SPATIAL AND TEMPORAL STRUCTURE OF

A CANID COMMUNITY IN NEBRASKA

by

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Understanding patterns of space-use by individuals, their distribution, and how they coexist with ecologically similar species is crucial to address various issues in ecology, evolution, conservation biology, and wildlife management. However, the study of such patterns challenging because the relationship among species and their environment is shaped by multiple ecological processes, many of which are acting at different scales, often in a hierarchical manner. In the Canidae family, for instance, where interference competition appears critical, larger species such as coyotes (*Canis latrans*), can often affect smaller species, such as red fox (*Vulpes vulpes*) and swift fox (*Vulpes velox*), by killing or displacing foxes. As such, increases in the abundance and distribution of coyote following the development of the western Nebraska may have inadvertently restricted the range of swift fox (state endangered species) despite the availability of suitable habitat. In this study we aimed (1) to understand how land cover variables were associated with species occurrence and test the effect that presence of intraguild competitors have on the predictive distribution of the focal species (swift fox); (2) to investigate if temporal segregation among species may be the mechanism allowing their coexistence; and (3) to assess the genetic structure and diversity of swift fox population in Nebraska and explored whether or not genetic structure could be influenced by landscape feature and habitat constraints. Overall, our results reiterated the importance

of native shortgrass prairies, at small scale, for the occurrence and distribution of swift fox, and showed that increases of tree, row-crops, and developed areas, at larger scales, would have negative effects on the species' occupancy. Intraguild interactions do not seemed to be a significant force affecting swift fox occupancy. We found seasonal differences in activity patterns overlap among species and that differences in canid body size can predict the degree of their temporal separation. Our result suggest that swift fox population in Nebraska is restricted to two subpopulations within its available habitat, but without clear genetic structure and geographic isolation; gene flow among populations is occurring within Nebraska and across the larger region. However, our findings draw attention to the potential for future reduction of genetic diversity due to swift fox small population size in light of increasingly diminished and fragmented suitable habitat.

To all the migrants around the world.
May your voices be heard, and your rights respected.

ACKNOWLEDGEMENTS

Graduate school is, besides a series of lessons that clarify your strengths and weaknesses, a period of time in which you must be willing to fail from the very moment you start the program to the very end of it. The skills you gather along this process, by thinking and implementing possible solutions to your failures, are probably one of the most valuable learning experiences you will have. Ultimately, graduate school will put to the test your limits and broaden your horizons, and at the end you will learn. If I have to choose one of the most important lessons that graduate school has given me is that science is a team endeavor, and I say "team" in the broadest sense of the word. This work would not have been possible without the guidance, hard work, patience, support and trust of many people. As I prepare to finish this long-sought Ph.D., I realize that I am deeply thankful to more people that it is possible to name here.

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Last, but not least, I am thankful to my family. I have been incredibly fortunate to have a husband who has strived to understand my graduate student experience and who has unconditionally supported and helped me to keep a firm psychological stance. I thank my mom, my dad, and bother who, even though far away, have made my tough days easier to bear and the happier moments even brighter.

As a graduate student I saw life pass away and be born again. I saw the passing of one of the most loved, important and influential persons in my life, my dad, who missed the opportunity to visit the vastness and beauty of Nebraska's prairies but with whom I always talked about them. His support was invaluable until his death, earlier this year. I wish very much that he were here to see the grande finale of this graduate career he helped me go through. And as crazy as life is, I also became a mother, a transition that was neither smooth nor natural for me, and which took me to the limits in every aspect of my life and forced me to redefine myself. Motherhood also made me realize that finding

a life-work balance was not optional anymore; this balance is one of the first things graduate students give up. I thank Leo for giving me, during the last two years of my Ph.D., the secret benefits of being a parent, an unbreakable mandate on being more balanced; thank him for forcing me to stay physically and mentally healthy, and for the invaluable gift of being made to feel reassured regardless of how many times I fail.

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PREFACE

Grasslands are vast and dynamic ecosystems covering one-quarter of the Earth's land area, making grasslands the largest terrestrial biome (Coupland 1979, Savage 2004). In North America, temperate grasslands naturally extend over 3.5 million square kilometers (Ricketts et al. 1999, Savage 2004). During the last hundred thousand years, grasslands have experience constant changes in climate and thus community composition, but over the last two hundred years, grasslands have undergone dramatic changes in response to increasing human disturbance. Humans have severely altered grasslands leading to dramatic shifts in the plant and animal communities (Benedict et al. 1996). As a result, temperate grasslands, such as the prairies in the Great Plains, are among the most temporally and spatially unstable, and therefore, threatened ecosystems on earth (Samson and Knopf 1996, Ricketts et al. 1999, Benedict et al. 1996).

The modern prairie mammal community of the Great Plains reflects the dynamic changes that the prairies have experienced (Benedict et al. 1996). Most of the mammals that currently dominate the Great Plains originally evolved in the surrounding ecosystems, but their diverse habitat requirements allow them to emigrate into the grasslands (Risser et al. 1981, Jones et al. 1983, Armstrong et al. 1986). Only 12 percent of the mammal species found in the central and northern plains are believed to have evolved in the Great Plains, the majority of which are found in the short and mixed-grass prairies of the western Great Plains (Armstrong et al. 1986). Among the short and mixed grasslands specialists is the swift fox (*Vulpes velox*). The smallest native canid of the North America's grasslands, the swift fox went from being the emblematic "true" fox of the Great Plains, with a population perhaps numbering in the hundreds of thousands prior to European settlement, to an extremely rare and displaced species across most of

its former range (Johnson 1969, Licht 1997, Allardyce and Sovada 2003, Sovada et al. 2009). Listed as threatened or endangered in half of the states in which it formerly occurred, the causes underlying the decline of swift fox populations remains largely unknown. Habitat loss, persecution, changing community dynamics, and even climate change may all contribute to the ongoing population decline (Gauthier and Licht 2003, Allardyce and Sovada 2003, Sovada et al. 2009), but the subtle ecological mechanisms are thought to be more complex. Given the continued decline across much of their range, there is an urgent need to improve upon our limited knowledge of the ecological processes driving swift fox's populations if we expect to prevent the extinction of this iconic species.

Here, I seek to garner knowledge regarding the factors that influence swift fox occurrence, distribution, and the persistence of the species. In Chapter I, I present a species account that provides life history information for the species, detailed information regarding distribution and habitat, diet, behavior, breeding, current population status and conservation. In Chapter II, I assess the relationship between landcover and swift fox occupancy, and explore the consequences of future changes in landcover to the species. I develop species distribution models for swift fox and other two sympatric canid species (red fox and coyote) found in the shortgrass and mixedgrass prairies of Nebraska, USA, whose presence and interaction with swift fox have been consider two of the most serious limiting factors to swift fox establishment and use of suitable habitat, and significantly reduce swift fox survival through a combination of interference and exploitative competition. I explore the question: Do intraguild competitors influence spatial patterns in habitat selection and geographic distribution of swift fox? In Chapter III, I examine temporal activity patterns of the three canid species and their overlap as a way to

understand if temporal avoidance could be the mechanism by which these canid species compensate for the absence of spatial separation or buffer the effects of spatial overlap among them. Finally, in Chapter IV, I evaluate the genetic structure and diversity of swift fox in Nebraska and explored whether or not there are genetically distinct groups that could be influenced by landscape feature and habitat constraints, both at a local and regional scale. I provide a model of the genetic diversity and structure of swift fox in Nebraska, a state with among the largest intact grasslands left in North America. By combining information from genetic analysis and landscape features, I give some insight into potential genetic structure and how it may translate into gene exchange between swift fox populations in the face of increasingly grasslands loss and fragmentation.

CHAPTER I

SWIFT FOX (VULPES VELOX)

Abstract

The swift fox (*Vulpes velox*) is the smallest canid species native to the short- and mixed-grass prairies of the Great Plains of North America. Swift fox are well suited to the dynamic conditions of the arid prairies, having adapted physiologically (e.g., body size, coloration, digging capacity, speed, thermoregulation and specialized digestive/excretory adaptations) and behaviorally (e.g., fossorial, nocturnal life, opportunistic and generalist forager) to survive in wide-open spaces with limited shelter and water, and frequent disturbances including fire, drought, and other extreme weather conditions. Historically, swift fox were present from southern Canada to eastern New Mexico and northwestern Texas, but less than five decades after the first human settlement of the Great Plains, swift fox populations greatly declined. Currently, swift fox appear extirpated from more than half of its historic range, with the species survival in danger from the pressures of human population growth. Preservation of the swift fox requires understanding the swift fox's needs and threats. Here we compiled research about the swift fox's life history, ecology, historic and current distribution, population status, and current threat (e.g., land use conversion and intraguild competition). We provide an overview of management and conservation actions taken to protect the swift fox populations. Finally, we highlight the gaps in our knowledge of the species needed to improve the conservation of the species.

Classification

Kingdom: Animalia
  Phylum: Chordata
    Class: Mammalia
      Order: Carnivora
        Family: Canidae
         Genus: Vulpes
Species: *Vulpes velox*
Common name: Swift fox

Distinguishing Characteristics

The swift fox (*Vulpes velox*; Say 1823) is one of the smallest canid species on Earth, and the smallest wild canid in the North American grasslands, with an average weight of 2.4 kilograms (Moehrenschlager and Sovada 2004). Males are slightly larger than females weighing 2.4 kg (5.4 pounds) on average versus 2.3 kg (5.0 pounds) for females (Scott-Brown et al. 1987). An adult swift fox is approximately 30 cm tall and 80 cm long (Moehrenschlager and Sovada 2004, Scott-Brown et al. 1987, Carbyn 1998). Other recorded swift fox measurements are 28 cm for length of the tail, 3 cm for length of hind foot, and 0.8 cm for length of ear (Carbyn 1998).

Swift fox pelage is light grey with orange-yellow-tan coloring across the lower sides, legs, and the ventral surface of the tail and characteristic dark marks on the snout, and a black tipped tail (Egoscue 1979). Both sexes show the same pelage coloration. The winter coat of the swift fox is a dark buffy gray across the back extending into a yellow-tan coloration on the sides, legs, and ventral surface of the tail (Scott-Brown et al. 1987). The swift fox can be distinguished from it close relative the kit fox (*Vulpes macrotis*) by its shorter and more widely spaced ears, its shorter tail, and its more rounded and doglike head (compared with the broader head and narrower snout of the kit fox; Egoscue 1979). Swift fox dental formula: 3/3-1/1-4/4-2/3=42 (Moehrenschlager and Sovada 2004).

Historical and Current Distribution

The swift fox is native to the shortgrass and mixedgrass prairies of the Great Plains in North America (Egoscue 1979). The historical range of the swift fox is estimated to be approximately 1.5 million km^2 (Sovada et al. 2009), where swift fox occupied regions from central Canada in the north, including the Alberta, Saskatchewan, and Manitoba provinces, into New Mexico and Texas in the south, and from the Rocky Mountains in the west into Iowa and Minnesota to the east; however, there are no verified records of occurrence in either state (Sovada and Scheick 1999, Moehrenschlager and Sovada 2004).

The most recent estimate of the current distribution range for the swift fox in the United States and Canada was published in 2009, and estimates that swift fox occupy 44% of their historical range in the United States and 3% in Canada (Sovada et al. 2009). Today, swift fox can be found in a small areas in Alberta and Saskatchewan, in Canada, and Montana, in the US, which constitutes the northern limit of its range, and are reestablished populations from a reintroduction program in Canada (Moehrenschlager and Moehrenschlager 2001, Moehrenschlager and Sovada 2004), through the Great Plains to New Mexico and north-wester Texas. Swift fox remains absent from part of its historical range in North Dakota, South Dakota, Nebraska, Kansas, and Texas (Sovada et al. 2009). Recent work have documented swift fox have recolonization in a small area in extreme southwestern North Dakota (Dowd 2017; Table 1.1).

Taxonomy

Although referred as "kit" fox, the earliest published record of a swift fox was in an 1801 fur trade shipment inventory of the Pembina Post of the Northwest Company's

Red River District in North Dakota owned by Alexander Henry (Reid and Gannon 1928). A few years later, in 1805, Lewis and Clark wrote in their journal the first description of the swift fox, referring to it as the "burrowing fox" and highlighting its remarkable small size, its fast and agile movements, and its ability to refuge in very deep burrows. However, it was not until 1823 that the species was scientifically described and named as *Canis velox* by Thomas Say, during his expedition on the western United States (Clark 2011). Later, in 1851, the species was reassigned to the genus *Vulpes* by Audubon and Bachman (Clark 2011). Swift fox taxonomic classification has changed through the decades as more tools, including genetic analysis, became available. For example, in the early literature, the English names "kit fox" and "swift fox" were often interchanged, but today "kit fox" refers to *Vulpes macrotis* and "swift fox" to *V. velox* as they have been identified genetically as two different species (Wilson and Cole 2000).

Subspecies and Related Species

Historical studies often led to conflicting conclusions regarding the number and location of specific species or subspecies recognized and referred to as swift or kit fox (Dragoo and Wayne 2003). Swift and kit foxes, currently classified as different species, are very close related and once considered the same species (Dragoo and Wayne 2003, Wayne et al. 2004, Clark 2011). In the early 1900s there was limited knowledge of the fox species found in the prairies and desert habitats of North America (Dragoo and Wayne 2003). Taxonomic questions were recurrent mid and late 20th century (Merriam 1902, Elliot 1903, Nelson and Goldman 1909, Grinnell 1913, Grinnell 1923, Miller 1924, Seton 1929, Hall 1946, Goldman 1931, Nelson and Goldman 1931, Grinnell et al. 1937, Dragoo and Wayne 2003). However, much of the literature published during those times used morphology and physical; therefore, it presented contradictory classification of

species and subspecies referring as swift or kit foxes (Dragoo and Wayne 2003). For example, in 1902, C. H. Merriam described three new taxa for Vulpes that included the subspecies *Vulpes velox hebes* (the Canadian *V. velox*), based on specimen collected in Calgary, Alberta, and that in his view they looked larger and grayer than *velox* to be apart from the *V. velox* of the southern United States, which he renamed as *V. v. velox*. Merriam described *V. macrotis neomexicanus* (the New Mexican subspecies of *V. macrotis*), which was apparently larger and heavier than a *macrotis*; and *V. muticus* (the San Joaquin kit fox), which he found similar to *macrotis* but larger with a longer tail and hind foot and geographically to distant. In the coming years, more new subspecies of *V. macrotis* kept been added to the list, such as *V. m. devia* (Nelson and Goldman 1909), *V. m. mutica* and *V. m. arsipus* (Grinell 1913), and *V. m. arizonensis*, *V. m. nevadensis* and *V. m. tenuirostris* (Goldman 1931).

As genetic analysis became available, the early morphologically based classifications were revisited, and foxes were classified into fewer species (Creel and Thornton 1971, Thornton and Creel 1975, Dragoo et al. 1990, Mercure et al. 1993, Maldonado et al. 1997). The arid land foxes of North America are habitat specialist and poor dispersers; thus, they may show a pronounced pattern of genetic differentiation making their taxonomic status dynamic and a point of controversy (see Dragoo and Wayne 2003 and Clark 2011). Currently, most researchers agree on distinguishing as swift fox (*Vulpes velox*) all the populations to the east of the Rocky Mountains and as kit fox (*V. macrotis*) those to the west (Wilson and Reeder 2005).

Adaptations

Like other species of the Great Plains, swift fox have adapted to survive in wide-open spaces with few trees or other shelter, limited water, and frequent disturbances including fire, drought, severe storms and other extreme weather conditions (Benedict et al 1996). Swift fox adaptations are both physiological (e.g., body size, coloration, digging capacity, speed, thermoregulation and specialized digestive/excretory adaptations) and behavioral (e.g., fossorial, nocturnal life). Swift fox coloration allow them to blend with the vegetation of the shortgrass and mixedgrass prairies. Swift foxes can satisfy most of their water needs from their prey and small amounts of vegetable materials (Egoscue 1962). Water gain through food is another adaptation to survive in the grasslands where there is little free-standing water available. Swift fox are built to run at speeds up to 60 km/hr, allowing them to hunt rapid prey such as jackrabbits and help them to escape from predator such as coyote (Moehrenchlager and Sovada 2004). Swift fox's small body size allow it to survive on smaller prey, such as insects and small mammals that tend to be abundant and easy to catch, and thus minimize hunting time to meet its energy requirements and reduce exposure to extreme weather conditions and predators (Macdonald and Sillero-Zubiri 2004).

Habitat

The swift fox is a true prairie obligate that requires from 500 to 1,500 ha of shortgrass or mixedgrass prairie to support a pair (Cameron 1984; Jones 1987; Rongstad et al. 1989). Swift fox habitat characterization varies along its distribution range and depends on the geo-physiographic area, but it is generally described as short and mixed-grass prairie ecosystems with relatively flat to gently rolling topography (Kilgore 1969,

Hillman and Sharps 1978, Egoscue 1979, Carbyn 1998, Sovada et al. 1998, Sovada et al. 2003). Swift fox prefer landscapes with relatively flat topography (<15 percent slope), abundant prey, and few predators or competitors (Cutter 1958a, Hillman and Sharps 1978, Hines 1980, Fitzgerald et al. 1983, FaunaWest 1991, Carbyn et al. 1993).

Some studies have documented swift foxes using non-native habitat within prairie ecosystems such as croplands, including fallow, stubble, and small grains fields (Sovada et al. 1998, Matlack et al. 2000, Criffield et al. 2010); however, as a general trend swift fox tend to avoid agricultural or otherwise altered habitat (Kamler et al. 2003, Finley et al. 2005, Nicholson et al. 2007) . Although the results of some investigations indicate some plasticity in habitat use and population parameters in different landscapes have been examined, the extent to which the swift fox can adapt to different non-native habitats within the grassland ecosystem and how landscape structure and disturbances thresholds affect the species abundance and may lead to exclusion is not well studied (Kahn et al. 1997, Moehrenschlager et al. 2004, Thompson and Gese 2012).

Food Habits

Diet

Swift fox are opportunistic foragers and hunters; their dietary diversity is considered high (Kamler et al. 2007a, Lemons et al. 2010). Their dietary habits vary according to season and food availability (Sovada et al. 2001, Moehrenchlager et al. 2004, Kamler et al. 2007a); however, insects and small rodents dominate the diet of swift fox in all seasons (Uresk and Sharps 1986, Hines and Case 1991, Sovada et al. 2001, Kamler et al. 2007a,b). They feed mainly on small animals, especially rodents and rabbits (e.g., murid rodents were the most frequently occurring prey in swift fox diets in

Nebraska and Kansas; prairie dogs (*Cynomys ludovicianus*) was the primary prey item in South Dakota), but also small birds, such as meadowlarks (*Sturnella* spp.) and lark buntings (*Calamospiza melanocorys*), and bird eggs (Kilgore 1969; Uresk and Sharps 1986; Sovada et al. 2001), and occasionally reptiles and amphibians (Cutter 1958, Uresk and Sharps 1981, Scott-Brown et al. 1987, Kilgore 1969, Hines and Case 1991, Sovada et al. 2001, Kamler et al. 2007a). Insects are frequently found in their diet, primarily beetles and grasshoppers (Cutter 1958b, Kilgore 1969), and in the winter swift fox will use carrion as a food source (Zumbaugh et al. 1985, Sovada et al. 2001). Although in less proportion, swift fox consume some plant materials such as wild plums and sunflowers seeds in agricultural areas (Sovada et al. 2001, Cypher 2003, Moehrenchlager and Sovada 2004).

Foraging

Swift fox forage mostly throughout the night, but they also exhibit crepuscular activity, hunting mainly diurnal birds, ground squirrels, and insects (Sovada et al. 2001). Swift fox are mostly solitary hunters (Moehrenchlager and Sovada 2004). Swift fox seems to be random and non-selective forager (Kilgore 1969), and is known to cache excess food under snow during the winter (Banfield 1974).

Behavior

Activity and Locomotion

Swift foxes are nocturnal, and they limit their diurnal activity near den sites, even most of their nighttime activity may occur near dens (Kilgore 1969, Kitchen et al. 1999, Andersen et al. 2003). Swift fox spend most of the day lounging underground, avoiding

predators, and the dry and often extremely hot or cold weather that typifies the Great

Plains (Hines and Case 1991, Kitchen et al. 1999, Andersen et al. 2003). Swift fox can

travel an average of 18.5 km/day during the nighttime activity period (Covell et al. 1996),

covering roughly an area of 8–10 km^2 at a speed up to 3–4 km/hr (Clark and Stromber

1987). Hines (1980) reported distance traveled of 1.22–1.30 km/hr between 2000–0300

hours, when swift fox were more active. Locomotion costs (estimated from daily

movement distance in winter, using an allometric equation) accounted for at least 21% of

total daily expenditure, the highest proportion reported for a mammal (Covell et al 1996).

Communication: Vocalization and Non-vocal Signaling

Foxes communicate using a variety of vocalizations (Darden et al. 2003, Darden

et al. 2006). The swift fox vocal repertoire includes eight different vocalizations:

courting/territorial call, agonistic chatter, submissive whine, submissive chatter,

precopulatory call, growls, excited yip/bark, and social yips (Avery 1990); however, this

characterization of swift fox vocalization was done from recordings made of captive

foxes. Darden and Dabelsteen (2008) found that male swift foxes used long-ranging

vocalization (i.e., barking sequence) for territory defense. Swift foxes also communicate

using growls and barks in agonistic interaction with conspecifics (Cameron 1984, Avery

1989). Swift foxes, as other canid species, routinely scent mark their territories using

urine and feces. This may be particularly important along home range core area

boundaries and during breeding season (Darden et al. 2003).

Territoriality

Although early studies described swift fox as not territorial (Hines 1980, Cameron

1984), more recent data have provided evidence of territoriality (Pechacek 2010,

Thompson and Gese 2012, Lebsock et al. 2012, Poessel and Gese. 2013). Swift fox home range overlap can be extensive, but the core areas are used exclusively by resident individuals or small family groups (Ralls and White 1995, Zoellick et al. 2002, Andersen et al. 2003).

Home Ranges

Home range estimates reported in the literature for swift fox range from approximately 3–6 km^2 (Rongstad et al. 1989) to 27–32 km^2 (Hines and Case 1991; Table 1.2). Published home range estimates for swift fox are variable and difficult to compare because different techniques and criteria have been used to do the calculations (Allardyce and Sovada 2003). Swift fox home range sizes differ between areas and over time; for instance, home ranges estimated for on the Piñon Canyon Maneuver site in Colorado averaged 22.8 km^2 from 1986 to 1987 (Andersen et al. 2003) and 7.6 km^2 from 1997 to 1998 (Kitchen et al. 1999, Macdonald and Sillero-Zubiri 2004). Swift fox home ranges in South Dakota averaged 10.4–12.3 km^2; in Albany, Wyoming 7.7–11.7 km^2 (Pechacek et al. 2000); in Nebraska averaged 32.3 km^2 for males and 27.5 km^2 for females (Hines and Case 1991); in Wallace and Sherman counties, Kansas, averaged 15.9 km^2 (Sovada 2001). A good review that presents detailed estimates for home range size for swift fox by location can be found in Moehrenschlager et al. (2004).

Social Behavior

Swift fox generally pair for life (Kilgore 1969). The typical social group consists of a mated pair with pups. Sporadically there are social groups formed by three or four individuals, which can be a group of two males and two or three females, with one

breeding female and non-breeding helpers (Kilgore 1969; Covell 1992; Sovada et al. 2003; Tannerfeldt et al. 2003). Pups remain with the parents until dispersal.

Sexual Behavior

Swift fox are described primarily as socially monogamous (Kilgore 1969, Asa and Valdespino 2003, Moehrenschlager et al. 2004). Members of social groups form long-term bonds, generally share home ranges, and most commonly remain together until the death of one group member (Kilgore 1969, Cypher 2003). Swift fox can use a mixed mating strategy, with foxes in a stable breeding group engaging in extra pair mating with residents of neighboring ranges (Kitchen et al. 2006). Also, Kitchen et al. (2006) reported that some foxes deviated from the monogamous pair family group by forming groups of three individuals.

Denning

Swift fox is among the most fossorial fox species (Allardyce and Sovada 2003). Swift foxes live in the same habitat year-around and are strongly den dependent (Carby 1998, Dark-Smiley and Keinath 2003). They use their dens in every season, which is different from other canid species, such as coyote and red fox, which use dens only during breeding season (Cutter 1958, Egoscue 1979, Hines 1980). Despite their dependence on dens, swift foxes rarely dig dens, relying on the construction efforts of other fossorial mammals such as prairie dogs (*Cynomys ludovicianus*), ground squirrels (*Spermophilus* spp.), and American badgers (*Taxidea taxus*). Within their home range, a swift fox often has several dens, each with a multitude of entrances, which they use for raising their offspring, evading predators, and protecting themselves from the extreme

weather (Kitchen et al. 1999, Pruss et al. 1999, Moehrenchlager et al. 2004, Schauster et al. 2002, Poessel and Gese 2013).

It seems to be a general consensus that predator avoidance (Moehrenschlager et al. 2004, White et al. 1994; Arjo et al. 2003 for *V. macrotis*) and proximity to resources are the two most important factors that drive den site selection in swift fox (Hines and Case 1991, Pruss et al. 1999). Cutter (1958) found dens in cultivated fields, along fence rows, overgrazed pastures, and culvert in Texas; Kilgore (1969) reported swift fox using dens in cultivated fields in Oklahoma.

Breeding

Swift fox is monestrous (Kilgore 1969, Asa and Valdespino 2003, Moehrenschlager et al. 2004) with a seasonal breeding, where the timing of breeding is dependent upon latitude as a response to changes in photoperiod so that reproduction occur earlier at lower latitudes (Asa and Valdespino 2003). Later breeding periods and birth dates are generally reported at latitudes further north (Hines 1980), and successful breeding may vary annually due to ecological variability (e.g. food availability; Moehrenschlager et al. 2004), but generally the breeding season is from December 20 to March 1 (Hines 1980, Carbyn 1998, Finley et al. 2005, Martin et al. 2007). Sexual maturity in males and females is generally reach after one year (Sovada 2003). The mean length of gestation is estimated to be 51 days (Schroerder 1985), but is only known from captive breeding ((Schroerder 1985). Whelps emerge from the natal den after approximately 4 weeks, and are weaned at 6–7 weeks of age (Kilgore 1969; Hines 1980).

Data on many aspect of swift fox's reproduction cycle and behavior is limited, for example, there has not been reported in the literature the length of the different phases of

the typical reproductive cycle (proestrus, estrus, diestrus and anestrus). Length of reproductive period has been reported to be from 1 to 70 days (Finley et al. 2005, Martin et al. 2007).

Litter Size

The swift fox produces one litter of pups per year (Kilgore 1969). Average litter size based on counts of pups at natal dens is 2.4–5.7 (Kilgore 1969, Hillman and Sharps 1978, Covell 1992, Carbyn et al. 1994, Schauster et al. 2002, Andersen et al. 2003, Moehrenschlager et al. 2004). Mean litter size is 4.6 (95% CI 3.8-5.3) from pups observed with their parents (Olson and Lindzey 2002). The sex ratio at birth has been reported to be 1:1 (Olson and Lindzey 2002).

Parental Care

Both members of the pair provide for the young and young foxes remain with the adults for 4–6 months (Covell 1992). The extent of male parental care is unknown. Some studies have suggested that both parents share in pup rearing (Kitchen et al. 2006). However, the roles of male and female swift foxes in parental care have not been thoroughly studied, even less related to the mating tactic.

Dispersal

Swift fox tend to disperse between 9.8–18 months, but dispersal generally occurs at one year of age. Young females may delay dispersal and remain in the natal home ranges and assists parents in rearing the next litter of pups or stay until the death of parents (Kilgore 1969, Covell 1992, Olson 2000, Sovada et al. 2003, Moehrenschlager et al. 2004, Kamler et al. 2004a). Dispersal varies along latitude, starting in August or

September in the southern portion of the distribution (e.g., New Mexico and Texas),
September to October in Nebraska, Colorado, and Kansas (Hines 1980, Covell 1992;
Sovada et al. 2003), and August in Canada (Pruss 1994).

Swift fox juvenile mean dispersal has been reported to be as long as 13.1 km
(Kitchen et al. 1999, Schauster 2001, Sovada 2001), where males disperse longer
distances than females; for example, Covell (1992) reported mean dispersal distances of
9.4 km for males and 2.1 km for females in Colorado. Swift fox dispersal is typically
male biased (Kamler et al. 2004b, Ausband and Moehrenschlager 2009) and the
proportion of individual dispersing and dispersal distances vary spatially and temporally
with population density, mortality rates among parents, and available resources
(Koopman et al. 2000, Cypher 2003, Kamler et al. 2004a).

Interspecific Interactions

Interspecific interaction, in particular interference competition with other canid
species, is extremely important for swift fox because it can influence distribution and
habitat use (Allardyce and Sovada 2003). Predation and competition with coyotes (*Canis
latrans*) and the expansion of red fox (*Vulpes vulpes*) may be the two most serious
limiting factors for swift fox (Moehrenschlager and Sovada 2004). There is clear
evidence from several studies that predation by coyotes are one of the principal causes of
swift fox mortality (Covell 1992, Carbyn et al. 1994, Sovada et al. 1998, Kitchen et al.
1999, Schauster et al. 2002a, Andersen et al. 2003, Thompson and Gese 2004). For
example, coyotes have been reported as the major mortality factor both in cropland and
rangeland areas in Kansas (Sovada et al. 1998). Swift fox survival, density, and
recruitment rates of juvenile increased after coyotes were removed Rita Blanca National

Grassland in Texas (Kamler et al. 2003b). Thompson and Gese (2004) examined swift fox-coyote interaction and found that coyotes are aligned with resource availability, and swift fox used resources under the influence of predation risk. Karki et al. (2007) studied impacts of coyote removal on swift fox at the Piñon Canyon site in Colorado, and noted that reduction of populations of coyotes did not increase density, due to compensatory dispersal, or reproduction of swift foxes, but did positively influence survival of adults.

Intraguild aggression can also occur between swift fox and red fox (*Vulpes Vulpes*), and can constitute a source of mortality for swift fox. Red fox occupancy may be a substantial barrier to swift fox range expansion, as it had been suggested for San Joaquin kit foxes (Ralls and White 1995, Sovada et al. 1998). However, studies looking specifically at the interaction of sympatric swift fox and red fox have not been published.

Demography and Populations

Life Span and Survivorship

Swift foxes usually live between 3 and 6 years in the wild, but may live up to 14 years in captivity (Sheldon 1992, Kitchen 2004, Moehrenschlager and Sovada 2004). Swift fox survival rates range from 0.50 to 0.92 for adults and 0.05 to 0.78 for juveniles (Rongstad et al. 1989, Sovada et al. 1998, Olson and Lindzey 2002, Schauster et al. 2002, Kamler et al. 2003, Karki et al. 2007, Gese and Thompson 2014, Nevison 2017). The high variation in swift fox survival rates is believed to be influenced by fluctuating environmental conditions, such as annual precipitation and the resulting vegetation growth and vegetation height that may affect dispersal, or changes in food availability, as well as differences in predation and competition with other canid species (Gese and Thompson 2014) .

Disease and Body Parasites

Swift foxes host a variety of internal and external parasites (Kilgore 1969; Pybus and Williams 2003, Criffield et al. 2009). Fleas (*Opisocrostos hirsutus*, *Pulex irritans, P. simulans*) are the most common and abundant ectoparasite (Harrison et al. 2003, Gese et al. 2004, Pence et al. 2004, McGee et al. 2006, Salkeld et al. 2007, Criffield et al. 2009). Other ectoparasites include two flea species (*Dactylopsylla percernis*, *Euhoplopsyllus affinis, Orchopeas agilis* and *O. caedens*) and one species of tick (*Ixodes sculptus*; Harrison et al. 2003; Pence et al. 2004). Among the internal parasites reported in swift fox are nematodes (i.e., *Toxascaris, Physaloptea, Trichuris vulpis, Toxocara, Capillaria*), cestodes (i.e., *Taenia*), and mites (e.g., *Demodex;* Pybus and Williams 2003, Criffield et al. 2009). Swift fox is rarely affected by plague (*Yersinia pestis*) and they are thought to play only a minor role in plague epidemiology of black-tailed prairie dog (*Cynomys ludovicianus*) colonies (McGee et al. 2006, Salkeld et al. 2007).

Causes of Mortality

The main causes of mortality documented for swift foxes are coyote (*Canis latrans*) intraguild predation and vehicle collisions (Covell 1992, Carbyn et al. 1994, Sovada et al. 1998, Kitchen et al. 1999, Moehrenschlager 2000, Schauster et al. 2002, Andersen et al. 2003, Thompson and Gese 2004, Nevison 2017). Other mortality causes documented are due to raptor depredation (e.g., golden eagles *Aquila chrysaetos*) and American badgers (*Taxidea taxus*; Carbyn et al. 1994; Moehrenschlager 2000; Andersen et al. 2003, Nevison 2017). Additionally, canine distemper has been reported as cause of death of swift fox (Olson 2000), but no significant disease outbreaks have been documented in swift fox populations.

Status of the Populations

Historically distributed across the shortgrass and mixed-grass prairies of the Great

Plains from south-central Canada to the southern plains of Texas and New Mexico, swift

fox have experienced a significant range reduction since European settlement. Currently,

swift fox are presumed extirpated from as much as 60% of their historical range (Sovada

et al 2009).

Following the extirpation of the species in Canada, a swift fox reintroduction

program started on Canada in 1983. By 1997, 942 foxes were released (Moehrenschlager

and Macdonald 2003). Canada conducted repeated census using catch-and-release

methods in 1996-1997, 2000-2001, and 2005-2006. The first census documented a

population estimate of 289 foxes; the second census, which expanded the survey area into

northern Montana, estimated that swift fox population consisted of 887; and the last

census estimated a population around 1,162 foxes (Moehrenschlager and

Moehrenschlager 2001, 2006). Swift fox is still rare in Montana, North Dakota, South

Dakota, and Nebraska (SFCT Reports). The population established in northern Montana

is isolated from the rest of the species range in the United States (Moehrenschlager and

Sovada 2004), but connected with the population in southern Canada. Recent swift fox

population estimates for north central Montana reported a population of 221 foxes in

years 2000–2001, 515 for the period 2005–2006, and ~175 from 2014–2015 (DeVore et

al. 2017 in SFCT Report for 2015–2016). In South Dakota, populations are small and

fragmented, their numbers have probably been increased as result of four reintroductions

that started in 1999 (Bad River Ranches, Lower Brule Sioux Tribal Land, Badlands

National Park and Pine Ridge Indian Reservation) all completed in 2010 with a total

number of 538 foxes. The current status of the populations in North Dakota, Nebraska

and Texas is unknown, but swift fox numbers appear to be recovering. Swift fox populations in New Mexico, Oklahoma, Wyoming, Colorado, and Kansas have been described as relatively stable, but no population estimates have recently been published (Dowd 2017, SFCT 2015-2016).

In the United States, population monitoring results conducted by state wildlife agencies can be found in the SFCT annual reports. Results are often only for limited study areas, such as eastern Colorado (Finley et al. 2005, Martin et al. 2007), Piñon Canyon Maneuver Site in southeastern Colorado (Schauster et al. 2002b), or Oklahoma's Panhandle (Criffield et al. 2010).

Historical Perspective: Swift Fox in the Native American Traditions

For centuries, swift fox have been an iconic figure of the Great Plains together with bison and prairie dogs (Litch 1997), including playing an important role in some Native American tribes' creation myths and stories. The swift fox is associated with the sacred pipes of the Arapahos, and with warrior societies in the Cheyenne and Lakota tribes, named the Swift Fox or Kit Society (the Lakota made no distinction between the swift fox and its kit fox cousin). These warrior societies were comprised of prominent warrior men from the tribe chosen to serve in the tribal police, or guard unit, which were responsible for tribal defense, internal security, enforcement of tribal law and raids, leadership during times of war, and the organization of the annual buffalo hunt (Timber and Liberty 1998, Santoro 2009).

Among the (Swift and Kit) Fox Societies, fox fur and other parts were used to make various types of clothing and regalia, mostly for decorative and symbolic reasons. Fox skin and jaws, together with other symbolic objects such as pipes, lances, whips, and

drums, were signs of membership to the society and were attire to rituals and ceremonies (Gilman 2003). Swift fox was important as a medicine animal in many Native American cultures and it is still considered a messenger of danger, symbol of good power, and a guardian. Swift fox represents pride, regality, and loyalty in Native American traditions, and it remains an important symbol and character of stories and ceremonies (Lake-Thom 1997).

Conservation and Management

Effects of Human Activity

Although the exact reasons remain unclear, the decline in swift fox population is linked to human activities (Licht 1997, Gauthier and Licht 2003, Allardyce and Sovada 2003, Sovada et al. 2009). The westward migration of Europeans dramatically altered the local fauna. By the late 1800s, the American bison was largely extirpated from the Great Plains. A keystone herbivore, bison along with fire, affected the distribution and overall vitality of the historic grass and forb community of the prairies (Sanderson et al. 2008), and thus the suitability of habitat for swift fox. Like bison, wolves were also quickly extirpated from the expansive grasslands. As top predator, wolves killed large mammals, the left over carrion providing an important winter food source for swift fox. At the same time, wolves kept coyote populations under control, reducing competition between coyotes and swift fox and altering the canid community dynamic (Carbyn 1986, Licht 1997, Gauthier and Licht 2003). The indirect effects of removing wolves likely cascaded through the ecosystems to affect swift fox, but the direct implications of the eradication effort was also significant. Bison and cattle carcasses laced with strychnine

indiscriminately killed numerous species of predators, including swift fox, with unknown implications for the population (Seton 1909, Young 1944 in Allardyce and Sovada 2003).

By that time, large scale ranching and farming began to arrive on the Great Plains in the late 1800s, the prairies were already substantially different, but human settlement further affected the ecosystem. Following a series of Homestead Acts, the endless prairies were quickly replaced by fields of grain as the population of the Great Plains boomed section by section. Where grasslands remained intact, concerns over competition for grazing lands led to government efforts to remove prairie dogs. Prairie dogs were an important prey animal for swift fox and prairie dog towns provide the shortgrass and abundant den sites that swift fox prefer (Nicholson et al. 2006, Zielinski 2015). An increasingly agrarian landscape created a mosaic of challenges for swift fox including habitat loss and fragmentation, reductions in rodent prey base, and a changing predator community. By the middle of the 20th century, swift fox were largely extirpated from much of the northern and eastern portions of their range. Isolated populations, mostly in the southwestern swift fox range, were all that remained of this historically abundant species (Martin and Sternberg 1955, Glass 1959, Jones 1964, Long 1965, Van Ballenberghe 1975, Hines 1980, Allardyce and Sovada 2003, Sovada et al. 2009).

Poisoning

Inadvertent poisoning from strychnine-laced baits used for wolf control has been described as the most important direct cause of swift fox population declines in North America during the beginnings of the 20th century (Seton 1909, Grinnell 1914, Baily 1926, Young 1944), and the recovery of swift fox populations in some areas has been

attributed to the prohibition of the use of chemicals poisons (Allardyce and Sovada 2003).

Trapping and Hunting

The history of the swift fox description as a species is linked first to the fur trade industry that started in the sixteenth century, and then to the exploration of the western North America by naturalists during the nineteenth and twentieth centuries (Reid and Gannon 1928, Hillman and Sharps 1978, Allardyce and Sovada 2003, Clark 2011). Swift fox pelts became a valuable transatlantic trade commodity by the mid-1800s. Native Americans were the primary hunters and trappers, transporting and trading pelts to European intermediaries in exchange of a range of goods, including knives, firearms, shots and powder, awls and twine, kettles and blankets (Carlos and Lewis 2010).

Swift fox fur trade stretched back for centuries in North America, but its economic value peaked from mid-1800s to the early 1900s (Carlos and Lewis 2012). Fur buyers' records are the first evidence of the relative abundance and vulnerability of the swift fox to trapping (Clark 2011). The American Fur Company received 10,614 swift fox pelt from their upper Missouri and Sioux outfits between 1835 and 1838 (Clark 2011), while only 1,989 red fox and 108 gray fox (*Urocyon cinereoargenteus*) were taken from that region during the same period (Johnson 1969 in Clark 2011). The Hudson's Bay Company, which in the twentieth century was one of the largest North American retailers, reported selling almost 5,000 swift fox pelts annually in London, England, between 1853 and 1877 (Rand 1948 in Sovada et al. 2009). By the beginning of the twentieth century, swift foxes were considered common and abundant in much of its original range, but swift fox numbers and distribution quickly began a marked decline.

Early in European settlement, the fur trade may have played a role in reducing swift fox populations (Clark 2011). Trapping continues to occur throughout the range of the swift fox, but swift fox pelts are not particularly valuable (Arnold 1925; Jones 1987; FaunaWest 1991) and most harvest is incidental (McDaniel 1976; Sharps 1984; Jones 1987). Although the direct effects of trapping on swift fox populations remains debatable.

Management and Conservation Status

Conservation Measures Proposed and Taken

In 1992, the US Fish and Wildlife Service (USFWS) received a petition to list the swift fox as an endangered species, under the authority of the Endangered Species Act, in the northern portion of its range (Montana, North Dakota, South Dakota, and Nebraska), if not the entire range (Federal Register 1994). Two years later, the USFWS placed the species on the candidate list, which encouraged state wildlife agencies to form the Swift Fox Conservation Team (SFCT) to work cooperatively on swift fox management and conservation (Kahn et al. 1997). The Swift Fox Conservation Team was formed by 10 state agencies (Colorado, Kansas, Montana, Nebraska, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, and Wyoming), 6 federal agencies (list the federal agencies since you list everything else), and the Alberta Fish and Wildlife Division (Canada). The main goals of the SFCT are to: 1) Enhance the distribution of swift fox to maintain genetic diversity and health within the species, 2) Maintain current areas of abundance and manage additional populations for increased abundance, and 3) Elevate the management status of the species throughout the distribution and develop incentives for private landowners to manage swift fox (Kahn et al. 1997). One of the first tasks of the SFCT was the preparation of the Swift Fox Conservation Assessment and

Conservation Strategy (CACS) to guide management and conservation of the species while allowing state wildlife agencies to retain the management authority of the species, as an alternative to a federally recovery effort (Kahn et al. 1997, Allardyce and Sovada 2003, Dowd 2011). One of the objectives of the CACS is the implementation of research on swift fox, thus the SFCT has been encouraging investigation of biological and ecological parameters of the species. Updating the distribution maps of swift fox was a major area of emphasis in research, partly in response to the needs of an assessment of the population status for the potential listing review process (Dowd 2011).

In 1998, an International Symposium on Swift Fox was held in Saskatoon, Saskatchewan, Canada, organized by the CWS and the U. S. Geological Survey's Northern Prairie Wildlife Research Center. The symposium was aimed at facilitating information exchange, updating the species status in its entire range, identifying the "state-of-the-science" of the swift fox ecology (Sovada and Carbyn 2003), and creating a strategy to best manage the species to increase distribution and viability of the existing populations. This symposium was a venue to present research that had been done in the years following the petition for listing of swift fox under ESA. As a result of new information, some of which was research presented in the symposium and many other papers published after it, the USFWS removed the swift fox from the candidate species list in 2001 (Federal Register 2001).

Conservation Status

Reductions in population size, and subsequently a significant range contraction, led to the first proposed federal protection of swift fox in 1970. The U.S. Fish and Wildlife Service listed the northern swift fox (*Vulpes velox hebes*) as endangered (35 FR

8485), but the designation was quickly removed due to controversy over taxonomy (Federal Register 1994). At the same time, Canada designated swift fox as endangered (45 FR 49844), but by the late 1970s swift fox were considered extirpated from Canada (Carbyn et al. 1993). In 1992, the U.S. Fish and Wildlife Service again implemented protective measures, and swift fox were under consideration as a threatened species under the Endangered Species Act until 2001 when an alternative management strategy was devised (Allardyce and Sovada, 2003).

Through ongoing conservation efforts, swift fox populations have shown some improvement, although the species continues to occupy less than 50% of its historic range (Sovada et al. 2009). No longer a candidate for federal protection, the status of swift fox remains a concern across much of the species distribution (Allardyce and Sovada 2003). Internationally, swift fox are considered 'vulnerable' (NatureServe Global rank G3, last reviewed 19 June 2006) and some federal agencies, including the U.S. Forest Service, prioritize their conservation and management by designating swift fox as a "sensitive species". Lacking any formal federal regulatory status, swift fox management and legal protection falls under state and provincial authority (Table 1.3), with the specific regulatory status varying from a harvestable game species to endangered (Dowd 2011; Table 1.4).

History of Swift Fox Research

In this section, we present a historical perspective of our knowledge of swift fox. We examine over 170 publications, which we obtained from two major online bibliography databases (JSTOR and Web of Science), and one web-based search engine (Google Scholar) to search for articles available from 1900 to 2017 that contained 'vulpes

velox', or 'swift fox' in their title or as a topic. We examined all publications using an automated content analysis framework with the text analysis tool Leximancer (V4.5; Leximancer Pty Ltd; Brisbane, Australia) to uncover the predominant topics. Leximancer uses algorithm for text-mining and visualizing complex text data (Smith 2003, Nunez-Mir et al. 2016) that allows to automatically identify and map recurrent concepts and themes by relaying on word frequency and co-occurrence of terms (Smith and Humphreys 2006). We used Leximancer's output to create a list of the topics and subtopics that repeatedly appear among the publications and manually subset the literature to address our topics of interest (Table 1.5).

Most of the early studies of swift fox were natural history descriptions of mammalian fauna, primarily species checklists or notes of mammal species distributions (Coues 1867, Knox 1875, Baker 1889). Well into the 1900s, little was known about the biological and ecological characteristics of swift fox. Early efforts to further understand swift fox at the turn of the 20th century focused on taxonomic questions aimed at identifying and differentiating swift and kit fox populations (Swift fox: Merriam 1902, Seton 1929, Hall 1946. Kit fox: Elliot 1903, Nelson and Goldman 1909, Grinnell 1913, Grinnell 1923, Miller 1924, Goldman 1931, Nelson and Goldman 1931, Grinnell et al. 1937, Dragoo and Wayne 2003). Beside publications on taxonomy specific to foxes, in the following decades most studies were focused on the species distribution (Swift fox: Hardy 1945, Long and Long 1964 in Stromberg and Boyce. 1986, Blus et al. 1967. Kit fox: Halloran 1945, Anderson and Hadary 1965, Miller and McCoy 1965, Baker 1968), description, and natural history (Swift fox: Martin and Sternberg 1955, Birney 1965, Kilgore 1969. Kit fox: Benson 1938, Bunker 1940, Egoscue 1956, 1962, 1964, 1966),

with a couple of articles looking at denning and food habits specifically for the two fox species (Swift fox: Cutter 1958a, 1958b. Kit fox: Hawbecker 1943, Burns 1960)

Over the following decades, 1980s and 1990s, swift fox attracted more attention, not only because of the Canadian reintroduction project, but also because of its limited reappearance in portions of its historical range and the limited knowledge on aspects of its biology and ecology (Hines 1980). Subsequently, more research was done on the species and the topics studied expanded to include physiology (Flaherty and Plakke 1986, Womer and Richards 1990), parasites and diseases (Mainka 1988, Miller et al. 1998), behavior (Carbyn 1986, Uresk et al. 1986, Hines 1991, Covell et al. 1996, Pruss 1999), food and feeding (Zumbaugh and Fox 1985, Hines 1991, Wilson 1993), demography (Sovada et al. 1998), interspecific interactions (Sargeant et al. 1987, Cohn 1998, Kitchen et al. 1999) and management on reintroduced populations (Sharps and Whitcher 1984, Stromberg and Boyce 1986, Carby 1994). The first publication of hematology and biochemistry was done on the captive swift foxes at two breeding programs in Canada (Mainka 1988). As improvements in genetic analysis became available during the 90s, the early morphologically based classifications were revisited, and foxes were classified into fewer species. Studies that combined both morphometric and genetic data started to be published (Dragoo et al. 1990, Mercure et al. 1993, Maldonado et al. 1997).

The process of petitioning the listing (1970, 1992) and then delisting of swift fox (2001), the creation of the SFCT and the formulation of the CACS prompted an increase in funding for swift fox research. Consequently, most of the literature available for swift fox (56% of all publications since 1900s) were published during the first decade of the 21st century, from 2000 to 2010, and the topics range from general description of the species (e.g., Harrison 2003) and what is known about the species current distribution

(e.g., Finley et al. 2005, Sovada et al. 2009) to behavioral characteristics (30 % of publications from 2000-2010), which included breeding, denning, movement (local and dispersal movements), sociality and territoriality (Asa and Valdespino 2003, Moehrenschlager et al. 2004, Martin et al. 2007, Kitchen et al. 2006, Tannerfeldt et al. 2003, Schauster et al. 2002, Olson 2000, Sovada et al. 2003, Kamler et al. 2004a, Andersen et al. 2001, Schauster 2001, Sovada 2001, Zoellick et al. 2002, Andersen et al. 2003). The articles published during this decade also emphasized survey techniques (17 % of articles published 2000-2010) to assess the presence and abundance of swift foxes in native prairies (e.g., Harrison et al. 2002, Olson et al. 2003, Sargeant et al. 2003). Studies on parasites and diseases that affect swift foxes increased from previous decades (Harrison et al. 2003, Gese et al. 2004, Pence et al. 2004, McGee et al. 2006, Salkeld et al. 2007, Criffield et al. 2009) and more studies on interspecific relationships, specifically looking at antagonistic interactions of swift fox and other larger canids such as coyote and red fox, were published (Kamler et al. 2003, Karki et al. 2007, Gese and Thompson 2014).

In the past seven years, from 2010 to 2017, the trend of dominance of some topics, such as behavior, population estimates and survey techniques, continued (e.g., behavior: Pechacek 2010, Thompson and Gese 2012, Lebsock et al. 2012, Poessel and Gese. 2013; population estimates: Criffield et al. 2010; Sasmal et al. 2016; and survey techniques: Stratman and Apker 2014); but until 2017 the total number of publications equals just one third of the number of publications from the 2000 to 2010. Population genetics appears more in the published literature both for native and reintroduced populations (e.g., Cullingham et al. 2013, Sasmal et al. 2013, Schwalm et al. 2014), as well as genetics as survey technique (e.g., Cullingham et al. 2010, Hebert et al. 2011).

Other survey techniques highlighted by the articles published in this period are camera

traps (e.g., Stratman and Apker 2014) and scat identification by classification trees

(Lonsinger et al. 2015). Other publications relate to capture or handling techniques

(Kamler et al. 2002, Kozlowski et al. 2003, Moehrenschlager et al. 2003), aging

techniques (Richholt and Carbyn 2003), and the use of barking sequence analysis to

classify individual captive animals (Darden et al. 2003).

Recently, some studies have gone beyond only distribution of swift fox and

looked into the species landscape ecology. Efforts have been made to assess the effect of

landscape structure and fragmentation on population connectivity and to develop

predictive maps of core habitat and identify potential movement corridors in the Great

Plains (Cushman et al. 2013, Gese and Thompson 2014, Schwalm et al. 2014, Alexander

et al. 2016). Such papers have emphasized the need for conservation measures to

maintain connectivity among swift fox populations and protect future gene flow in light

of expected higher landscape fragmentation and decreases of habitat availability.

Texas and Colorado have been at the forefront in the number of studies done on

swift foxes, 1/3 of all the publications found since 1900 used these states as study area. In

both states, studies on behavior predominate the literature published (Colorado with 36 %

and Texas with 40% of all the publications respectively). These states also have

published more about interspecific interactions and parasites/disease along with

Oklahoma.

Aspects of swift fox behavior have been studied in almost all the states within the

distribution range of the species. Publications on survey techniques for swift fox have

also been published for almost all the states. There is lack of recent research on

population estimates in states such as North Dakota, Nebraska, and New Mexico. Studies focused on food and feeding for swift fox have been primarily done in Texas (Cutter 1958b, Kamler et al. 2007a, b; Lemons et al. 2010). Research on parasites and disease has been conducted along the swift fox range except in the states of Montana, Nebraska, South Dakota and Wyoming. Publications on management of the species come from Colorado, South Dakota, Montana and Canada, mostly due to reintroduction programs.

Priorities for Future Research

In general, research on swift fox has followed the same patterns as other fields of study and for other species in which as the scientific literature has expanded, the scope of each publication has contracted, and the empirical studies have replaced natural history descriptions and interpretation. Despite the fact that North American foxes are among the most thoroughly studied mammal canid species (Cypher 2003), questions remain unanswered for the smallest species like the swift fox.

A recurrent research need is to assess population estimates and the demography of the species, in particular within human dominated landscapes. Consistent information has been generated on individual swift fox populations scattered throughout their distribution range. Nonetheless, there is a lack of research regarding the variation between populations and what habitat factors contribute to differences in population parameters and demographic rates (Gese and Thompson 2014). More studies are warranted assessing how vegetation structure influences swift fox ecology as a result of shifts in prey base or predation pressure. There is still lack of updated empirically developed fine-scale maps of swift fox distribution to allow the visualization of the overall range and connectivity for the species, as a tool for managers to develop conservation strategies.

To achieve a successful restoration and conservation of the swift fox in its increasingly fragmented landscape will required more research on the relationship among landscape composition and dispersal and gene flow between populations, as a way to assess not only structural but also functional connectivity, and to examine which factors, natural or anthropogenic, influence connectivity (Schwalm 2012). Understanding the role of habitat fragmentation on gene flow and genetic structure in and between the existing swift fox populations is crucial for decision making regarding the species management and conservation in the long term (Murphy and Evans 2011, Schwalm 2012). Assessing population functional connectivity is challenging due to the persistent uncertainty there is about species distribution, and limited understanding on how different landscape features affect movement, added to incomplete knowledge of the species dispersal abilities (Cushman 2006, Rudnick et al. 2012; Cushman et al. 2013). In addition, studies on fine-scale genetic structures within swift fox population are insufficient, and it has not been explored closely the effect of swift fox reproductive strategies on the genetic structure of its populations. Furthermore, it is expected that factors affecting structural and functional connectivity at different scales will be impacted by global climate change, but such impacts are not well-understood for grassland ecosystems and, thus, beg further scientific inquiry.

Interspecific competition may be particularly important for specialist species that have experienced declines in distribution and abundance due to substantial changes in the habitat in which they are specialized (e.g., grassland obligates; Samson and Knopf 1994), especially if changes to the ecosystem favor increases in dominant habitat generalists (Benedict et al.1996). Coyotes and red fox may be excluding swift fox from suitable habitat, restricting its distribution, therefore, further investigation on swift fox, coyote

and red fox interaction is required. Interference competition among canid species should keep being a topic of study to determine whether this competition is occurring, and in what degree is favoring one species over the other.

There are not studies examining the effects of grassland management practices (e.g., prescribed burning, controlled grazing during appropriate times of the year, mechanical reduction of woody vegetation or crop management to reduce crop stubble) on swift fox populations. Given that these practices can reduce vegetation density and grass height, and consequently could increase the availability and quality of habitat for swift fox, there is an apparent need. Uncertainty also remains regarding landscape scale habitat requirements and arrangements for swift fox. Further research is needed to help improve techniques for understanding how restoring agricultural land to grassland vegetation communities may influence swift fox population persistence.

Another particularly important issue to address is zoonotic diseases carried by foxes that may affect their populations and transfer to domestic species. There is a lack of specific knowledge of the diseases and parasites that affect swift fox. Pybus and Williams (2003) presented a review of what has been reported in the literature for swift fox and also extrapolated to swift fox what is known about diseases in other fox species and wild canids. These generalizations may not be adequate, however, because even closely related species can differ in its response to a given pathogen (William and Thorne 1996, Pybus and Williams 2003). More research is needed in determine the serology and health of swift foxes and sympatric canids. It is important to determine the prevalence and likelihood of disease transmission between swift foxes, red foxes, coyotes, and domestic dogs; as well as determine the haematology and parasite load of swift foxes (Sillero-Zubiri et al. 2004).

Lastly, there is also a need to address research toward the human dimensions and perceptions of the public about the swift fox. Education has an important role in conserving swift fox, because it influences public perception and attitudes toward the species and any management or conservation action. At present, there is still very little knowledge on public perception and attitudes to swift fox and issues that exists, or may arise, as a result of the species listing and protection in some portion of its distribution range (e.g., Nebraska). To provide a framework to help plan and implement effective conservation campaigns to improve public understanding, it is required to investigate methods and actions for effective education campaigns at local level (Sillero-Zubiri et al. 2004).

Potential Topics for Research Identify by Swift Fox Conservation Team

Research needs are discussed and prioritized at annual meetings of the SFCT. The SFCT has identified the advances and challenges that researchers and managers face regarding swift fox conservation and management, and has highlighted significant research areas that are indispensable to addressing swift fox management and conservation in the coming decades; the most prevalent topics are presented below.

– Monitor swift fox response to landscape level changes in different habitats, such as restoration of native rangeland, shifts from dryland cropping systems to irrigated cropping, and changes in CRP enrollment.

– Evaluate the effects of native prairie patch size and juxtaposition of agricultural lands and prairies on swift foxes.

– Monitor swift fox populations in habitats dominated by cropland to determine if these populations are sustained long-term.

– Examine why swift fox use of cropland is variable.

– Evaluate the influence of competitive exclusion by other canids on swift fox dispersal and potential growth.

– Potential impact of the loss of historic disturbance regimes on swift foxes.

– Potential impact of the difference in grazing patterns of cattle and bison on swift foxes.

– Influences of drought conditions on availability of food resources in rangeland-dominated landscapes.

– Potential impact of energy development (impacts from infrastructure and habitat loss) on swift foxes.

– Potential impact of biofuels; i.e., habitat loss from conversion of native habitat to monoculture.

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TABLES

Table 1. 1 Current swift fox occurrence by state

State	Counties with verified occurrences
Montana	Glacier, Liberty, Hill, Blaine, Phillips, Valley, Richland, McCone, Dawson, Garfield, Meagher, Golden Valley, Musselshell, Prairie, Wibaux, Fallon, Custer, Rosebud, Treasure, Yellowstone, Gallatin, Madison, Big Horn, Powder River, Carter
North Dakota	Bottineau, Billings, Mercer, Stark, Morton, Burleigh, Slope, Cass, Bowman
South Dakota	Pennington, Jackson, Fall River, Oglala Lakota, Meade, Butte, Harding, Perkins
Wyoming	Laramie, Platte, Goshen, Converse, Natrona, Weston, Niobrara
Nebraska	Banner, Cheyenne, Dawes, Garden, Hitchcock, Kimball, Morrill, Scotts Bluff, Sheridan, Sioux
Colorado	Weld, Morgan, Adams, Washington, Elbert, Lincoln, Kit Carson, El Paso, Cheyenne, Pueblo, Crowley, Kiowa, Otero, Bent, Prowers, Huerfano, Las Animas, Baca
Kansas	Cheyenne, Rawlins, Sherman, Thomas, Sheridan, Wallace, Logan, Gove, Greeley, Wichita, Scott, Lane, Hamilton, Kearny, Finney, Hodgeman, Stanton
Oklahoma	Cimarron, Beaver
New Mexico	Chaves, Colfax, Curry, De Baca, Guadalupe, Harding, Lea, Mora, Quay, Roosevelt, San Miguel, Union
Texas	Known from western one-third of state east to Menard County
Canada	Alberta, Saskatchewan

Table 1. 2 Swift fox home range characteristics along its the distribution range.

Home range	Value	Reference
Maximum size	32 ± 9.8 km^2	Hines and Case (1991)
Minimum size	7.6 ± 0.5 km^2	Kitchen et al. (1999)
Maximum overlap (no breeding season	0.22 ± 0.24	Adapted from Schauster et al. (2002)
Home range size by state:		
Nebraska	Mean 32.3 km^2 (MCP)	Hines & Case (1991)
South Dakota	Mean 8.83 ± 2.87 km^2 (female in rearing season)	Sasmal (2011)
Colorado	Mean 7.6 km^2 (AK)	Kitchen et al. (1999)
	8.7 ± 0.5 km^2 (males in breeding season)	Darden (2008)
Wyoming	Mean 11.7 ± 1.3 km^2 (95% AK) Mean 7.7 ± 1.1 km^2 (100% CP)	Pechacek et al. (2000)
New Mexico	Mean 21.9 ± 7.6 km^2 (AK) Mean 14.9 ± 4.9 km^2 (MCP)	Harrison (2003)

Table 1. 3 State institution responsible of swift fox management and conservation in the United States and member of the Swift Fox Conservation Team

State	State Agency
Montana	Montana Fish, Wildlife and Parks
North Dakota	North Dakota Game and Fish Department
South Dakota	South Dakota Game, Fish, and Parks
Wyoming	Wyoming Game and Fish Department
Nebraska	Nebraska Game and Parks
Colorado	Colorado Parks and Wildlife
Kansas	Kansas Wildlife, Parks and Tourism
Oklahoma	Oklahoma Department of Wildlife Conservation
New Mexico	New Mexico Department of Game and Fish
Texas	Texas Parks and Wildlife

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Table 1. 4 State legal status, harvest seasons, and management activities for swift fox up to 2018

State	District	Legal Status	Harvest Season	Season Start Date	Season End Date	Limits / Quota	State Wildlife Action Plan
Montana	Districts 1-5 and 7	Species of concern	Closed				S3 (SGCN3[1])
	District 6	Furbearer	Closed (01/10/2018)	November 1, 2019	March 1, 2019	3/10	
North Dakota	Statewide	Non-game					S2 (CP2[2])
South Dakota	Statewide	Threatened					S1[3]
Wyoming	Statewide	Non-game					S2 (NSS4-Cb, Tier II)
Nebraska	Statewide	Endangered					S2 (Tier I)
Colorado	Statewide	Furbearer	Open	November 1	February 28	No limit	S3 (SC-Tier II[4])
Kansas	Statewide	Furbearer	Open	November 14	February 15	No limit	S2 (SGCN-Tier II)
Oklahoma	Statewide	Furbearer	Closed	December 1	February 28	No limit	S2, S3 (SGCN 2, 3-Tier II)
New Mexico	Statewide	Furbearer	Open	November 1	March 15	No limit	?
Texas	Statewide	Furbearer	Open	September 1	August 31	No limit	S3

[1] Species of Greatest Conservation Need (SGCN)
[2] Species of Conservation Priority (SCP), Level II: species having a moderate level of conservation priority or high level of conservation priority but a substantial level of non-SWG funding is available to them.
[3] G1 S1: Critically imperiled because of extreme rarity (5 or fewer occurrences or very few remaining individuals or acres) or because of some factor(s) making it especially vulnerable to extinction. Species for which the State has a mandate for recovery
[4] SC: species of special concern

Table 1. 5 Frequent main topics and subtopics found on the publications for swift fox (*Vulpes velox*) available from 1900 to 2017.

Main topic	Specific topic
Distribution and habitat	
Description of the species	Life history general
	Systematics
	Taxonomy
	Morphology
	Physiology
Habitat selection	
Behavior	
	Foraging
	Denning
	Breeding
	Movement
	Social
	Territoriality
	Communication
Food and feeding	
Demography	
Population	Structure
	Genetics
	Occupancy
	Abundance and density
	Recruitment
	Mortality
Parasites and disease	Parasites
	Diseases
	Plague
	Hematology
Interspecific interactions	Coyote
	Foxes
	Prey
Comparative Biology	
Management	
	Conservation status
	Reintroductions
Survey techniques	

CHAPTER II

SPECIES DISTRIBUTION MODEL OF CANIDS IN NEBRASKA

Abstract

Niche theory has frequently been used as a framework to integrate environmental variables and species interactions to describe species geographic distribution; yet the scale at which species respond to the environment and other species is rarely considered in species distribution modeling. Here we examined the effect of spatial scale on species distribution modeling of canid species, which are known for resources competition and intraguild aggression, across a complex landscape. Specifically, we examine the relationship between the occurrence of three canid species (swift fox, *Vulpes velox*; red fox, *Vulpes vulpes*; and coyote, *Canis latrans*) and land cover variables at different spatial scales and tested the effect of intraguild competition on predictive distribution of one of the species (swift fox, the smallest and subordinate species). We described the geographical distribution of swift fox, red fox, and coyote, and their responses to changes in the landscape by identifying how species select habitat and at what scales. Our results showed that each species responded differently to the land cover features at different spatial scales. However, our results did not provide evidence of intraguild interaction affecting swift fox occupancy. Nevertheless, our findings highlight challenges of incorporating ecological mechanisms into occurrence and distribution models.

INTRODUCTION

Patterns of space-use by individuals and subsequent species distribution are fundamental to the ecology of animal populations and shape social structures, mating systems, demography, and the distribution of prey and competitors (Moorcroft et al. 2006). Consequently, understanding where species exist and how they use habitats is crucial to address various issues in ecology, evolution, conservation biology, and wildlife management (Guisan and Thuiller 2005). Traditionally, studies of species distribution have focused on identifying the habitat attributes, most notably vegetation, that best predict the spatial patterns observed in nature. However, the relationship between a species and its environment is shaped by multiple ecological relationships beyond simple habitat characteristics, many of which are acting at different scales, often in a hierarchical manner (Pearson et al. 2004, Guisan and Thuiller 2005).

Predictive models of species occupancy and distribution have become an increasingly important tool to study distribution patterns and the processes that predict species occurrence (Guisan and Thuiller 2005). Models are constructed in accordance with ecological factors limiting species occurrence (Scott et al. 2002, Franklin 2009) and reflect a species' niche (Hutchinson 1957, 1978). Once described, the niche is mapped to produce a potential distribution (Franklin 2009), and subsequently used to predict the likelihood that a species occurs at a location (i.e., the probability of the species presence in an area). In general, species are expected to be present where the abiotic conditions are favorable (i.e., density-independent fitness is positive), an appropriate suite of species is present (e.g., prey and other food resources) and absent (e.g., competitors and predators), and the areas are accessible to the species (i.e., no dispersal limitation, Soberón and Peterson 2005). Additionally, the ecological processes that shape the niche of a species

are expected to act at multiple spatial scales (Levin 1992, Boyce 2006, Sandel and Smith 2009, Chase and Jonathan 2011).

The complexity of ecological interactions, and the multitude of scales at which they may interact can make understanding the distribution of any given species exceptionally challenging. For example, even if the distribution of a species at a larger scale is determined by the availability of food and shelter, at a smaller scale the species may be excluded from suitable habitats due to competition, predation, or anthropogenic change. Therefore, although habitat availability and suitability are often cited as the primary predictors of species distribution and abundance (Austin 2002, McDonald et al. 2012), the ecological mechanisms underlying species occurrence are often more complex.

In canid systems, for example, there is clear evidence that intraguild interactions play an important role in predicting species distribution and habitat use, particularly for smaller canid species (Palomares and Caro 1999, Kamler et al. 2007, Ballard et al. 2003). Intraguild interactions are manifested through exploitative (i.e., indirect competition for shared resources) or interference (i.e., direct interaction through aggressive behaviors) competition, each resulting in asymmetrical impacts on the smaller species (Ballard et al. 2003). Intraguild competition may be particularly important for specialist species that have experienced declines in distribution and abundance due to substantial changes in the habitat in which they are specialized (e.g., grassland obligates; Samson and Knopf 1994), especially if changes to the ecosystem favor increases in dominant habitat generalists (Benedict et al.1996). For instance, the distribution and likely densities of generalist carnivores including coyote (*Canis latrans*) and red fox (*Vulpes vulpes*), have increased throughout North America (Hill et al. 1987, Gompper 2002, Lovell et al. 1998, Prange and Gehrt 2007), while closely related grassland obligate carnivores such as swift fox (*V.*

velox) and kit fox (*V. macrotis*) have and continue to undergo significant declines

(Meaney et al. 2006, Sovada et al. 2009).

In Nebraska, where shortgrass prairie is highly altered due to the removal of

native grazers and natural fire regimes, the introduction of invasive species and

agriculture, and more recently increasing exploration for oil, gas, and wind energy

resources (Benedict et al. 1996, Benedict et al. 2000, Samson and Knopf 1994, Samson

and Knopf 1996), grassland obligated species have experienced significant reductions in

habitat availability and suitability. In canids, the grassland obligate swift fox is estimated

to occupy 20–25% of its historic range (Sovada et al. 2009), while coyote and red fox are

thought to have increased both in numbers and range throughout the state (Prange and

Gehrt 2007). Swift fox are listed as a sensitive species by the U.S. Department of

Agriculture (USDA) and the U.S. Forest Service (USFS), and in Nebraska, swift fox has

been a state endangered species since 1972 (Andelt 1995). Generalists such as coyotes

and red fox are more capable of thriving in highly altered human landscapes (Gese and

Bekoff 2004), thus it is not surprising that their distribution has increased. As the largest

canid in Nebraska, coyotes are dominant to swift fox and often cited as an important

source of mortality for swift fox (Covell 1992, Sovada et al. 1998, Schauster et al. 2002,

Karki et al. 2007). As such, increases in the abundance and distribution of coyote

following the development of the Great Plains may have inadvertently restricted the

range of swift fox despite the availability of suitable habitats. With increasing interest in

developing infrastructure in the shortgrass prairie, there is a clear need to identify the

mechanisms limiting the distribution of grassland obligate species such as swift fox, and

how continuing anthropogenic change is likely to alter important ecological relationships.

To assess the current geographic distribution of swift fox and further our understanding of how its occurrence may be affected by the interaction with other sympatric canid species, we model the distribution of the three canid species (swift fox, red fox, and coyote) and attempted to identify the processes shaping their distribution. Foxes and coyotes in Nebraska are thought to have high overlap in habitat use, home range, food habits, and reproductive period (Harrison et al. 1989, Lemons et al. 2001, Kamler et al. 2007). Therefore, intraguild interactions may play an important role in predicting species occurrence and distribution and specially to have a negative impact on swift fox population. Here we examined the extent to which land cover variables were associated with species occurrence on the spatial scales relevant to each species and tested the effect that presence of intraguild competitors have on the predictive distribution of the focal species (swift fox). Our objectives were: (1) to assess the relationship between land cover variables, measured at different spatial scales, and canid species occurrence; (2) evaluate whether the inclusion of predicted presence of competitor/predator affected swift fox response to land cover variables and the performance of the models predicting its distribution; and (3) using the predictive models created, to examine the potential effects of changes in land cover on species occurrence.

METHODS

Study Area

Our study area comprised the western third of Nebraska, US within the historical range of swift fox in the state, including 24 counties and encompassing approximately 68,605 km^2 (Figure 2.1). Western Nebraska is dominated by dry short-grass prairie and

mixed-grass prairie, in addition to patches of sand-sage prairie, pine woodlands, badlands, and other vegetation types (Schneider et al. 2011). Most of the northwest portion of the study area is primarily grass used for cattle production and most of the southeast part of the study area has been converted to agricultural croplands, mainly irrigated and dryland corn, wheat, and sugar beets (Bishop et al. 2011, Schneider et al. 2011). The region presents a relative diverse topography, which includes several areas of rocky escarpments, and a great variety of soil types, which range from sands to clays. The climate is semi-arid and is characterized by low humidity, moderate to high winds, and a large daily and seasonal range in temperature (Chapman et al. 2001, Schneider et al. 2011). Annual precipitation ranges from 300 to 430 mm. Mean annual wind speed at 100 m range from 21.5 to 34.3 km/h, and mean temperature ranges from -6° C in January to 32° C in July (Schneider et al. 2011).

Data Collection and Preparation

Site Selection

We selected survey sites to optimize our ability to record presence/absence of swift fox across different land covers based on a method described initially by Findley et al. (1999, 2005). We divided the study area into grids of 31 km^2, an area that exceeded the mean home range size of swift fox in Nebraska (Hines 1980, Hines and Case 1991). By setting our scale of assessment to exceed the home range size of swift fox we hoped to increase the validity of our sampling effort by decreasing double sampling, increasing the overall geographic area we were able to sample, and possibly allowing more direct comparisons with other studies (Finley et al. 1999, 2005; Martin et al. 2007, Knox and Grenier 2010, Stratman 2012). We classified each grid by the percentage of potential

suitable habitat based on a priori assessments of 'suitable' habitat from the literature. A grid was defined as "suitable" if it was composed of ≥ 25% suitable land cover (i.e., short- and mix-grass prairie) and ≥ 45% suitable slope (i.e., < 10% of slope) because those habitat characteristics reliably predicted occupancy and detection of swift foxes (Findley et al. 2005, Martin et al. 2007, Knox and Grenier 2011).

We used the Spatially Balanced Points tool, an ArcGIS 10.0 Geostatistical Analyst extension by ESRI, to select 100 sites from all available grids. The Spatially Balanced Points tool was developed based on the Reverse Randomized Quadrant-Recursive Raster algorithm (Stevens and Olsen 2004, Theobald et al. 2007), which is used to map two-dimensional space into a one-dimensional space where successive samples are randomly and spatially balanced according to an unequal inclusion probability of the grids. The Reverse Randomized Quadrant-Recursive Raster algorithm works in a three-step process that includes: generating a sequence grid or raster, filtering the sequence generated against a probabilistic grid (i.e., probability of observing the target species in a specific location), and selecting unique grids (Theobald et al. 2007, ESRI 2010). Thus, grids were selected based on perceived importance and relative to other locations in the raster. Spatially Balanced Sampling selects grids by taking into account the potential spatial pattern of the population and optimizing the sampling based on the probability of observing a target species in a specific point. Spatially Balanced Sampling reduces spatial autocorrelation (Theobald and Norman 2006), allows for flexibility in survey design to remove a location from the survey if needed and replace the location with a replicate site, or add new locations, and conserves the random and spatially balanced qualities necessary for study effective study design (i.e., make it possible to update sample locations according to accessibility of the sites, budget, etc.).

Survey Design

We conducted surveys from March to May (spring season) and again from September to November (fall season) of 2014, 2015 and 2016, except 2016 when we only conducted a fall survey. Surveys coincide with two main life history stages: (1) in the spring, during breeding season, to detect resident adults, because the persistence of swift fox populations depends on the distribution and abundance of breeding adults; and (2) in the fall, during juvenile dispersal, to maximize detection when populations are most abundant and most active (Olson et al. 2003, Finley et al. 2005, Martin et al. 2007).

We deployed lured trail cameras (Bushnell Trophy Cam HD and Moultrie M-880) along transects on existing trails (e.g., cow trails, unpaved roads) or fence lines (Knox and Grenier 2010). Each camera was spaced a minimum of 1.6 km apart to maximize detection rates within the sampling grid and reduce overlap between sampling efforts, as the distance between cameras also optimized scent attraction based on volatilization rates of fatty acid to maximize the probability to detect swift fox (Roughton and Sweeny 1982, Kahn et al. 1996, Harrison et al. 2002, Sargeant et al. 2003). We selected locations to take advantage of the presence of fences, posts, gates, and intersections, because canids tend to travel along such landscape features. At each location, a camera was hung on a post 40 cm above the ground and the location recorded using a hand-held GPS. We set a wooden stake 3 m in front of each camera with 40 cm exposed above the ground, which served as a base for the lure, a focal point for the camera, and a metric for estimating animal body size. The lure consisted of 15 ml of a skunk-based attractant produced by heating 385 ml of petroleum jelly to liquid form, adding 15 ml of skunk essence (F&T Fur Harvester's Trading Post, Alpena, MI), and allowing the lure to solidify. Cameras were set up to take bursts of 3 photographs no less than 5 seconds apart each time motion and/or a heat

signature was detected. We left cameras traps out for a minimum of 10 consecutive nights to minimize the trade-off between detection probability (i.e., reducing false negatives) and sampling time (Corral unpublished data).

Data Extraction and Preparation

All images were downloaded, and the GPS location and total number of photos taken for each camera recorded. We processed images using Timelapse Image Analyser software (Greenberg 2015, Greenberg and Godin 2012) recording the presence of any canid species. The resulting data for each camera was saved as hourly detection histories (i.e., presence was counted when at least one individual of the target species was photographed during each hour of the survey). The data on presence/absence of each canid species was the response variable for our analysis, while the data on landscape characteristics at each location formed the basis of the explanatory variables.

The land cover variables were derived from the Rainwater Basin Joint Venture Nebraska Landcover dataset (version 11; Bishop et al. 2016). We re-classified the original land cover layer into nine classes (i.e., shortgrass prairie, mixed-grass prairie, sandsage prairie, sandhill prairie, woodlands, small grains, row crops, roads, and development), and calculated the proportion of each land cover type surrounding camera traps at seven different buffer sizes: 500 m, 1, 2, 3, 4, 5, and 10 km radii (Table A.1). Land cover variable, each measured at seven spatial scales, were entered in our models as covariate for occurrence of the species, while year and day of the year were included as covariate in the detection process of the model. We examined linear and quadratic effects between the species occupancy and land cover at each site. Because the linear and quadratic values of land cover variables-are highly correlated, for each variable we

calculated the orthogonal values of the first and second degree using the 'poly' function in stats package in R to improve stability and computational efficiency (Chambers and Hastie 1992, Scheiner and Gurevitch 2001). We assumed land cover did not significantly change among surveyed years.

Statistical Analysis

We used a Bayesian hierarchical multi-season occupancy model to estimate occupancy of each canid species and the influence of land cover on the occupancy of each species (MacKenzie et al. 2002, Royle and Kery 2007, Royle and Dorazio 2008, Kery et al. 2009). Bayesian hierarchical models are well suited for highly complex multi-level models and have the advantage of explicitly incorporating multi-level uncertainty by making probabilistic statements about the accuracy of the relationships given the data (Kery and Schaub 2012, Stuber et al. 2017). Multi-season occupancy models require that sample points are surveyed multiple times within a "closed" period, which assumes occupancy remains constant within each sampling period (Sauer et al. 2002); here we used season as each sampling period. We used Bernoulli-Bernoulli mixture model, which is a zero-inflated binomial model. Two important assumptions of our model are closure and lack of false-positive errors. We assume that the occupancy state of a location did not change over the duration of the survey, such that that the location is either occupied or not with no temporarily change within a survey season (i.e, spring and fall). However, we considered that there may be changes in occupancy at a location from one year to the other, thus we modeled occupancy separately for each period of closure (i.e., year).

Our hierarchical model links two binary regression models: a process model for occupancy of the species, and an observational model for the detection conditional on

occupancy of the species (Goijman et al. 2015). The model assumes the site-specific

occupancy as a binary state $z(t,j)$ as a 'true' presence or absence of the target species at

year $t = 1,2,…T$ and site $j = 1,2,…,J$; where $z(t,j) = 1$ if species occurs in site j at year t,

and is zero otherwise (eq. 1). We modeled occurrence as a latent variable, since true

occurrence is unknown, with a Bernoulli distribution with probability $\psi_{t,j}$ that the species

occurs at site j at year t (eq. 2). We observe $y(t,j,k)$ in year t, at site j, period $k = 1,2,…,K$,

for our target species, which also followed a Bernoulli distribution with $p_{t,j,k}$ as the

probability that species was detected in site j at period k on year t, and $y(t,j,k) = 1$ when

the species is detected and zero otherwise (eq. 3). The detection probability of the species

was conditional on the species being present (i.e., $z(t,j) = 1$).

We examined linear effects for all land cover variables and additionally examined

quadratic relationships for the uncorrelated land cover types (short-grass, woodlands,

small grain, and row crop). We modeled detection probability of the species in site j at

period k to account for survey-specific variables such as year and day of the year.

Because our locations were clustered within sites, we included a random 'site' effect on

the occupancy model as a means of controlling for potential sources of spatial

autocorrelation and variation among sites (Kéry et al. 2009, Jorgensen et al. 2014,

Goijman et al. 2015). In the simplest specification of the model, the occurrence and

detection probabilities, ψ and p, are determined by location and survey specific effects.

The effects are incorporated into the model on the logit-probability scale as logit $(\psi_{t,j}) =$

$\alpha_{c0} + \alpha_1 x_1 + … + \alpha_n x_n$ and logit $(p_{t,j,k}) = \beta_0 + \beta_1 x_1 + … + \beta_n x_n$, where α represent coefficients

of occurrence predictors and β represent coefficients of detection predictors (eq. 2 and

4). The general form of the model is:

$$z_{t,j} \sim \text{Bern}\,(\psi_{t,j}) \tag{1}$$

$$\text{logit}\,(\psi_{t,j}) = \alpha_{c0} + \alpha_1 x_1 + \ldots + \alpha_n x_n \tag{2}$$

$$\alpha_c \sim \text{Norm}\,(\mu_{\alpha 0},\, \sigma_{\alpha 0})$$

$$y_{t,j,k} \sim \text{Bern}\,(z_{t,j} * p_{t,j,k}) \tag{3}$$

$$\text{logit}\,(p_{t,j,k}) = \beta_0 + \beta_1 x_1 + \ldots + \beta_n x_n \tag{4}$$

Because we did not know at which scale species were responding to the landscape, we used the Bayesian Latent Indicator Scale Selection (BLISS; Stuber et al. 2017) function for selecting the spatial scale for each land cover variable that best explained the data (i.e., we analyze scale selection accuracy and selected the scale with the highest posterior probability as the "best" scale for each predictor) while estimating the effects of predictors (Stuber et al. 2017). All our models were estimated using JAGS ('just another Gibbs sampler', Plummer 2003) and packages R2jags and rjags (Plummer 2013), which uses Markov Chain Monte Carlo (MCMC) to estimate the posterior distribution of the parameters of interest. We used weak, normally distributed priors for the coefficients with large prior variance (i.e., normal distribution from 0 to 0.01). We ran one chain with 20,000 iterations to calculate the posterior distribution after a burn-in period of 5,000 iterations.

We monitored parameter convergence visually by using trace plots and effective sample size (ESS), which is a calculation of the number of independent samples that would contain the same posterior accuracy as the correlated samples from an MCMC (de Valpine et al. 2017) in the coda package (Plummer et al. 2006). The larger the ESS more accurate is the estimation (Kruschke 2015). Once the parameters converged, we

calculated the mean and 95% credible interval for each parameter based on the posterior distribution.

Spatial Modeling and Validation

We created a predictive spatially-explicit model by integrating our hierarchical model with the independent land cover variables using raster package (Hijmans 2017). Since the statistical model was fit on transformed covariates, the resulting model parameters had to be back-transformed from the poly-quadratic transform data to be applied to the land cover data and then from the log-transformation resulting from the binomial model. Species distribution maps were created with geographic information system tools (maptools package, Bivand and Lewin-Koh 2018; and ArcGIS 10.3.1, Environmental Systems Research, Redlands, CA).

We used in-sample validation to evaluate the prediction performance of the model by comparing expected detections (i.e., detection of the species predicted using the model's estimates of detection probability and the data-only prevalence) and observed detections (i.e., raw detections). Specifically, we predicted the detection of the species if the detection probability estimate was larger than the data-only prevalence (i.e., the proportion of the surveys at which the species was recorded was used as a threshold for predicting detection; Cramer 2003; Liu et al. 2005). Then we calculated six predictive accuracy metrics based on an error matrix: overall accuracy, omission, commission, sensitivity, specificity, and true skill statistic (TSS). The overall predictive accuracy of the model gives the percent of correct predictions. Omission and commission present the models failure to predict true presence and over-prediction of presence, respectively. Sensitivity evaluates the model on its ability to predict true presence, while specificity

evaluates the model on the ability of predict true absences. Lastly, true skill statistic (TSS = sensitivity + specificity -1) normalize the overall accuracy by the accuracy that might have occurred by chance alone (i.e., accounts for both omission and commission error, and success as a random outcome). TSS values ranges from – 1 to + 1, where + 1 indicates that predictions correspond perfectly to actual detections and values of zero or less indicates that prediction are no better than random (Allouche et al. 2006).

As a dominant competitors and predators, coyote and red fox are expected to influence swift fox occupancy and detection probabilities (i.e., swift fox should be sensitive to coyote and red fox occupancy). We evaluated the importance of coyote and red fox on swift fox's occupancy by re-running the model described above for swift fox with the estimated occupancy probability for coyote and red fox as a predictor variables. We then compared the difference between the predictive maps of the two swift fox models by computing a cell-by-cell comparison. We calculated covariance and correlation matrices (i.e., correlation equals the ratio of the covariance between datasets divided by the product of their standard deviations; Snedecor and Cochran 1968), as well as, basic statistical parameters, such as the values of minimum, maximum, mean, and standard deviation for each dataset (i.e., predictive map).

RESULTS

Capture Records

Across all years we obtained 929,633 trap nights, with a total of more than 6.5 million pictures with 23,136 pictures of canids—2,298 pictures of swift fox (0.10

detections/trap night), 1,306 pictures of red fox (0.06 detections/trap night), and 19,532 of coyote (0.84 detections/trap night). Out of the 902 camera-trap stations , swift fox were recorded at 63 camera-trap stations, red fox at 43, and coyote at 638.

Spatial Scale Selection

Species' selected scales for land cover variables ranged from the minimum (0.5 km) to the maximum (10 km) scales tested, with posterior probabilities of selected scales from 0.15 to 0.76. In general, BLISS showed significant differences in scale selection among species for four of the land cover types (mixed-grass, sage-grass, row crop, and roads; Figure 2.2). The remaining land covers had non-extreme differences in scale selected.

The scales selected for sandhills, trees, small grain, and development were similar for all canid species (i.e., smaller scales for sandhills and small grain, medium scales for development, and larger scales for trees; Figure 2.2). The scales selected for short-grass were the smallest scale (0.5 km) for coyote (posterior distribution: 0.28) and medium scales for both fox species (swift fox—scale: 2 km, posterior distribution: 0.65; red fox—scale: 3 km, posterior distribution: 0.19). Scales selected for mixed-grass and row crop were the smallest for red fox (posterior distribution of 0.18 and 0.40, respectively) and the largest scale (10 km) for swift fox and coyote (swift fox—posterior distribution: 0.15 and 0.21; coyote—posterior distribution: 0.17 and 0.44). Contrary, the scale selected for sage-grass was the smallest scale for swift fox and coyote (posterior distribution: 0.20 and 0.19, respectively) and the largest scale for red fox (posterior distribution: 0.16). Finally, the scale selected for roads was the smallest for red fox, medium for coyote, and

the largest for swift fox (posterior distributions: 0.21, 0.23, and 0.46, respectively; Table 2.1).

We identified two predictors that were clearly selected at well-differentiated spatial scales in predicting swift fox occupancy, the proportion of short-grass and row crop. The proportion of short-grass was estimated to predict swift fox occupancy at medium scale (2 km) with posterior distribution of 0.65, while row crop affected swift fox occupancy at the largest spatial scales tested (10 km) with high posterior distribution of 0.76. Row crop at the largest scale was also unambiguously selected for coyote with a posterior probability of 0.44, and at the smallest scale for red fox with a posterior probability: 0.40. Additionally, development at medium scale (4 km) was clearly identified as predictor of red fox, with a posterior probability: 0.46 (Table 2.1).

Covariate and Occupancy Estimation

Detection and Occupancy Probability

Mean detection probabilities for the three canid species in our study were low (detection probability $p > 0.25$, Table 2.2),significantly different among species (Kruskal-Wallis chi-squared $= 554.57$, df $= 2$, p-value $< 2.2e^{-16}$), and the response to percentage of each land cover type varied by species.

Mean occupancy probabilities for both fox species were low (swift fox: 0.04, red fox: 0.03), especially when compared to coyote (0.66; Table 2.3). Occupancy of all species remained constant among surveyed years. Using location as a random effect on the intercept of the occupancy model accounted for variation among sites on occupancy and that was not explained by year in the study area.

Landcover Effects on Occupancy

Of the nine land cover variables we investigated, the proportion of short-grass and row crop best explained the variability in swift fox occupancy at the medium and large scale, respectively, with swift fox responding positively to short-grass and negatively to row crop (Figure 2.3). Swift fox occupancy also responded positively to sage-grass and roads. Row crop at small scale and development at medium were the best variables to explain occupancy of red fox, responding positively to both land cover types (Figure 2.4). Finally, short-grass and sage-grass, both at a small scale, best predicted occupancy of coyote showing a positive response (Table 2.1, Figure 2.5).

Overall, both swift fox and red fox responded negatively to increases on the proportion of mixed-grass, sandhills, and trees; while coyote responded positively to the same land cover types. In contrast, both species of fox responded positively to roads; while coyote responded negatively. Swift fox and coyote response to increases of short-grass (positive response), sage-grass (positive response), development (negative response) were similar and inverse to red fox response to the same land cover types. Only swift fox was negatively affected by row crop, and all the species appeared to be positively affected by small grain; however, the effect of small grain in swift fox occupancy is marginal and showed, as well as coyote, a threshold up to which an increase in the proportion of small grain begin to have a negative effect on occupancy (Figure 2.3–2.5).

Based on the species distribution model, swift fox populations were predicted to be most abundant in the northwestern and southwestern regions of Nebraska (Figure2.6). As expected, higher occupancy probabilities occurred in Sioux, Dawes, Banner, and

Kimball counties, located in the panhandle region of the state. Red fox were predicted to occur mainly in mixed agricultural habitats and on the margins of urban areas (Figure 2.7). Lastly, as we expected, coyote showed to be the most wide-spread canid, occurring in most living available habitats throughout the study area (Figure 2.8).

Assessment of Model Fit

We evaluated the performance of our models using in-sample validation and six accuracy metrics presented in Table 2.4. The models developed for swift fox and red fox were accurate between 94–96% of the time accurate, and the model developed for coyote was close to 50% accurate. Although both fox models did not incorrectly predict presences (i.e., the models for both species predicted 100% of the true presences, and 5% and 4% incorrectly over-predicted for swift fox and red fox, respectively), models were strongly influenced by the low occurrence of the two species (detections represented the 7% and 5% of the data for swift fox and red fox, respectively). The low occurrence resulted in models that were extremely accurate in showing where foxes are not. The model for coyote failed only 7% of the time to predict true presence, but it also presented a 50% over-prediction rate (Table 2.4).

We performed a cell-by-cell comparison between swift fox predictive maps (i.e., output datasets of predictive occupancy probability models) with and without red fox and coyote occupancy included as a covariate (Datasets are as follow A: swift fox predicted occupancy probability without other canid species as covariate; B: swift fox predicted occupancy probability with red fox occupancy as covariate; C: swift fox predicted occupancy probability with coyote occupancy as covariate, Table 2.5). The covariance of datasets A, B, and C were close to zero, indicating a weak relationship among metrics

and all datasets were highly linearly correlated (Correlation value ≥ 0.99; Table 2.5).

Therefore, the inclusion of red fox or coyote occupancy as covariate do not appear to

improve swift fox predicted occupancy probability maps. Likewise, swift fox predicted

occupancy was not influenced by increases in red fox nor coyote occupancy (Figure 2.9).

DISCUSSION

Using a niche-based species distribution model approach, we examined the

habitat association of a suite of canid species individually and the response of the focal

species (swift fox) to the presence of a competitor/predator (red fox and coyote). As a

result, our models yielded projections of occupancy probability and geographical

distribution of the species based on the environmental variables and potential intraguild

interaction combined, where both were used as spatially explicit factors. Not surprisingly,

we found that each canid species responded to unique combinations of land cover

variables at different spatial scales. For example, the increase of mixed-grass prairies

negatively affected the probability of occurrence of both fox species (swift fox and red

fox), but had a positive effect on coyote occurrence. Interestingly, however, mixed-grass

prairies influenced swift fox and coyote occupancy at the larger scale than red fox, which

were affected at the local scale. In contrast, the proportion of small grains and trees,

affected all species at the same spatial extent (1km and 10km respectively), but in

different ways. Indeed, while the proportion of trees in the landscape appears to constrain

swift fox and red fox occupancy, the presence of trees appears beneficial to supporting

coyote populations. Small grains on the other hand had a positive affect for all species,

but at some point the benefits associated with increasing small grain coverage diminished for swift fox and coyotes, while continuing to benefit red fox population.

Our findings are congruent with what we would expect. While swift fox can use a variety of habitats and prey (Jackson and Choate 2000, Matlack et al. 2000, Sovada and Carbyn 2003, Sovada et al. 2009), they are sensitive to thresholds in vegetation structure (i.e., shortgrass specialist beyond which they are excluded, and the persistence of populations compromised (Thompson and Gese 2012, Gese and Thompson 2014). For instance, swift fox abundances is generally negatively related to mean grass height and adult survival is positively related to shrub density (Gese and Thompson 2004). Suitable habitat for swift fox is thought to represent a balance between a low average grass height to allow predator detection and easy movement, and medium shrub density to maintain prey (Kamler et al. 2003, Thompson and Gese 2007, Gese and Thompson 2014). Furthermore, swift fox appear to follow an "adaptive compromise" behavior (Sih 1980), in which they trade safety (i.e., avoidance of intraguild predation, mainly by coyotes) for greater food resources during periods food scarcity (e.g., during winter; Thompson and Gese 2012).

Therefore, it is not surprising that swift fox and red fox are slightly negatively affected by increases in percentage of mixed-grass prairies, given that the habitat is positively related with coyote occupancy and thus represents higher risk of predation for both fox species, but especially for swift fox. Our finding that mixed-grass prairies affected swift fox at a larger scale may be a reflection of its requirement for a permanent safe core area, but with access to resource-rich surroundings (mixed-grass prairies present a vegetation structure that enhance rodent prey availability) even if those areas present higher predation risk due to potential encounters with coyotes (Thompson and Gese

2012). Similarly, trees in immediate proximity may represent barriers to swift fox foraging and movement and constitute a risk, given their presence favored coyote occupancy and as roost sites for aerial predators.

The presence of small grains is widely known to be positive related with some ground birds and small mammal abundance (Kaufman and Kaufman 1990, Robertson et al. 1993, Jorgensen et al. 2014); therefore, we expected to see a positive effect of this landcover on all canid species. However, small grains cover do not necessarily fulfill the other life history requirement of swift fox (e.g., high-quality den site and cover) and it might present trade-off related to the proximity with human activity and the increase intraguild competition. This could explain the pattern we observed for both foxes and coyote, in which small grains cover may be beneficial as a resource-rich habitat, but only to a certain point beyond which swift fox and coyote won't benefit. In contrast, red fox, appears better adapted than swift fox and coyotes to cropland dominated areas (Harrison and Schmitt 2003), and thus it is the only species that did not show a threshold in the benefits gained from increases in small grain cover.

As predicted, and congruent with previous studies (e.g., Findley et al. 2005), we found that occupancy probability of swift fox, the grassland obligate, showed a positive relationship with the proportion of native short-grass prairie habitat, and a negative relationship with row-crop and development. Red fox and coyote, on the other hand, both generalist, were positively related with the proportion of crops, and in the case of red fox strong positive influence of developed areas.

Our results for swift fox of positive relationship between occupancy and the percent of short-grass prairies, and negative relationship with percent of row-crops is

congruent with the notion that conversion of native prairies is one of the most important factors for the contraction of swift fox range (Hillman and Sharps 1978, Egoscue1979, Eklund 1994, Allardyce and Sovada 2003). The alteration of the landscape due to the conversion of grasslands to row-crops likely influences local and seasonal prey availability, leads to changes in canid community intensifying interspecific competition, and increases predation risk on swift fox (Ralls and White 1995, Sovada et al. 1998, Allardyce and Sovada 2003). Additionally, the establishment of row-crop on native shortgrass prairies may change soil characteristics, structure, and composition, and reduce the qualities that made soils suitable for excavation and maintenance of multiple den sites for year-around use. Moreover, swift fox may be completely excluded from previous occupied areas converted to croplands due to some farming practices such as irrigation, frequent plowing, or herbicide application (Harrison and Whitaker-Hoagland 2003). As other studies have indicated, agricultural development has rapidly turned complex grassland systems into homogeneous landscapes, reducing the quality of the landscape for swift fox and other grassland species (Thompson and Gese 2012).

We found that both species of fox responded positively to the presence of roads in the landscape, while coyote populations responded negatively. Smaller canids are vulnerable to interference competition from larger canids (Macdonald and Sillero-Zubiri 2004). By selecting areas near human developments that may be otherwise avoided by larger canids (Hines and Case 1991, Pruss 1999), foxes may potentially avoid coyotes. Indeed, swift fox often associate den sites with roads, potentially to minimize encounters with coyotes (Hines and Case 1991, Pruss 1999). Although swift fox movement is not yet well understood, there is a general consensus that road can act as dispersal corridors (e.g., individuals could potentially move easily through roads than across high and dense

vegetation, especially in winter when locomotion costs is a substantial portion of swift fox energy expenditure—locomotion accounted for > 20% of total daily expenditure; Covell et al. 1996), and, when the road network is limited, secondary roads appear to facilitate dispersal and gene flow in swift fox populations (Schwalm 2012). However, roads have been reported as high source of mortality for swift fox (Covell 1992, Carbyn et al. 1994, Sovada et al. 1998, Kitchen et al. 1999, Moehrenschlager 2000, Schauster et al. 2002, Andersen et al. 2003, Thompson and Gese 2004, Nevison 2017). Consequently, we would expect that beyond an unknown threshold, the expansion of the road network will have more negative effects than benefits on swift fox, and may ultimatley limit connectivity of among populations (Schwalm 2012). Lastly, the expansion of the road network, as well as, agricultural and urban development will intensify and accelerate the phenomenon of habitat loss and fragmentation (Fahrig 2003), possibly leading to reduced fitness of populations and localized extinction (Wilcove et al. 1998, With and King 1999, Reed and Frankham 2003, Kolb 2008), affecting mainly specialist species with narrower niches, such as swift fox.

Predation and competition by coyote and red fox is cited as important limiting factors for swift fox distribution and habitat use (Allardyce and Sovada 2003, Moehrenschlager and Sovada 2004, Covell 1992, Carbyn et al. 1994, Sovada et al. 1998, Kitchen et al. 1999, Schauster et al. 2002, Andersen et al. 2003, Thompson and Gese 2007); however, we found no evidence of the negative effects of interference competition on swift fox occupancy probability. Although initially surprising, there are sound reasons why we might expect occupancy of one species to be relatively insensitive to another, even if there is the potential for significant interference competition. Most notably, depending on the competitive abilities of the species involved, competition would be

reflected in their population numbers, and here we are not incorporating estimate abundance of the species.

Although there is sound theory to suggest why we failed to find any evidence of interference competition, we cannot rule out issues of study design. We chose to focus our efforts on occupancy rather than measures of abundance because we were concerned with issues associated with model performance. Detection and occupancy rates of canids are generally low (Sillero-Zubiri et al. 2004). In our case, the extremely low occupancy values resulted in a highly zero-inflated data set that reduced model fit and thus sensitivity to additional sources of explanatory variation (Hobbs and Hooten 2015). Indeed, in the case of swift fox most of our data reflect locations where swift fox are not present (numerous zeros in the input data). As a result, our model was highly accurate (95% correctly predicted presences) at predicting the presence or absence of swift fox, but that the probability of finding a swift fox is extremely low and thus extremely insensitive to identifying sources of variation in occupancy rates.

When working with rare species, occupancy models may afford the benefit of reducing sources of uncertainty (Thompson 2004). Reducing errors of omission (i.e., failure to predict true presence) and identifying model sensitivity (i.e., model's ability to predict true presence) are extremely important to ensuring conservation success, but the tradeoff is that occupancy data may be a less sensitive measure of the outcome of ecological interactions (MacKenzie et al. 2006). In modelling species interactions using occupancy data, rare and abundant populations are afforded a similar likelihood of interacting assuming each is detected. In reality, however, the absolute abundance of a species has significant implications for how it interacts with other species (Brown 1984). Swift fox may be less likely to occupy areas with high coyote abundance (Kamler et al.

2003, Karki et al. 2007), but unaffected by the presence of coyotes per se. For example, temporal avoidance of coyotes may be an important mechanism by which swift fox evade the potential interference competition. Swift fox may also expand their diurnal activity, to avoid a mainly nocturnal competitor like coyote. Furthermore, swift fox's fossorial behavior has been documented as one of the mechanisms that allows them to deal with interference competition with coyotes (Kitchen et al. 1999, Cypher et al. 2001). We might thus expect detailed interactions between landscape features such as soil conditions and ecological features such as the presence of coyotes to interact, a question that remains beyond our ability to assess here.

In general, we had low detection rates for all canid species. The highest probability of detection was for swift fox (0.14), likely due to the selection for survey locations that favored swift fox detection. Detection probability for red fox and coyote were similar (~ 0.10). Detection probability for the three species seemed to be affected by day of the year, with little variation among years except for swift fox detection probability. As predicted, day of the year, affected detection, with the higher detection probabilities occurring during the fall, especially for swift fox. During the fall juveniles disperse and adults form pairs and establish territories; consequently, populations are most abundant and most active (Olson et al. 2003, Finley et al. 2005, Martin et al. 2007). Given the higher detection probability in the fall, and assuming Type II error is the greatest risk when assessing populations of rare species (citations), we recommend conducting canid surveys in the fall, in an attempt to maximize detection probability.

Surprisingly and contrary to our expectations, coyote had the lowest probability of detection even though they had the highest occupancy (Gese et al. 1988, Person and Hirth 1991, Chamberlain et al. 2000, Kays et al. 2008, Gehrt and Riley 2010). Although we are

uncertain, we speculate that coyote's low detection rates may be due to avoidance of the camera trap stations due to their location in areas close to human infrastructure and activity (e.g., roads), an clear outcome of our modelling efforts. Alternatively, coyote have larger home ranges (home range sizes of adult male coyote average 24.85 km^2, and adult female average 14.67 km^2; Bekoff and Gese 2003) than red fox (home range sizes average 0.08–6.31 km^2; Baker and Harris 2004) or swift foxes (home range size of adult fox averages 15.9 km^2; Sovada et al. 2003), which may result in lower detection rates simply because of the probability of individuals actually interacting with the lures at the scale they are interacting with their environment.. Low detection probability generally translate in low sample size, which itself limits our ability to obtain precise parameters and affect the strength of population estimates (Foster et al. 2011). Still, although the low detection rates of coyotes limited our ability to definitively state how coyotes shape swift fox distribution, it may provide valuable information about other underlying ecological mechanisms that may be influencing occurrence and distribution of swift fox. For example, that the addition of distribution information for both coyote and red fox did not appreciably improve our understanding of swift fox distribution suggests that swift fox are capable of occupying areas with other canids. Indeed, habitat suitability for swift fox is likely more reflective of sufficient resources available, such as prey and suitable refugia that are reflected by larger landscape attributes than the presence or absence of other guild members per se.

CONCLUSIONS

We were able to describe the geographical distribution of three canid species and their potential responses to changes in the proportion of the land cover types studied by identifying how species select habitat and at what scales. Our results corroborated that each species respond differently to the land cover features, depending on the spatial scale. Moreover, our findings confirmed the importance of native short-grass and sage-grass prairies, at small scale, for the occurrence and distribution of swift fox, and showed that increases of tree, row-crops, and developed areas, at larger scales, would have negative effects on the species' occupancy and distribution. Although our results did not provide evidence of intraguild interactions affecting swift fox occupancy (i.e., we did not find that red fox and coyote occupancy affected swift fox occupancy probability), our study highlights the challenges of making inferences about the ecological mechanisms that determine the occurrence and distribution of a rare and elusive species. We suggest that future research should consider fine-scale spatial and temporal avoidance that may play an important role in minimizing the effects of interference competition and promoting the coexistence of sympatric canid species.

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TABLES AND FIGURES

Table 2. 1 Estimated coefficients (posterior mean) and their associated 95% credible intervals (CI) at selected spatial scales based on BLISS applied to occupancy models for three canid species in Nebraska, US.

	Coefficient	Spatial scale (km)	Scale posterior probability	Posterior mean (95% CI)
SWIFT FOX				
Occupancy model	Intercept			-4.97 (-5.73, -4.32)
	Short-grass	2	0.65	28.31 (14.47, 42.03)
	Short-grass^2	2	0.65	4.84 (-5.05, 14.81)
	Mixed-grass	5	0.15	-6.51 (-23.38, 9.42)
	Sage-grass	1	0.20	8.94 (-2.03, 19.58)
	Sandhills	0.5	0.19	-10.02 (-26.01, 5.33)
	Trees	10	0.35	-12.1 (-26.73, 0.95)
	Trees^2	10	0.35	8.16 (-5.79, 21.21)
	Small grain	0.5	0.24	3.36 (-9.75, 16.05)
	Small grain^2	0.5	0.24	-8.26 (-20.95, 3.69)
	Row crop	10	0.76	-20.32 (-34.66, -6.62)
	Row crop^2	10	0.76	10.00 (-2.96, 22.58)
	Roads	10	0.21	5.62 (-6.44, 17.19)
	Development	2	0.29	-8.59 (-20.11, 2.33)
Detection model	Intercept			-1.99 (-2.17, -1.81)
	Year			0.15 (0.01, 0.28)
	Day of the year			0.69 (0.46, 0.91)
RED FOX				
Occupancy model	Intercept			-4.57 (-5.44, -3.9)
	Short-grass	3	0.19	3.75 (-9.75, 17.21)
	Short-grass^2	3	0.19	-7.74 (-18.79, 2.99)
	Mixed-grass	0.5	0.18	-6.17 (-20.99, 7.3)
	Sage-grass	10	0.16	-8.65 (-24.59, 5.41)
	Sandhills	1	0.16	-10.54 (-26.24, 4.35)
	Trees	5	0.27	-12.15 (-27.05, 0.78)

	Coefficient	Spatial scale (km)	Scale posterior probability	Posterior mean (95% CI)
	Trees^2	5	0.27	5.84 (-7.79, 18.55)
	Small grain	1	0.22	10.74 (0.67, 20.87)
	Small grain^2	1	0.22	5.03 (-3.55, 13.09)
	Row crop	0.5	0.40	-0.85 (-11.95, 9.7)
	Row crop^2	0.5	0.40	11.76 (2.89, 20.73)
	Roads	0.5	0.23	5.56 (-4.18, 15.24)
	Development	4	0.46	13.54 (7.52, 19.92)
Detection model	Intercept			-2.15 (-2.47, -1.87)
	Year			0.14 (-0.04, 0.33)
	Day of the year			0.23 (-0.01, 0.49)
COYOTE				
Occupancy model	Intercept			0.80 (0.59, 1.02)
	Short-grass	0.5	0.28	10.1 (2.5, 17.59)
	Short-grass^2	0.5	0.28	1.23 (-3.94, 6.58)
	Mixed-grass	5	0.17	3.14 (-3.88, 10.58)
	Sage-grass	1	0.19	10.33 (3.06, 19.22)
	Sandhills	2	0.17	6.42 (-0.95, 14.16)
	Trees	10	0.24	1.79 (-3.44, 7.31)
	Trees^2	10	0.24	-2.71 (-8.18, 2.64)
	Small grain	1	0.28	6.37 (0.51, 12.43)
	Small grain^2	1	0.28	-4.4 (-9.54, 0.69)
	Row crop	10	0.44	5.1 (-0.65, 11.1)
	Row crop^2	10	0.44	-1.31 (-7.05, 4.63)
	Roads	2	0.23	-5.14 (-10.25, -0.05)
	Development	4	0.24	-5.11 (-9.85, -0.4)
Detection model	Intercept			-2.19 (-2.24, -2.13)
	Year			0.04 (-0.01, 0.88)
	Day of year			0.25 (0.19, 0.30)

Table 2. 2 Mean detection probability of canid species

Species	Detection probability (95% CI)	SD
Swift fox	0.1420 (0.1384, 0.1456)	0.0551
Red fox	0.1077 (0.1064, 0.1090)	0.0199
Coyote	0.1029 (0.1019, 0.1040)	0.0158

Table 2. 3 Mean occupancy probability of canid species

Species	Occupancy probability (95% CI)	SD
Swift fox	0.04425 (0.0357, 0.0527)	0.1295
Red fox	0.03243 (0.0260, 0.0388)	0.0976
Coyote	0.66215 (0.6478, 0.6764)	0.2187

Table 2. 4 Values of six cross-validated model accuracy measures for swift fox, red fox, and coyote predictive occupancy models that used presence/absence data of each species as response variable and associated with land cover explanatory variables as predictors.

	Swift Fox	Red Fox	Coyote
Overall accuracy (95% CI)	0.947 (0.944 - 0.949)	0.957 (0.954 - 0.959)	0.532 (0.526 - 0.538)
Omission [1]	0	0	0.0743
Commission [2]	0.054	0.043	0.497
Sensitivity [3]	0.946	0.957	0.503
Specificity [4]	1	1	0.926
TSS [5]	0.946	0.957	0.428

[1] Failure to predict true presence, [2] Over-prediction of presence, [3] Model's ability to predict true presence, [4] Model's ability of predict true absences, [5] True Skill Statistic (TSS = sensitivity + specificity -1) normalizes the overall accuracy by the accuracy that might have occurred by chance alone

Table 2. 5 Basic statistical parameters (values of minimum, maximum, mean, and standard deviation), covariance and correlation matrices of datasets of swift fox predictive occupancy probability models, with and without red fox and coyote occupancy included as a covariate.

Dataset	Min	Max	Mean	SD	Covariance matrix			Correlation matrix		
					A	B	C	A	B	C
A	0	0.2127	0.0125	0.0246	0.00033	0.00033	0.00033	1	0.99997	0.99998
B	0	0.2208	0.0129	0.0253	0.00033	0.00034	0.00034	0.99997	1	0.99992
C	0	0.2125	0.0127	0.0249	0.00033	0.00034	0.00034	0.99998	0.99992	1

A: swift fox predicted occupancy probability without other canid species as covariate; B: swift fox predicted occupancy probability with red fox occupancy as covariate; C: swift fox predicted occupancy probability with coyote occupancy as covariate
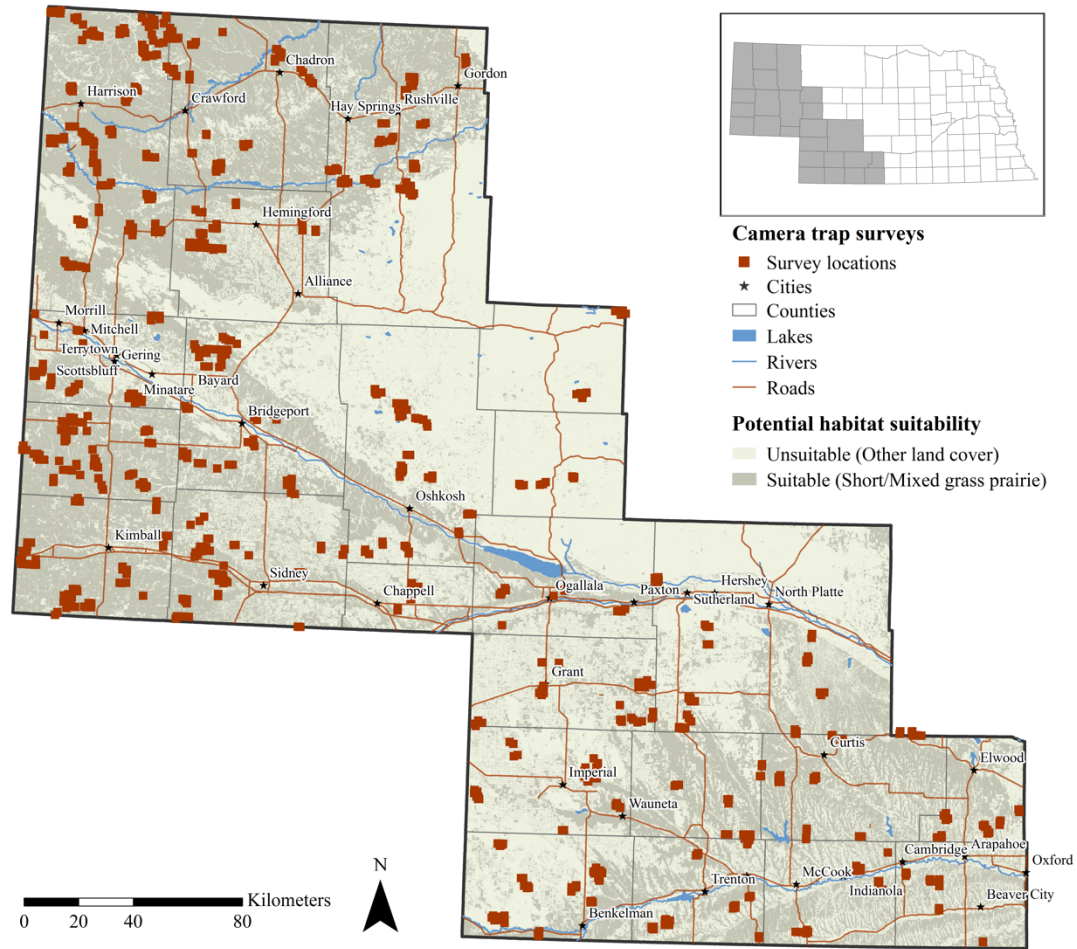
Figure 2. 1 Map of survey locations distributed within the historical range of swift fox (*Vulpes velox*) in Nebraska. Camera trap surveys were conducted in 902 locations (red squares) throughout western Nebraska. Survey data was used to fit statistical models to predict occurrence of canids species.
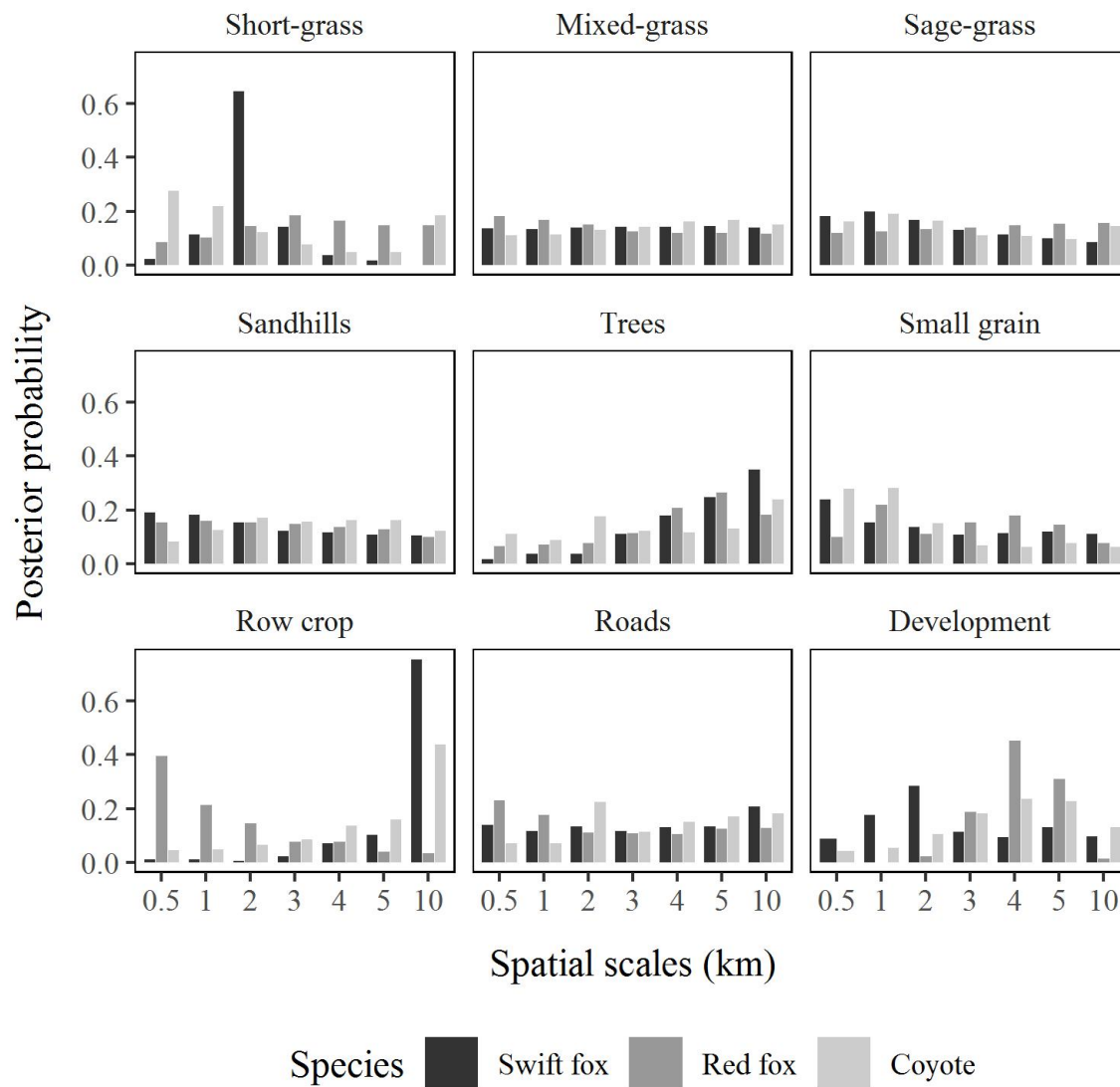
Figure 2. 2 Posterior distributions of the spatial scales (km) of the land cover occupancy predictors for three canid species in Nebraska as estimated by BLISS
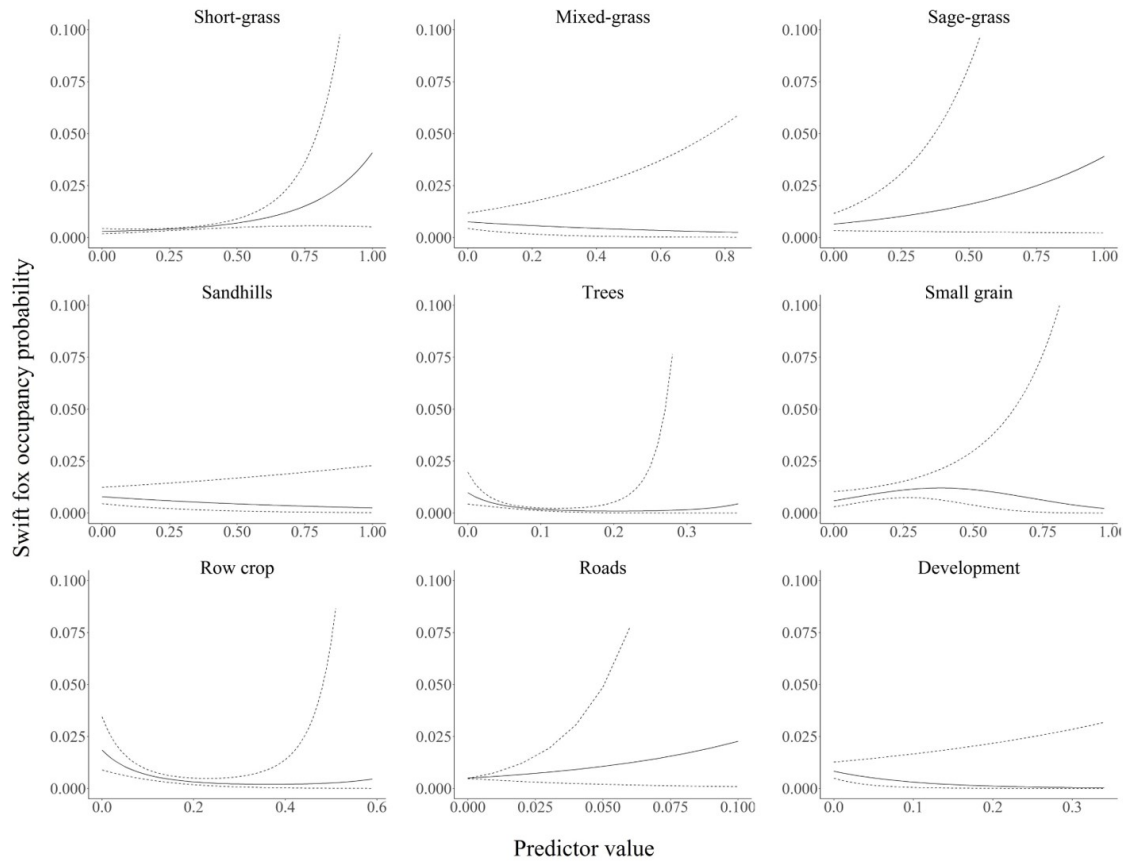
Figure 2. 3 Relationship between land cover predictors and swift fox occupancy probability. Solid lines represent mean marginal effects and the dashed lines represent the 95% credible intervals. The range of the x-axis represents values of the predictor variables measured as proportions sampled in Nebraska.
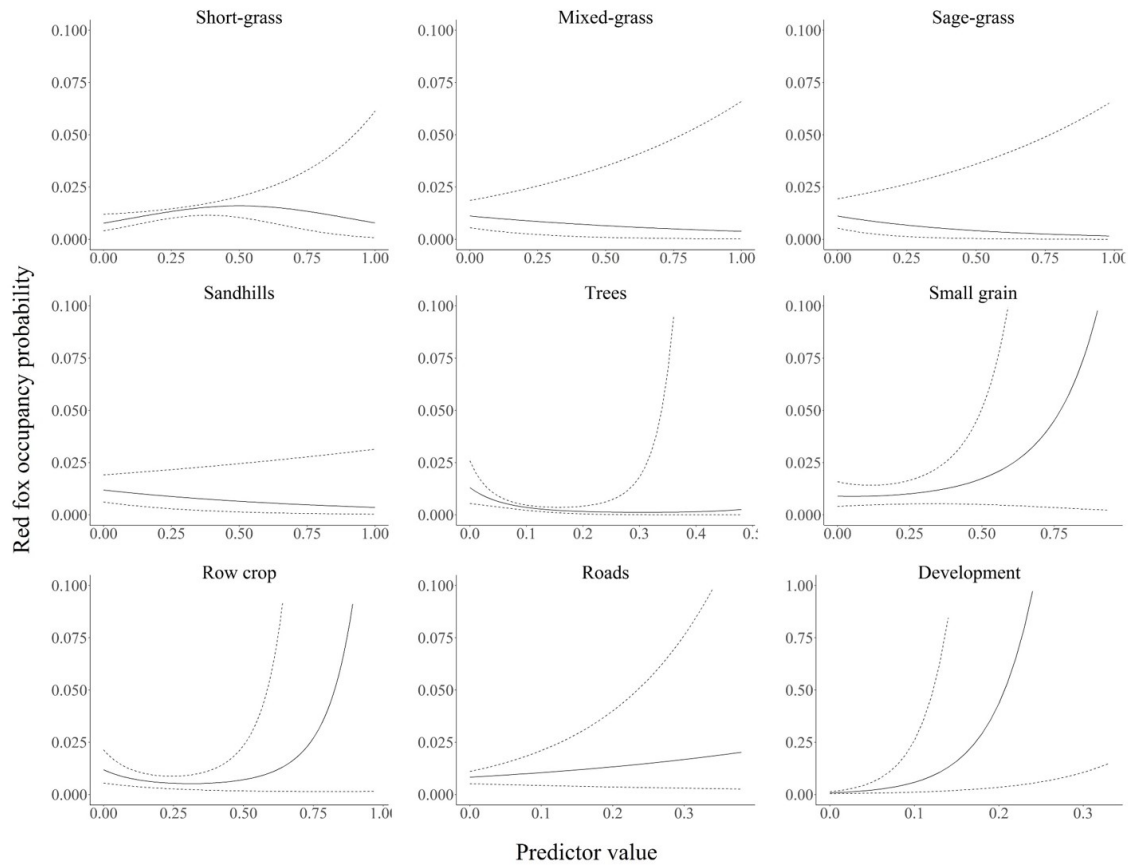
Figure 2. 4 Relationship between land cover predictors and red fox occupancy probability. Solid lines represent mean marginal effects and the dashed lines represent the 95% credible intervals. The range of the x-axis represents values of the predictor variables measured as proportions sampled in Nebraska.
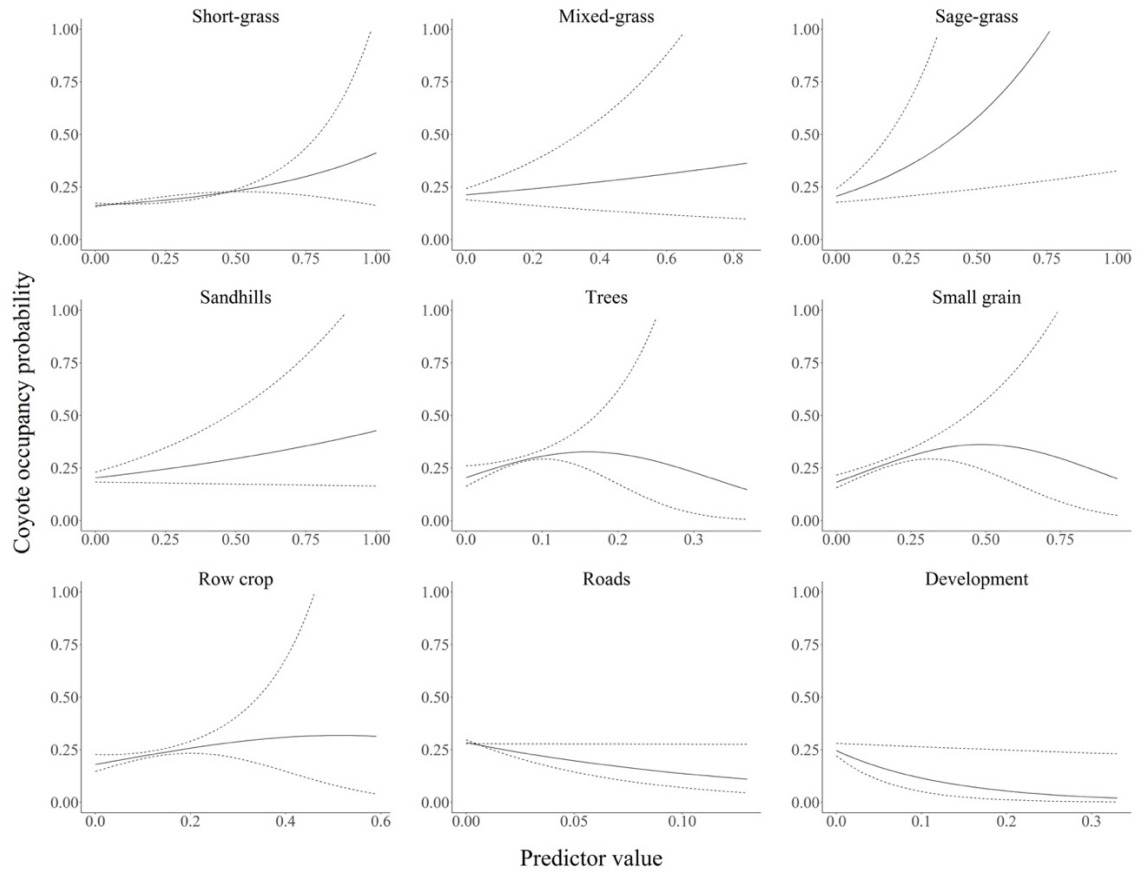
Figure 2. 5 Relationship between land cover predictors and coyote occupancy probability. Solid lines represent mean marginal effects and the dashed lines represent the 95% credible intervals. The range of the x-axis represents values of the predictor variables measured as proportions sampled in Nebraska.
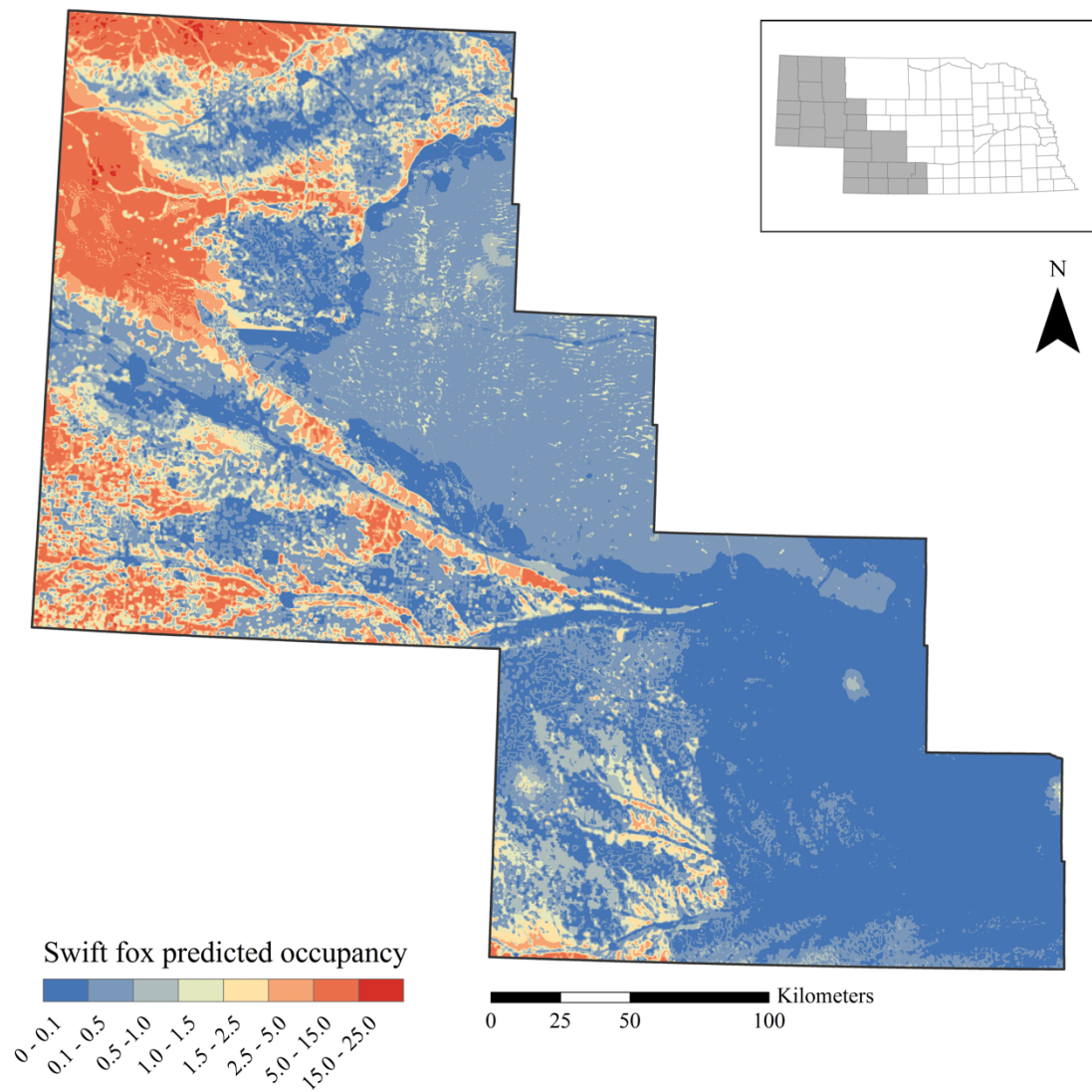
Figure 2. 6 Predicted swift fox (*Vulpes velox*) species distribution model for western Nebraska based on land cover variables. The range of predicted values was divided into eight categories based on geometrical intervals classification for non-normally distributed data. Classifying the relative predicted occupancy values using this approach allows the visualization of heavily skewed data by a preponderance of repeated values, e.g., 39% of the features have a value of 0.1.
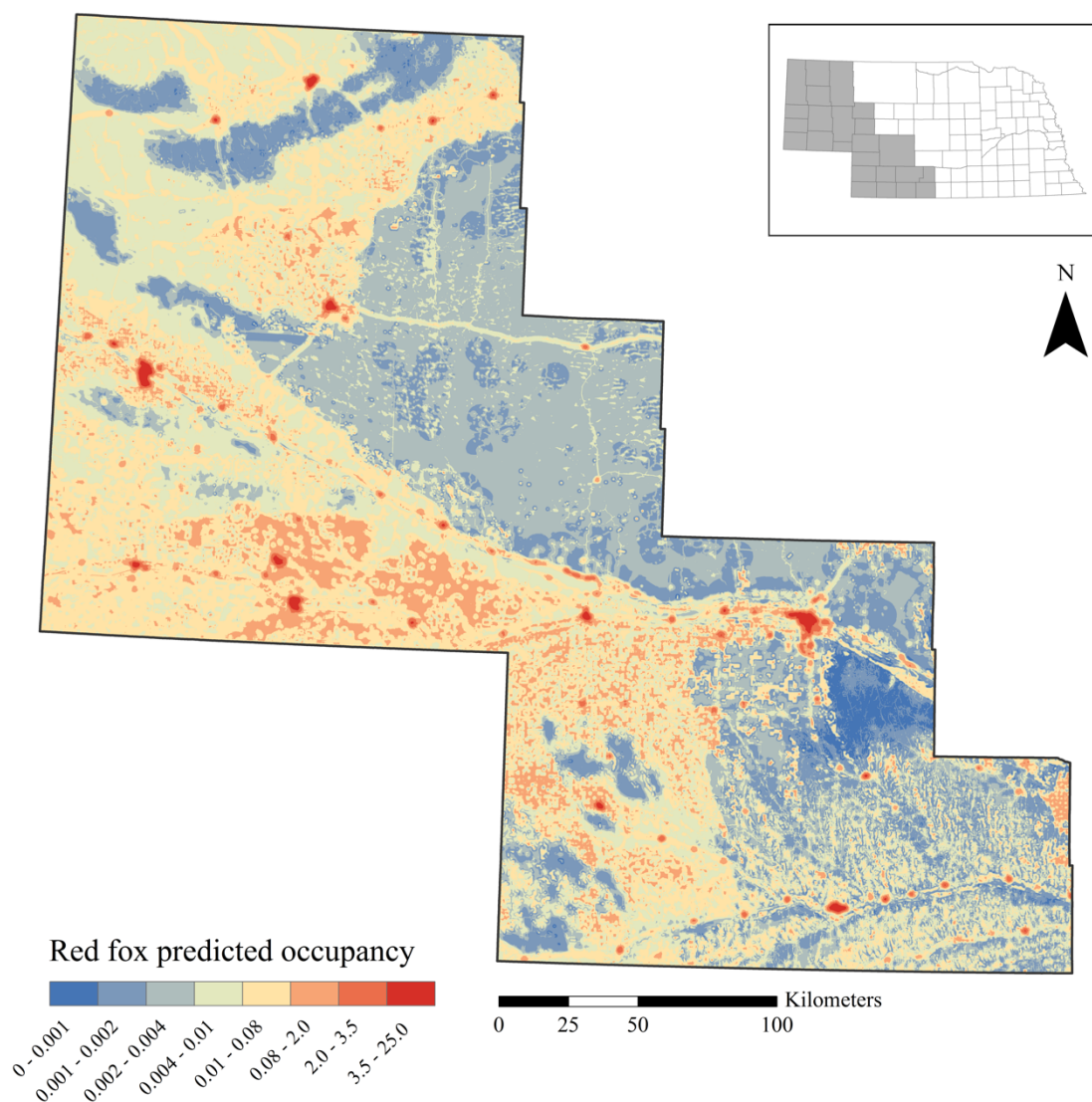
Figure 2. 7 Predicted red fox (*Vulpes vulpes*) species distribution model for western Nebraska based on land cover variables. The range of predicted values was divided into eight categories based on geometrical intervals classification for non-normally distributed data. Classifying the relative predicted occupancy values using this approach allows the visualization of heavily skewed data by a preponderance of repeated values, e.g., 22% of the features have a value of 0.002. The areas within Nebraska that contain the highest predicted occupancy probability are shown in bright red.
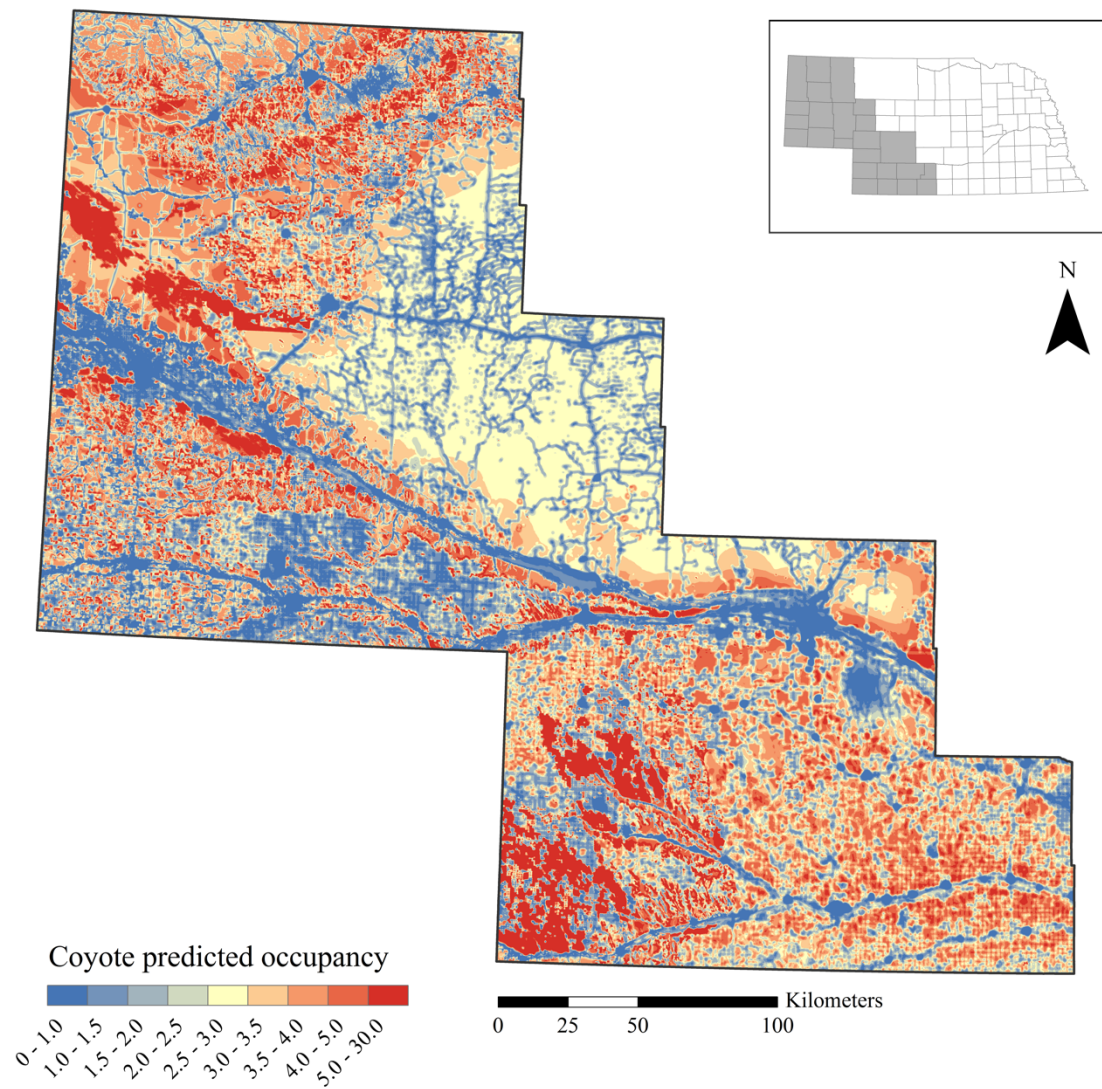
Figure 2. 8 Predicted coyote (*Canis latrans*) species distribution model for western Nebraska based on land cover variables. The range of predicted values was divided into nine categories based on geometrical intervals classification for non-normally distributed data. Classifying the relative predicted occupancy values using this approach allows the visualization of heavily skewed data by a preponderance of repeated values, e.g., 25% of the features have a value of 2.6. The areas within Nebraska that contain the highest predicted occupancy probability are shown in bright red.
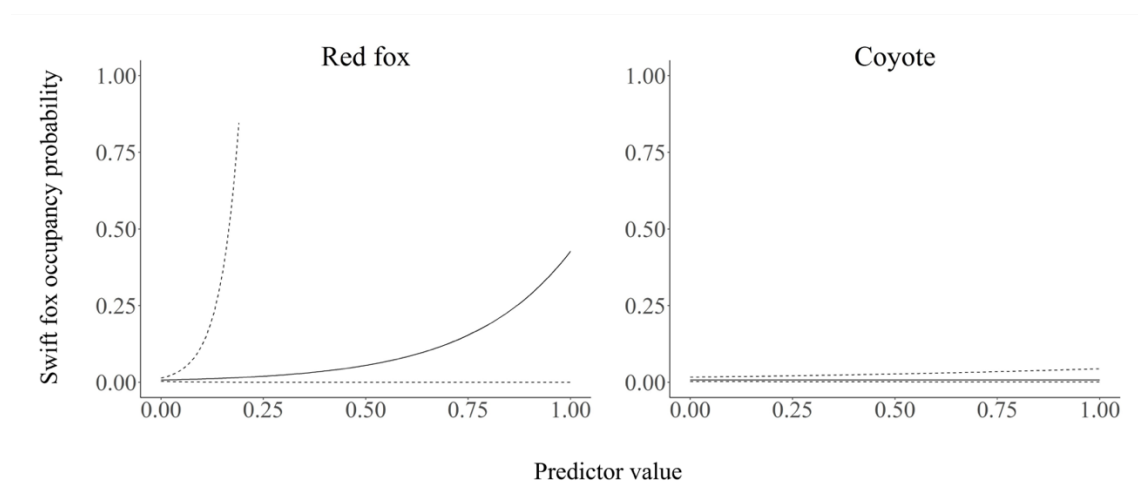
Figure 2. 9 Relationship between red fox and coyote occupancy and swift fox occupancy probability. Solid lines represent mean marginal effects and the dashed lines represent the 95% credible intervals.

APPENDIX

Table A.1. The range, mean, standard deviation and median values of the proportion of land cover types within seven spatial scales

Variable	Scale	Min	Mean	Stand. Dev	Median	Max
Shortgrass prairie	500 m	0.000	0.382	0.374	0.346	1.000
	1 km	0.000	0.392	0.377	0.346	1.000
	2 km	0.000	0.393	0.376	0.336	1.000
	3 km	0.000	0.393	0.370	0.331	1.000
	4 km	0.000	0.393	0.364	0.347	1.000
	5 km	0.000	0.393	0.359	0.356	1.000
	10 km	0.000	0.387	0.339	0.402	0.999
Mixed-grass prairie	500 m	0.000	0.070	0.191	0.000	1.000
	1 km	0.000	0.068	0.181	0.000	0.978
	2 km	0.000	0.064	0.169	0.000	0.873
	3 km	0.000	0.065	0.166	0.000	0.854
	4 km	0.000	0.064	0.164	0.000	0.842
	5 km	0.000	0.065	0.164	0.000	0.846
	10 km	0.000	0.066	0.163	0.000	0.799

Table A.1. The range, mean, standard deviation and median values of the proportion of land cover types within seven spatial scales

Variable	Scale	Min	Mean	Stand. Dev	Median	Max
Sandsage prairie	500 m	0.000	0.035	0.167	0.000	1.000
	1 km	0.000	0.036	0.166	0.000	1.000
	2 km	0.000	0.037	0.164	0.000	1.000
	3 km	0.000	0.037	0.161	0.000	1.000
	4 km	0.000	0.037	0.158	0.000	1.000
	5 km	0.000	0.037	0.155	0.000	0.999
	10 km	0.000	0.038	0.145	0.000	0.985
Sandhill prairie	500 m	0.000	0.101	0.272	0.000	1.000
	1 km	0.000	0.102	0.274	0.000	1.000
	2 km	0.000	0.100	0.267	0.000	1.000
	3 km	0.000	0.102	0.268	0.000	1.000
	4 km	0.000	0.103	0.269	0.000	1.000
	5 km	0.000	0.105	0.270	0.000	0.996
	10 km	0.000	0.108	0.274	0.000	0.987
Badlands	500 m	0.000	0.003	0.031	0.000	0.556
	1 km	0.000	0.003	0.032	0.000	0.526
	2 km	0.000	0.004	0.034	0.000	0.665
	3 km	0.000	0.004	0.034	0.000	0.584
	4 km	0.000	0.004	0.033	0.000	0.495
	5 km	0.000	0.004	0.032	0.000	0.409
	10 km	0.000	0.004	0.024	0.000	0.248
Woodlands	500 m	0.000	0.010	0.048	0.000	0.572
	1 km	0.000	0.014	0.055	0.000	0.546
	2 km	0.000	0.016	0.055	0.002	0.554
	3 km	0.000	0.019	0.055	0.003	0.494
	4 km	0.000	0.020	0.055	0.003	0.476
	5 km	0.000	0.021	0.055	0.004	0.480
	10 km	0.000	0.022	0.046	0.007	0.375
Small grains	500 m	0.000	0.124	0.215	0.000	0.976
	1 km	0.000	0.133	0.206	0.007	0.949
	2 km	0.000	0.135	0.184	0.056	0.950
	3 km	0.000	0.135	0.172	0.071	0.921
	4 km	0.000	0.135	0.165	0.079	0.895
	5 km	0.000	0.135	0.161	0.090	0.861
	10 km	0.000	0.135	0.144	0.100	0.722

Table A.1. The range, mean, standard deviation and median values of the proportion of land cover types within seven spatial scales

Variable	Scale	Min	Mean	Stand. Dev	Median	Max
	500 m	0.000	0.096	0.186	0.000	0.970
Row crops	1 km	0.000	0.108	0.180	0.001	0.922
	2 km	0.000	0.116	0.162	0.041	0.863
	3 km	0.000	0.121	0.150	0.059	0.851
	4 km	0.000	0.123	0.140	0.073	0.807
	5 km	0.000	0.124	0.135	0.080	0.731
	10 km	0.000	0.127	0.127	0.092	0.596
Roads	500 m	0.000	0.093	0.077	0.111	0.383
	1 km	0.000	0.056	0.043	0.065	0.289
	2 km	0.000	0.034	0.023	0.034	0.138
	3 km	0.000	0.029	0.018	0.028	0.128
	4 km	0.000	0.025	0.016	0.025	0.107
	5 km	0.000	0.024	0.014	0.022	0.098
	10 km	0.000	0.022	0.012	0.020	0.101
Development	500 m	0.000	0.042	0.069	0.000	0.432
	1 km	0.000	0.027	0.043	0.009	0.388
	2 km	0.000	0.018	0.029	0.010	0.349
	3 km	0.000	0.015	0.024	0.010	0.341
	4 km	0.000	0.014	0.022	0.010	0.334
	5 km	0.000	0.013	0.021	0.010	0.343
	10 km	0.000	0.013	0.016	0.010	0.315

CHAPTER III

ACTIVITY PATTERNS AND TEMPORAL OVERLAP AMONG CANID SPECIES IN NEBRASKA

Abstract

Habitat and diet preferences are often considered major aspects of niche differentiation among species; however, partitioning of habitat and resource use temporally is often ignored in modeling coexistence. The plasticity of temporal activity patterns of individuals may influence the species' response to selective forces and long-term persistence. Temporal avoidance may be a mechanism by which subordinate species can reduce the likelihood of direct competition with sympatric dominant species. Here, we examine temporal activity patterns of three canid species (swift fox *Vulpes velox*, red fox *Vulpes vulpes*, and coyote *Canis latrans*) to determine how temporal activity patterns and activity overlap varies among species. We found that all species presented seasonal differences in activity patterns. When activity patterns were compared among species, the estimates of activity overlap in the spring season (i.e., breeding and pup-rearing periods) were higher than the activity patterns in the fall (i.e., juvenile dispersal and pair-formation periods); however, activity pattern overlap among species were significant only during the fall. Overall, these patterns revealed a close temporal overlap between swift fox (subordinate species) and both red fox and coyote (dominant species), which provides new insight into conditions under which time partitioning may not be as clear as predicted, and some other mechanisms are in place to allow coexistence for the subordinate species. Considering swift fox population decline and distribution contraction across the North American grasslands, investigating temporal activity patterns of the

canid species may reveal the implications of altering such patterns for individual animals, populations, and ecosystems.

INTRODUCTION

Understanding the mechanisms driving the patterns in the distribution, diversity, and abundance of species in ecological communities is crucial for the wildlife conservation (Menge and Olson 1990, Farris et al. 2015). Community structure is shaped by multiple spatiotemporal interactions within and among species. Classical ecological niche theory (e.g., Hutchinson 1957, 1959; MacArthur 1958, MacArthur and Levins 1967) proposes that the coexistence of species that fill similar ecological roles is facilitated by differences in resource-use involving the segregation of habitat, food, or time (Schoener 1974, Kronfeld-Schor and Dayan 2003). Habitat and food are most often considered the major resources for niche differentiation (Schoener 1974); however, partitioning the temporal niche dimension as a mechanism enabling coexistence is equally important (Pianka 1973, Richards 2002, Kronfeld-Schor and Dayan 2003, Farris et al. 2015). Temporal activity patterns of individuals, which are affected by ecological and physiological costs and constraints, may influence the plasticity of a species' response to selective forces and therefore the potential persistence of a species through time (Halle and Stenseth 2000, Kronfeld-Schor and Dayan 2003). Investigating temporal activity patterns can aid in understanding behavioral and ecological components of the life history of a species; for example, by giving insight into the complex balance of risk-avoidance and energetic needs (Rowcliffe et al. 2014).

In some guild communities, such as among canids, there is evidence that top predators kill and harass smaller predators (Macdonald and Sillero-Zubiri 2004), and such interaction (i.e., interference competition) affect the distribution and population dynamics of the smaller species (Swanson et al. 2016). Temporal avoidance may be a mechanism by which subordinate species can reduce the likelihood of direct interference competition with sympatric dominant species and promote coexistence. In the Canidae family, where interference competition appears critical, larger species such as coyotes (*Canis latrans*), can often affect smaller species, such as swift fox (*Vulpes velox*) and kit fox (*V. macrotis*), by killing or displacing foxes (Cypher and Spencer 1998, Ralls and White 1995).

Foxes and coyotes in Nebraska are believed to have considerable overlap in habitat use, home range requirements, food habits, and reproductive timing (Kamler et al. 2003, Kamler et al. 2007). As the largest canid in Nebraska, coyotes are dominant to swift fox and are often cited as an important source of mortality (Covell 1992, Sovada et al. 1998, Schauster et al. 2002, Karki et al. 2007). Similarly, red fox, (*Vulpes vulpes*) is considered to be a barrier preventing swift fox populations from expanding into unoccupied, but suitable areas (Sovada et al. 1998). Swift fox are listed as a sensitive species by the U.S. Department of Agriculture (USDA) and the U.S. Forest Service (USFS), and in Nebraska it has been a state endangered species since 1972 (Andelt 1995). Coyote and red fox, on the contrary, have increased both in abundance and range throughout the state (Hill et al. 1987, Gompper 2002, Lovell et al. 1998, Prange and Gehrt 2007). Declines in distribution or abundance of a specialist species due to changes in the habitat in which they specialize (e.g., grassland obligates; Samson and Knopf

1994) may increase the importance of time partitioning, particularly if the ecosystem changes favor increases in dominant habitat generalists (Benedict et al. 1996).

Here, we examine the temporal activity patterns of three canid species (swift fox, red fox, and coyote) to determine how activity varies among species and to quantify activity levels overlaps. We focused on three main questions: (1) Is there a temporal segregation among a group of potential competitors? (2) Is the degree of segregation predictable such that smaller species are more likely to differentiate from larger species and the degree of body size differentiation predicts the degree of segregation?, and (3) Is temporal segregation consistent through time or is it determined by trade-offs driven by predictable shifts in life history?

We hypothesize first, that activity levels (i.e., detections occurring within a 24-hour period) of the canid species will be similar due to the relatively high dietary overlap (Kitchen et al. 1999, Kamler et al. 2007) and their feeding (i.e., generalist and opportunistic) and foraging behavior (i.e., primarily nocturnal and crepuscular activity; Kitchen et al. 1999, Moehrenschlager 2000, Sovada et al. 2001, Moehrenschlager and Sovada 2004). Second, we hypothesize that body size differences can predict the degree of temporal separation and that activity levels are influenced by competitive interaction and avoidance; and third, that activity levels change seasonally, given that breeding season occurs during the spring and juvenile dispersal occurs in the fall (Olson et al. 2003, Finley et al. 2005, Martin et al. 2007). Therefore, we predict the difference in size to drive increasing temporal separation such that smaller canid species would be negatively influenced by the activity of a larger dominant species , and the activity of all species would increase in the fall when populations are larger, and their life history predicts greater movement. Specifically, we examined diel activity patterns of individual

canid species, the overlap among species, seasonal difference on activity overlap, and, lastly, explored the potential of fine-scale temporal activity of foxes depending on coyote density.

METHODS

Study Area and Study Species

Our study area encompassed approximately 68,605 km^2 of western Nebraska, US (Figure 3.1), an area dominated by dry shortgrass and mixedgrass prairie (Schneider et al. 2011). The study area was primarily native rangeland with some areas converted to cropland, mainly irrigated and dryland corn, wheat, and sugar beets (Bishop et al. 2011, Schneider et al. 2011). Additional patches of other native habitat, such as woodlands and wetlands, are scattered throughout the study area. The region presents a relatively diverse topography, which includes several areas of rocky escarpments and a great variety of soil types, which range from sands to heavy clay. The climate is semi-arid, characterized by low humidity, moderate to high winds, and a large daily and seasonal range in temperature (Chapman et al. 2001, Schneider et al. 2011). Annual precipitation ranges from 300–430 mm. Mean annual wind speed at 100 m ranges from 21.5–34.3 km/h, and mean temperature ranges from -6º C in January to 32º C in July (Schneider et al. 2011).

The swift fox is endemic, restricted to the short-grass and mixed-grass prairies, and is the smallest Nebraska canid species (average weight of 2.4 kg; Moehrenschlager and Sovada 2004). The red fox is found in diverse habitats such as shrubland, bushland, forested areas, grasslands, mixed agricultural habitats, as well as on the margins of some

urban areas, and is an intermediate size (average weight of red fox 5.8 kg; Macdonald and Reynolds 2004). Lastly, coyotes are the largest (average weight of 10.8 kg) and most wide-spread canid, living in almost all available habitats throughout the state (Gese and Bekoff 2004, Sillero-Zubiri et al. 2004). Differences in canid body masses has a tight relationship with prey body masses—e.g., larger species specialize in larger prey—and consequently the use of space differs between species (Rosenzweig 1966, Carbone and Gitlleman 2002, Radloff and Du Toit. 2004). Nonetheless, in the grasslands the three canid species, use similar habitat, have overlapping prey use (swift fox and coyote: Kitchen et al. 1999, Kamler et al. 2007, red fox and coyote: Fuller and Harrison 2006, Mueller et al. 2018), and are thought to be primarily active at night (Sillero-Zubiri et al. 2004). Coyotes exhibit interference and exploitation competition with both fox species, especially swift fox, through intraguild predation (Kamler et al. 2003, Nelson et al. 2007, Sillero-Zubiri et al. 2004). Therefore, variation in the use of food resources and space may not be sufficient to describe and explain the canid community structure, where activity patterns may play an important role in determining interspecific relationships (Jacomo et al. 2004).

Data Collection

We investigated activity patterns and temporal overlap among canid species through camera-trap records obtained during surveys conducted from March to May (spring season) and from September to November (fall season) of 2014 and 2015, and in the fall of 2016. To optimize detections of a diversity of canid species, we selected survey sites across different land covers representing potential differences among species in habitat requirements. We then divided the study area in a grid of 31 km^2, the estimated home range size of the smallest species we were considering (Findley et al. 1999, 2005),

and thus the finest spatial resolution for which we might expect differences among species to manifest. At each survey site, we placed multiple camera-trap stations, consisting of baited trail cameras (Bushnell Trophy Cam HD and Moultrie M-880 models) along existing trails (e.g., cow trails, unpaved roads) or fence lines, each spaced a minimum of 1.6 km apart. Each camera was hung on a post 40 cm above the ground and the location recorded using a hand-held GPS (Garmin eTrex 10). We set a wooden stake 3 m in front of each camera (Hegglin et al. 2004) with 40 cm exposed above the ground, which served as a base for the lure, a focal point for the camera, and a metric for estimating animal body size. The lure consisted of approximately 15 ml of a skunk-based attractant produced with petroleum jelly and skunk essence (F&T Fur Harvester's Trading Post, Alpena, MI). We selected locations for camera-traps to take advantage of the presence of fences, posts, gates, and intersections because canids tend to travel along such landscape features. The interval between cameras also optimized scent attraction based on volatilization rates of fatty acid to maximize the probability to detect swift fox (Roughton and Sweeny 1982, Kahn et al. 1997, Harrison et al. 2002).

Cameras were set up to take bursts of 3 photographs no less than 5 seconds apart each time motion and/or heat signature was detected (Bushnell: optical field of view = 45°, approximate detection range = 12 m, response time = 0.6 sec; Moultrie: optical field of view = 50°, approximate detection range = 12 m, response time = 0.8 sec). We left cameras-traps running for a minimum of 10 consecutive nights to minimize the trade-off between detection probability (i.e., reducing false negatives) and sampling time (Corral unpublished data).

Data Analysis

We recorded minute-by-minute detections histories for three canid species. Under the assumption that activity patterns were similar across the years of our surveys and due to small sample size for rare species, we pooled all records across years (2014, 2015 and 2016). We treated detections as separated data points, thus included in the analysis multiple captures of the same individual in subsequent images (Carver et al. 2001). We assumed that the probability of individuals detection during a single minute approximates activity at the population level and reflects individual level trade-offs, including competition and predation risk.

Because daylight length varies seasonally and our target species are described as predominantly nocturnal, we adjusted each record's "clock time" to the specific sunrise and sunset of that date at that location and then converted to a day of 12-h length with sunrise at 0600 h and sunset at 1800 h, which allowed us to standardize temporal and geographical variation in daylight (Carver et al. 2011, Nouvelle et al. 2012). Sunrise and sunset were estimated based on date, location, and the algorithms provided by the National Oceanic and Atmospheric Administration (NOAA) using the 'sun-methods' function in R-package 'maptools' (Bivand and Lewin-Koh 2013, 2018).

We determined the temporal activity patterns of our target species and estimated the overlap of activity patterns between the species using a two-step procedure. First, density curves were fitted to the data using a non-parametric von Mises kernel density function corresponding to a circular distribution (Ridout and Linkie 2009, Rowcliffe 2016, Meredith and Ridout 2018). Second, kernel density curves for the target species were compared to each other based on a sample of each species and the estimated area

lying under both of the density curves (i.e., coefficient of overlapping; Weitzman 1970). The coefficient of overlapping (Δ) is defined as the area under the curves formed by the minimum of the two density functions at each point in time. The value of Δ lies between 0-1, with $\Delta = 0$ if there is no overlap between densities and $\Delta = 1$ if there is complete overlap (Ridout and Linkie 2009, Linkie and Ridout 2011, Meredith and Ridout 2018). We used $\Delta 1$ for samples < 50 records and $\Delta 4$ for samples > 75 records (the estimator was chosen based on the size of the smaller of the two samples), and used smoothing parameter 0.8 and 1.0 to estimate Δ respectively (Ridout and Linkie 2009, Merdith and Ridout 2018). We calculated 95% confidence intervals of each overlap index using smoothed bootstrap with 10,000 resamples (Meredith and Ridout 2018, Azevedo et al. 2018).

Since the coefficient of overlap is merely descriptive, we used the function 'compareCkern' in the R-package 'activity' (Rowcliffe 2016) to test the probability that the two sets of circular observations come from the same distribution. CompareCkern uses a randomization test that calculates overlap index for the observed data samples, then generates a null distribution of overlap indices using data sampled randomly with replacement from the combined data, and uses the randomized distribution to estimate the probability that the observed overlap is given by chance (Ridout and Linkie 2009, Rowcliffe 2016). Additionally, to compare activity patterns, we computed a Wald test for each pair of activity levels estimates. All analyses were performed in R version 3.4.3 (R Development Core Team 2017) using the 'overlap' and 'activity' R-packages (Rowcliffe 2016, Meredith and Ridout 2018).

As our camera-trap locations were clustered within sites, we investigated the potential relationship between coefficient of overlap of our target species and the density

of the dominant canid species (i.e., coyote) at each site (e.g., if the coefficient of overlap between subordinate species and coyote was proportionally related to coyote density at the site). For this analysis, the first step consisted of calculating coyote density at each site. Second, we estimated each species activity pattern and the coefficient of overlap between species separately for each site. Third, we fitted linear regression to examine coefficient of overlap as a function of coyote density. We analyzed the data on a log scale (natural logarithm).

RESULTS

Capture Records

Across all years of camera-trap surveys, we obtained 929,633 records (sampling effort on average was 1,070 cameras at 168 sites for minimum of 10 nights trap by years) with a total of 23,136 pictures of canids—2,298 pictures of swift fox (0.10 detections/trap night), 1,306 pictures of red fox (0.06 detections/trap night), and 19,532 of coyote (0.84 detections/trap night). Out of the 902 camera-trap stations, swift fox were recorded at 63 camera-trap stations, red fox at 43, and coyote at 638. We attained 4,371 activity records (by minute) of the three canid species, including swift fox (n = 442), red fox (n = 226), and coyote (n = 3,703). The three canid species were detected primarily between midnight (2400 h) and noon (1200 h), and considerably fewer records were obtained during the spring (n = 980) than the fall (n = 3,391; Figure 3.2).

Overall Temporal Activity Patterns

In general, swift fox, red fox, and coyote concentrated their daily activity between midnight and a few hours after sunrise (Figure 3.3), but all the species presented some difference in their activity cycles. Swift fox showed higher levels of activity between midnight and sunrise, and were more active during the morning hours than red fox and coyotes. Red fox presented two distinct peaks of activity, one between midnight and sunrise (0230 h) and another right before noon (1100 h). Coyote was active mainly between midnight and noon (Figure 3.4).

The comparison of activity patterns between canid species showed a mean coefficient of activity overlap (Δ) of 0.73 (SE = 0.048). The highest activity overlap was observed between coyote and swift fox ($\Delta = 0.81$, $p < 0.001$), followed by coyote and red fox ($\Delta = 0.73$, $p < 0.001$), and the lowest activity overlap between red fox and swift fox ($\Delta = 0.65$, $p < 0.001$; Figure 3.5).

Relationship between Difference in Body Size and Degree of Segregation

When testing the relationship between the differences between body sizes and the degree of segregation (i.e., equal to 1 - coefficient of activity overlap) between the species, we found the variables are negatively linearly related with a strong association (Figure 3.6), and the correlation coefficient was statistically significant ($F_{(1,1)} = 7485$, $p = 0.007$, $R^2 = 0.99$; Table 3.1).

Seasonal Activity Patterns Overlap

Seasonal activity patterns overlap ranged from $\Delta = 0.56$ to $\Delta = 0.84$ and were statistically different for all the target species (Figure 3.7, Table 3.1). Swift fox showed

the lowest overlap in activity patterns between spring and fall ($\Delta = 0.56$, $p < 0.005$). During the spring, swift fox presented a distinct initial peak of activity approximately four hours after midnight (0350 h) and activity declined gradually afterwards until noon. During the fall, swift fox did not seem to present an initial peak of activity but a steady increase of activity after sunset, with maximum activity between 0100-0200 h, followed by relatively constant activity until a decline after noon. Minimum activity occurred between 1800-1900 h (Figure 3.7.a). Red fox showed a higher seasonal activity overlap ($\Delta = 0.62$, $p = 0.005$) than swift fox, but lower than coyote and exhibited a marked peak of activity around sunrise (0500-0700 h) during the spring, but two distinct peaks of activity during the fall, one between midnight and sunrise (0230 h) and another right before noon (1100 h; Figure 3.7.b). Coyote, with the highest seasonal overlap of activity patterns between spring and fall ($\Delta = 0.84$, $p < 0.005$), have a similar activity pattern between seasons, characterized by a high peak after midnight (spring: 0300-0330 h; fall: 0100-0200 h) and a steep decline before noon (Figure 3.7.c).

Compared with either red fox or coyote, swift fox exhibited different coefficients of overlap each season (Table 3.3). No differences were found between activity pattern overlap in the spring, but the estimates of overlap were significantly different in the fall (Table 3.3, 3.4; Figure 3.7). However, the spring overlap estimate confidence intervals are much wider due to smaller sample size. Swift fox have the highest overlap with coyote ($\Delta = 0.88$) in the spring and the lowest overlap with red fox ($\Delta = 0.60$) in the fall. Although the seasonal activity patterns are different to those of swift fox, red fox presented similar values of coefficient of overlap with coyote in both seasons (spring: $\Delta = 0.89$; fall: $\Delta = 0.70$), but only the fall overlap coefficient was statistically significant (Table 3.4).

Coyote Density and Activity Coefficient of Overlap

From a total of the 206 sites, swift fox and coyotes were found together in 35

sites, and red fox and coyote at 28 sites. Coyote density ranged from 0.12–4.06

coyotes/km2 in locations where swift fox and coyote were detected together, and 0.02–

2.12 coyotes/km2 in sites where red fox and coyote were detected. Where swift fox and

coyote were detected, the activity coefficients of overlap were 0.29–0.75, while in the red

fox and coyote sites the coefficients of overlap ranged 0.14–0.60. However, it is

important to clarify that out of all the sites where coyote were present together with swift

fox or red fox, only 16 sites in each pair (i.e., swift fox and coyote, red fox and coyote)

had the minimum number of records for both species that allowed us to calculate

estimates of overlap based on smoothed bootstrapped samples, thus the above results of

coefficient of overlap include only 16 sites.

The results of the regression, to test if coyote density predicted the activity

coefficient of overlap between foxes and coyotes (Figure 3.8), indicated that coyote

density had no significant effect on the coefficient of overlap for swift fox ($F_{(1, 14)} =$

0.130, $p > 0.05$, $R^2 = 0.009$; Table 3.5) or red fox ($F_{(1, 14)} = 0.3543$, $p > 0.05$, $R^2 = 0.025$;

Table 3.6).

DISCUSSION

Natural selection is expected to favor behavioral responses that reduce the cost of

interspecific competition. Here we examine temporal separation as a mechanism that

favor the coexistence of three canid species believed to compete in areas of sympatry

(Covell 1992, Carbyn et al. 1994, Ralls and White 1995, Sovada et al. 1998, Kitchen et al. 1999, Schauster et al. 2002, Andersen et al. 2003, Thompson and Gese 2004). We found evidence for temporal separation, with differences among species pairs that yield insights about the factors permitting co-occurrence of wild canids.

Similar to previous studies (e.g., Andelt 1985, Kitchen et al. 1999, Sovada et al. 2001), our results showed that swift fox, red fox, and coyote are primarily nocturnal and crepuscular, with activity concentrated between sunset and sunrise, but also all three species can be active throughout the day, suggesting some flexibility in their activity patterns (Monterroso et al. 2014). Our findings revealed a strong temporal overlap among the species, which we expected based upon the considerable overlap in diet among the species we considerd (White et al. 1994, 1995; Moehrenschlager 2000, Sovada et al. 2001, Moehrenschlager and Sovada 2004, Moehrenschlager et al. 2004, Kitchen et al. 1999, Kamler et al. 2007).

We found support for our hypothesis that difference in body size can predict the degree of temporal separation in canid species, as has been found in other studies of co-occurring carnivores (Macdonal and Sillero-Zubiri 2004, Sunarto et al., 2015). In our study, red fox and swift fox (mean weight difference of 3.4 kg) showed the highest degree of separation with 35% of temporal separation on their daily activity patterns, followed by coyote and red fox (mean weight difference of 5.0 kg) with 27% of temporal separation, and, lastly, coyote and swift fox (mean weight difference of 8.4 kg) that presented the lowest degree of separation with 18% of temporal separation on their daily activity patterns. Congruent with the generality, we found that the pair of species more similar in size, and thus potentially with more similar diets and space requirement, had greater degree of temporal segregation (Macdonal and Sillero-Zubiri 2004). Our finding

are in line with evidence that dominant species are more likely to harass, and potentially kill, only those subordinate species that are sufficiently smaller than itself to minimize the risk of injury (Ralls and White 1995, Peterson 1995, Sargeant et al. 1987, Tannerfeldt et al. 2003); therefore, pair of species with more similar size (e.g., red fox and swift fox) might try to segregate themselves from each other in a greater extent than less similar-size species (e.g., coyote and swift fox), because the high cost of an encounter with each other.

Animals' daily routines constitute adaptive strategies to cope with the time structure of their environment and, similar to other elements of animals' behavior, are the outcome of natural selection constantly refined by the individual experiences (Daan 1981). Consequently, it is not surprising that swift fox, red fox, and coyotes, members of the same family living in the same environment, have analogous activity patterns, limited to a precise part of the diel cycle to which they are adapted anatomically, physiologically, and behaviorally (Daan 1981, DeCoursey 2004). However, the habitat of most animals are subject to seasonal fluctuations and, hence, individuals need to develop strategies to adapt and cope with such fluctuations (Gwinner 1981). For instance, many life history traits of a species, such as reproduction and dispersal, are concentrated or restricted to certain times of the year, timed in a way that they occur when they are more likely to be successful (Gwinner 1981). Given the existence of such annual cycles, we hypothesized that the activity patterns of our target species change seasonally, and that temporal overlap is determined by trade-offs driven by predictable shifts in life history stage.

As expected, we found differences in seasonal activity patterns and overlap for each of the three canid species. Additionally, our data showed that activity patterns, when compared between species, were different during the fall, but not during the spring, and

we observed higher estimates of activity patterns overlap in the spring than in the fall. Typically, during the spring, environmental conditions start to become more favorable (e.g., increase in day length, higher temperatures and precipitation, increase in prey availability, etc.). As a results, individuals may experience less competitive pressure and conditions are propitious for breeding. Assuming that individuals respond to stimuli to maximize fitness, and considering the life history of the species, we could attribute the high overlap in activity patterns during the spring to the occurrence of the breeding and rearing periods, when adult fox energetic needs are higher as they reproduce, raise and feed young and, thus, they must increase their activity (e.g., foraging) despite being exposed to potentially higher predation risk. Ultimately, the decision of an individual to be active or not at specific time is related to physical condition, which encompasses body condition and energetic needs. Individuals' physical condition at the end of the winter and beginning of the spring may be poor compare to other seasons, imposing the necessity to increase foraging and activity levels to meet high energetic needs for breeding. The result is higher activity overlap and no difference in activity patterns among the target canid species in the spring. Our spring results were consistent with previous studies looking at spatial-temporal avoidance of coyotes in swift foxes' movement patterns, where no evidence of spatial-temporal avoidance was found at any time during the day (Kitchen et al. 1999). However, it is worth noting the lack of difference between coefficients of overlap in the spring could also reflect the low statical power associated with lower sampling rates during this period (i.e., low detection for both species of foxes).

The higher detection rates obtained for the fall are thought to be a result of higher densities and dispersal of individuals. During the fall season, pair-formation and juvenile

dispersal take place. Young forage on their own and adults are more active and range farther from their dens (Olson et al. 2003, Finley et al. 2005, Martin et al. 2007) and have larger home-ranges and core areas compare to the spring (Olson and Lindzey 2002). Additionally, this is a period of low prey abundance and availability. Foxes and coyotes have a generalist and opportunistic feeding behavior, and changes in food availability associated with seasonal changes impact composition of their diets (Kilgore 1969, Scott-Brown et al. 1987, Kitchen et al. 1999, Kamler et al. 2007). In most seasons, mammals have been documented as the dominant item in both foxes and coyote diets (Kamler 2007). Even though coyotes tend to consume larger prey than red fox and swift fox, the relatively low prey diversity and abundance in the fall make coyotes and foxes have higher dietary overlap (Kitchen et al. 1999, Lemons 2001, Kamler et al. 2007). Consequently, the high dietary overlap in the fall could be imposing strong competitive pressure to the smaller subordinate fox species, especially to swift fox that had been reported to experience high killing rates from coyotes during the fall (Kamler et al. 2003), and be a reason for the lower activity overlap and significantly different activity patterns we observed.

Although described as predominantly nocturnal and crepuscular, in the fall swift fox and red fox also showed diurnal activity. Swift fox was the most active species during daylight hours, which may be a behavioral strategy to avoid risk of predation while still fulfilling energetic needs, even though this may affect the accessibility of certain food items. Coyote, the dominant larger canid species, may select to be active according to food availability and risk unrelated to other carnivore species. Coyote may be able to forage more at night when there is a greater abundance of nocturnal rodents and no humans or domestic dogs around (i.e., humans and dogs were only photographed during

day light); whereas swift fox is active in a wider range of time during the day, potentially based upon coyote presence. Red fox may also pose a similar threat to swift foxes, because their activity pattern overlap is high, but in our study area red foxes occur in lower numbers than coyotes, potentially due to habitat related factors (i.e., red foxes select different habitats such as shrubland, bushland, woodlands, mixed agricultural habitats, and close to urban areas).

Our results were inconclusive to the hypothesis of temporal avoidance between the smaller canid species (i.e., swift fox) and the larger dominant species (i.e., coyotes). If temporal avoidance of coyotes is indeed not a distinctly important mechanism by which swift fox evade the potential interference competition, there should other life-history traits that allow swift fox to persist in areas where other dominant canid species are present. Swift foxes' fossorial behavior has been documented as one of the mechanisms that allows them to deal with interference competition with coyotes (Kitchen et al. 1999, Cypher et al. 2001). Swift fox have several dens underground within their home range and they are usually not far from the denning area (Sovada et al. 1998, Kitchen et al. 1999). Swift fox use their dens all year, while coyote and red fox use dens only during breeding season. Furthermore, based on our results, we propose that another mechanism that may allow swift fox populations to persist in sympatry with coyotes and red foxes is an expansion of their diurnal activity, instead of strictly temporal avoidance of coyotes, particularly in the fall when the potential of interference competition increases due to dispersal of young individuals and low food availability. Alternatively to displacement, limiting similarity theory predicts that, depending on the competitive abilities of the species involved, competition would be reflected in their population numbers (Abrams

1983), therefore the swift fox small population size could be an indication of the competitive interaction with other canid species.

Against to our expectations, we did not find a difference in activity pattern overlap of any of the fox species as a function of coyote density. Even in sites where the density of coyotes is relatively high, neither swift nor red foxes showed differences in their activity pattern overlap with coyotes. This result is interesting considering the general consensus in the literature that predation by coyotes is one of the leading causes of mortality in swift fox populations (e.g., Covell 1992, Sovada et al. 1998, Schauster et al. 2002). Interactions between species in relation to their activity patterns are difficult to understand given the fact that the activity pattern of a species on a diel cycle is not only regulated by competition or the risk of predation, but it is also regulated by species' endogenous timekeeping mechanisms (circadian 'clock') and their relationship to other abiotic factors, such as environmental light and darkness, weather events, or ambient temperature (Kronfeld-Schor et al. 2013). Unique individual characteristics, such as age, sex, reproductive status, and personality, may also shape the response to the environment and affect activity patterns, and so mask patterns at the population level (Hertel et al. 2017, Gaynor et al. 2018).

It is important to keep in mind that we are assuming that our camera-trap detection rates at a given time during the day was proportional to the level of activity of the populations of our target species at that same time, and that all the animals were active when the camera trap rate reaches the maximum value for diel activity (Zimmermann et al. 2016). Another assumption we undertook was that the lure we used did not introduce bias in activity of the target species. However, the above mentioned and other factors (e.g., animal size, animal speed while active, camera field of view and

response time, camera detection range during the day versus night) could potentially affect detection rates regardless the proportion of the population being active (Rowcliffe et al. 2008). Moreover, we need to be conservative when interpreting activity curves generated from small sample size data sets, such as ours, because they are limited on accuracy and precision of the estimates.

Given the importance of activity on fundamental ecological processes, and that interspecific competition can be a highly limiting force, efforts to understand species temporal patterns as a response to competitors in different landscapes is imperative. For instance, if swift fox could be indeed reducing nocturanal activities due to interference competition, as our results suggested, this can have far-reaching consequences (e.g., mismatches between the environment and the species traits; Gaynor et al. 2018) that could impose substantial fitness costs on individuals and, imperil population persistence through time. By altering typical activity patterns, species may need to adjust their diet, foraging behavior, or reproductive strategies; in conjunction with this, animals inhabiting areas with more human presence may experience stronger effects from shifting activity patterns, particularly specialist species like swift fox. It is clear that further research on this matter is needed. Which is the role of different landscape configurations in the likelihood of canids temporal activity shifts? Are some landscapes more conductive to shifts in activity patterns than others? Are the subordinate rare species more susceptible to shifts in activity patterns than dominant more common species? Overall, the hypotheses of our study just scratch the surface of this wide range of questions raised when trying to understand temporal activity patterns and canid community temporal dynamics, as well as the impacts that interference competition could have on a subordinate species and the role of time as a niche axis.

CONCLUSIONS

Our study quantified the degree of overlap in activity patterns among three canid species (swift fox, red fox, and coyote). We found that all species presented seasonal differences in activity patterns. When such activity patterns were compared between species, the estimates of activity overlap in the spring season (breeding and pup-rearing periods) were higher than the estimates in the fall (juvenile dispersal and pair-formation periods); however, the activity pattern overlaps between species were significant only during the fall. Overall, these patterns revealed a close temporal overlap between swift fox (subordinate species) and both red fox and coyote (dominant species), contrary to our expectations, which provides new insight into conditions under which time partitioning may not be as clear as predicted, and some other mechanisms are in place to allow coexistence for the subordinate species. For instance, despite coyote mortality has been cited as the primary source of mortality for swift fox, the two species appear to partition resources (e.g., habitat, diet, time) in a way that allows a certain degree of coexistence in spatial sympatry.

At minimum, the results of our study raise a warning of potential shifts in activity patterns of a specialist and subordinate species (swift fox) in the face of increasing pressure due to fragmentation and alteration of the habitat in which it specialized, which may also favor generalist and common dominant species (coyote). Considering swift fox population decline and distribution contraction across the North American grasslands, it is important to investigate more about temporal activity patterns of canid species and the implications of altering such patterns for individual animals, populations, and ecosystems.

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TABLES AND FIGURES

Table 3. 1 Estimated regression parameters, standard error, *t*-values and *p*-values for the degree of segregation between canid species as a function of the difference of body weight between species.

	Estimated value	Std. Error	*t*-value	*p*-value	
Intercept	-0.176	0.014	-12.63	0.050	.
Coyote density	-0.709	0.008	-86.52	0.007	**

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table 3. 2 Wald statistic on a chi-square distribution with one degree of freedom to test significant differences at the 5% level between overall activity patterns between spring and fall of each canid species.

	Diff.	SE	*W*	p
Swift fox	-0.284	0.068	17.295	0.000
Red fox	0.173	0.078	4.916	0.027
Coyote	-0.073	0.025	8.653	0.003

Table 3. 3 Estimate of activity pattern overlap (Δ) between swift fox, red fox, and coyote, sample size (*n*) and p-values.

	Activity overlap					
	Spring			Fall		
	n	Δ	p	*n*	Δ	p
Coyote vs. Swift fox	917/43	0.88	0.45	2786/399	0.79	< 0.005
Red fox vs. Swift fox	20/43	0.87	0.68	206/399	0.60	< 0.005
Coyote vs. Red fox	917/20	0.89	0.85	2786/206	0.70	< 0.005

Table 3. 4 Wald statistic (difference, standard error, Wald test, and p-values) on a chi-square distribution with one degree of freedom to test significant differences at the 5% level between overall activity patterns of three canid species.

	Spring				Fall			
	Diff.	SE	*W*	p	Diff.	SE	*W*	p
Coyote vs. Swift fox	-0.059	0.044	1.776	0.183	0.152	0.057	6.976	0.008
Red fox vs. Swift fox	0.004	0.085	0.002	0.961	0.462	0.060	58.469	0.000
Coyote vs. Red fox	-0.063	0.076	0.705	0.401	-0.310	0.032	93.649	0.000

Table 3. 5 Estimated regression parameters, standard error, *t*-values and *p*-values for the swift fox/coyote activity coefficient of overlap as a function of coyote density.

	Estimated value	Std. Error	*t*-value	*p*-value	
Intercept	-0.660	0.071	-9.348	< 0.001	***
Coyote density	0.023	0.063	0.361	0.724	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table 3. 6 Estimated regression parameters, standard error, *t*-values and *p*-values for the red fox/coyote activity coefficient of overlap as a function of coyote density.

	Estimated value	Std. Error	*t*-value	*p*-value	
Intercept	-1.218	0.283	-4.308	< 0.001	***
Coyote density	-0.080	0.134	-0.595	0.561	

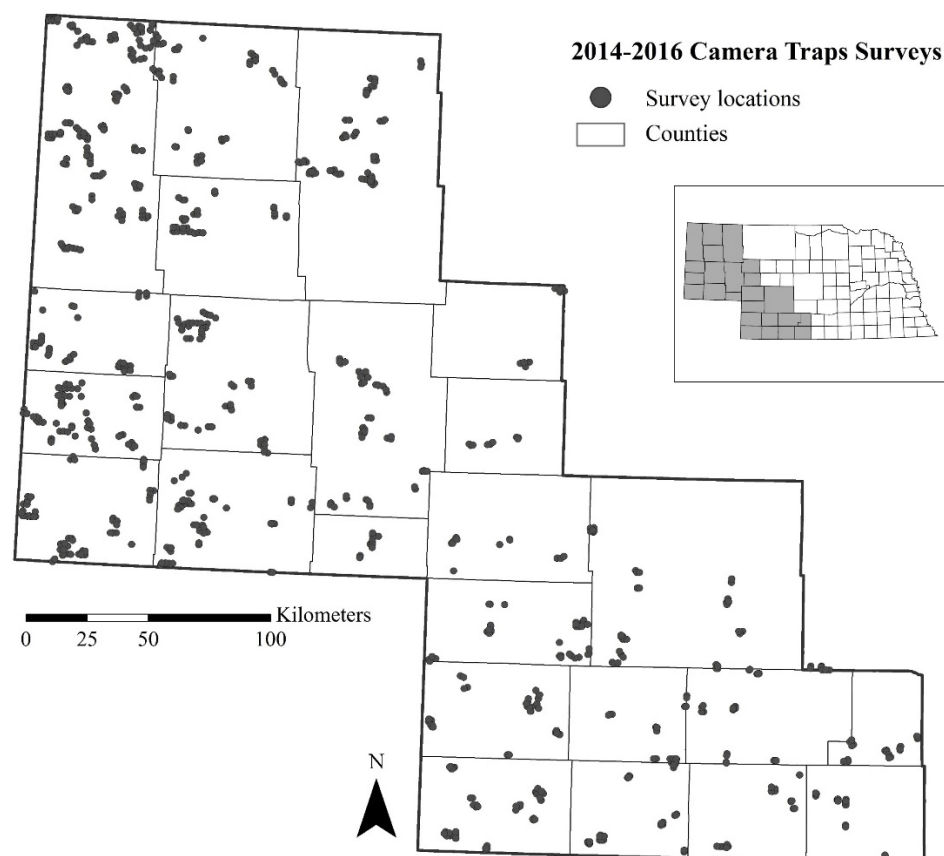Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Figure 3. 1 Map of camera traps surveys.
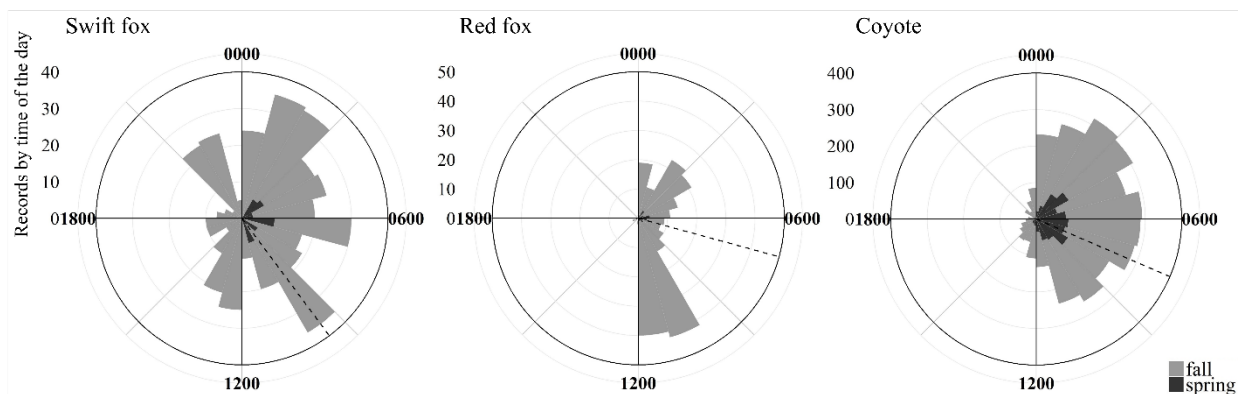
Figure 3. 2 Times of total records of three canid species from camera-traps. Time has been standardized to a day of equal length of day and night (sunrise at 0600 h and sunset at 1800 h). Light grey bars represent records for the fall season and dark grey bars for the spring season. The dashed lines represent mean value vectors.
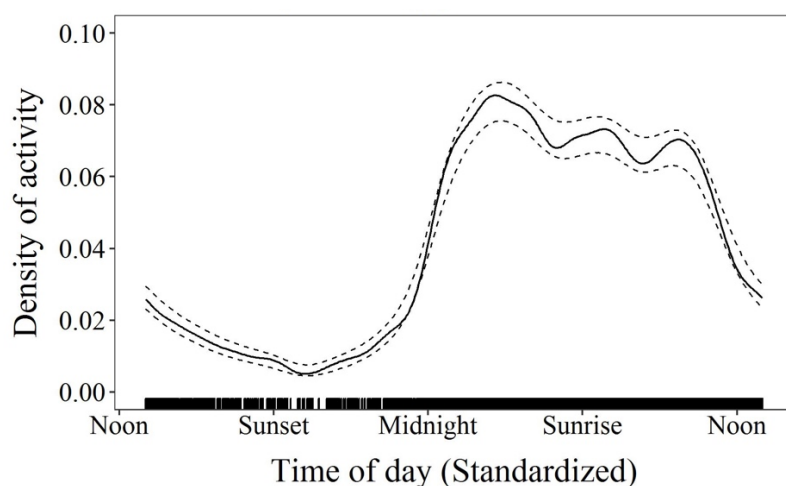
Figure 3. 3 Density estimates of daily activity for three canid species (swift fox, red fox, and coyote) combined. The solid lines are density estimates for the spring, whereas the dashes lines are estimates for the fall. The shaded areas represent 95% confidence intervals (CI).

Figure 3. 4 Density estimate for daily activity by species. The yellow line are density estimates for swift fox, red line for red fox, whereas the blue line are estimates for coyote. The dashed lines represent 95% confidence intervals (CI)

Figure 3. 5 Overlap plots of the density estimates of daily activity patterns for swift fox and coyote (a), swift fox and red fox (b), and red fox and coyote (c) in western Nebraska, US. The yellow lines are density estimates for swift fox, red lines for red fox, whereas the blue lines are estimates for coyote. The dashed lines represent 95% confidence intervals (CI) and the coefficient of overlap (Δ) equals the shaded area below both curves.

Figure 3. 6 Relationship between difference in body weight and the degree of segregation between canid species (R^2 = 0.99). The solid line represents the regression line and shaded areas represent the 95% CI.
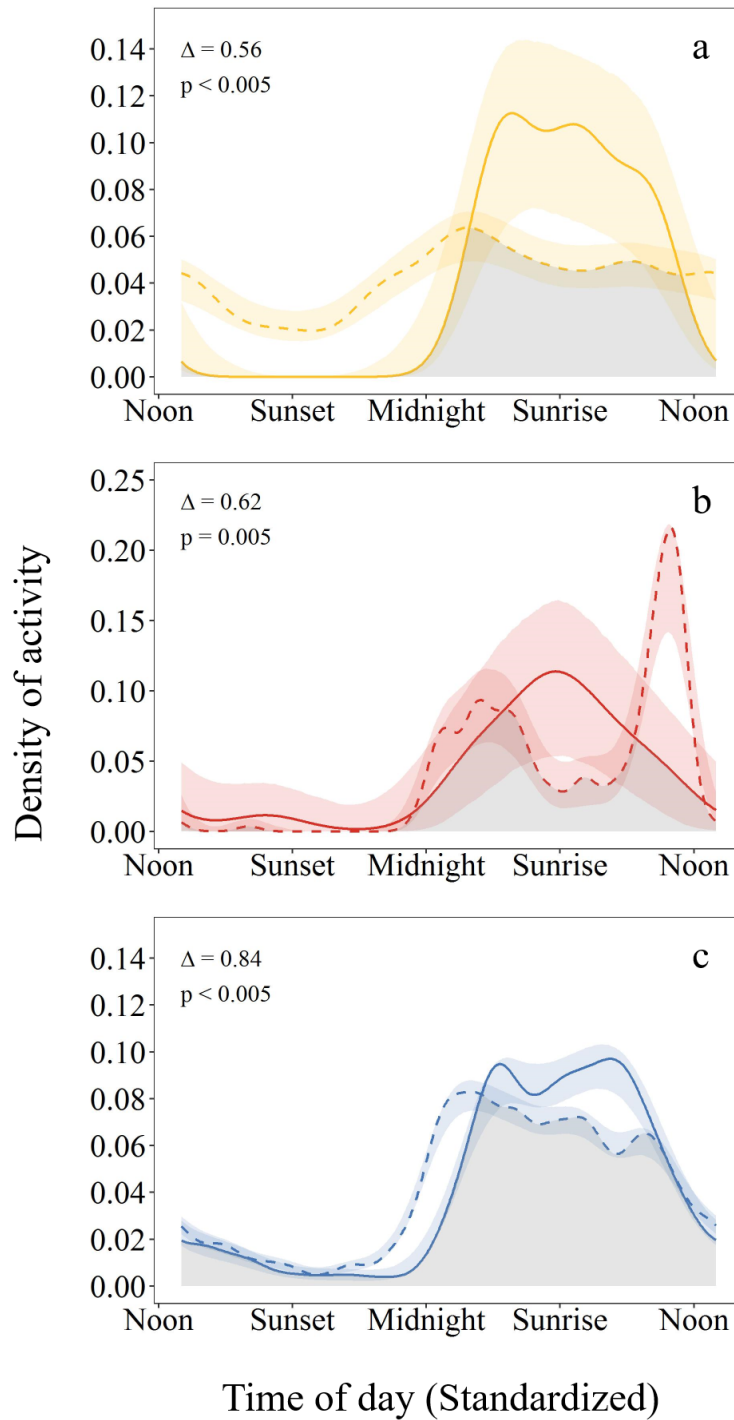
Figure 3. 7 Density estimates of daily activity patterns during two season for swift fox (a), red fox (b), and coyote (c). The solid lines are density estimates for the spring, whereas the dashes lines are estimates for the fall. The shaded areas represent 95% confidence intervals (CI).
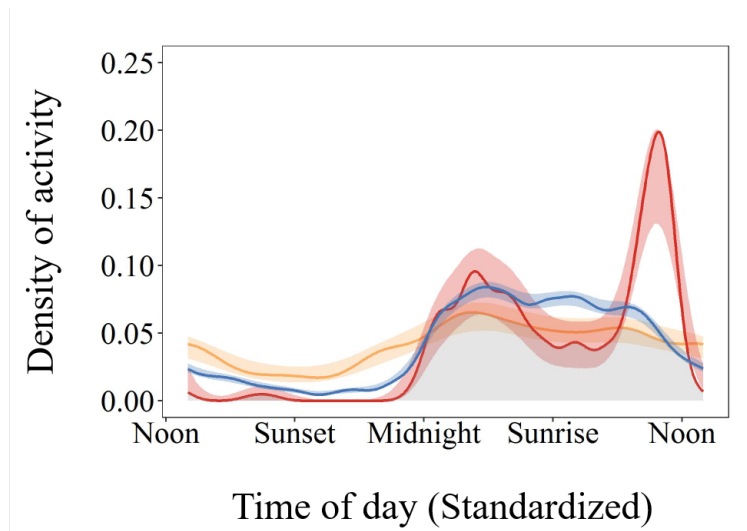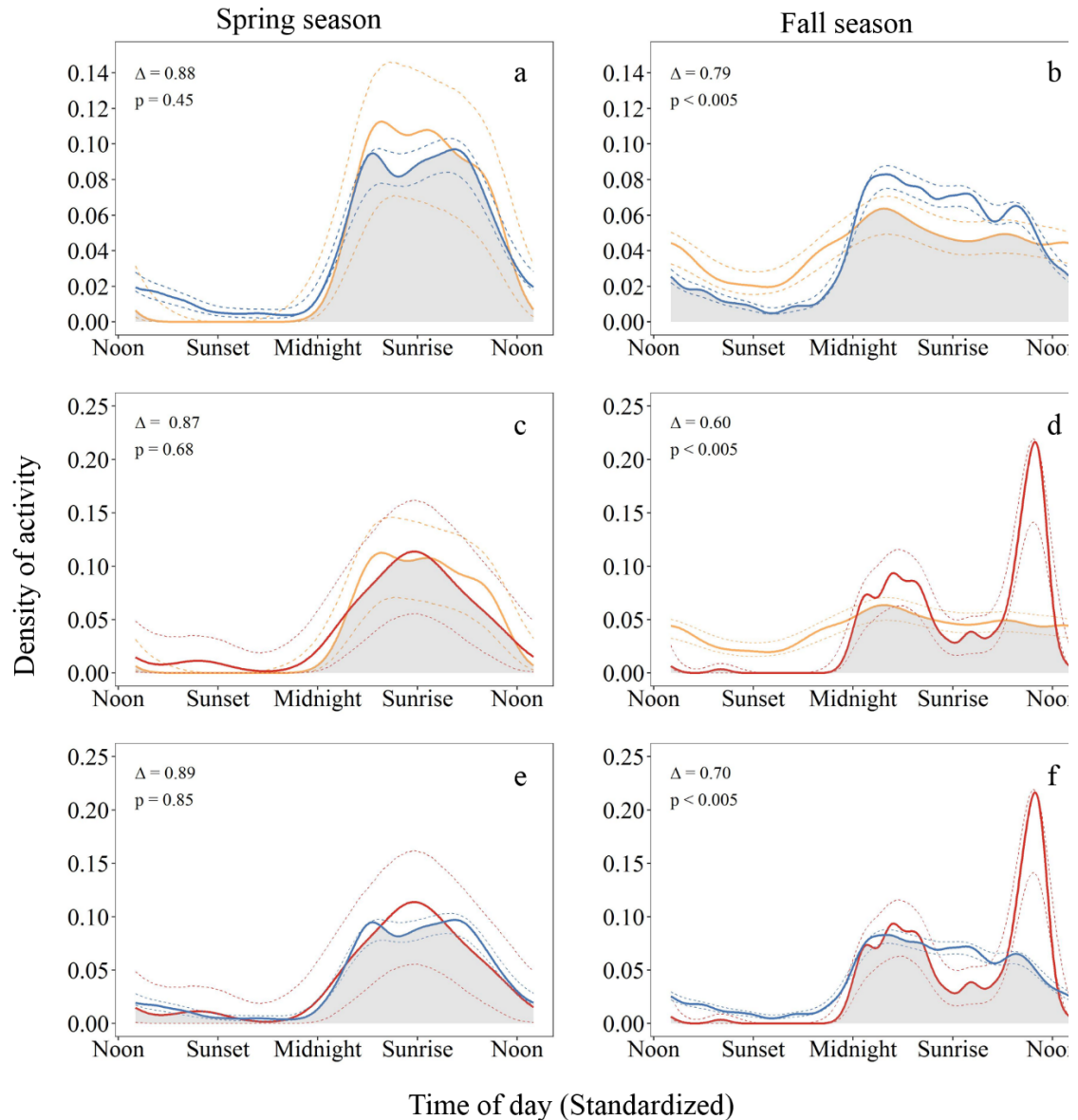
Figure 3. 8 Overlap plots of the density estimates of daily activity patterns during two season for swift fox and coyote (a, b), swift fox and red fox (c, d), and red fox and coyote (e, f) in western Nebraska, US. The yellow lines are density estimates for swift fox, red lines for red fox, whereas the blue lines are estimates for coyote. The dashed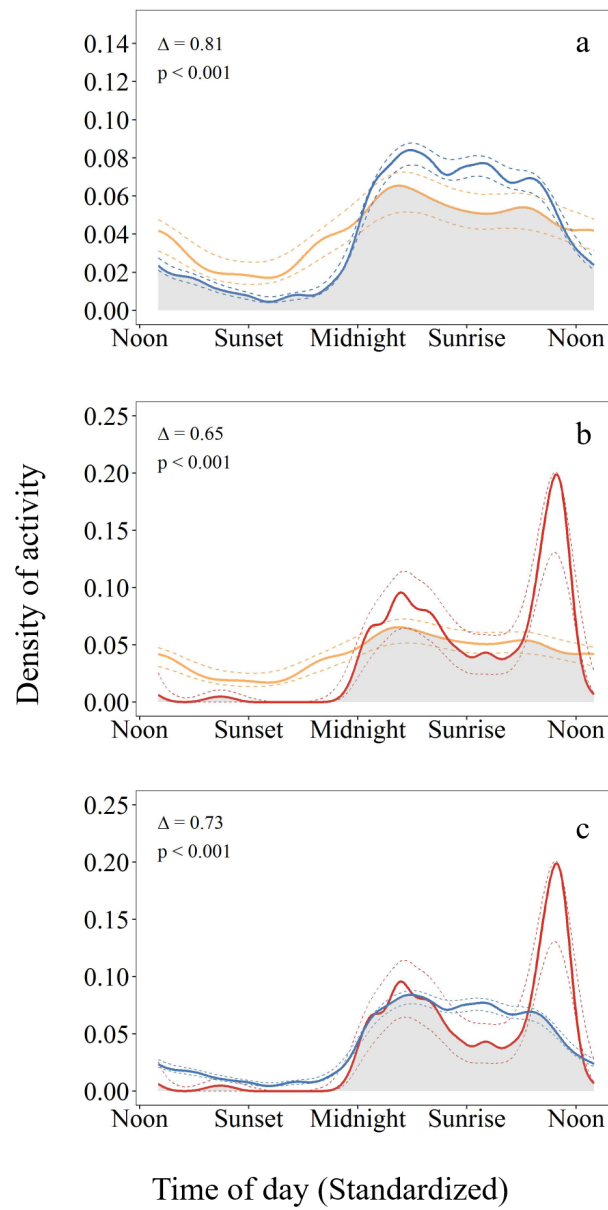 lines represent 95% confidence intervals (CI) and the coefficient of overlap (Δ) equals the shaded area below both curves.
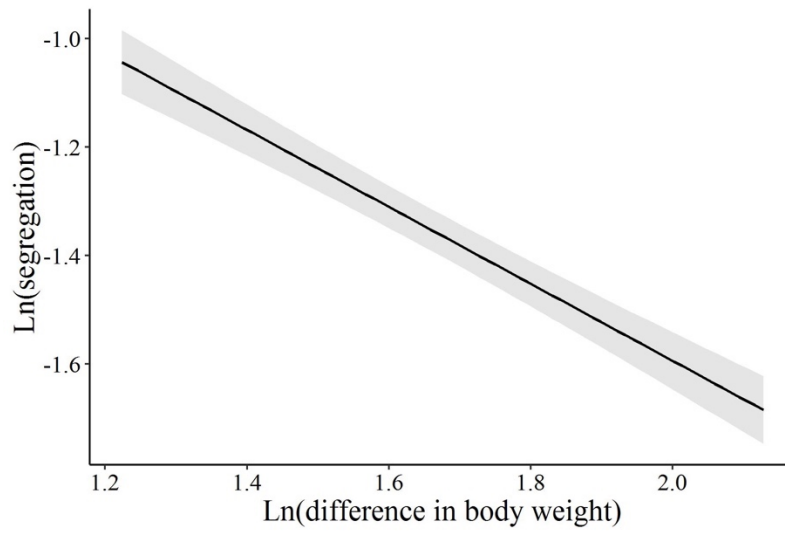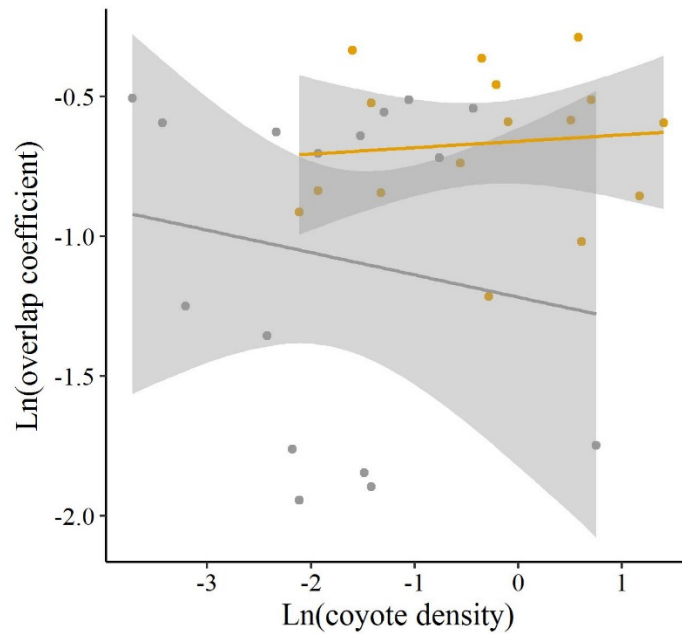
Figure 3. 9 Relationship between coyote density and the coefficient of overlap of coyote/swift fox (yellow dots and line, $R^2 = 0.009$) and coyote/red fox (grey dots and line, $R^2 = 0.024$). Solid lines represent the regression line for coefficient of overlap. Shaded areas represent the 95% CI.

CHAPTER IV

GENETIC STRUCTURE AND DIVERSITY OF SWIFT FOX POPULATION IN NEBRASKA

Abstract

Genetic diversity is a fundamental component of the intrinsic viability of a population. The loss of genetic diversity in a population is expected to reduce the population's adaptive capacity to respond to environmental changes. and could lead to increasing probability of inbreeding depression. Dispersal increases gene flow among populations and consequently promotes genetic diversity; therefore, the capacity for individuals to disperse across the landscape is a determinant of genetic structure of populations. Habitat loss and fragmentation present potential barriers to gene flow that would negatively affect genetic diversity in and among populations. We assessed the local genetic structure and diversity of swift fox (*Vulpes velox*) populations in Nebraska and explored whether or not there are genetically distinct groups that could be influenced by landscape feature and habitat constraints. We also studied genetic structure of the species in Nebraska as part of a larger geographic area that includes three neighboring states (Wyoming, Colorado, and Kansas). Our result suggest that swift fox population in Nebraska is restricted to two pockets within its available habitat, but no genetic structure, nor geographic isolation, existed between the two. They also indicated that the population is genetically healthy and stable because of the relatively high levels of heterozygosity and high genetic diversity. Our findings suggest historic genetic exchange and current gene flow among swift fox populations is occurring within Nebraska and across the larger region. However, there is the potential for future reduction of genetic diversity due

to small population sizes and landscape fragmentation that could further isolate the populations.

INTRODUCTION

Habitat loss and fragmentation is among the primary causes of biodiversity decline, with broad ranging effects on population and community dynamics as well as ecosystem function (Gibbs 2001, Frankham 2006, Keyghobadi 2007, Hughes et al. 2008, Allendorf et al. 2013). The loss and increasing isolation of native grasslands, for example, has resulted in widespread reductions in wildlife habitat availability and suitability, particularly for grassland specialists such as the swift fox (*Vulpes velox*). Endemic to the short- and mixed-grass prairies of the Great Plains in North America, swift fox were extirpated from the majority of their historic range by the 1950's (Allardyce and Sovada 2003). The remaining populations of swift fox are closely associated with remnants of native shortgrass prairie, resulting in a spatially disconnected distribution that reflects the fragmented conditions of the habitat (Schwalm et al. 2014).

Increasingly isolated, swift fox may face escalating risks to long-term population viability if continued fragmentation limits gene flow. A lack of gene flow can limit the genetic variability within a population with significant implications for the ability of the population to cope with additional anthropogenic stressors such as climate change (Dixon et al. 2009, Keller and Waller 2002, Frankham et al. 2002, Frankham 2005). Although, there is a cursory understanding of the relationship among swift fox populations structure, gene flow and landscape structure at a broad scale (i.e., the entire species' distribution range in North America; Schwalm et al. 2014), the local effects of

fragmentation and potential barriers to gene flow are less well understood. Moreover, there is no current model of genetic diversity and structure of swift fox in Nebraska, a state with among the largest intact grasslands left in North America. Consequently, we lack crucial pieces of information about the genetic status of the species, potential barriers for gene flow and the possible impacts of landscape changes on the population genetic diversity, processes especially important for species with small population size like swift fox in some regions of its distribution range (Sovada et al. 2009).

Here, we assessed the genetic structure and diversity of swift fox in Nebraska using nuclear DNA microsatellite analysis and explored whether there are genetically distinct groups that could be influenced by landscape feature and habitat constraints. Additionally, to assess the possibility of gene flow among swift fox populations at larger spatial extents, we studied contemporary genetic structure of the species in Nebraska as part of a larger geographic area that includes Wyoming, Colorado, and Kansas from which we have genetic information of several previous swift fox generations. By combining information from genetic analysis and landscape features, we give some insight into swift fox genetic structure, and how it translates into gene exchange among populations facing increasing habitat loss and fragmentation.

METHODS

Study Site

Our study area encompassed approximately 68,605 km^2 of western Nebraska, US. The area is dominated by dry shortgrass and mixedgrass prairies (Schneider et al. 2011). The study area was primarily native rangeland with some areas converted to cropland,

mainly irrigated and dryland corn, wheat, and sugar beets (Bishop et al. 2011, Schneider et al. 2011). Additional patches of other native habitat, such as woodlands and wetlands, are scattered throughout the study area. The region presents a relatively diverse topography, which includes several areas of rocky escarpments and a great variety of soil types, which range from sands to heavy clay. In general, levels of transportation infrastructure, human population densities and urbanization range from low to moderate. The climate is semi-arid, characterized by low humidity, moderate to high winds, and a large daily and seasonal range in temperature (Chapman et al. 2001, Schneider et al. 2011). Annual precipitation ranges from 300–430 mm. Mean annual wind speed at 100 m ranges from 21.5–34.3 km/h, and mean temperature ranges from -6º C in January to 32º C in July (Schneider et al. 2011).

Sample Collection

Survey sites were established between 2014-2016 across the study area, where we monitored more than 900 camera-trap stations that consisted of remotely-triggered camera traps lured with a skunk-based attractant to draw animals into our camera stations (see chapter 2 for details). Where swift fox was detected, we reset camera traps, cleared of any previous scat within a circle area of 5 m radius, and baited with cat food. We poked holes in the top and bottom of the cat food can, and then stake it down in front of the camera. The foxes feel compelled to mark the station and defecate on or near the can (B. L. Cypher and D. Schwalm pers. comm.) Two to five days after baiting the camera trap, we revisited the site to collect every scat pellet found within a 5 m radius. We stored scat deposits separately, identified by the date, survey site location, and GPS coordinates, and verified scat identification with pictures taken by the camera. Tissue and hair samples

were also collected opportunistically from road-killed individuals (Figure 4.1). We stored the scat samples at room temperature in paper bags within a container with a silica desiccant, and tissue and hair sample frozen until reaching the lab at Oregon State University, where samples were processed, following standard protocols for DNA extraction, and genotyping was performed.

DNA Extraction and Amplification

DNA Extraction

Tissue and hair samples – We extracted whole genomic DNA from tissue and hair samples using the Qiagen DNEasy blood and tissue kit (Qiagen, Valencia, CA) with the following modifications: we incubated samples for 8-12 hours at step 3 of the Qiagen protocol and used 210 µl of ethanol at step 6. For tissue analyses, we used ~15 mg of dried tissue cut from a larger sample stored in silica desiccant beads. Due to the difficulty of identifying and isolating individual follicle roots for extraction, we rolled ~20 follicles into a tight ball between gloved fingertips and ensured the ball was fully immersed in the reagent mixture during incubation.

Scat samples – We collected a 0.04-0.07g fecal sample from each dried scat by scraping the exterior with a razor blade, taking care to remove only the outermost material. We then extracted whole genomic DNA using the AquaGenomic Stool and Soil protocol (Multitarget Pharmaceuticals, LLC, Colorado Springs, CO) with the following modifications: use of 1.0 mm silica/zirconium beads (BioSpec Products Inc., Bartesville, OK) and a 15-minute bead beating step immediately after adding AquaGenomics and 2.5µl proteinase K to the fecal sample; addition of 150 µl of AquaPrecipi solution (Multitarget Pharmaceuticals, LLC) to remove additional PCR inhibitors after the

completion of both rounds of incubation followed by separation via spinning at 12000xg; and a final overnight rehydration of DNA pellets using 110 µl of 1x TE buffer. Following rehydration, the sample was spun for 2 minutes at 12,000xg and the supernatant was stored in a screw-top cryovial.

DNA Amplification

We included 15 microsatellite primers in 3 multiplexes using the Qiagen Multiplex Kit (Qiagen). The forward primer in each primer pair was labeled with a fluorescent dye at the 5'end with NED, PET, VIC (ABI) or 6-FAM (Sigma-Aldrich, St. Louis, MO), while the reverse primer was unlabeled (Integrated DNA Technology, Coralville, IA). Information regarding multiplex membership and dye color, as well as primer reference, is provided in Table A.1. Polymerase change reactions (PCR) were conducted in a 7 µl reaction consisting of 1 µl genomic DNA, 1x Master Mix, 0.5x Q Solution and 0.09-0.57 uM of each primer (Table A.1 lists individual primer concentrations); PCR reactions were brought to volume with nuclease-free water.

For hair and tissue samples, thermalcycling profiles were identical for a given multiplex except that 5 additional cycles were used for hair samples. Individual themalprofiles for each multiplex are shown in Table A.2. For scat samples, we followed the protocol for DNA amplification described above, excluding differences in primer concentrations (Table A.1) and individual themalprofiles for each multiplex (Table A.3).

All samples were run in triplicate in parallel PCRs for each multiplex and a consensus genotype was constructed from the replicates. To be included in the consensus genotype, a homozygous allele had to be observed in all three replicates, while each allele of a heterozygous genotype had to be observed twice. Where an allele was observed

singularly, a maximum of three additional replicate PCRs were run to confirm allele

identity and presence. Where confirmation was not possible, the sample was considered

to have missing data at that locus.

PCR products for all sample types were visualized on an ABI 3730 sequencer

(Applied Biosystems, Carlsbad, CA, USA) with 500 LIZ size standards (Applied

Biosystems). PCR products for hair and tissue were diluted to a 1:10 concentration (i.e., 1

μl of PCR product and 9 μl of sterilized water), but scat PCR products were not diluted.

We used Genotyper v 4.1 software (Applied Biosystems) to construct genotypes from the

microsatellite data.

Individual Identification

Because it is possible for multiple samples to represent the same individual, in

particular when using scat samples of unknown origin, we used computer program

Cervus v 3.0.7 (Marshall et al. 1998, Kalinowski et al. 2007) to identify duplicate

genotypes in the dataset. The Cervus program performs the identity analysis by reading a

text-based file of genotypes, and compares each row of genotype data against every other

row in the file; then it records any IDs that occur more than once in the file, and

separately records any genotypes that occur more than once (Kalinowski et al. 2007).

After removing duplicate records, we calculated PID, the probability of mistakenly

assigning genotypes to different individuals when they in fact are from the same

individual, by dividing the number of unique genotypes (number of unique individuals

identified) by the total number of genotypes obtained.

Genetic Data from Neighboring States

Genetic data from Wyoming, Colorado, and Kansas was obtained from Schwalm (2012, 2014). DNA extraction, PCR and genotyping from microsatellite and mitochondrial DNA followed similar laboratory protocols (see Schwalm et al. 2014). Since differences in lab equipment, in particular sequencers, can result in inconsistent allele identities, we standardized allele identities between the older dataset (Schwalm 2012, 2014) and the new dataset for NE by first repeating DNA amplification and visualization for a subsample (n = 10) of the older dataset under the new laboratory conditions, identifying differences in allele identity between the old and new datasets, and then using the differences to align the two datasets.

Data Analysis

To ensure that the observed diversity in our samples was sufficient to discriminate between unique individuals, we produced genotype accumulation curves for each population using the R package poppr (Kamvar and Grünwald 2014). The accumulation curves are constructed by randomly re-sample loci without replacement and counting the number of multilocus genotypes (MLGs) observed. The process is then repeated 1,000 times for 1 locus up to n-1 loci and the output plotted to represent the n-1 distributions of observed MLGs (Kamvar and Grünwald 2014). The number at which the curve reaches a plateau (Figure 4.4) determines the minimum number of loci necessary to discriminate individuals. We then looked for missing data, rare alleles, and overall dataset quality by computing basic locus statistics using the 'poppr' package (Kamvar and Grünwald 2014). The microsatellite markers were checked for accordance to Hardy–Weinberg equilibrium (HWE), and the presence of linkage disequilibrium (LE) with the index of association (I_A,

Brown et al.1980; Smith et al. 1993) using R package adegenet (Jombart 2008). We

removed from further analysis all loci with missing data ≥ 0.20 (20%), and loci suspected

of not being in HWE with $p \leq 0.01$.

A priori Genetic Structure Hypothesis

Prior to testing for genetic structure, we predicted the number and location of

genetically distinct groups for swift fox, first within Nebraska (Figure 4.2) and then

between Nebraska and three neighboring states (Colorado, Kansas, and Wyoming; Figure

4.3). We based our predictions on the presence of natural and anthropogenic landscape

features that may limit swift fox dispersal, including rivers, mountain ranges, high-traffic

roads and agricultural development. In Nebraska we identified three main groups that we

hypothesized might currently be genetically distinct and two outliers (due to their distant

geographical location in relation with the other samples) that may be dispersing foxes

from neighboring states, which were included in a larger analysis (Figure 4.3). For the

regional analysis, we predicted the formation of five groups, which we hypothesized as

genetically distinct based on potential barrier to gene flow (Figure 4.3).

Analysis of Genetic Diversity and Structure

We measured genetic variability of the microsatellite markers for each locus by

the number of alleles (Na), gene diversity (H_{exp}, expected heterozygosity), observed

heterozygosity (Ho), and evenness. To assess population diversity and structure, we first

examined genetic variation within and among groups using F_{ST} (Wright 1969) and G_{ST}

(Nei 1973). F_{ST} is a measure of genetic divergence among subpopulations (Allendorf and

Luikart 2008). The value of F_{ST} ranges between one and zero, where zero indicates

complete randomly mating populations and indicates complete isolation between two

populations. We tested statistical significance of F_{ST} values by using Goudet's G-statistic Monte Carlo test. Specifically, we used Hedrick's standardized G_{ST} (Hedrick 2005) to measures the amount of variation between individuals and groups (i.e., hypothesized distinct genetic groups), relative to the total population variation, but without specifying the identity of the alleles involved. An index of $G_{ST} = 0$ indicates no differentiation, whereas $G_{ST} = 1$ indicates that individuals/populations are segregating for differing alleles.

Second, we investigated the genetic structure and individual assignments by identifying and describing groups or clusters of genetically related individuals based on our hypothesized geographical differentiation using a discriminant analysis of principal components (DAPC: Jombart et al. 2010). The DAPC is a multivariate approach that combines principal component analysis (PCA) and discriminant analysis (DA), which maximizes the separation between groups while minimizing within groups variation. DAPC does not make any assumption on the population genetic models and may be more efficient at identifying genetic groups and hierarchical structure (Jombart et al. 2010). However, DAPC requires the selection of *a priori* number of groups; thus, we selected the number of groups using the sequential *K*-means clustering method. We used the Bayesian Information Criterion (BIC) for choosing the number of groups (*K*) from 1 to 5 (i.e., *K* with the lowest BIC value is ideally the optimal number of groups). The number of principal components that explained > 90% of the cumulative variance was retained. For display of DAPC plots we centered (Jombart et al. 2009), but did not scale the data. All DAPC and *k*-means analyses were performed in the R package adegenet (Jombart, 2008).

Because genetic structure can be a result of geographic distance (i.e., isolation by distance; Wright 1943), we ran a Mantel test to identify the relationship between genetic distance and geographic distance among samples. We first calculated individual-based pair-wise genetic distance (Edward's distance) and geographical distance (Euclidean distance), and then tested the correlation between matrices (Jombart 2015).

RESULTS

Population Genetic Analysis for Nebraska

Amplification and Genotyping Error Rate

We analyzed 15 hair and tissue samples, and 86 scat samples, of which 86.65% of hair and tissue samples, and 48.84% scat samples produced usable genotypes. Our amplification success was 54.46% and our genotyping error rates were 0 % for hair and tissue samples and 1.5 % for scat samples. We identified 3 individuals that were sampled more than once, and duplicate genotypes were removed from the analysis. Additionally, we excluded from the Nebraska analysis two additional samples deemed as outliers from the focal geographical area of study, but included both in the larger regional analysis. After removing all but the first record in instances of duplicate records and the outlier samples, the final number of unique genotypes was 49.

Although the 15 microsatellites we assessed have proven robust for assessments of swift fox population genetics (Kitchen et al. 2006, Sasmal et al. 2012, Cullingham et al. 2013, Schwalm et al. 2014), degraded DNA in our scat samples led to poor amplification and thus required that we removed three loci from our analysis (CXX263,

CXX403 and VVE5-33). We estimated the probability of identity (PID) and genotype accumulation curve to assess the power of the 12 loci dataset in discriminate between unique individuals, and found that both indicated high power to identify individuals (PID < 0.0001). The overall genotype accumulation curve increased logarithmically as the number of loci sampled increased, and 100% of multilocus genotypes (MLGs) were resolved with six loci (Figure 4.4).

Locus Summary Statistic and Missing Data

All 12 microsatellite loci were polymorphic. The number of alleles per locus varied from 3 to 17 (Table 4.1). Observed and expected heterozygosity were similar, where observed heterozygosity ranged from 0.53 (CXX377) to 0.88 (VVE2-110), while expected heterozygosity ranged from 0.54 to 0.89 for the same loci. Evenness for all locus ranged from 0.57 (CXX377) to 0.94 (VVE2-111, the locus that had the most evenly distributed alleles; Table 4.1).

None among the 12 loci tested was significant for linkage disequilibrium (I_A = 0.687, p = 0.392; r_d = 0.063, p = 0.408) and only one locus (CXX173) showed a significant departure from HWE (p < 0.01) for two of the three groups (Table 4.1). We found that missing data per loci ranged between 2–22%, with an average of 10% missing data for all loci (Figure A.1). We removed from further analysis two loci (CXX109 and VVE2-110) with missing data ≥ 0.20 (20%), and one locus (CXX173) suspected of not being in HWE.

Genetic Diversity

The genotype richness of MLGs varied in each hypothesized group with the minimum of 14 within groups 1 and 3 and with the maximum of 21 genotypes within

group 2 (Table 4.2). However, when the sampling effort was considered, the expected

MLG (eMLG) based on rarefaction at the largest, shared sample size (n = 14), richness

was the same for all three groups. The Shannon–Weiner Index (H) and the unbiased

genotypic diversity (H_{exp}), which is an analog of expected heterozygosity, were 2.64–3.04

and 0.69–0.73, respectively (Table 4.2). The value of genotype evenness in each group

was the same and equal to that of all the groups pooled together, showing perfect

evenness (1.0), which suggests that all MLGs were equally distributed in each group. We

found no linkage disequilibrium at any possible locus combination, either within or

among groups, values of *Ia* ranged from 0.55–0.78 and values of r_d from 0.07–0.10.

The pairwise F_{ST} values between groups were low, ranging from 0.019 to 0.034

(Table 4.3) suggesting groups did not differ (p = 0.34). As expected, G_{ST} value were also

low and indicated no differentiation among groups, ranging from 0.014 to 0.096 (p =

0.31). When estimating F_{ST} and $G"_{ST}$ for only two groups, we obtained FST = 0.045 and

$G"_{ST}$ = 0.239, both with p values of 0.01.

Based on the discriminant analysis of principal components (DAPC), the initial

three hypothesized genetic groups did not differ from each other (Figure 4.5–4.7); instead

two genetic groups were considered optimal to describe the data (lowest BIC value

Figure A.2). Additionally, we performed a DAPC stratified cross-validation analysis to

confirm that the appropriate number of PCs (i.e., number of PCs associated with the

lowest Mean Squared Error; Jombart et al. 2010) was selected for the DAPC analysis

(Figure A.3). The three genetic groups (clusters) were not geographically restricted

(Figure 4.5 and 4.6), thus indicating high levels of admixture (Figure 4.7).

We assessed which alleles contributed the most to the observed pattern and found three (CXX2062.137, VVE2-111.128 and VVE2-111.137) contributed more than 10% (Figure A.4). We found no evidence of isolation by distance in the swift fox distribution in Nebraska. The geographic distance between populations cannot explain the genetic pattern observed given the correlation is small and non-significant (Mantel $r = 0.032$, $p = 0.205$; Figure 4.8).

Lastly, we conducted a DPCA using the number of PCs that explained 92% of variance and the number of clusters (K) suggested by lowest value of the BIC versus K diagram (i.e., K=2). The results for the DAPC using two hypothesized groups showed two clearly distinct groups (Figure 4.9.a) with almost complete segregation of membership probability (Figure 4.9.b).

Population Genetic Analysis for Four States (Wyoming, Colorado, Nebraska, and Kansas)

Genetic Diversity

The resulting regional dataset comprised 447 unique genotypes based on 12 microsatellite markers and representing 5 hypothesized groups. The number of alleles per locus varied from 3 to 40. Observed and expected heterozygosity ranged from 0.51 (CXX109) to 0.94 (VVE2-110), while expected heterozygosity ranged from 0.61 to 0.71 for the same locus. Evenness range from 0.61(CXX109) to 0.96 (CPH3; Table 4.4). None among the 12 loci tested was significant for linkage disequilibrium ($I_A = 0.259$, p = 0.545; $r_d = 0.024$, p = 0.543). We found that missing data per loci ranged between 0–14%, with an average of 2% (Figure A.5).

The Shannon–Weiner Index (H) and the unbiased genotypic diversity (H_{exp}) were 3.74–6.10 and 0.68–0.73, respectively (Table 4.5). The value of genotype evenness in each group was the same and equal to that of all the groups pooled together, showing perfect evenness (1.0), which suggests that all MLGs were equally distributed in each group.

Genetic Structure

The pairwise F_{ST} values between groups range from 0.013 to 0.031, and G_{ST} value range from 0.071 to 0.185 (Table 4.6). Even though the values for F_{ST} and G_{ST} are relatively low, they both suggest significant group differentiation ($p < 0.01$). However, when we applied DAPC to the microsatellite genotypes from the four states, we found no clear genetic stratification was supported. First, we examined the genetic structure of five *a priori* hypothesized genetically distinct sampled groups. In this DAPC we retained 90 principal components of PCs during the preliminary variable transformation, accounting for 99.5% of the total genetic variability, and we used five clusters (K = 5; Figure 4.10-4.11). The eigenvalues of the analysis showed that the genetic structure was captured by the first four discriminant functions (DA eigenvalues; Figure 4.10). All individual genotypes were plotted to examine group membership and the result suggests high levels of admixture (Figure 4.12). Second, we carried out a DPCA using the number of clusters (K) suggested by lowest value of the BIC versus K diagram (i.e., K=7; Figure A.6) from a stratified cross-validation analysis and the number of PCs that explained 99% of variance. The results for the DAPC using K = 5 are presented in Figures 4.10–4.12, and results from DAPC K = 7 in Figures 4.13–4.15. In both cases the DAPC suggested genetic subdivision, although overlapping is also present, and the group membership proportion estimates revealed groups with some level of admixture.

We found evidence of IBD in the swift fox populations along the four states (Mantel $r = 0.136$, p = 0.001). Even though the correlation coefficient was relatively small, it suggested that the geographic distance and genetic distance are positively linearly related (Figure 4.16).

DISCUSSION

Genetic Diversity

Overall, the swift fox population in Nebraska appears genetically stable (observed genetic diversity 1-D = 0.71; heterozygosity $H_{exp} = 0.71$), as Nebraska's swift fox population presented similar heterozygosity to other swift fox populations (0.53-0.73, Schwalm et al. 2014; 0.73-0.78, Sasmal et al. 2013; 0.30-0.79, Kitchen et al. 2005; 0.70, Harrison et al. 2002; 0.70, Cullingham et al. 2010). The heterozygosity of a healthy mammal population is considered to be 0.677 ± 0.012 (Garner et al. 2005), and our diversity estimates for swift fox in Nebraska is high in comparison with other closely related species (i.e., San Joaquin kit fox – *Vulpes macrotis mutica*, 0.389, Schwartz et al. 2005; red fox – *Vulpes velox*, 0.576, Roy et al. 1996; coyote – *Canis latrans*, 0.75, Williams et al. 2003; grey wolf – *Canis lupus*, 0.605, Forbes and Boyd 1996). However, our analysis is limited by a relatively small sample size (n < 50), and sample size can affect genetic diversity measures. Previous work has shown that small sample sizes increase bias and reduce precision and accuracy of the genetic diversity estimates given that the most frequent alleles are expected to be detected in small sample sizes (Pruett and Winker 2008, Smith and Wang 2014). Additionally, small sample sizes can lead to a larger variance and thus a smaller probability of statistical significance for heterozygosity

estimators (Smith and Wang 2014). Even though the estimates of diversity have shown to be biased downwards with a reduction in sample size, especially in low levels of population differentiation ($F_{ST} < 0.05$) and when a small number of microsatellite loci is used (Gorman and Renzi 1979, Smith and Wang 2014), which implies that our heterozygosity estimate is underestimated and thus be consider conservative, we should still interpret our results with caution.

Prior to analysis, we identified potential gene flow barriers that represented both anthropogenic and natural sources of grassland fragmentation, and hypothesized the presence of three genetically distinct groups in Nebraska (Figure 4.2), but our results suggest the existence of two distinct genetic groups instead of three. Moreover, the two genetically distinct groups we identified are not geographically isolated from each other, suggesting that habitat fragmentation may thus far had limited implications for gene flow among swift fox populations (Figure A.9 and Figure A.10). Still, although the low $F_{ST}/G"_{ST}$ values indicate that genetic exchange is occurring between the groups and with the larger population of swift fox from neighboring states, genetic differentiation is relatively slow. That we find two distinct genetic groups suggests despite apparent gene flow may suggest that there is a current and ongoing reduction of gene flow, and that swift fox populations in Nebraska, at least, may be in the early stages of becoming isolated. While some gene flow may be still occurring between swift fox in Nebraska and even though restricted gene flow and genetic structure can occur naturally, the reduction of connectivity due to more recent and spatially extensive anthropogenic disturbances may impose a greater threat to gene flow. Small population, such as the swift fox population in Nebraska, are vulnerable to demographic, environmental, and genetic stochasticity (Mills et al. 2005). The loss of genetic variation in individuals as well as

populations may negatively impact demographic rates and exacerbate susceptibility to environmental perturbations (Lacy 1993).

Similar to our local examination of gene flow barriers, our larger regional examination failed to support our initial predictions (Figure 4.3). Although there is clear evidence that groups that are spatially proximate are less differentiated than groups that are geographically distant, our analysis suggests there is a seven, not five groups (Figure A.10, Figure A.12). Still even though there is apparent barriers to admixture, there is no clear genetic structure pattern. Groups show significant overlap, indicating, as we found within in Nebraska, the hypothesized barriers to gene flow are permeable at some degree. Although, these loosely subdivided seven groups were not clearly isolated, they seemed to support at least two of the hypothesized barriers (i.e., Barriers B and D; Figure 4.3). As predicted, we found two distinct groups on either side of the South Platte River, and on each side of the agricultural development between Colorado and Kansas (Figure A.10). Schwalm et al. (2014) also reported high degree of differentiation among swift fox populations (i.e., unique genetic groups) due to the barrier concurrent with the South Platter River. They also found different groups between central Colorado and Kansas, presumed to be due to agricultural development. The north and south groups, identified at both sides of the South Platte River (barrier B), may signal differentiation due to the climatic variation along the latitudinal gradient; or conversely, these groups may derive from two expanding source populations in two geographic extremes, representing species recovery post-extirpation (Schwalm 2012). The west and east groups, identified on both sides of the agricultural development between Colorado and Kansas, may represent an anthropogenic-induced and more recent differentiation. In general, our results of genetic structure suggested there are limited barriers to gene flow among swift fox populations

within the Central Great Plains, which may reflect their historical and current connectivity. However, populations show a weak locally genetic sub-structure related in some degree to natural and anthropogenic barriers. Colorado and Kansas swift fox populations showed connectivity, but some level of differentiation may be related to agricultural development, which could negatively influence gene flow (Schwalm et al. 2014).

While apparently genetically healthy, the swift fox population in Nebraska is relatively small (Tier I At-risk Species in Nebraska; Schneider et al. 2011); thus, interactions with populations in the surrounding states may be especially important for maintaining genetic diversity. Indeed, the high genetic diversity we found within Nebraska may reflect the mixture of multiple source population, which could include larger populations in Wyoming and Colorado. Additionally, the current low level of structure in the Nebraska's swift fox population could potentially be due to a time lag and founding effects, if the population is reestablishing after been extirpated from the majority of its historic range in the state. The low level of genetic structure may be a product of immigration of small number of individuals from Wyoming and Colorado populations, and to a lesser extent from Kansas, considering that 10–20 years (genotype data from Wyoming, Colorado, and Kansas are from years 1998 to 2009) provide enough time for several generations to disperse and establish in new areas. Alternatively, our results could reflect a genetic bottleneck event within the state. We would expect swift fox populations in to be subject of marked population size fluctuations resulting from the variation in annual rainfall and the associated reduction on prey, as has been observed on its close relative the kit fox (Cypher et al. 2000, Schwartz et al. 2005). Such declines make swift fox population vulnerable to genetic bottleneck effects .The extreme dry

conditions that were pervasive in the Great Plains in 2013, right before the collection of data for this study, may have reduced the population size to an extent that created a founder effect from the survivors, in the case of local extinctions followed by colonization events.

Even though previous studies have suggested relatively large areas of suitable habitat for swift fox in Nebraska (i.e., 42% of Nebraska continues to contain seemingly high-quality swift fox habitat; Sovada et al. 2009), swift fox have a relatively restricted distribution (Chapter II). The swift fox population seemed to be restricted to two regions within its available habitat, one in the north extreme and other in the south extreme of the Nebraska's Panhandle; however no clear genetic structure was found between the two regions. With no evidence of barriers, it appears clear that swift fox have the potential to continue to expand in Nebraska if suitable habitat is available.

CONCLUSIONS

Our study provides an assessment of the genetic health of swift fox in Nebraska, and explores regional genetic diversity and structure for context. Swift fox in Nebraska could be consider genetically healthy and stable given the relatively high levels of heterozygosity and high genetic diversity compared with other populations of the species and other canids. The swift fox population in Nebraska seemed to be restricted to two pockets within its available habitat, but no genetic structure, nor geographic isolation, existed between the two. Our findings suggested historic genetic exchange and current gene flow among swift fox populations is sufficient as gene flow is occurring through migration/dispersal of individual foxes within Nebraska and across the larger region.

While genetic diversity of the swift fox population in Nebraska may not be motive of concern at present, given that it showed to be genetically healthy, there is the potential for future reduction of genetic diversity due to its small population size in light of increasingly fragmented landscapes that isolates wildlife into even smaller populations. Populations that lose genetic diversity are more prone towards becoming extinct in comparison to those that maintain higher levels of genetic diversity (Koons 2010). Efforts should be made to expand the scope of this study by analyzing functional connectivity, and we stress the need to incorporate both demographic and genetic information simultaneously and with a broader regional context.

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TABLES AND FIGURES

Table 4. 1 Allele frequency (Na) per locus, observed genetic diversity index (1-D, Simpson index), expected heterozygosity (H_{exp}, Nei's 1978 gene diversity), evenness of alleles (*E*), and test for HWE using chi^2 statistic for Nebraska's swift fox (*Vulpes velox*) population.

Locus	Locus summary statistics				Hardy-Weinberg equilibrium			
	Na	1-D	H_{exp}	*E*	chi^2	df	Pr(chi^2>)	Pr_{exact}
CPH3	6	0.80	0.81	0.91	12.72	15	0.62	0.58
CXX173	3	0.56	0.57	0.82	18.49	3	0.00	0.00
CXX20	8	0.78	0.79	0.84	76.01	28	0.00	0.01
CXX250	8	0.76	0.77	0.75	14.86	28	0.98	0.83
CXX377	6	0.54	0.54	0.57	13.33	15	0.58	0.31
FH2054	6	0.68	0.69	0.76	32.67	15	0.01	0.02
CXX109	5	0.60	0.61	0.69	16.74	10	0.08	0.24
CXX2062	4	0.68	0.69	0.85	10.20	6	0.12	0.07
VVE2_111	3	0.64	0.64	0.94	3.30	3	0.35	0.31
VVE2_110	17	0.88	0.89	0.73	127.31	136	0.69	0.09
VVE3_131	5	0.72	0.73	0.89	11.80	10	0.30	0.16
VVE_M19	13	0.83	0.84	0.70	111.79	78	0.01	0.17
Mean	7	0.71	0.71	0.79	-	-	-	-

Table 4. 2 Genotypic richness, diversity, and evenness for hypothesized groups

Group	N	MLG	eMLG	H	G	Lambda	E.5	H_{exp}	Ia	r_d
K = 3										
1	14	14	14	2.639	14	0.929	1	0.730	0.549	0.069
2	21	21	14	3.045	21	0.952	1	0.720	0.642	0.081
3	14	14	14	2.639	14	0.929	1	0.690	0.782	0.101
K = 2										
1	19	19	19	2.944	19	0.947	1	0.687	0.108	0.014
2	30	30	19	3.401	30	0.967	1	0.705	0.828	0.104
Total	49	49	14,19*	3.892	49	0.980	1	0.722	0.482	0.061

N = number of individuals observed; MLG = number of multilocus genotypes observed; eMLG = number of expected MLG at the smallest sample size ≥ 10 based on rarefaction; H = Shannon-Wiener Index of MLG diversity (Shannon 2001); G = Stoddart and Taylor's Index of MLG diversity (Stoddart and Taylor 1988); lambda = Simpson's Index (Simpson 1949); E.5 = Evenness, E5 (Pielou 1975; Ludwig and Reynolds 1988; Grünwald et al.,2003); Hexp = Nei's unbiased gene diversity (Nei 1978); Ia = Index of association, I_A (Brown et al. 1980; Smith et al. 1993); r_d = standardized index of association. * eMLG = 14 for three groups and eMLG = 19 for two groups

Table 4. 3 Pairwise for F_{ST} and G_{ST} values for three swift fox groups (hypothesized genetically distinct groups) in Nebraska

	F_{ST}			G'_{ST}		
	Group 1	Group 2	Group 3	Group 1	Group 2	Group 3
Group 1	0	-	-	0	-	-
Group 2	0.025	0	-	0.066	0	-
Group 3	0.034	0.019	0	0.096	0.014	0

Table 4. 4 Number of observed alleles (Na) per locus, diversity index (Simpson index), gene diversity (Nei's 1978 gene diversity), and evenness (E) for swift fox (*Vulpes velox*) populations in four states (Wyoming, Colorado, Nebraska, and Kansas).

Locus	Na	1-D	H_{exp}	E
CPH3	6	0.819	0.820	0.958
CXX173	3	0.534	0.534	0.799
CXX20	10	0.788	0.789	0.880
CXX250	9	0.790	0.791	0.818
CXX377	7	0.648	0.648	0.647
FH2054	7	0.623	0.623	0.633
CXX109	6	0.511	0.512	0.608
CXX2062	5	0.705	0.705	0.874
VVE2-111	5	0.651	0.652	0.882
VVE2-110	40	0.936	0.937	0.714
VVE3-131	7	0.743	0.744	0.865
VVE-M19	26	0.908	0.909	0.787
Mean	10.917	0.721	0.722	0.789

Table 4. 5 Genotypic richness, diversity, and evenness for hypothesized groups in four states (Wyoming, Colorado, Nebraska, and Kansas)

Group	N	MLG	eMLG	H	G	Lambda	E.5	H_{exp}	Ia	r_d
1	77	77	42	4.34	77	0.99	1	0.70	0.56	0.05
2	100	100	42	4.61	100	0.99	1	0.68	0.32	0.03
3	118	118	42	4.77	118	0.99	1	0.72	0.09	0.01
4	42	42	42	3.74	42	0.98	1	0.73	0.92	0.08
5	110	110	42	4.70	110	0.99	1	0.68	0.08	0.01
Total	447	447	42	6.10	447	1.00	1	0.72	0.26	0.02

N = number of individuals observed; MLG = number of multilocus genotypes observed; eMLG = number of expected MLG at the smallest sample size $\geq$ 10 based on rarefaction; H = Shannon-Wiener Index of MLG diversity (Shannon 2001); G = Stoddart and Taylor's Index of MLG diversity (Stoddart and Taylor 1988); lambda = Simpson's Index (Simpson 1949); E.5 = Evenness, E5 (Pielou 1975; Ludwig and Reynolds 1988; Grünwald et al.,2003); Hexp = Nei's unbiased gene diversity (Nei 1978); Ia = Index of association, I_A (Brown et al. 1980; Smith et al. 1993); r_d = standardized index of association.

Table 4. 6 Pairwise for F_{ST} and G_{ST} values for five swift fox groups (hypothesized genetically distinct groups) in four neighboring states (Wyoming, Colorado, Nebraska, and Kansas).

	F_{ST}					$G"_{ST}$				
Group	1	2	3	4	5	1	2	3	4	5
1	0	-	-	-	-	0	-	-	-	-
2	0.014	0	-	-	-	0.075	0	-	-	-
3	0.013	0.024	0	-	-	0.071	0.142	0	-	-
4	0.029	0.028	0.013	0	-	0.178	0.185	0.093	0	-
5	0.025	0.031	0.016	0.021	0	0.151	0.175	0.094	0.143	0
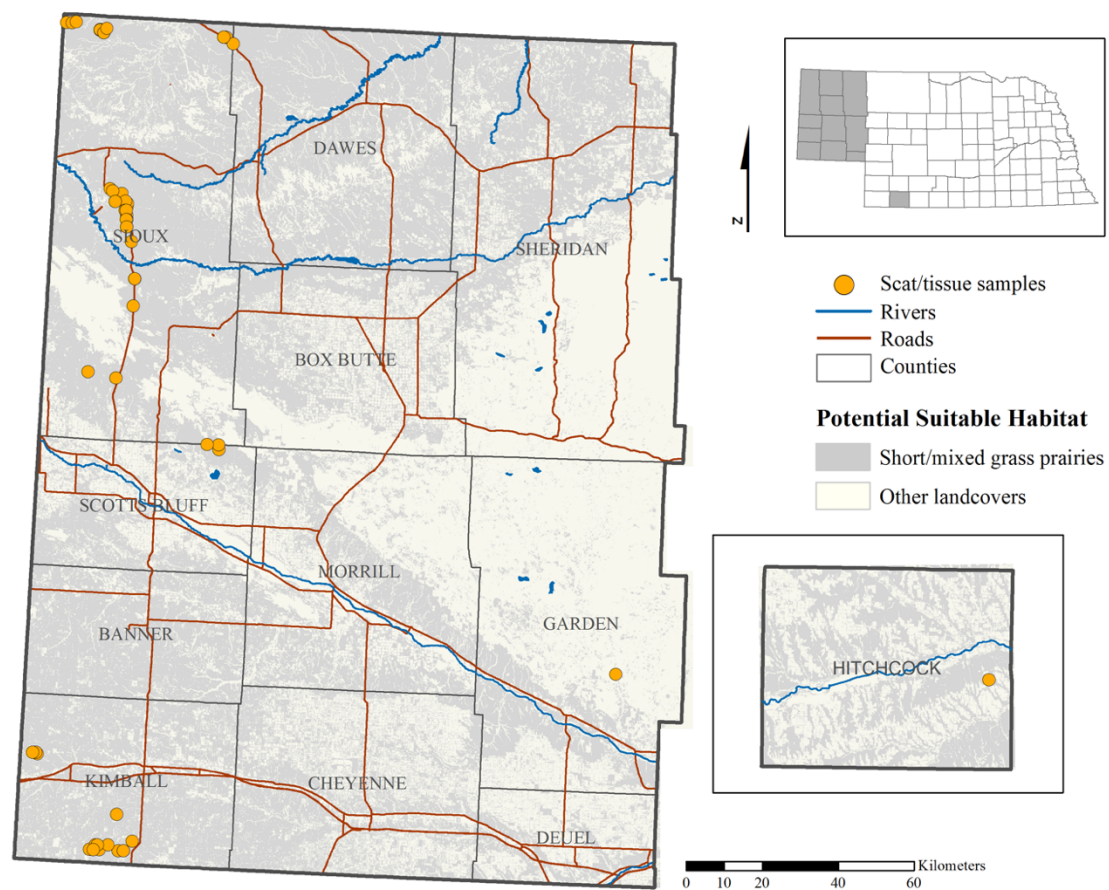
Figure 4. 1 Map of DNA samples (scat, hair and tissue samples) from swift fox (*Vulpes velox*) collected in Nebraska.
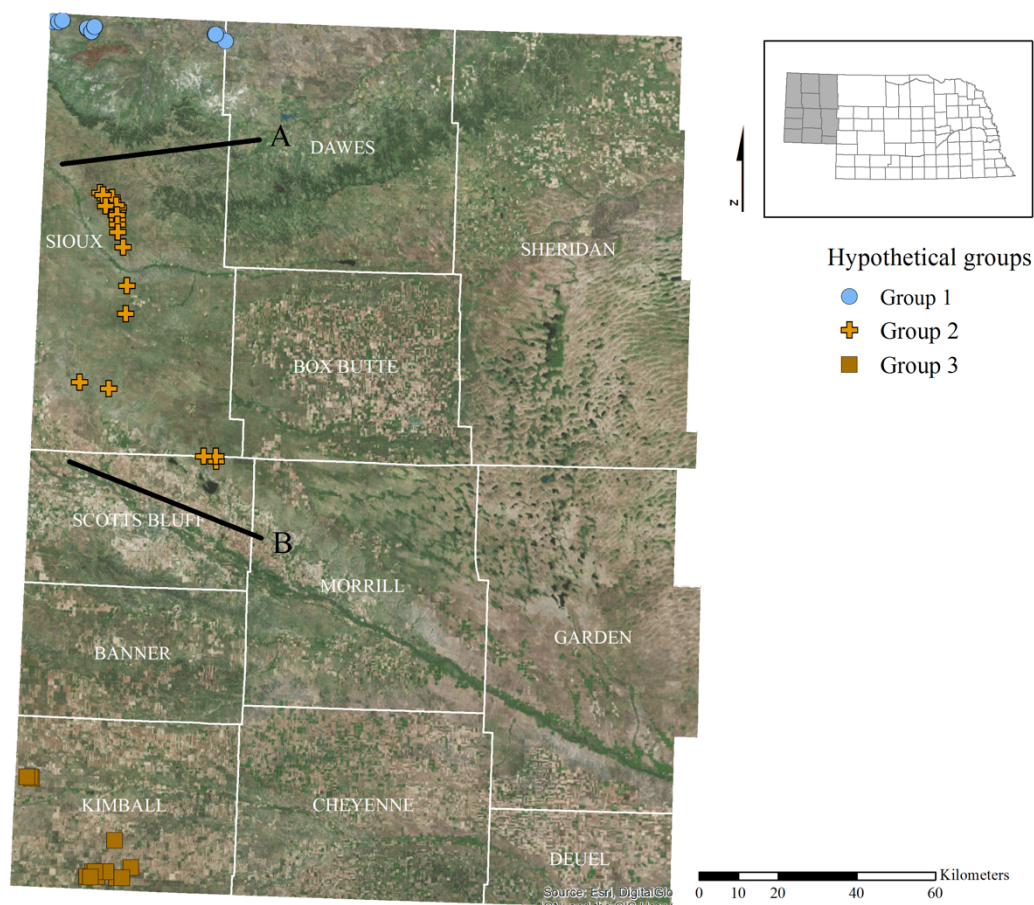
Figure 4. 2 Geographic location of hypothesized genetically distinct swift fox groups and general gene flow boundaries. Barrier A corresponds with the Pine Ridge ant the Niobrara River; barrier B corresponds with the North Platte River, Hwy 26 and I-80 additionally to agricultural lands.
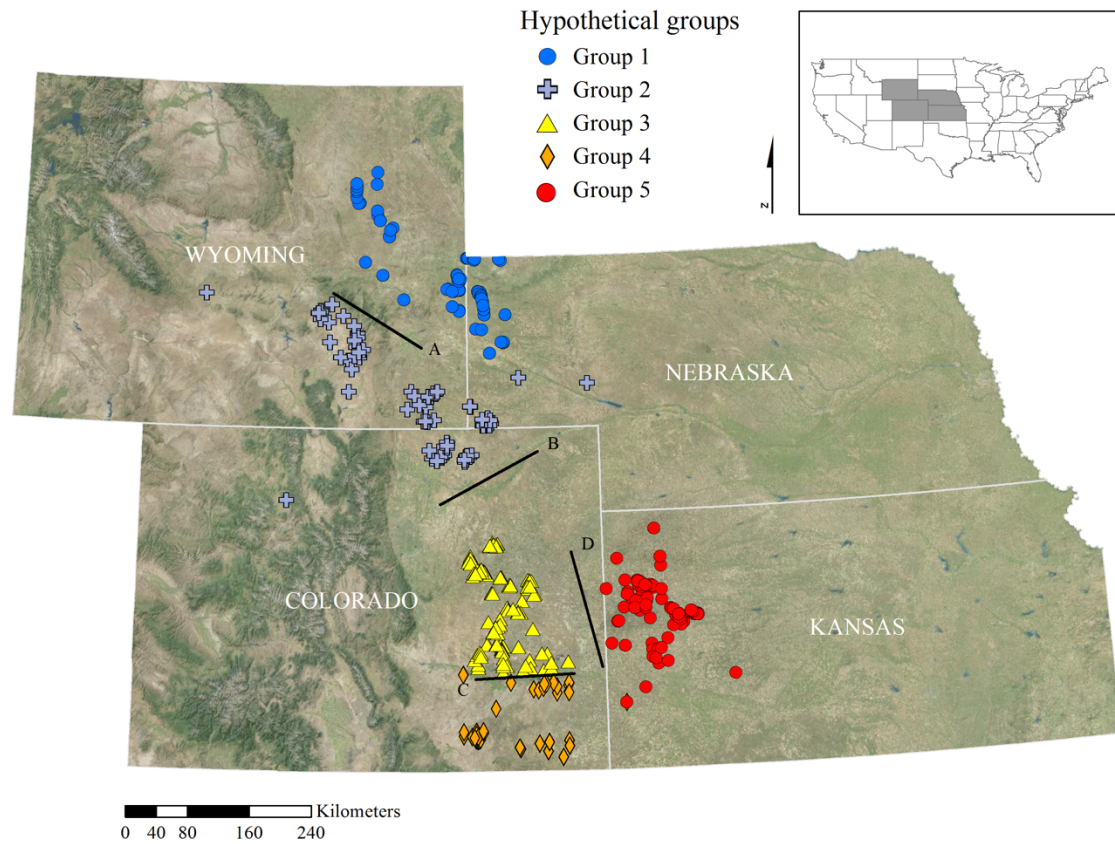
Figure 4. 3 Geographic location of hypothesized genetically distinct swift fox groups and general gene flow boundaries. Barrier A corresponds with the Laramie Mountains, barrier B corresponds with the South Platte River and agricultural development, barrier C corresponds with Arkansas river, and barrier D corresponds with agricultural development (Based on Schwalm et al. 2014).
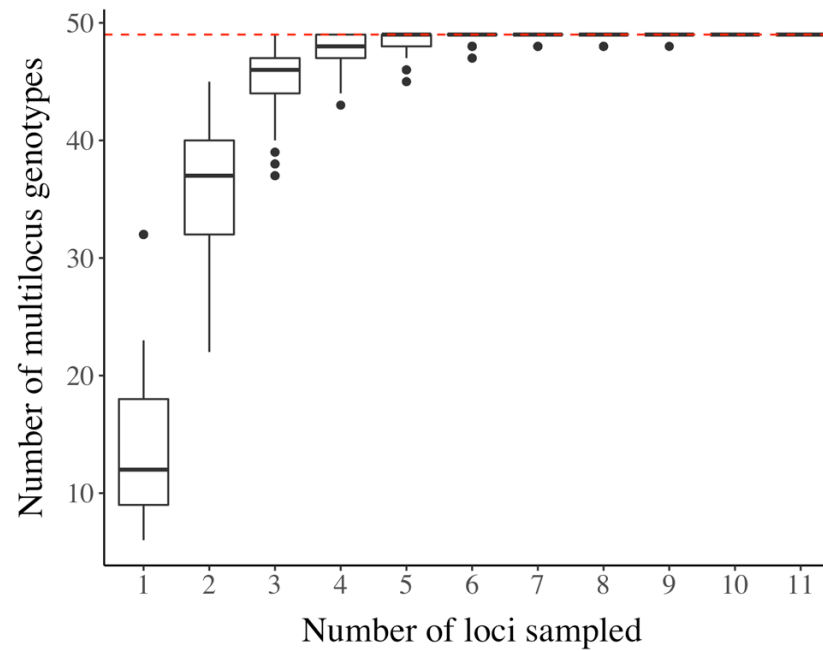
Figure 4. 4 Genotype accumulation curve for Nebraska's swift fox (*Vulpes velox*) population. The x axis denotes the number of observed MLGs and y axis indicates the number of loci randomly sampled without replacement. Each boxplot contains 1,000 random samples representing different possible combinations of *n* loci. The horizontal red dashed line represents 100% of MLG resolution.
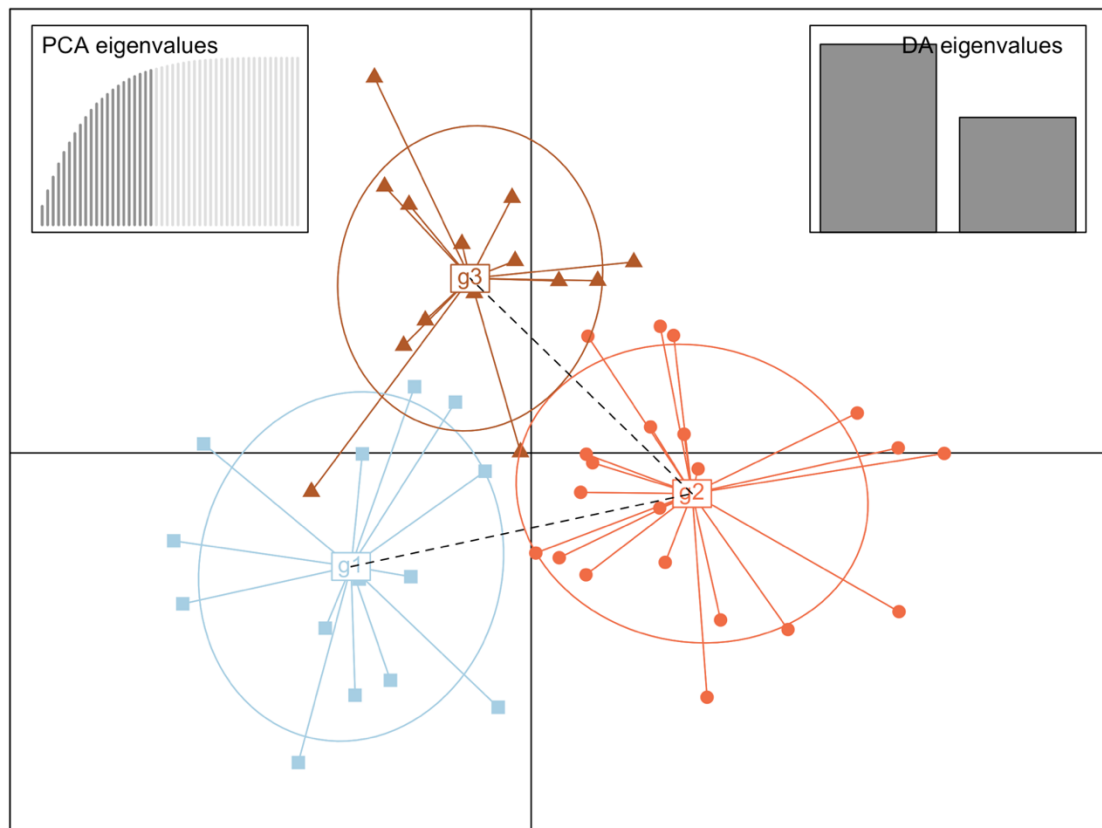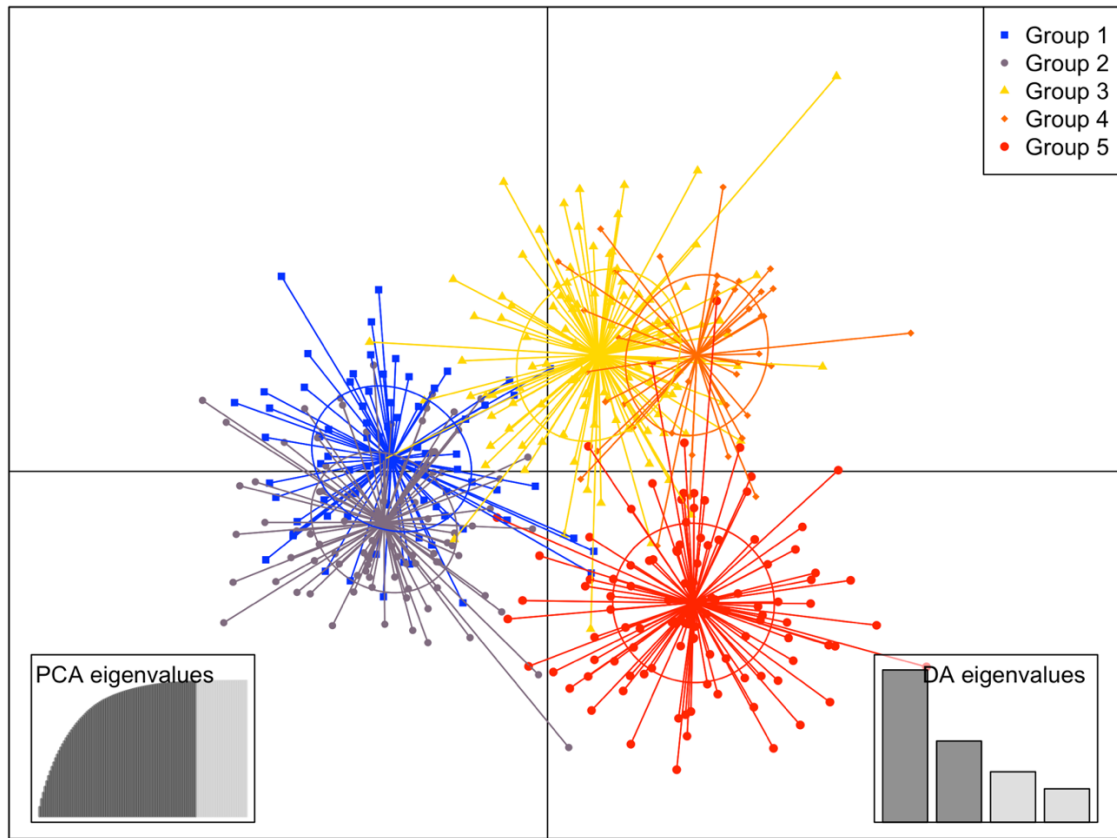
Figure 4. 5 DAPC analysis of the first two principal components in swift fox (*Vulpes velox*) samples from three different hypothesized groups. Groups are indicated by different colors and ellipses, with dots representing haplotypes in each group. In the top left and top right, insets of principal component analysis (PCA) and discriminant analysis (DA) eigenvalues are shown, respectively. The number of axes retained was 21 for the PCA and 2 for the DA.
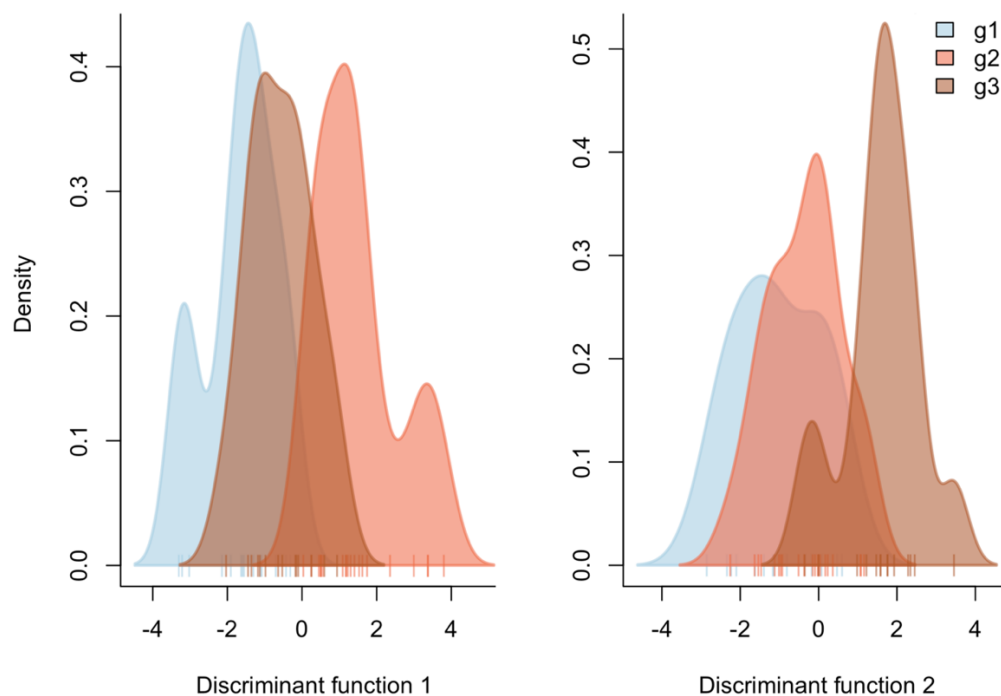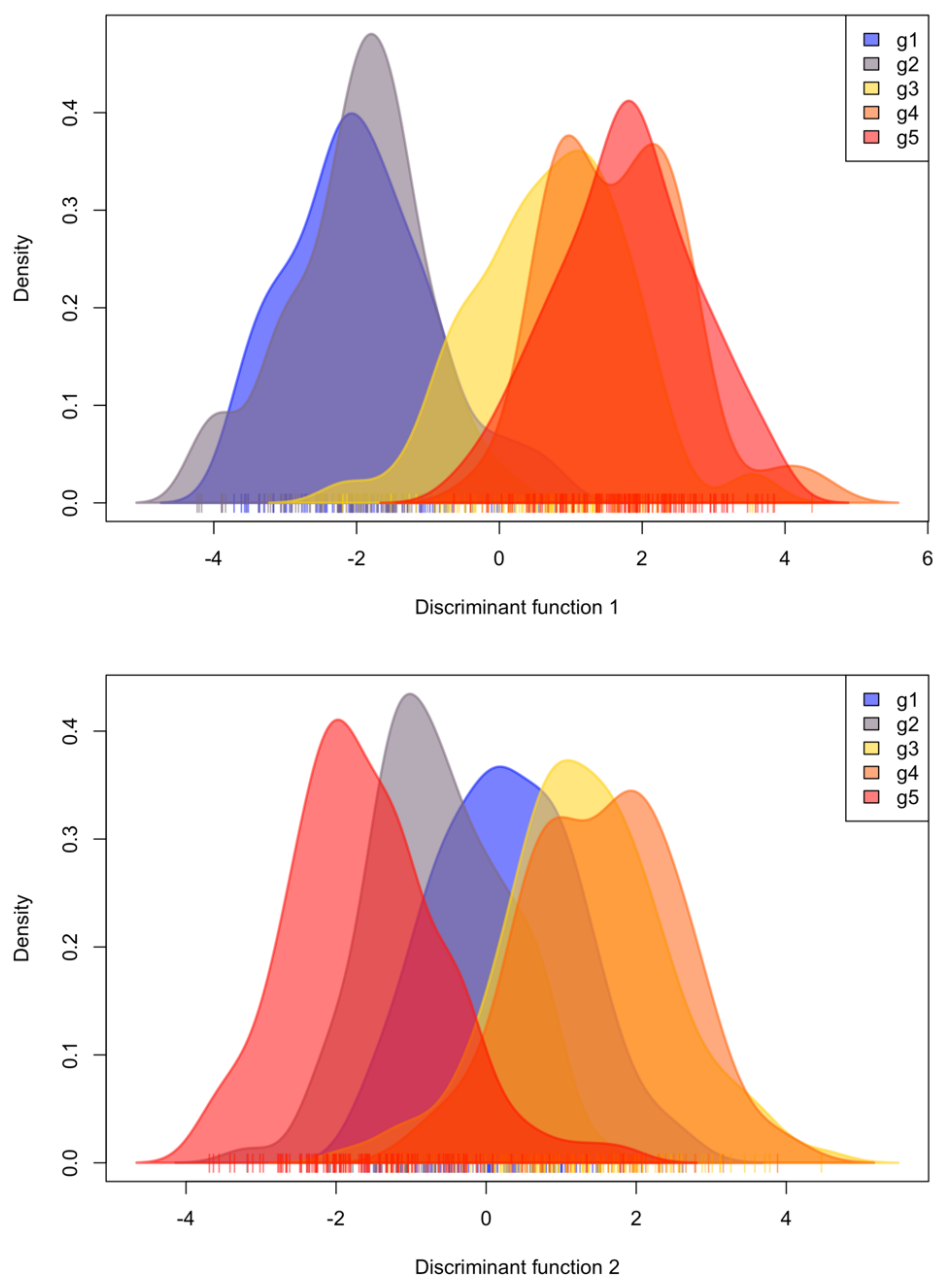
Figure 4. 6 Plot of the densities of individuals on the two retained discriminant functions on DAPC analysis for swift fox (*Vulpes velox*) samples from three different hypothesized groups in Nebraska.
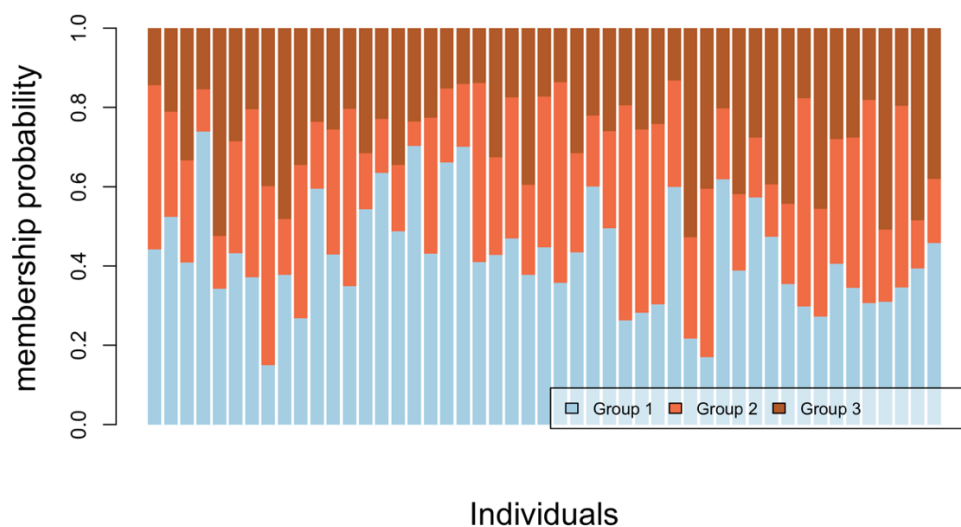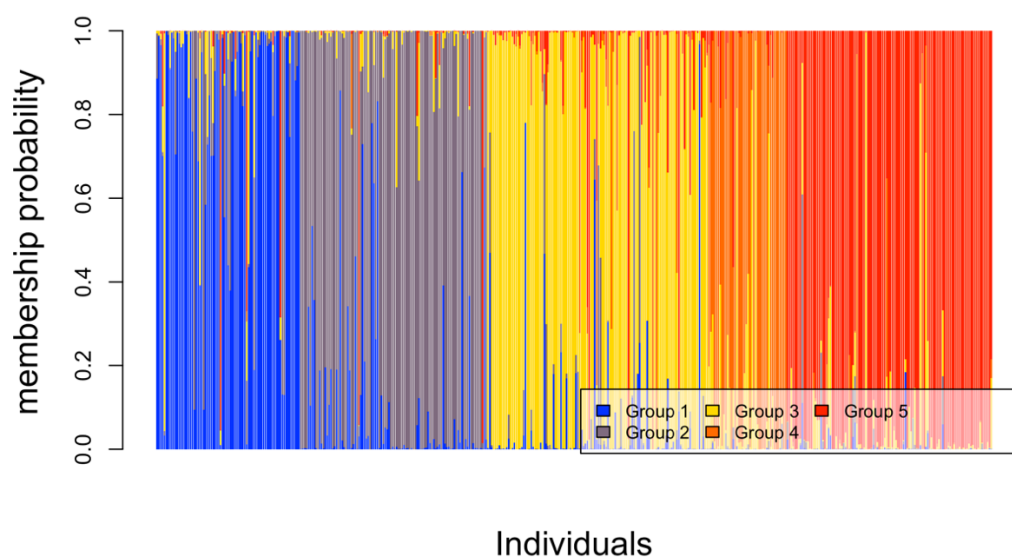

Figure 4. 7 Mean proportion of ancestry in each hypothesized group for swift fox (*Vulpes velox*) in Nebraska.
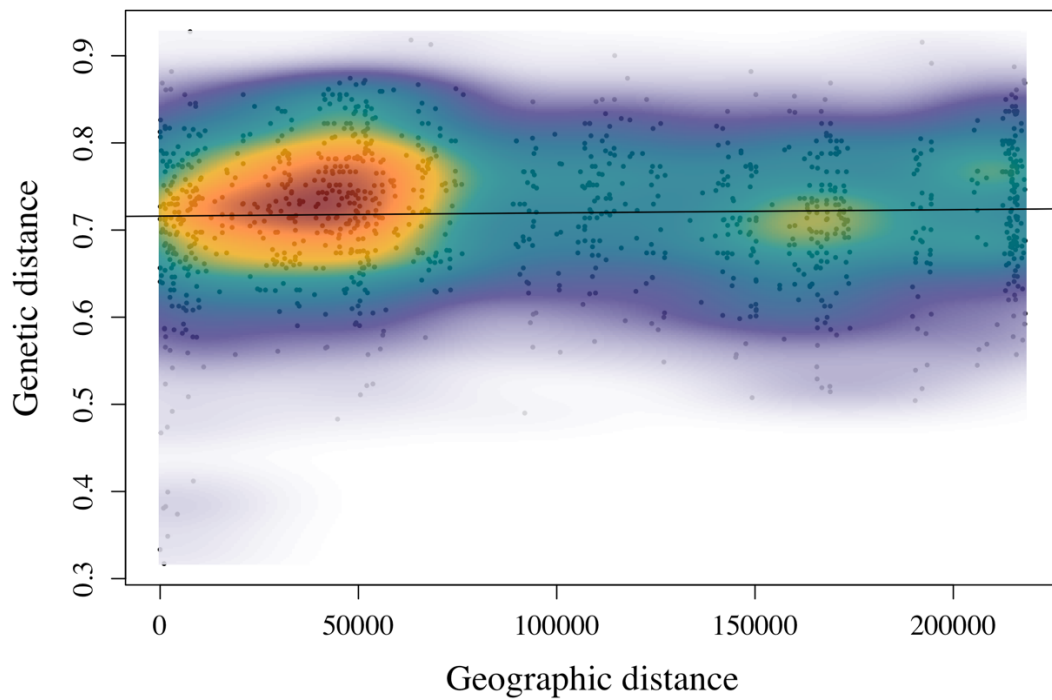
Figure 4. 8 Estimated genetic differentiation among swift fox (*Vulpes velox*) in relation to geographic distance. Multilocus estimates of genetic differentiation based on (Edward's distance) are plotted against the geographic distance (m). The scatterplot suggests the absence of spatial structure given that there is one main cloud of point, without discontinuities which would have indicated an isolation by distance pattern.
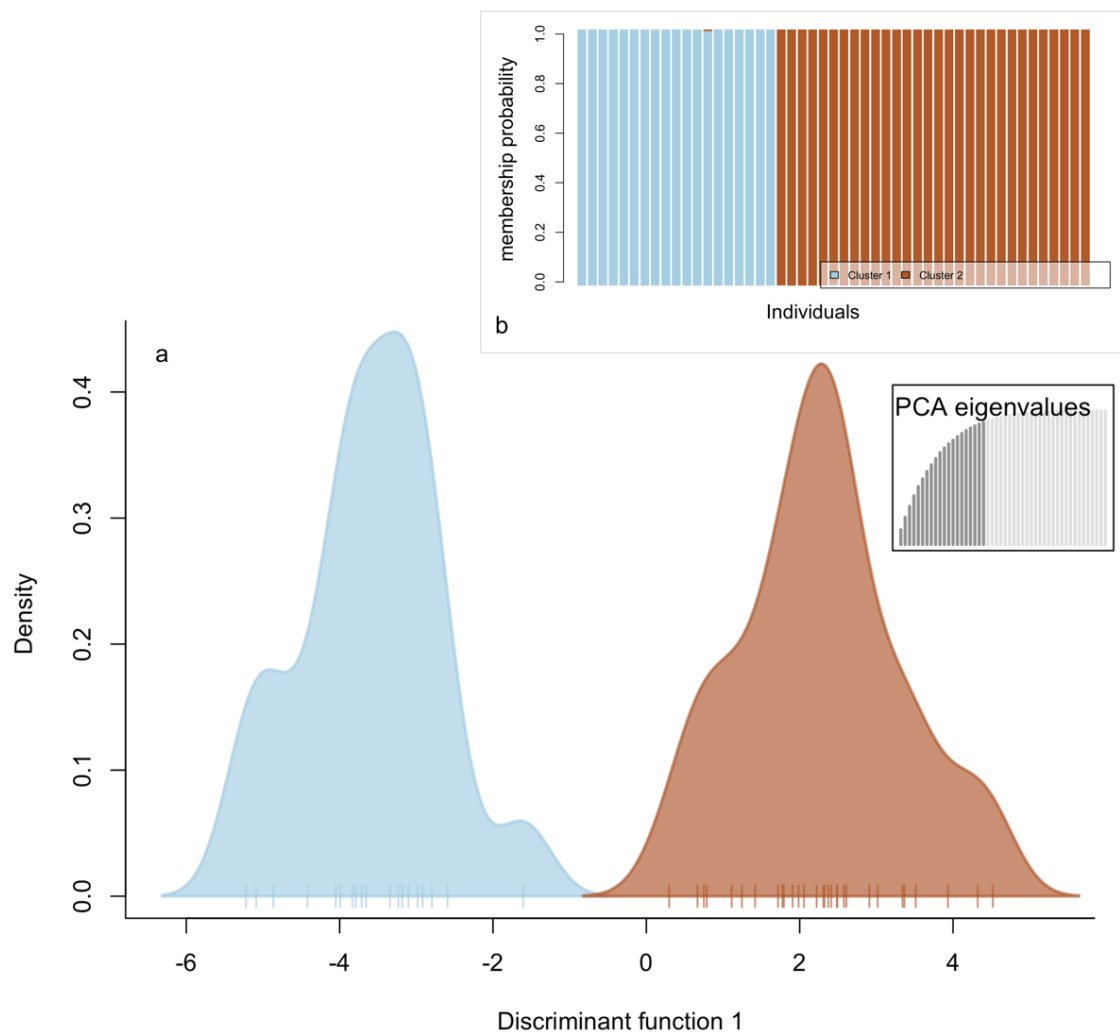
Figure 4. 9 Plot of the densities of individuals on one retained discriminant functions (a) and stacked barplot of group distribution (b) for two potential groups of swift fox (*Vulpes velox*) in Nebraska.
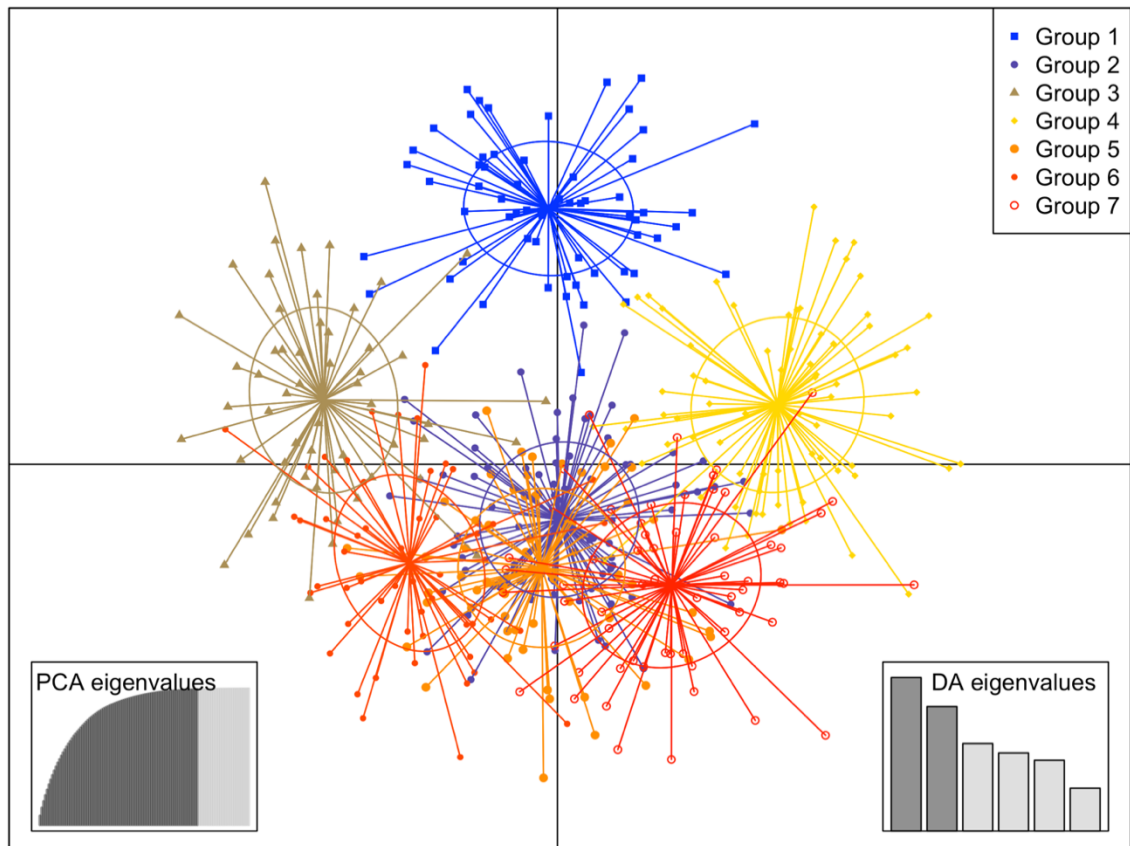
Figure 4. 10 DAPC analysis of the first two principal components in swift fox (*Vulpes velox*) samples from five different hypothesized groups. Groups are indicated by different colors and ellipses, with dots representing haplotypes in each group. In the top left and top right, inserts of principal component analysis (PCA) and discriminant analysis (DA) eigenvalues are shown, respectively. The number of axes retained was 90 for the PCA and 4 for the DA.
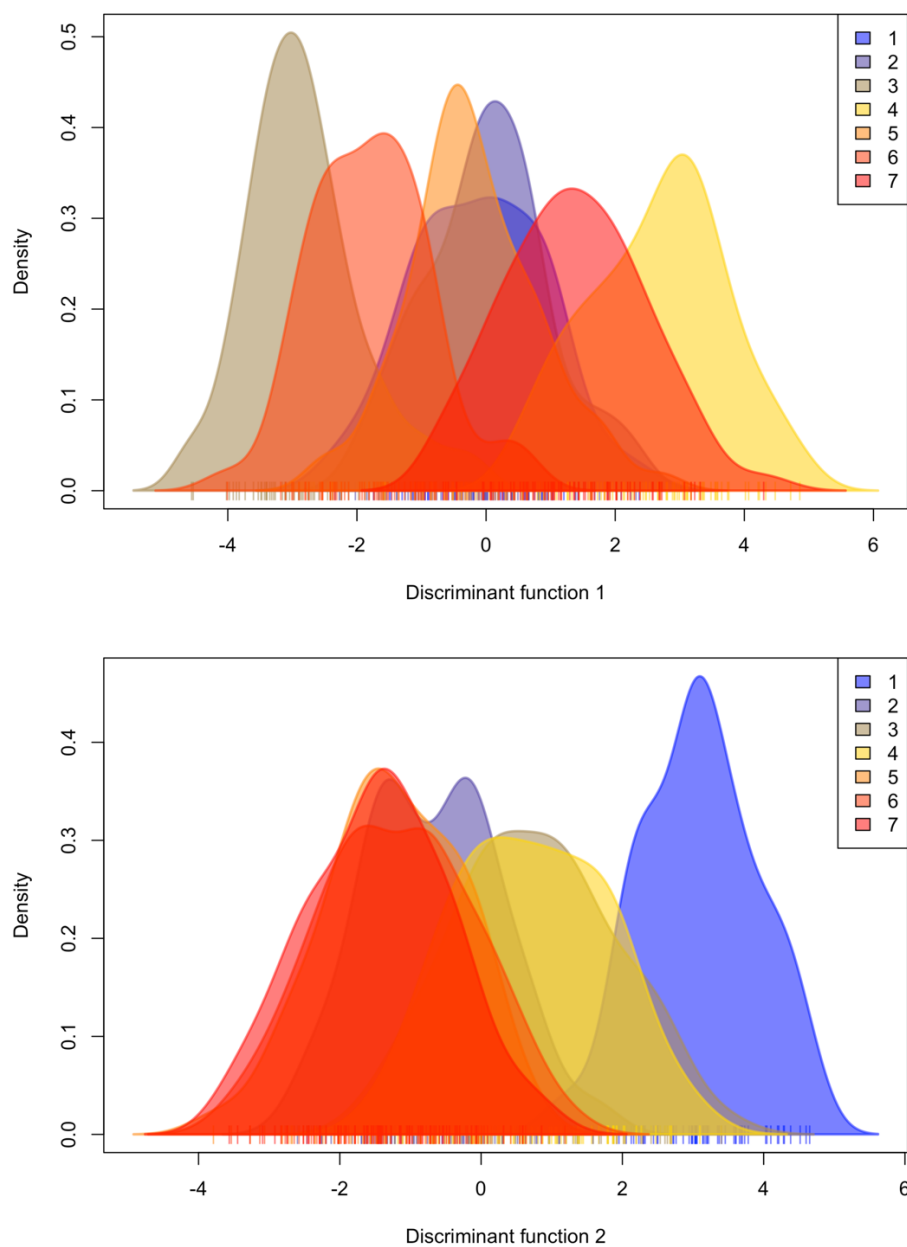
Figure 4. 11 Plot of the densities of individuals on two of the retained discriminant functions used in DAPC analysis for swift fox (*Vulpes velox*) samples from five different hypothesized groups.
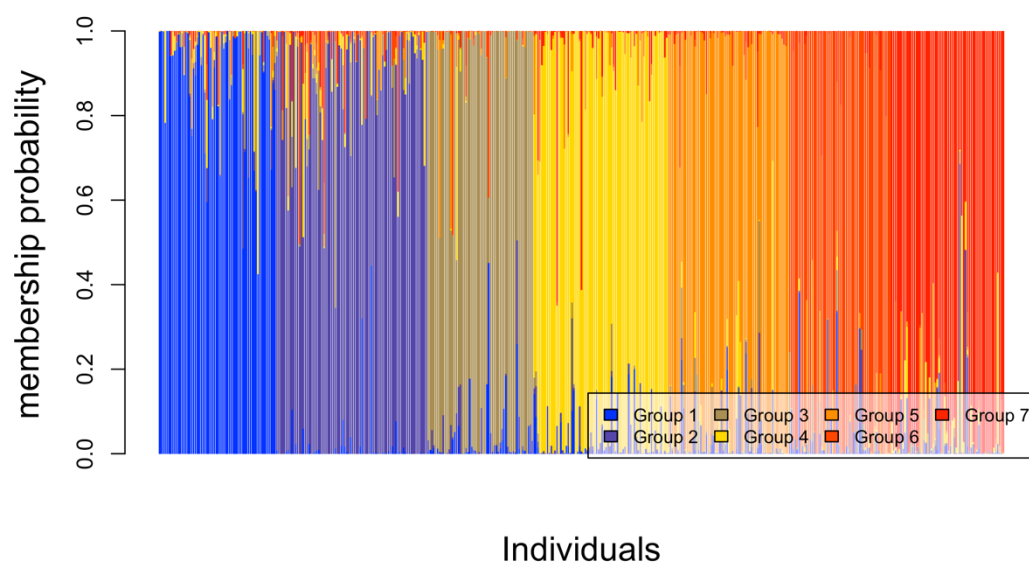
Figure 4. 12 Mean proportion of ancestry for five hypothesized groups of swift fox (*Vulpes velox*) in four states (Wyoming, Colorado, Nebraska, and Kansas).

Figure 4. 13 DAPC analysis of the first two principal components in swift fox (*Vulpes velox*) samples from seven different hypothesized groups. Groups are indicated by different colors and ellipses, with dots representing haplotypes in each group. In the bottom left and bottom right, inserts of principal component analysis (PCA) and discriminant analysis (DA) eigenvalues are shown, respectively. The number of axes retained was 90 for the PCA and 6 for the DA.

Figure 4. 14 Plot of the densities of individuals on two of the retained discriminant functions used in DAPC analysis for swift fox (*Vulpes velox*) samples from seven different hypothesized groups.

Figure 4. 15 Mean proportion of ancestry for seven hypothesized groups of swift fox (*Vulpes velox*) in four states (Wyoming, Colorado, Nebraska, and Kansas).
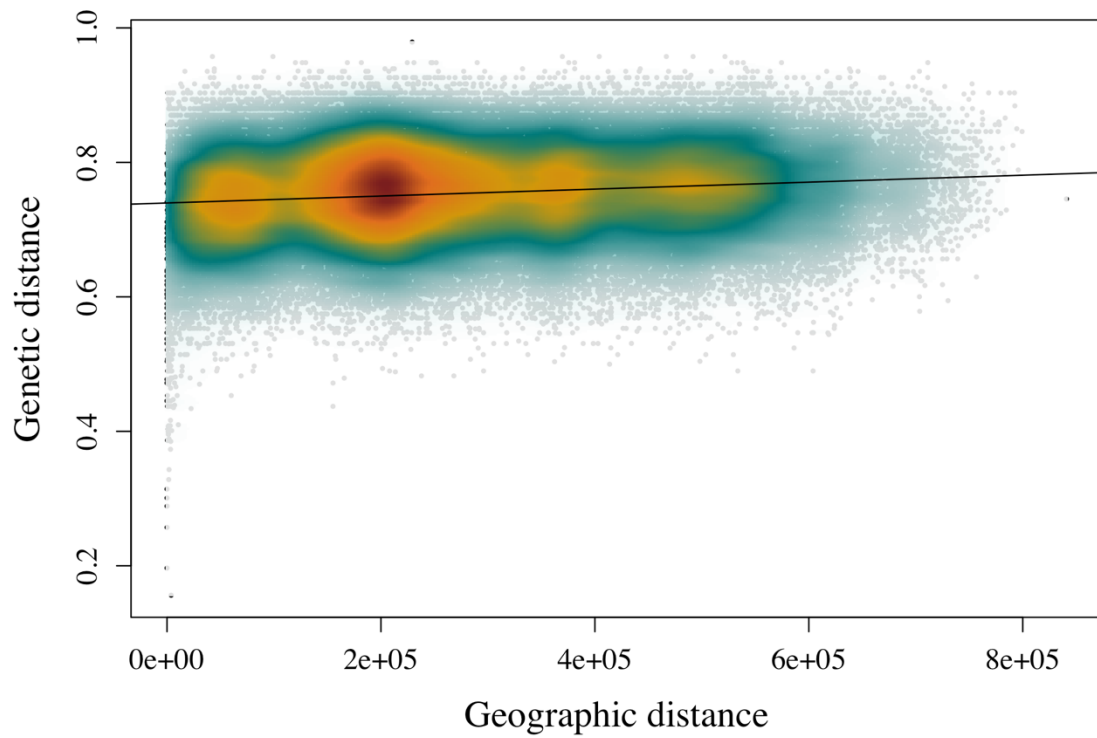
Figure 4. 16 Estimated genetic differentiation among swift fox (*Vulpes velox*) in relation to geographic distance. Multilocus estimates of genetic differentiation based on (Edward's distance) are plotted against the geographic distance (m). The scatterplot suggests the presence of spatial structure given that there is a positive correlation between the variables (Mantel $r = 0.136$, $p = 0.001$) indicating an isolation by distance pattern.

APPENDIX

Table A.1. Microsatellite loci used to construct genotypes for swift fox from samples received from the University of Nebraska, including multiplex panel, number of alleles, allele size range, dye label, and primer pair concentration (separately shown for tissue/hair and scat PCRs). SIDL, HI6145 and H3R were used in a species ID test described by De Barbara et al. 2014. Fragment analysis was conducted using an ABI 3730 (Applied Biosystems, Inc. Carlsbad, CA, USA) at the Center for Genomic Research and Biocomputing at Oregon State University.

Locus	Multiplex Panel	# Alleles	Allele Size (bp)	Dye Label	Primer Concentration Tissue and Hair (uM)	Primer Concentration Scat (uM)
CPH3[1]	1	6	152-162	6FAM	0.20	0.20
CXX20[2]	1	8	116-139	VIC	0.24	0.24
CXX173[2]	1	3	122-126	NED	0.10	0.10
CXX250[2]	1	8	127-141	PET	0.20	0.20
CXX377[3]	1	6	169-187	VIC	0.09	0.09
CXX403[3]	1	3	268-276	VIC	0.39	0.39
FH2054[4]	1	6	163-187	NED	0.11	0.11
CXX109[2]	2	5	160-166	NED	0.14	0.14
CXX263[2]	2	5	94-120	6FAM	0.14	0.21
FH2062[4]	2	4	133-146	6FAM	0.14	0.14
VVE2-111[5]	2	3	128-137	NED	0.14	0.14
VVE5-33[5]	2	8	189-221	NED	0.50	0.57
VVE-M19[5]	3	13	224-278	VIC	0.09	0.09
VVE2-110[5]	3	18	239-337	6FAM	0.36	0.36
VVE3-131[5]	3	5	156-189	PET	0.11	0.11
SIDL[6]	3 (scat only)	-	-	PET	-	0.29
HI6145[6]	3 (scat only)	-	-	-	-	0.20
H3R[7]	3 (scat only)	-	-	-	-	0.10

Table A.2. Multiplex protocols for each of three individual multiplex PCRs used to amplify DNA extracts from swift fox hair and tissue samples.

Multiplex 1		
Initial denaturation	95°C	15 min
Touchdown		
Number of cycles	14	
Denaturation	94°C	30 sec
Annealing	55°C – 0.3°C	90 sec

Table A.2. Multiplex protocols for each of three individual multiplex PCRs used to amplify DNA extracts from swift fox hair and tissue samples.

Elongation	72°C	1 min
Cycling		
Number of cycles	25 (hair)	20 (tissue)
Denaturation	94°C	30 sec
Annealing	51°C	90 sec
Elongation	72°C	1 min
Final Elongation	60°C	30 min
Multiplex 2 & Multiplex 3		
Initial denaturation	95°C	15 min
Touchdown		
Number of cycles	12	
Denaturation	94°C	30 sec
Annealing	53°C – 0.5°C	90 sec
Elongation	72°C	1 min
Cycling		
Number of cycles	33 (hair)	28 (tissue)
Denaturation	94°C	30 sec
Annealing	47°C	90 sec
Elongation	72°C	1 min
Final Elongation	60°C	30 min

Table A.3. Multiplex protocols for each of three individual multiplex PCRs used to amplify DNA extracts from putative swift fox scat samples.

Multiplex 1		
Initial denaturation	95°C	15 min
Touchdown		
Number of cycles	14	
Denaturation	94°C	30 sec
Annealing	55°C – 0.3°C	90 sec
Elongation	72°C	1 min
Cycling		
Number of cycles	25	
Denaturation	94°C	30 sec
Annealing	51°C	90 sec
Elongation	72°C	1 min
Final Elongation	60°C	30 min
Multiplex 2		
Initial denaturation	95°C	15 min
Touchdown		
Number of cycles	4	
Denaturation	94°C	30 sec
Annealing	51°C – 1°C	90 sec

Table A.3. Multiplex protocols for each of three individual multiplex PCRs used to amplify DNA extracts from putative swift fox scat samples.

Elongation	72°C	1 min
Cycling		
Number of cycles	28	
Denaturation	94°C	30 sec
Annealing	47°C	90 sec
Elongation	72°C	1 min
Final Elongation	60°C	30 min
Multiplex 3		
Initial denaturation	95°C	15 min
Touchdown		
Number of cycles	12	
Denaturation	94°C	30 sec
Annealing	53°C – 0.5°C	90 sec
Elongation	72°C	1 min
Cycling		
Number of cycles	33	
Denaturation	94°C	30 sec
Annealing	47°C	90 sec
Elongation	72°C	1 min
Final Elongation	60°C	30 min
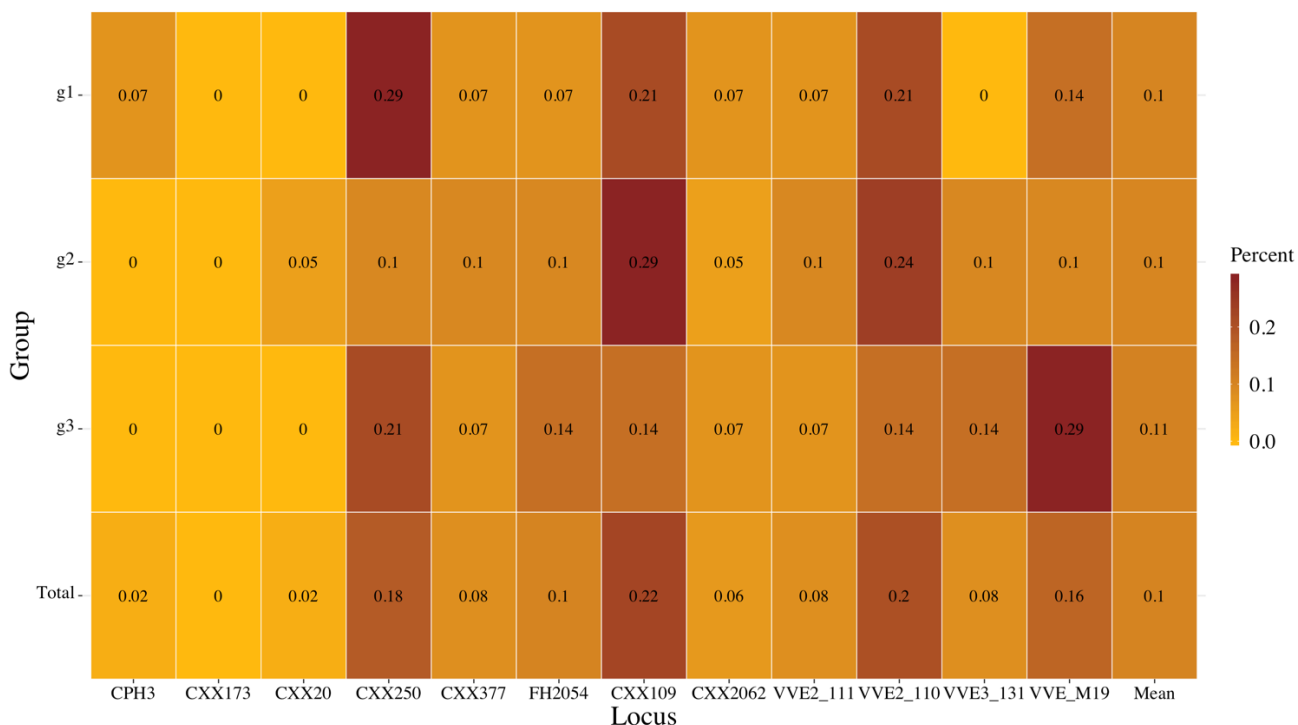
Figure A.1. Percent of missing data per locus and hypothesized group for Nebraska's swift fox (*Vulpes velox*) population.
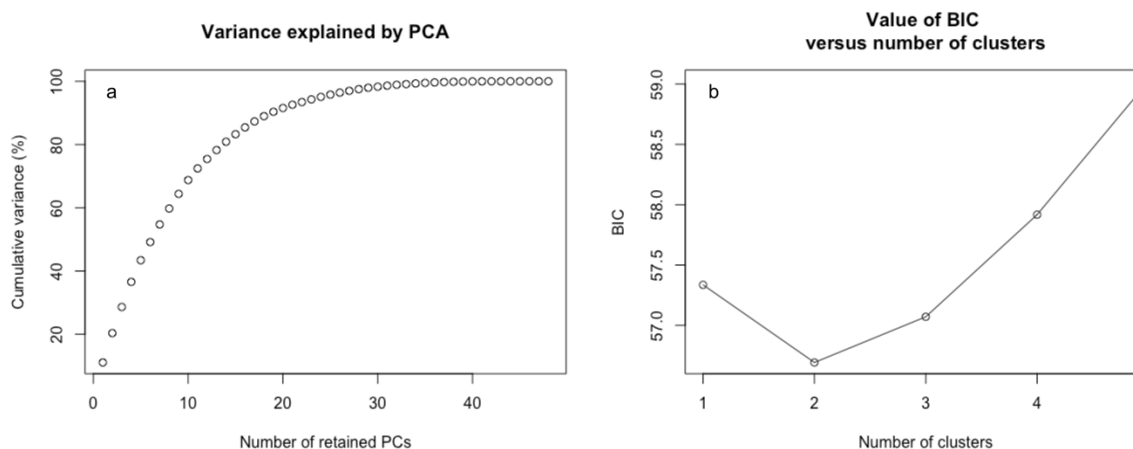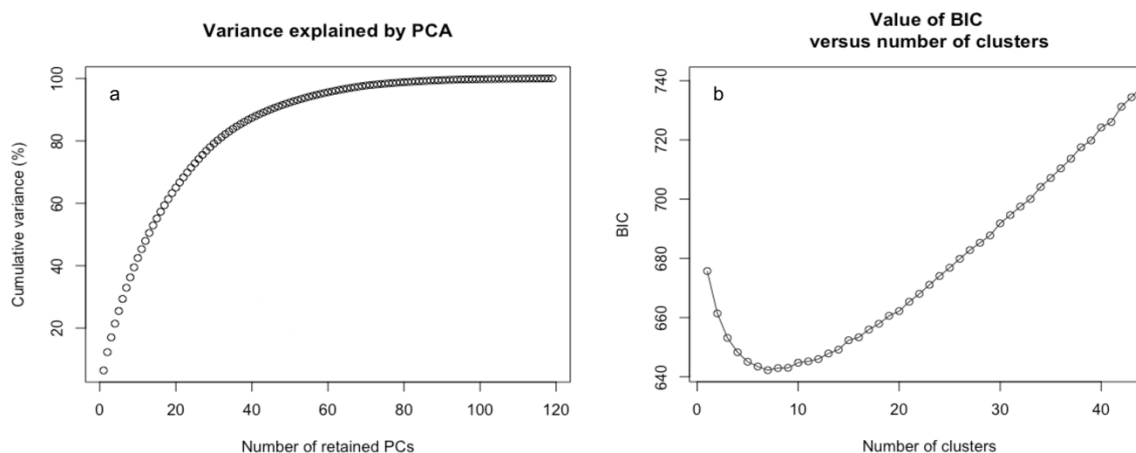

Figure A.2. Number of principal components retained (a) and number of clusters (K=2), based on cumulative explained variance (0.92) and Bayesian Information Criterion (BIC) curve (b), used in DAPC analysis on Nebraska swift fox population. More than 90% of the variance was explained by choosing >20 PCs. The BIC curve decreased sharply at K=2, indicating that the data clusters optimally into two groups and thus we selected it as the most probable number of clusters
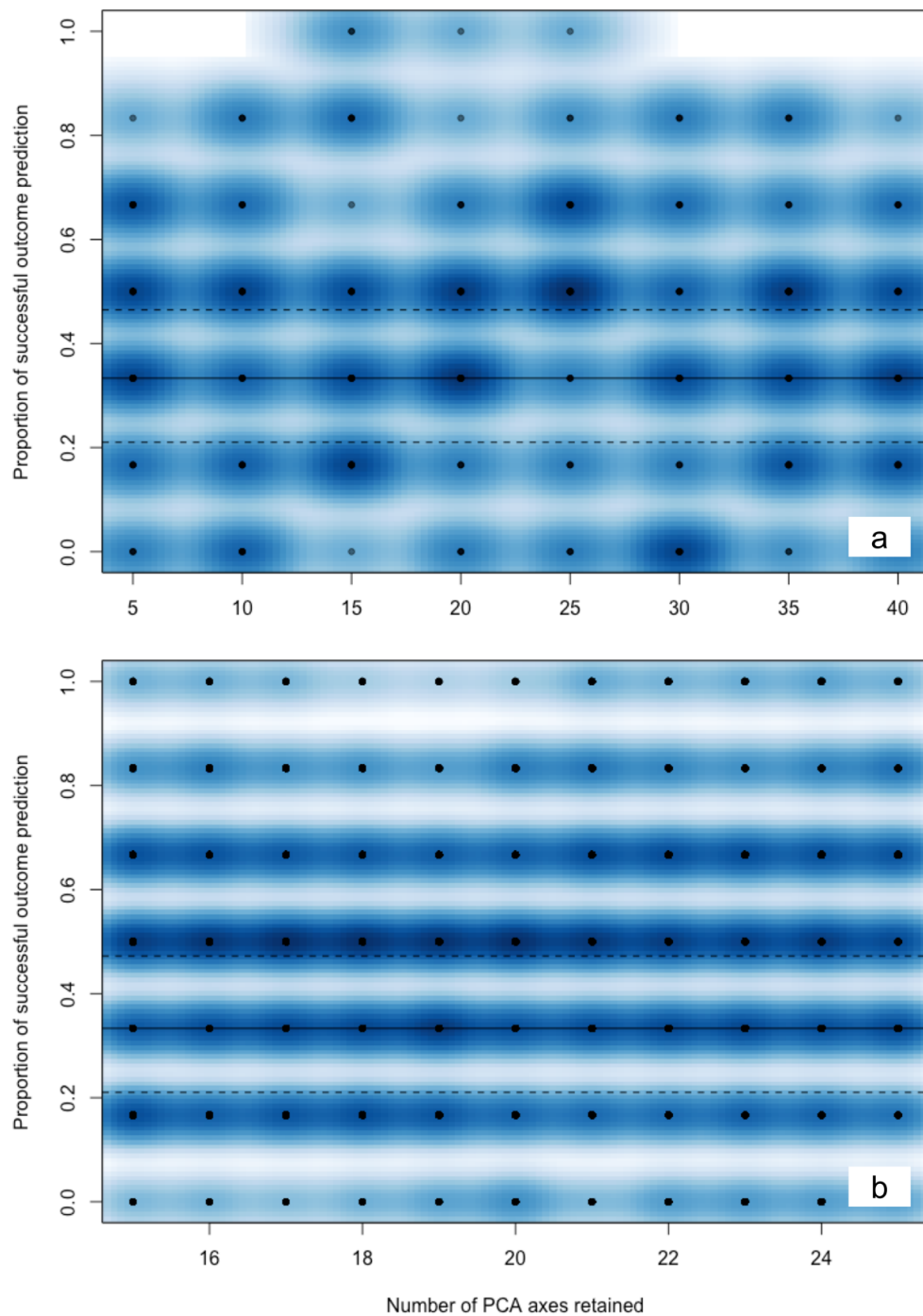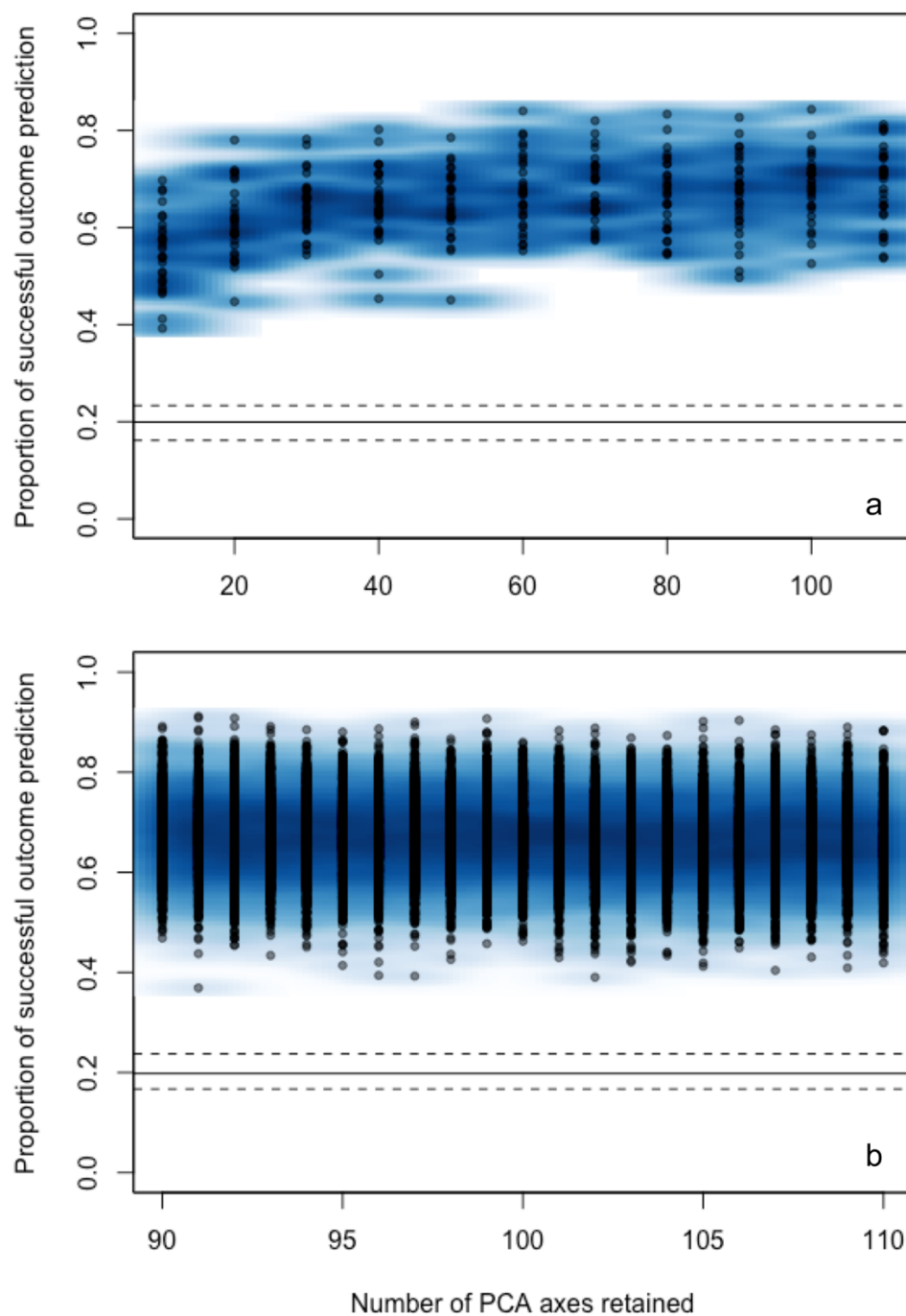
Figure A.3. DAPC stratified cross-validation running 30 replicates and a number of PCs less than the total number of alleles in the data (a) and running 1000 replicates with 15-25 PCs retained, for both kept the number of discriminant functions fixed. The number of PCs that gave the highest percent of correctly predicted subsamples with the lowest error was 21. DAPC analysis on swift fox populations for Nebraska.
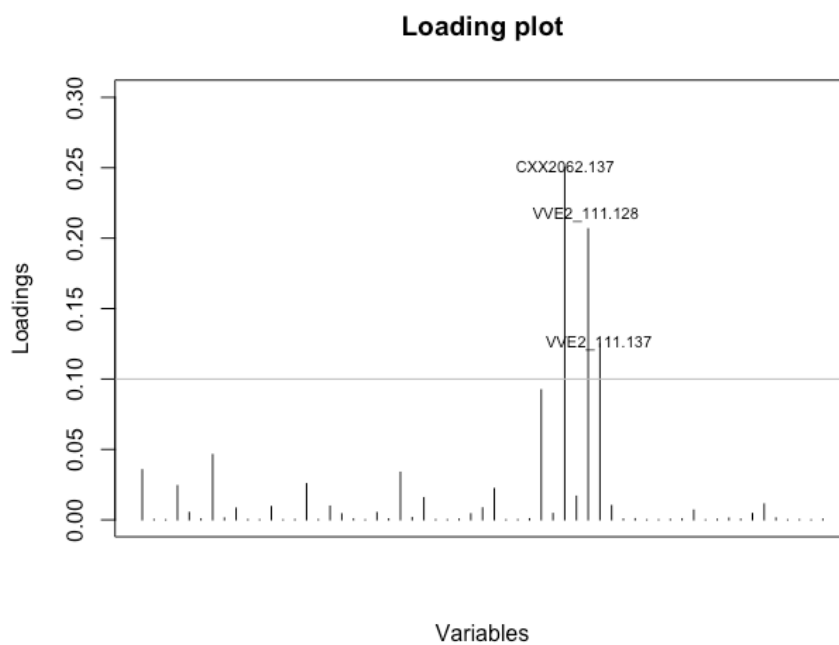
Figure A.4. Weight of each variable (locus loading) in DAPC analysis for swift fox population in Nebraska.
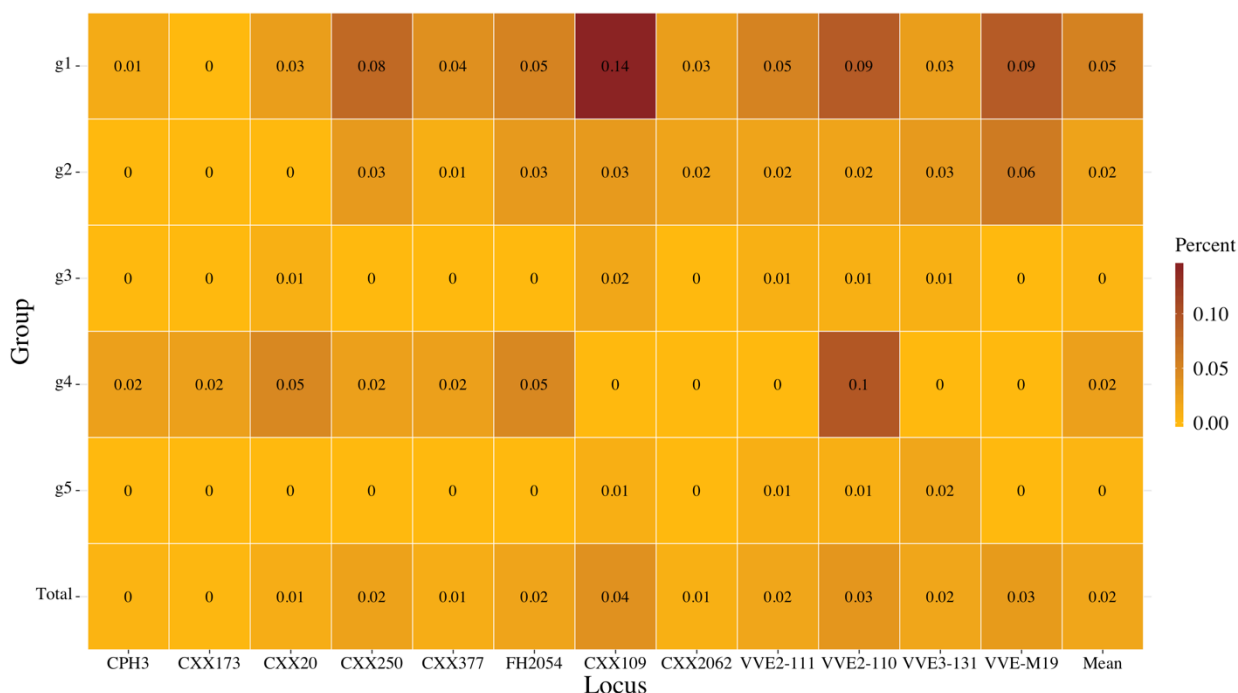
Figure A.5. Percent of missing data per locus and hypothesized group for swift fox (*Vulpes velox*) populations in four states (Wyoming, Colorado, Nebraska, and Kansas).

Figure A.6. Number of principal components (n=90) retained (a) and number of clusters (K=7), based on cumulative explained variance (0.99) and Bayesian Information Criterion (BIC) curve (b), used in DAPC analysis on swift fox populations for four neighboring states (Wyoming, Colorado, Nebraska, and Kansas). More than 99% of the variance was explained by choosing >90 PCs. The BIC curve decreased sharply at K=7, indicating that the data clusters optimally into seven groups.

Figure A.7. DAPC stratified cross-validation running 30 replicates and a number of PCs less than the total number of alleles in the data (a) and running 1000 replicates with 80-100 PCs retained, for both kept the number of discriminant functions fixed. The number of PCs that gave the highest percent of correctly predicted subsamples with the lowest error was 90. DAPC analysis on swift fox populations for four neighboring states (Wyoming, Colorado, Nebraska, and Kansas).
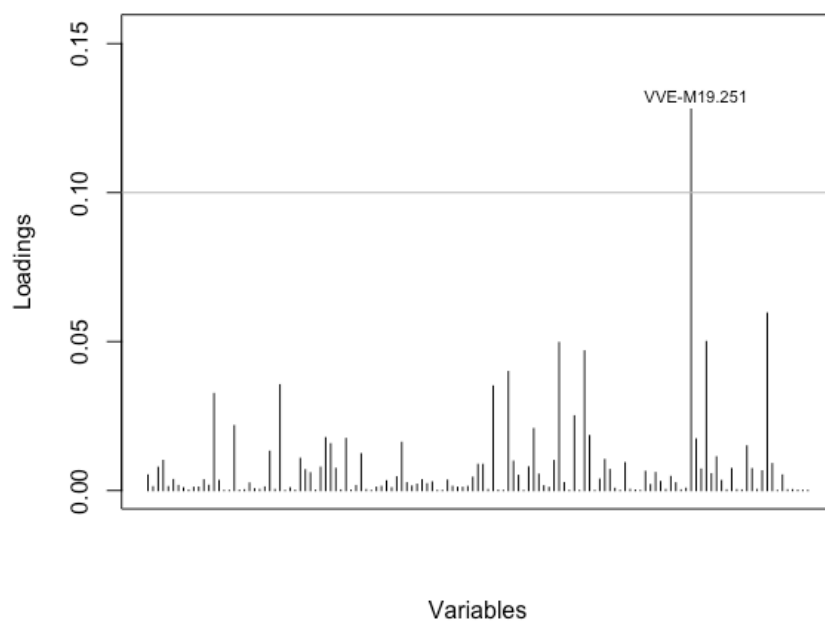
Figure A.8. Weight of each variable (locus loading) in DAPC analysis for swift fox population in four neighboring states (Wyoming, Colorado, Nebraska, and Kansas).
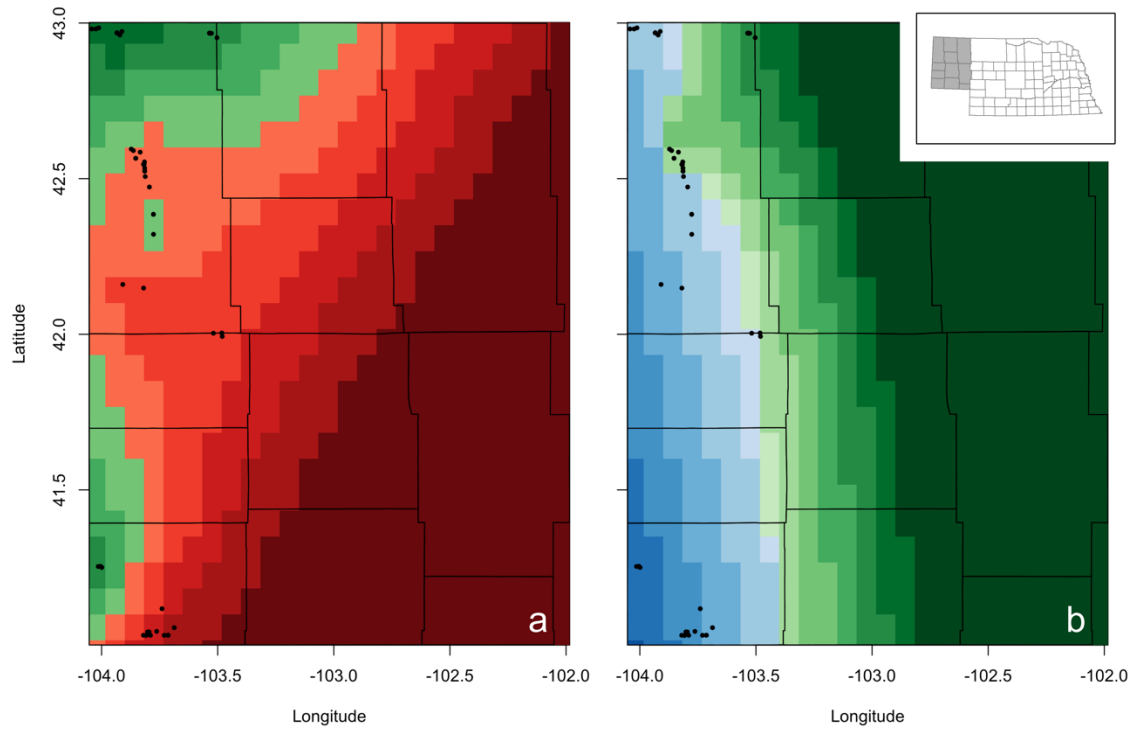
Figure A.9. Interpolated values of admixture coefficients using K = 2 (a) and K = 3 (b) for swift fox in Nebraska. Computed spatial estimates of admixture coefficients to depict the spatial predictions on geographic maps. Here the group with the maximal local contribution to membership is represented at each geographic point of the map.
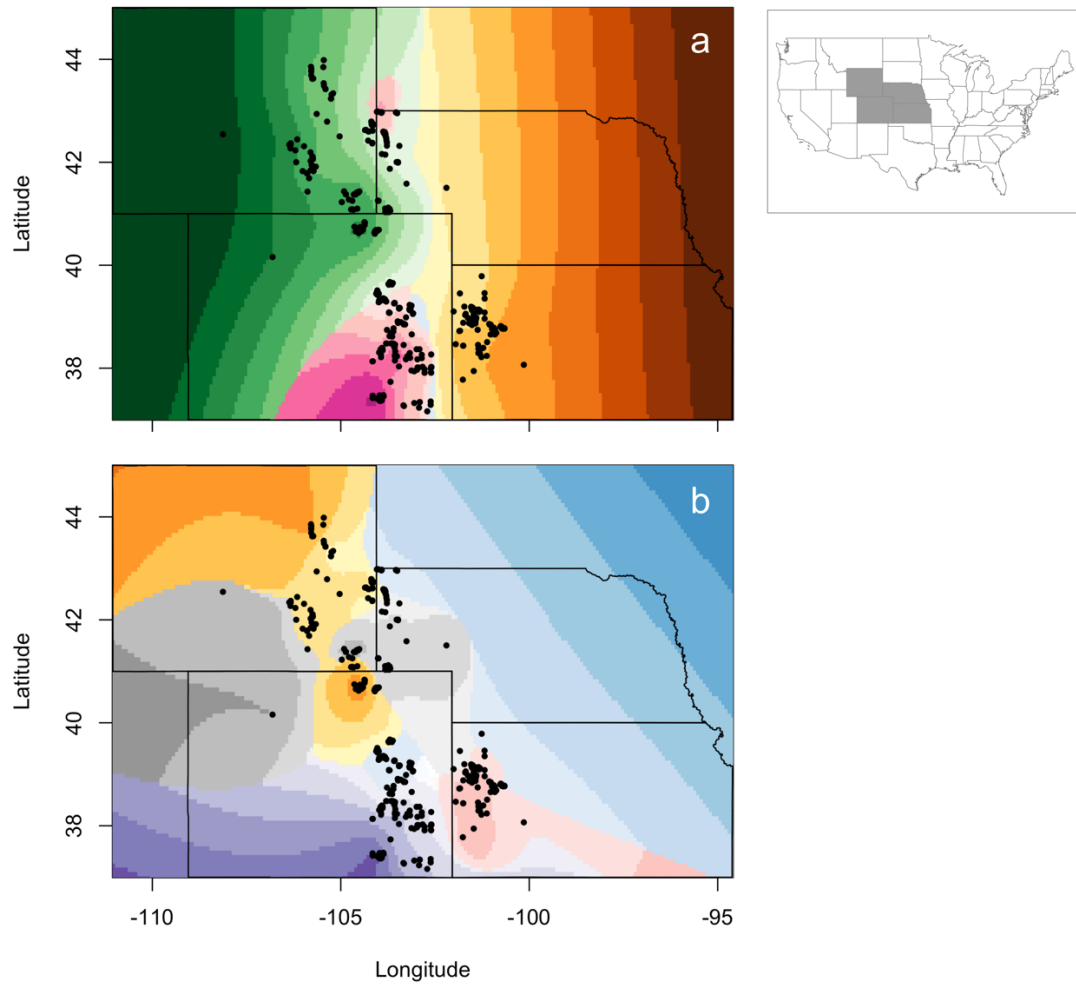
Figure A.10. Interpolated values of admixture coefficients using K = 5 (a) and K = 7 (b) for swift fox. Computed spatial estimates of admixture coefficients to depict the spatial predictions on geographic maps. Here the group with the maximal local contribution to membership is represented at each geographic point of the map.
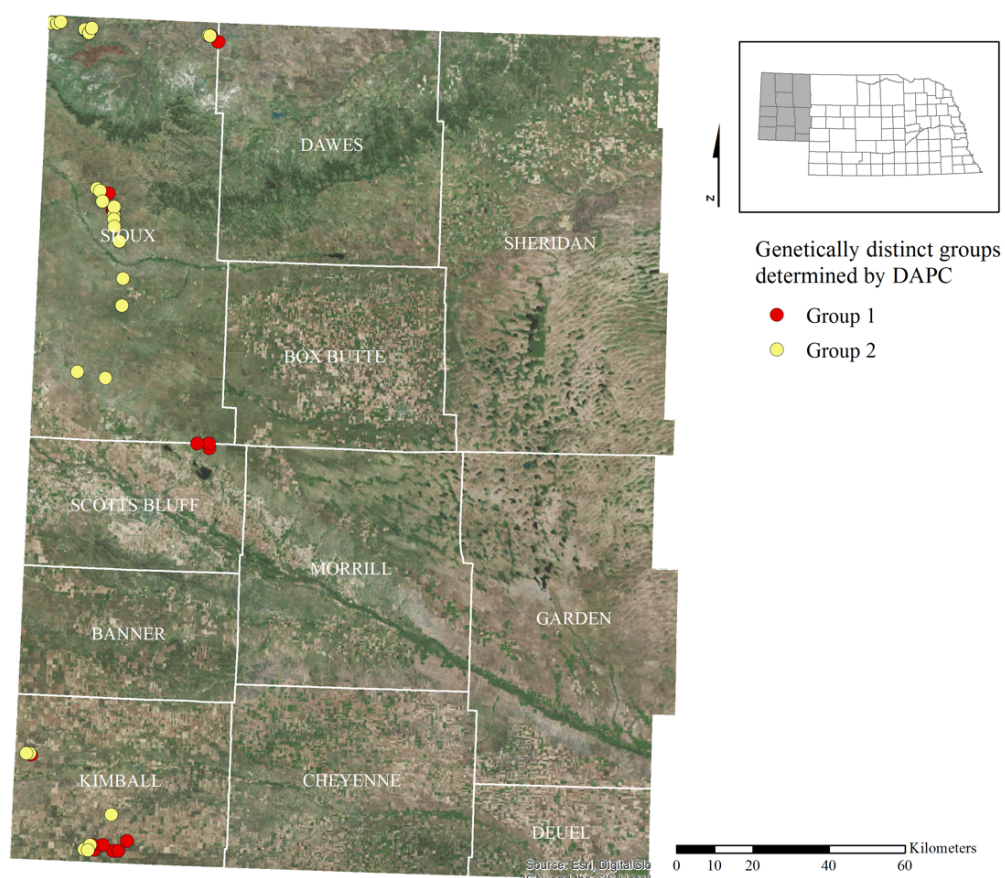
Figure A.11. Geographic location of samples assigned to two genetically distinct swift fox groups obtained by DAPC in Nebraska.
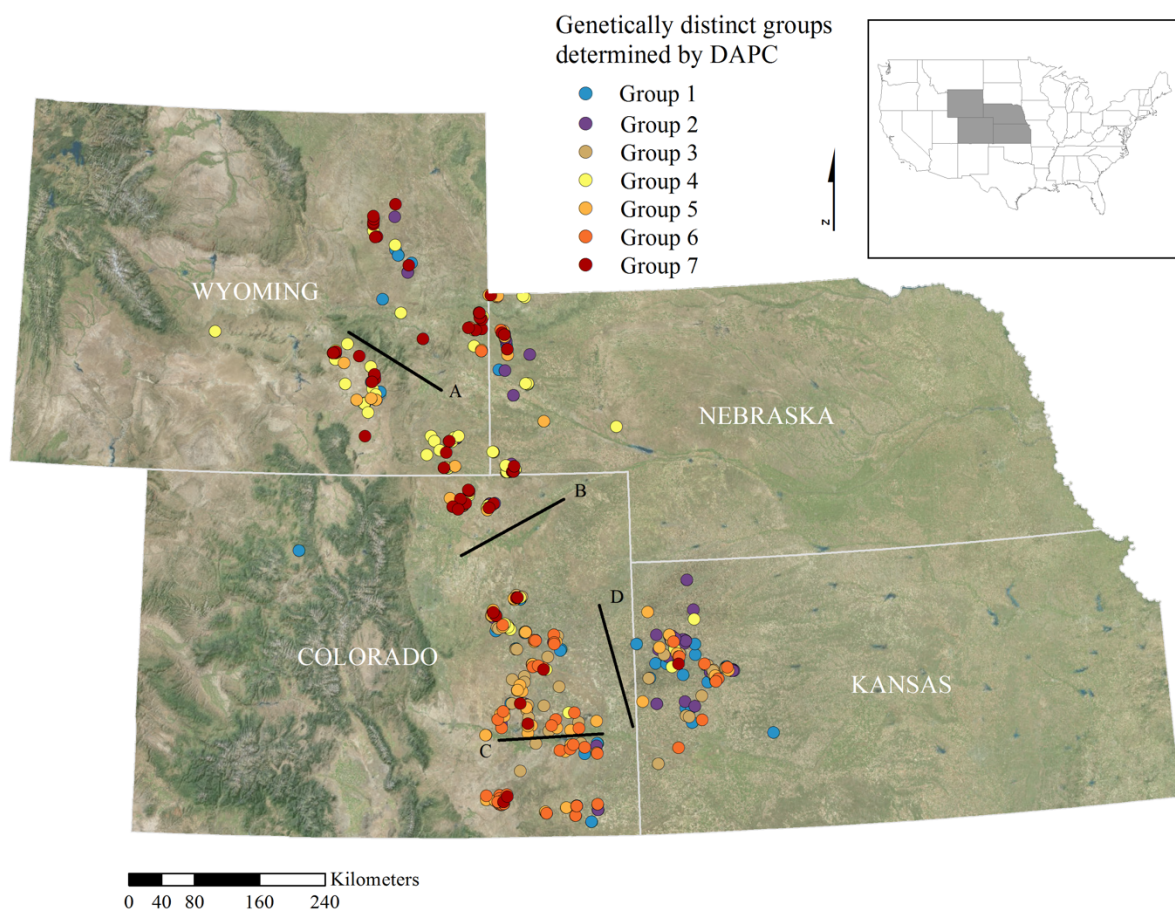
Figure A.12. Geographic location of samples assigned to seven genetically distinct swift fox groups obtained by DAPC in Wyoming, Colorado, Nebraska and Kansas.