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DISTRIBUTION, ECOLOGY, DISEASE RISK, AND GENETIC DIVERSITY OF SWIFT FOX (*VULPES VELOX)* IN THE DAKOTAS

BY

EMILY LOUISE MITCHELL

A thesis submitted in partial fulfillment of the requirements for the

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DISTRIBUTION, ECOLOGY, DISEASE RISK, AND GENETIC DIVERSITY OF SWIFT FOX (*VULPES VELOX)* IN THE IN THE DAKOTAS

EMILY LOUISE MITCHELL

This thesis is approved as a creditable and independent investigation by a candidate for the Master of Science in Wildlife and Fisheries Science degree and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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"When we try and pick out anything
by itself, we find it hitched
to everything else in the universe."
- John Muir

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ABSTRACT

DISTRIBUTION, ECOLOGY, DISEASE RISK, AND GENETIC DIVERSITY OF SWIFT FOX (*VULPES VELOX)* IN THE DAKOTAS

EMILY L. MITCHELL

2018

The swift fox (*Vulpes velox*), a native species once abundant throughout the Northern Great Plains (NGP), has declined due to changes in land use, historic predator eradication programs, and predation by larger canid species. Currently, the species is estimated to occupy 44% of its historic range. In the NGP, the status of the swift fox varies by state, ranging from furbearer to endangered species. However, knowledge of the current status of swift foxes in the NGP is lacking due to an absence of systematic population monitoring. Improving the current state of knowledge concerning swift fox populations in the NGP is necessary to assess the population status of the species and will be instrumental in assisting managers in conservation and, if needed, restoration of this rare species. The swift fox is considered rare in North Dakota and state threatened in South Dakota. We evaluated the distribution of swift fox, red fox (*Vulpes vulpes*), and coyote (*Canis latrans*) populations, investigated ecology and life history of swift fox, and assessed disease risk and genetic diversity of resident swift foxes in northwest South Dakota and southwest North Dakota. To accomplish these objectives, we first conducted a systematic camera-trap survey to assess occupancy and distribution of swift fox, coyotes, and red fox. Using camera trap detections and anecdotal sightings, we live-trapped, radio-collared, and tracked swift foxes to locate den sites to assess den site habitat selection. Using samples collected during camera-trap surveys and radiocollaring, we conducted disease and genetic diversity analyses. We conducted occupancy and distribution models at two different scales (sympatric canids: double-home range, 6.68 km, and home range, 3.34 km; swift fox: sub-home range, 30 m, and home range, 3.34 km); both scales created overfit models, producing inaccurate distribution maps for swift fox. Therefore, we do not suggest using either of these models for management purposes. However, we found that coyotes occupied 63-69% of the study area while red fox occupied 46-53% of the study area. We documented average litter sizes (3.25 pups), large home ranges (55.38 km^2), late dispersal (February), large dispersal distances (17.20 km), high survival (0.857), and found dens farther from roads than other studies, with no correlation between den-site location and vegetation height. We also found high prevalence of canine parvovirus (71.43%) and *Francisella tularensis* (67.74%), but low prevalence of canine distemper virus (10.34%) and *Yersinis pestis* (3.32%). The high prevalence of canine parvovirus and exposure to canine distemper are cause for concern, due to their typically highly fatal outcomes. This swift fox population occupying northwestern South Dakota and southwestern North Dakota is genetically viable, with high intrapopulation connectivity and no sign of a genetic bottleneck. Our study is the first of its kind in northwest South Dakota and southwest North Dakota and most of our findings can and should be used in future monitoring, conservation, and restoration plans for this native species in the Dakotas.

CHAPTER 1

INTRODUCTION

Distribution

The swift fox (*Vulpes velox*) inhabits short and mixed-grass prairies in the North American Great Plains (Egoscue 1979, Scott-Brown et al. 1987). Historically, the species ranged from southern Alberta, Manitoba, and Saskatchewan provinces in Canada south to New Mexico and Texas in the United States (Moehrenschlager and Sovada 2004). Once abundant throughout the Great Plains, by the early 1900's the species had greatly declined and was considered rare or extirpated in most of its historical range. This reduction was largely associated with conversion of native short-grass prairies to agriculture, changes in land use, historic unregulated hunting and trapping, and predator eradication efforts (Egoscue 1979, Sovada et al. 1998, Schauster et al. 2002, Kilgore 1969, Carbyn et al. 1994, Allardyce and Sovada 2003).

In 1992, the swift fox was petitioned to be listed as threatened under the Endangered Species Act, but by 1994 the United States Fish and Wildlife Service (USFWS) determined the threatened listing was warranted but precluded by higher priority species and thus, the species was placed on the candidate list (Federal Register 1994, Federal Register 1995). In response, wildlife agencies within the historic range of the species formed the Swift Fox Conservation Team (SFCT) to aggregate existing data, gather new data, and implement monitoring and management programs to gain a better understanding of the species’ status (Allardyce and Sovada 2003). In 2001, the USFWS reviewed the status of the swift fox and determined the species did not warrant listing and removed it from the candidate list (Federal Register 2001).

By the mid 1950's, changes in predator control methodology allowed gradual swift fox recovery in portions of its range (Egoscue 1979). The swift fox is now estimated to occupy 44% of the historic species range (Sovada et al. 2009). However, some populations, such as the peripheral populations in the Northern Great Plains (NGP), have continued to exhibit low densities and remain extirpated or rare in much of their historic range. The swift fox is currently considered threatened in South Dakota and rare in North Dakota, while anecdotal evidence implies small isolated populations are all that remain in Montana, South Dakota, Nebraska, and parts of Wyoming (Merrill et al. 1996, Redmond et al. 1998, North Dakota Game and Fish Department 2017, South Dakota Game, Fish, and Parks Department 2014, Soper 1964, Sovada and Scheick 1999, Allardyce and Sovada 2003). Reintroduction efforts were conducted in parts of Canada and Montana in the 1980's and 1990's (Carbyn 1998, Moehrenschlager and Moehrenschlager 2006, Ausband and Foresman 2007) and in the early to mid-2000's in South Dakota (Schroeder 2007, Goodman et al. 2012, Sasmal et al. 2015, S. Grassel, LBST, personal communication). Despite partial recovery of the species and reintroduction efforts, populations in the NGP remain small and isolated.

The majority of extant swift fox populations in the NGP are the result of reintroduction efforts, rather than natural recovery (Smeeton and Weagle 2000, Montana Fish, Wildlife and Parks Department 2006, Ausband and Foresman 2007). In South Dakota 459 swift fox were released between 2002 and 2010 (Honness et al. 2007, Swift Fox Conservation Team 2006, Swift Fox Conservation Team 2011, Oglala Sioux Parks and Recreation Department 2012). These reintroductions occurred in four areas in the west-central portion of the state: Bad River Ranches (Stanley and Jones counties), Lower

Brule Sioux Tribal Land (Lyman county), Badlands National Park (Pennington and Jackson counties), and Pine Ridge Indian Reservation (Oglala Lakota county). Today, swift foxes are known to exist around Badlands National Park and in Fall River County (a remnant population) South Dakota (Swift Fox Conservation Team 2011, Swift Fox Conservation Team 2014). Beginning in 2006, intermittent swift fox sightings in northwest South Dakota and southwest North Dakota were recorded via aerial telemetry, incidental capture, or recovered mortality, implying the potential re-establishment of swift fox in the region (unpublished data, Turner Endangered Species Fund and South Dakota Game, Fish and Parks). Systematic surveys conducted in 2017 confirmed the presence of a swift fox population in the area; however, the species distribution is patchy and swift fox occur at low densities.

Life History and Ecology

Swift foxes are typically monogamous, pairing with a mate for life, and living together as a breeding pair or sometimes as a group with one breeding female and nonbreeding "helper" foxes (Kilgore 1969, Covell 1992, Ralls et al. 2001). They breed once a year, beginning in March in the northern portion of their range (Kilgore 1969, Hines 1980, Carbyn et al. 1994, Asa and Valdespino 1998). The average liter size is 2.4-5.7 pus (Kilgore 1969, Hillman and Sharps 1978, Covell 1992, Carbyn et al. 1994, Roell 1999, Schauster et al. 2002, Anderson et al. 2003, Nevison 2017). Both parents contribute to rearing pups, and pups typically stay with their parents for four to six months (Rongstad et al. 1989, Covell 1992). Pups typically disperse from September to January, with males often dispersing sooner and farther than females (Zoellick et al.

1989, Covell 1992, Sovada unpublished data, Kitchen et al. 1999); dispersal distances range from 2.1 km to 25 km (Sovada unpublished data, Covell 1992).

The cause and extent of mortality in wild canids, such as the swift fox, are often difficult to assess. Their elusiveness, and in the case of the swift fox their low abundance, often make the likelihood of finding mortalities low. However, a better understanding of mortality factors is vital to managing for the species persistence. Potential predators of the swift fox include coyotes, red fox (*Vulpes vulpes*), bobcats (*Lynx rufus*), and large raptors (Sovada et al. 1998). Human factors, including vehicle collisions, secondary poisoning, shooting, and trapping, contribute to mortality (Kilgore 1969, Rongstad et al. 1989, Carbyn et al. 1994). Most studies have found coyote predation and vehicle collisions to be the top causes of swift fox mortality (Covell 1992, Carbyn et al. 1994, Sovada et al. 1998, Kitchen et al. 1999, Olsen and Lindzey 2002, Kamler et al. 2003, Nevison 2017).

The swift fox is one of the most den-dependent canid species in North America (Jackson and Choate 2000). Swift foxes use dens as natal and pup rearing sites and as escape refugia from inclement weather and predators throughout the year (Herrero *et al.* 1986, Pruss 1999). Often having more than one den within their home range, swift foxes move among dens throughout the year (Kilgore 1969, Chamber 1978, Hillman and Sharps 1978, Hines and Case 1991). Dens are usually located in open areas with sparse vegetation, low slope, and well-drained soils (Cutter 1958, Kilgore 1969). In South Dakota, dens may be located in active black-tailed prairie dog (*Cynomys ludovicianus*) colonies and heavily grazed pastures (Uresk and Sharps 1986, Sasmal et al. 2011). Swift fox population viability is, in part, dependent on the availability of suitable den sites

(Egoscue 1979, Russell and Scotter 1984, Pruss 1999, Harrison and Whittaker-Hoagland 2003).

Swift foxes are predominantly nocturnal, with the exception of some daytime activity around the den site (Laurion 1988, Kilgore 1996, Kitchen et al. 1999, Anderson et al. 2003). Their nocturnal activity, elusiveness, and often low abundance make estimating home range sizes difficult and variable between studies. Radio collared individuals must be tracked throughout the night to accurately document movement (Sasmal et al. 2011). This can make it difficult for researchers to schedule tracking activities, and gaining access to areas occupied by swift fox can be complicated, often resulting in studies obtaining few data points for analyses. Also, not all studies use the same methodology to estimate home range, making it difficult to compare swift fox home range sizes among study areas and regions. Estimates of home range have been found to vary widely from as low as 7.6 km^2 to a high of 32.3 km^2 (Worton 1989, Hines and Case 1991, Kitchen et al. 1999, Anderson et al. 2003, Sovada unpublished data, Zimmerman et al. 2003).

Study Objectives

Investigating potential drivers for the continued local rarity of the species is necessary to inform swift fox conservation in this area. Potential drivers include interspecific competition with larger canids (Ralls and White 1995, White et al. 1994, Kamler et al. 2003, Pamperin et al. 2006), exposure to disease (Johnson et al 1994, Pence et al. 1995, Gese et al. 1997, Miller et al. 2000, Olson and Lindzey 2002, Gese et al. 2004, Sobrino et al. 2008, Di Sabatino et al. 2014), loss of genetic diversity (Ouborg

2009, Koons 2010, Sasmal et al. 2012), and lack of suitable habitat (Egoscue 1979, Sovada et al. 1998). A better understanding the characteristics and behaviors of this population and the individuals in it can be used to enhance current and future management, conservation, and reestablishment efforts of the species in the Dakotas.

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CHAPTER 2

DEN SITE SELECTION, SURVIVAL, AND HOME RANGE OF SWIFT FOXES (*VULPES VELOX*) IN SELECTED AREAS OF THE DAKOTAS, USA

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ABSTRACT

Conservation of small populations is difficult because often times data and information regarding life history characteristics and ecological factors influencing the survival of the population are either lacking or missing all together. Small, isolated populations are especially difficult to study and are often times subject to Allee effects, consecific attraction, and experience adverse reactions to settlement costs due to habitat selection by dispersal. We studied a small, re-colonizing population of swift fox (*Vulpes* velox) in northwest South Dakota and southwest North Dakota (hereafter "Dakotas") in an attempt to better understand the life history characteristics and ecological factors that may be influencing this population. We monitored 26 swift foxes to assess reproductive success, survival, den site selection, and home range, from July 2016 to December 2017. We documented 4 litters with an average litter size was 3.25 and first emergence of pups on 5 May. Estimated survival was 0.857, with predation by coyotes (*Canis latrans*) as the leading cause of mortality. Den sites were found to be farther from roads (average of 570.99 m), and in areas with no correlation between den site selection and vegetation height. The average number of den entrances was 1.38. Juveniles dispersed from natal home ranges from 23 October to 14 February, with most dispersal events occurring in February. Juveniles dispersed an average distance of 17.20 km, with dispersal distances ranging from 4.75 km to 29.64 km. Home range size varied from 21.53 km^2 to 132.44 km^2, with an average of 55.38 km^2 and core area of 12.20 km^2. Our results indicate that swift foxes in the Dakotas occur at a low density likely due to predator avoidance and anthropogenic activities that disturb life history characteristics associated with established populations.

INTRODUCTION

Habitat-selection theory generally assumes that individual fitness declines as a function of density, that social interaction among settlers are solely competitive (Greene and Stamps 2001). However, when animals settle at low densities, other fitness distributions (e.g., Allee effects (Allee 1951)) and positive interactions (e.g., conspecific cueing (Greene and Stamps 2001) are possible. One form of habitat selection is through dispersal, which can be divided into 3 stages: search, settlement, and residency (Stamps 2001). This process affects distribution, density, and fitness of the individuals in different habitats (Hilden 1965, Morris 1991, Stamps 1994). Habitat selection by dispersers can have great effects on population size and dynamics (Pulliam and Danielson 1991, Lima and Zollner 1996), population persistence (Kokko and Sutherland 2001, Greene 2003), and the management of endangered species (Schlaepfer et al. 2002, Morris 2003). Understanding dispersal in low density populations is necessary in single-species conservation to predict the movements of a threatened species, especially in a fragmented landscape (Lande 1988, Lamberson et al. 1992, Goss-Custard et al. 1995).

Allee effects (Allee 1951) occur when fitness increases as a function of low density (Greene and Stamps 2001), and influences the amount of habitat used (Fretwell and Lucas 1970). Settlement costs reduce individual fitness during the settlement period (Greene and Stamps 2001). Conspecific attraction, which occurs when the presence of conspecifics increases the probability that other individuals will settle in same area, can occur at low population densities (Stamps 1988, Stamps 1991, Schmitt and Holbrook 1996). The benefits of having neighbors includes increased efficiency of removing intruders (Eason and Stamps 1993, Meadows 1995), reduced the risk of predation (Smith

1986, Wisenden and Sargent 1997), and improved access to mates (Levitan and Young 1995, Wagner 1997). It has also been found that individuals exposed to certain stimuli as juveniles are likely to select a new habitat containing those stimuli (Wecker 1963, Hilden 1965, Klopfer and Gonzhorn 1985, Arvedlund and Nielson 1996), and those individuals that do choose a post-dispersal habitat similar to that of their pre-dispersal habitat achieve higher reproductive success (Stamps 2001). This is likely due to more developed perceptual and motor skills, increasing foraging performance (Oretega-Reyes and Provenza 1993, Mclean 1996, Yoerg and Shier 1997), anti-predator behavior (Curio 1993), and social interactions (Nelson 1997, West et al. 1997). A better understanding of dispersal characteristic and drivers of species with low population density is necessary to increase the success of current and future management and conservation strategies.

The swift fox (*Vulpes velox*) inhabits short and mixed-grass prairies in the North American Great Plains (Egoscue 1979, Scott-Brown et al. 1987). Historically, the species ranged from the Canadian provinces of Alberta, Manitoba, and Saskatchewan south to New Mexico and Texas in the United States (Moehrenschlager and Sovada 2004). Once abundant throughout the Great Plains, by the early 1900's the species had greatly declined and was considered rare or extirpated in most of its historical range. This reduction was largely associated with conversion of native short-grass prairies to agriculture, changes in land use, historically unregulated hunting and trapping, and predator eradication efforts (Kilgore 1969, Egoscue 1979, Carbyn et al. 1994, Sovada et al. 1998, Schauster et al. 2002, Allardyce and Sovada 2003). The swift fox is considered warranted for listing under the endangered species act, but precluded by species with greater need. It is listed as threatened in South Dakota, and rare in North Dakota (South Dakota Game, Fish, and Parks 2014, North Dakota Department of Game and Fish 2017).

The majority of extant swift fox populations in the northern Great Plains are the result of reintroduction efforts, rather than natural recovery (Smeeton and Weagle 2000, Montana Fish, Wildlife and Parks Department 2006, Ausband and Foresman 2007). For South Dakota, specifically, 459 swift fox were released between 2002 and 2010 (Swift Fox Conservation Team 2006, Honness et al. 2007, Swift Fox Conservation Team 2011, Oglala Sioux Parks and Recreation Department 2012, Sasmal 2012, Sasmal 2016). These reintroductions occurred in four areas in the west-central portion of South Dakota: Bad River Ranches (Turner Endangered Species Fund), Lower Brule Sioux Tribal Land (Lower Brule Sioux Tribe Department of Wildlife, Fish and Recreation and the Maka 4 Foundation), Badlands National Park (National Park Service), and Pine Ridge Indian Reservation (Oglala Sioux Parks and Recreation Authority). Prior to this study, swift foxes are known to exist around Badlands National Park and in Fall River County (a remnant population), South Dakota (Swift Fox Conservation Team 2011, Swift Fox Conservation Team 2014, Nevison 2017).

Anecdotal evidence indicates that swift fox may also occur in northwest South Dakota and southwest North Dakota. This population is assumed to exhibit low densities and to be small overall, given the intermittent nature of opportunistic observations. However, swift fox ecology, including litter size, home range size, dispersal timing and distance, survival, and den site characteristics have not been assessed in this region. Understanding these factors specific to the swift fox population in this area will inform habitat needs of the species and drivers of the assumed continued low density, which can be used to enhance current and future management, conservation, and reestablishment efforts of the species in the Dakotas. We hypothesize that due to this populations, likely, small size swift fox will have larger home ranges and juveniles will disperse longer distances than swift fox populations with higher densities and larger overall population size. We also hypothesis that swift foxes in the Dakotas will select den sites close to roads, with low vegetation density. Finally, we hypothesize that this population will have low levels of mortality, with the leading cause of death being coyotes, likely because of Allee effects. A better understanding of these life history characteristics and ecological factors influencing the swift fox population in the Dakotas is vital to encourage an enhance management and conservation efforts in the region.

STUDY AREA

The study area included Harding, Butte, Perkins, and Meade counties in South Dakota and Slope, Bowman, Adams, and Hettinger counties in North Dakota (Figure 1). The study was conducted on state, federal (i.e., Forest Service and Bureau of Land Management), and private lands within the region. The study area encompassed approximately 4,099,174 ha dominated by mixed grass prairie, interspersed with sagebrush (*Artemisia* spp.). Prominent grasses of the mixed grass prairie in the area were: western wheatgrass (*Pascopyrum smithii*), green needlegrass (*Nassella viridula*), needle-and-thread (*Hesperostipa comata*), blue grama (*Bouteloua gracilis*), and side-oats grama (*Bouteloua curtipendula*). Topography was largely flat to gently rolling hills with occasional buttes. The primary soil types were clays derived from Cretaceous Pierre Shale (Johnson et al. 1995). Predominate water features included Shadehill Reservoir, Belle Fourche Reservoir, and the Belle Fourche River. Lands were primarily used for cattle and sheep grazing.

Since 2006 regular swift fox sightings have been reported in northwest South Dakota, with three marked foxes from the Bad River Ranches reintroduction found via aerial telemetry, incidental capture, and mortality (unpublished data, Turner Endangered Species Fund and South Dakota Game, Fish and Parks). Starting in 2008, in southwest North Dakota an increase in fatalities due to vehicles collisions also indicated potential for an existing population in the area. These opportunistic records indicate that swift fox populations may exist in northwest South Dakota and southwest North Dakota.

MATERIALS AND METHODS

Capture and radio telemetry:

We live captured swift fox from July 2016 to April 2017, using modified wire box traps (Model 108SS; Tomahawk Live Trap Co., Tomahawk, WI, USA) of dimensions 81.30 cm × 25.40 cm × 30.50 cm (Sovada et al. 1998). We manually restrained captured swift fox while we determined and recorded sex, age (juvenile or adult, determined by tooth wear), weight, and body condition. We also collected blood and skin samples for disease and genetic analyses. We microchipped (AVID Identification Systems Inc., Norco, CA) each fox dorsally between the scapulae. We fitted foxes weighing over 2 kg with mammal necklace-type VHF radio collars (Model 1830, Advanced Telemetry Systems, Isanti, MN, USA).

We located radio-collared swift foxes from July 2016 to December 2017 once weekly, after dark. We used a null peak vehicle mounted system to locate foxes from July 2016 to October 2016 (Brinkman et al. 2002). Winter weather and access issues such as absence of roads and private landownership precluded continued tracking of swift fox from the ground, thus we located foxes from the air from October 2016 to December 2017, pending pilot availability and weather conditions, using wing mounted antennae on a fixed wing aircraft. We tracked each fox after dark and when we located the signal, the pilot would maneuver the airplane in increasingly tight circles around the signal to improve accuracy of the presumed location, which we recorded with a handheld GPS unit (GPSMAP 62s, Garmin International Inc., Olathe, KS, USA). All live capture, handling, and tracking were approved by the South Dakota State University Institutional Animal Care and Use Committee (permit # A3958-01).

Den site/habitat selection:

We tracked radio-collared foxes on the ground during the day to locate den sites, from September 2016-December 2016 and May-August 2017. We attempted to locate at least one den per fox during the study. We recorded the number of entrances, distance to road, and visual obstruction at each den site, as well as at one random site per den. We intended to capture visual obstruction from the perspective of a swift fox, which can be important for avoiding ambush by coyotes or other predators. We measured visual obstruction using a modified Robel pole with alternating black and white bands that were 2.54 cm wide (Robel et al. 1970). We recorded the lowest band that was totally obstructed from a distance of 25 m with an eye height of 40 cm, roughly the eye level of a swift fox (Egoscue 1979), in each of the four cardinal directions. We chose random sites using a random number generator (R N G Random Number Generator, Version 1.01, mobile application, A. Rutkowskij). We generated a random bearing (1-360°) and a random distance (200-500 m) from the den site, allowing assessment of selection of sites from local habitat features available to the fox, rather than habitat features within the whole home range of the fox. We used the statistical computing environment R (R Development Core Team, cran.r-project.org, accessed 1 May 2016) to evaluate den site characteristics using linear regression; we used analysis of variance (ANOVA) to compare visual obstruction at den sites to random sites. Alpha was set at $\alpha \leq 0.05$ when considering significance of statistical analyses.

Reproduction:

We did not systematically monitor assumed male-female pairs to confirm reproduction. Rather, we conducted litter counts opportunistically in April and May 2017, as new den sites were discovered. It is unknown how many pups were born to each female, because parturition occurs within the den and pups remain underground for approximately three weeks (Asa 2003). We determined litter size post-emergence of pups. We did this by conducting litter counts using two methods. First, we used motion activated, infrared trail cameras (Black Ops HD, Browning, Morgan, UT) placed 3-4 meters from the den entrance and checked biweekly to determine litter count (Nevison 2017), where the litter count was considered to be the maximum number of pups observed in a single photo. Second, we used binoculars to conduct observation of natal dens that were on private property and could not be accessed, but were close to major public roads. These dens were observed for at least 60 minutes of pup activity to determine the maximum number of pups around the den site at one time.

Home range and dispersal:

Using the weekly tracking data we estimate home range size, core area size, dispersal date, and dispersal distance. Using the Geospatial Modeling Environment

(GME; Spatial Ecology LLC, Hawthorne L. Beyer, 2001-2014) and ArcGIS (ESRI, Redlands, CA, USA) we modeled the 95% kernel density estimate (home range; Worton 1989) and the 50% kernel density estimate (core area; Sovada et al. 2003) for each radio collared fox. We used the 95% kernel density method with LSCV bandwidth (Horne and Garton 2006) to estimate home range similar to previous swift fox studies (Kitchen et al. 1999, Pechacek et al. 2000, Kamler et al. 2003*a*, Sovada et al. 2003). We calculated home ranges from foxes with over 13 tracking locations, with the number of locations ranging from 13 to 53. We estimated juvenile dispersal date as the date of the first observation of a juvenile fox ≥4.82 km from their original capture location. This was the shortest distance a juvenile was observed to move and leave the natal natal home range. Dispersal distance was the farthest a juvenile fox traveled from the original capture location once it was met the criteria for dispersal defined previously. For juvenile foxes that had two distinct home ranges, one prior to dispersal and one after dispersal, we calculated home range after dispersal was completed.

Survival:

We used weekly tracking data to model survival, using known fate in Program MARK (White and Burnham 1999) to estimate the probability of survival to the end of the study. Due to the fact that we live captured foxes sporadically from August 2016 to March 2017 foxes were entered into the model using staggered entry (Pollock et al. 1989); foxes that disappeared throughout the study were censored. We developed *a priori* models that included age, sex, and time covariates, selecting the best fit model with the lowest AIC value. Cause of mortality was determined by field necropsy. Swift fox carcasses with hemorrhaging and puncture wounds consistent with coyote bites, evidence of being shaken (e.g., broken neck and/or back), and/or punctures on the radio collar consistent with coyote bites were classified as coyote predations (Sovada et al. 1998, *Olson and Lindzey* 2002*a*, Kamler et al. 2003*a*). Carcasses found on roads and showing visible signs of trauma from vehicles (e.g., shattered bones and/or having flattened portions of the carcass) were classified as vehicle collisions.

RESULTS

We live captured 41 individual swift foxes, in 376 trap nights, throughout the study area sporadically from August 2016 to March 2017. Of these, 23 were female (5 adults and 18 juveniles), 16 were male (12 adults and 4 juveniles), and 2 were of undetermined sex (Table 1). We fit radio collars on 26 foxes, including: 2 adult females, 13 juvenile females, 10 adult males, and 1 juvenile male. We monitored eight den sites in late April and early May 2017 to obtain litter counts. Three of these dens were monitored visually from a distance, while the remaining five dens were monitored via trail camera. Of these, pups were observed and counted at four dens. Average litter size per den was estimated at 3.25 pups. However, due to camera malfunctions we were only able to record one emergence date, which occurred on 5 May 2017.

Four of the 26 radio collared swift fox died, 2 from coyote predation, 1 from a vehicle collision, and 1 unknown (Table 1). An additional 5 swift fox were censored because they disappeared during the sampling period, thus the total number of foxes included in survival analyses was 21. At the time of mortality, all four foxes were adults, and were comprised of one female and three males. However, the vehicle collision, which was the lone female mortality, occurred after the sampling period and was not included in our survival estimate. The time model (AIC = 29.85; Table 2) was found to be the best fit for our data. Using this model, the probability of surviving the study was estimated as 0.86 (SE=0.08, 95% CI=0.64-0.95) and the leading cause of death was coyote predation.

We conducted 27 den surveys throughout the study. The distance to the nearest road from den sites ranged from 1 to 4,232 m and from random sites from 0 to 4,393 m at random sites. Average distance to the nearest road at den sites was 570 m (SD = 923 m) while it was 630 m (SD = 995 m) at random sites. Average visual obstruction at den sites was 31 cm (SD = 33 cm) and 30.57 cm (SD = 25.51 cm) at random sites; visual obstruction at den sites and random sites did not differ significantly ($p = 0.929$, DF = 1).

Of the 14 juvenile radio-collared foxes, 7 were observed to disperse a minimum of 4.82 km from their original capture location. Dispersal dates ranged from 23 October to 14 February, with most juveniles dispersing in February ($n = 5$; Table 3). Dispersal distances ranged from 4.82 km to 29.64 km (Table 3); average distance dispersed was 17.20 km (SD = 8.76 km). However, only one fox dispersed less than 10 km; excluding this outlier average dispersal was 19.27 km (SD = 7.48). We estimated the 95% kernel density home range and the 50% kernel density core area for 24 of 26 radio collared foxes; we did not calculate home range or core range estimates for the remaining 2 foxes because they either never settled down enough to form a home range or the fox disappeared within 2 weeks of its capture. We completed these analyses with a total of 364 fixes for adults and 439 fixes for juveniles; the minimum number of fixes for any individual was 13. Home range size varied from 21.53 km^2 to 132.44 km^2, while core area ranged from 3.62 km^2 to 37.34 km^2 (Table 4). Average home range size (95% kernel density) was 55.38 km^2 (SD = 28.62 km^2) and average core area size (50% kernel density) was 12.19 km^2 (SD = 7.69 km^2). However, 3 individuals had exceptionally large home ranges, exceeding 100 km^2. Excluding these 3 individuals the average home range size was 46.61 km^2 (SD = 16.64 km^2) and average core area size was 9.83 km^2 (SD = 3.80 km^2).

DISCUSSION

The swift fox population in the Dakotas that we studied is assumed to be a small isolated population, but has not previously been studied or monitored. When the swift fox selects habitat by dispersal it effects distribution, density, and fitness of the individuals in the population (Hilden 1965, Morris 1991, Pulliam and Danielson 1991, Stamps 1994, Lima and Zollner 1996). Low population density can effect fitness distributions (Allee effects), conspecific interactions, and the amount of habitat used (Allee 1951, Fretwell and Lucas 1970, Stamps 1988, Stamps 1991). A better understanding of the litter size, home range size, dispersal timing and distance, survival, and den site characteristics is necessary to evaluate and manage the population. Our study provides a first look into the general ecology of the swift fox population in northwest South Dakota and southwest North Dakota.

The average swift fox litter size in northwest South Dakota and southwest North Dakota (average litter size = 3.25) was within the range of estimates in similar studies conducted throughout the species range (Table 5; Kilgore 1969, Moehrenschlager 2000, Olson and Lindzey 2002*a*, Sovada et al. 2003, Karki 2007, Nevison 2017). However, it was slightly lower than the combined average of these studies (i.e., 3.57). It is unclear if this difference is biologically significant to swift fox recovery in the area. However, it indicated that this is likely a viable re-colonization, with comparable litter sizes to other established populations. It is possible that lower pup counts could be related to a high prevalence of canine parvovirus and/or canine distemper virus in the population (E. Mitchell in prep), although this relationship has yet to be studied in swift foxes. Production of pups in kit fox is likely related to prey abundance (White and Ralls 1993, White et al. 1996, Cypher et al. 2000), and is likely the case for swift foxes as well. We hypothesize that the prey abundance in the Dakotas is similar to other areas with swift fox, due to our comparable litter sizes. However, we suggest further examination of diet selection and prey abundance in this population to better understand the possible food limitations in the region. The motion activated cameras at den sites allowed monitoring of dens continuously, potentially providing more accurate pup counts than visual observations while also reducing labor and logistic demands. This study and that of Nevison (2017), conducted at Badlands National Park in South Dakota, are the only studies to date that have used motion activated cameras to conduct swift fox pup counts.

Our results are consistent with many other studies that have found that coyotes are the leading cause of mortality of swift and kit foxes (*Vulpes macrotis*) (Laurion 1988, Covell 1992, Carbyn et al. 1994, Ralls and White 1995, Sovada et al. 1998, Olson and Lindzey 2002*a*, Schauster et al. 2002, Ausband and Foresman 2007, and Cypher et al. 2009). Overall, however, swift fox survival rates were higher in the study area compared to values reported elsewhere. For example, reported swift fox survival rates in the Northern Great Plains range from 0.26, 0.39, and 0.50 for reintroduced populations in South Dakota (Sharps and Whitcher 1984, Sasmal et al. 2016, Nevison 2017), 0.48 and 0.53 for resident individuals in Colorado (Rongstad et al. 1989, Covell 1992), 0.58 for resident individuals in Wyoming (Olson and Lindzey 2002*a*), 0.51 for resident individuals in Canada (Moehrenschlager et al. 2007), and up to 0.73 for resident individuals in a reintroduced population in northern Montana (Ausband and Foresman 2007). The large confidence intervals surrounding this estimate indicate uncertainty in the measure and imply that survival may be within the range reported for other populations (Table 6). This variance is potentially influenced by modest sample size and a limited time period for data collection; survival estimates in other portions of the species distribution are generally calculated over multiple years and, further, show high inter-annual variation (Olson and Lindzey 2002*a*, Kamler et al. 2003*a*, Nevison 2017). Thus, it is unclear if survival in the Dakotas is sustained at the rate we detected, or if it fluctuates as in other populations. One notable difference between the Dakotas and other regions where survival has been estimated is the extensive predator removal programs in the region, of which coyotes are a primary target. Karki et al (2007) reported increased survival of both juvenile and adult swift fox during experimental coyote removal; the effect was temporary in their study but could easily be extended when coyote control is a sustained, year-round management strategy, as is the case in the Dakotas. With presumably small, isolated, populations, adult survival is important, as adult fecundity is generally higher than juvenile fecundity (Sovada et al. 1998, Nevison 2017), a vital factor in population growth. Conversely, low juvenile survival and recruitment may be a limiting factor in swift fox population density and expansion (Sovada et al. 1998, Kamler et al. 2003a, Nevison 2017). Assessing survival rates over multiple years and exploring the potential link between coyote control and swift fox survival may elucidate unique factors shaping swift fox survival and, ultimately, re-colonization in this region.

Although there was no statistically significant difference in the distance to the nearest road from den sites and random sites our study found den sites to be generally farther from roads that similar studies. Swift fox den sites in the Dakotas are an average of 570.99 m from the nearest road. This is contrary to most other studies, which found dens tend to be much closer to roads (range = 161 m - 267 m) than those in our study area. For example, Olson (2000) recorded an average distance of 215 m to the nearest road in Wyoming. In a previous study in southwestern South Dakota, dens were an average of 160.90 m from the nearest road (Nevison 2017). Finally, swift fox dens in Canada were an average of 267 m from the nearest road (Pruss 1999). Only Harrison (2003) reported findings similar to our study; he documented dens sites an average of 660 m from roads. We suggest two possible explanations for this disparity. First, it is possible that swift fox in the Dakotas select den sites farther from roads due to increased risk of anthropogenic sources of mortality near roadways. For example, swift fox are frequently mistaken for coyote pups and shot in other parts of the species distribution; although swift fox are protected in South Dakota, it is possible that mistaken identity may result in higher mortality for swift foxes near roads. In addition, although adults denning near roads may persist for many years, pup mortality is often very high (Nevison 2017). Finally, vehicle strikes are a common source of mortality for swift foxes (Sovada et al. 1998, Matlack et al. 2000, Kamler et al. 2003a, Nevison 2017) and, in one study, exceeded coyotes as the primary source of mortality in swift foxes (Kamler et al. 2003a). Second, extensive coyote control throughout the study area may release swift fox from intraguild predation risk and facilitate denning further from the anthropogenic shield provided by roadways in other parts of the species distribution, where coyote control is less intense. Distance to road is considerably lower for the only other swift fox population in South Dakota in which it has been studied (Nevison 2017); notably, coyote control in that region is neither as intense nor as systematic as in the study area.

Our study found an average visual obstruction of 31.28 cm compared to 30.57 cm in height at random sites. There was no significant difference in vegetation density between den and random sites, indicating that swift foxes were not selecting den sites based on the parameters we measured or the scale we used. Vegetation is often considered a primary tool for prey species to hide from predators (DePerno et al. 2003). However, in the case of the swift fox, tall vegetation likely allows its primary competitor, the coyote, to remain undetected when at close proximity to foxes, enhancing the chance of mortality (Kitchen 1999, Harrison 2003). Cutter (1958) and Cameron (1984) located swift fox dens in areas with little to no vegetation, whereas Jackson and Choate (2000), Uresk et al. (2003) and Kitchen et al. (2006) observed foxes selecting for denser vegetation or not selecting based on vegetation, but simply using what was available to them. With conflicting results, the role of vegetation in den site selection is currently uncertain. Similar to our study, Kitchen et al. (2009) failed to detect factors which influenced swift fox dens site selection at the scale of the den site, but location within the home range was an important predictor of use. It is possible that den site selection by swift foxes is influenced by factors at broader scales than the one we used. It is also possible that swift fox habitat selection, and there for den site selection, is driven by an environmental factor not included in either study.

Juvenile swift foxes are generally thought to disperse from the natal home range beginning in September through February (Covell 1992, Sovada et al. 2003, Kamler et al. 2004). Swift foxes in Oklahoma have been documented to disperse in August/September

(Kilgore 1969), whereas foxes in Colorado were found to disperse in September/October (Covell 1992), and Sovada et al. (2003) observed that swift foxes in Kansas dispersed in November. In a comprehensive assessment of dispersal in 109 adult and 114 juvenile swift fox in Colorado, New Mexico, and Texas, Kamler et al. (2004) reported bimodal dispersal patterns, with two pulses occurring in September-October and January-March. Our results are consistent with these findings and further, imply that swift fox dispersal in the NGP may be biased towards the later peak in dispersal. This later timed dispersal could possibly be caused by high resource availability around the natal den, encouraging pups of the year to stay with the family group until the mating season (February-March; Tannerfeldt et al. 2003). All seven juveniles with recorded dispersal events were female, which contrasts with male-biased juvenile dispersal rates reported for swift fox elsewhere (Sovada et al. 2003, Kamler et al. 2004). All other juvenile foxes were either radio-collared after they dispersed, including those individuals radio collared in March 2017, or remained within the natal home range. We were also unable to locate two juveniles after 14 February and for the remainder of the study, both of which were female.

Average dispersal distance in this study (17.20 km; range 4.82 km - 29.64 km) was larger than values reported in most similar studies; when a single, exceptionally short dispersal distance is removed from our data set, this average increases to 19.27 km (range 12.07 km - 29.64 km). Swift foxes in Colorado were found to disperse an average of 12.60 km (range 8.40 – 15.90 km; Schauster 2002), foxes in Canada were observed to disperse 12.10 km on average (Moehrenschlager 2000), and swift foxes in Kansas dispersed 14.70 km on average (SE = 4.80; Sovada et al. 2003). In Texas, average dispersal distance differed by individual status and habitat fragmentation (Nicholson et al.

2007). Average dispersal distances for juveniles and resident adults (13.10 km +/- 0.30 km and 10.00 km +/- 4.70 km, respectively) were less than the dispersal average we report here, but the average dispersal distance of transients was greater (25.40 km +/- 9.10). Average dispersal distance, regardless of status, was greater in fragmented habitats than contiguous habitats (27.40 km +/- 21.40 km vs 21.80 km +/- 22.50 km). Both estimates exceed the average dispersal distance we report here, but when only juveniles are considered then dispersal in contiguous habitats is lower and dispersal in fragmented habitats is higher (9.30 km +/- 8.70 km vs 25.90 km +/- 20.80 km, respectively) than average juvenile dispersal reported here. We hypothesize that the longer dispersal distances in the Dakotas were due to the population being small and isolated, causing Allee effects to occur. Juveniles must travel longer distances to find a non-family member with which to mate (Creel and Creel 2002). High levels of relatedness in the population (Mitchell et al. in prep) may exacerbate individuals' search for an unrelated mate, increasing dispersal distances.

Although we documented a larger average juvenile dispersal distance than most other studies, only about 40% of our juveniles dispersed. The other 60% stayed within their natal home range. We documented a much lower dispersal rate than other studies; of the 10 swift foxes in a Kansas study 7 dispersed (70%; Sovada et al. 2003), of the 114 juvenile swift foxes in Colorado, New Mexico, and Texas 59 dispersed (52%; Kamler et al. 2004), of the 25 swift foxes in northwestern Texas 18 dispersed (72%; Nicholson et al. 2007). However, we observed a higher dispersal rate than Schauster (2002), who recorded 8 dispersed juvenile swift fox of the 25 monitored in Colorado (32%). The low percentage of dispersing individuals in this study could be due to high resource availability at natal sites, possibly high availability of mates near natal sites, due to clustering of different family groups. Swift fox are likely dispersing at low rates due to conspecific attraction occurring near natal dens, and reducing the want/need to disperse at all. We did document one juvenile with exploratory movements prior to dispersal. This fox left the natal home range, traveling distances ranging from 3.70 km to 15.26 km before returning, and eventually dispersed into a new home range. We likely missed other exploratory movements due to the limit frequency at which data was collected using the VHF radio collars.

Swift fox have been documented to disperse extreme distances compared to their body size in some instances. For example, Ausband and Moehrenschlager (2009) recorded a straight-line dispersal distance of 181 km by a juvenile swift fox in Montana, while Olson and Lindzey (2002*b*) report a dispersal distance of 67 km by a yearling female and Nicholson et al (2007) reports multiple instances of individual dispersal distances exceeding 60 km. While we observed larger than typical average dispersal distances, we did not record any such long-distance dispersal events, although the fate of 4 individuals in the population is unknown and long-distance dispersal cannot be ruled out.

The average home range size of 55.38 km^2 for swift foxes in our study area is higher than those estimated in other studies of swift fox. This estimate includes three exceptionally large home ranges which exceed 100 km^2 (Table 7); however, when these three home ranges are excluded, the average home range remains large (46.61 km^2). It is difficult to compare home range sizes from study to study due to different monitoring and data analysis techniques, e.g., some studies used the 95% kernel density method and others used the minimum convex polygon method; variation in the number of locations used between studies also influences these calculations. Six studies found swift fox home ranges to vary between 7.60 km^2 and 32.20 km^2, with an average of 14.92 km^2 (Hines and Case 1991, Kitchen et al. 1999, Pechacek et al. 2000, Zimmerman et al. 2003, Kamler et al. 2003, Sovada et al. 2003). Prior to beginning this study, we hypothesized that swift fox home ranges in the Dakotas would be larger than other populations, due to their assumed low abundance. This low abundance likely allows them to exploit more of the resources in a larger area and causes them to travel longer distances to find a mate. We hypothesize that the larger home range size is a result of Allee effects, due to the low population density. In general, reported average home ranges are larger for swift foxes in the northern end of the species distribution (Olson and Lindzey 2002*b,* Hines and Case 1991) including in this study. This implies that swift fox in the northern Great Plains may experience different resource availability (e.g., prey abundance, amount of suitable habitat, interspecific competition) or other population-level factors (e.g., disease, human inflicted mortality) compared to swift fox in the central or southern Great Plains. Further research is necessary to determine the mechanisms regulating swift fox densities, and therefore, swift fox home range size in the northern portion of the species' distribution.

Little was known about the swift fox population in northwest South Dakota and southwest North Dakota prior to this study. With the species listed as threatened in South Dakota and considered rare in North Dakota a better understanding of the fox populations that do currently exist is vital to the success of future conservation efforts. This is especially important since the evidence we present here implies that this population may be different in many ways from populations in southerly regions, where more empirical information has been generated for this species. These differences may be attributed to a possible lack of resources, the likely low swift fox abundance, and/or predator removal practices. Further research is necessary to determine the mechanisms that result in lower litter size, higher survival rates, den site locations, dispersal patterns, and large home ranges. Understanding the mechanisms behind the ecology of this population will allow wildlife managers to develop site-specific conservation plans and programs, thus encouraging continued reestablishment of the species in this region.

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Figure 1. The map includes the focal counties in southwest North Dakota (Bowman, Adams, Hettinger, and Slope) and northwest South Dakota (Harding, Perkins, Meade, and Butte) where swift fox were captured. Individual fox trapping locations are shown as black dots, reintroduction sites are shown as black triangles, and the remnant population is shown as a black star.

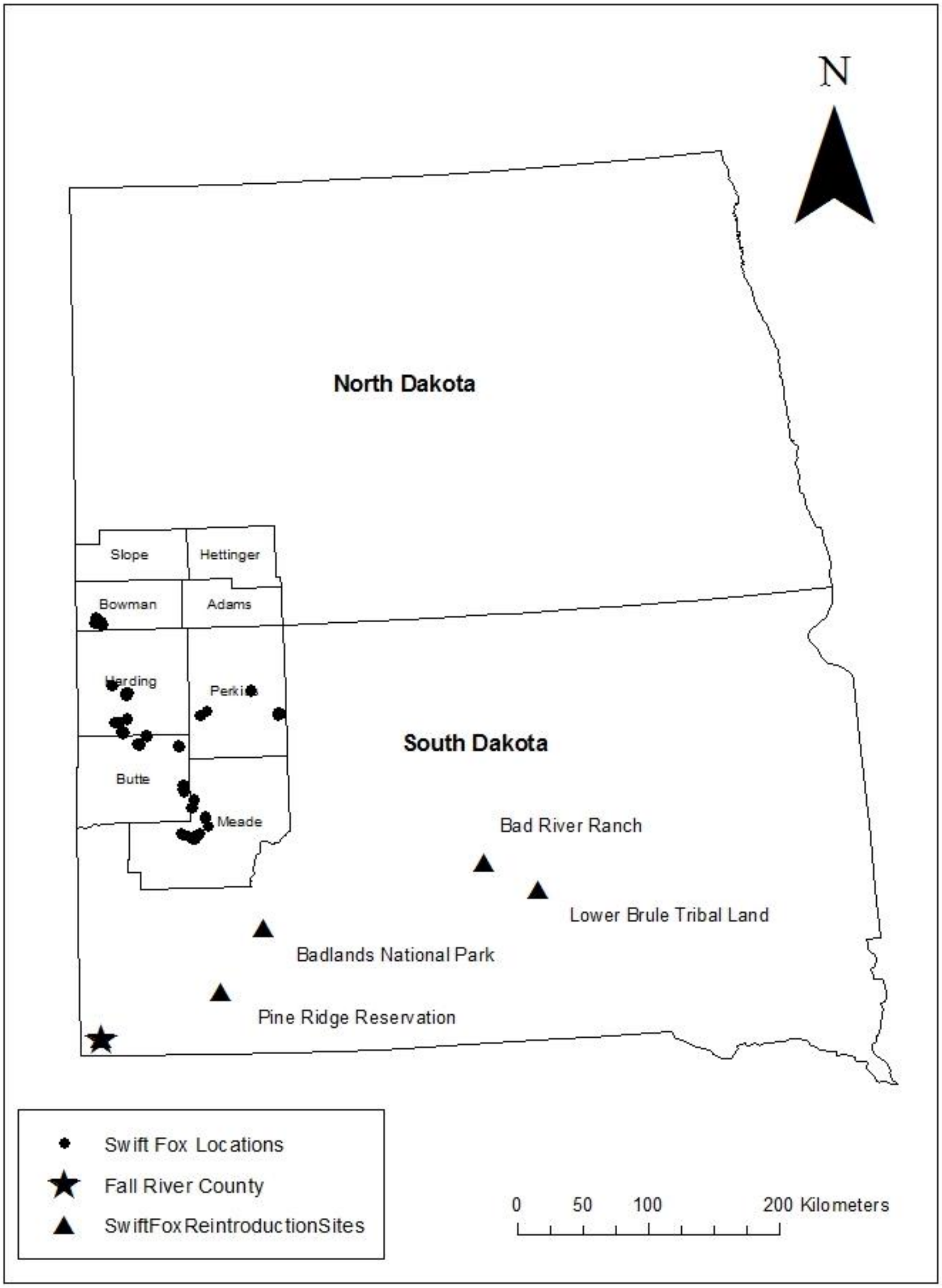

Table 1. Radio collared swift fox capture, sex (F = female, M = male), age (A = adult, J = juvenile), and mortality data.

Fox ID	Date Captured	County	Sex	Age	Mortality Date	Mortality Cause
1602	7/26/2016	Bowman	F	J		
1604	7/26/2016	Bowman	F	A		
1606	9/14/2016	Meade	F	J		
1608	9/14/2016	Meade	M	J		
1609	9/14/2016	Meade	F	J		
1611	9/14/2016	Meade	F	J		
1612	9/14/2016	Meade	F	J		
1614	9/17/2016	Bowman	M	A		
1615	9/27/2016	Meade	F	J		
1616	9/28/2016	Meade	F	J		
1617	10/11/2016	Perkins	M	A		
1618	11/12/2016	Perkins	F	J		
1621	11/6/2016	Perkins	F	J		
1622	11/6/2016	Perkins	M	A		
1623	11/11/2016	Butte	M	A	11/7/2017	unknown
1624	11/26/2016	Harding	M	A		
1625	12/13/2016	Harding	F	J		
1702	1/14/2017	Harding	F	J		
1704	1/26/2017	Harding	F	J	11/24/2017	vehicle
1705	2/3/2017	Harding	M	A	8/25/2017	coyote
1707	3/28/2017	Harding	F	J		
1708	3/28/2017	Harding	M	A		
1709	3/30/2017	Meade	M	A	8/28/2017	coyote
1710	3/31/2017	Butte	M	A		
1711	3/31/2017	Meade	F	A		
1714	4/1/2017	Butte	M	A		

Table 2. Swift fox survival model results for known fate in program MARK. The best fit model (t; time, the number of weeks monitored) was decided by lowest AIC value.

Model	**AICc**	**Delta AICc**	**AICc Weight**	**Model Likelihood**	**Number of Parameters**	**Deviance**
{S(t)}	29.85	0.00	0.99	1.00	3.00	23.82
{s(.)}	41.85	12.01	0.00	0.00	1.00	39.85
{S(age*sex)}	53.70	23.86	0.00	0.00	3.00	47.68
{S(age+sex)}	60.50	30.66	0.00	0.00	2.00	56.49
{S(sex)}	399.11	369.26	0.00	0.00	2.00	395.09
{s(age)}	728.90	699.05	0.00	0.00	2.00	724.89

Table 3. Radio collared juvenile swift fox age, dispersal dates, distances, and the fate (i.e., survival status/reproductive status) of the fox for 15 individuals. Seven of the juvenile radio collared swift fox were documented to have an obvious dispersal event, moving at least 4.82 km from their original capture location. All seven dispersing individuals were female.

Fox ID	Sex	Dispersal Event	Dispersal Date	Dispersal Distance (km)	Fate
1602	F	N	lost 2/14	----------	unknown
1606	F	N	----------	----------	survived/ unknown
1608	M	Y	3-Nov	26.95	survived/ unknown
1609	F	Y	23-Oct	12.07	survived/ reproduced
1611	F	Y	3-Nov	4.82	survived/ reproduced
1612	F	Y	3-Feb	19.05	survived/ unknown
1615	F	N	lost 2/14	----------	unknown
1616	F	Y	3-Feb	15.57	survived/ unknown
1618	F	Y	14-Feb	29.64	survived/ unknown
1621	F	Y	3-Feb	12.35	survived/ unknown
1625	F	N	----------	----------	survived/ unknown
1702	F	N	----------	----------	survived/ reproduced
1704	F	N	----------	----------	died - vehicle collision
1707	F	N	----------	----------	survived/ did not reproduce
1708	M	N	----------	----------	survived/ unknown

Table 4. Radio collared swift fox home range estimates, using 95% Kernel Density Estimate (KDE; home range) and 50% Kernel Density Estimate (core area), with sex (F = female, M = male), age (A = adult, J = juvenile), and number of telemetry fixes for each fox.

Fox ID	Sex	Age	# Fixes	95% KDE	50% KDE
1602	F	J	22	29.70	6.49
1604	F	A	52	32.90	6.09
1606	F	J	46	49.48	7.79
1609	F	J	42	105.54	21.44
1611	F	J	45	55.87	10.85
1612	F	J	26	132.44	37.34
1614	M	A	53	49.11	10.84
1615	F	J	19	37.20	9.35
1616	F	J	32	58.46	14.75
1617	M	A	50	28.87	5.57
1618	F	J	29	16.73	3.62
1621	F	J	45	71.19	12.84
1622	M	A	16	70.32	16.09
1623	M	A	40	112.20	27.5
1624	M	A	44	21.53	4.69
1625	F	J	39	39.01	9.05
1702	F	J	35	29.01	4.85
1704	F	J	32	44.27	7.37
1705	M	A	21	45.45	11.47
1707	F	J	27	46.52	10.86
1708	M	A	26	58.88	12.06
1709	M	A	13	73.45	16.26
1711	F	A	26	53.27	11.46
1714	M	A	27	67.64	14.06
Average				**55.37667**	**12.19542**

Table 5. Average swift fox litter sizes reported by similar studies throughout the range of the swift fox.

Location	**Average Litter**	**Sample Size**	**Reference**
Badlands National Park, South Dakota	4.30 (±0.30)	17	Nevison 2017
Southeastern Colorado	2.50 (±1.90)	51	Karki 2007
Kansas	3.10 (±0.40)	10	Sovada et al. 2003
Southeastern Wyoming	4.60 (±0.40)	25	Olson and Lindzey 2002*a*
Alberta/Saskatchewan	3.90 (±1.8)	29	Moehrenschlager 2000
Southeastern Colorado	2.40 (±0.30)	13	Covell 1992
Beaver County, Oklahoma	4.30 (±1.10)	4	Kilgore 1969
AVERAGE	**3.57**		
Southwest South Dakota/Northwest North Dakota	3.25 (±0.50)	4	*This study*

Table 6. Swift fox survival estimates with in the Northern Great Plains region and throughout the species range.

Location	**Survival Probability**	**Sample Size**	**Method**	**Reference**
Badlands National Park, South Dakota	0.38-0.47	22	Kaplan-Meier	Nevison 2017
Badlands National Park, South Dakota	0.20-0.47	341	Cormack–Jolly–Seber	Sasmal et al. 2016
Southeast Wyoming	0.40-0.69	56	Kaplan–Meier	Olson and Lindzey 2002*a*
Montana	0.46	11	Kaplan–Meier	Zimmerman 1998
Colorado	0.13-0.53	94	Kaplan-Meier	Covell 1992
Northern Montana	0.47-0.73	58	Matlab ‘‘eigenall’’	Ausband and Foresman 2007
Piñon Canyon Maneuver Site, Colorado	0.55-0.75	90	MICROMORT	Schauster 2001
Western Kansas	0.55-0.67	65	Kaplan-Meier	Sovada et al. 1998
Texas	0.52-0.66	42	MICROMORT	Kamler et al. 2003*a*
Southwest South Dakota/Northwest North Dakota	0.86	26	known-fate	*This study*

Table 7. Average home range size of 5 similar studies, throughout the swift fox range. Comparing results can be difficult due to different methods of analyzing data. 95% adaptive kernel density (ADK) and minimum convex polygon (MCP) are the most common.

Location	**Average Home Range (km^2)**	**SE/range**	**Sample Size**	**Method**	**Reference**
Kansas	15.90	SE = 1.60	21	95% ADK	Sovada et al. 2003
Colorado	7.60	SE = 0.50	73	95% ADK	Kitchen et al. 1999
Texas	11.70	SE = 1.00	17	MCP	Kamler et al. 2003*a*
Nebraska	32.20	7.70-79.30	7	MCP	Hines and Case 1991
Montana	10.40	7.30-16.90	5	MCP	Zimmerman et al. 2003
AVERAGE	**14.92**				
Southwest South Dakota/Northwest North Dakota	55.38	SE = 5.84	24	95% ADK (LSCV)	*This study*

CHAPTER 3

AFFECT OF SYMPATRIC CANIDS ON DISTRIBUTION OF SWIFT FOXES (*VULPES VELOX*) IN THE DAKOTAS, USA

ABSTRACT

Interspecific competition between coyotes (*Canis lupis*), red fox (*Vulpes vulpes*) and swift fox (*Vulpes velox*) is likely a factor determining species distribution throughout the landscape. We conducted a systematic survey of suitable swift fox habitat in 6 counties and all suitable home ranges in 2 counties from August - December 2015 (North Dakota), and 2016 (South Dakota) to shed light on how these species interactions affect swift fox distribution. We placed the camera stations 6.68 km apart, roughly two swift fox home ranges, and each camera station was deployed for 7 consecutive trap nights. We detected swift fox at 10 camera sites, coyotes at 191 camera sites, and red fox at 190 camera sites in 3,929 effective trap nights. We live captured swift fox and tracked weekly, from July 2016 to April 2017; capturing 41 swift fox, deploying 26 radio collars, collecting 611 locations. We also located 32 active den locations, confirmed 7 incidental sightings, and located 9 road mortalities. We used the camera detection data to model occupancy of coyotes and red fox at two different scales, double-home range (6.68 km) and home range (3.34 km). At the double-home range scale, we estimated a detection probability of 0.176 (SE = 0.013) for coyotes, a detection probability of 0.195 (SE = 0.0119) of red fox. We estimate that coyotes occupy 63% of the study area, while red fox occupy 53%. At the home range scale, we estimated a detection probability of 0.175 (SE = 0.013) for coyotes, a detection probability of 0.802 (SE = 0.137) of red fox. We estimate that coyotes occupy 69% of the study area, while red fox occupy 46%. We used Random Forest (RF) and the combined detection data (camera, trapping, tracking, den sites, mortalities, and incidental sightings) to model distribution of swift fox, adding the sympatric canid occupancy models in as predictor variables, also at two different scales, the sub-home range (30 m) and the home range (3.34 km). The swift fox distribution model at the sub-home range scale had an overall out-of-bag (OOB) of 0.108, OOB error of presence of 0.140, and an OOB of absence of 0.078. The top prediction variables were elevation, coyote occupancy, red fox occupancy, percent sand in soil, and road density. Of the 40,632.49 km^2 study area only about 5,000 km^2, or 12%, has a ≥ 50% chance of being used by swift fox. While at the home range scale, overall out-of-bag (OOB) of 0.480, OOB error of presence of 0.256, and an OOB of absence of 0.559. The top prediction variables were red fox occupancy, roughness, percent scrub, coyote occupancy, and greenness. With this model about 14,000 km^2, or 34%, has a ≥ 50% chance of being used by swift fox. Both models were overfit, but both also found coyote and red fox occupancy to be negatively correlated with swift fox habitat use. This study is one of the first to explicitly incorporate interspecific three-way interactions into a species distribution model, and it is the first of its kind to do so for swift foxes. The results illustrate the importance of including the effect of sympatric canid occupancy in future assessments of swift fox distribution.

INTRODUCTION

Apex predators, species that occupy the top trophic position in a community, have been found to play a leading role in suppressing populations of mesopredators (Crooks and Soulé 1999, Johnson et al. 2007, Berger et al. 2008, Ritchie and Johnson 2009). Apex predators can affect abundance and distribution of mesopredators directly through lethal encounters, as well as indirectly by inducing behavioral changes to reduce mortality risk (Ritchie and Johnson 2009). Mesopredator release hypothesis predicts an increase in mesopredators abundance when apex predator abundance is reduced (Soulé et al. 1988). This is thought to be due to a decrease in intraguild predation and competition.

One form of lethal encounter between apex predators and mesopredators is interspecific killing, where the mesopredator is killed for reasons other than food consumption (Minta et al. 1992, Gese et al. 1996, Palomares and Caro 1999, Helldin et al. 2006). Interspecific killing is especially common among canid species (Carbyn 1982, Paquet 1992, Thurber et al. 1992, White et al. 1994, Ralls and White 1995, Palomares and Caro 1999, Kamler et al. 2003*b*, Pamperin et al. 2006), and is generally associated with interspecific competition for food resources (Donadio and Buskirk 2006). In some cases the rate of interspecific killing has direct, negative demographic effects on the smaller canid species (Caro 1987, Palomares and Caro 1999, Sergio and Hiraldo 2008). For example, Ralls and White (1995) demonstrated that coyote predation can cause significant population declines in kit fox (*Vulpes macrotis*). Interspecific killing can also create a landscape of fear response (Brown et al. 1999), causing mesopredators to alter their behavior to avoid high-risk areas. This ultimately results in spatial displacement of smaller canids by the larger canids which kill them, as has been well documented in coyote and red fox interactions (Voigt and Earle 1983, Major and Sherburne 1987, Sargeant et al. 1987) and in red fox and arctic fox interactions (reviewed in Hof et al. 2012).

In the Dakotas, the coyote is considered an apex predator, due to the extirpation of wolves (*Canis lupus*; Crooks and Soulé 1999). Coyotes are sympatric, in the mixed grass prairies of the Dakotas, with two smaller canid species, red fox and swift fox. Of these species, the swift fox is considered rare in North Dakota and is listed as threatened in South Dakota (North Dakota Game and Fish 2017, South Dakota Game, Fish, and Parks 2017). The current swift fox distribution is unknown, and could be negatively affected by the presence of coyotes, and potentially also by red fox. For example, interspecific killing is a well-documented outcome of coyote/swift fox interactions (Kamler at al. 2003*a*, White et al. 1994, Ralls and White 2016, Karki et al. 2007), and coyotes have been found to be the primary cause of mortality in swift fox, resulting in suppression of swift fox populations (Covell 1992, Carbyn et al 1994, Sovada et al. 1998, Olson and Lindzey 2002, Schauster et al. 2002, Kamler et al. 2003*b*, Ausband and Foresman 2007). Swift fox home ranges have been found to not overlap coyote core areas, presumably to avoid the predation threat (Kamler et al. 2003*b*, Thompson and Gese 2007). Neither interspecific killing nor exclusion of swift fox by red fox has been described. Nonetheless, red fox are known to kill arctic fox and kit fox to remove them from preferred habitat (Frafjord et al. 1989, Ralls and White 1995, Pamperin et al. 2006), so it is likely that red fox also kill swift fox. Likewise, behavioral avoidance of red fox by arctic fox has been observed at den sites (Frafjord et al. 1989) and the presence of red fox is the primary factor limiting arctic fox recolonization of areas from which it was extirpated in Fennoscandia (Hamel et al. 2013), thus it seems probable that red fox may negatively influence the local distribution of swift fox in the Dakotas.

Taken together, the evidence of both coyote and red fox predation on and exclusion of smaller fox species provides clear evidence that interspecific interactions between canid species, in addition to habitat attributes, likely play an important role in understanding species distribution and habitat use for smaller canids like the swift fox. To date, most investigations of swift fox distribution have focused on habitat characteristics (e.g., Finley et al. 2005, Martin et al. 2007, Corral 2012) or focused on site-specific characteristics such as vegetation height, slope, soils, and distance to road (e.g., Cutter

1958, Kilgore 1969, Chambers 1978, Hillman and Sharps 1978, Roy and Dorrance 1985, Hines and Case 1991, Sovada et al. 2001). It is currently unclear whether or not red fox or coyotes affect swift fox space use in the study site. Our objective was to assess the influence of the presence of sympatric canids, in addition to habitat characteristics, on swift fox home range distribution in an area where the species is rare and appears to be in the process of recolonization. To meet this objective, we conducted a systematic camera survey to record species presence, and used a unique approach which combined occupancy model outputs for coyotes and red fox into a species distribution model (SDM) for swift fox. If either coyotes or red fox were to displace swift fox, we expect to observe a negative relationship between swift fox presence and the probability of occupancy of either sympatric canid. We also hypothesize that sympatric canids can displace swift fox from their preferred habitat. If this were the case, we would expect to observe habitat relationships that are opposite or unusual (e.g. a negative relationship with % cover of grass) based on what is known for swift fox in other areas. Lastly, we hypothesize that there is a tri-trophic interaction between coyotes, red fox, and swift fox; with coyotes excluding both red fox and swift fox, likely encouraging red fox to then exclude swift fox.

STUDY AREA

The study area included Harding, Butte, Perkins, and Meade counties in South Dakota and Slope, Bowman, Adams, and Hettinger counties in North Dakota (Figure 1). The study was conducted on state, federal (i.e., Forest Service and Bureau of Land Management), and private lands within the region. The study area encompassed approximately 40,600 km^2 dominated by mixed grass prairie, interspersed with sagebrush

(*Artemisia* sp.). Prominent grasses of the mixed grass prairie in the area were: western wheatgrass (*Pascopyrum smithii*), green needle grass (*Nassella viridula*), needle and thread (*Hesperostipa comata*), blue grama (*Bouteloua gracilis*), and side-oats grama (*Bouteloua curtipendula*). Topography was largely flat to gently rolling hills with occasional buttes. The primary soil types were clays derived from Createaceous Pierre Shale. Predominate water features included Shadehill Reservoir, Belle Fourche Reservoir, and the Belle Fourche River. Lands use was primarily cattle and sheep production. 77% of the study area was deemed suitable swift fox habitat via a habitat suitability index (Olimb et al. 2018).

MATERIALS AND METHODS

Camera survey:

We used ArcGIS (ESRI, Redlands, CA) and Geospatial Modeling Environment (GME; Spatial Ecology LLC, Hawthorne L. Beyer, 2001-2014), and a swift fox habitat suitability index, created by World Wildlife Fund (WWF; Olimb et al. 2018), to generate a grid of survey sites 6.68 km apart, about two swift fox home ranges (Sovada et al. 2003) for Meade and Perkins counties in South Dakota and Slope, Bowman, Adams, and Hettinger counties in North Dakota. In all but two counties, locations are within swift fox predicted high-quality habitat. However, camera locations in Harding and Butte County in South Dakota were similarly spaced but were chosen without regard to habitat type or suitability. This was done to obtain samples from areas not defined as suitable by the swift fox habitat suitability index. When access to the site centroid could not be obtained, we placed cameras in the nearest accessible habitat, maintaining a minimum spacing of 3.34 km (one swift fox home range) to reduce the likelihood of the same swift fox being detected at multiple sites (Figure 1). We sampled sites by placing a Browning Black Ops HD (Browning Trail Cameras) or Moultrie (EBSCO Industries Inc.) trail camera on an existing structure (i.e., fence post or power pole) in the highest quality swift fox habitat nearest the site centroid. We placed cameras approximately 40 cm above the ground, facing various directions. We did not face them due east or west in order to avoid glare from the sun. We then applied a scent lure, such as Canine Call (Carman's, New Milford, PA) and/or Powder River (O'Gorman Enterprises, Broadus, MT), to a wooden stake placed 3 m in front of the camera. We also applied sent lure to the ground at random locations between the camera and the stake. To provide an additional attractant, we punched 8 holes in a can of cat food, and staked it to the ground 2-3 inches in front of the wooden stake (Figure 2).

Camera trapping occurred for 7 consecutive days at each site from August to December in 2015 (North Dakota) and 2016 (South Dakota). We chose fall sampling because swift fox pups begin to forage independently, juveniles begin to disperse, and adults are more active and travel farther from their dens during this time (Olson et al. 2003). This increased activity maximized the chance of detecting individuals in this small population (E. Mitchell in prep.). We defined a sampling occasion to be a 24 hour period beginning at the time of set up. We defined encounter history as detected, "1", if the animal was photographed at least once in a sampling occasion and undetected, "0", if it was not.

Live capture and radio telemetry:

We captured swift foxes from July 2016 to April 2017 using 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). We fitted captured foxes weighing over 2 kg with a necklace-type VHF radio collars (model 1830, Advanced Telemetry Systems, Isanti, MN, USA) and released them at the capture site. We located radio collared swift foxes after dark once weekly, on average, between July 2016 and December 2017. We used a null peak vehicle mounted system (Brinkman et al. 2002) for radio telemetry until snow closed the roads in October 2016. From then until sampling ended in December 2017 we located foxes from a fixed-wing aircraft with wing-mounted antennae when weather conditions allowed and pilots were available. We located foxes after dark and recorded a GPS location using aerial telemetry or triangulation. We tracked foxes using handheld antennae to find den sites.

Predictor Variable Selection:

We chose predictor variables that were likely to represent important determinants of swift fox and sympatric canid habitat suitability based on previously published literature (Table 1). We obtained these predictor variables from publically available landcover, soil type, DEM, and road GIS layers. We calculated separate GIS layers for crop, grass, forest and scrub land cover types using the National Land Cover Database (NLCD 2012). For each layer, we calculated the proportion of the target land cover type using a moving window with a 1 km radius implemented in the Geomorphometry and Gradient Metrics add-on toolbox in ArcGIS 10.0 (Evans and Oakleaf 2012). We used the tasseled cap transformation (ESRI 2010) to measure brightness of soil (brightness), presence and density of green vegetation (greenness), and soil and vegetation moisture content (wetness) from the Global Land Survey dataset (GLS 2010). We calculated percent sand from a soil composition layer based on the NRCS General Soil Map (NRCS

USDA 2006; Sarah Olimb/WWF). We created measures of topographic complexity (i.e., roughness and surface relief ration (SRR)), slope (degrees) and northness (a cosine transformation of aspect) using a Digital Elevation Model (DEM; USDA NRCS datagateway.nrcs.usda.gov accessed 1 May 2012). To calculate slope and northness we used the slope and aspect functions in ArcToolbox (ArcGIS 10.3.1). We calculated roughness and SRR using a moving window with a 1 km radius implemented in the Geomorphometry and Gradient Metrics add-on toolbox in ArcGIS 10.0 (Evans and Oakleaf 2012). We created a road density layer using the density function in ArcToolbox (ArcGIS 10.3.1), based on the North and South Dakota primary and secondary roads map (USDA NRCS datagateway.nrcs.usda.gov accessed 1 May 2012). Because we built occupancy models for coyotes and red fox (double home range and home range scale, see *Sympatric canid occupancy*, bellow), as well as species distribution models for swift fox (sub-home range and home range scales, see *Swift fox distribution*, below), we resampled all layers >30 m resolution (e.g., % crop, % forest, % grass, % scrub, elevation, slope, northness, roughness, surface relief ration, road density, brightness, and wetness) to 30m resolution for the double-home range scale and the sub-home range scale. For the home range scale, we resampled the original rasters for all predictor variables to 3.34 km, roughly the size of one swift fox home range. We calculated a Pearson correlation coefficient (Pearson 1896) to evaluate collinearity between landscape variables, excluding one variable if pair-wise correlations were > 0.59, and continuing until no correlated variables remained.

To generate predictor variables associated with red fox and coyote occupancy, we used the following steps. First, we converted the predicted occupancy tables for coyotes and red foxes (see *Sympatric canid occupancy*, below) into point shapefiles in ArcMap (ArcGIS 10.3.1). We then converted the point shapefiles into raster layers using the occupancy prediction at each point on the grid. As part of the raster creation process, we made the occupancy rasters to have the same spatial resolution, extent, and projection as the rest of the predictor variables (i.e., 30 m). We used the resulting raster layers of coyote and red fox occupancy as additional predictor variables in the distribution model for swift fox (Random Forest). For the model attempt at the swift fox home range scale, we used the coyote occupancy layer as an additional predictor variable in the red fox occupancy model.

Sympatric canid occupancy:

We used the "unmarked" package in the R statistical computing environment (Fiske and Chandler 2011; R Development Core Team, cran.r-project.org, accessed 1 May 2016) to model site occupancy of sympatric carnivores, coyote and red fox, using two different scales intended to model occupancy at the double-home range scale (6.68 km) and home range scale (3.34 km). We followed a two-step methodology to estimate the probability of detection and occupancy (Richmind et al. 2010). We first held occupancy constant and modeled detection probability as a function of environmental covariates that may affect the probability that red fox or coyote would be detected by the cameras when present ($\Psi(.)$, p(covariate); Table 2). Covariates used that may affect detection were % crop, % scrub, % forest, and wetness. They were chosen because they indicate environmental factors that could block the camera, inhibiting the ability to detect an animal in front of it. We chose the detection model with the lowest AIC value, and began fitting models representing biological hypothesis, such as habitat characteristics coyotes or red foxes select for, that may explain occupancy (Burnham and Anderson 2002; Table 2 and Table 4). We standardized continuous environmental covariates using z-scores to facilitate the interpretation of coefficients (Cooch and White 2006, Silva et al. 2017). We ranked candidate models using the Akaike Information Criterion (AIC) (Burnham and Anderson 2002). We used environmental covariates for all models, except the red fox occupancy model, at the home range 3.34 km scale. In which we also used coyote occupancy as an added covariate, due to the potential influence interspecific completion with coyotes may have on red fox occupancy.

Swift fox distribution:

We used a machine learning approach, random forest (RF) (Brieman 2001), to model distribution of swift foxes at two scales (sub-home range and home range). We chose random forest because it has high classification accuracy and has been found to create better species range maps in under sampled areas (Guisan and Thuiller 2005, Cutler et al. 2007, Drew et al. 2011, Mi et al. 2017). Random forest uses regression trees to model species distribution (Breiman 2001), where the response variable is recursively partitioned into increasingly homogenous groups through binary splits of one predictor variable at a time (Breiman et al. 1984). At each node, the threshold value and the predictor variable(s) are selected at random from the entire suite of predictors, so that the difference between the resulting branches is maximized. For greater predictive accuracy, random forest combines predictions from many regression trees (Breiman 2001). A major advantage of the random forest approach is that it is non-parametric and lacks distributional assumptions about study design, allowing use of multiple data sources (Cutler et al. 2007). Here, we used live trapping and radio tracking records to include swift fox detections in areas where the camera survey failed to detect the species. However, care must be taken to avoid over fitting and bias associated with non-random sampling (Domingos 2012). We attempted to avoid over fitting by having binary splits of three predictor values at a time, rather than one, and reducing the number of decision trees from 1501 (sub-home range scale) to 1001 (home range scale), and for the model at the home range scale we altered cutoffs to accept more sensitivity.

We preformed random forest analysis using the "randomForest" package in the R statistical computing environment (Liaw and Wiener 2002; R Development Core Team, cran.r-project.org, accessed 1 May 2016) to model the potential distribution of swift fox, using two different scales intended to model habitat suitability at the sub-home range scale (30 m) and home range scale (3.34 km). We used swift fox presence data from multiple sources, including camera detections, road kills, confirmed incidental sightings, and tracked locations of radio collared foxes. For the model at the sub-home range scale we used all known such locations. Conversely, for the model at the home range scale we deemed the centroid of each cell either occupied or not occupied regardless of the number of known swift fox locations within the cell. We then used a random number generator to randomly select 33% of the absence locations to remove, in an attempt to reduce the effect of pseudo-absences (Hanberry et al. 2012). We used landscape and topographical variables of elevation metrics, as well as the probability of predicted occupancy of sympatric red fox and coyotes. After removing correlated variables, for the 30m scale model the total number of predictor variables was 13, total number of trees was 1501, and total number of variables at each split was 3. For the 3.34 km scale model the total number of predictor variables was 6, total number of trees was 1001, and total number of variables at each split was 3. To assess prediction error in the generated Random Forest, we withheld 33% of samples in an out-of-bag (OOB) sample random forest model. We then applied a predictive classifier, "raster" package in the R statistical Computing environment (Hijman and van Etten 2012; R Development Core Team, cran.r-project.org, accessed 1 May 2016) to produce a map of predicted distribution for swift fox (Figure 3 and 4). To investigate model fit, at both scales, we calculated Out of Bag (OOB) error, Area Under the Receiver Operating Characteristic curve (AUROC; Fawcett 2006), sensitivity, and specificity for each model.

RESULTS

We deployed trail cameras at 582 locations on the grid of 590 potential survey sites, 56 of these in North Dakota and 526 in South Dakota, for a total of 3,929 trap nights. We recorded >300,000 photographs, and swift fox at 10 camera stations on 25 nights, coyotes at 191 camera stations on 304 nights, and red fox at 105 camera stations on 190 nights. We obtained 611 locations from 26 radio-collared swift foxes. Collared animals included: 15 females (2 adults and 13 juveniles) and 11 males (10 adults and 1 juvenile). We recorded 27 den locations by tracking radio-collared individuals. We found 5 dens, 7 live foxes and 9 road mortalities independently of the telemetry effort. This effort resulted in the detection of swift fox in 126 sample units that were used for random forest modeling.

Sympatric canid occupancy (double-home range scale):

We detected coyotes on 304 of the 3,929 effective trap nights, a global trapping rate of 7.46 captures/100 trap nights or 1 coyote capture every 13.4 trap days. The constant detection model was the chosen to best fit the data, and the detection probability was 0.176 (SE = 0.0134). There were 6 models with AIC < 2 (Table 2). All of these top six models include different covariates. Although model selection uncertainty was high, the best model predicted that the probability a site was occupied by coyotes was positively related to percent grass cover (Table 3). Sixty-three percent of the study area was predicted to have ≥ 50% likelihood of being used by coyotes (~25,700 km^2; Figure 5).

We detected red fox on 190 of 3,929 effective trap nights, with a global trapping rate of 4.66 captures/100 trap nights or 1 red fox capture every 21.56 days. Detection probability for red fox was negatively related percent roughness and positively related to the percent of scrub (Table 3), and the probability that red fox occupied a site was negatively related to percent sand in the soil (Table 3). There were only 2 models with AIC < 2 (Table 4). Both of these top models include percent sand in the soil as a covariate, indicating that percent sand is an important variable in predicting red fox occupancy. Fifty-four percent of the study area was predicted to have ≥ 50% likelihood of being used by red foxes (~21,700 km^2; Figure 7).

Sympatric canid occupancy (home range scale):

Similar to the previously discussed coyote model the constant detection model was the chosen to best fit the data. The detection probability was 0.175 (SE = 0.013). However, model selection uncertainty was higher at this scale, because there were 10 models with AIC < 2 (Table 2). Four of these top models include percent grass as a covariate, indicating that percent grass is an important variable when predicting coyote occupancy. Sixty-nine percent of the study area was predicted to have ≥ 50% likelihood of being used by coyotes (~29,000 km^2; Figure 6).

Red fox detection probability estimate was 0.802 (SE = 0.137). There were only 1 model with AIC < 2 (Table 2). Red fox detection probability was negatively related to the percent of crop and the data the survey station was set (Table 3). The occupancy probability a site was negatively related to percent sand in the soil and the slope (Table 3). Forty-six percent of the study area was predicted to have ≥ 50% likelihood of being used by red foxes (~19,200 km^2; Figure 8).

Swift fox distribution (sub-homerange scale):

The overall out of bag error (OOB) estimate was 0.108; the specific measure of OOB for presence was 0.140, and absence was 0.078. Area Under the Receiver Operating Characteristic curve was 0.494, sensitivity was 93.24%, and specificity was 86.14%. Of the variables included in the model elevation, coyote occupancy, red fox occupancy, percent sand in soil, percent forest, road density, and percent grass are the most important variables in the model, with elevation being the most important of them all (Figure 9). Elevation, coyote, and red fox occupancy have a negative correlation with swift fox distribution (Figure 11). Percent sand in soil has a positive correlation with swift fox distribution, until a certain point (~38) when it them becomes a negative correlation. This is likely due to too much sand inhibiting their digging ability. Percent forest has a slightly negative correlation. Road density had a positive correlation to swift fox occupancy, likely due to swift fox using roads as travel corridors. Twelve percent of the study area was predicted to have ≥ 50% likelihood of being used by swift foxes (~5,000 km^2).

Swift fox distribution (home range scale):

The larger scale model had more variables that were collinear. Of the 6 variables included in the model red fox occupancy, surface relief ratio, roughness, percent scrub, coyote occupancy, and greenness are the most important variable in the model, with red fox being the most important variable of them all (Figure 10). The overall out of bag error (OOB) estimate was 0.480; the specific measure of OOB for presence was 0.256, and absence was 0.559. Area Under the Receiver Operating Characteristic curve was 0.502, sensitivity was 75.40%, and specificity was 43.26%. Of the top variables in the model, red fox has a negative correlation with swift fox distribution, likely due to interspecific competition with red fox (Figure 12). Roughness and coyote occupancy has a positive correlation, until a certain point (roughness ~110 and coyote ~0.35). This is likely due to and the inability to traverse very rough terrain and increased interspecific competition as coyote occupancy increases. Percent scrub and surface relief ratio are negatively correlated with swift fox distribution, until a certain point (percent scrub ~0.2 and surface relief ratio ~0.3). This is odd because swift fox are usually assumed to select specifically ofr short grass or mixed grass prairies and not areas with scrub. Brightness does not have an effect on swift fox distribution, until ~135 when it begins to have a positive correlation and then ~175 it begins to have a negative correlation. This is likely due to some sand in the soil being good for digging, but too much making digging dens harder. Thirty-four percent of the study area was predicted to have ≥ 50% likelihood of being used by swift foxes (~14,000 km^2).

DISCUSSION

We found that both coyote and red fox occupancy have a negative correlation with swift fox distribution. This result was expected because coyotes have been found to spatially displace swift fox by killing them and/or causing them to avoid certain areas (Kamler et al. 2003*b*, Thompson and Gese 2012). Our observation that swift fox tend to occur in areas with lower probability of occupancy by both coyote and red fox suggests that they are avoiding the larger canids. This is also true in the case of the coyote and red fox; red fox occupancy is negatively related to coyote occupancy in both the occupancy model attempts, suggesting that red fox are avoiding coyotes. Mesopredator release could be assisting in natural re-colonization of the area. This relationship is likely driven by competition and prey availability, due to the swift fox highly overlapping prey with coyotes and red fox (Robinson et al. 2014). The extensive predator removal programs in northwest South Dakota and southwest North Dakota may be benefitting swift fox by releasing them from predation or competition from both dominant predators (Rayner et al. 2007, Trewby et al. 2008, Ritchie and Johnson 2009, Cupples et al. 2011).

We found that fewer sites were predicted to be occupied by coyotes than expected. We hypothesize that this is due to the large scale predator removal that occurs in the area. However, it is also possible that we simply did not have enough survey stations to adequately survey for the species. Swift fox survival and recruitment has been shown to increase after reducing the coyote population, by removing coyotes via aerial gunning (Kamler et al. *2003b*, Karki et al. 2007*)*. Although not conclusive, this lower than expected occupancy of sympatric canids could be a factor in the recent success of the swift fox in the area (Carbyn et al 1994, Ralls and White 1995, Sovada et al. 1998, Olson and Lindzey 2002).

We hypothesized that red fox play a role in swift fox mortality and displacement due to their documented predation on smaller arctic and kit fox (Ralls and White 1995, Pamperin et al. 2006). Although swift fox mortality by red fox has not been confirmed, both random forest models predicted that the presence of red fox is negatively impacted the presence of swift fox. This implies that swift fox are being displaced or killed by red fox, or both. Our study is the first to show a negative relationship between swift fox and red fox.

We observed, trapped, and tracked a number of swift foxes that were not detected by the cameras, indicating limitations in the ability to detect swift foxes in low-density populations with the survey method used. Of the cameras with swift fox detections 40% had 1 detection, 20% had 2 detections, 20% had 3 detections, 10% had 5 detections, and 10% had 6 detections. This is in contrast to results from a swift fox survey conducted in Montana using identical methodology, where swift fox were observed to visit the camera station repeatedly during the survey period (Schwalm unpublished data). We hypothesis that the use of the single-camera survey method is likely providing a low detection probability and the use of multiple cameras at survey sites would greatly increase detection probability (Pease et al. 2016). Since the completion of this study a swift fox survey in Texas has taken into account the observed low detection probability generated here and is using multiple cameras per survey grid (D. Schwalm personal communication). Similar camera surveys are often completed through the range of the swift fox in order to calculate and monitor swift fox occupancy (Cudworth et al. 2011, Stratman 2012, Corall 2016). All of these surveys used a grid system with 5 to 10 cameras per grid. We suggest that future studies use a multi-camera survey design.

In Random Forest models, out-of-bag (OOB) measures model reliability through estimation of misclassification error, or the incorrect classification of a presence as an absence or vice versa, with lower values indicating higher classification accuracy. Our first attempt at Random Forest generated a distribution model of swift fox, at the sub-home rage scale, demonstrating high accuracy on average, with an OOB of 10.8%. However, the OOB error of presence (14.0%) is higher than the OOB error of absence (7.8%) is indicating that the model overestimates the probability of absence. It may be possible to reduce overfitting by changing the scale, subsetting the telemetry locations, and accounting for false absences, or pseudo-absence. Having an OOB error of absence higher than an OOB error of presence, indicates that the model is not over predicting swift fox distribution. The sensitivity value (93.24%) indicates that this model predicts presence of swift fox correctly 93.24% of the time, while the specificity value (86.14%) indicates that the model predicts absence of swift fox correctly 86.14% of the time. However, the low AROCC value (0.494) indicates imperfect balance between specificity and sensitivity, and therefore poor model performance at the level class.

After increasing the scale to one swift fox home range (3.34 km), subsetting swift fox detection locations to only have one record per cell, and randomly removing 33% of the absences we re-ran the Random Forest analysis. This approach generated a distribution model of swift fox demonstrating low accuracy on average, with an OOB of 48.03%. It is still over fitting, with an OOB error of presence of 25.91%, an OOB error of absence of 55.86%, an AUROC of 0.502, sensitivity of 75.50%, and specificity of

43.26%. However, this model is overestimating the probability of presence. Indicating an over prediction of suitable habitat. The sensitivity value indicates that this model predicts presence of swift fox correctly 75.50% of the time, while the specificity value indicates that the model predicts absence of swift fox correctly 43.26% of the time. However, the AROCC value (0.502) indicates no discrimination between sensitivity and specificity. There are multiple reasons why our model may still be over fitting including inappropriate scale, possible high pseudo absence, failure to include one or more important environmental variables, limited presence data (due to the small population size) and/or Random Forest may not be the appropriate model (Wiens 2002, Guisan and Thuiller 2005). In the future I suggest testing multiple scales, reducing the number of absences, and re-running the Random Forest analysis, or using a presence only species distribution model (e.g., Maxent (CITE) to correct for the potentially high frequency of pseudo-absences in the dataset.

Multiple attempts at modeling swift fox distribution in the Dakotas resulted in swift fox distribution models which are over fit. More specifically, these models appear to underperform in the accurate identification of potential species distribution, based on the recurrent and highly skewed misclassification error of presence records. The models presented here, and their associated spatial predictions, should be interpreted as inaccurate and not suitable for use in swift fox management decisions or as accurate representations of swift fox ecology. Future attempts at modeling swift fox distribution are necessary for assessing the status of the swift fox in this area, and we intend to continue with this work. This study has provided vital information regarding potential project design setbacks, and we suggest that future swift fox distribution studies which intend to use trail camera surveys consider using multiple cameras within each grid cell and, potentially, at each individual camera location. Additional monitoring efforts may be necessary to better assess swift fox distribution in the Dakotas.

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Figure 1. The study area surveyed for swift fox and sympatric canids in 2015 and 2016. Survey locations in North Dakota are represented as blue dots, and survey locations in South Dakota are represented as pink dots. All survey locations were space 6.68 km (two swift fox home ranges) apart in predicted suitable habitat, except for those in Harding and Butte County in South Dakota in which a survey station was set every 6.68 km regardless of habitat suitability. These added survey locations are represented as orange stars.

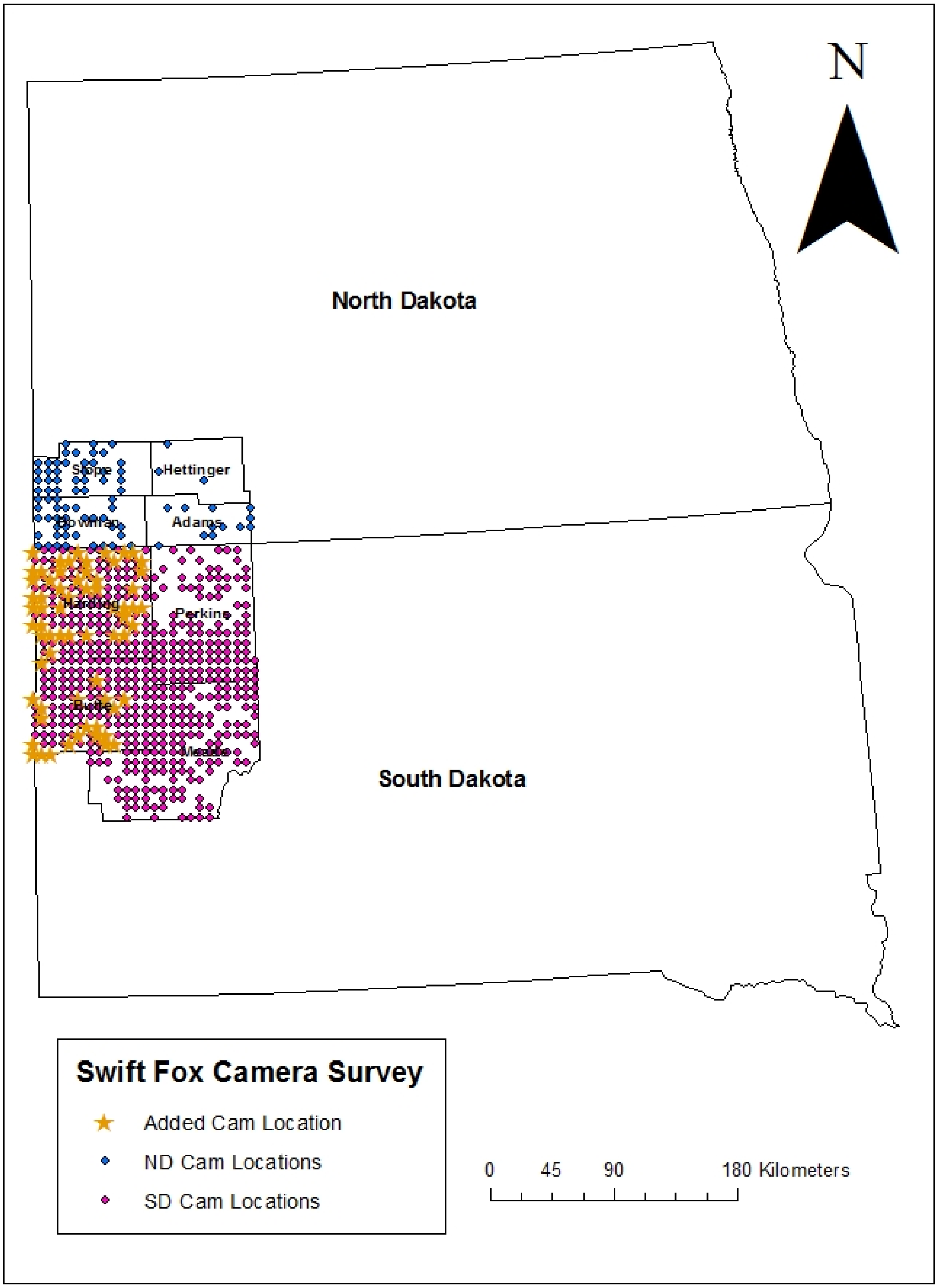


Figure 2. Diagram of survey station setup used to detect swift fox and sympatric canids in the western Dakotas. A camera was placed ~40 cm above the ground on an existing structure. A wooden stake was placed 3 meters in front of the camera. A scent lure was applied on the top of the stake and at random locations between the camera and the stake. 8 holes were punched into a can of cat food, and it was staked to the ground 2-3 inches in front of the wooden stake.

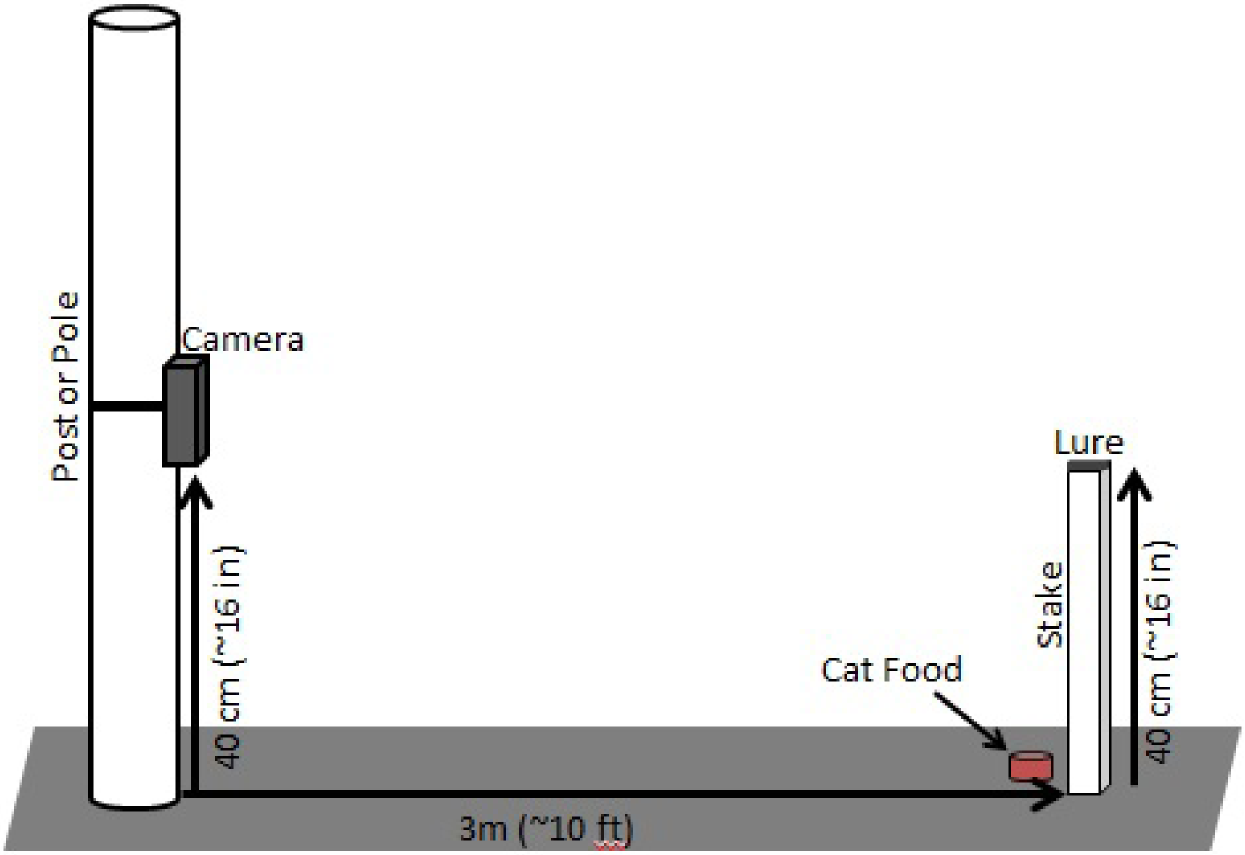


Figure 3. Predicted distribution of swift fox in the Dakotas, using Random Forest (Breiman 2001) at the 30 m scale. Overall out of bag error (OOB) was 0.108, OOB for records of presence was 0.140, and OOB for records of absence was 0.078. Of the roughly 40,600 km^2 in our study area, about 5,000 km^2, or 12%, have a likelihood of ≥ 50% of swift fox presence.

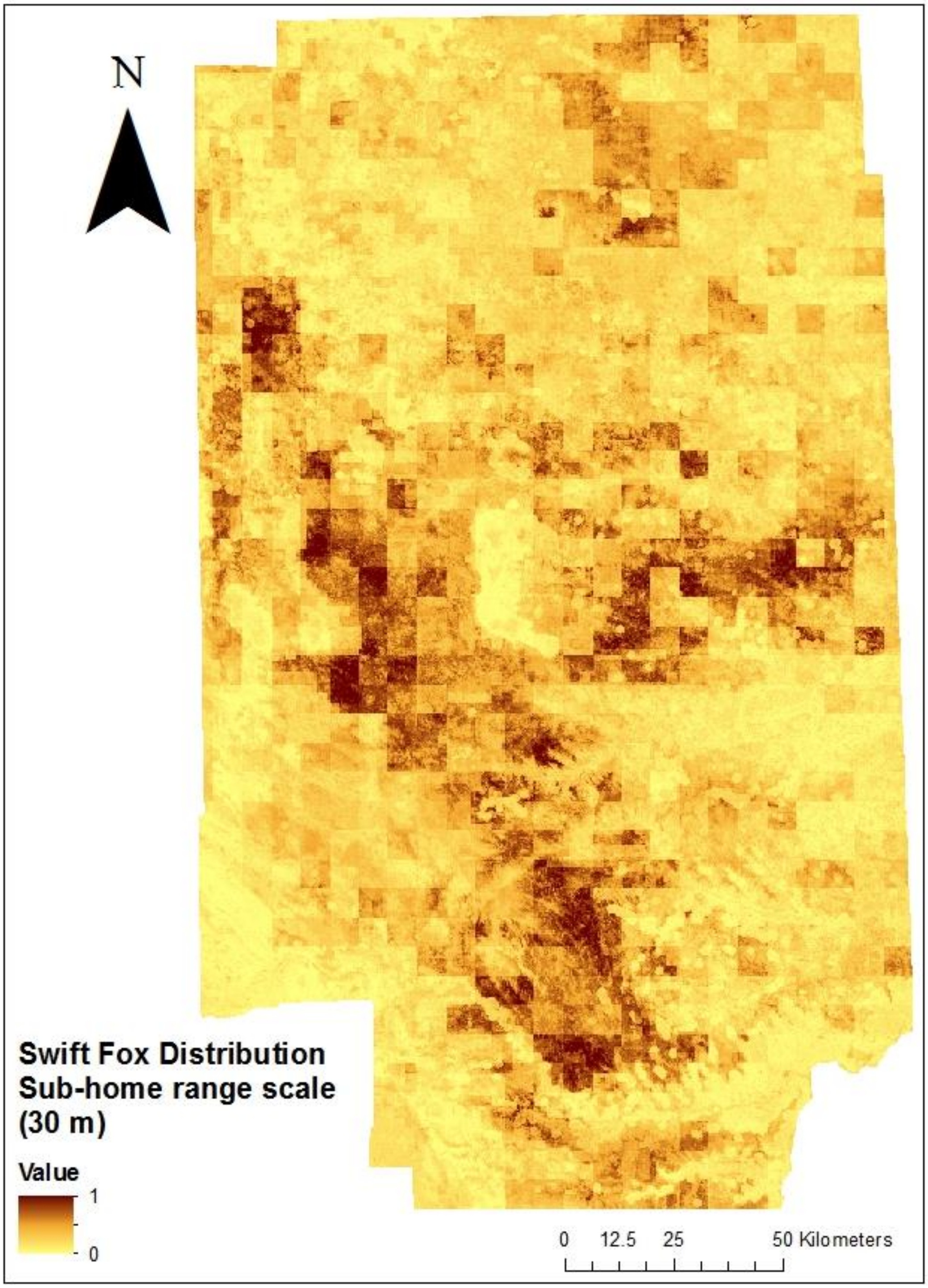


Figure 4. Predicted distribution of swift fox in the Dakotas, using Random Forest (Breiman 2001) at the 3.34 km scale. Overall out of bag error (OOB) was 0.480 OOB for records of presence was 0.259, and OOB for records of absence was 0.559. Of the roughly 40,600 km^2 in our study area, about 14,000 km^2, or 34%, have a likelihood of ≥ 50% of swift fox presence.

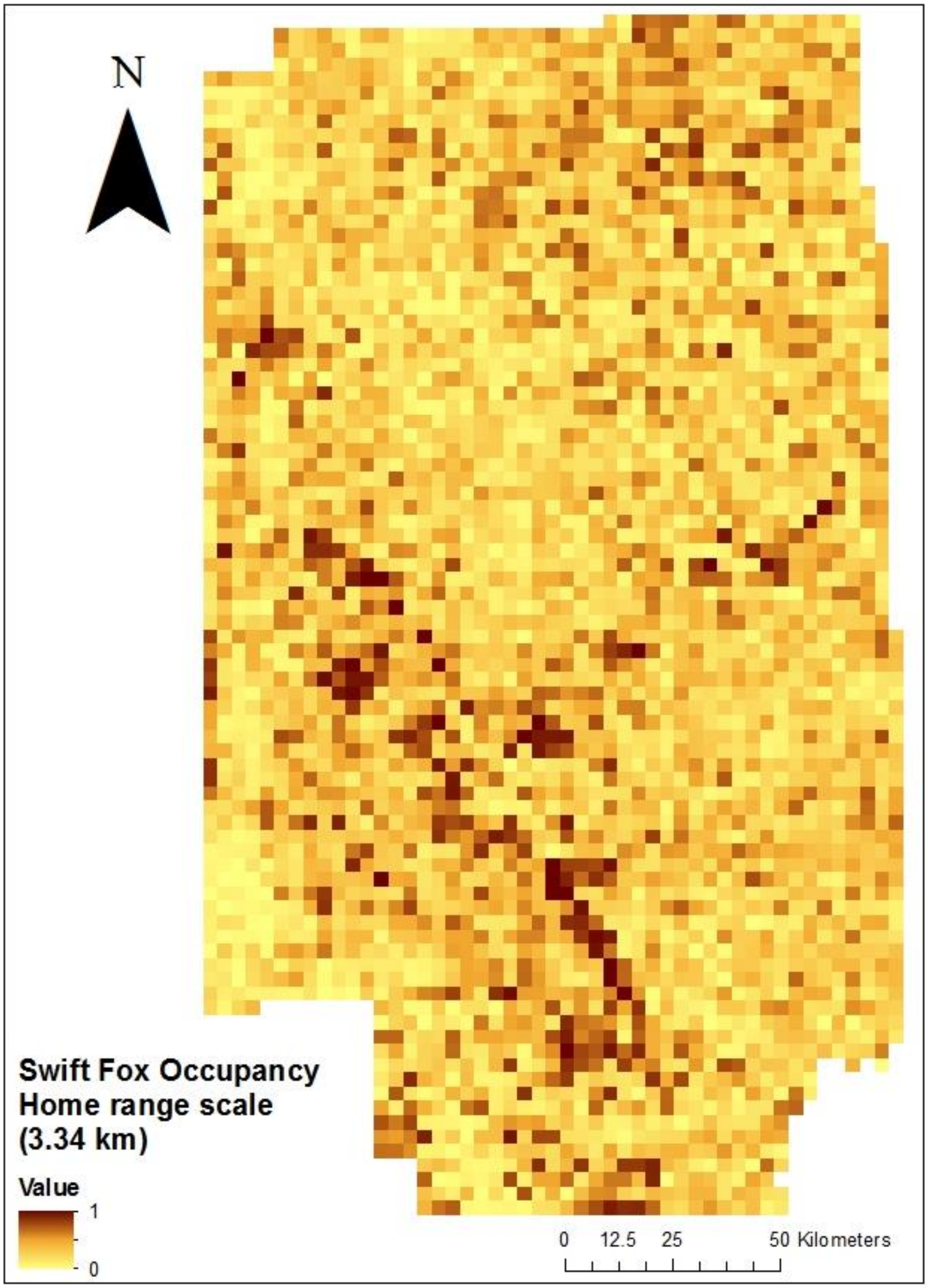


Figure 5. Predicted occupancy of coyotes in the Dakotas, using the most parsimonious model (Ψ(grass), p(.)) at the double-home range (6.68 km) scale. Of the roughly 40,600 km^2 in our study area, about 25,700 km^2, or 63%, have a likelihood of ≥ 50% of coyote occupancy.

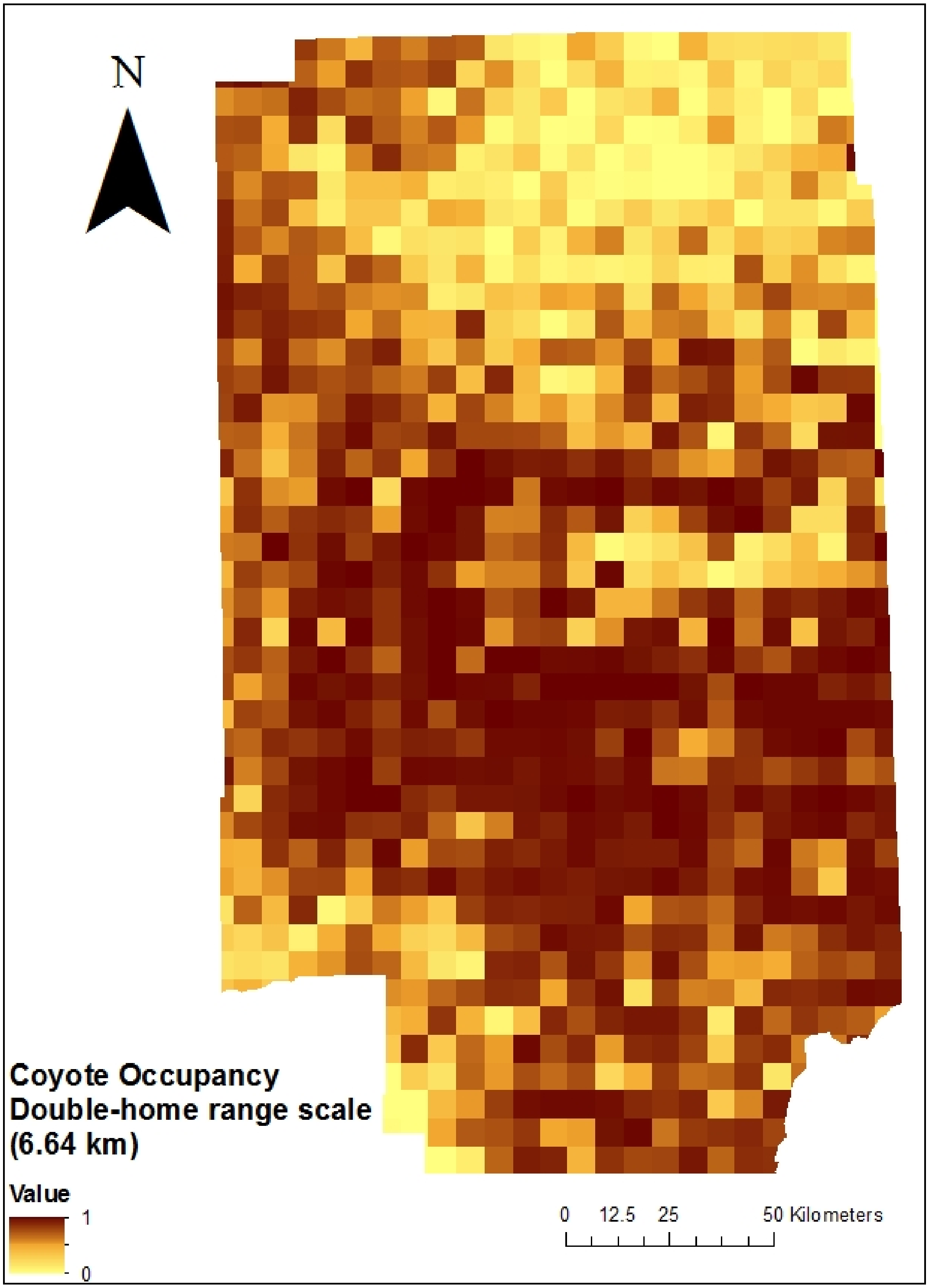


Figure 6. Predicted occupancy of coyotes in the Dakotas, using the most parsimonious model (Ψ(grass), p(.))at the home range (3.34 km) scale. Of the roughly 40,600 km^2 in our study area, about 29,000 km^2, or 69%, have a likelihood of ≥ 50% of coyote occupancy.

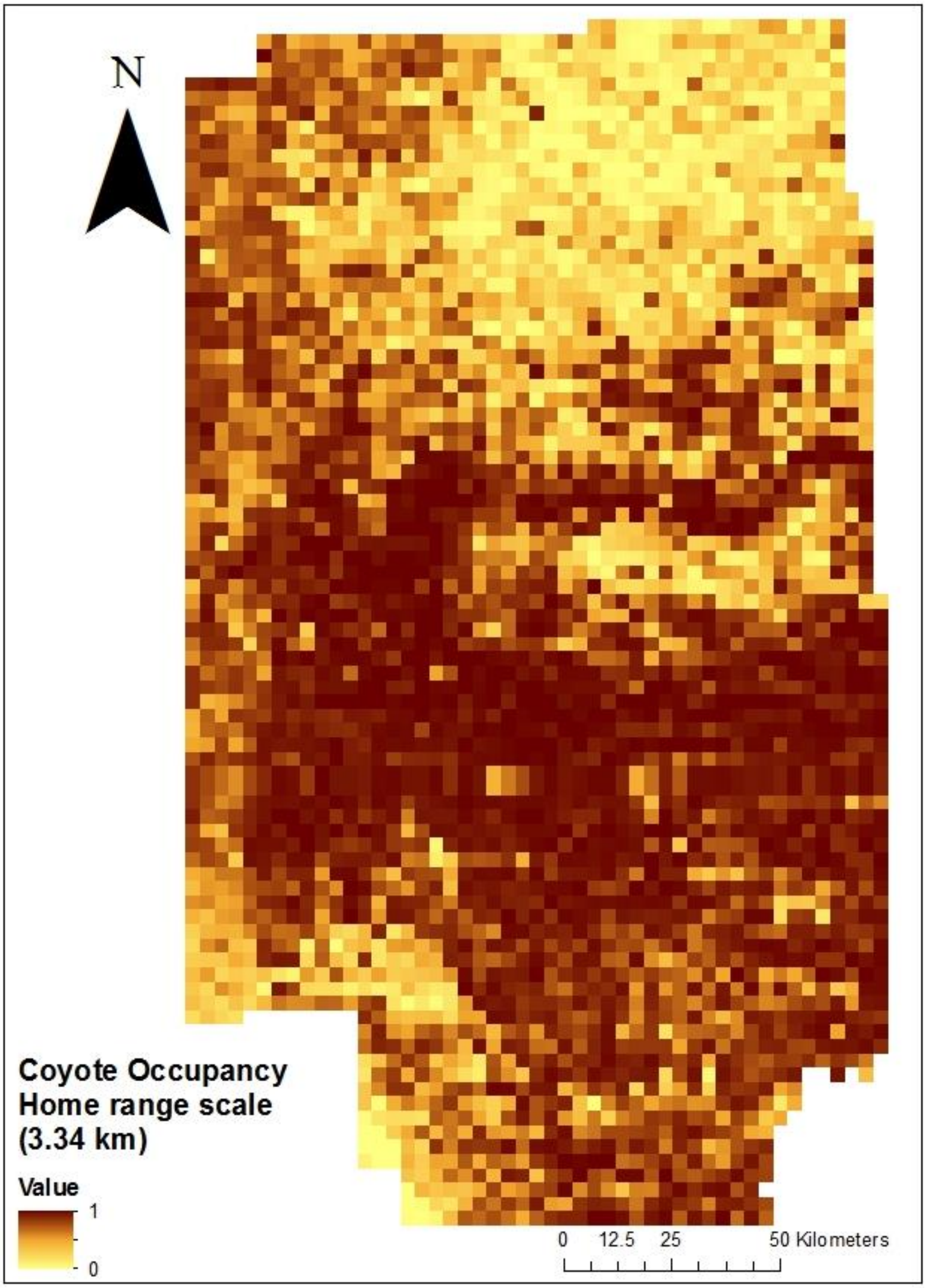


Figure 7. Predicted occupancy of red fox in the Dakotas, using the most parsimonious model (Ψ(sand), p(scrub+rough)) at the double-home range (6.68 km) scale. Of the roughly 40,600 km^2 in our study area, about 21,700 km^2, or 54%, have a likelihood of ≥ 50% of red fox presence.

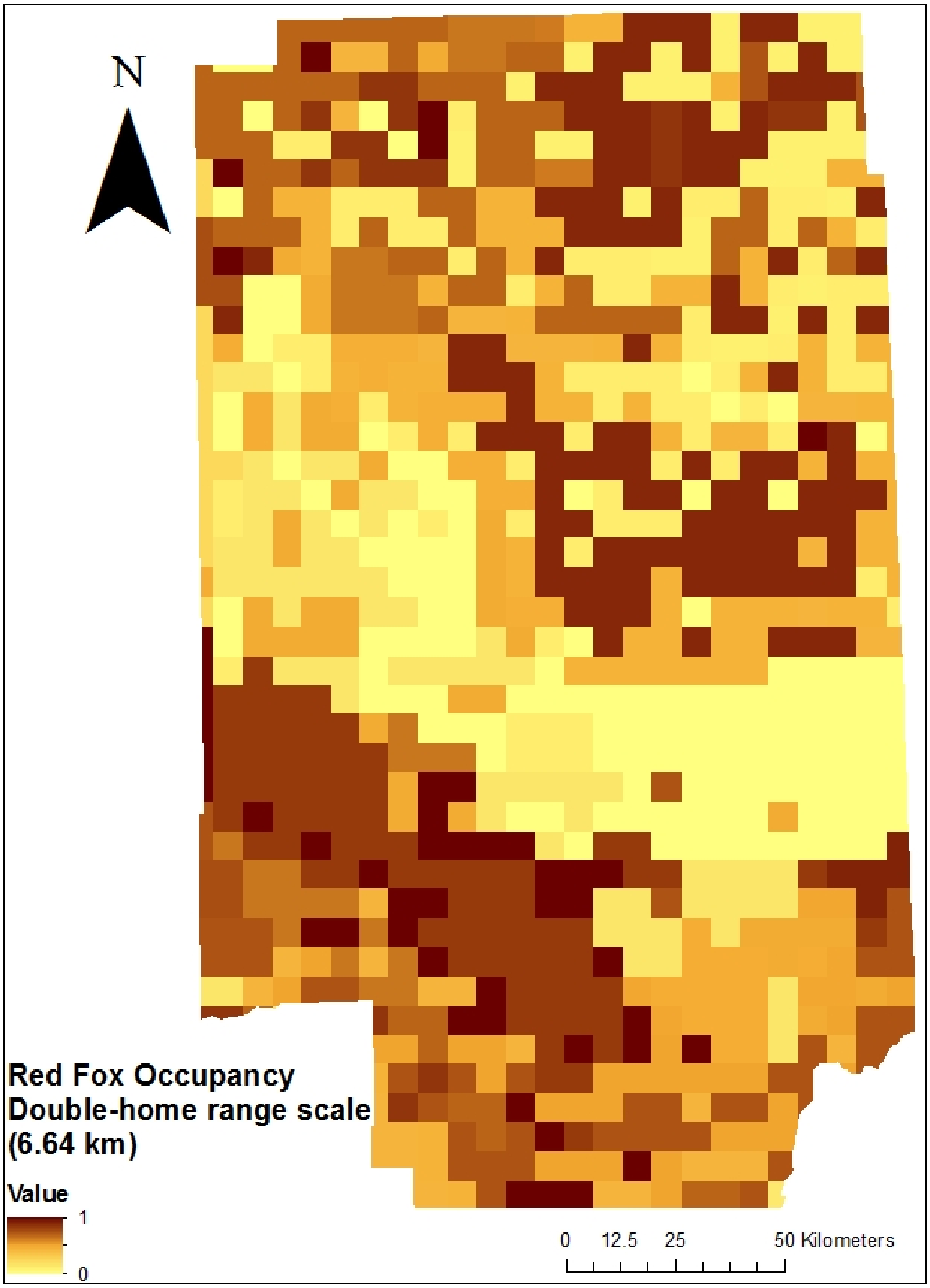


Figure 8. Predicted occupancy of red fox in the Dakotas, using the most parsimonious model (Ψ(grass), p(.)) at the home range (3.34 km) scale. Of the roughly 40,600 km^2 in our study area, about 19,200 km^2, or 46%, have a likelihood of ≥ 50% of red fox occupancy.

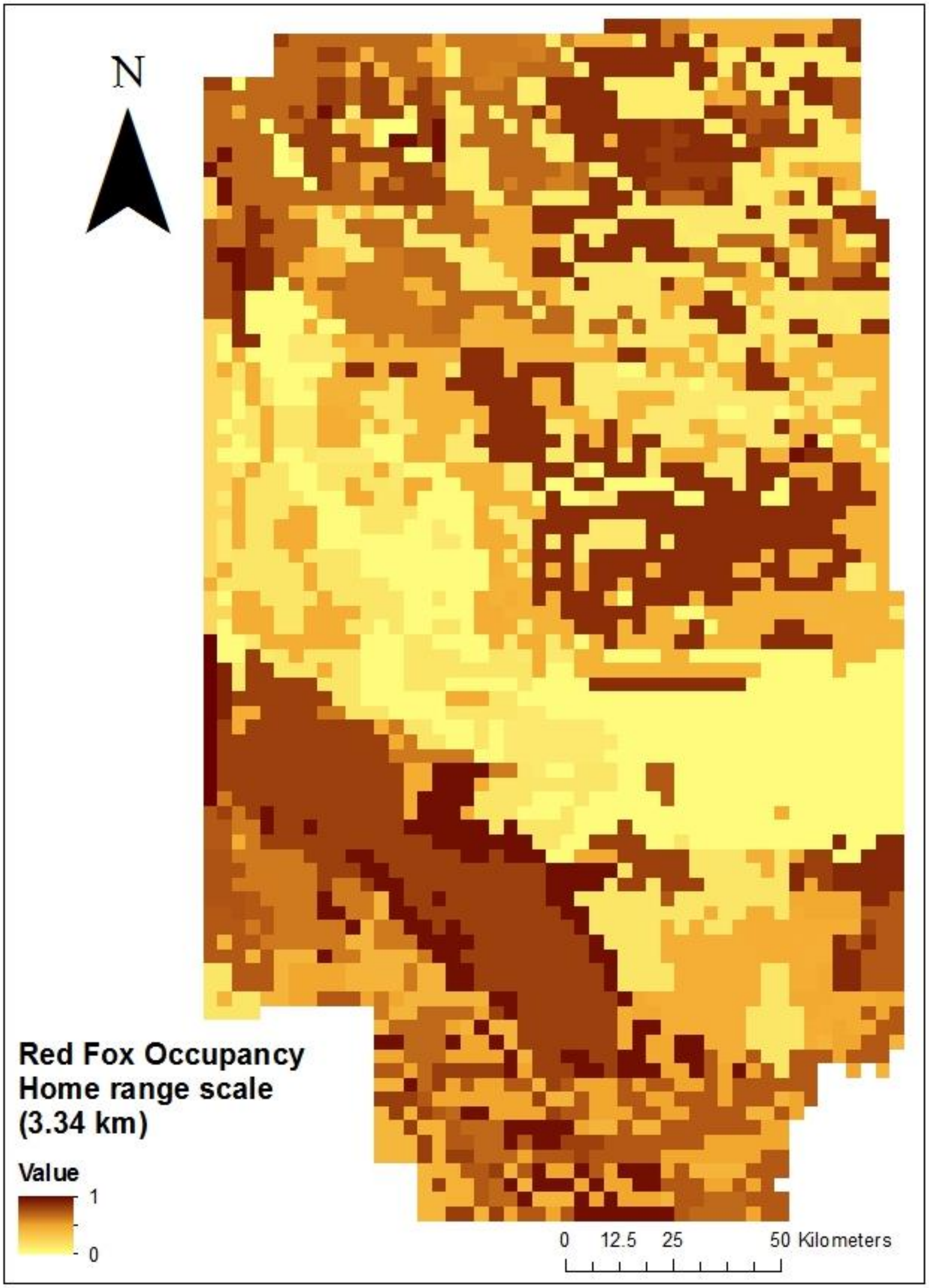


Figure 9. A measure of variable importance in the sub-home range (30 m) scale swift fox distribution model. Of the variables included in the model elevation (“elev”), followed by coyote occupancy (“coy”) and red fox occupancy (“rfox”) had the highest effect on classifying correctly.

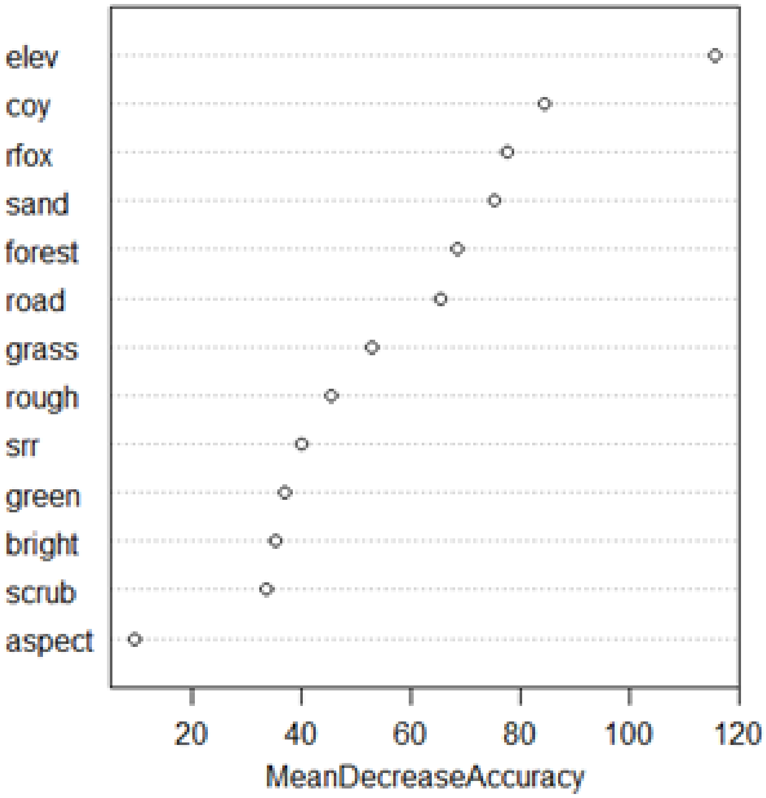


Figure 10. A measure of variable importance in the home range (3.34 km) scale swift fox distribution model. Of the variables included in the model red fox occupancy ("rfox") had the highest effect on classifying correctly.

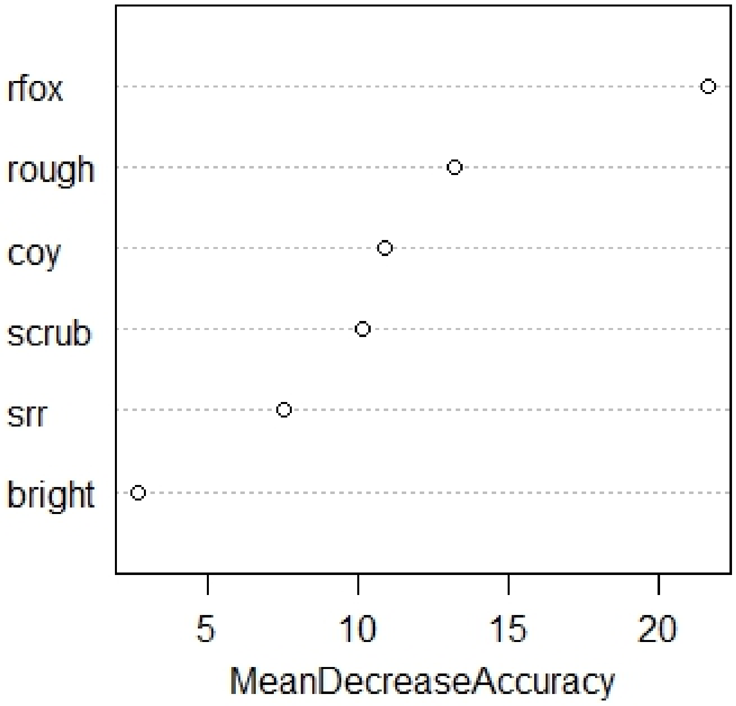


Figure 11. Partial dependence plots of the top variables in the swift fox distribution model at the sub-home range (30 m) scale. Elevation, coyote, and red fox occupancy have a negative correlation with swift fox distribution. Percent sand in soil (“sand”) has a positive correlation with swift fox distribution, until a certain point (~38) when it them becomes a negative correlation. This is likely due to too much sand inhibiting their digging ability. Percent forest (“forest”) has a slightly negative correlation. Road density (“road”) had a positive correlation to swift fox occupancy, likely due to swift fox using roads as travel corridors.

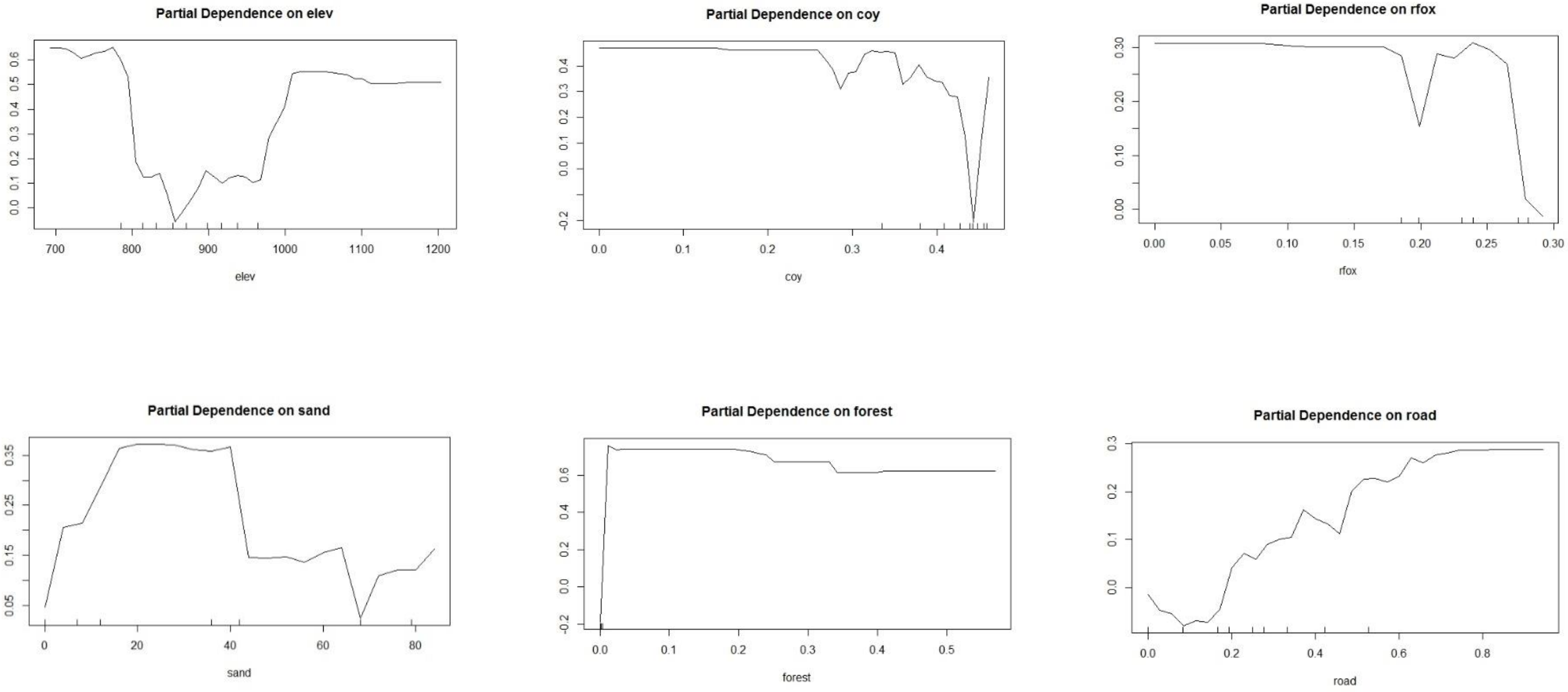
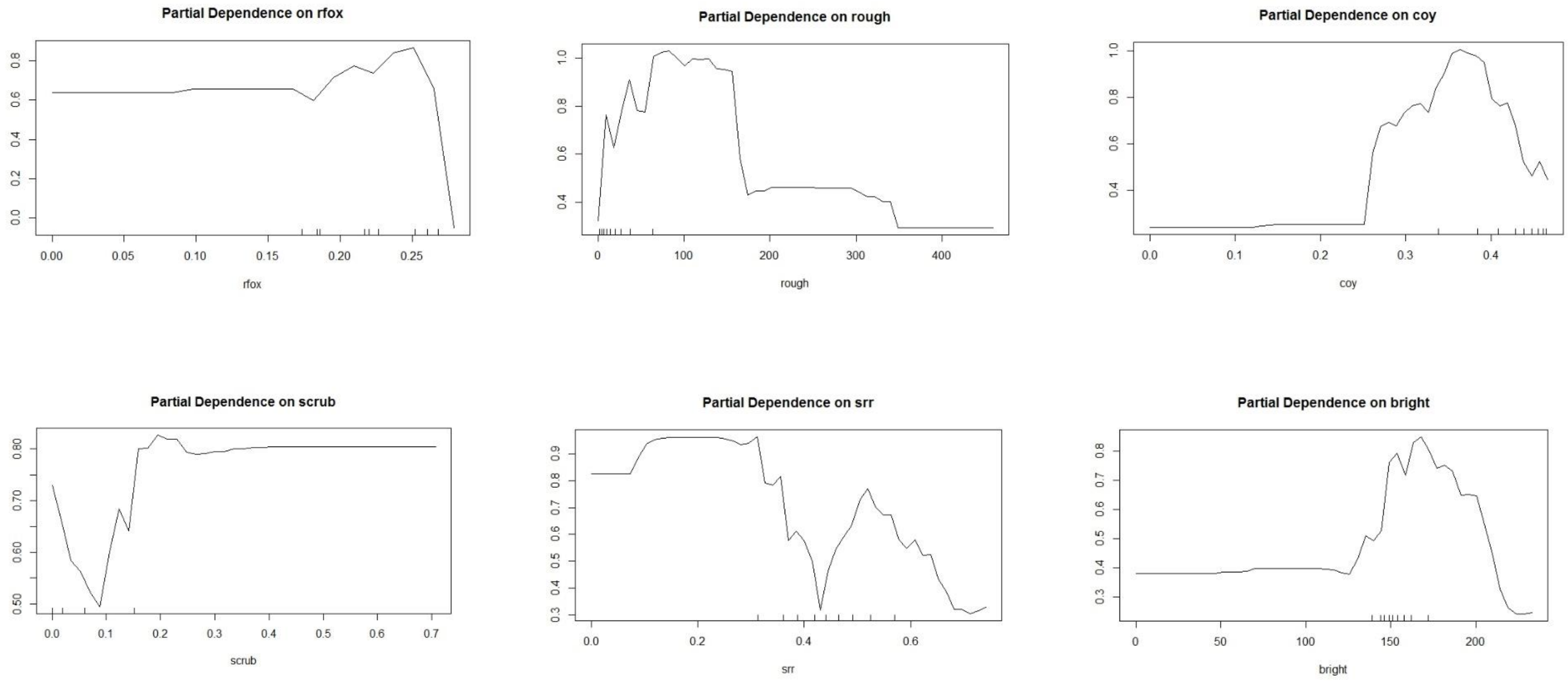


Figure 12. Partial dependence plots of the affect the top variable have on swift fox distribution at the home range (3.34 km) scale. Red fox (“rfox”) has a negative correlation with swift fox distribution. Roughness (“rough”) and coyote occupancy (“coy”) has a positive correlation, until a certain point (roughness ~110 and coyote ~0.35). Percent scrub (“scrub”) and surface relief ratio (“srr”) are negatively correlated with swift fox distribution, until a certain point (percent scrub ~0.2 and surface relief ratio ~0.3). Brightness (“bright”) does not have an effect on swift fox distribution, until ~135 when it begins to have a positive correlation and then ~175 it begins to have a negative correlation.



Partial Dependence on rfox

Partial Dependence on rough

Partial Dependence on coy

Partial Dependence on scrub

Partial Dependence on srr

Partial Dependence on bright

Table 1. Variable name, description, and ecological justification for inclusion of 16 predictor variables used to assess swift fox distribution, and 14 predictor variables used to assess coyote and red fox distribution.

Variable	**Variable description**	**Ecological justification**
forest[124]	percent of the landscape that is forest	Influences pop size, habitat connectivity, habitat availability
grass[124]	percent of the landscape that is grass	Influences pop size, habitat connectivity, habitat availability
sand[124]	percent of sand in the soil	Influences ability to dig in soil, create dens
road[124]	road density	Influences survival and acts as travel corridors
green[1234]	greenness- a measure of vegetation	Influences pop size, habitat connectivity, habitat availability
bright[1234]	brightness- a measure of soil	Influences ability to dig in soil, create dens
wet[23]	wetness- a measure of vegetation	Influences pop size, habitat connectivity, habitat availability
slope[124]	slope in degrees	Influences habitat availability
crop[124]	percent of the landscape that is forest	Influences pop size, habitat connectivity, habitat availability
scrub[1234]	percent of the landscape that is scrub	Influences pop size, habitat connectivity, habitat availability
elev[1]	elevation	In-site shelter, between site traversability
rough[1234]	surface roughness	In-site shelter, between site traversability
srr[13]	surface relief ration	In-site shelter, between site traversability
aspect[1]	northness	Influences den site selection
coy[135]	coyote occupancy	Influences survival
rfox[13]	red fox occupancy	Influences survival

[1] Used in sub-home range swift fox distribution (Random Forest) model.
[2] Used in double-home range coyote and red fox occupancy models.
[3] Used in home range swift fox distribution (Random Forest) model.
[4] Used in home range coyote and red fox occupancy models
[5] Used in home range red fox occupancy model.

Table 2. Results of AIC model selection, and ecological justification, applied to coyotes camera trapped on a systematic grid in suitable habitat for swift fox in southwest North Dakota and northwest South Dakota, USA, August-December 2015 and 2016. Of the 3,929 trap nights coyotes were detected on 304 trap nights.

Model	K	AIC	ΔAIC	AICwt	Ecological justification
double-home range (6.68 km) scale:					
Ψ(grass), p(.)	3	2014.46	0	0.109	Habitat availability
Ψ(grass+road), p(.)	4	2015.32	0.87	0.87	Habitat availability and travel corridors
Ψ(bright), p(.)	3	2015.45	1	0.066	Ability to dig in soil
Ψ(sand), p(.)	3	2015.51	1.05	0.065	Ability to dig in soil
Ψ(grass+rough), p(.)	4	2015.85	1.39	0.054	Habitat suitability and in-site shelter
Ψ(scrub), p(.)	3	2016.08	1.63	0.048	Habitat suitability
Ψ(rough), p(.)	3	2016.99	2.54	0.031	In-site shelter
Ψ(sand+rough), p(.)	4	2017.14	2.69	2.69	Ability to dig in soil and in-site shelter
Ψ(road), p(.)	3	2017.23	2.78	0.027	Travel corridor
Ψ(scrub+rough), p(.)	4	2017.25	2.79	0.027	Habitat suitability and in-site shelter
home range (3.34 km) scale:					
Ψ(grass), p(.)	3	2005.23	0	0.1134	Habitat availability
Ψ(grass+wet), p(.)	4	2005.8	0.57	0.0854	Habitat availability
Ψ(wet), p(.)	3	2005.96	0.72	0.0789	Habitat availability
Ψ(grass+road), p(.)	4	2006.1	0.87	0.0735	Habitat availability and travel corridors
Ψ(.), p(.)	2	2006.29	1.06	0.0666	Constant
Ψ(sand), p(.)	3	2006.38	1.15	0.064	Ability to dig in soil
Ψ(bright), p(.)	3	2006.45	1.22	0.0615	Ability to dig in soil
Ψ(sand+bright), p(.)	4	2006.53	1.3	0.0591	Ability to dig in soil
Ψ(grass+rough), p(.)	4	2006.66	1.43	0.0554	Habitat suitability and in-site shelter
Ψ(scrub), p(.)	3	2006.92	1.69	0.0487	Habitat availability

Table 3. Regression coefficients (a) and standard error (SE) for all of the occupancy models with ΔAIC < 2.

Model	**a**	**SE**
Sub-home range scale:		
Coyote (Canis latrans)		
Ψ(grass), p(.)	0.187	0.11
Ψ(bright), p(.)	-0.124	0.109
Ψ(sand), p(.)	0.0667	0.106
Ψ(scrub), p(.)	0.0441	0.104
Ψ(rough), p(.)	0.146	0.106
Ψ(road), p(.)	0.148	0.107
Red Fox (Vulpes vulpes)		
Ψ(sand), p(scrub+rough)	-0.211	0.116
Ψ(sand+bright), p(scrub+rough)	0.0754	0.114
Home range scale:		
Coyote (Canis latrans)		
Ψ(grass), p(.)	0.191	0.11
Ψ(grass+wet), p(.)	-0.324	0.129
Ψ(wet), p(.)	-0.166	0.109
Ψ(grass+road), p(.)	-0.325	0.128
Ψ(.), p(.)	-0.32	0.127
Ψ(sand), p(.)	0.148	0.107
Ψ(bright), p(.)	0.144	0.107
Ψ(sand+bright), p(.)	-0.326	0.128
Ψ(grass+rough), p(.)	-0.324	0.128
Ψ(scrub), p(.)	-0.127	0.109
Red Fox (Vulpes vulpes)		
Ψ(slope+sand), p(crop+date)	1.40141	0.86593

Table 4. Results of AIC model selection, and ecological justification, applied to red fox camera trapped on a systematic grid in suitable habitat for swift fox in southwest North Dakota and northwest South Dakota, USA, August-December 2015 and 2016. Of the 3,929 trap nights red fox were detected on 190 trap nights.

Model	K	AIC	ΔAIC	AICwt	Ecological justification
Double-home range (6.68 km) scale:					
Ψ(sand), p(scrub+rough)	5	1367.26	0	0.304	Ability to dig in soil
Ψ(sand+bright), p(scrub+rough)	6	1369	1.74	0.1276	Ability to dig in soil
Ψ(sand+rough), p(scrub+rough)	6	1369.26	2	0.1121	Ability to dig in soil and in-site shelter
Ψ(bright), p(scrub+rough)	5	1370.25	2.99	0.0621	Ability to dig in soil
Ψ(road), p(scrub+rough)	5	1370.44	3.18	0.0621	Travel cooridor
Ψ(grass), p(scrub+rough)	5	1370.49	3.23	0.0606	Habitat availability
Ψ(rough), p(scrub+rough)	5	1370.49	3.36	0.0566	In-site shelter
Ψ(scrub+rough), p(scrub+rough)	6	1370.98	3.72	0.0472	Habitat availability and in-site shelter
Ψ(grass+road), p(scrub+rough)	6	1372.12	4.86	0.0267	Habitat availability and travel cooridor
Ψ(grass+rough), p(scrub+rough)	6	372.48	5.22	0.0223	Habitat availability and in-site shelter
Ψ(.), p(.)	2	1380.55	13.29	0.0004	Constant
Home range (3.34 km) scale:					
Ψ(slope+sand), p(crop+date)	6	1348.09	0	9.90E-01	Habitat availability and ability to dig in sand
Ψ(scrub+rough), p(crop+date)	6	1357.76	9.67	7.90E-03	Habitat availability and in-site shelter
Ψ(scrub), p(crop+date)	5	1364.21	16.12	3.10E-04	Habitat availability
Ψ(sand+rough), p(crop+date)	6	1364.58	16.49	2.60E-04	Habitat availability and in-site shelter
Ψ(sand+rough+coy), p(crop+date)	7	1365.25	17.17	1.90E-04	Ability to dig in sand, habitat availability, and survival
Ψ(wet), p(crop+date)	5	1366.09	18	1.20E-04	Habitat availability
Ψ(sand+scrub+coy), p(crop+date)	7	1366.34	18.25	1.10E-04	Ability to dig in sand, habitat availability, and survival
Ψ(rough), p(crop+date)	5	1366.75	18.66	8.80E-05	In-site shelter
Ψ(grass+rough), p(crop+date)	6	1366.97	18.88	7.90E-05	Habitat availability and in-site shelter
Ψ(wet+aspect), p(crop+date)	6	1367.21	19.12	7.00E-05	Habitat availability and den site selection

CHAPTER 4

SEROLOGIC SURVEY OF INFECTIOUS DISEASES IN SWIFT FOXES (*VULPES VELOX*) IN THE DAKOTAS, USA

Intended for publication in the Journal of Wildlife Diseases

ABSTRACT

Infectious diseases are a recognized threat to carnivore species worldwide. To determine the prevalence of *Yersinis pestis*, *Francisella tularensis*, canine distemper virus (CDV), and canine parvovirus (CPV) in swift foxes in northwest South Dakota and southwest North Dakota we collected blood samples from 31 individual swift fox. Of these, 1 was antibody-positive for *Y. pestis* (3.23%) and 21 were antibody-positive for *F. tularensis* (67.74%). Of the 29 fox samples tested for CDV, 3 were antibody-positive (10.34%), and of 28 swift fox samples tested for CPV, 20 were found to be antibody-positive (71.43%). Disease results were not related to age or sex of foxes. *F. tularensis* and CPV prevalence was higher than documented in similar studies, while *Y. pestis* prevalence was lower than in similar studies; results for CDV were similar to other studies. Evidence of high mortality in canines infected with CPV and our indication of a high prevalence of CPV antibodies suggest that this disease is likely a concern for swift fox population conservation and re-establishment within the western Dakotas. Effects of *F. tularensis* on swift fox are largely unknown; however, our finding of high prevalence in the study population could be cause for concern. Low prevalence of *Y. pestis* suggests that plague exposure in swift fox is limited in this region of the Dakotas at this time. In the future, infectious diseases should be considered an important factor in swift fox conservation efforts.

INTRODUCTION

Disease has become a worldwide conservation threat, especially for carnivore species (Murray et al. 1999). Wild carnivores can be exposed to infectious diseases through contact with both wild and domestic carnivores (Woodroffe et al. 2004). The prevalence of such diseases has begun to increase due to an increase in the wildlandurban interface (Woodroffe et al. 2004, Nelson et al. 2012). Diseases such as sylvatic plague (*Yersinia pestis*), tularemia (*Francisella tularensis*), canine parvovirus (CPV), and canine distemper virus (CDV) have been found to infect swift foxes throughout the Great Plains region and may be a threat to the continued success of both established and re-colonizing populations (Miller et al. 2000, Olson and Lindzey 2002, Harrison 2003, Gese et al. 2004, Nevison 2017, S. Grassel personal communication, and K. Bly personal communication).

Sylvatic plague (*Yersinia pestis*) is associated with fleas found in black-tailed prairie dog (*Cynomys ludovicianus*) populations throughout the species distribution (USFWS 2014), including North and South Dakota (Dyer and Huffman 1999, Nevison 2017). Swift foxes have been found to carry *Y. pestis* antibodies in studies conducted in northwestern Texas and southeastern Colorado (McGee et al. 2006, Gese et al. 2004), as well as in Wyoming, Colorado, and Kansas (Turner Endangered Species Fund, Badlands National Park, and *Lower Brule* Department of Wildlife, Fish and Recreation, unpublished data). However, canids, such as swift fox, typically do not exhibit clinical symptoms of the disease (Von Reyn et al. 1976, Barnes 1982, Pybus and Williams 2003, Gage and Kosoy 2005, Malmlov et al. 2014), a finding supported by post-exposure survival of swift fox captured for translocation in Wyoming (Turner Endangered Species Fund, unpublished data). Serologic testing of carnivores can help establish the presence of plague among local rodent populations (Willeberg et al. 1979, Thomas and Hughes 1992). With nearly 66% of the prairie dog range affected by *Y. pestis* (USFWS 2014), it is likely that swift foxes in these affected areas within the Northern Great Plains (NGP) have been exposed to the disease. In South Dakota, swift foxes use prairie dog towns for den sites and as a source of food, especially during the pup-rearing season (Sasmal 2011, Russell 2006). A recent study in west-central South Dakota (Badlands National Park and Buffalo Gap National Grasslands) found swift foxes were 69.6% seropositive for *Y. pestis* (Nevison 2017).

CDV and CPV have been found to cause high morbidity and mortality in wolves (*Canis lupus*; Johnson et al 1994, Pence et al. 1995, Di Sabatino et al. 2014; *Canis latrans* Gese et al. 1997), while CDV caused the disappearance in the last wild population of black-footed ferrets (*Mustela nigripes*) in Spain (Sobrino et al. 2008). CDV affects all canine species (Montali et al. 1987), but few swift foxes and kit foxes (*Vulpes macrotis*) sampled throughout the western United States were exposed to this potentially deadly disease (Miller et al. 2000, Olson and Lindzey 2002, Gese et al. 2004). Effects of CPV on swift fox survival and population trends is unknown because most studies have not tested for it, and of those that did, all reported positive CPV tests in a captured swift fox (Miller et al. 2000, Harrison 2003, Gese et al. 2004). Swift fox have been documented to succumb to CDV in two instances (Olson and Lindsey 2002). Studies on coyotes (*Canis latrans*) and wolves have also documented mortality associated with the disease, especially in pups (Johnson et al. 1994, Gese et al. 1997, Mech et al. 2008).

F. tularensis is a known infectious agent in species swift fox commonly prey on (e.g., lagomorphs and rodents; Brown et al. 2015, Mani et al. 2016). Tularemia has been found in black footed ferrets in South Dakota, implying that prairie dogs in the state are also infected (Prairie Wildlife Research unpublished data). However, the impact tularemia has on canid species in unknown (Gese et al. 1997). It is likely that canids contract the disease, but are relatively unsusceptible and healthy individuals are able to recover (Gier and Ameel 1959, Zarnke and Ballard 1987). In general, the prevalence of *F. tularensis* in the NGP, frequency of exposure for swift foxes, and effect of that exposure is unknown.

Infectious disease can be a threat to the viability of small populations, such as the swift fox populations in the Dakotas, and exposure to infectious disease pathogens could threaten recovery efforts for this species (Miller et al. 2000). Because the exposure rate and impact of these diseases on swift foxes is largely unknown, we evaluated disease exposure of swift foxes in the western Dakotas to inform species conservation efforts in the region

STUDY AREA

The study area included Harding, Butte, Perkins, and Meade counties in South Dakota and Slope, Bowman, Adams, and Hettinger counties in North Dakota (Figure 1). The study was conducted on state, federal (Forest Service and Bureau of Land Management), and private lands within the region. The study area encompassed approximately 4,099,174 ha dominated by mixed grass prairie, interspersed with sagebrush (*Artemisia* sp.). Prominent grasses of the mixed grass prairie in the area were: western wheatgrass (*Pascopyrum smithii*), green needle grass (*Nassella viridula*), needle and thread (*Hesperostipa comata*), blue grama (*Bouteloua gracilis*), and side-oats grama (*Bouteloua curtipendula*). Topography was largely flat to gently rolling hills with occasional buttes. The primary soil types were clays derived from Createaceous Pierre Shale. Predominate water features included Shadehill Reservoir, Belle Fourche Reservoir, and the Belle Fourche River. Lands were primarily used for cattle and sheep grazing.

MATERIALS AND METHODS

Swift foxes were live captured from July 2016 to April 2017 using modified wire box traps (Model 108SS; Tomahawk Live Trap Co., Tomahawk, WI, USA) of dimensions 81.3 cm × 25.4 cm × 30.5 cm, baited with road killed deer or rabbit. Captured swift fox were manually restrained while we collected a blood sample. Up to 5 mL of blood was drawn with a 20 gauge needle from the saphenous vein (Salkeld et al. 2007). Immediately after releasing the captured fox the needle was removed from the syringe and the blood was placed in serum separator tubes (Monoject Blood Collection Tube, Covidien, Dublin, Republic of Ireland), with polymer gel. Within 12 hours of collection, the serum separator tubes were centrifuged for 30 minutes and the serum collected and stored at -20 C (Gese et al. 1997, Arjo et al. 2003, Mech et al. 2008). All methods were approved by the Institutional Animal Care and Use Committee (IACUC) at South Dakota State University (permit # A3958-01).

The serum samples were analyzed at the Department of Microbiology, Immunology & Pathology, Colorado State University, Fort Collins, Colorado (USA) for antibodies against *Y. pestis* and *F. tularensis* and at the Colorado State University Veterinary Diagnostic Laboratory, Fort Collins, Colorado (USA) for CDV and CPV. *Y. pestis* antibody titers of fraction 1 capsular antigen protein (F1) and low calcium response V antigen protein (LcrV) were determined using enzyme-linked immunosorbent assay (ELISA) for immunoglobin G (IgG) as described by (Rocke et al. 2004) with modifications; modifications included use of recombinant antigens F1 and LcrV (BEI Resources, Manassas, VA) to coat plates and horseradish peroxidase conjugated Protein A/G (at 1:10,000; Pierce Biotechnology, Rockford, IL) used for the secondary antibody.

Presence of either antigen in the blood indicated exposure to *Y. pestis* bacterium (Gomes-Solecki et al. 2005). It was previously thought that the F1 antigen was an important virulance factor that added to the effectiveness of *Y. pestis* immunosuppression; however, F1 negative strains have been reported (Gomes-Solecki et al. 2005). Due to this finding, samples also were tested for the LcrV antigen, which has been confirmed to be an essential virulence factor (Gomes-Solecki et al. 2005).

A positive plague titer was considered ≥ 1:50 dilution concentration (L. Baeten, Colorado State University, personal communication; Nevison 2017). If a positive titer was detected at 1:50, the sample was subsequently diluted to 1:150 or 1:450 to assess highest concentration, with 1:450 being the most concentrated. Elution scores were assessed visually based on color change after samples were eluted in ELISA buffer, ranging from 1–4. Elution scores of 3 and 4 are considered reliable for negative titer results, while elution scores of 1 and 2 can produce false negatives because of the lower quality of the sample (L. Baeten, Colorado State University, personal communication). A positive result at any elution score is considered reliable

F. tularensis antibodies were detected using an enzyme-linked immunosorbent assay, as described by Brown et al. (2015) with the modification of horseradish peroxidase conjugated Protein A/G (at 1:10,000; Pierce Biotechnology, Rockford, IL) used for the secondary antibody. Samples with 3 standard deviations (SDs) above the mean of a negative-control domestic rabbit serum were considered positive.

Antibodies for CDV were detected using the serum virus neutralization test (Appel and Robinson 1973). A titer level of ≥ 1:32 was considered positive for CDV.

Antibodies for CPV were detected using hemagglutination inhibition (HI) test (Carmichael et al. 1980). A titer level of ≥ 1:64 was considered positive for CPV.

Each individual fox was used as the sampling unit for all statistical analyses. To statistically analyze the prevalence of antibodies among age class and sex we used Fisher's exact test of independence (Fay 2010). A p-value $\leq$ 0.05 was considered significant. All statistical analyses were performed with the computer software R (R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

We collected blood samples from 31 swift foxes from July 2016 to April 2017; sex and age class are reported in Table 1. All 31 foxes were tested for *Y. pestis* and *F. tularensis*. However, due to limited blood samples, 29 foxes were tested for CDV and 28 were tested for CPV. Foxes 1606, 1703, and 1714 were not tested for CPV and fox 1606 and 1703 were not tested for CDV (Table 1).

Seroprevalence of *Y. pestis* was 3.23%, with only one fox, an adult male, testing positive for antibodies (fox # 1617) (Table 2). There was no correlation between age or sex of the fox and positive results (Fisher's exact test: age: p = 0.4194; sex: p = 0.4839). The number ofantibodies were 1:150 in the F1 analysis and 1:50 in the LcrV analysis.

Laboratory analysis for *F. tularensis* indicated that 21 foxes were positive for titers, with a seroprevalence of 67.74%. Of these, 12 were juveniles, 9 were adults, with equal numbers of males and females (10 males and 10 females), and 1 of unknown sex. However, there was no relationship between age or sex of the fox and positive lab results (Fisher's exact test: age: p = 1; sex: p = 0.8028).

Analysis for CDV titers indicated that 3 foxes were positive for titers; seroprevalence was 10.34%. Of these, 1 was a juvenile and 2 were adults, with 1 female and 2 males represented. There was no relationship between age or sex of the fox and positive lab results (Fisher's exact test: age: p = 0.5534; sex: p = 0.6264). However, adults and males had higher seroprevalance (adults: 16.67%, juveniles: 5.56%; males: 15.38%, and females: 6.25%). Positive antibodies ranged from 1:64, 1:256, to 1:2048, with the only positive juvenile having the lowest number of antibodies.

Analysis for CPV titers indicated that 20 foxes were positive for titers, with a seroprevalence of 71.43%. Of these, 12 were juveniles, 9 were adults, with equal numbers of males and females (10 males and 10 females), and 1 of unknown sex. There was no correlation between age or sex of the fox and positive lab results (fisher's exact test: age: p = 0.4087; sex: p = 1). Positive antibodies ranged from 1:64 to 1:2048.

DISCUSSION

Our study is the first to assess swift fox exposure to CDV, CPV, and *F. tularensis* in the Northern Great Plains, and the only assessment of swift fox exposure to *Y. pestis* in the study area. Seroprevalence tests were positive for all four diseases, with results for CPV and *F. tularensis* particularly high, indicating regular exposure of swift fox to harmful or potentially harmful diseases. Swift fox populations in the Dakotas are small and disease could play a role in both long-term population viability and the ability of the populations to expand into suitable habitat. Knowing and understanding the exposure to and effect of infectious diseases could be an important factor in future conservation and reestablishment of these populations. Below, we place our results in the context of similar studies in different parts of the species distribution, and discuss potential implications in terms of population viability and future conservation action.

We documented high prevalence of antibodies for *F. tularensis* (67.74%) and CPV (71.43%) in swift foxes. Studies conducted for both swift fox and the closely related kit fox found considerably lower antibody prevalence for these two diseases. For example, lower seroprevalence was reported for CPV in Colorado (39%), California (10%), Utah (22%), and Arizona (30%) (Miller et al. 2000, White and Ralls 1993, Disney and Spiegel 1992). Similarly low seroprevalence was reported for *F. tularensis* in Colorado (0%) and California (8% and 31%) (Gese et al. 2004, McCue and O'Farrell 1988). The high prevalence of CPV antibodies is particularly concerning given high juvenile mortality rates associated with CPV infection in other canid species (Mech et al. 2008, Murray et al. 1999, Deem at al. 2000, Kreeger et al. 2003, Pratelli et al. 2006, Almberg et al. 2009, Nandi and Kumar 2010, Mech and Goyal 2011, Johnson 1994, Gese et al. 1997). High prevalence suggests a high rate of exposure to the disease; however, because prevalence is measured only in surviving animals, our results are not directly indicative of a negative impact (Arjo et al. 2003). Therefore, the effect of CPV on individual survival and the overall trajectory of the swift fox population in the Dakotas is unknown. Given high mortality rates in other canid species, at least some mortality in swift fox can be assumed. Improved monitoring and, potentially, intervention (e.g., vaccination) would benefit swift fox recovery in this small population.

Swift foxes are likely exposed to *F. tularensis* through their prey (i.e., rabbits [*Sylvilagus* sp.], Hestvik et al. 2015, Cutter 1958; prairie dogs and other rodents, Baird 1858, Kilgore 1969). The effect of *F. tularensis* on canids, including the swift fox, is largely unknown (Gese et al. 2004). However, Keuhn et al. (2013) proposed that red fox (*Vulpes vulpes*) could be an indicator of the spread of *F. tularensis* due to the species ability to develop antibodies. This could also be true of the swift fox. The role foxes play in the *F. tularensis* cycle has rarely been investigated (Ebani et al. 2017). However, regular testing of swift fox could be used to monitor *F. tularensis* prevalence regionally.

CDV antibody prevalence in this study was low (10.34%) compared to similar studies of swift fox and kit fox elsewhere. For example, low seroprevalence was reported for swift fox or kit fox in Colorado (18%), Kansas (20%), California (0%), New Mexico (0%), Utah (13%), and Arizona (0%) (Miller et al. 2000, White and Ralls 1993, Disney and Spiegel 1992). Low seroprevalence could be because close contact is necessary for the transmission of the disease, and because CDV does not survive long in the environment (Gorham 1966). It may be indicative of low survival of infected individuals, which could succumb to the disease prior to being tested. This is particularly true given high mortality rates in other canid species from CDV infection (Johnson et al. 1994, Gese et al. 1997, Mech et al. 2008). The high rate of mortality in other canid species and our finding of CDV positive animals within the population in the Dakotas may indicate that CDV is a serious threat to the continued survival of this population. Regular monitoring may help elucidate the influence of CDV on swift fox populations in the Dakotas.

We found a low prevalence of *Y. pestis* (3.23%) in our study area. However, a recently completed study in west-central South Dakota documented high prevalence for *Y. pestis* (69.6%) in swift fox population sympatric to prairie dog towns with a high prevalence of the disease (i.e., Canata Basin region and Buffalo Gap National Grassland) (Nevison 2017). Because swift foxes typically do not exhibit clinical symptoms (Gese et al. 2004), we conclude that *Y. pestis* likely does not directly impact swift foxes in northwest South Dakota and southwest North Dakota. They likely are an indicator species (Gese et al. 2004). However, indirect effects may be considerable given the high susceptibility exhibited by common swift fox prey species (e.g., rabbits and rodents) (Von Reyn et al. 1976, McGee et al. 2006, Russell 2006). In addition, epizootic plague outbreaks can substantially reduce prairie dog availability, reducing availability of suitable habitat for swift foxes; this may have contributed to swift fox population declines at Badlands National Park in South Dakota (Kristy Bly, personal communication; Nevison 2017). Monitoring for *Y. pestis* and, potentially, treating prairie dog colonies to limit epizootic events may aid swift fox recovery in the area.

Infectious disease prevalence in wild canid populations is believed to have increased due to rural development, expansion of urban areas, and an increase in domestic dog (*Canis familiaris*) and feral cat (*Felis cattus*) populations (Arjo et al. 2003). As a result, disease is recognized as a growing threat to carnivore conservation worldwide (Murray et al. 1999). Carnivore conservation and restoration efforts should incorporate the potential risks presented by infectious diseases. Despite significant efforts to recover swift fox in the Dakotas through reintroduction, populations remain small and are potentially in decline (Nevison 2017), leaving them vulnerable to perturbations such as those imparted by disease outbreaks. Our results, combined with those of Nevison (2017), demonstrate that swift fox in the Dakotas are regularly exposed to four infectious agents; of these, two have demonstrated negative impacts on the survival of canids, one has a strong negative association with the survival of key swift fox prey species, and the other is highly prevalent but the impact on swift fox is not understood. If these diseases are causing large mortality events in this small, re-colonizing, population it is likely slowing or completely halting the natural re-colonization process. This could be very devastating to the future of swift fox populations, especially small ones like this. Future conservation efforts in the Dakotas should include improving understanding of the effects of these diseases on swift fox population recovery and developing mediation actions where warranted.

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Figure 1. Focal counties in southwest North Dakota (Bowman, Adams, Hettinger, and Slope) and four counties in northwest South Dakota (Harding, Perkins, Meade, and Butte) where swift fox were captured for disease testing. Individual fox locations are shown as black dots.

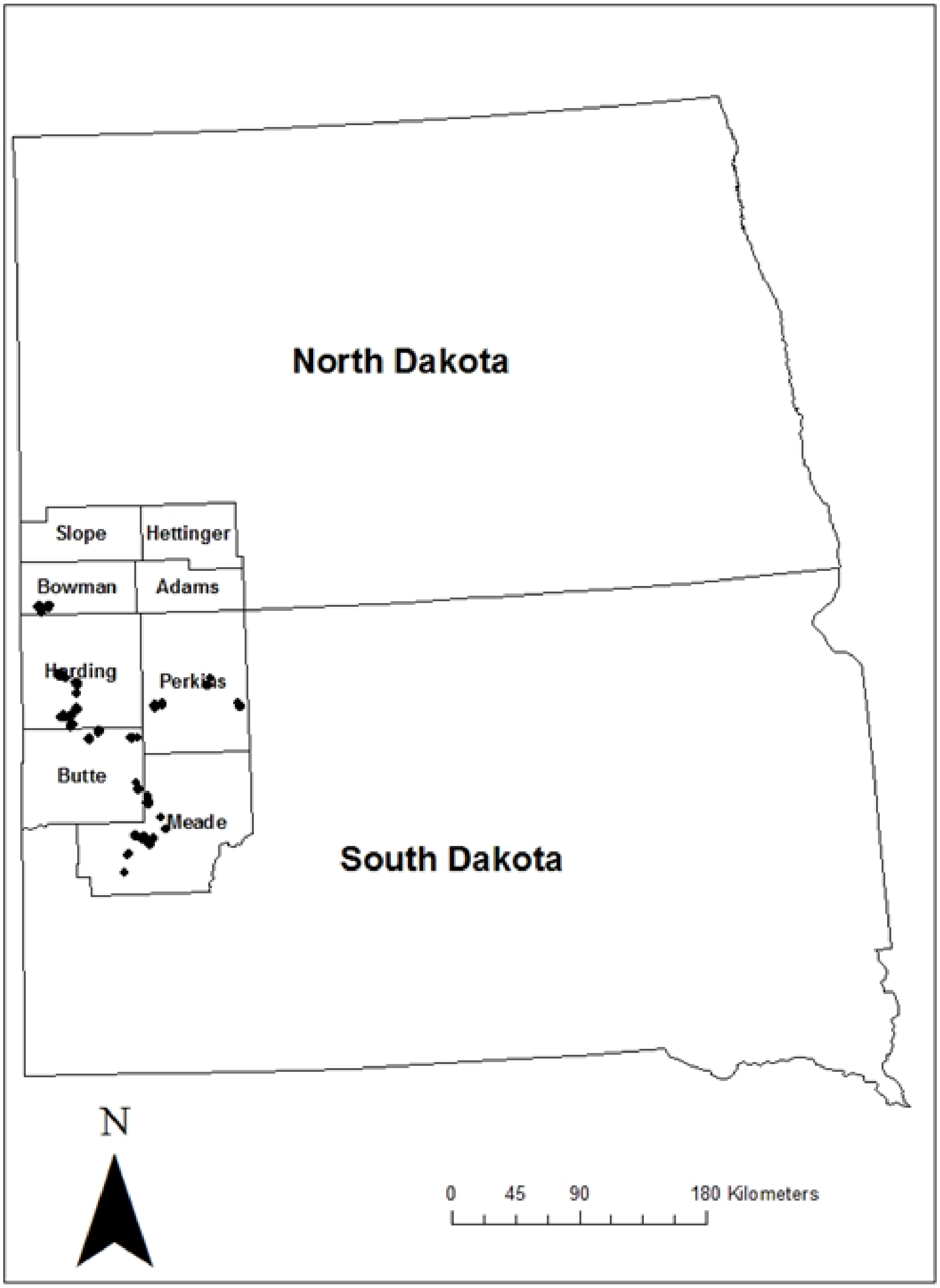

Table 1. Results of *Yersinia pestis, Francisella tularensis,* canine distemper virus (CDV), and canine parvovirus (CPV) for each swift fox in the study. P represents positive antibodies and N represents negative antibodies. Samples that were not available for testing are represented with an NA.

Fox #	**Age**	**Sex**	**Y. pestis**	**F. tularensis**	**CDV**	**CPV**
1602	J	F	N	N	N	P
1602	J	F	N	N	N	P
1603	J	F	N	P	N	N
1605	J	F	N	N	N	N
1606	J	F	N	P	NA	NA
1607	J	M	N	P	N	P
1608	J	M	N	P	N	P
1609	J	F	N	P	N	P
1610	J	Unk	N	P	N	P
1611	J	F	N	P	N	P
1612	J	F	N	P	N	P
1613	J	F	N	N	N	P
1614	A	M	N	P	N	N
1615	J	F	N	N	N	P
1616	J	F	N	N	N	P
1617	A	M	P	P	P	P
1618	J	F	N	N	N	P
1619	A	M	N	N	N	P
1621	J	F	N	P	P	N
1622	A	M	N	N	N	P
1623	A	M	N	P	N	N
1624	A	M	N	P	N	P
1702	J	F	N	P	N	P
1703	A	M	N	N	NA	NA
1704	J	F	N	P	N	P
1705	A	M	N	P	N	P
1707	J	F	N	P	N	N
1708	A	M	N	N	P	P
1709	A	M	N	P	N	N
1710	A	M	N	P	N	N
1711	A	F	N	P	N	N
1714	A	M	N	P	N	NA

Table 2. Seroprevalence of four diseases [*Yersinia pestis*, *Francisella tularensis*, canine distemper virus (CDV), and canine parvovirus (CPV)] in swift foxes in the Dakotas from 2016-2017, reported as the proportion of all swift foxes tested, all males tested, all females tested, all adults tested, and all juveniles tested which yielded a positive result.

Category	***Y. pestis***	***F. tularensis***	**CDV**	**CPV**
All Foxes (n = 31)	3.23	67.74	10.34	71.43
Males (n = 14)	7.14	71.43	15.38	66.67
Females (n = 16)	0	62.50	6.25	68.75
Adults (n = 12)	7.69	69.23	16.67	54.55
Juveniles (n = 19)	0	66.67	5.88	82.35

CHAPTER 5

ASSESSMENT OF GENETIC DIVERSITY IN A RECENTLY RE-ESTABLISHED SWIFT FOX POPULATION

Intended for publication in the Journal of Conservation Genetics

ABSTRACT

The swift population found in the Dakotas is assumed to be a small, isolated population resulting from recolonization by founders from either reintroduced populations in central South Dakota or a naturally occurring population in northern Wyoming. To assess the genetic diversity and viability of this population we collected 59 scat and tissue samples for microsatellite DNA analysis. Of these 59 samples 50 were successfully genotyped to 15 microsatellite loci, representing a total of 50 individuals. We observed a mean observed heterozygosity of 0.66 (SD = 0.19), a mean expected heterozygosity of 0.64 (SD = 0.18), and allelic richness of 6.18 (SD = 3.52). Four loci significantly deviated for Hardy-Weinberg equilibrium with the majority indicating heterozygote deficit; we also observed evidence of inbreeding ($F_{IS} = 0.0324$; $p = 0.0005$). Using the random and monogamous models in program NEstimator, we estimated an effective population size between 33.6 and 68.9 individuals. We used kinship analysis to identify 24 first order, 34 second order, and 186 third order relationship within the population, and further found that all individuals exhibited at least one third order relationship with another individual. These relationships were found to be distributed throughout the study area. We determined that there was no evidence of a recent bottleneck in the population. We concluded that the swift fox population in northwest South Dakota and southwest North Dakota is a small, but genetically viable population with high interapopulation connectivity. This is the first study to assess genetic composition in a recolonizing population of swift foxes, and one of the only detailed genetic assessments of a small, low density swift fox population more generally.

INTRODUCTION

Monitoring genetic indices can provide vital insight into demographic and evolutionary processes in populations (Barrett et al. 2005), and can be a helpful tool in assessing the status of and documenting changes in those populations being monitored. The genetic diversity of populations is an important measure of the intrinsic viability of each population. Genetic theory predicts that levels of genetic variation should increase with effective population size (Frankham 1996). Small, isolated populations are highly susceptible to loss of genetic variation through genetic drift and inbreeding (Brook et al. 2002, Frankham et al. 2002, Frankham et al. 2005, Jamieson et al. 2006). Isolated populations have been found to lose genetic variation at a faster rate than connected populations due to the lack of migration and genetic exchange; making populations with limited genetic diversity prone to extinction (Ouborg 2009, Koons 2010). A reduction in genetic diversity might cause inbreeding depression, reduce adaptability, increase mortality and physical abnormalities which, in small populations, can reduce long-term viability of a species population (Allendorf and Ryman 2002).

Inbreeding is known to reduce reproduction, and therefore survival, of species (Darwin 1876, Charleworth and Charlesworth 1987, Falconer and Mackay 1996, Lynch and Walsh 1998). It can have negative impacts on reproduction through sperm production, mating ability, female fecundity, juvenile survival, mothering ability, age at sexual maturity, and adult survival (Frankham et al 2005). The effects of inbreeding can only be reduced following crossbreeding with individuals from unrelated populations (Speilman and Frankham 1992, Falconer and Mackay 1996, Westemeier et al. 1998, Schwartz and Mills 2005).

Species re-colonization occurs through migration and dispersal. Often, these new populations are founded by a small number of individuals (Schwaegerle and Schaal 1979), and exhibit founder effects, where the genetic diversity of the newly formed population is limited to that contained within the founders, and not the species as a whole. Similarly, a reduction in population size to a few individuals, followed by rapid expansion is known as a bottleneck (Allendorf et al. 2010). Both founder effects and bottlenecks result in a loss of genetic diversity (Wright 1931, Nei et al 1975, Denniston 1978, Allendorf 1986). However, adaptive alleles can be quickly restored after re-establishment even with low rates of gene flow from other populations (Carlquist 1966, MacArthur and Wilson 1967, Williamson and Charlesworth 1976). Monitoring genetic characteristics of a re-colonizing population, including inbreeding, heterozygosity, effective population size, allelic diversity, evidence of a bottleneck or founder effect, and relatedness can be used to determine population viability and to evaluate when the population has reached a critical threshold that requires management action (Schwartz et al. 2006).

Anecdotal evidence implies small isolated populations of swift fox (*Vulpes velox*) are all that remain in Montana, South Dakota, Nebraska, and parts of Wyoming (Merrill et al. 1996, Redmond et al. 1998, North Dakota Game and Fish Department 2017, South Dakota Game, Fish, and Parks Department 2014, Soper 1964, Sovada and Scheick 1999, Allardyce and Sovada 2003). The majority of extant swift fox populations in the Northern Great Plains, in particular in Montana and the Dakotas, are the result of reintroduction efforts, not natural recovery (Smeeton and Weagle 2000, Montana Fish, Wildlife and Parks Department 2006, Ausband and Foresman 2007). Due to state-wide extirpation, 459 swift fox were released in South Dakota between 2002 and 2010 (Honness et al. 2007, Swift Fox Conservation Team 2006, Swift Fox Conservation Team 2011, Oglala Sioux Parks and Recreation Department 2012, Sasmal et al. 2012). These reintroductions occurred in four areas in the west-central portion of the state: Bad River Ranches (Turner Endangered Species Fund), Lower Brule Sioux Tribal Land (Lower Brule Sioux Tribe Department of Wildlife, Fish and Recreation and the Maka 4 Foundation), Badlands National Park (National Park Service), and Pine Ridge Indian Reservation (Oglala Sioux Parks Recreation Authority). Today, swift foxes are known to exist around Badlands National Park and in Fall River County (a remnant population) South Dakota (Swift Fox Conservation Team 2011, Swift Fox Conservation Team 2014). Since the start of these reintroduction efforts, regular swift fox sightings have been reported in northwest South Dakota and there has been a spike in regular fatalities due to vehicles in southwest North Dakota, indicating potential for an existing, yet small, population in the area. This area is outside of the boundaries of recent reintroduction projects, where swift fox were not known to occur; it is not clear if these foxes are descendants of reintroduced foxes, natural dispersal from nearby Wyoming and Montana, or both potential sources.

It is unknown if the genetic variation within the re-established population is reduced. The apparent small population size and patchy distribution of individuals imply potential for reduced genetic variation, while the history of multiple reintroductions from genetically diverse source populations (Sasmal et al. 2012, Schwalm et al. 2014) combined with potential immigration from nearby populations may counteract the effects of size and distribution – or, in the instance of reintroductions specifically, could confound losses through founder effects and genetic bottlenecks. The objective of this study was to measure genetic diversity and assess population genetics characteristics such as founder effects, bottlenecks, inbreeding and relatedness in a small, recolonizing swift fox population, of which little is known about the distribution, abundance, connectivity, or genetic diversity. Notably, we provide one of the first studies of the genetic composition of a naturally re-colonizing swift fox population and one of few studies of genetic diversity in newly re-established population of vertebrates.

STUDY AREA

The study area included Harding, Butte, Perkins, and Meade counties in South Dakota and Slope, Bowman, Adams, and Hettinger counties in North Dakota (Figure 1). The study area encompassed approximately 4,099,174 ha dominated by mixed grass prairie, interspersed with sagebrush (*Artemisia* sp.). Prominent grasses of the mixed grass prairie in the area were: western wheatgrass (*Pascopyrum smithii*), green needle grass (*Nassella viridula*), needle and thread (*Hesperostipa comata*), blue grama (*Bouteloua gracilis*), and side-oats grama (*Bouteloua curtipendula*). Topography was largely flat to gently rolling hills with occasional buttes. The primary soil types were clays derived from Createaceous Pierre Shale. Predominate water features included Shadehill Reservoir, Belle Fourche Reservoir, and the Belle Fourche River. Lands were primarily used for cattle and sheep grazing. The southwestern edge of the study area is roughly 33.70 km from the BNP reintroduction site, 8.46 km from the Pine Ridge Reservation reintroduction site, 143.23 km from the Bad River Ranch reintroduction site, 186.68 km from the Lower Brule Reservation reintroduction site, and 119.09 km from the remnant population in Fall River County in South Dakota. Its western boarder likely abuts the small southeastern Montana population and the slowly expanding Wyoming population. It is roughly 413.60 km from the north central Montana reintroduction site.

MATERIALS AND METHODS

Sample collection and preservation

We captured swift foxes from July 2016 to April 2017 using modified wire box traps (Model 108SS; Tomahawk Live Trap Co., Tomahawk, WI, USA) of dimensions 81.30 cm × 25.40 cm × 30.50 cm (Sovada et al. 1998). We manually restrained captured fox while we recorded sex, age (juvenile or adult, determined by tooth wear), and collected a 3-mm tissue sample 2.54 cm from the outer edge of the ear using a sterile biopsy punch (Schwalm et al. 2012). We also collected tissue samples from any opportunistically obtained swift fox carcasses, typically from road mortalities. We then stored tissue samples at room temperature in a 0.70 ml screw-cap cryovial filled with lysis buffer (Longmire et al. 1997).

In addition to tissue samples, we collected scat samples during a systematic camera survey conducted from August 2016-December 2016 (Mitchell et al, in prep). We also collected scats left at live trapping sites, outside of the traps. We allowed scat to dry in a paper bag at room temperature for 7 days then placed the paper bag in a sealed plastic bag with silica beads. We collected 49 swift fox tissue samples and 10 potential swift fox scats.

Laboratory analyses

We extracted whole genomic DNA from tissue samples using the QIAGEN DNeasy tissue and blood kit (QIAGEN Inc., Valencia, California, USA) except we modified the Qiagen protocol to include a 12-hour incubation at step 3 and 210 µl of ethanol at step 6. We next generated individual genotypes using 15 microsatellite primer sets previously used for swift fox (Kitchen et al. 2005; Cullingham et al. 2007, Sasmal et al. 2012, Schwalm et al. 2014; Table 1). We included primer pairs in one of three multiplexes using the QIAGEN Multiplex Kit. PCR conditions (7µl final volume) for multiplex one were 1µM sample, 1X Master Mix, 0.5X Q solution, 0.07µM both primers for locus CXX173, 0.06µM both primers for locus CXX377, 0.08µM both primers for locus FH2054, 0.17µM both primers for locus CXX20, 0.10µM both primers for loci CPH3 and CXX250, and 0.27µM both primers for locus CXX403. The PCR thermoprofile included initial denaturation for 15 min at 95ºC, 14 cycles of 30 s at 94ºC, 90 s at 55ºC (decreasing 0.3ºC per cycle to 50.8ºC) and 1 min at 72ºC, followed by 25 cycles of 30 s at 94ºC, 90 s at 51ºC and 1 min at 72ºC, then final elongation at 60ºC for 30 min.

PCR conditions for multiplex two were 1µM sample, 1X Master Mix, 0.5X Q solution, 0.15µM both primers for locus CXX263, 0.10µM both primers for locus VVE2-111, 0.10µM both primers for locus FH2062, 0.40µM both primers for locus VVE5-33, and 0.10µM both primers for locus CXX109. PCR conditions for multiplex three were 1µM sample, 1X Master Mix, 0.5X Q solution, 0.06µM both primers for locus VVE-M19, 0.08µM both primers for locus VVE3-131, and 0.25µM both primers for locus VVE2-110. For scat samples only, species ID markers described by De Barbara et al. (2014) also were included in this multiplex. These were SIDLF (0.20 µM both primers), HI6145R (0.14 µM both primers) and H3RR (0.07 µM both primers). The PCR thermoprofile for multiplex two and three included initial denaturation for 15 min at 95ºC, 12 cycles of 30 s at 94ºC, 90 s at 53ºC (decreasing 0.3ºC per cycle to 49.4ºC) and 1 min at 72ºC, followed by 25 cycles of 30 s at 94ºC, 90 s at 47ºC and 1 min at 72ºC then final elongation at 60ºC for 30 min. For all multiplexes, an additional 10 cycling steps were added for scat samples.

We completed DNA extraction and amplification in the Epps' lab for Conservation Genetics at Oregon State University, which has dedicated space for DNA analysis of low-quality/low-quantity samples generated from feces. PCR products were run on an ABI 3730 capillary DNA sequencer (Applied Biosystems, Inc.) at the OSU Center for Genome Research and Biocomputing. We determined allele size, number of alleles and individual genotypes using GeneMapper 3.7 (Applied Biosystems, Inc.).

All tissue samples were successfully genotyped. Of the 10 scat samples we collected, 7 failed to amplify, 1 was identified as a red fox (*Vulpes vulpes)* scat, and 2 were identified as swift fox scats. Of these two swift fox scats, one was successfully genotyped while the other produced a partial genotype and was not used in further analyses. Thus, in total, we generated genotypes for 50 unique swift fox.

Data analysis

Using Arlequin 3.5.2.2 (Excoffier and Lischer 2010), we estimated observed and expected heterozygosity. Using FSTAT 2.9.3.2 (Goudet 2001), we tested for linkage disequilibrium to determine if there were any significant associations between all pairs of microsatellite loci, and we corrected for multiple tests using Bonferroni corrections (Rice 1989). We also tested for Hardy-Weinberg equilibrium (HWE), correcting for multiple comparisons with a sequential Bonferroni correction at a nominal α value of 0.05. We estimated pairwise relatedness (R) among individuals, accounting for null alleles, with ML-Relate (Kalinowski et al. 2006). We estimated genetic effective population size (i.e., number of breeding individuals, N_e) using NEstimator 2.1 (Do et al. 2014). For these analyses, we used both the monogamous-mating model and the random-mating model, since swift fox are not always strictly monogamous (Kamler et al. 2004, Kitchen et al. 2006). Lastly, we tested for signs of a genetic bottleneck using the Wilcoxon tests in BOTTLENECK 1.2.02 (Cornuet and Luikart 1997).

RESULTS

There were no signs of linkage disequilibrium between any pair of loci ($p > 0.05$ in all instances). Observed heterozygosity at each locus ranged from 0.18 to 0.86 and expected heterozygosity at each locus ranged from 0.17 to 0.863 (Table 1). Estimated expected global heterozygosity (H_e) was 0.64 (SD = 0.18) and observed global heterozygosity (H_0) was 0.66 (SD = 0.19). Allelic richness at each locus ranged from 3.99 to 15.92 and the number of alleles detected ranged from 3 to 16 (Table 1). Allelic richness (AR) was 6.18 (SD = 3.52). We found 4 loci with significant deviation from HWE, with significant heterozygote deficiencies. Many factors can influence HWE, but because our population had some clustering of relatives these deviations may be due to the Wahlund effect (Wahlund 1929). This phenomenon has been reported in swift fox populations elsewhere (Kitchen et al. 2005). We also found evidence of inbreeding (F_{IS} = 0.03, p = 0.0005). Using the random mating model and monogamous mating models, respectively, we estimated a genetic effective population size (N_e) between 33.60 (95% CI: 33.60-57.50) and 68.90 (95% CI: 68.90 - 116.50) individuals. We found 24 first order relationships (i.e., parent/offspring), 34 second order relationships (i.e., full sibling), and 186 third order relationships (i.e., half sibling, grandparent-grandchild, aunt/uncle-niece/nephew) throughout the entire data set (Table 2). All individuals had at least one third order relationship with another individual in the dataset and 68% of individuals (n = 34) exhibited at least one second order relationship with another individual in the dataset. These relationships were distributed throughout the study area. None of the models used (i.e., I.A.M., T.P.M, and S.M.M) showed evidence of a bottleneck within the population ($p > 0.05$ in all cases).

DISCUSSION

We observed no evidence of a genetic bottleneck in the study population, similar to reintroduced and re-colonizing populations (Forbes and Boyed 1996*a*, Forbes and Boyed 1996*b*). However, we did observed evidence of high individual relatedness within the population and reduced genetic diversity compared to neighboring swift fox populations. Combined, the small to modest sized effective population estimate, current evidence of inbreeding and reduced genetic diversity, and the high relatedness of individuals in the population imply that the population is at risk of inbreeding and loss of genetic diversity over time. This is particularly true if the population is isolated from immigration nearby populations in Montana and Wyoming. The relationship to and level of connectedness between swift foxes in the Dakotas, Montana, and Wyoming is currently unknown, and would be a useful topic for further study.

The observed heterozygosity and allelic richness we report here are comparable to those found by Schwalm et al. (2014) for the seven unique swift fox genetic groups that encompass the majority of the species range in the United States (H_0 range = 0.50 to 0.68; AR range = 3.70 to 4.73; Table 4). Garner et al. (2005) reported that across mammal species an average heterozygosity of 0.69 is an indicator of genetic health. Our global heterozygosity level (H_o = 0.66), is not only close to this indicator of genetic health but also is very similar to that of other stable canid populations (Forbes and Boyd 1996*a*, Kitchen et al. 2005, Williams et al. 2003, Cullingham et al. 2010, Cullingham and Moehrenschlager 2013). Thus, we conclude that the swift fox population in northwest South Dakota and southwest North Dakota is a genetically viable population currently. However, given that the population in the Dakotas exhibits reduced genetic diversity compared to putative source populations including BNP, Wyoming, and Colorado, it should be monitored to ensure that this reduction is not symptomatic of ongoing decline in genetic diversity.

Observed heterozygosity (H_o = 0.66) wass higher than expected heterozygosity (H_e = 0.64) indicating an isolated-breaking effect, also known as the Wahlund effect, or the mixing of two previously isolated populations (Wahlund 1928). This supports our hypothesis that the swift fox population in northwest South Dakota and southwest North Dakota is a re-colonizing population, likely including dispersing individuals from from reintroduced populations and from distant natural source populations.

Genetic effective population size (N_e) is a key determinant in the rate of loss of genetic diversity and is the best overall metric of genetic diversity (Lande and Barrowclough 1987, Hoehn et al. 2012). The longer a population remains small, the more likely it will experience adverse effects from inbreeding (i.e. inbreeding depression). Estimates of N_e for the swift fox population in the Dakotas ranged from 33.60 (95% CI: 33.60-57.50) to 68.90 (95% CI: 68.90 - 116.50), with higher precision indicated for the smaller of these two estimates. N_e estimates assume the population is closed, however there is a knowledge gap in the Dakotas related to swift fox population connectivity on a regional scale. It is possible that this population is influenced by immigration from neighboring Wyoming and/or Montana populations. If this is the case then the N_e estimate in this study may be inflated. The low genetic effective population estimate was expected yet concerning, considering the 50/500 rule (Franklin 1980).

The 50/500 rule proposes that genetic N_e be > 50, in the short term and > 500 in the long term, to avoid inbreeding depression. Following this guideline the population in the Dakotas is likely at risk to experience inbreeding depression, in both the long term and short term. Indeed, we found support for inbreeding in the study population (F_{is} = 0.03, p = 0.0005), and observed that what seems to be exceptionally high relatedness throughout the population, with 48% (n = 24) of individuals sharing a parent-offspring relationship with another individual, 68% (n = 34) of individuals sharing at least a full sibling relationship with another individual and 100% (n = 50) of individuals sharing at least a half sibling, grandparent-grandchild or aunt/uncle-niece/nephew relationship with another individual in the dataset. The majority (n = 46; 92%) were related to multiple individuals in the dataset. Thus, the risk of mating with a relative is high in this population. This may, in part, explain the high spatial dispersion of these relationships, as well as the relatively large movements and home ranges observed in the population (Mitchell et al. in prep), which could be the result of individuals seeking mating opportunities with non-relatives (Gandon 1999) although it is unknown if swift foxes are able to recognize relatives outside of parents and litter-mates.

The spatial dispersion of closely related individuals in the study area also points to high intra-population connectivity, which can positively affect the retention of genetic diversity in populations (Gandon 1999). This study found that closely-related individuals

(2nd and 3rd order) were distributed throughout the study area, with related individuals separated by large distances (E. Mitchell, unpublished data). Conversely, we also observed evidence of kin clusters (1st and 2nd order relatedness) in some parts of the study area, similar to those reported in a swift fox population by Kitchen et al. (2005) and those in a kit fox population by Ralls et al. (2001). Kin clusters occur when neighboring foxes are closely related, and can result in an increased level of tolerance and overlapping home ranges. This is supported by telemetry data, which shows overlapping home ranges between closely related individuals within the population in some instances (E Mitchell et al., in prep). The long-term effect of kin clustering on genetic diversity in swift fox populations is unknown, although it appears to be a naturally occurring phenomenon and could be linked to cooperative breeding intermittently observed in swift fox populations (Kitchen et al. 2006, Kamler et al. 2004), which also has been documented in other vulpid species (Ralls et al. 2001, Kamler et al. 2013).

These findings suggest that the swift fox population in the western Dakotas is currently a small, but viable population, exhibiting good genetic diversity. Related individuals are broadly scattered throughout the population implying gene flow across the study area, which may positively influence the rate of loss of genetic diversity (decreasing it). Nonetheless, genetic diversity was lower than reported in many other swift fox populations including those populations that are the likely sources of recolonization in the study area, estimated effective breeding size was lower than recommended for both short and long term viability, and evidence of inbreeding was observed. All three findings point towards a need to monitor the genetic composition of this population in the future; the heterozygosity levels, allelic richness, and estimated genetic effective population size we report here provide as a baseline for such future assessments. In addition, gene flow between this population and surrounding populations in South Dakota, Wyoming, and Montana should be explored; region-wide processes of immigration and emigration may play a large role in the long-term viability of the swift fox population in the Dakotas.

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Figure 1. Location of individual swift fox samples, shown as black dots, collected in the study area from August 2016 – July 2017. The study area is comprised of four counties in southwest North Dakota (Bowman, Adams, Hettinger, and Slope) and four counties in northwest South Dakota (Harding, Perkins, Meade, and Butte). The four reintroduction sites are shown as black triangles and the remnant population is shown as a black star.

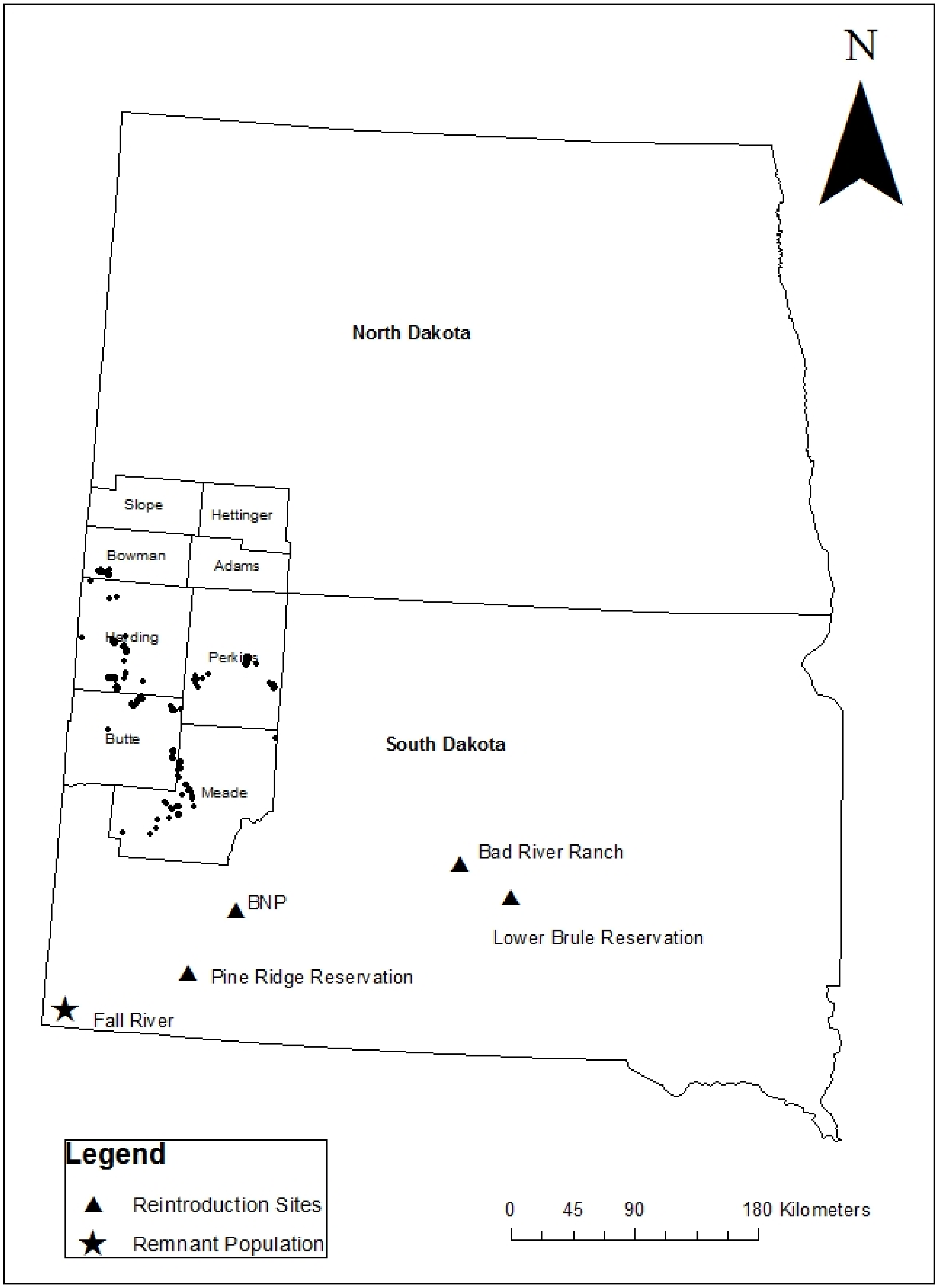

Table 1. Size range and observed polymorphisms per microsatellite locus pair used to analyze 50 swift fox scat and tissue samples. Samples are shown grouped in the PCR multiplex in which they were run. For reference the # of alleles known to occur throughout the species distribution (i.e., # Alleles Distrib.), reported by Schwalm et al. 2014, are also shown.

Multiplex	Locus	Size range (bp)	# Alleles	# Alleles Distrib.
1	FH2054[1]	171-183	4	7
	CPH3[2]	152-162	6	6
	CXX20[3]	116-136	5	9
	CXX173[3]	122-126	3	4
	CXX250[3]	127-139	7	10
	CXX377[3]	169-187	6	8
	CXX403[3]	268-276	3	5
2	CXX109[3]	160-164	5	6
	CXX263[3]	112-120	4	5
	FH2062[1]	133-146	4	6
	VVE2-111[4]	128-141	5	5
	VVE5-33[4]	197-217	3	9
3	VVE-M19[4]	249-274	12	27
	VVE2-110[4]	239-336	16	40
	VVE3-131[4]	156-189	5	6

Francisco et al. 1996[1]
Fredholm et al. 1995[2]
Olstrander et al. 1993[3]
Cullingham et al. 2007[4]

Table 2. Observed (H_o) and expected (H_e) heterozygosity, allelic richness (AR), number of alleles per loci, and results of Hardy-Weinberg equilibrium (HWE; $p < 0.05$), mean observed and expected heterozygosity and allelic richness for each of 15 microsatellite loci used to assess genetic diversity in a swift fox population in the Dakotas. Four loci deviating from HWE are indicated with an asterisk. Heterozygosity, allelic richness, and number of alleles per loci were calculated using Arlequin 3.5.2.2 and HWE was calculated using FSTAT 2.9.3.2 with a Bonferroni correction.

Alleles	**H_0**	**H_e**	**AR**	**# alleles**
CPH3	0.84	0.81556	6	6
CXX173*	0.32	0.44505	3	3
CXX20	0.7	0.75677	5	5
CXX250	0.8	0.79778	7	7
CXX377	0.6	0.53495	5.88	6
CXX403	0.18	0.16909	3	3
FH2054	0.6	0.65475	4	4
CXX109	0.66	0.65919	4.94	5
CXX206	0.78	0.72949	4	4
CXX263*	0.52	0.55859	3.997	4
VVE2-111*	0.64	0.68889	4.94	5
VVE5-33	0.6383	0.67582	8	8
VVE2-110	0.77083	0.86272	15.916	16
VVE3-131	0.86	0.76768	5	5
VVE-M19*	0.74	0.85576	11.988	12
Mean	**0.643275**	**0.664806**	**6.1774**	**6.2**

Table 3. Number of first order (parent/offspring), second order (full sibling), and third order (half sibling) relationships per individual fox. Relatedness was calculated using ML-Relate.

Fox ID	1st Order	2nd Order	3rd Order
ND1701		1	6
ND1702		1	9
ND1703			4
ND1704			10
SD1701	1		9
SD1702	1	1	1
SD1703	2	1	4
SD1704		1	7
SD1705			6
SD1706	1	4	2
SD1707	1	2	2
SD1708	1	3	2
SD1709	1	2	2
SD1710	4		5
SD1711		1	3
SD1712		2	2
SD1713R		1	4
SD1714			5
SD1715			1
SD1716	1		4
SD1718		1	3
SD1719		1	3
SD1720	2		3
SD1721			3
SD1722		1	2
SD1723			4
SD1724		2	3
SD1725			3
SD1726			3
SD1727	2	2	4
SD1728		1	2
SD1729R			2
SD1730		1	3
SD1731			2
SD1732			1
SD1733	4		1

SD1734		1	1
SD1735		1	3
SD1736			2
SD1737			4
SD1738		2	2
SD1739			1
SD1741			5
SD1742	1	1	6
SD1743			5
SD1744			5
SD1745	1		5
SD1746	1		7
SD1747			5
SDS03			5
Total	**24**	**34**	**186**