Landscape effects on carnivore community dynamics in an agro-prairie ecosystem

by

Ty Jordan Werdel

B.S., Chadron State College, 2013
M.S., South Dakota State University, 2017

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Horticulture and Natural Resources
College of Agriculture

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Abstract

The Great Plains region has undergone extensive conversion of native prairies to agriculture production and energy development since European colonization. Temperate prairies, including remaining prairies within the Great Plains, are considered among Earth's most imperiled ecosystems. Prairie patches now exist as components of a landscape mosaic proportionately dominated by cultivated agriculture. These contemporary human-modified landscapes may structure species' distributions, influence community dynamics, and supplant established abiotic range-limiting processes. Understanding the direction and scale of these processes, and how they are affected by landscape composition and configuration, is necessary to enhance conservation efforts. Carnivore communities may be most affected by landscape changes due to negative interactions with humans and their inherent biological traits; however, information regarding landscape-scale effects on the existing suite of carnivores in the Great Plains is lacking. I examined how landscape composition and characteristics influenced site occupancy probabilities and turnover rates by swift foxes (*Vulpes velox*), the spatial and temporal interactions between swift foxes and coyotes (*Canis latrans*), and carnivore richness in agro-prairie ecosystems. Additionally, I strategically identified native prairie areas to focus conservation and management of remaining swift fox habitat.

During 2018-2020, I used detection/non-detection data from camera traps at 381 randomly selected sites distributed throughout a landscape mosaic comprising the westernmost 31 counties (7.16 million ha) of Kansas, USA. I subsequently used presence/absence data from these sites across three years to infer species-specific responses to landscape change and carnivore community dynamics. To evaluate effects of landscape composition and configuration on site occupancy probabilities and turnover rates by swift fox, I used a distance-weighted scale

of effect of landscape metrics within multi-season occupancy models. Swift foxes were more likely to occur at sites with moderate landcover diversity within 254.47 ha, greater proportion of shortgrass prairie (7.07 ha) and loamy soil types (0.79 ha), and lower proportions of Conservation Reserve Program (CRP) landcover (78.54 ha). Swift foxes were more likely to colonize sites with less diverse landcover, a greater proportion of loamy soil types, and lower proportions of CRP landcover. Swift foxes were insensitive to the proportion of row-crop agriculture surrounding sites (3.14 ha). To evaluate landscape composition effects on swift foxes and coyote (the apex predator in the region) spatiotemporal interactions, I used a Bayesian hierarchical multi-season occupancy model to evaluate spatial interactions, and a coefficient of overlap of temporal activity to assess factors affecting temporal interactions. Mean persistence of swift foxes differed across sites where coyotes were not detected (0.66; SE = 0.001) and where coyotes were detected (0.39; SE=0.001). The coefficient of overlap at sites surrounded by lower proportions of CRP ($\geq$0.10) differed (95% CIs did not overlap) from coefficient of overlap of all other landscape effects. The spatial distribution of swift foxes was positively influenced (Species Interaction Factor [SIF] > 1) by coyote presence through space and time at low proportions of CRP ($\leq$0.04). SIF decreased as proportion of CRP increased; however, Bayesian confidence intervals overlapped SIF = 1, suggesting that swift foxes were spatially distributed independent of coyotes through space and time at greater proportions of CRP (>0.04).

I used a structural equation model to test hypotheses of multiple direct and indirect relationships between landscape composition and configuration and prey availability on carnivore richness. My hypothesized model ($X^2 = 23.92$, df = 24, $P = 0.47$) explained 27% of the variance of carnivore richness. Agriculture, native prairie, landcover diversity, CRP, water availability, prey occurrence, and sampling effort all had direct positive effects on my measure of carnivore richness, while loamy tableland soil had only an indirect effect. To strategically identify native prairie areas for conservation of swift fox habitat, I created a predicted swift fox occupancy map based on my most-supported, stacked single-season occupancy model. I identified predicted occupancy rate (range = 0.01–0.46) where sensitivity equaled specificity (0.09) within a receiver operating characteristic curve, and reclassified the predicted occupancy map to include only predicted occupancy rates >0.09, and again for a more targeted approach with predicted occupancy rates >0.18. These two maps were intersected with a map of grassland proportions >0.60 to identify areas that were expected to have relatively high occupancy and survival rates by swift fox. Swift foxes were more likely to occur at sites with low levels of landscape diversity (β = -0.411 ± 0.140), greater proportions of native grassland (β = 0.375 ± 0.154) and loamy tableland soils (β = 0.944 ± 0.188), and lower proportions of CRP landcover (β = -1.081 ± 0.360). Identified native grassland conservation areas totaled 84,420.24 ha (mean patch size = 162.66 ha [SE = 29.67]). Conservation areas located on privately owned working lands included 82,703.86 ha, while conservation areas located within the boundaries of federal, state, and non-governmental organizations (NGO) parcels included 1,716.38 ha.

My results provide a unique understanding of how landscape composition and configuration, intraguild competition, and prey availability drive carnivore community dynamics in agro-prairie ecosystems. Additionally, my research elucidated constraints to range expansions for an iconic prairie-obligate carnivore (swift fox) at the edge of their range, while also identifying areas for strategic conservation for their populations.

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I am certain I have inadvertently left people out who truly deserve acknowledgement, so if that's you, I apologize, and thank you. I have worded this dissertation in the first-person form of "I", but for those of you reading, understand that this was the result of many people's collaborative work, support, and encouragement.

Dedication

This dissertation is dedicated to my grandmother, Phyllis Pettie, and my dad, Ron Werdel. I miss you both and hope you are proud of me.

Introduction

Biodiversity worldwide has continuously declined since the mid-1900s, with most losses in biodiversity in the last 100 years attributed to effects of human modified landscapes in the form of resource consumption, habitat loss and degradation, invasive species, and overharvest (Collen et al. 2009, Butchart et al. 2010). Vertebrates are particularly vulnerable to biodiversity loss, with 16 to 33% of species considered globally threatened (Schipper et al. 2008, Hoffmann et al. 2010). Among vertebrates, mammalian carnivores (hereafter carnivores) have experienced substantial population declines and are at increased risk of species extinction, mainly due to negative interactions with humans (e.g., unregulated harvest, persecution, loss of prey base) and biological traits (e.g., large body sizes, large home-ranges, low densities, slow life histories) which make them highly vulnerable to habitat loss and fragmentation (Cardillo et al. 2004, Ripple et al. 2014, Di Minin et al. 2016a, b). Habitat loss and fragmentation is substantially driven by agricultural expansion (Foley et al. 2005, 2011), making agricultural conversion of natural landscapes a significant threat to carnivore persistence (Woodroffe and Ginsberg 1998, Di Minin et al. 2016b)

Native grasslands (hereafter prairie) are climatically determined and occur where precipitation is below the minimum requirement for forests, but receive enough precipitation (usually seasonally) to sustain grass species (Poaceae; Lauenroth, 1979). It is important to distinguish between native prairie, comprised of mainly original plant communities (i.e., never cultivated or plowed), and prairie that has been established following anthropogenic conversion, such as deforestation to improve grazing production (DeFries et al., 1999; Lark et al., 2019). Native prairie coverage worldwide was once estimated at 25% of the earth’s land surface, or roughly 33 million km^2 (Shantz, 1954). These native prairies have provided many ecosystem services for millennia, including livestock forage, improvement of water quality, flood mitigation, wildlife habitat (greater wildlife biodiversity), and carbon sequestration superior to restored or planted grasslands (Bakker and Higgins, 2009).

In North America, native prairies once covered a great swath down the center of the continent, known as the Great Plains, and included approximately 162 million ha before the arrival of colonial Europeans (Samson and Knopf, 1994). As Euro-Americans settled western North America, there was a systematic conversion of native prairies to production agriculture, resulting in a loss of 70% of historical Great Plains prairie land area (Samson et al., 2004). Demand for biofuels and the continued rise in crop prices (e.g., corn [*Zea mays*]) will likely continue driving conversion of native prairies to cropland (Lark et al., 2020, 2019). Conversely, the Conservation Reserve Program (CRP), enacted in the United States in the 1985 Food Security Act, is a concerted effort to reduce soil loss in highly erodible agricultural lands by removing it from production, with additional benefits to wildlife including restoration of prairie habitat in these areas (Dunn et al., 1993).

Western Kansas, USA appropriately represents both a suite of carnivore species and an agriculturally dominated landscape matrix indicative of the contemporary short and mixed-grass prairie region of the Great Plains. Along with loss and conversion of native prairies in Kansas, carnivores such as gray wolves (*Canis lupus*), grizzly bears (*Ursus arctos horribilis*), and mountain lions (*Puma concolor*) were locally extirpated due to anthropogenic factors from most of the region during the 19th century (Choate 1987). The removal of these large apex carnivores left a void at the upper trophic level, likely benefitting medium-sized sympatric carnivores (e.g., coyotes [*Canis latrans*]; Levi and Wilmers 2012), while restricting small carnivores due to intraguild competition with coyotes (Mac Nally 1983, Palomares and Caro 1999, Fedriani et al. 2000, Linnell and Strand 2000).

A small carnivore species that may have been most negatively affected by prairie conversion in Kansas are swift foxes (*Vulpes velox*), small (~3 kg), prairie-obligate carnivores that occur at relatively low densities (range = 0.16 – 0.31 swift fox/km2 [Schauster et al. 2002; Karki et al. 2007]) across their geographic range (Sovada et al. 2009, Schwalm et al. 2014, Butler et al. 2020, Olimb et al. 2021). Their prey includes small mammals, insects, and birds (Kilgore 1969) and they dig burrows in suitable soils for protection from predators and to raise kits (Kitchen et al. 1999; Jackson and Choate 2000; Harrison 2003; Olimb et al. 2021). Swift fox populations were once extirpated across much of their range due to habitat loss and overkill (e.g., bounties, trapping, poisoning [Sovada et al. 2009]). They have since recolonized once-extirpated areas, but populations remain patchy, especially along contemporary range edges. The eastern edge of their current distribution is now a mosaic of remnant prairies, primarily grazed pastureland, embedded in a heterogeneous matrix of row-crop agriculture, energy development, urbanization, and other human infrastructure (Drummond et al. 2012; Samson and Knopf 1994).

Interspecific competition and predation risk among carnivores influence species distributions, resource selection, and population dynamics (Brown et al. 1999, Chase et al. 2002, Vanak et al. 2013). Intraguild predation and interference are apparent in systems where multiple species vie for similar resources, (Polis et al. 1989, Holt and Polis 1997, Linnell and Strand 2000, Vanak et al. 2013). Sympatric carnivores generally coexist at different trophic levels within a system, where apex carnivores exert a top-down advantage over less-dominant species (Fedriani et al. 2000, Jensen and Humphries 2019). Apex carnivores may restrict prey availability for subordinate species through interference, forcing smaller carnivores to forage under threat of predation (Holt and Polis 1997, Brown et al. 1999, Ritchie and Johnson 2009). Intraguild predation among carnivores is common and likely reduces densities and distributions of smaller species, resulting in local extirpation or exclusion (Mac Nally 1983, Palomares and Caro 1999, Fedriani et al. 2000, Linnell and Strand 2000).

Carnivore community richness has been shown to be influenced by environmental variables such as prey availability (i.e., occurrence; [Li et al. 2021]), landscape composition (Wait et al. 2018), landscape configuration (Moore et al. 2022), landcover diversity (Pita et al. 2009), water availability (Schuette et al. 2013), and suitable denning substrates (i.e., soil types; Kaufman et al. 2005). Native carnivore species known to occupy western Kansas include coyote, red fox (*Vulpes vulpes*), swift fox, bobcat (*Lynx rufus*), striped skunk (*Mephitis mephitis*), long-tailed weasel (*Mustela frenata*), black-footed ferret (*Mustela nigripes*), least weasel (*Mustela nivalis*), American badger (*Taxidea taxus*), and raccoon (*Procyon lotor* [Kansas Mammal Atlas 2022]).

During my dissertation research, I test the hypotheses that landscape composition and configuration, along with environmental variables, influence species' distributions, community dynamics, and range-limiting processes.

In Chapter 1, I examine how landscape composition and configuration influence occupancy, colonization, and extinction rates of swift fox at the eastern edge of their geographic range. I present strong evidence that swift fox occupancy and colonization are positively influenced by shortgrass prairie and loamy soil types, negatively associated with CRP, and insensitive to row-crop agriculture based on the current conditions of my study area.

In Chapter 2, I examine how landscape composition and configuration influence the spatial and temporal interactions of swift fox and coyotes. I show that proportion of area enrolled in CRP has the greatest effect on both spatial and temporal interactions between the two carnivores.

In Chapter 3, I identify native prairie areas for strategic conservation of swift fox habitat. I report that native grassland conservation areas totaled 84,420.24 ha. Conservation areas located on privately owned working lands included 82,703.86 ha, while conservation areas located within the boundaries of federal, state, and NGO parcels included 1,716.38 ha.

In Chapter 4, I examine how landscape composition and configuration influence carnivore richness. I show that 27% of the variance of carnivore richness can be explained through direct and indirect pathways of landscape and environmental variables.

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Chapter 1 - Scale-specific landscape effects impose range-limiting constraints on the distribution of a prairie-obligate carnivore

This chapter has been submitted to Landscape Ecology *and is formatted to journal specifications.*

Abstract

Human-modified landscapes can structure species' distributions and supplant traditional biotic range-limiting processes. Understanding the direction and scale of these processes is necessary to enhance species conservation efforts. I investigated how the distribution of a prairie-obligate carnivore, swift fox (*Vulpes velox*), is influenced by landscape pattern at the eastern edge of their occupied range. I also assessed the effects of a popular conservation effort, the Conservation Reserve Program (CRP), on swift fox distributions. I used three years of detection/non-detection data (2018 – 2020) from camera traps at 381 sites to evaluate the spatial distribution of swift foxes at the eastern edge of their extant range in Kansas, USA. I used Gaussian Kernel functions to identify optimal scales of effect for measured landscape covariates and multiseason occupancy models to reveal potential range-limiting constraints.

Swift foxes were more likely to occur at sites with moderate landcover diversity within 254.47 ha, greater proportion of shortgrass prairie (7.07 ha) and loamy soil types (0.79 ha), and lower proportions of CRP landcover (78.54 ha). Swift foxes were more likely to colonize sites with less diverse landcover, a greater proportion of loamy soil types, and lower proportions of CRP landcover. Swift foxes were insensitive to the proportion of row-crop agriculture surrounding sites (3.14 ha). Loamy soils and distribution of shortgrass prairie ecosystems may shape the periphery of the distribution for swift foxes. Landscape-scale use of CRP may constrain swift fox

distributions at their range edge because managed vegetation structure of CRP does not mimic native shortgrass prairie.

Introduction

Range-limiting processes for species are complex and do not always conform to climatic or geographic boundaries (Oldfather et al. 2020). Human-modified landscapes (e.g., urbanization, agriculture, energy development) occurring along species' range edges can create patchy and isolated habitats, further limiting species' distributions (Pfeifer et al. 2017). Carnivores are particularly susceptible to these changes due, in part, to their large home-range size requirements, relatively low densities, and frequent conflict with humans (Crooks 2002; Di Minin et al. 2016; Farris et al. 2015). Widespread changes over the last century have altered landscape composition and configuration in the Great Plains of North America (Hoekstra et al. 2005; Olimb and Robinson 2019) and likely affected the distribution patterns of carnivores in the region (Laliberte and Ripple 2004; Wait et al. 2018). Understanding the direction and scale of these range-limiting effects is necessary to help facilitate species' recolonization or more generally for conservation of carnivore species (Wolf and Ripple 2017).

Species distribution models can reveal the effects of landscape change on the spatial extent of species ranges (Caughley et al. 1988; Heim et al. 2017), but are sensitive to scale (Oldfather et al. 2020). Covariates used to characterize landscapes are often derived by extracting information (e.g., landscape composition and configuration) from within circular buffers surrounding discrete sampling sites where species' presence is known or estimated (e.g., Jackson and Fahrig 2015; Wait et al. 2018). This method assumes that all variables derived from within a particular buffer have a constant effect on a species regardless of distance from the measured response (Miguet et al. 2017). This assumption is likely unrealistic, prompting a more robust investigation of appropriate scales to assess effects (Zeller et al. 2014; Chandler and Hepinstall-Cymerman 2016; McGarigal et al. 2016; Miguet et al. 2017; Moll et al. 2020; Stuber and Gruber 2020). For instance, Moll et al. (2020) found that mammal species responded to urbanization at a maximal scale of effect, with the ecological response diminishing as distance from the response increased. The scale of effect varied among species, with no relationship between effect scale and species' body size or mobility, indicating that species-specific conservation efforts may not be effective when considering a static scale (e.g., home-range size; Moll et al. 2020).

Swift foxes (*Vulpes velox*) are small (~3 kg), prairie-obligate carnivores that occur at relatively low densities (range = 0.16 – 0.31 swift fox/km^2 [Schauster et al. 2002; Karki et al. 2007]) across their geographic range (Sovada et al. 2009; Schwalm et al. 2014; Butler et al. 2020; Olimb et al. 2021). Their prey includes small mammals, insects, and birds (Kilgore 1969) and they dig burrows in suitable soils for protection from predators and to raise kits (Kitchen et al. 1999; Jackson and Choate 2000; Harrison 2003; Olimb et al. 2021). Swift fox populations were once extirpated across much of their range due to habitat loss and overkill (e.g., bounties, trapping, poisoning [Fig. 1.1; Sovada et al. 2009]). They have since recolonized once-extirpated areas, but populations remain patchy, especially along contemporary range edges. The eastern edge of their current distribution is now a mosaic of remnant prairies, primarily grazed pastureland, embedded in a heterogeneous matrix of row-crop agriculture, energy development, urbanization, and other human infrastructure (Drummond et al. 2012; Samson and Knopf 1994). Good-quality swift fox habitat has been characterized as areas with greater proportions of native prairie (< 30 cm tall grasses; Kamler et al. 2003; Thompson and Gese 2007; Martin et al. 2007; Butler et al. 2020), with historical boundaries of swift fox ranges limited to within the extent of shortgrass and mixed-grass prairies. Additionally, areas with loamy soils (soils containing equal amounts of silt, sand, and clay textures; Weil and Brady 2016) can provide suitable substrates for swift fox den-sites (Jackson & Choate 2000).

The Conservation Reserve Program (CRP; FSA 2018) has been an effective conservation effort used, in part, to restore populations of prairie-obligate species (Herkert 1998; Dahlgren et al. 2016). For instance, researchers forecasted enhanced distributions of lesser prairie-chicken (*Tympanuchus pallidicinctus*, a threatened prairie-obligate grouse species; Sullins et al. 2019) populations when considering spatial prioritization of future CRP enrollments in the Great Plains. However, there is limited understanding of how the presence and amount of CRP landcover affects swift fox populations, though this conservation practice is prevalent throughout the eastern portion of their range in the United States (USDA Farm Service Agency 2021).

I used 3 years of detection/non-detection data from camera-trap sites distributed across western Kansas, USA to assess how landscape composition structures swift fox distributions along the eastern edge of their range. Additionally, my goal was to create a fine-scale contemporary swift fox distribution map at their range edge and identify potential range-limiting constraints. Because swift foxes are considered prairie-obligate carnivores, I predicted greater probabilities of site occupancy and greater rates of colonization at sites with greater proportions of shortgrass prairie. I also predicted greater occupancy and colonization rates at sites composed of more loamy soil coverage, as these areas may provide suitable substrates for burrow construction. I expected areas converted to row-crop agriculture and other land-use types would not mimic the structure and composition of shortgrass prairie ecosystems. Thus, I predicted lower occupancy and colonization rates at sites with greater proportions of row-crop agriculture and diversity of landcover types. CRP is the most widespread conservation effort (initially implemented to reduce soil erosion and improve water quality) in my region (547,750 ha; FSA 2018), designed in part, to restore and bolster populations of species associated with prairie landcover. The vegetative structure of CRP plantings, however, do not mimic historical shortgrass prairie ecosystems and may preclude swift foxes from recolonizing into these areas. Thus, I predicted lower occupancy and colonization rates at sites with greater proportions of land devoted to CRP.

Methods

Study Area

My study occurred within the 31 westernmost counties of Kansas, USA (7,160,077 ha; -100.815301, 38.492366 [center]; Fig. 1.1), and encompassed the contemporary eastern edge of swift fox range within the state (Sovada et al. 2009). Average annual precipitation ranged from 31 to 107 cm, and temperatures ranging from 10 to 14° C (PRISM Climate Group 2021). This region was characterized by four major land resource areas (NRCS Soils 2021): Central High Tableland, Rolling Plains and Breaks, Southern High Plains, and Central Rolling Red Plains. The region was sparsely populated (1 – 13 people per km^2) and included a moderate elevation gradient (412 – 1355 m). My study area was historically comprised of short, mixed, and sand-sage prairies, but has undergone substantial conversion since the colonization of Euro-American settlers. Within the study area, row-crop agriculture was the dominant land-use type (62%) followed by shortgrass (15%) and mixed-grass prairie (12%). Energy development was also widespread, including active oil wells (*n* = 20,093) and wind turbines (*n* = 1,429) distributed throughout the study area (Kansas Geological Survey 2021).

Site Selection and Camera Placement

I randomly selected 381 sites, separated by ≥ 2-km ($\bar{x}$ = 8.16 km, SD = 3.61) to limit the possibility of a single swift fox captured on multiple cameras (swift fox home-range ≈ 12.56 km^2 [Kamler et al. 2003]), using a geographic information system (ArcMap v. 10.8). Each site consisted of a single motion-sensing camera trap (Bushnell Trophy Cam®; Bushnell Corporation, Overland, KS, USA) and represents swift fox habitat use at that site. All sites were considered spatially independent (Kitchen et al. 1999; Kamler et al. 2003; Sovada et al. 2009; Lebsock et al. 2012). I established camera traps nearest their exact randomly generated location unless impractical due to inaccessible private land or increased likelihood of camera destruction (e.g., center of agricultural fields). In these cases, I adjusted the camera-trap location to the nearest suitable location. I affixed camera traps to a metal post 40 cm above ground and oriented North or South to avoid solar interference. To potentially increase detections of swift foxes, I used an olfactory attractant at each site, which was a mixture of skunk essence (F&T Fur Harvester's Trading Post, Alepna, MI, USA) and petroleum jelly smeared on a wooden stake positioned 3 m in front of the camera (Stratman and Apker 2014). I removed any herbaceous material (hand-held weed cutter) within the field-of-view of each camera that might cause visual obstructions or result in a large number of images resulting from wind-blown vegetation. Camera traps were functional at each site for 28 days (Wait et al. 2018). I returned to each site every ~14 days to refresh skunk essence and replace batteries and digital memory cards.

I sampled sites from 5 May – 2 November 2018 (*n* = 375), 20 May – 2 October 2019 (*n* = 361), and 22 April – 28 September 2020 (*n* = 360). Due to changing accessibility on private lands, I could not sample all sites during 2019 and 2020. I archived site-specific photo data in a custom database (Colorado Parks and Wildlife Photo Warehouse 4.0, Colorado Parks and

Wildlife, Fort Collins, CO, USA) and manually scanned all photos from each site for detection/non-detection of swift foxes. I considered a site occupied during a given year if I observed ≥ 1 photo of a swift fox during the 28-day sampling period for that year.

Landscape Characterization

I created a custom landcover raster (30x30 m) by merging and reclassifying three raster datasets to accurately represent biologically important spatial data: lands enrolled in CRP (FSA 2018), CropScape (CropScape 2018), and PRAIRIEMAP (PRAIRIEMAP 2003). The final reclassified raster map included 14 landcover classes. I converted soil distribution polygons to raster format to characterize the spatial distribution of soil types across my study area (30x30 m; Web Soil Survey 2018). The extent of all raster layers extended 10 km beyond the boundaries of my study area to ensure raster information would be incorporated into site buffers near the edge of my study area.

Distance Weighted Scale of Effect

I created 200 concentric buffers centered on each site, each with a radii increasing by 50 m increments from 50 – 10,000 m (Moll et al. 2020). From within each buffer, I extracted landcover proportions of shortgrass prairie (SGP), row-crop agriculture (AG), CRP, and loamy soil (LOAMY), as well as diversity of landcover (SHDI; Table 1.1), using R 4.0.3 (R Core Team 2021) “landscapemetrics” package (Hesselbarth et al. 2019).

To determine the scale of effect for each covariate, I employed a distance-weighted smoothing function, assuming that the effect of a particular covariate is strongest near the sampled site and would diminish with distance (Miguet et al. 2017; Yeiser et al. 2018; Moll et al. 2020). To determine the optimal scale of effect for each covariate (C_w), I calculated the weighted average of C_w at each of *j* sites following methods similar to Miguet et al. (2017) and Moll et al. (2020):

$$C_{w(j)} = \sum_{m} w_m \times C_{m(j)}$$

in which $C_{m(j)}$ is the mean raster value of the covariate of interest (e.g., SGP raster extracted from landcover raster) in ring *m* encircling site *j*, while w_m is the weight of ring *m* calculated according to a Gaussian kernel:

$$w_m = \frac{\exp\left(-\frac{d_{m(j)}^2}{2\sigma^2}\right) \times A_m}{\sum_m exp\left(-\frac{d_{m(j)}^2}{2\sigma^2}\right) \times A_m}$$

where $d_{m(j)}$ is the radius of ring *m* encircling site *j*, A_m is the area of ring *m*, and σ is a scaling parameter (a larger σ value produces a flat kernel, whereas a smaller σ value produces a sharply declining kernel as distance increases; Moll et al., 2020) indicating how rapidly the effect of a covariate decays with increasing distance (Chandler and Hepinstall-Cymerman 2016; Yeiser et al. 2018). All kernels (n = 200) for each site were estimated from a range of σ (50 – 10,000 m), at 50 m increments. I used optimal scales of effect for each covariate to create model sets within a pseudo-optimized multiple scales framework as defined by McGarigal et al. (2016). Akaike's Information Criterion (corrected for small sample sizes; $\mathrm{AIC_C}$) scores were used to identify the optimal scale of effect for each covariate within multi-season occupancy models (R 4.0.3, unmarked package v.1.0.1; Fig A.1 [MacKenzie et al. 2003; Miguet et al. 2017; Chandler et al. 2020]). These analyses revealed the optimal scale of effect (buffer radius = σ [m]), and associated area of landscape (area of buffer with radius = σ [ha]), for each covariate: SGP = 150 m (7.07 ha), AG = 100 (3.14 ha), CRP = 500 m (78.54 ha), LOAMY = 50 m (0.79 ha), and SHDI = 900 m (254.47 ha, Fig 1.2).

Multi-Season Occupancy Modeling

I used multi-season occupancy models to assess my measured covariate effects on site detection, occupancy, and colonization by swift foxes (R 4.0.3, unmarked package v.1.0.1; MacKenzie et al. 2003; Chandler et al. 2020). I assumed that the probability of swift fox occurrence and turnover at sites reflected habitat use during a biologically closed sampling season (i.e., no dispersal and females were rearing kits). All covariates were standardized prior to analysis, and I did not include any correlated ($|r| \geq 0.60$) covariates within the same model. I structured my detection histories to include 28 independent, 1-day surveys at each site, each year (*sensu* (Fidino et al. 2020). I developed three detection covariates to control for survey-specific variation in swift fox detection. To control for unmeasured within-year effects on detection, I modeled the day of year (DOY; days since 1 January of survey year; range = 112 – 308]). I controlled for the potential of diminishing attractant by including a covariate representing the number of days since scent was applied or reapplied at each site (Scent). Camera traps were occasionally destroyed or knocked down by cattle or farm equipment during the 28-day survey period (resulting in a decreased or ineffective camera view field), so I developed a covariate to include the number of days cameras were inactive or had altered field-views at each site (Altered). I created a candidate detection model set ($n = 8$) using models incorporating the single (DOY, Scent, Altered) and additive effects of these covariates (DOY + Scent, DOY + Altered, Scent + Altered, DOY + Scent + Altered) along with a constant model (Intercept Only). To determine if my sampling approach provided an adequate duration to detect swift foxes, I assessed the cumulative daily detection probability ($1 - [1\text{-P}]^k$, where P = daily detection probability from my most-supported detection model, k = number of daily surveys; Mackenzie 2006) across the entire 28-day sampling period.

I used a sequential-by-sub model strategy, with each subsequent sub-model dependent upon the selected model structure from the previous stage (Morin et al. 2020). I first identified my most-supported detection model, then included this model in all subsequent models of initial site occupancy and colonization (also included most-supported initial site occupancy model). Because of model convergence issues, I did not model covariates for local extinction (extinction was held constant). I developed *a priori* candidate model sets for initial site occupancy and colonization (pseudo-optimized multiple scales [(McGarigal et al. 2016]) including: optimal scale of effects of SGP (σ = 150 m), AG (σ = 100 m), CRP (σ = 500 m), LOAMY (σ = 50 m), and SHDI (σ = 900 m). I assessed 48 models for both initial occupancy and colonization model sets including single and additive effects of these covariates, and a constant model (Intercept Only; Table A.1). Models were ranked using $\mathrm{AIC_C}$, and models $\leq$2.00 $\Delta\mathrm{AIC_C}$ were considered competitive (Burnham and Anderson 2002). Within each competitive model set, I selected my most-supported model by assessing relative changes in model deviance (Burnham and Anderson 2002; Arnold 2010). I further assessed predictor importance by assessing cumulative model weights. Once I identified my most-supported site occupancy model, I created a contemporary predictive swift fox distribution map using its associated covariate estimates (ArcMap v. 10.8; Karanth et al. 2009; Long et al. 2011).

Results

I collected 5,217,641 photos (2018 = 1,734,588; 2019 = 1,942,072; 2020 = 1,540,981) over 27,954 camera-trap days (2018 = 10,351; 2019 = 9,478; 2020 = 8,125). Cameras were active an average of 25 days (SE = 0.154, range = 2-28) and unaltered an average of 22 days (SE = 0.222, range = 0-28). I observed swift foxes in 341 photos from 55 sites across all three years. I did not observe swift foxes at 326 sites; no sites were occupied for three consecutive years.

Naïve site occupancy (2018 = 0.08 [sites = 32], 2019 = 0.04 [sites = 16], 2020 = 0.06 [sites = 23]), colonization (2019 = 0.04 [sites = 13], 2020 = 0.05 [sites = 17]), extinction, (2019 = 0.07 [sites = 27], 2020 = 0.03 [sites = 10]), and persistence (2019 = 0.01 [sites = 3], 2020 = 0.01 [sites = 5]) were dynamic among years.

My only competitive detection model included the additive effects of DOY, Scent, and Altered (Table 1.2). I was more likely to detect swift foxes later in the year (β = 0.006 ± 0.002). Additionally, I was less likely to detect swift foxes as my scented bait diminished (β = -0.056 ± 0.020) and when the camera field-view was altered (β = -1.296 ± 0.356). Sampling sites for 28 days yielded a 0.973 cumulative detection probability (per survey detection from most-supported detection model = 0.121 [SE = 0.017]). On average, I documented my first observation of a swift fox at a site nine days after the camera was first activated (SE = 0.933, range = 1-26; Fig 1.3).

My most-supported model for initial occupancy included the quadratic effect of SHDI and linear effects of SGP, LOAMY, and CRP (*w* = 0.61, Table 1.2). Swift foxes were more likely to occur at sites with moderate levels of landscape diversity (linear β = -1.523 ± 0.484, quadratic β = -0.816 ± 0.279; Fig 1.4A), greater proportions of shortgrass prairie (β = 0.574 ± 0.235; Fig 1.4B) and loamy tableland soils (β = 1.240 ± 0.273; Fig 1.4C), and lower proportions of CRP landcover (β = -1.707 ± 0.671; Figs 1.4D and 1.5). AG was present in the competitive model set (95% CI overlapped 0), but its addition did not improve model fit (Table 1.2). Occupancy probabilities adjusted for detection (2018 = 0.09 [SE= 0.02], 2019 = 0.07 [SE= 0.02], 2020 = 0.07 [SE= 0.02]) varied slightly among years. Models including LOAMY, SGP, $SHDI^2$, and CRP were included in 1.00, 0.86, 1.00, and 1.00 model weights, respectively.

There was moderate model-selection uncertainty in my colonization model set which included five competitive models (Table 1.2). My top and most-supported model (LOAMY +

CRP + SHDI) was the most parsimonious. Inclusion of other covariates (AG, SGP, and $SHDI^2$) did little to improve model fit and those covariates had 95% CI overlapping zero. Model estimates suggest swift foxes were more likely to colonize sites with less diverse landcover types (SHDI, $\beta = -0.429 \pm 0.196$; Fig 1.6A), a greater proportion of loamy tableland soils (LOAMY, $\beta = 0.622 \pm 0.199$; Fig 1.6B), and lower proportions of CRP landcover (CRP, $\beta = -1.697 \pm 0.738$; Fig 1.6C). Colonization rates adjusted for detection (2019 = 0.04 [SE= 0.01], 2020 = 0.06 [SE= 0.01]) varied between years. Models including variables LOAMY, CRP, and SHDI were represented in 0.95, 0.89, and 0.53 model weights, respectively.

Discussion

As predicted, swift foxes were more likely to occupy sites with greater proportions of shortgrass prairie and loamy tableland soil, and less likely to occupy sites with greater proportions of CRP. Swift foxes were also more likely to occur at sites with moderate amounts of landcover diversity within 900 m (255 ha); however, occupancy probabilities diminished as landcover diversity increased. Swift foxes were also more likely to colonize areas with greater proportions of loamy soil, and less likely to colonize areas with greater proportions of CRP and greater landcover diversity. Swift fox distributions seemed insensitive to the amount of row-crop agriculture on the landscape.

Consistent with previous research, swift foxes were more likely to occur in areas with greater proportions of shortgrass prairie. I identified this effect at a much finer scale (~7 ha) than previously documented (Butler et al. 2020 [314 ha]; Kamler et al. 2003 [~10,000 ha]; Martin et al. 2007 [3072 ha]). This result may reflect the relatively small mean patch sizes of shortgrass prairie within my study area (3.24 ha; SE = 0.17; range = 0.09 – 25,554 ha; median = 0.18 ha). Within my study site on the eastern edge of their range, my results suggest that swift foxes are occupying relatively small patches of shortgrass prairie embedded in agroecosystems. By using smaller patches of shortgrass prairie embedded within other landcover types, swift foxes may be minimizing intraspecific or interspecific resource competition and maximizing population fitness in contemporary landscapes (Durrett and Levin 1998; Thompson and Gese 2007; Kozlowski et al. 2008). Although outside the scope of this study, intraguild competition with coyotes (*Canis latrans*) may also preclude swift foxes from using the good-quality habitats in my study area (Polis et al. 1989; Thompson and Gese 2007). Coyotes and swift foxes exploit many of the same prey species (Kilgore 1969; Gese et al. 1988), and coyotes may exclude swift foxes from areas with greater prey densities through direct predation (Sovada et al. 1998) or spatiotemporal shifts in space use driven by fear of predation (Brown et al. 1999; Laundré et al. 2010). My results also suggest that swift foxes may not necessarily need large contiguous patches of shortgrass prairie, but even relatively small patches (often overlooked by managers) may be capable of sustaining populations. Further investigation of functional thresholds for shortgrass prairie patch sizes and isolation distances on swift fox population demographics are timely and warranted (Goodwin and Fahrig 2002).

The amount of loamy soil coverage was positively associated with both site occupancy and colonization and most influential at a finer scale (~1 ha) compared to other covariates. Swift fox dens in this region occur across both agriculture and grassland areas, but are uniformly present in loamy soil types (Jackson and Choate 2000). Loamy soil types are friable enough for digging and cohesive enough to not result in den structural failure (Jackson and Choate 2000; Weil and Brady 2016), providing an adequate substrate for swift fox dens. Small mammals also utilize loamy soils for burrowing (black-tailed prairie dog [*Cynomys ludovicianus*]; Desmond et al. 2000; Kretzer and Cully 2001) and may provide an indirect indication of prey availability.

Soil textures (e.g., percentage of sand and clay), at a similar scale (1 ha), were important for determining habitat suitability for swift foxes in the Northern Great Plains (Olimb et al. 2021). Loamy soil types in my region occur in areas with gentle slopes (0-15%) and are generally greater in fertility, making these areas candidates for conversion to row-crop agriculture (EDIT 2021; Web Soil Survey 2021). Managers cannot actively expand the distribution of loamy soil types as they were formed over millennia (Weil and Brady 2016). The distribution of this soil type, however, may serve as geologic boundary for swift foxes along their range edges, suggesting that targeted conservation of native shortgrass prairies in these soil types may aid in recolonization efforts.

My results suggest swift foxes use areas with less diverse landcover types, likely because greater landcover diversity reduces the amount, or modifies the configuration or patch size, of shortgrass prairie present on the landscape. Swift fox occupancy was greater at sites with moderate landcover diversity up to a threshold (SHDI = 1.35, range = 0.55 – 2.25; ~255 ha), but as the number of landcover types surrounding sites increased they were less likely to occupy those sites. Additionally, swift foxes were less likely to colonize areas with greater landcover diversity. As landcover diversity increases, shortgrass prairie patch sizes may also decrease, further reducing good-quality swift fox habitat or connections between good-quality habitats (Kamler et al. 2003; Martin et al. 2007; Butler et al. 2020). Moving through non-shortgrass prairie landcover types may expose swift foxes to predation or human conflict (Sovada et al. 2003; Thompson and Gese 2007). Re-establishing connectivity between shortgrass prairie patches may be necessary to facilitate recolonization of swift foxes at the edge of their range (Cushman et al. 2013; Schwalm et al. 2014).

Swift foxes were less likely to occupy and colonize sites surrounded by greater proportions of CRP at a larger scale (~80 ha). Although CRP has clearly been a successful conservation tool for prairie-obligate species including lesser prairie chickens (Dahlgren et al. 2016; Sullins et al. 2019), grasshopper sparrows (*Ammodramus savannarum*; Herkert 1998), and coyotes (Kamler et al. 2005), these efforts may be indirectly constraining distributions of swift foxes on the edge of their range. Seeding mixtures associated with CRP focus on creating vegetation communities not associated with short grass prairie communities (Sovada et al. 2003; Plumb et al. 2019), resulting in taller vegetation (e.g., big bluestem [*Andropogon gerardii*], switchgrass [*Panicum virgatum*]) suitable for other species such as non-native ring-necked pheasant populations (*Phasianus colchicus*; Nielson et al. 2008). CRP seeding mixtures that shift vegetation composition to taller species (>30 cm) may inhibit the visual range of swift foxes and increase predation risk in these areas (Kamler et al. 2003; Thompson and Gese 2007). Increasing amounts of CRP along swift fox range edges may reduce functional connectivity among habitats and further isolate populations. Vegetation structure along the eastern edge of swift fox range is dynamic, oscillating between mixed and shortgrass species depending on climate and precipitation (Küchler 1972). CRP is also somewhat variable in species composition and structure, varying by time since contract year (succession), annual average precipitation at site, and management application (Sullins et al. 2019). It is clear that future work should focus on understanding the population-level consequences for swift foxes (e.g., survival, population growth) in areas with greater proportions of CRP landcover. Fine scale information (e.g., contract year, management plan, patch-specific characteristics) may provide a clearer picture of how CRP influences swift fox populations. Additionally, it may be necessary to understand how the spatial pattern of CRP, along with other human-modified landcover types, affects swift fox distributions and population demography.

My study found swift fox distributions were insensitive to the amount of row-crop agriculture surrounding sites, although Butler et al. (2020) suggested row-crop agriculture was poor habitat for swift foxes in northeastern Montana, USA at a much larger scale (314 ha), particularly during periods of greater crop height (i.e., July-August in Kansas; Sovada et al. 2003). It is unclear why I did not detect a similar negative effect of row-crop agriculture on swift fox distributions in my study area. Small mammals can be most abundant within tall vegetation that provide more food resources (Benedek and Sîrbu 2018), and grassy row-crop field borders (i.e., fencerows, roadsides, and crop edges) may provide refugia (Bilenca et al. 2007). For instance, deer mice (*Peromyscus maniculatus*) can be more abundant in landscapes dominated by row-crop landcover (Heisler et al. 2013) and small mammal abundance may be greatest in post-harvested fields (Kaufman et al. 2000). Swift foxes may be exploiting prey resources available in these prairie field edges though they may not represent large, contiguous tracts of short grass prairie. Swift foxes select natal den sites in the spring and early summer (Pruss 1999), which coincides with early growth spring-planted crops (e.g., corn), winter conservation cover crops, and harvest of fall-planted crops (e.g., wheat) in Kansas. Swift foxes select den sites during seasons when vegetation height is very low, appearing to be kit-rearing habitat (i.e., low visual obstruction to detect predators, increased prey abundances; Pruss 1999), but vegetation growth or harvest of crops may reduce habitat quality in these areas once dens are established. Although anecdotal, I observed a swift fox den (with kits) in a fallow agricultural field that was disked under while producers were preparing to plant crops in late spring. Future research should investigate the annual effects of row-crop agriculture on swift fox population demographics and spatial ecology.

Changing landscapes may supplant historic abiotic range-limiting processes for swift foxes occurring in the Great Plains (e.g., climate, elevation, precipitation; Gaston 2003) and future climate change will likely further exacerbate the effects of landscape change (Hickling et al. 2006; Moritz et al. 2008; Hetem et al. 2014). Thus, identifying range-limiting factors within human-dominated ecosystems may help managers forecast and mediate the negative effects of landscape change in light of climate change. My study revealed scale-specific effects that may limit range expansions of swift foxes at the eastern edge of their contemporary range. There is opportunity for swift foxes to expand their range to include areas once occupied before extirpation (Olimb et al. 2021), but conservation efforts must identify and focus on scale-specific adaptive management of landscapes at range edges to realize range expansions.

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Table 1.1 Descriptions of covariates, origin of spatial data, and associated summary statistics used to model initial site occupancy probability and colonization rates of swift fox (*Vulpes velox*) in western Kansas, USA.

Covariate	**Description**	**Mean**	**Minimum**	**Maximum**	**SD**
SGP	Proportion of site composed of shortgrass prairie landcover (PRAIRIEMAP 2003)	0.18	0.00	1.00	0.16
AG	Proportion of site composed of row-crop agriculture landcover (CropScape 2018)	0.37	0.00	1.00	0.20
CRP	Proportion of site composed of landcover enrolled in the Conservation Reserve Program (FSA 2018)	0.09	0.00	1.00	0.12
LOAMY	Proportion of site composed of loamy tableland soils (Web Soil Survey 2018)	0.33	0.00	1.00	0.34
SHDI	Shannon-Wiener Diversity Index of landcover surrounding site (PRAIRIEMAP 2003; CropScape 2018; FSA 2018)	1.67	0.55	2.25	0.25

Table 1.2 Model-selection statistics for competitive models of detection, initial site occupancy (2018), and site colonization (2019-2020) by swift fox (*Vulpes velox*) in western, KS, USA. I present competitive models ($\leq 2\ \Delta\text{AIC}_\text{C}$) along with the null model (Intercept Only) for each parameter. Covariates include day of year (DOY), number of days since bait was applied or reapplied at each site (Scent), and days with an altered camera view field (Altered), and distance-weighted effects of landcover diversity (SHDI), proportion shortgrass prairie (SGP), loamy tableland soils (LOAMY), proportion of conservation reserve program (CRP), and proportion of agriculture (AG). K = number of model parameters, $\Delta\text{AIC}_\text{c}$ = difference between AIC_c model value compared to the top model, *w* = Akaike weight, -2LL = log-likelihood * (-2), indicating model fit.

Model	**K**	**AIC_C**	**$\Delta\text{AIC}_\text{C}$**	***w***	**-2LL**
Detection					
DOY + Scent + Altered	7	1728.33	0.00	0.96	1714.04
Intercept Only	4	1755.90	27.57	0.00	1747.80
Occupancy					
LOAMY + CRP + SGP + SHDI^2	12	1670.07	0.00	0.61	1645.22
LOAMY + CRP + SGP + SHDI^2 + AG	13	1671.84	1.77	0.25	1644.84
Intercept Only	7	1728.33	58.26	0.00	1714.04
Colonization					
LOAMY + CRP + SHDI	15	1633.33	0.00	0.23	1602.02
LOAMY + CRP + SHDI + AG	16	1634.72	1.39	0.11	1601.24
LOAMY + CRP + SHDI + SGP	16	1634.76	1.43	0.11	1601.28
LOAMY + CRP + AG	15	1635.01	1.68	0.10	1603.70
LOAMY + CRP + SHDI^2	16	1635.17	1.84	0.09	1601.68
Intercept Only	11	1685.74	52.41	0.00	1663.04

Figure 1.1 Study area in Kansas, USA (7,160,077 ha) where I sampled camera-trap sites (2018 = 375, 2019 = 361, 2020 = 360) for detection of swift fox (*Vulpes velox*) for 3 years (2018-2020). County-level historical (i.e., pre-European encroachment and colonization) and contemporary swift fox range in the U.S.A. (Sovada et al., 2009) is displayed relative to my sampling sites.

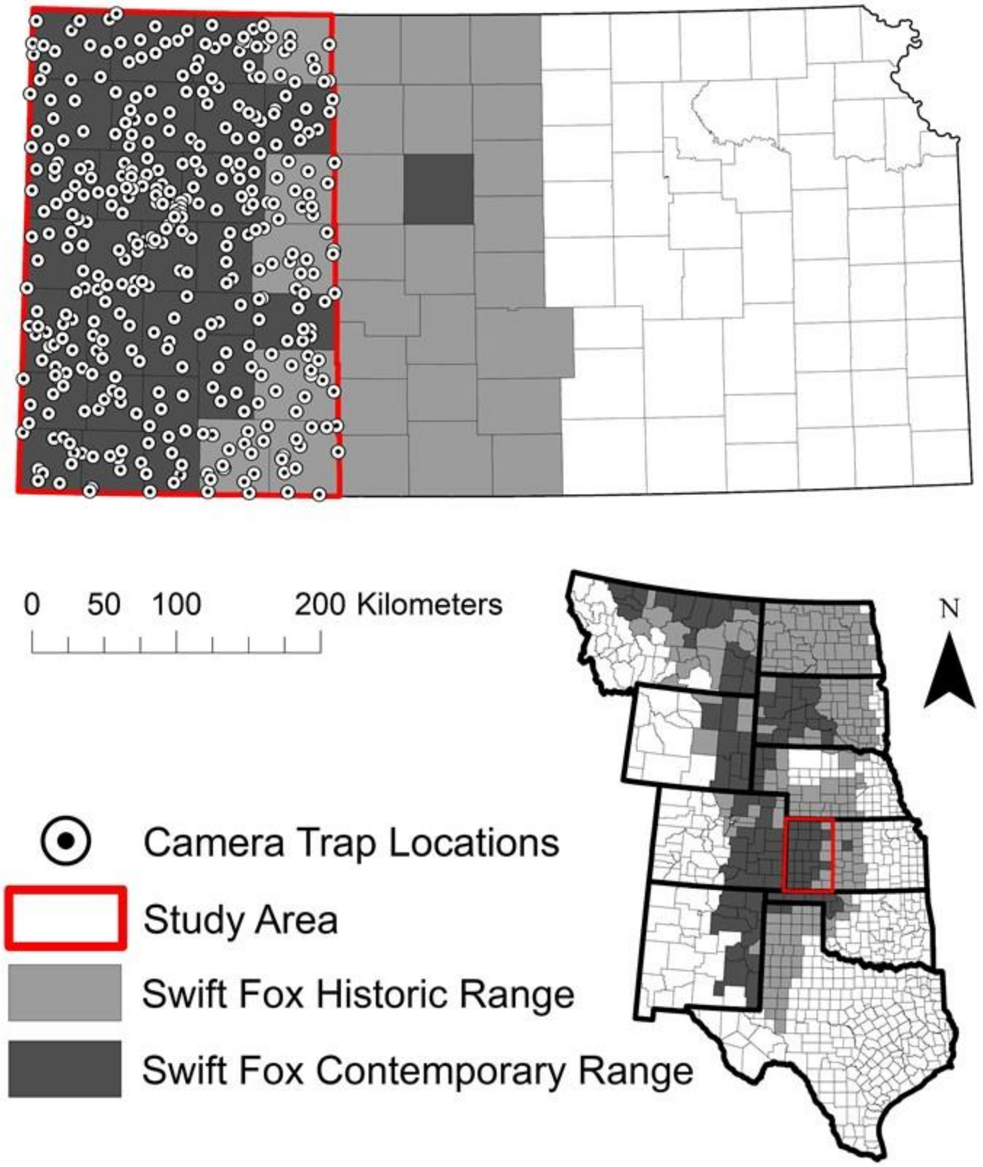


Figure 1.2 Distance weight functions for optimal scale of effect (σ) for proportion of loamy tableland soil (A; σ = 50 m), row-crop agriculture (B; σ = 100 m), shortgrass prairie (C; σ = 150 m), Conservation Reserve Program (D; σ = 500 m), and landcover diversity (E; Shannon-Weiner Diversity Index; σ = 900 m).

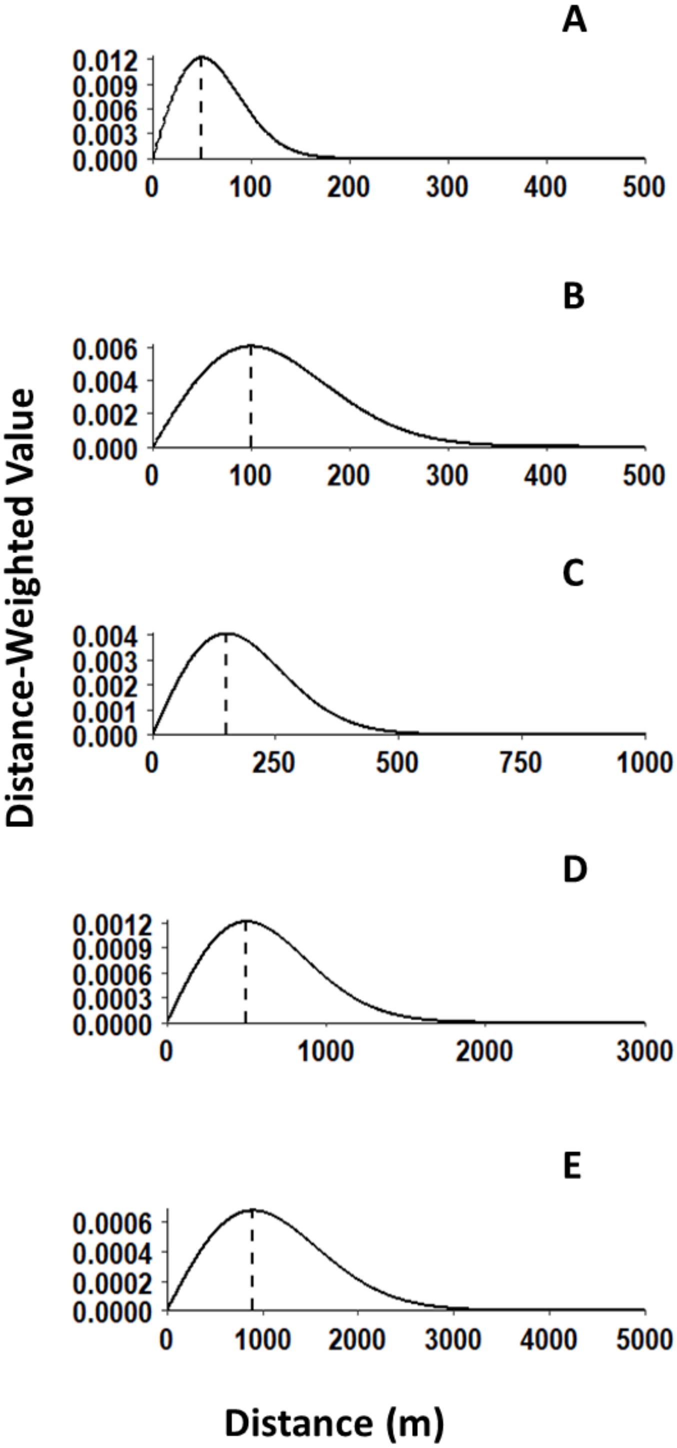


Figure 1.3 Swift fox (*Vulpes velox*) cumulative detection probability (dotted line) derived from my most-supported detection model, and smoothed frequency histogram (solid line) modeled with frequency of initial swift fox detections (i.e., first day a swift fox was detected at a site). I documented site occupancy using a single motion-sensing camera-trap at each site (2018 = 375, 2019 = 361, 2020 = 360) for 28 days per year for three consecutive years (2018-2020) in western Kansas, USA. Note increase in frequency of initial swift fox detections once scent was reapplied and offset cameras were readjusted.

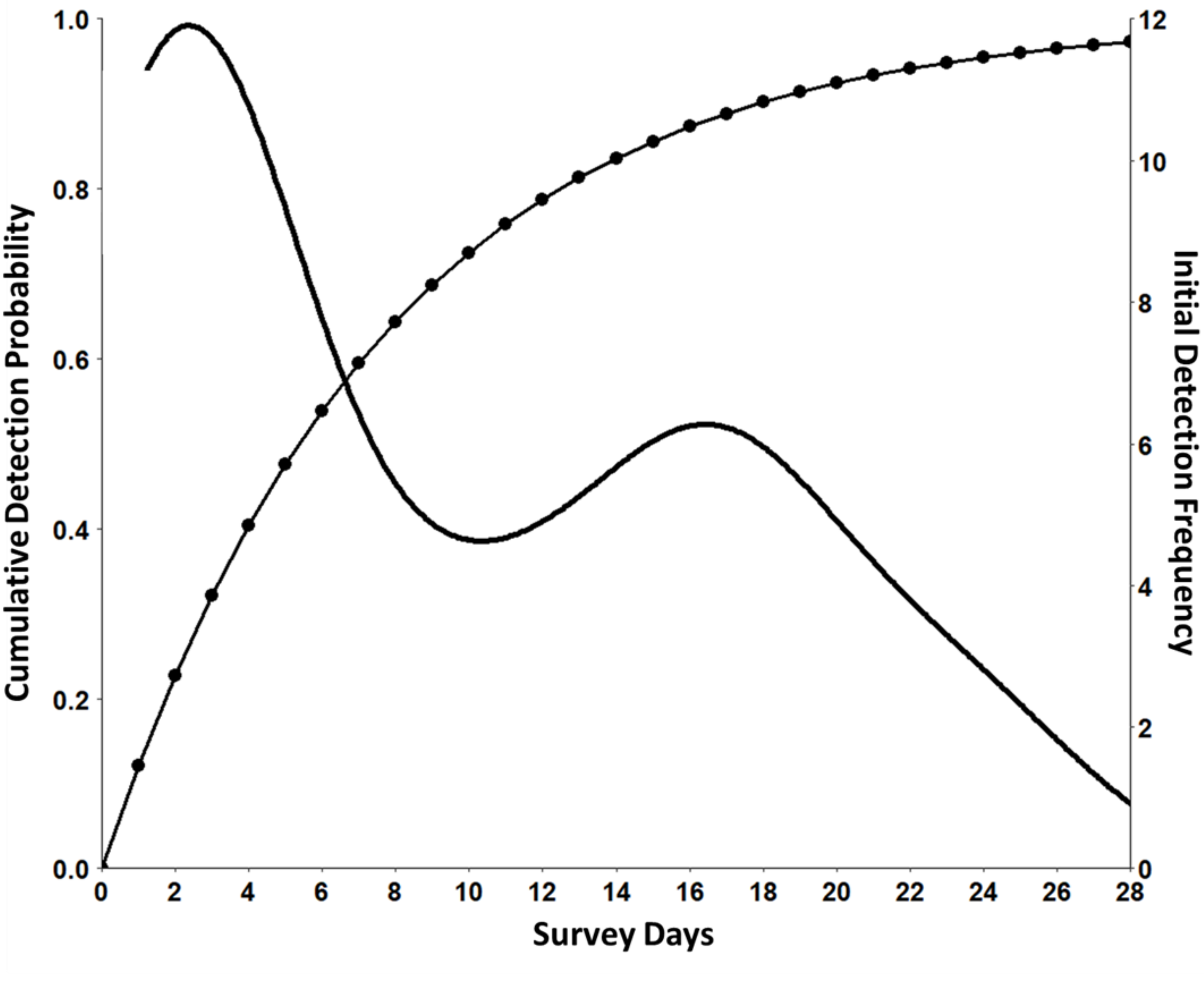


Figure 1.4 Site occupancy probabilities (and 95% CI) for swift fox (*Vulpes velox*) in relation to the quadratic effect of landcover diversity (A), proportion of shortgrass prairie (B), proportion of loamy tableland soils (C), and proportion of lands enrolled in the Conservation Reserve Program (D) surrounding camera-trap sites. I assessed presence/absence of swift fox using camera traps at sites (2018 = 375, 2019 = 361, 2020 = 360) distributed across western Kansas, USA. Site occupancy probabilities were derived from my most-supported initial occupancy model. Note scale of y-axes.

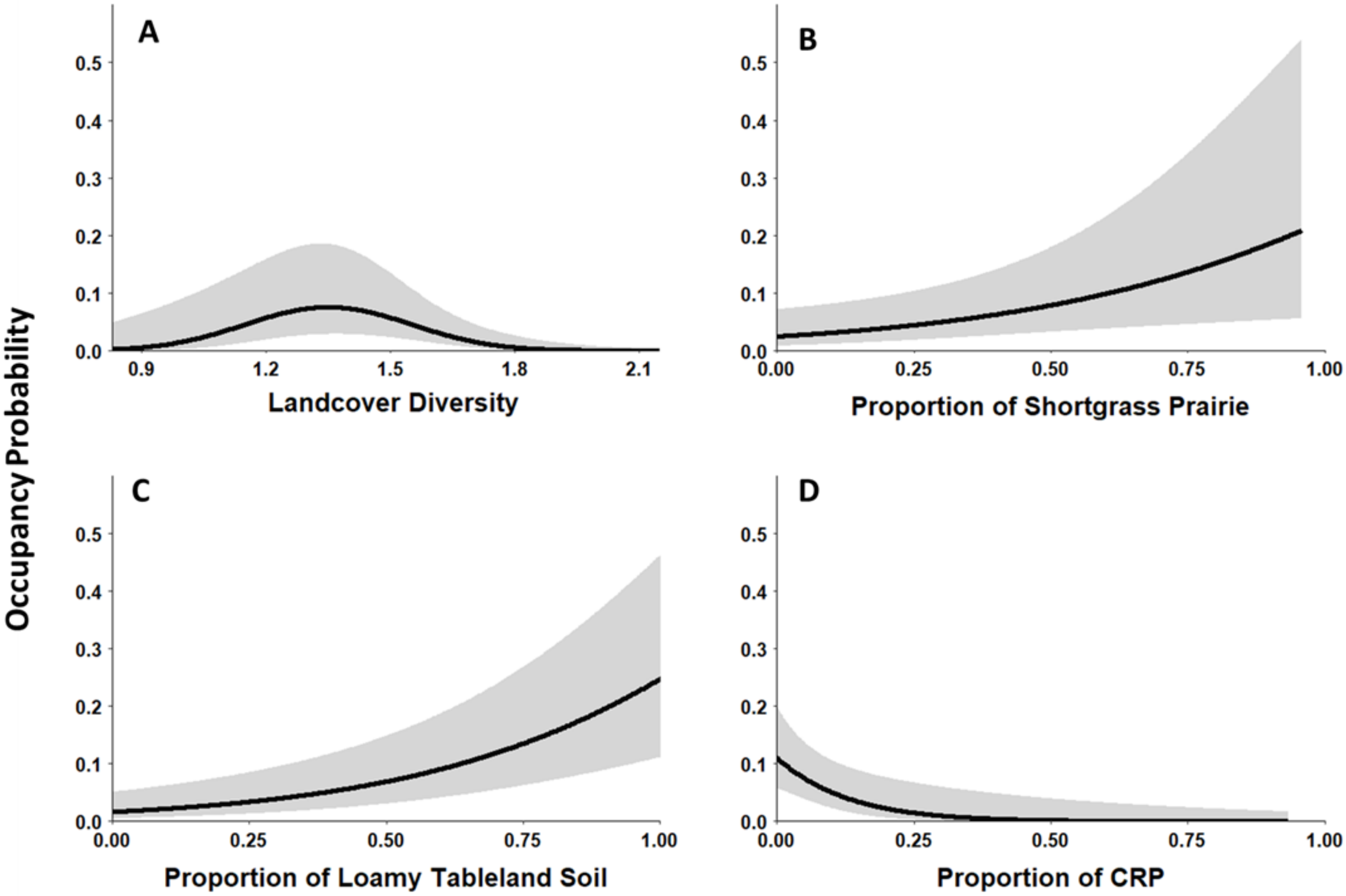


Figure 1.5 Modeled scaled range (0 – 1; lowest to highest probability of occurrence) of site occupancy predictions for swift fox (*Vulpes velox*) in western Kansas, USA. Predictions were based on the influence of the additive effects of my distance-weighted covariates within my most supported initial occupancy model. I assessed swift fox site occupancy at sites (2018 = 375, 2019 = 361, 2020 = 360) using camera traps distributed across western Kansas, USA.

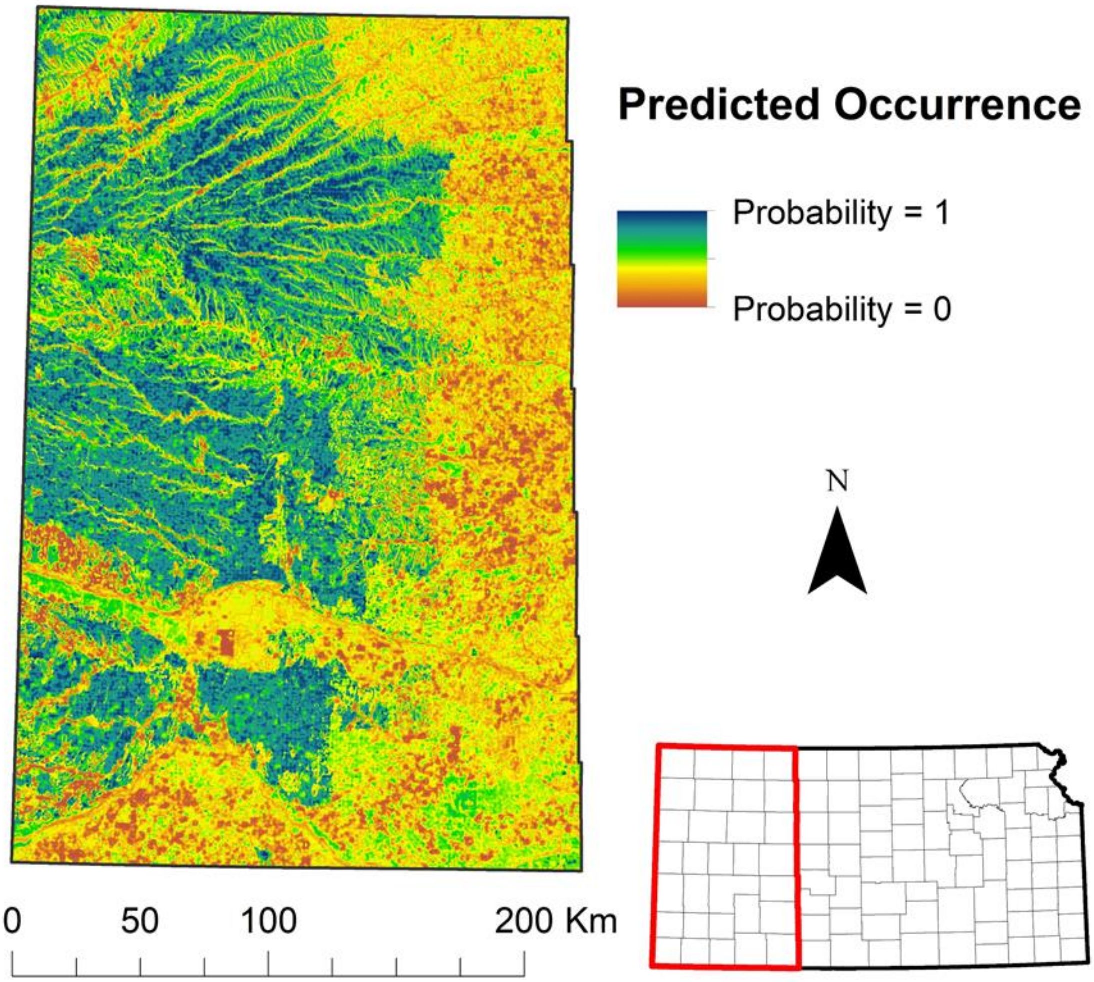
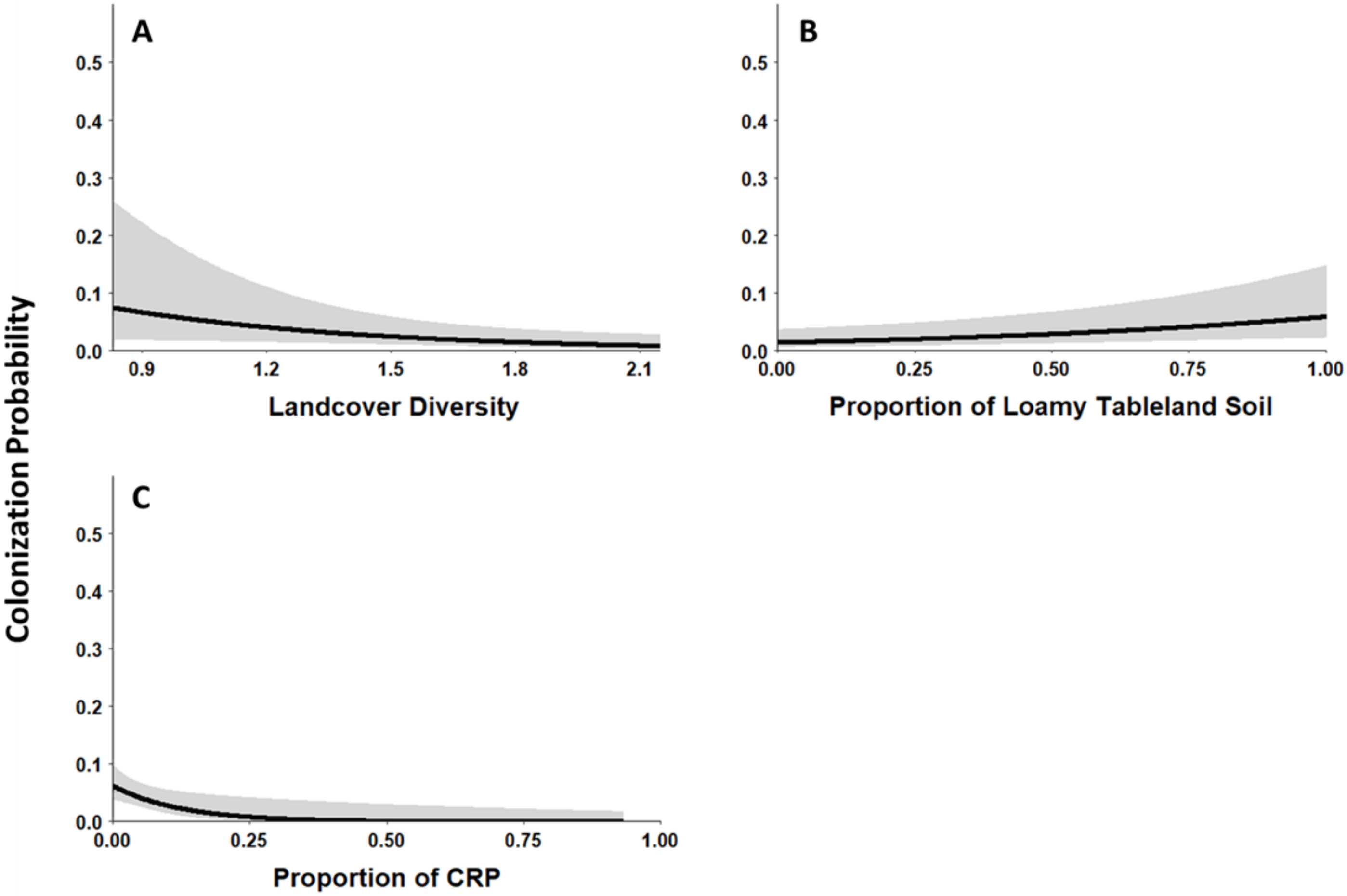


Figure 1.6 Influence of landcover diversity (A), proportion of loamy tableland soils (B), and proportion Conservation Reserve Program (C) on site colonization rates (and 95% CI) by swift fox (*Vulpes velox*). I assessed swift fox site detection at camera trap sites (2018 = 375, 2019 = 361, 2020 = 360) across western Kansas, U.S.A. during 2018-2020. Predicted estimates were derived from my most-supported colonization model. Note scale of y-axes.



Appendix A - Chapter 1 Supplemental Material

Table A.1 Model-selection statistics for all models of detection (*n* = 7), initial site occupancy (*n* = 47; 2018), and site colonization (*n* = 47; 2019-2020) by swift fox (*Vulpes velox*) in western, Kansas, U.S.A. I present all models along with the null model (Intercept Only) for each parameter. Covariates include day of year (DOY), number of days since bait was applied or reapplied at each site (Scent), and days with an altered camera view field (Altered), and distance-weighted effects of landcover diversity (SHDI), proportion shortgrass prairie (SGP), loamy tableland soils (LOAMY), proportion of conservation reserve program (CRP), and proportion of agriculture (AG). K = number of model parameters, ΔAIC_c = difference between AIC_c model value compared to the top model, *w* = Akaike weight, -2LL = log-likelihood * (-2), indicating model fit.

Model	**K**	**AIC_C**	**ΔAIC_C**	**w_i**	**-2LL**
Detection					
DOY + Scent + Altered	7	1728.33	0.00	0.96	1714.04
DOY + Altered	6	1734.81	6.48	0.04	1722.58
Altered	5	1743.46	15.14	0.00	1733.30
DOY + Scent	6	1744.17	15.84	0.00	1731.94
DOY	5	1753.49	25.16	0.00	1743.34
Intercept Only	4	1755.90	27.57	0.00	1747.80
Scent + Altered	6	1827.03	98.70	0.00	1814.82
Scent	5	1838.32	109.99	0.00	1828.16
Occupancy					
LOAMY + CRP + SGP + SHDI2	12	1670.07	0.00	0.61	1645.22
LOAMY + CRP + SGP + SHDI2 + AG	13	1671.84	1.77	0.25	1644.84
LOAMY + CRP + SHDI2	11	1673.93	3.87	0.09	1651.22
LOAMY + CRP + SHDI2 + AG	12	1675.66	5.59	0.04	1650.82
LOAMY + CRP + SGP + SHDI	11	1680.18	10.11	0.00	1657.46

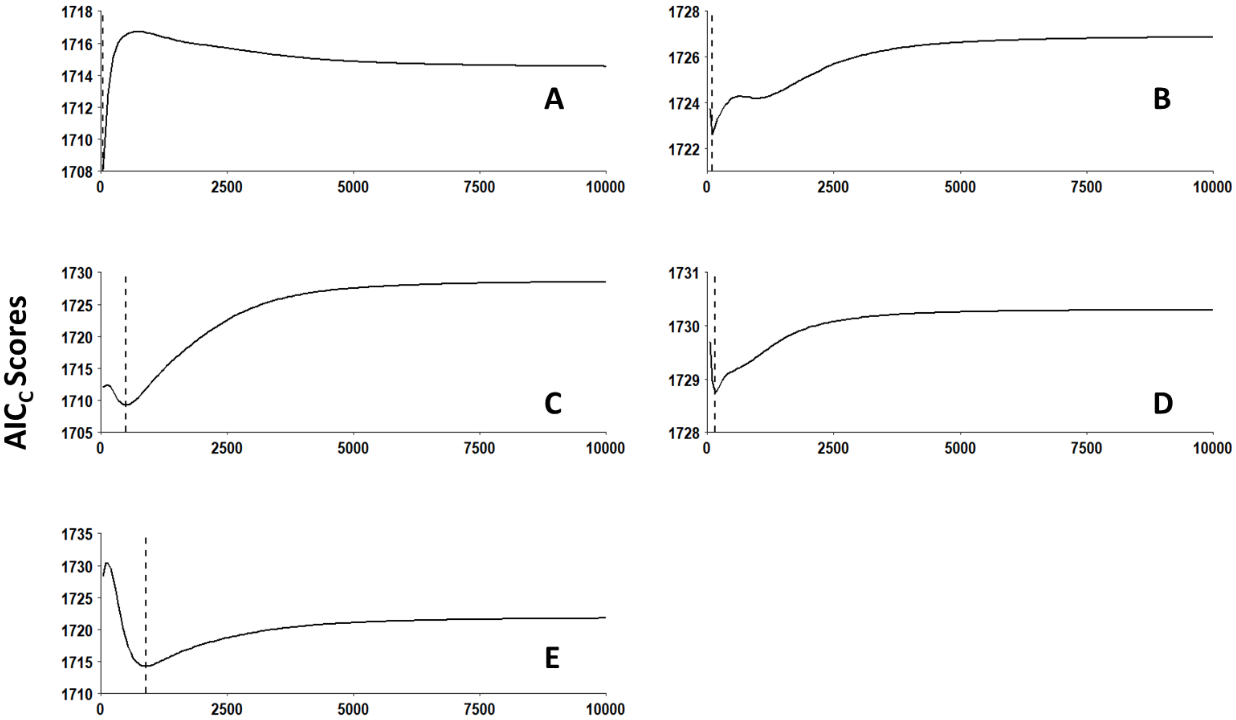
LOAMY + CRP + SGP	10	1680.84	10.77	0.00	1660.24
LOAMY + SGP + SHDI2 + AG	12	1681.39	11.32	0.00	1656.54
LOAMY + CRP + SGP + SHDI +AG	12	1682.27	12.21	0.00	1657.44
LOAMY + CRP + SGP + AG	11	1682.51	12.45	0.00	1659.80
LOAMY + CRP	9	1683.35	13.29	0.00	1664.88
LOAMY + SGP + SHDI2	11	1684.07	14.00	0.00	1661.36
LOAMY +CRP + SHDI	10	1684.39	14.32	0.00	1663.80
LOAMY + CRP + SHDI + AG	11	1684.98	14.91	0.00	1662.26
LOAMY + CRP + AG	10	1685.27	15.20	0.00	1664.68
LOAMY + SGP + SHDI	10	1692.00	21.93	0.00	1671.40
LOAMY + SGP + SHDI + AG	11	1692.03	21.97	0.00	1669.32
CRP + SHDI2	10	1693.14	23.07	0.00	1672.54
CRP + SHDI2 + AG	11	1694.22	24.16	0.00	1671.50
LOAMY + SHDI2	10	1694.49	24.43	0.00	1673.90
CRP + SGP + SHDI2 + AG	12	1694.83	24.76	0.00	1669.98
CRP + SGP + SHDI2	11	1695.06	24.99	0.00	1672.34
LOAMY + SGP + AG	10	1695.13	25.07	0.00	1674.54
LOAMY + SHDI2 + AG	11	1695.99	25.92	0.00	1673.28
SGP + SHDI2 + AG	11	1700.51	30.44	0.00	1677.80
LOAMY + SGP	9	1701.45	31.38	0.00	1682.96
CRP + SHDI	9	1702.23	32.16	0.00	1683.74
LOAMY + SHDI	9	1702.45	32.39	0.00	1683.96
CRP + SGP + SHDI	10	1703.55	33.49	0.00	1682.96

CRP + SHDI + AG	10	1704.26	34.20	0.00	1683.68
LOAMY + SHDI + AG	10	1704.44	34.38	0.00	1683.86
CRP + SGP + SHDI + AG	11	1704.80	34.74	0.00	1682.10
SGP + SHDI2	10	1705.87	35.80	0.00	1685.28
SHDI2 + AG	10	1706.01	35.95	0.00	1685.42
SHDI2	9	1706.78	36.72	0.00	1688.30
LOAMY + AG	9	1707.87	37.80	0.00	1689.38
CRP + AG	9	1708.25	38.18	0.00	1689.76
LOAMY	8	1708.26	38.19	0.00	1691.88
CRP + SGP + AG	10	1708.64	38.57	0.00	1688.04
CRP	8	1709.25	39.19	0.00	1692.86
SGP + SHDI + AG	10	1710.60	40.53	0.00	1690.00
CRP + SGP	9	1711.33	41.27	0.00	1692.84
SGP + SHDI	9	1712.42	42.35	0.00	1693.94
SHDI	8	1714.24	44.18	0.00	1697.86
SHDI + AG	9	1715.48	45.42	0.00	1697.00
SGP + AG	9	1717.17	47.11	0.00	1698.70
AG	8	1722.65	52.58	0.00	1706.26
Intercept Only	7	1728.33	58.26	0.00	1714.04
SGP	8	1728.71	58.64	0.00	1712.32
Colonization					
LOAMY + CRP + SHDI	15	1633.33	0.00	0.23	1602.02
LOAMY + CRP + SHDI + AG	16	1634.72	1.39	0.11	1601.24

LOAMY + CRP + SGP + SHDI	16	1634.76	1.43	0.11	1601.28
LOAMY + CRP + AG	15	1635.01	1.68	0.10	1603.70
LOAMY + CRP + SHDI2	16	1635.17	1.84	0.09	1601.68
LOAMY + CRP	14	1635.97	2.64	0.06	1606.82
LOAMY + CRP + SHDI2 + AG	17	1636.34	3.01	0.05	1600.66
LOAMY + CRP + SGP	15	1636.36	3.03	0.05	1605.04
LOAMY + CRP + SGP + SHDI2	17	1636.50	3.17	0.05	1600.82
LOAMY + CRP + SGP + SHDI + AG	17	1636.64	3.31	0.04	1600.96
LOAMY + CRP + SGP + AG	16	1636.91	3.58	0.04	1603.42
LOAMY + CRP + SGP + SHDI2 + AG	18	1638.27	4.94	0.02	1600.40
CRP + SHDI + AG	15	1639.62	6.29	0.01	1608.32
CRP + SGP + SHDI	15	1639.81	6.48	0.01	1608.50
CRP + SHDI	14	1640.81	7.48	0.01	1611.66
CRP + SGP + SHDI + AG	16	1640.90	7.57	0.01	1607.42
CRP + SHDI2 + AG	16	1641.07	7.74	0.00	1607.58
CRP + SGP + SHDI2	16	1641.51	8.18	0.00	1608.02
CRP + SGP + SHDI2 + AG	17	1642.32	8.99	0.00	1606.64
CRP + AG	14	1642.58	9.25	0.00	1613.44
CRP + SHDI2	15	1642.74	9.42	0.00	1611.44
CRP + SGP + AG	15	1643.81	10.48	0.00	1612.50
LOAMY + SHDI + AG	15	1645.00	11.67	0.00	1613.70
LOAMY + SHDI2 + AG	16	1646.58	13.25	0.00	1613.10
LOAMY + SHDI	14	1646.61	13.28	0.00	1617.46

LOAMY + SGP + SHDI + AG	16	1646.63	13.30	0.00	1613.14
SHDI + AG	14	1647.16	13.83	0.00	1618.02
CRP + SGP	14	1647.31	13.98	0.00	1618.16
LOAMY + AG	14	1647.57	14.24	0.00	1618.42
LOAMY + SGP + SHDI2 + AG	17	1648.15	14.82	0.00	1612.48
SHDI2 + AG	15	1648.62	15.29	0.00	1617.32
LOAMY + SHDI2	15	1648.63	15.30	0.00	1617.32
LOAMY + SGP + SHDI	15	1648.78	15.45	0.00	1617.48
LOAMY + SGP + AG	15	1649.15	15.82	0.00	1617.84
SGP + SHDI + AG	15	1649.24	15.91	0.00	1617.94
SGP + SHDI2 + AG	16	1650.70	17.37	0.00	1617.22
LOAMY + SGP + SHDI2	16	1650.82	17.49	0.00	1617.32
SHDI	13	1651.10	17.77	0.00	1624.12
AG	13	1652.38	19.05	0.00	1625.40
CRP	13	1652.49	19.16	0.00	1625.50
SGP + SHDI	14	1652.65	19.32	0.00	1623.50
SHDI2	14	1653.15	19.82	0.00	1624.00
SGP + AG	14	1654.45	21.12	0.00	1625.32
SGP + SHDI2	15	1654.71	21.38	0.00	1623.40
LOAMY	13	1658.47	25.14	0.00	1631.48
LOAMY + SGP	14	1660.37	27.04	0.00	1631.24
Intercept Only	12	1670.07	36.74	0.00	1645.22
SGP	13	1670.16	36.83	0.00	1643.18

Figure A.1 Optimal distance-weighted representation of each covariate, based on Akaike's Information Criterion, corrected for small sample sizes (AIC$_C$), from the weighted average of each covariate (C$_w$). AIC$_C$ scores representing 200 initial occupancy site models corrected for detection. Ring distance with the lowest AIC$_C$ values were utilized in initial site occupancy and local colonization models. Vertical dashed lines represent lowest AIC$_C$ values.



Chapter 2 - Landscape composition mediates spatiotemporal interactions among sympatric canids in a prairie ecosystem

This chapter has been prepared for submission to Oikos *and is formatted to journal specifications.*

Abstract

Apex carnivores influence subordinate carnivores through intraguild predation and competition. Landscape composition and configuration may mediate interactions between sympatric carnivores though landscape-scale effects are relatively unknown. I examined the influence of landscape composition and configuration on the spatial and temporal interactions of two carnivore species (coyotes and swift foxes) native to shortgrass prairies. Additionally, due to expected intraguild competition shaping swift fox distributions, I investigated the effect of coyote presence on swift fox occupancy, colonization, and persistence. I used three years of detection/non-detection data (2018 – 2020) from camera traps at 381 sites to compare swift fox and coyote spatial and temporal interactions in relation to common landscape characteristics in Kansas, USA. Mean persistence of swift foxes differed across sites where coyotes were not detected (0.66; SE=0.001) and where coyotes were detected (0.39; SE=0.001). The coefficient of overlap at sites with CRP proportion ≥0.10 was significantly different (95% CIs did not overlap) from coefficient of overlap of all other tested parameters. Swift foxes were spatially distributed dependent upon coyotes through space and time at low proportions of CRP (≤0.04). At CRP proportions >0.04, 95% confidence intervals overlapped SIF=1, indicating that even though the regression curve tends to have a negative relationship with proportion of CRP, swift foxes were shown to be spatially distributed independent of coyotes through space and time at high proportions of CRP. Swift foxes practice avoidance when predation risk by coyotes is

heightened. Results from my study show that landscape, and its inherent structure and composition (e.g., vegetation height), influence the intraguild interactions of swift foxes and coyotes in western Kansas.

Introduction

Intraguild predation and interference competition among carnivores can influence species distributions, resource selection, and population dynamics (Brown et al. 1999, Chase et al. 2002, Vanak et al. 2013), and occurs in systems where multiple species vie for similar resources (Polis et al. 1989, Holt and Polis 1997, Linnell and Strand 2000, Vanak et al. 2013). Sympatric carnivores generally coexist at different trophic levels within a system, where apex carnivores exert a top-down advantage over less-dominant species (Fedriani et al. 2000, Jensen and Humphries 2019). Apex carnivores may restrict prey availability for subordinate species through interference, forcing smaller carnivores to forage under threat of predation (Holt and Polis 1997, Brown et al. 1999, Ritchie and Johnson 2009). Intraguild predation among carnivores is common (Prugh and Sivy 2020) and likely reduces densities and distributions of smaller species, resulting in local extirpation or exclusion (Mac Nally 1983, Palomares and Caro 1999, Linnell and Strand 2000, Fedriani et al. 2000).

Although competition among carnivores is common, landscape composition and configuration can mediate these interactions (Finke and Denno 2002, Moll et al. 2018). Landscape characteristics, such as vegetation structure (e.g., vegetation height and heterogeneity), can influence both spatial and temporal activity partitioning between sympatric carnivores (St-Pierre et al. 2006, Thompson and Gese 2007, Schooley et al. 2021). For instance, Davies et al. (2021) found that African wild dogs (*Lycaon pictus*) avoid African lions (*Panthera leo*) by selecting heterogenous landscape features that may provide greater cover to enhance avoidance strategies. Many studies assessing how landscape characteristics effects influence species interactions, however, have generally used smaller bodied species (< 1 kg) as models in small-scale experiments (< 10 ha; Morris and Grant 1972, Keen 1982, Rosenheim et al. 1993). Although these types of studies are relatively easy to manipulate and replicate, they may not provide strong inference across broader landscapes and contexts (Lawton 1999, Schmitz et al. 2017). Understanding how landscape characteristics can mediate spatiotemporal interactions among carnivores is timely and warranted as land-use changes are occurring at rapid paces (Winkler et al. 2021, Kuipers et al. 2021).

Shortgrass prairie ecosystems throughout the North American Great Plains have undergone significant changes since colonization by Euro-Americans (Hartnett et al. 1997, Licht 1997, Brockway et al. 2002). These areas have largely been converted to agriculture (Hart and Hart 1997, Brockway et al. 2002) resulting in a patchy, human-dominated landscape mosaic throughout the Great Plains (Engle et al. 2008, Ott et al. 2021). Western Kansas, USA is characterized by these contemporary landscapes, and sustains biodiversity within a patchwork of various land-use types (Samson et al. 2004). Remnant shortgrass prairie patches in this region provide habitat for native carnivores including swift fox (*Vulpes velox*) and coyote (*Canis latrans*). Coyotes (~50 cm tall, ~ 11 kg; Henke and Bryant 1994) are the apex predator in the region and a significant cause of swift fox mortality (Sovada et al. 1998, 2009). Swift foxes are small (~30 cm tall, ~2.4 kg; Dark-Smiley and Keinath 2003) prairie-obligate carnivores that were once nearly extirpated from the region though have recolonized remnant prairie patches through their range. Because both canid species are primarily nocturnal and crepuscular (Lemons et al. 2003, Andelt and Gipson 1979) and forage on similar prey items (e.g., small mammals and insects; Kamler et al. 2007), there is potential for increased negative interactions. A previous study found swift fox must balance predation risks by foraging in areas with reduced shrub densities while coyotes freely foraged in areas with increased prey availabilities (Thompson and Gese 2007). It remains unclear, however, how both species partition diel activity patterns to facilitate coexistence in multiuse landscapes.

Native prairies are the ongoing target of landscape-scale restoration efforts (Berger et al. 2020). The most common restoration effort in the USA is the Conservation Reserve Program (CRP; Baer et al. 2002); a voluntary program that pays farmers to remove marginal cropland from production and reestablish grassland vegetation (Reichelderfer and Boggess 1988). Initially created to decrease soil erosion and crop surpluses (Reichelderfer and Boggess 1988), CRP may indirectly improve habitat for some native carnivores (e.g., coyotes; Kamler et al. 2005). Many CRP plantings, however, use relatively taller grassland species (e.g., big bluestem [*Andropogon gerardii*], switchgrass [*Panicum virgatum*]) into shortgrass prairie ecosystems of western Kansas (Kamler et al. 2003). Tall (> 30 cm) and dense vegetation has historically restricted swift fox distributions at the eastern edge of their range (Egoscue 1979). The main agent of grassland conversion, row-crop agriculture, is used as habitat for many native carnivores including American badgers (*Taxidea taxus*; Piper et al. In Revision), coyotes (Kamler et al. 2005), and swift fox (Werdel et al. In Revision). Concurrently, fragmentation and conversion of native prairies with alternate land-use types have created edges that may provide corridors for carnivore movements or represent good-quality foraging areas (e.g., small mammals; Frey and Conover 2006, Bilenca et al. 2007, Červinka et al. 2011, Andersen et al. 2017). Although coyotes and swift foxes cooccur in these contemporary landscapes it is unclear if novel landscape compositions or configurations mediate their spatiotemporal interactions.

I examined the influence of landscape composition and configuration on the spatial and temporal interactions of swift fox and coyote using three years of occupancy data from camera-trap sites distributed across western Kansas. Additionally, I assessed the evidence for effects of coyote presence on site occupancy, colonization, and persistence by swift fox. Because coyotes exhibit top-down pressure through intraguild competition and predation on smaller canids (Kitchen et al. 1999), I expected swift foxes to avoid landcover that increased chances of predation (i.e., taller vegetation in relation to shortgrass prairie) by adjusting spatiotemporal activity patterns when coyotes were present.

Methods

Study Area

My study occurred within the westernmost counties of Kanas, USA (-100.815301, 38.492366; 7,160,077 ha; Fig. 2.1). This region was historically characterized by native shortgrass prairie but now is now a heterogenous matrix of native short (15%, 1,035,347 ha) and mixed-grass (12%, 859,209 ha) prairie, row-crop agriculture (62%, 4,439,247 ha), CRP (7%, 501,205 ha), and energy development (oil wells = 20,093, wind turbines = 1,429; Kansas Geological Survey 2021). Remaining native short- and mixed-grass prairie species include side-oats grama (*Bouteloua curtipendula*), buffalo grass (*Bouteloua dactyloides*), big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), witchgrass (*Panicum capillare*), tumblegrass (*Schedonnardus paniculatus*), Indiangrass (*Sorghastrum nutans*), blue grama (*Bouteloua gracilis*), and sand dropseed (*Sporobolus cryptandrus*). The spatial distribution of both swift foxes and coyotes overlap completely within my study area. Other similar-sized sympatric carnivores occurring in this region included bobcat (*Lynx rufus*) and American badger (*Taxidea taxus*) – neither of which have reported associations with swift foxes.

The region is characterized by low annual precipitation (31-107 cm), with temperatures ranging from -9 to 49° C (PRISM Climate Group 2021).

Site Selection and Camera Placement

Initial site locations (*n* = 381) were randomly selected using a random-point generator in a geographic information system (ArcMap v. 10.8) and consisted of a single motion-sensing camera (Bushnell Trophy Cam®; Bushnell Corporation, Overland, KS, USA) affixed to a metal T-post (40 cm high with a north/south orientation to avoid solar interference). I established sites nearest the random generated location unless the likelihood of camera destruction was high (e.g., center of production agriculture, pasture, or fields). In these cases, I relocated cameras to the nearest fence line or field edge to avoid interference. I placed a wooden stake 3 m (40 cm high) in front of the camera and smeared with an olfactory attractant (skunk essence and petroleum jelly [F&T Fur Harvester's Trading Post, Alepna, MI, USA]) to lure individuals to pass in front of the camera's field of view (Stratman and Apker 2014). Vegetation in front of the camera was removed with a hand-held weed cutter to reduce visual obstruction. Distance between sites was ≥ 2-km ($\bar{x}$ = 8.16 km, SD = 3.61), roughly equal to mean swift fox and resident coyote home ranges (Gese et al. 1988, Kitchen et al. 1999, Kamler et al. 2003, Nicholson et al. 2007, Sovada et al. 2009, Lebsock et al. 2012), reducing chances of multiple cameras capturing a single swift fox or coyote in a trap-day. Each camera was in place at sites for 28 days and I replaced lure, batteries, and digital memory cards every ~14 days.

Data Collection

I sampled sites during spring and summer, as coyote and swift fox dispersal generally occurs during late fall and early winter (Harrison 1992, Nicholson et al. 2007). Thus, I considered my annual sampling timeframe as biologically closed (e.g., no emigration or immigration). Due to changing landowner access issues, I sampled 375 sites in 2018 (5 May – 2 November), 361 sites in 2019 (20 May – 2 October) and 360 sites in 2020 (22 April – 28 September 2020), for a total of 381 unique sites. I established cameras at approximately 1/3 of the sites (~125) within the study area for the first ~28 days of the field season, then moved cameras to the next 1/3 of sites for the following ~28 days, and again for the final ~28 days to complete my sampling effort each year. I adjusted the timing of camera placement in subsequent years to not sample the same sites at the same time each year. I archived photographs within a Microsoft Access database (Colorado Parks and Wildlife Photo Warehouse 4.0, Colorado Parks and Wildlife, Fort Collins, CO, USA). I tagged site and time-stamped specific photos for detection (1) or non-detection (0) of swift foxes and coyotes each year. I considered a site occupied by a particular species if I detected ≥ 1 photo of that species during the 28-day sampling period during a given year. Detections were considered independent observations if >30 min between observations.

Landscape Characterization

I created a landcover raster (30x30 m) of my study area by merging information from 2018 CRP enrollments (Farm Service Agency 2018), CropScape (CropScape 2018), and PRAIRIEMAP (PRAIRIEMAP 2003). From this raster, landcover was classified into 3 classes (CRP, shortgrass prairie, and row-crop agriculture). I created 2-km radius buffers surrounding each site (Wait et al. 2018), which reasonably encompasses both swift fox and resident coyote home ranges (12.56 km^2 [Gese et al. 1988, Nicholson et al. 2007]). I considered 500 m, 1 km, and 5 km radii, but proportion of landcover classes among buffer sizes was correlated ($r>0.80$). I extracted landcover class proportions and total edge from circular buffers using R (v. 4.0.3) “landscapemetrics” package (Hesselbarth et al. 2019).

Spatial Overlap

I quantified if coyote presence influenced site occupancy by swift fox with a Bayesian dynamic occupancy model for interacting species adapted from Gallo et al. (2019), which controls for imperfect detection. Briefly, this model assumes that the site occupancy status of a subordinate species (i.e., swift fox) may vary due to the presence of a dominant species (i.e., coyote). As a dynamic occupancy model, I estimated four probabilities for coyote across *i* in 1,…,*I* sites and *t* in 1,…,*T* sampling seasons. Leaving site and sampling season subscripts out for ease of presentation, these probabilities included initial occupancy at $t = 1$ (ψ^{c}), colonization (γ^{c}), persistence (ϕ^{c}), and detection (ρ^{c}). Because occupancy status of swift fox was conditional on coyote presence, I estimated eight probabilities for swift fox which included initial occupancy given coyote presence ($\psi^{s|c}$) or absence ($\psi^{s|c-}$), colonization given coyote presence ($\gamma^{s|c}$) or absence ($\gamma^{s|c-}$), persistence given coyote presence ($\phi^{s|c}$) or absence ($\phi^{s|c-}$), and detection given coyote presence ($\rho^{s|c}$) or absence ($\rho^{s|c-}$). Using the logit-link I made each of these eleven probabilities a function of covariates. To test influence of landscape on logit-linear predictors (i.e., initial site occupancy, colonization, persistence, and detection) I created a function for each landcover class (CRP, shortgrass prairie, row-crop) and characteristic (total edge). All covariates were centered and scaled prior to analyses.

To quantify whether coyote and swift fox co-occurred more or less than expected by chance, I derived species interaction factors (SIF) along a landcover gradient from the estimated probabilities of my model (MacKenzie et al. 2004, Richmond et al. 2010, Gallo et al. 2019). An estimated SIF <1 indicates that two species co-occurred less frequently than expected by chance and an SIF >1 indicates species co-occurred more frequently than expected by chance.

I followed Gallo et al.'s (2019) approach to calculate a SIF such that

$$SIF = \frac{\psi^c \psi^{s|c}}{\psi^c(\psi^{s|c} + (1 - \psi^c) \times \psi^{s|c-})}$$

Where $\psi^c$is the unconditional occupancy probability of coyotes, $\psi^{s|c}$is the occupancy probability for swift foxes given coyotes are present, and $\psi^{s|c-}$ is the occupancy probability for swift foxes given coyotes are absent. As future occupancy states are a function of local colonization and persistence rates, I used Mackenzie et al.'s (2017) recursive equation, $\psi_{t+1} = \psi_t \phi_t + (1 - \psi_t)\gamma_t$, to derive subsequent occupancy probabilities estimated by my occupancy model and to calculate SIFs between coyotes and swift foxes for each sampling season (Gallo et al. 2019).

I fit this model in JAGS (v. 4.2.0 [Plummer 2003]) using the "runjags" package (Denwood 2016) in R. I sampled the posterior distribution 200,000 times across two chains following a 10,000-step adaptation and 10,000 step burn-in phase. Chains were thinned by two for a total of 100,000 posterior samples. Model convergence was assessed by visually inspecting trace plots and ensuring that Gelman-Rubin diagnostics were < 1.1 (Gelman et al. 2013; Table B.1 and B.2). For logit-scale parameter estimates I determined evidence of an effect and calculated 95% credible intervals (CI) for each parameter and checked whether or not they overlapped zero. Similarly, I calculated 95% credible intervals for the SIF, though I checked whether credible intervals for each SIF overlapped one.

Temporal Overlap

I exported activity data (site and time of detections) specific to swift foxes and coyotes from my Microsoft Access database (Colorado Parks and Wildlife Photo Warehouse 4.0, Colorado Parks and Wildlife, Fort Collins, CO, USA) for use with the "activity" (Rowcliffe 2021) and "overlap" (Meredith and Ridout 2021) packages in R (v. 4.0.3, R Core Team 2020). I selected overlap estimators (Δ) based on sample sizes for each comparison with Δ_1 used if the less frequently detected population had fewer than 75 detections and Δ_4 used if the smaller detected population had greater than 75 detections (Ridout and Linkie 2009, Hardouin et al. 2021, Searle et al. 2021). I considered four site-level landscape characteristics that had potential to mediate temporal partitioning among swift foxes and coyotes including proportion of CRP, agriculture, and shortgrass prairie landcover surrounding sites and total habitat edge (m) surrounding sites. I analyzed temporal overlap 1) among all swift fox and coyote detections at sites, 2) at sites that only included detections of both species, 3) at sites where both species were detected that included landcover class proportions or characteristics $\geq$ the mean (CRP proportion $\bar{x}$ = 0.10 [range = 0.00 - 0.62], row-crop proportion $\bar{x}$ = 0.37 [range = 0.00 - 0.90], shortgrass prairie proportion $\bar{x}$ = 0.18 [range = 0.00 - 0.77], total edge $\bar{x}$ = 312,183 m [range = 91,950 - 851,280]), and 4) at sites where both species were detected and included landcover class proportions or characteristics that were $<$ the mean values. I estimated 95% confidence intervals for each coefficient of overlap, and compared among overlap parameters, using smoothed bootstrapping with 10,000 resamples (Meredith and Ridout 2021). I used the function compareCkern in the “activity” R package (Rowcliffe 2021) to test for significant differences ($P<0.05$) between species’ temporal activity (Searle et al. 2021).

Results

I documented 3,624 photos of coyotes (2018 = 1,307; 2019 = 988; 2020 = 1,329) and 341 photos of swift foxes (2018 = 207; 2019 = 40; 2020 = 94) over 27,954 camera-trap days (2018 = 10,351; 2019 = 9,478; 2020 = 8,125).

Multi-Species Occupancy

Median detection-corrected initial site occupancy across all sites for coyotes was 0.67 (95% CIs = 0.62-0.71; Table 2.1). Median colonization (0.56 [95% CIs = 0.50-0.62]) and persistence (0.61 [95% CIs = 0.57-0.66]; Table 2.1) across all sites for coyotes were similar. Median site detection, colonization, and persistence rates by swift foxes were lower with coyotes present, but not significantly different (Table 2.1). Swift foxes were more likely, however, to occupy coyote-absent sites (0.10 [95% CIs = 0.06-0.14]) than sites where coyotes were present (0.01 [95% CIs = 0.01-0.02]; Table 2.1).

Spatial Overlap

Credible Intervals (CI; 95%) of spatial overlap between coyotes and swift foxes overlapped SIF=1 across all landscape metrics except for the proportion of CRP surrounding sites. SIF and CI were >1 at sites where the proportion of CRP was ≤0.04 (CIs above 0 from 0 – 0.04; Fig. 2.4), thus swift foxes were spatially influenced (positive association) by coyotes. However, at sites where the proportion of CRP land-use was >0.04, CI overlapped SIF=1 indicating swift foxes were spatially independent of coyotes.

Temporal Overlap

All coyote (independent observations [Obs]=3624) and swift fox (Obs=341) activity results yielded a coefficient of overlap (Δ_4) of 0.92 (95% CI=0.87-0.94; Fig. 2.2A). When both species were present at sites (coyote Obs=379, swift fox Obs=297), Δ_4=0.89 (95% CI=0.84-0.93; Fig. 2.2B). When both swift foxes and coyotes were present at sites where CRP proportion was <0.10 (coyote Obs=326, swift fox Obs=261), Δ_4=0.89 (95% CI=0.86-0.95; Fig. 2.2C), and at sites where both were present (coyote Obs=53, swift fox Obs=36) and CRP proportion was ≥0.10, Δ_1=0.67 (95% CI=0.46-0.75; Fig. 2.2D). The Δ_1 at sites with CRP proportion ≥0.10 was significantly different (95% CIs did not overlap) from Δ of all other landscape characteristics (Fig. 2.3).

Discussion

Site occupancy and persistence rates by swift fox were lower at sites where coyotes were present compared to sites where coyotes were not present. However, only 95% Credible Intervals (CI's) of occupancy rates of swift foxes did not overlap when comparing sites where coyotes were and were not also present. Habitat use by swift foxes was independent of coyote presence in relation to my measured landscape characteristics except at sites with lower proportions of CRP landcover (≤0.04). Also, as predicted, swift foxes adjusted their temporal activity patterns at sites surrounded by greater proportions of CRP (≥0.10) – likely to avoid interactions with coyotes. Notably, the proportion of agriculture, shortgrass prairie, and total landcover edge at sites did not affect temporal activity patterns of swift foxes.

Swift foxes were less likely to occupy sites where coyotes were also present, supporting my hypothesis that coyotes likely exert top-down pressure on swift fox distributions. Previous research suggests subordinate carnivores either avoid landscapes where predation risk is high (i.e., safety matching by avoiding tall vegetation; Thompson and Gese 2007) or persist in landscapes where prey abundance is insufficient for larger, more dominant carnivores to persist (Robinson et al. 2014). Intraguild predation theory suggests stable coexistence between sympatric carnivores may only occur if the abundance of the dominant carnivore is low enough that predation upon the subordinate carnivore is insufficient enough to eliminate the species (Holt and Polis 1997). Because site colonization rates by swift fox were insensitive to coyote presence (95% CI's overlapped), it is likely that swift foxes were exhibiting spatial niche partitioning, where swift foxes would persist only in areas with reduced coyote densities

(Schuette et al. 2013). Unfortunately, I did not evaluate cause-specific mortality or relative densities of either species. Future research should address variation in swift fox survival across gradients of coyote population densities.

Management of CRP easements within my study area incorporated seeding mixtures producing taller vegetation communities (e.g., big bluestem [*Andropogon gerardii*], switchgrass [*Panicum virgatum*]) that differed from native shortgrass prairie vegetation communities (Sovada et al. 2003, Plumb et al. 2019). This interspersed shift in vegetation structure to taller species likely increases predation risk for swift foxes, as their visual range is impaired when vegetation is taller than their body height (30 cm; Kamler et al. 2003, Thompson and Gese 2007). My results support my hypothesis that swift foxes altered their temporal activity patterns, likely to reduce predation risk in landscapes with taller vegetation structure, such as CRP landuse. However, there was no significant difference in temporal activity patterns in relation to the amount of row-crop agriculture or total landcover edges surrounding sites. CRP is a successful conservation tool for multiple species including lesser prairie chickens (*Tympanuchus pallidicinctus*; Sullins et al. 2019), grasshopper sparrows (*Ammodramus savannarum*; Herkert 1998), and coyotes (*Canis latrans*; Kamler et al. 2005). Additionally, small mammal densities may be greater in CRP than in surrounding shortgrass prairie (Stanley 2010). Because coyotes are the apex carnivore in my system, their densities likely correspond with prey (e.g., small mammals) densities which are expected to be greater in areas with increase CRP landcover (Thompson and Gese 2007, Stanley 2010). When coyotes and swift foxes both occur in areas with increased proportions of CRP landcover, my data suggests swift foxes alter temporal overlap with coyotes.

I expected landcover type (CRP, shortgrass prairie, and row-crop agriculture) and characteristics (total edge) to influence spatial activity patterns of swift foxes and coyotes, but found that across all classes and characteristics, only the amount of CRP on the landscape mediated their spatial interactions. At sites with lower proportions of CRP (≤0.04), swift foxes were influenced by presence of coyotes through space and time. This suggests in landscapes with no or low amounts CRP landcover, coyotes and swift foxes co-occur on the landscape more often than expected by chance, likely also indicating that swift fox mortality from coyote predation in these landscapes was sufficiently low for the two species to coexist (intraguild predation theory; Holt and Polis 1997). Conversely, as proportion of CRP landcover surrounding sites increased, SIF approached zero, suggesting coyotes and swift foxes co-occur on the landscape less often than expected by chance. Although 95% CI's of my estimated SIF overlapped zero, these results follow the predicted influence of tall vegetation cover on swift fox and coyote interactions; swift foxes and coyotes interact less than expected where predation risk is perceived to be higher (Thompson and Gese 2007). Another hypothesis would suggest that coyotes may be resource matching and their densities will be greater in landscapes with more CRP landcover, with swift fox actively avoiding these areas (Nelson et al. 2007). The introduction of CRP onto the landscape may create landscape heterogeneity that allows coexistence of locally competing carnivores (Davies et al. 2021). Contrary to my hypotheses, amount of row-crop agriculture and total landcover edge surrounding sites did not affect swift fox and coyote spatial interactions even though small mammal densities are likely greater in these areas compared to surrounding shortgrass prairie landcover (Bilenca et al. 2007, Heisler et al. 2013, Benedek and Sîrbu 2018). Agricultural landscapes may be poor quality swift fox habitat (Butler et al. 2020), however, because crop cover varies by season (i.e., crop height increases from spring to summer; Sovada et al. 2003) and confirmed sightings of swift foxes in row-crop agriculture fields during my study, swift foxes may be using these fields intermittently throughout the year (Werdel et al. In Revision).

Similar to previous studies documenting intraguild competition between sympatric carnivores (Thompson and Gese 2007, Nelson et al. 2007, Kozlowski et al. 2008, Robinson et al. 2014), swift foxes also likely practice spatiotemporal avoidance of coyotes in areas with increased predation risks. Results from my study suggest that CRP landcover proportions, and its inherent structure and composition, influence the intraguild interactions of swift foxes and coyotes. Carnivores worldwide are at increased risk of species extinction, primarily due to negative interactions with humans and sensitivity to habitat loss and fragmentation (Cardillo et al. 2004, Ripple et al. 2014, Di Minin et al. 2016a, b). Agriculture conversion of natural landscapes is the primary cause of habitat loss and fragmentation in remaining prairie ecosystems, with expanding agriculture landscapes creating a significant threat to carnivores worldwide (Woodroffe and Ginsberg 1998, Foley et al. 2005, 2011, Di Minin et al. 2016b). Investigations into species interactions within these novel landscapes may help managers identify and conserve important habitats or help us better understand factors that structure tropic-level interactions among carnivores.

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Table 2.1 Parameter summaries from my dynamic occupancy model which assumed that site occupancy of swift fox (*Vulpes velox*) varies due to the presence of coyotes (*Canis latrans*). "Coyote" refers to all sites where coyotes were observed, "Swift Fox without Coyote" refers to sites where swift foxes were observed but coyotes were not, and "Swift Fox with Coyote" refers to sites where swift foxes and coyotes were observed at the same sites. I assessed presence/absence of swift foxes and coyotes using camera traps at sites (2018 = 375, 2019 = 361, 2020 = 360) distributed across western Kansas, USA.

Species	Median	Lower – Upper 95% CI
Coyote		
Detection	0.129	0.124 – 0.134
Occupancy	0.666	0.617 – 0.713
Colonization	0.563	0.504 – 0.621
Persistence	0.612	0.565 – 0.658
Swift Fox without Coyote		
Detection	0.010	0.002 – 0.027
Occupancy	0.096	0.062 – 0.138
Colonization	0.016	0.003 – 0.057
Persistence	0.535	0.242 – 0.874
Swift Fox with Coyote		
Detection	0.001	0.000 – 0.003
Occupancy	0.013	0.008 – 0.020
Colonization	0.001	0.000 – 0.004
Persistence	0.402	0.129 – 0.862

Figure 2.1 Study area in Kansas, USA (7,160,077 ha) where I sampled 381 camera-trap sites for detection of coyotes (*Canis latrans*) and swift foxes (*Vulpes velox*) for three years (2018-2020). Study area encompasses furthest eastern extent of contemporary swift fox range and is comprised of an agro-prairie landscape matrix.

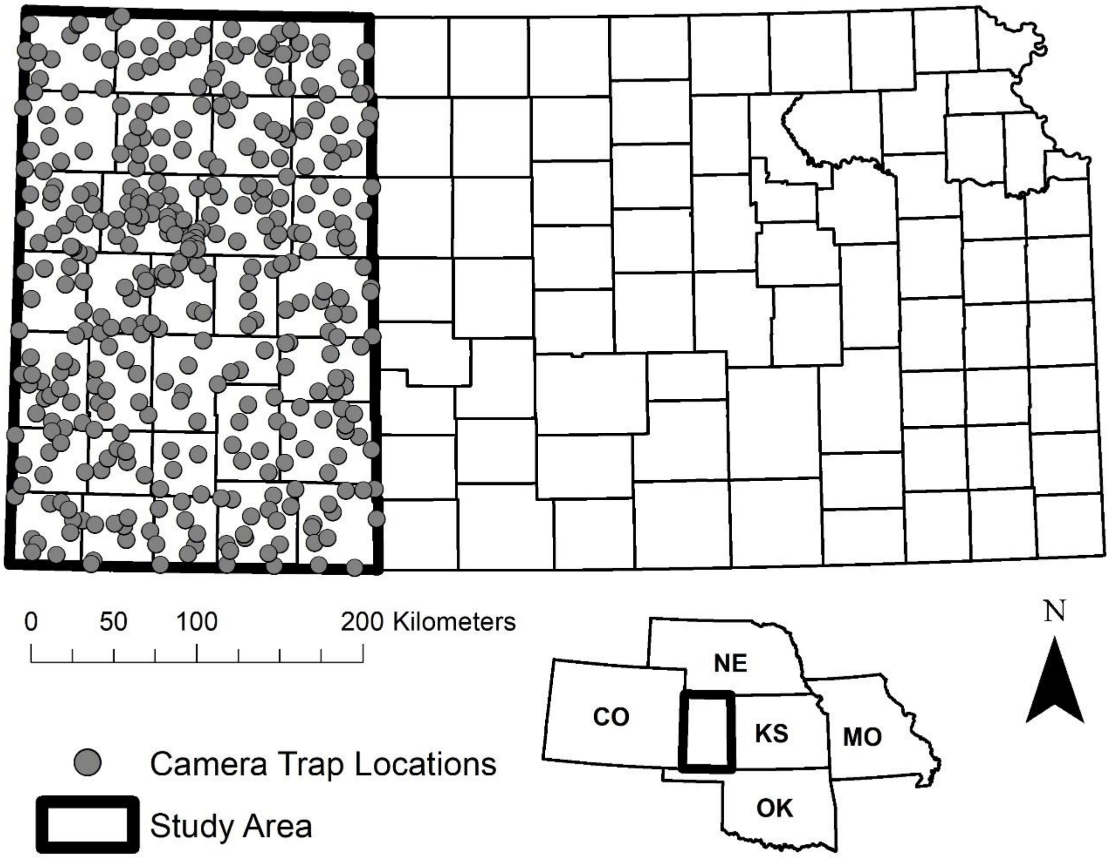


Figure 2.2 Kernel density function plots of coyote and swift fox activity in Kansas, USA (2018-2020). Kernel density functions and overlap estimation (Δ_1 if swift fox detections were <75, Δ_4 if swift fox detections at >75]) of (A) all coyote and swift fox activity, (B) coyote and swift fox activity when both are present at a site, (C) coyote and swift fox activity when both are present at sites with proportion of Conservation Reserve Program (CRP) landcover <0.10, and (D) coyote and swift fox activity when both are present at sites with proportion of CRP landcover ≥0.10.

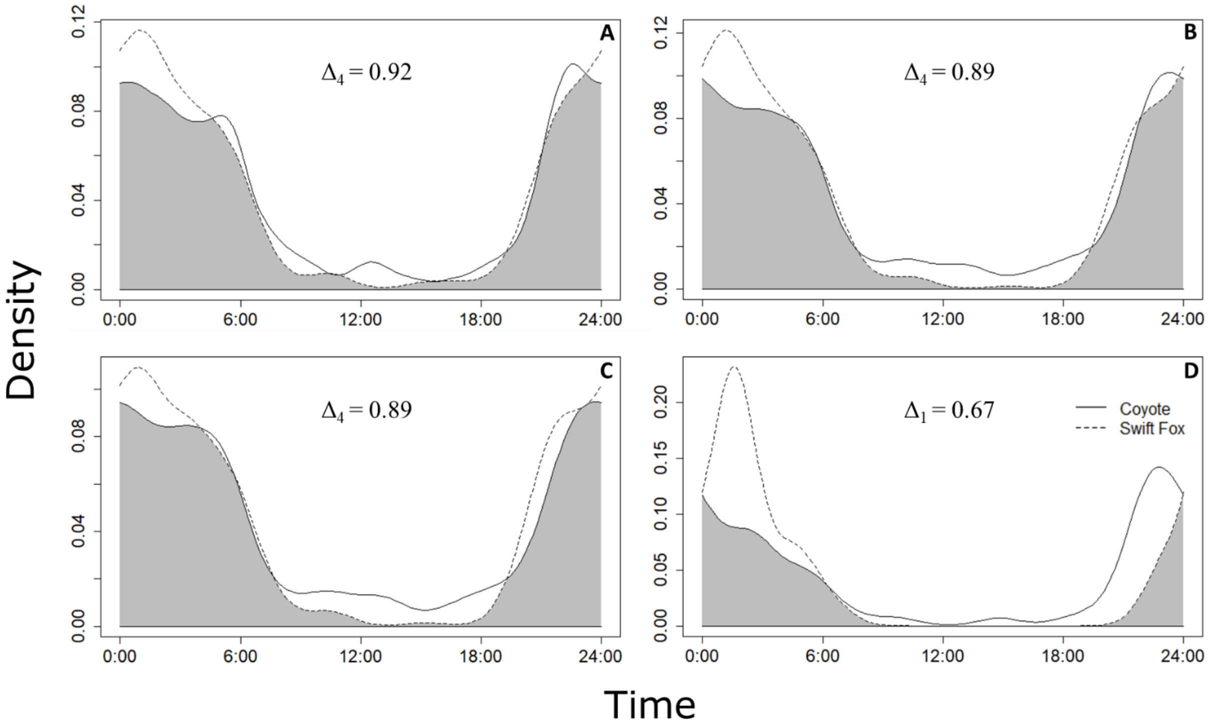


Figure 2.3 Bootstrapped means and 95% confidence intervals (CI's) of activity coefficient of overlap among swift foxes and coyotes in Kansas, USA (2018-2020). Coefficient of overlap means and CI's of all coyote and swift fox activity (All), coyote and swift fox activity when both are present at a site (Both), coyote and swift fox activity when both are present at sites with proportions of Conservation Reserve Program (CRP) landcover <0.10 (LCRP), and coyote and swift fox activity when both are present at sites with proportions of CRP landcover ≥0.10 (HCRP).

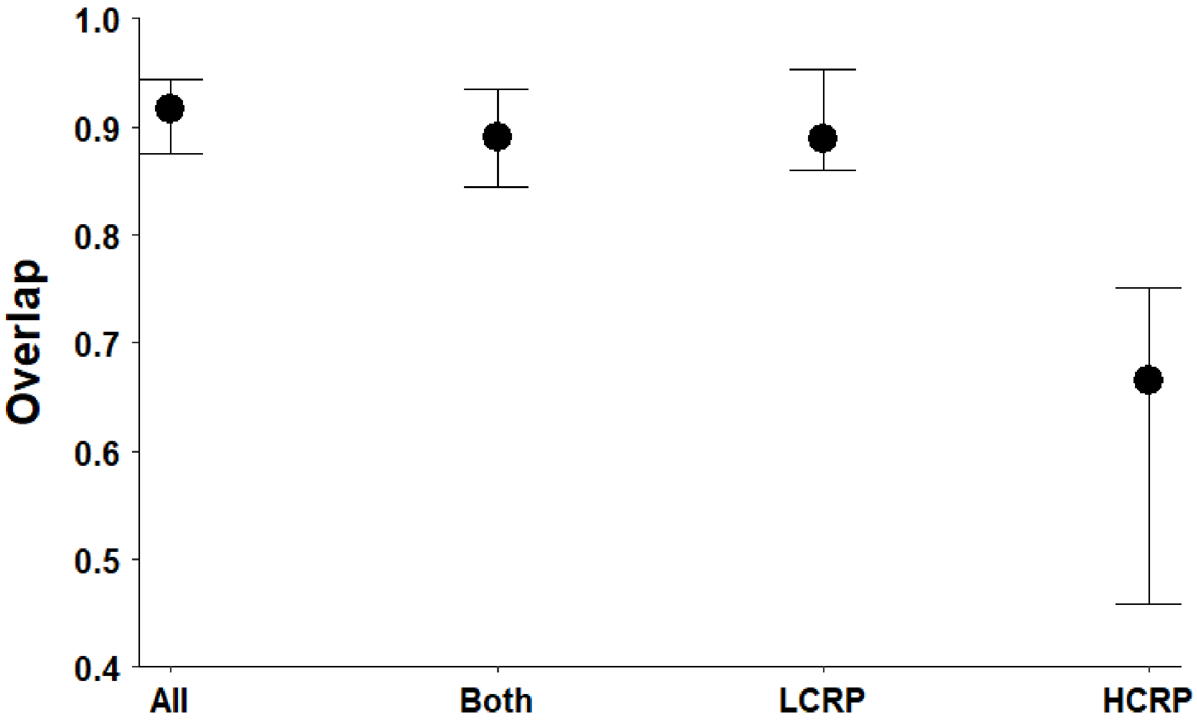
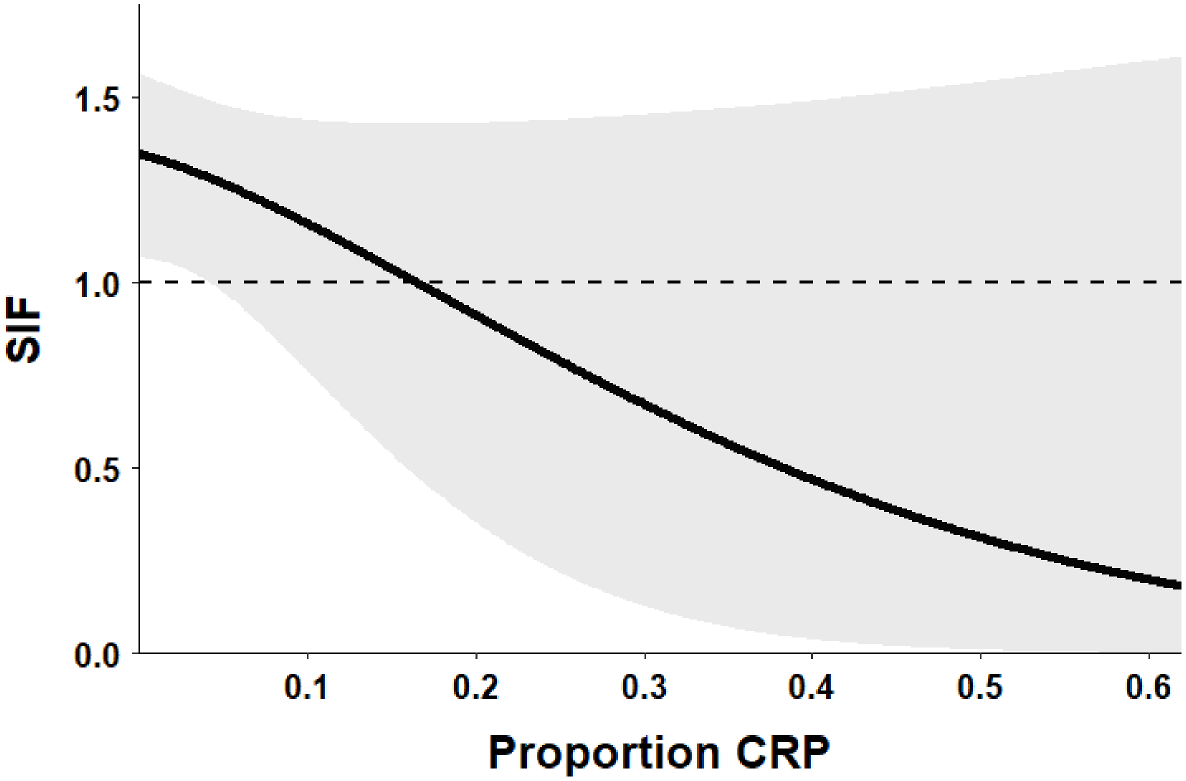


Figure 2.4 Species Interaction Factor (SIF) of swift foxes and coyotes in relation to the proportion of Conservation Reserve Program (CRP) landcover within 2km buffers in Kansas, USA (2018-2020). An SIF of 1 indicates expected spatial overlap, while an SIF > 1 indicates the species interact more often than expected, and an SIF < 1 indicates the species interact less often than expected.



Appendix B - Chapter 2 Supplemental Material

Table B.1 Metadata table for parameters used to estimate detection, occupancy, colonization, and persistence rates between swift fox (*Vulpes velox*, A) and coyote (*Canis latrans*, B) within a dynamic occupancy model. Effective sample size is the calculation of the equivalent number of independent samples that would contain the same posterior accuracy as the correlated samples from a Markov chain Monte Carlo. Model convergence was assessed by visually inspecting trace plots and ensuring that Gelman-Rubin diagnostics were < 1.1 (all parameters were < 1.1). I assessed presence/absence of swift foxes and coyotes using camera traps at sites (2018 = 375, 2019 = 361, 2020 = 360) distributed across western Kansas, USA.

Parameter	Scale	Description
a[x,y,z]	logit	Species by Parameter by Process array for the influence of coyote on swift fox colonization and persistence. For the first index, the 2 represents swift fox. For the second index, a 1 represents the average log-odds difference coyote presence has on the given process and a 2 represents the log-odds difference coyote presence has on swift foxes' response to proportion of CRP landcover. For the third index, a 1 represents colonization while a 2 represents persistence.
da[x,y]	logit	Species by Parameter array for the influence of coyote on swift fox detectability. For the first index, 2 = swift fox. For the second index, the 1 represents the average log-odds difference coyote presence has on swift fox detectability while the 2 represents the log-odds difference coyote presence has on swift foxes' response to proportion of CRP landcover.
psi0[i]	logit	Initial Occupancy intercept [species]. 1 = coyote. 2 = swift fox.
psi_crpi]	logit	Initial Occupancy Slope Term [species] 1 = coyote. 2 = swift fox.
pmu[i]	logit	Persistence Intercept [species]. 1 = coyote. 2 = swift fox.
lp[i]	logit	Detection Intercept [species]. 1 = coyote. 2 = swift fox.
gmu[i]	logit	Colonization Intercept [species]. 1 = coyote. 2 = swift fox.
gb[i]	logit	Colonization Slope Term [species]. 1 = coyote. 2 = swift fox.
pb[i]	logit	Persistence Slope Term [species]. 1 = coyote. 2 = swift fox.
lpb[i]	logit	Detection Slope Term [species]. 1 = coyote. 2 = swift fox.

Table B.2 Parameters used to estimate detection, occupancy, colonization, and persistence rates between swift fox (*Vulpes velox*, A) and coyote (*Canis latrans*, B) within a dynamic occupancy model. Effective sample size is the calculation of the equivalent number of independent samples that would contain the same posterior accuracy as the correlated samples from a Markov chain Monte Carlo. Model convergence was assessed by visually inspecting trace plots and ensuring that Gelman-Rubin diagnostics were < 1.1 (all parameters were < 1.1). I assessed presence/absence of swift foxes and coyotes using camera traps at sites (2018 = 375, 2019 = 361, 2020 = 360) distributed across western Kansas, USA. See Table B.1 for a description of each parameter and what each index represents.

Parameter	Median	Lower – Upper	Effective Sample Size
a[2,1,1]	-2.77	-3.47 – -2.20	17247
a[2,2,1]	-0.93	-1.89 – -0.15	17253
a[2,1,2]	-0.54	-1.49 – 0.29	28519
a[2,2,2]	0.00	-1.04 – 0.99	30944
da[2,1]	-2.07	-2.27 – -1.88	33819
da[2,2]	0.13	-0.11 – 0.36	34582
psi0[1]	0.69	0.47 – 0.91	40000
psi0[2]	-2.25	-2.72 – -1.83	25705
psi_crp1]	-0.18	-0.39 – 0.02	41037
psi_crp[2]	-0.56	-1.2 – -0.06	25234
pmu[1]	0.45	0.26 – 0.65	38150
pmu[2]	0.14	-1.14 – 1.94	4974
lp[1]	-1.91	-1.96 – -1.87	40000
lp[2]	-4.64	-6.04 – -3.57	7532
gmu[1]	0.25	0.01 – 0.50	40100
gmu[2]	-4.11	-5.85 – -2.81	19593
gb[1]	-0.09	-0.32 – 0.14	39162
gb[2]	0.05	-0.97 – 0.96	29627
pb[1]	-0.08	-0.27 – 0.12	37658
lpb[1]	-0.03	-0.08 – 0.02	40962
pb[2]	0.50	-1.06 – 3.50	4621
lpb[2]	-1.03	-3.09 – 0.32	7193

Chapter 3 - Strategic grassland conservation for swift foxes in a multi-use landscape

This chapter has been prepared for submission to Biological Conservation *and is formatted to journal specifications.*

Abstract

Native grasslands once covered approximately 162 million ha of North America prior to European colonization, but conversion of native grasslands has resulted in a 70% loss. Strategic conservation of remaining native grasslands is critical for the persistence of at-risk grassland wildlife and has become a global priority. Intact native grasslands are important for swift fox occupancy and survival, and I sought to identify priority native grasslands that included both greater swift fox site occupancy in landscapes with high proportions of native grassland. My goal was to strategically identify and prioritize areas of native grassland conservation to inform swift fox population conservation and management in an agro-prairie ecosystem. I modeled occupancy using three years of occupancy data (2018 – 2020) collected from camera-trap sites (381) covering the eastern edge of swift fox distribution in Kansas, USA, and a geographic information system to strategically identify potential native grassland conservation areas at an informative scale within (1-km) by intersecting predicted swift fox occupancy and grassland proportion layers. My occupied grassland assessment at two thresholds of predicted swift fox occupancy (≥ 0.09 and ≥ 0.18) identified 2,377,193 ha and 84,420.24 ha for conservation, respectively. Potential conservation areas were overwhelmingly located on privately owned working lands (98%).

Introduction

Native grasslands once covered approximately 162 million ha of North America prior to European colonization (Samson and Knopf, 1994). Native grasslands provided important ecosystem services including livestock forage, water quality improvement, flood mitigation, wildlife habitat, and carbon sequestration that were largely superior to those provided by restored or planted grasslands (Bakker and Higgins, 2009; Dodds et al., 2008). Conversion of native grasslands to production agriculture, however, resulted in a 70% loss of historical grassland landcover in the Great Plains (Samson et al., 2004). Demand for biofuels and increases in crop prices (e.g., corn [*Zea mays*]) will likely continue to drive conversion of remaining native grasslands to cropland or other alternative land uses (Lark et al., 2020, 2019). Conversely, the Conservation Reserve Program (CRP), enacted in the United States in the 1985 Food Security Act, is an effort to reduce soil loss in highly erodible agricultural lands by removing it from agricultural production, with additional benefits to wildlife including restoration of grassland habitat in these areas (Dunn et al., 1993). It is important, however, to distinguish between native grassland, comprised mainly of Indigenous plants (never cultivated or plowed), and grassland that has been re-established after conversion (DeFries et al., 1999; Lark et al., 2019), as not all prairie-obligate species respond positively to grassland restoration efforts through CRP efforts (Kamler et al., 2003; Werdel et al. In Revision).

Conservation of remaining native grasslands has become a priority across the world (Glaser, 2013). However, conservation of grasslands without regard to landscape composition and configuration does not account for ecological drivers that may have been altered, resulting in negative wildlife responses (Peterjohn and Sauer, 1999). Anthropogenic modifications influencing remaining grassland patches (e.g., grazing by fenced cattle, fire suppression, cultivation, invasive species) likely affect fidelity of ecosystem processes (Askins et al., 2007). Strategic applications of grassland conservation, rather than opportunistic implementations, may provide the most benefit to wildlife species of concern (Adkins et al., 2021; Sullins et al., 2018). Additionally, incorporating information from species' demography, natural history, and distribution (both historical and contemporary) are critical to the development of spatially explicit conservation actions (Sullins et al., 2018).

Swift foxes (*Vulpes velox*) are endemic to the Great Plains and distributed throughout remaining short and mixed grass grasslands (Sovada et al., 2009). Swift fox populations were extirpated throughout much of their historic range due to habitat loss and overharvest (e.g., bounties, trapping, poisoning; Sovada et al., 2009). Swift foxes have recolonized native grasslands where they were once extirpated, but due to their relatively low population densities (0.16 – 0.31 swift fox/km^2; Karki et al., 2007; Schauster et al., 2002), populations remain patchy across their contemporary distribution. Because of their small size (~3 kg), swift foxes primarily prey upon small mammals, insects, and birds (Kilgore, 1969). They also construct burrows in suitable loamy soils (containing equal amounts of silt, sand, and clay textures appropriate for den structure; Weil and Brady, 2016) to avoid predation and raise kits (Harrison, 2003; Jackson and Choate, 2000; Kitchen et al., 1999; Olimb et al., 2021). The eastern edge of swift fox contemporary distributions, where landscape change is likely most prolific, has become a patchy matrix of grazed and un-grazed remnant native grasslands, row-crop agriculture, and energy development (Drummond et al., 2012; Samson and Knopf, 1994; Sovada et al., 2009). Although CRP is used as a grassland restoration tool throughout swift fox distributions, it may restrict eastern recolonization due to taller vegetation structure (>30 cm) that can increase predation risk in these landscapes (Werdel et al. In Revision).

I used 3-years of occupancy rates (0-1) derived from camera-trap sites across the eastern edge of swift fox distributions in Kansas, USA to identify potential areas for swift fox conservation. My goal was to strategically identify and prioritize areas of native grassland conservation to inform swift fox population conservation and management in an agro-prairie ecosystem. My previous study (Werdel et al. In Review) used a dynamic, multi-season occupancy model to identify scale-specific landscape effects on swift fox initial site occupancy probability and colonization and turnover rates and I used this information to inform models in this study. Because intact native grasslands are important for swift fox occupancy (Werdel et al. In Revision) and survival (Butler et al. 2021), I identified priority native grassland conservation areas that included areas of both greater site occupancy and proportions of native grasslands >0.62.

Methods

Study Area

My study extent (7,160,077 ha) was bound by the 31 westernmost counties of Kansas, USA (-100.815301, 38.492366; Fig. 3.1). Historically, the region was comprised of native grassland but due to anthropogenic conversion, the contemporary region now consists of row-crop agriculture (62%, 4,439,247 ha) intermixed with remnants of native grassland (27%, 1,894,556 ha) and federally managed CRP easements (7%, 501,205 ha). Remaining short- and mixed-grass prairies is characterized by side-oats grama (*Bouteloua curtipendula*), buffalo grass (*Bouteloua dactyloides*), big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), witchgrass (*Panicum capillare*), tumblegrass (*Schedonnardus paniculatus*), Indiangrass (*Sorghastrum nutans*), blue grama (*Bouteloua gracilis*), and sand dropseed (*Sporobolus cryptandrus*). Annual average precipitation varied along a west-to-east longitudinal gradient (31-107 cm annually), and temperatures ranged from -9-49° C (“PRISM Climate Group 2021). Oil wells (*n* = 20,093) and wind turbines (*n* = 1,429) were also widespread throughout the region (Kansas Geological Survey 2021). My study area encompassed the entire contemporary distribution of swift foxes in Kansas (Sovada et al., 2009).

Camera Trap Placement

I initially selected 381 random camera trap locations (hereafter ‘site’), each ≥ 2-km apart (limiting individual swift fox detections at multiple sites [swift fox home range ~12.56 km^2; Kamler et al., 2003]). Each site consisted of a single motion-sensing camera (Bushnell Trophy Cam®; Bushnell Corporation, Overland, KS, USA) affixed to a metal T-post (40 cm high with a north/south orientation to avoid solar interference). I used a stake (40 cm high, positioned 3 m in front of the camera at each camera trap) with an olfactory attractant (mixture of skunk essence [F&T Fur Harvester’s Trading Post, Alepna, MI, USA] mixed into petroleum jelly [Stratman and Apker, 2014]) to lure swift fox into the camera field-of-view (Stewart et al., 2019). I removed vegetation within the field-of-view of each camera using a handheld cutter. Camera traps were functional for 28 days (Wait et al. 2018), and I returned to sites after ~14 days to refresh olfactory attractant and replace batteries and digital memory cards.

Camera traps were in place from 5 May – 2 November 2018 (n = 375), 20 May – 2 October 2019 (n = 361), and 22 April – 28 September 2020 (n = 360). Changes in accessibility on private lands reduced the total number of camera trap locations during 2019 and 2020. I manually scanned all photos from each site for detection (1) or non-detection (0) of swift foxes each year. I considered a site occupied during a given year if I observed ≥ 1 photo of a swift fox during the 28-day sampling period for that year.

Landscape Characterization

I created a landcover raster (30x30 m pixel size) covering the extent of my study area by merging information from 2018 CRP enrollments (Farm Service Agency 2018), CropScape (CropScape 2018), and PRAIRIEMAP (PRAIRIEMAP 2003). From this raster, landcover was classified into three classes (CRP, grassland, and row-crop agriculture). I also converted soil distribution polygons (Web Soil Survey 2018 [SSURGO]) to raster format to characterize the spatial distribution of soil types across my study area (30x30 m). I estimated the proportion of native grassland within a 1-km radius moving window which has been linked to swift fox survival (Butler et al. 2021). I extracted landcover class proportions and amount of landcover heterogeneity (SHDI) within 1-km of each site using circular buffers in R (v. 4.0.3) "landscapemetrics" package (Hesselbarth et al., 2019).

Predicting Contemporary Distribution of Swift Foxes

My previous study used a dynamic, multi-season occupancy model to identify distribution constraints of swift foxes at the eastern edge of their contemporary distribution (Werdel et al. In Revision). That model used detection histories from one year (2018) to estimate site occupancy probabilities, and the remaining years were used to model site turnover. Additionally, my previous model used scale-specific covariates to estimate site occupancy (2018) and turnover (2019-2020; did not include occupancy rates). To build a more robust occupancy model that incorporated detection histories from all three years and using a covariate scale informed by known-fate survival information (Butler et al. 2021), I used single-season, stacked occupancy models that considered each camera trap per year (2018, 2019, and 2020) to be an independent sampling effort (i.e., stacked design [Vanek et al., 2021]; R 4.0.3, unmarked package v.1.0.1). Thus, I structured detection histories (28 days per year) for 1096 sites. I assumed probability of swift fox occupancy at sites reflected habitat use during a biologically closed sampling season (i.e., no dispersal). All covariates were standardized (mean = 0) prior to analysis, and I did not include any correlated ($|r| \geq 0.60$) covariates within the same model. I structured my detection histories to include 28 independent, 1-day surveys at each site (*sensu* Fidino et al., 2020). I developed four detection covariates to control for survey-specific variation in swift fox detection. To control for unmeasured within-year effects on detection, I modeled day of year (DOY; days since 1 January of survey year; range = 112 – 308]). I controlled diminishing effects of my attractant by including a covariate representing the number of days since scent was applied or reapplied at each site (Scent). Camera traps were occasionally destroyed or knocked down by cattle (*Bos taurus*) or farm equipment (resulting in a decreased or ineffective camera view field), so I developed a covariate to include the number of days cameras were inactive or had altered field-views at each site (Altered). I controlled for the potential of dynamic yearly survey efforts by including a categorical covariate (Year) representing each year with subsequent model estimates in relation to my initial sampling year (2018). I developed a candidate detection model set ($n = 16$) using models incorporating the single (DOY, Scent, Altered, Year) and additive effects of these covariates, along with a constant model (Intercept Only; Table C.1).

I used a sequential-by-sub model strategy, with each subsequent sub-model dependent upon the selected model structure from the previous stage (Morin et al., 2020). I first identified my most-supported detection model, then included this model in all subsequent models of site occupancy. I developed *a priori* candidate model sets for site occupancy which included proportion within 1-km buffer of native grassland (Grass), row-crop agriculture (Ag), CRP, loamy soils (Loamy), and landcover heterogeneity (SHDI). I assessed 24 models within my site occupancy model set, including single and additive effects of covariates (Ag and Grass were not included together in any model; |*r*| = -0.68), and a constant model (Intercept Only; Table C.1). Models were ranked using AIC_C, and models ≤2.00 ΔAIC_C were considered competitive (Burnham and Anderson, 2002). I selected my best-supported model by assessing relative changes in model deviance (Burnham and Anderson 2002; Arnold 2010). I further assessed predictor importance by assessing cumulative model weights.

After identifying my most-supported site occupancy model, I evaluated model accuracy by calculating the area under (AUC) the receiver operating characteristic (ROC) curve (I used a cutoff value where sensitivity = specificity [0.09]; Long et al., 2011). ROC curves plot the true positive rate (sensitivity) against the false positive rate (1 – specificity) and AUC is the measure of a diagnostic test's discriminatory power with a maximum value of 1, indicating a perfect test, and a value of 0.5 indicating no discriminative value. AUC values >0.75 are considered diagnostically useful; Fan et al., 2006). I then created a baseline, raster-based predictive swift fox distribution map using its associated covariate estimates (ArcMap v. 10.8; Karanth et al. 2009; Long et al. 2011).

Identifying Conservation Areas

Results from my previous study (Werdel et al. In Review) and from my current, more robust occupancy analyses (see Results) indicated greater proportions of native grassland landcover positively influenced site occupancy by swift foxes. Additionally, increased grassland landcover was linked positively to swift fox survival (survival=0.95; Butler et al. 2021), underscoring the need to conserve remnant grassland landcover where swift fox populations occur. I used a geographic information system (ArcMap v. 10.8) to strategically identify potential native grassland conservation areas. To establish a minimum proportion of native grassland needed to maximize swift fox survival, I assumed swift fox survival (monthly) was ≥

0.95 when the proportion of grassland landcover was ≥ 0.62 within a 1-km moving window (following empirical results from Butler et al. 2021). I sought to identify potential conservation areas at two classes of predicted swift fox occupancy: ≥ 0.09 (mean predicted swift fox occupancy and cutoff value from my ROC analysis; see Results) and ≥ 0.18 (double the confidence of predicted occupancy and ≥ 80% of predicted occupancy values). I created a 15-km buffer (swift fox mean dispersal distance; Sovada et al., 2003) around raster cells with predicted values of occupancy for both classes. I used a 1-km moving window to identify mean proportion of native grasslands ≥ 0.62, that likely correspond with greater swift fox survival rates (Butler et al. 2021). After creating a raster of native grasslands with mean proportion values ≥ 0.62, I converted the raster to a polygon and created a 1-km buffer to include all areas used in the moving window analysis, and finally, intersected the buffer polygon with areas of predicted occupancy (both ≥ 0.09 and ≥ 0.18; Fig. 3.2). I used federal, state, and non-governmental organizations (NGO) shapefiles to delineate land ownership boundaries of conservation areas (Kansas DASC 2022) and compared the amount of potential conservation areas (ha) held by both private landowners and non-private landowners.

Results

I captured 5,217,641 photos during 27,954 camera-trap days. Cameras were active an average of 25 days (SE = 0.154, range = 2-28) each year and were unaltered an average of 22 days (SE = 0.222, range = 0-28) at each site. I observed swift foxes in 341 photos at 71 out of 1096 sites between 2018-2020 (naïve occupancy = 0.07).

My only competitive detection model included the additive effects of DOY, Scent, Altered and Year (Table C.1). I was more likely to detect swift foxes later in the year (β = 0.004 ± 0.002). Additionally, I was less likely to detect swift foxes as my olfactory attractant diminished (β = -0.059 ± 0.020) and when the camera field-view was altered (β = -1.221 ± 0.339). Survey year also affected detection (2019, β = -0.786 ± 0.273; 2020, β = -0.138 ± 0.199). Mean per-survey detection from my most-supported detection model = 0.092 (SE < 0.000).

My top and most-supported model for site occupancy included SHDI, Grass, Loamy, and CRP (*w* = 0.52). Swift foxes were more likely to occur at sites with less landcover heterogeneity (β = -0.411 ± 0.140; Fig 3.3A), greater proportions of native grassland (β = 0.375 ± 0.154; Fig 3.3B) and loamy tableland soils (β = 0.944 ± 0.188; Fig 3.3C), and lower proportions of CRP landcover (β = -1.081 ± 0.360; Fig 3.3D). Site occupancy probability adjusted for detection was 0.086 (SE = 0.003). The swift fox predictive distribution map created from my most supported model (Fig. 3.4) had sufficient discriminatory power (> 0.75) based on the area under the ROC curve (0.83; Fig. 3.5).

I identified 2,377,193 ha (predicted swift fox occupancy ≥ 0.09) and 84,420.24 (predicted swift fox occupancy ≥ 0.18) of potential native grassland conservation areas. Potential conservation areas were overwhelmingly located on privately owned working lands (98%; 2,327,575 ha [predicted swift fox occupancy ≥ 0.09] and 82,703.86 ha [predicted swift fox occupancy ≥ 0.18]), while only 2% of my identified conservation areas (49,618 ha [predicted swift fox occupancy ≥ 0.09] and 17,16.38 ha [predicted swift fox occupancy ≥ 0.18]) were located within federal, state or NGO lands (Fig. 3.6).

Discussion

As expected, my most supported occupancy model suggests that swift foxes were more likely to occur at sites surrounded by greater proportions of native grassland and loamy tableland soils, and less likely to occur in landscapes with greater proportions of CRP landcover and greater landcover heterogeneity. Diagnostic validation (AUC = 0.83) of my single-season occupancy model, incorporating a scale that was informed by known-fate survival information, supported the predictive power of my model and confidence in conserving my identified priority native grasslands. Although I acknowledge that landscape composition of loamy tableland soils, CRP, and landcover heterogeneity are important factors for habitat use by swift foxes, these additional effects are less likely, or impossible, to be managed for swift fox conservation.

Although there are several landscape-scale factors important for habitat use by swift foxes, actively managing landscapes solely for swift fox may be unrealistic. Restoration of loamy tableland soil is not actionable for swift foxes as these soil types developed over millennia (Weil and Brady, 2016). Additionally, expanding CRP easements with the direct goal of enhancing swift fox distributions will likely fail as this and previous work has identified these areas as low-quality habitat for swift foxes. Because of the multiple benefits associated with CRP (e.g., soil conservation, improved water quality, wildlife habitat; Reichelderfer and Boggess 1988), it is unlikely, and not recommended, that this program be suspended to benefit swift fox populations. Because increases in native grassland landcover can positively influence habitat use by swift foxes (Finley et al., 2005; Kamler et al., 2003), as well as enhance demographic factors such as survival (Butler et al., 2021) and population densities (Gese and Thompson, 2014), I think aggressive conservation of these areas are key for future landscape-scale conservation efforts for swift fox populations.

My approach to identify native grassland conservation areas by integrating occupancy models and known-fate survival information, will allow managers to strategically target grasslands beneficial to the persistence of swift fox populations. When considering areas in my first identification class, where predicted site occupancy cutoff was informed by my ROC and AOC analyses (≥ 0.09), all native grassland areas that were also large enough to maximize survival rates were included in my spatially-explicit strategic assessment. Although conserving the entirety of these native grassland areas would undoubtedly benefit swift foxes and other prairie-obligate species, it is improbable that any management agency could implement this level of conservation in a region primarily dependent on agriculture and energy development. Therefore, identifying native grasslands in my second assessment class where predicted occupancy cutoff ≥ 0.18 (top 20% of site predicted occupancies) in areas that also had sufficient grassland cover to maximize swift fox survival rates, allows conservation managers to prioritize and strategically target top-tier areas for grassland conservation.

Although my results are compelling, there were limitations to my study design. I do not have on-the-ground assessments of land-use for the extent of native grasslands I identified in my analyses. Understanding how grassland habitat quality has been affected by grazing intensity and fire regimes across both privately and non-privately owned grasslands, would likely improve my definition of priority conservation areas. Grazing intensity and fire frequency and intensity at grassland patches are likely dynamic and would need to be modelled in future assessments. I also used mean swift fox dispersal distance as a proxy for connectivity between grassland patches in my landscape-scale analyses. Connectivity between patches is likely affected by landcover, configuration, and anthropogenic infrastructure (e.g., roadways) within the matrix, and my models could be enhanced by accounting for functional connectivity between grassland patches. Unfortunately, the relative permeability of landcover types within my agro-prairie ecosystem by swift foxes is unknown. I further suggest that future research incorporate private landowner attitudes and beliefs towards conservation of swift foxes to enhance my model predictions of priority areas for grassland conservation.

Native grasslands identified as areas of priority conservation importance within my study area were overwhelmingly privately owned and managed (98% of total native grassland conservation area). Beef cattle production is the major enterprise on privately owned grasslands within my study area (Boyer et al., 2004) and likely to remain a significant land-use characteristic within the Great Plains in the future. Rangelands have experienced increasing recognition of their value to provide ecosystem services, with ecological stewardship becoming part of their recommended management framework (Chapin III et al., 2009; Havstad et al., 2007). Management of rangeland wildlife can compete with livestock production goals, especially when landowners derive no tangible benefits from wildlife (Ranglack and Toit, 2016). For strategic native grassland conservation to promote the sustainability of swift foxes in my study area, it is important for wildlife managers to provide incentives (e.g., monetary or social) to private landowners who contribute to conservation. Of note, the most intact temperate grassland in the world (Sand Hills of Nebraska) has no mandated conservation strategy, but forage benefits as a rangeland for grazing cattle and membership in local conservation groups acts as incentive (Scholtz and Twidwell, 2022).

Only 54.3% of carnivore species' geographic range worldwide is comprised of high-quality habitat, with only 5.2% of that high-quality habitat found within protected areas (Crooks et al., 2011). Protected conservation areas are vital for the biodiversity of both plant and animal species, especially in the contemporary era of rapid global change (Scholtz and Twidwell, 2022). Of terrestrial ecosystems, native grasslands are the most threatened on Earth (Suttie et al., 2005), and similar to my study area, these grasslands across the world have little to no federal or international protection (Carbutt et al., 2017). My study highlighted that state, federal, and NGO managed native grasslands made up a significantly small portion of native grasslands targeted in my analyses (2% of total native grassland conservation area). Although a small overall proportion, the continued management of these areas is integral in conserving native grassland dominated landscapes.

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Figure 3.1 Study area in Kansas, USA (7,160,077 ha) where I sampled camera-trap sites (2018 = 375, 2019 = 361, 2020 = 360) for detection of swift fox (*Vulpes velox*) for three years (2018-2020).

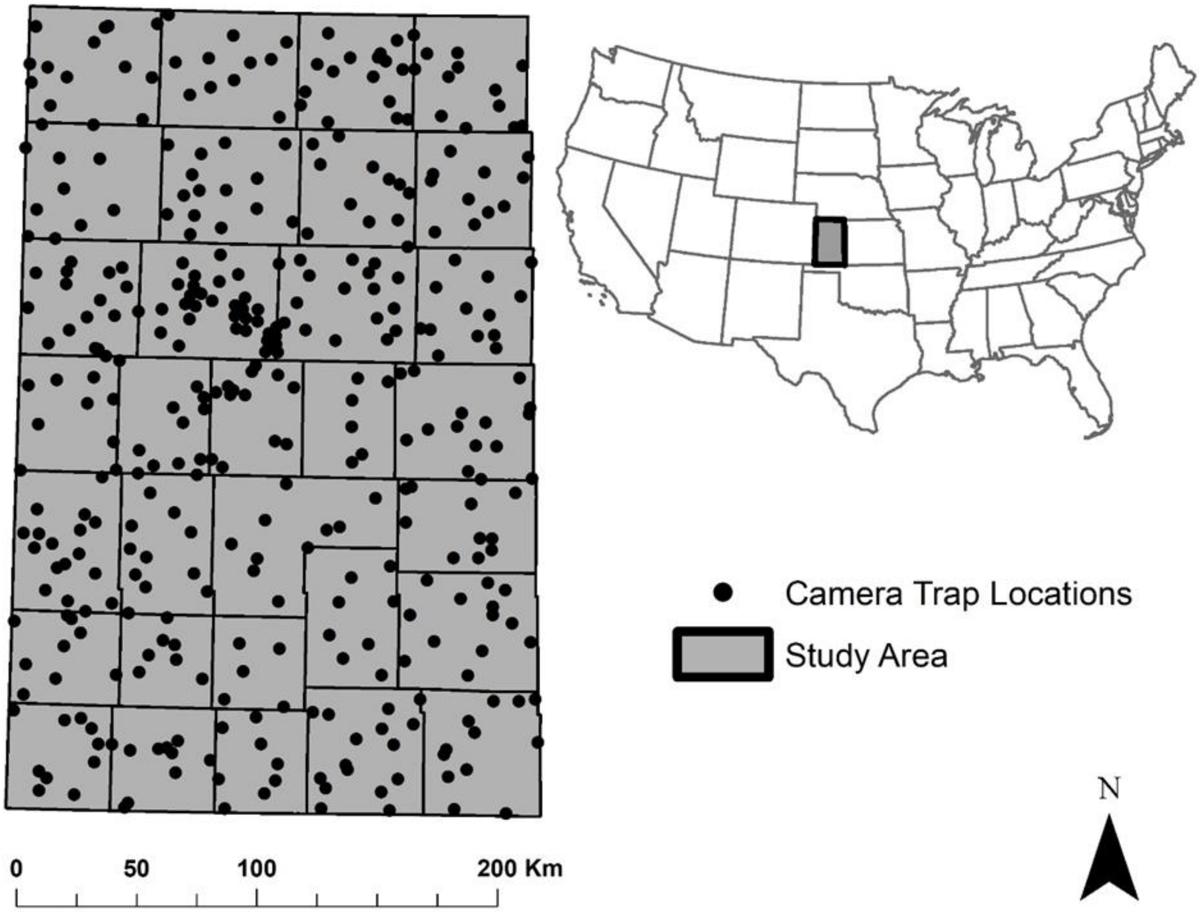


Figure 3.2 Geospatial workflow to strategically identify native grassland conservation areas for swift fox (*Vulpes velox*) in Kansas, USA using a geographic information system (ArcMap v. 10.8). Layers presented include swift fox predicted occupancy raster (A), swift fox predicted occupancy ≥ cutoff value (B), polygon (created from raster) B buffered by mean swift fox dispersal distance (C), 1-km moving window of native grassland proportions (D), native grassland proportions from raster D that were ≥ 0.62 to correspond with increased swift fox survival rates (E), polygon (created from raster) E buffered by 1-km (F), and intersection of polygons C and F (G).

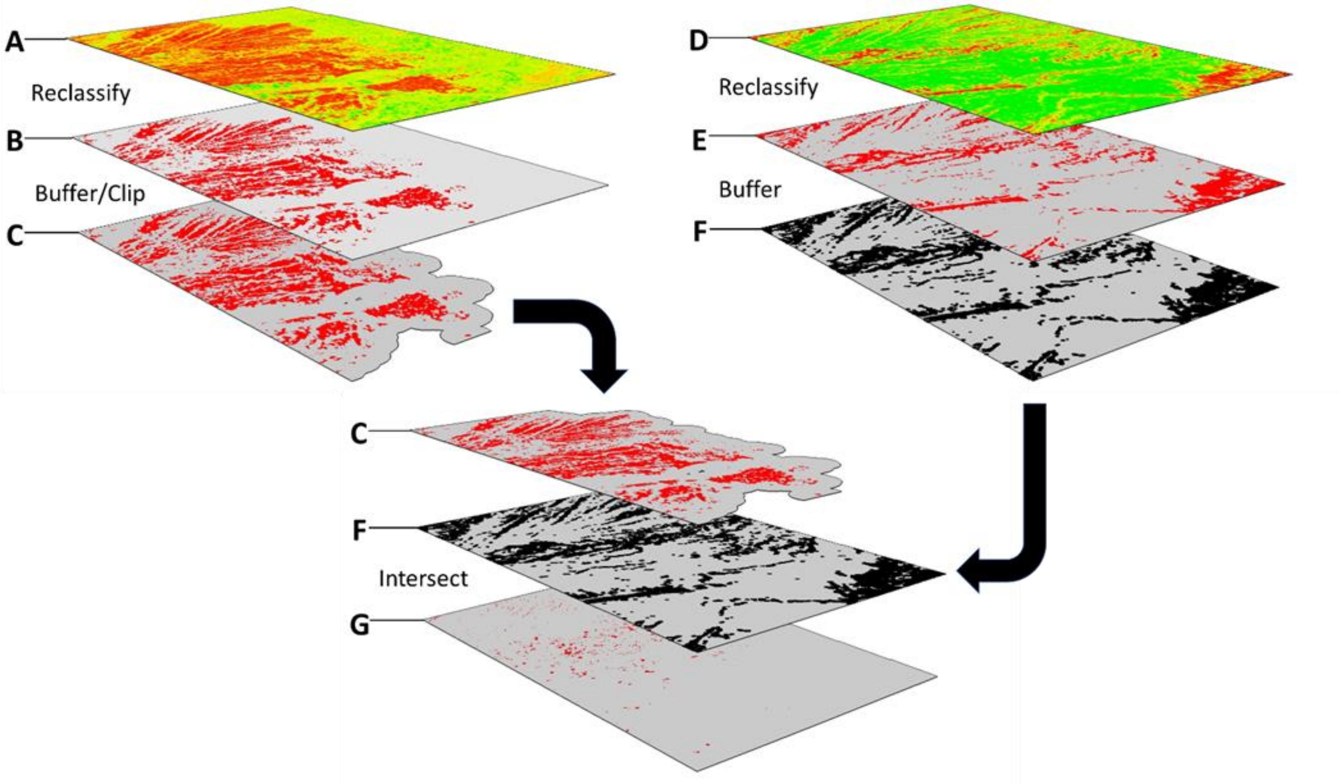


Figure 3.3 Site occupancy probabilities (and 95% CI) for swift fox (*Vulpes velox*) in relation to landcover heterogeneity (A), proportion of native grassland (B), proportion of loamy tableland soils (C), and proportion of lands enrolled in the Conservation Reserve Program (D) surrounding camera-trap sites. I assessed presence/absence of swift fox using camera traps at sites (2018 = 375, 2019 = 361, 2020 = 360) distributed across western Kansas, USA. Site occupancy probabilities were derived from my most-supported single-season occupancy model. Note scale of y-axes.

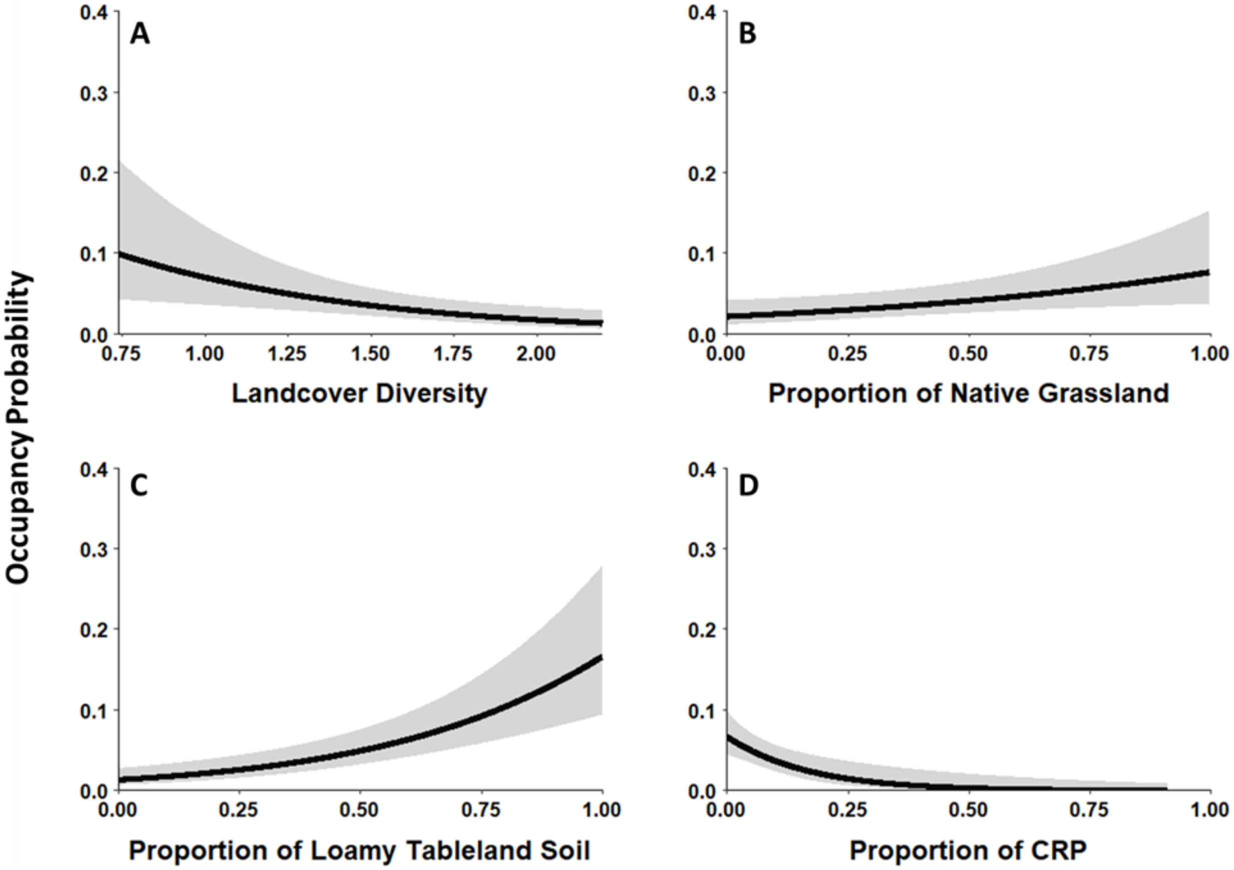


Figure 3.4 Site occupancy predictions for swift fox (*Vulpes velox*) in western Kansas, USA. Predictions were based on the influence of the additive effects of covariates within my most supported initial occupancy model. I assessed swift fox site occupancy at sites (2018 = 375, 2019 = 361, 2020 = 360) using camera traps distributed across western Kansas, USA.

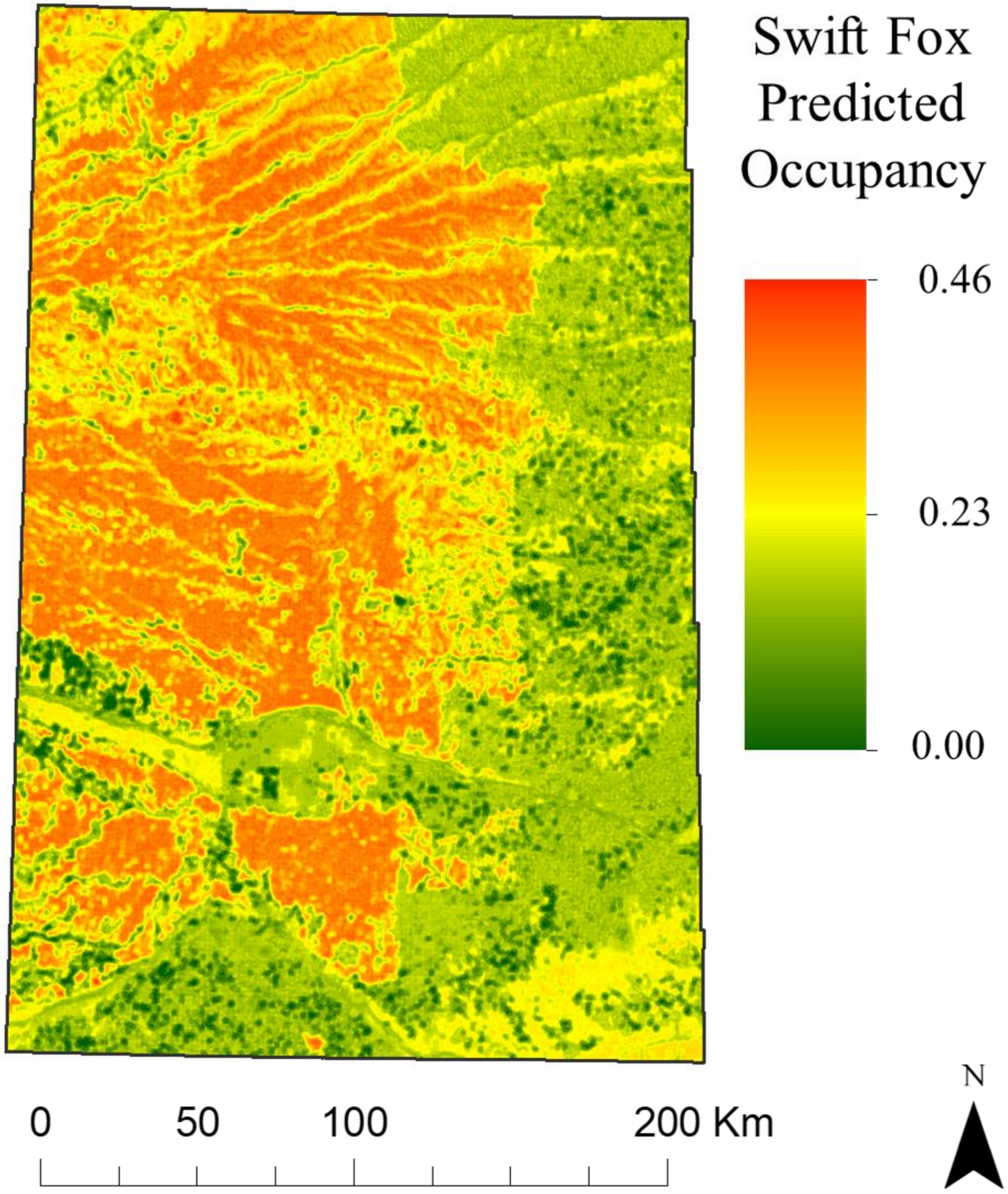


Figure 3.5 Receiver operating characteristic (ROC) of predicted swift fox site occupancy, based on the influence of the additive effects of covariates within my most supported initial occupancy model. Cutoff value method for swift fox predicted occupancy was the value of sensitivity = specific (0.09; represented as a diamond). Area under curve (AUC) = 0.83. I assessed swift fox site occupancy at sites (2018 = 375, 2019 = 361, 2020 = 360) using camera traps distributed across western Kansas, USA.

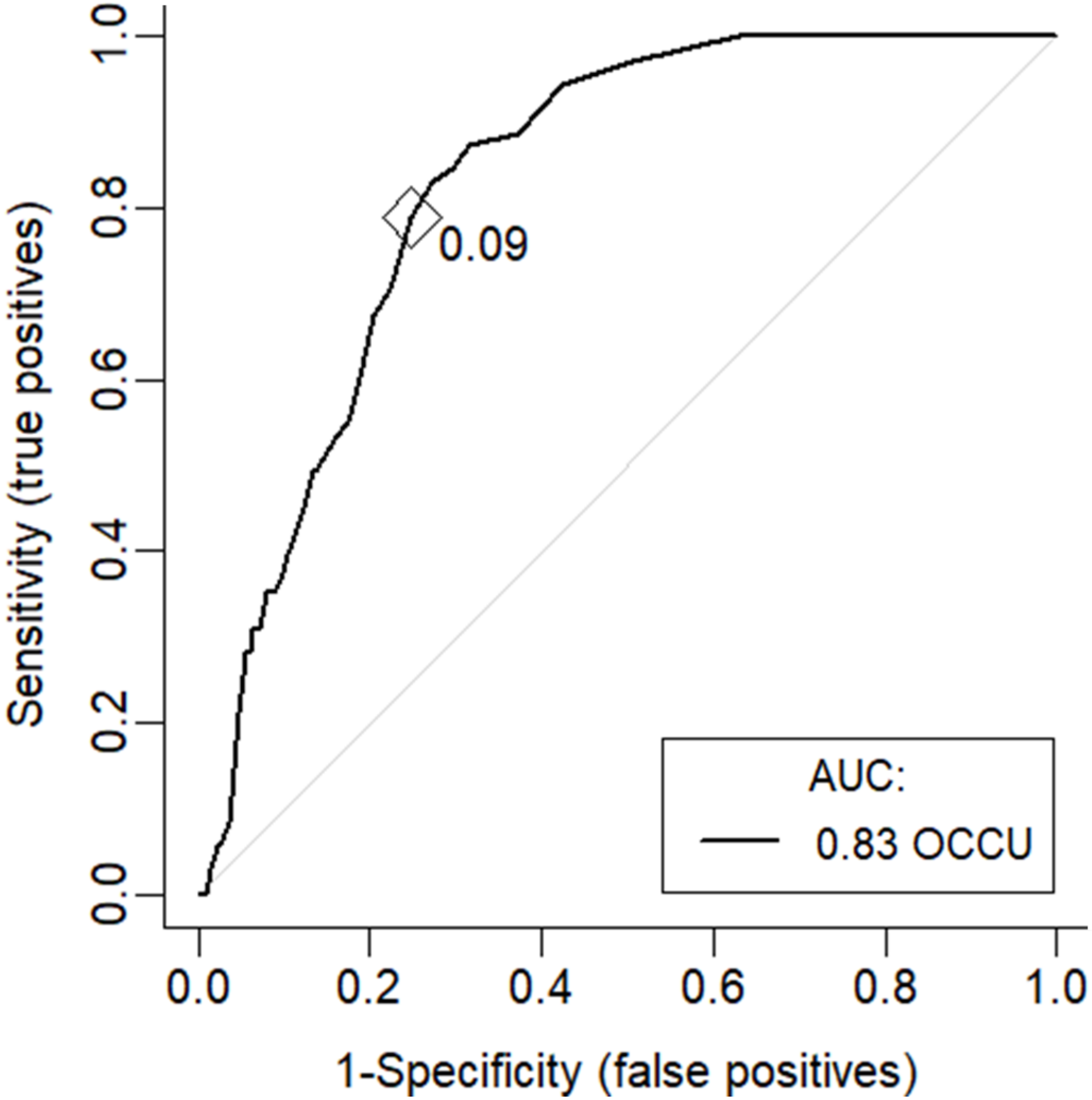
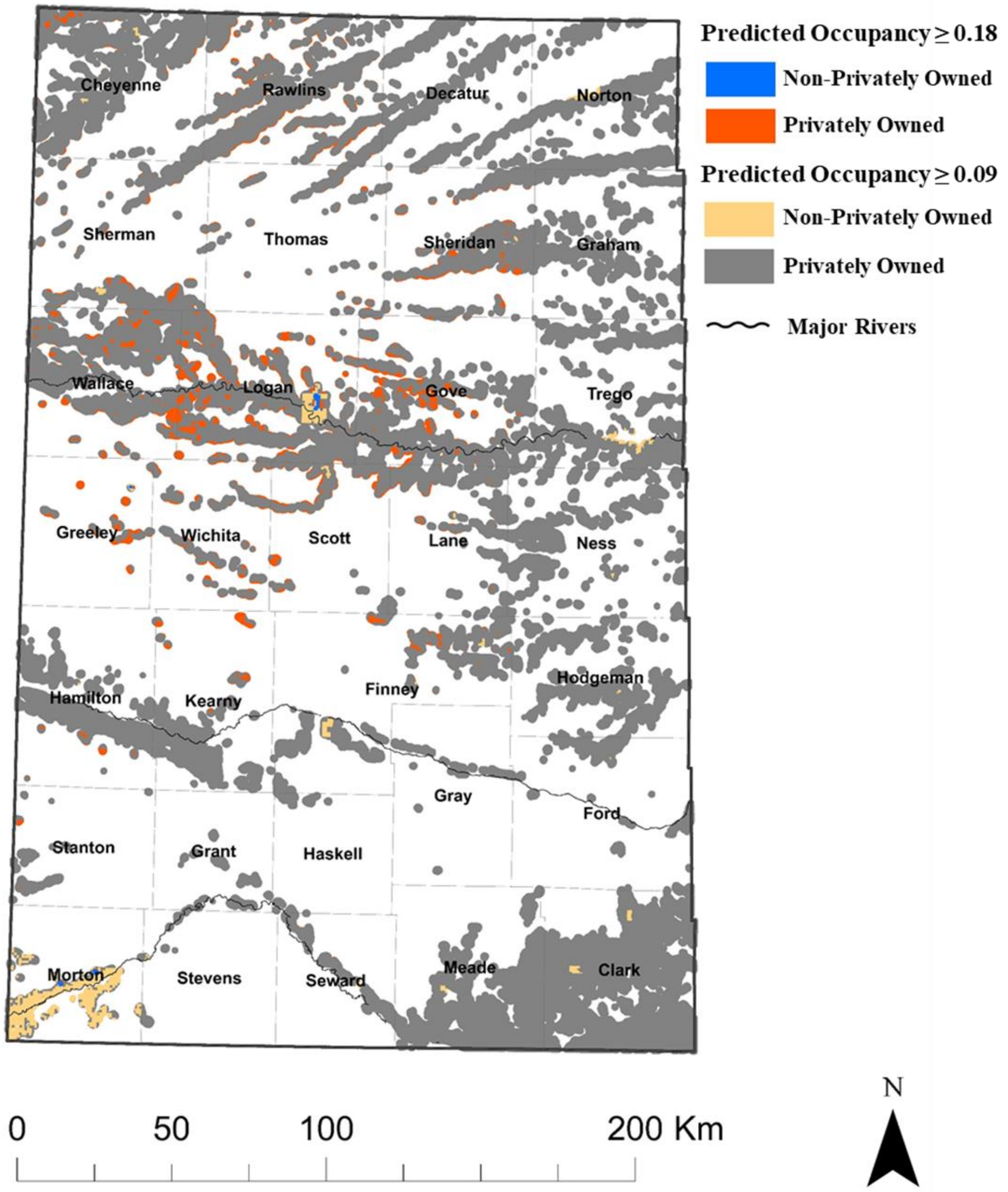


Figure 3.6 Strategically identified native grassland conservation areas using predicted swift fox site occupancy and proportion of native grassland. Minimum proportion of native grassland was ≥ 0.62 within a 1-km moving window (to maximize swift fox survival). I identified potential conservation areas at two classes of predicted swift fox occupancy: ≥ 0.09 (mean predicted swift fox occupancy and cutoff value from my ROC analysis) and ≥ 0.18 (double the confidence of predicted occupancy and ≥ 80% of predicted occupancy values) within my study area of western Kansas, USA. Privately owned grasslands for both predicted cutoff values covered 98% of the total conservation areas. Federal, state, and non-governmental organization (NGO) managed conservation lands (Non-Privately Owned) only made up 2% of total conservation area.



Appendix C - Chapter 3 Supplemental Material

Table C.1 Model-selection statistics for all models of detection (n = 16) and site occupancy (n = 24) by swift fox (*Vulpes velox*) in western, Kansas, U.S.A. I present all models along with the null model (Intercept Only) for each parameter. Covariates include day of year (DOY), number of days since bait was applied or reapplied at each site (Scent), days with an altered camera view field (Altered), year surveyed (Year), landcover heterogeneity (SHDI), proportion native grassland (Grass), loamy tableland soils (Loamy), proportion of conservation reserve program (CRP), and proportion of agriculture (Ag). K = number of model parameters, ΔAIC_c = difference between AIC_c model value compared to the top model, w = Akaike weight, -2LL = log-likelihood * (-2), indicating model fit.

Model	K	AIC_C	ΔAIC_C	w_i	-2LL
Detection					
DOY + Scent + Altered + Year	7	1752.28	0.00	0.71	1738.18
Scent + Altered + Year	6	1754.96	2.68	0.19	1742.88
DOY + Scent + Altered	5	1757.09	4.81	0.06	1747.04
DOY + Altered + Year	6	1759.27	6.99	0.02	1747.20
Altered + Year	5	1760.76	8.48	0.01	1750.70
DOY + Altered	4	1764.66	12.38	0.00	1756.62
Scent + Altered	4	1765.79	13.50	0.00	1757.76
Scent + Year	5	1766.90	14.62	0.00	1756.84
DOY + Scent + Year	6	1767.49	15.21	0.00	1755.42
DOY + Scent	4	1771.76	19.47	0.00	1763.72
Altered	3	1771.78	19.49	0.00	1765.76
Scent	3	1775.38	23.09	0.00	1769.36
Year	4	1775.59	23.31	0.00	1767.56
DOY + Year	5	1777.05	24.77	0.00	1767.00
DOY	3	1782.53	30.25	0.00	1776.52

NULL	2	1784.03	31.75	0.00	1780.02
<u>Occupancy</u>					
SHDI + Grass + Loamy + CRP	11	1662.45	0.00	0.52	1640.22
SHDI + Loamy + CRP + Ag	11	1663.06	0.61	0.38	1640.82
SHDI + Loamy + CRP	10	1666.45	4.01	0.07	1646.26
Grass + Loamy + CRP	10	1669.18	6.74	0.02	1648.98
Loamy + CRP	9	1671.39	8.94	0.01	1653.22
Loamy + CRP + Ag	10	1672.56	10.11	0.00	1652.36
SHDI + Grass + Loamy	10	1677.43	14.98	0.00	1657.24
SHDI + Loamy	9	1690.74	28.3	0.00	1672.58
SHDI + CRP	9	1690.74	28.3	0.00	1672.58
SHDI + Loamy + Ag	10	1691.02	28.57	0.00	1670.82
SHDI + Grass + CRP	10	1692.43	29.98	0.00	1672.24
SHDI + CRP + Ag	10	1692.52	30.08	0.00	1672.34
Grass + Loamy	9	1696.93	34.48	0.00	1678.78
CRP + Ag	9	1706.76	44.31	0.00	1688.60
Loamy	8	1708.93	46.48	0.00	1692.80
Loamy + Ag	9	1709.91	47.46	0.00	1691.74
Grass + CRP	9	1712.2	49.75	0.00	1694.04
SHDI	8	1712.79	50.34	0.00	1696.66
CRP	8	1713.81	51.37	0.00	1697.68
SHDI + Ag	9	1713.84	51.39	0.00	1695.68
SHDI + Grass	9	1713.86	51.41	0.00	1695.70

Ag	8	1737.39	74.94	0.00	1721.26
NULL	7	1752.28	89.84	0.00	1738.18
Grass	8	1754.35	91.91	0.00	1738.22

Chapter 4 - Landscape-scale effects structure carnivore communities in an agro-prairie ecosystem

This chapter has been prepared for submission to Journal of Mammalogy *and is formatted to journal specifications.*

Abstract

Carnivores have experienced substantial population declines and are at increased risk of extinction, mainly due to negative interactions with humans and biological traits which make them susceptible to habitat loss and fragmentation. Habitat loss and fragmentation is largely driven by agricultural expansion, making agricultural conversion of natural landscapes a significant threat to carnivore persistence. Carnivore community richness is likely influenced by multiple factors, but specific factors in shortgrass prairies have not been identified. My goal was to identify landscape-scale factors driving contemporary carnivore community richness in an agro-prairie ecosystem. I used three years of presence and absence data (2018 – 2020) from camera trap sites (381) distributed across western, Kansas USA to test *a priori* structural equation model (SEM) hypotheses to explain carnivore richness. My SEM explained 27% of the variance in carnivore richness ($X^2 = 23.92$, df = 24, P = 0.47). Measures of water availability, native prairie, and agriculture had positive influences on carnivore richness. Additionally, sampling effort (days camera active) and an index of lagomorph abundances had a direct positive effect on my measure of carnivore richness at sites. My results suggest that carnivore communities in human-dominated, agro-prairie landscapes are structured through multiple landscape-scale pathways. Contemporary agro-prairie mosaics may act as filters for carnivores' agricultural tolerance, with species more vulnerable to native prairie loss becoming locally extirpated.

Introduction

Biodiversity worldwide has declined, with most losses attributed to effects of human-modified landscapes including resource extraction, habitat loss and degradation, invasive species, and unregulated harvest (Collen et al. 2009, Butchart et al. 2010). Vertebrates are particularly vulnerable, with 16 - 33% of species considered globally threatened (Schipper et al. 2008, Hoffmann et al. 2010). Mammalian carnivores have experienced substantial population declines and are at increased risk of extinction, due to negative interactions with humans (e.g., overkill, persecution, loss of prey base) and biological traits (e.g., large body sizes, large home-ranges, low densities, slow life histories) which make them susceptible to habitat loss and fragmentation (Cardillo et al. 2004, Ripple et al. 2014, Di Minin et al. 2016*b*, *a*). Habitat loss and fragmentation is largely driven by agricultural expansion (Foley et al. 2005, 2011), making agricultural expansion a significant threat to carnivore persistence (Woodroffe and Ginsberg 1998, Di Minin et al. 2016*b*).

Landcover heterogeneity can structure species diversity across a wide range of taxa (Stein et al. 2014) including within carnivore communities (Davies et al. 2021). Still, local prey availability is likely the most important driver of carnivore diversity (Rich et al. 2017). Specialist carnivore species (e.g., guigna [*Oncifelis guigna*], swift fox [*Vulpes velox*]) are more obligately associated native landcover and sensitive to agricultural systems (Acosta-Jamett and Simonetti 2004, Ferreira et al. 2018), while generalist carnivores (e.g., coyotes [*Canis latrans*]) are often able to use agricultural landscapes even if small native habitat patches remain (Andrén 1994). However, if apex carnivores are locally extirpated due to land-use changes, populations of smaller carnivores may expand and use human-modified systems at greater densities (Crooks and Soulé 1999, Ritchie and Johnson 2009). Due to carnivores’ sensitivity to habitat loss and fragmentation, native carnivore species richness may indicate overall ecosystem health (Noss et al. 1996, Ordeñana et al. 2010).

Colonization of the North American Great Plains by European Americans resulted in large-scale prairie conversion to row crop agriculture and permanent grazing lands for cattle (*Bos taurus*) and sheep (*Ovis aries*; Hart and Hart 1997, Hartnett et al. 1997, Licht 1997, Brockway et al. 2002). Much of the Great Plains now supports a contemporary suite of carnivore species within a human-dominated landscape. Carnivores such as gray wolves (*Canis lupus*), grizzly bears (*Ursus arctos horribilis*), and mountain lions (*Puma concolor*) were locally extirpated from most of the region during the 19th century (Choate 1987). Removal of these large carnivores left a void at upper trophic levels, likely benefitting medium-sized sympatric carnivores (e.g., coyotes; Levi and Wilmers 2012), while restricting small carnivores due to intraguild competition with coyotes (Mac Nally 1983, Palomares and Caro 1999, Fedriani et al. 2000, Linnell and Strand 2000). However, it remains unclear how landscape-scale factors, including configuration and composition of contemporary land use types, structure carnivore richness in agro-prairie landscapes.

Carnivore community richness is influenced by many factors such as prey availability (Li et al. 2021), landscape composition (Wait et al. 2018) and configuration (Moore et al. 2022), landcover heterogeneity (Pita et al. 2009), water availability (Schuette et al. 2013), and suitable denning substrates (Kaufman et al. 2005). Most studies, however, have related carnivore richness patterns to landcover heterogeneity (Manlick et al. 2020, Davies et al. 2021) and human encroachment (e.g., urbanization, agriculture conversion; Ordeñana et al. 2010, Ferreira et al. 2018, Wait et al. 2018). I am unaware of studies assessing how carnivore richness varies across shortgrass prairie regions. Carnivore species representative of shortgrass prairie ecosystems include coyote, red fox (*Vulpes vulpes*), swift fox, bobcat (*Lynx rufus*), striped skunk (*Mephitis mephitis*), long-tailed weasel (*Mustela frenata*), black-footed ferret (*Mustela nigripes*), least weasel (*Mustela nivalis*), American badger (*Taxidea taxus*), and raccoon (*Procyon lotor* [Kansas Mammal Atlas 2022]). However, to my knowledge, factors structuring carnivore community richness in shortgrass prairies have not been identified.

Using three years of presence and absence data from camera trap sites distributed across western, Kansas USA, my goal was to identify landscape-scale factors driving carnivore community richness in an agro-prairie ecosystem. Due to the uncertainty of pathways by which landscape change may influence carnivore richness, I chose to test *a priori* hypotheses (Fig. 4.1) for model fit, with previous carnivore research informing my selection of model covariates. Based on previous studies, lagomorphs (e.g., black-tailed jackrabbits [*Lepus californicus*], eastern cottontail rabbits [*Sylvilagus floridanus*]) are a primary prey species for carnivores in the region (coyotes [Brillhart and Kaufman 1995], bobcats [Kamler and Gipson 2000]) and therefore, I expected that greater lagomorph abundances at sites would positively influence carnivore richness. I expected landcover composition (i.e., proportions of agriculture and shortgrass prairie land use) and configuration (i.e., landcover edge and diversity) of landcover types surrounding sites to have both positive (e.g., native prairies) and negative (e.g., rowcrop agriculture) influences on carnivore richness.

Methods

Study Area

My study area included the 31 westernmost counties of Kansas, USA (7.16 million ha; Fig. 4.2) and was dominated by row crop agriculture (62%; Winter wheat [*Triticum aestivum*; 1.27 million ha], Fallow/Idle [1.05 million ha], Corn [*Zea mays*; 1.05 million ha], Sorghum

[*Sorghum spp.*; 612,569 ha], and additional crop types totaling 429,580 ha), intermixed with conservation reserve program landcover (CRP; 7%) and remnant native prairies (28%). Native prairies were characterized by side-oats grama (*Bouteloua curtipendula*), buffalo grass (*Bouteloua dactyloides*), big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), witchgrass (*Panicum capillare*), tumblegrass (*Schedonnardus paniculatus*), Indiangrass (*Sorghastrum nutans*), blue grama (*Bouteloua gracilis*), and sand dropseed (*Sporobolus cryptandrus*), among other grass and forb species. Oil wells (*n*=20,093) and wind turbines (*n*=1,429) were also distributed throughout the region (Kansas Geological Survey 2021). The study area received 31-107 cm of precipitation annually (increasing West to East), with temperatures ranging from -9-49° C (PRISM Climate Group, Oregon State 2021).

Data Collection

I randomly selected a large number of site locations (*n* = 381) to increase the robustness of my samples and to compensate for expected low occupancy rates of secretive carnivores (e.g. bobcat [Long et al. 2011], swift fox [Werdel et al. In Revision]; Kays et al. 2020) using a random-point generator in a geographic information system (ArcMap v. 10.8). Each site consisted of a single motion-sensing game-camera (Bushnell Trophy Cam®; Bushnell Corporation, Overland, KS, USA) attached to a metal T-post (40 cm high) and oriented north/south to avoid solar interference. Sites were established nearest the location of the randomly generated points unless the likelihood of camera destruction by cattle, vehicles, or farm equipment was high; if destruction risk was high, sites were established at the nearest fence line or field edge. If I could not obtain permission by the landowner to establish a site, I moved my site location to the nearest location where access was granted. I placed a wooden stake 3-m in front of the camera, smeared with an olfactory attractant (skunk essence and petroleum jelly

[F&T Fur Harvester's Trading Post, Alepna, MI, USA]), to encourage carnivores to pass in front of the camera's field of view (Stratman and Apker 2014). I also removed grass and shrub vegetation in front of the camera-trap with a handheld weed cutter to reduce visual obstruction within the extent of camera's field of view. I left each camera-trap in place for 28 days, but replaced olfactory attractant, batteries, and digital memory cards at ~14 days.

I sampled each site for three years (2018-2020). Landowner access was dynamic throughout the study (e.g., property sales and increased hunting leases), so access was limited to 375 sites in 2018 (5 May – 2 November), 361 sites in 2019 (20 May – 2 October) and 360 sites in 2020 (22 April – 28 September 2020), for a total of 381 sites. Site-specific photographs were archived within a Microsoft Access database (Colorado Parks and Wildlife Photo Warehouse 4.0, Colorado Parks and Wildlife, Fort Collins, CO, USA). I tagged photographs for detection (1) or non-detection (0) of carnivore species during each 28-day sampling period each year. I defined carnivore species richness at sites as the cumulative number of species detected across all three sampling years. I quantified a relative index of prey abundance at each site using independent detections of lagomorphs (Eastern cottontail rabbit and black-tailed jackrabbit) across my 3-year sampling effort. Photographs of lagomorphs were considered independent detections if >30 minutes (O'Brien et al. 2003, Burton et al. 2015) had passed before the successive photograph of the same species; I identified total independent observations of all lagomorphs at each site.

Environmental Covariates

I merged spatial data from 2018 Conservation Reserve Program (CRP) enrollments (Farm Service Agency 2018), CropScape (CropScape 2018), and PRAIRIEMAP (PRAIRIEMAP 2003) to create a custom landcover raster (30x30 m) of my study area. I classified landcover from this raster into three classes: CRP, row crop agriculture (reclassified all crop types, including fallow into a single value [CropScape 2018]), and native prairie (reclassified short, mixed, and tallgrass prairie into a single value [PRAIRIEMAP 2003]). Loamy soil types provide important denning substrates for both prairie-obligate carnivores (Jackson and Choate 2000) and their prey (Desmond et al. 2000, Kretzer and Cully 2001); high loamy soil fertility (EDIT 2021) may also increase prey demographic factors (e.g., eastern cottontail rabbit litter size; Hill 1972). To investigate soil effects on carnivore richness, I converted soil distribution polygons to raster format to characterize the spatial distribution of loamy tableland soil within my study area (30x30 m; Web Soil Survey 2018). I created 2-km radius circular buffers (scale equivalent to previous studies [Wait et al. 2018] and home-range size of regional apex carnivore [coyote; Kamler et al. 2005]) surrounding each camera trap to extract landcover class proportions, landcover diversity, and edge (m) using the “landscapemetrics” package (Hesselbarth et al. 2019) in R (R Development Core Team 2022). I extracted metrics from stream shapefile data (TIGER; U.S. Census Bureau 2018) using the “Euclidean Distance” and “Line Density” tools in ArcMap (v. 10.8) to create distance to streams and stream density (within 2km) covariates. Black-tailed jackrabbits and eastern cottontail rabbits are important prey (Brillhart and Kaufman 1995, Kamler and Gipson 2000) that may influence carnivore richness. I obtained independent counts of lagomorphs from the total number of black-tailed jackrabbit and cottontail rabbit independent observations (separated by > 30 min) during the study period at each site. To account for site-level sampling effort (cameras were not consistently active throughout each 28-day sampling period [mean = 25 days, range = 0 – 28 days]) I included a variable describing camera trap sampling effort as total number of days camera was active.

Structural Equation Model

I investigated how landscape composition and structure, water availability, and prey availability affected carnivore species richness using a structural equation model (SEM; Grace et al. 2010). Due to hypothesized landscape and biological complexity within my system, SEM allows us to test multiple pathways that may directly or indirectly affect carnivore community richness (Grace et al. 2010, 2012). SEM provides a scientific framework in which multiple cause-effect hypotheses may be tested, allowing covariates to explain direct (i.e., explanatory variable [X] → response variable [Y]) and indirect effects (i.e., $X \rightarrow Y_1 \rightarrow Y_2$) within a network of interconnected variables that influence system processes (Grace et al. 2012,). I included both observed (measured) and latent (hypothesized and unmeasured) variables to describe variation in carnivore richness (Grace et al. 2010). I followed the Grace and Irvine (2020) outline of explanatory modeling process within SEM, and constructed my hypothesized conceptual diagram (Fig. 4.1) from which I tested multiple causal pathways.

I fit my SEM using the number of carnivore species observed across all sampling years at each site as a measure of carnivore richness (Wait et al. 2018). Within the SEM, I included the observed variable of loamy tableland soil to represent the effects of soil characteristics on carnivore richness. I hypothesized that proportions of row-crop agriculture and total row-crop edge surrounding camera trap sites would have a negative effect on the amount of native prairie surrounding sites, but a positive effect on overall carnivore richness due to increased prey abundances (Spanel and Geluso 2018). I expected proportions of CRP landcover and total CRP edge surrounding camera trap sites to have a positive effect on carnivore richness by providing secondary habitat for more generalist carnivore species of the region (Kamler et al. 2005). Due to the semi-arid climate of the region, I expected water availability (e.g., stream density and distance to streams [negative]) to positively influence carnivore richness. I also expected prey abundance (e.g., lagomorph observations) to be a positive driver of carnivore richness (Li et al. 2021). Because days camera was active increases opportunity to observe both prey and carnivore species, I expected this to have a positive effect on both lagomorph abundance and carnivore richness. I also expected landcover heterogeneity to be a positive influential observed variable on carnivore richness informed by previous research (Manlick et al. 2020, Davies et al. 2021). My latent variables included agriculture, CRP, and Water. Agriculture was represented by the indicator variables Rowcrop Proportion and Rowcrop Total Edge, CRP was represented by the indicator variables CRP Proportion and CRP Total Edge, and Water was represented by the indicator variables Stream Density and Distance to Streams.

I specified direct pathways to carnivore richness from Native Prairie, Agriculture, Landcover Heterogeneity, CRP, and Water surrounding sites (1-km), as well as Lagomorph abundances and Days Cameras were Active. I also included multiple indirect pathways that were mediated through appropriate effects (Fig. 4.3). Covariance terms were added to the SEM to improve model fit and included Rowcrop Total Edge and Landcover Heterogeneity, CRP Proportion, Loamy Tableland Soil, Native Prairie, and Stream Density; CRP Total Edge and Landcover Heterogeneity, Loamy Tableland Soil, Days Camera Active, Stream Density, and Distance to Streams; Rowcrop Proportion and Days Camera Active and Loamy Tableland Soil; and Stream Density and Loamy Tableland Soil and Days Camera Active.

I fit my SEM using the “lavaan” package (v. 0.6.9; Rosseel 2012) in R (R Development Core Team 2022). I scaled all observed variables with a standardized mean of zero before inclusion in the SEM to ensure all variances and regressions were similar in magnitude of influence. Following Kline's (2018) recommendations, I included both statistically significant (*p*

≤ 0.05) and not-significant ($p > 0.05$) individual path coefficients within the SEM and assessed model fit with a chi-square global fit statistic (X^2) to determine significant difference ($P > 0.05$) between the baseline and hypothesized models.

Results

I collected 5,217,641 photos (2018 = 1,734,588; 2019 = 1,942,072; 2020 = 1,540,981) and documented seven species of native carnivores and two species of lagomorphs over 27,954 trap days (2018 = 10,351; 2019 = 9,478; 2020 = 8,125). Pooled species-specific naïve site occupancy of carnivores varied (American badger = 0.66, bobcat = 0.10, coyote = 0.91, long-tailed weasel = 0.01, raccoon = 0.61, striped skunk = 0.67, and swift fox = 0.14). Additionally, pooled naïve site occupancy (black-tailed jackrabbit = 0.45, eastern cottontail rabbit = 0.38) and number of independent observations (black-tailed jackrabbit = 1263, eastern cottontail rabbit = 1085) of lagomorphs varied.

Collectively, my SEM model explained 27% of the variance in carnivore richness (X^2 = 23.92, df = 24, P = 0.47). Sampling effort (days camera active) had a direct positive effect on my measure of carnivore richness at sites, as well as my index of lagomorph abundances (Table 4.2 and Fig. 4.3). The latent variable for Agriculture surrounding sites positively influenced carnivore richness (β = 0.88 [SE = 0.27]; Table 4.2 and Fig. 4.3), and also affected carnivore richness through multiple indirect pathways (Table 4.2 and Fig. 4.3) as landcover diversity was lower at sites surrounded by more agriculture and native prairie proportion. The proportion of native prairie surrounding sites positively affected carnivore richness (β = 0.54 [SE = 0.22]; Table 4.2 and Fig. 4.3), though had a non-significant positive influence on my lagomorph abundance index. Carnivore richness was positively influenced by the distribution and density of water (β = 0.38 [0.10]; Table 4.2 and Fig. 4.3) indirectly through the amount of agriculture and landcover heterogeneity surrounding sites. My index of lagomorph abundance (Fig. 4.4), however, had minimal influence on carnivore richness ($\beta = 0.17$ SE = 0.05]; Table 4.2 and Fig. 4.3). The proportion of CRP landcover and landcover diversity surrounding sites both had non-significant direct effects on carnivore richness. The proportion of CRP landcover surrounding sites had significant negative influences on landcover diversity and proportion of prairie landcover. Loamy tableland soil affected carnivore richness through multiple indirect pathways, but had a direct positive relationship with agriculture and direct negative relationships with landcover heterogeneity and the proportion of remaining native prairie surrounding sites.

Discussion

My results suggest that carnivore communities in agro-prairie landscapes are structured through multiple landscape-scale pathways. As expected, greater proportions of native prairie, water availability, and prey abundance all positively influenced carnivore richness. Surprisingly, the amount of row-crop agriculture occurring on the landscape had a positive influence on carnivore richness. Distinct natural histories and habitat associations of carnivore species occurring in my system made it unlikely that a single factor could explain the landscape complexities likely structuring carnivore communities. My study, however, underscores the importance of both indirect and direct landscape-scale effects on carnivore communities in a rapidly changing landscape.

My study area was historically comprised of native short and mixed-grass prairies, and native carnivore species have coevolved and adapted in this semi-arid landscape (Küchler 1972). Thus, remaining native prairie likely represents good-quality habitat for specialist, prairie-obligate carnivores (e.g., swift fox; Ferreira et al. 2018, Werdel et al. In Review), and had a direct positive influence on overall carnivore richness. However, much like historic ecosystems worldwide, remnant native prairies are now included within a matrix of primarily agricultural landscapes (Perfecto and Vandermeer 2008). Due to juxtaposition of native prairie patches within an agriculturally dominated matrix, patch dynamics, landscape heterogeneity, and ecological processes are altered by anthropogenic pressures (Kupfer et al. 2006, Driscoll et al. 2013). These pressures are evident within my model as both CRP and agriculture have negative influences on native prairie, which in turn, indirectly affected carnivore richness.

Although agriculture directly converts and replaces native prairie landcover, my model suggests row crop agriculture can enhance carnivore richness. This result may be explained by greater prey (e.g., prairie vole [*Microtus ochrogaster*], western harvest mouse [*Reithrodontomys megalotis*], North American deermouse [*Peromyscus maniculatus*]) densities on agricultural peripheries (e.g., edges and road ditches; Spanel and Geluso 2018) and likely exploited by generalist carnivore species (e.g., coyotes, raccoons, badgers; Andrén 1994). Despite agriculture having a positive influence on carnivore richness, it is important to curb enthusiasm for promoting prairie conversion to agricultural production; native habitats still provide the greatest quality in most instances. Within my system, fertile loamy tableland soil types are primarily associated with agriculture, and the effects of both fertile soil (Hill 1972) and increased forage along agricultural edges for small mammals (Bilenca et al. 2007) likely accounts for agriculture's positive influence on lagomorph abundances (indexed through photographic rates). As expected, increased prey abundance drives carnivore occurrence (Rich et al. 2017), and an increase in lagomorph abundance at sites also had a positive influence on carnivore richness in my study.

In semi-arid environments, water availability likely affects the distribution of all flora and fauna including carnivores (Schuette et al. 2013). My model demonstrates that water availability at sites enhances carnivore richness, but also is associated with greater amounts landcover heterogeneity surrounding sites. I hypothesized that landcover heterogeneity would be important for carnivore richness due to spatial partitioning of coexisting species (Davies et al. 2021). Landcover heterogeneity had a weak positive effect on carnivore richness, but was important nonetheless, as it explained additional variance within my model; non-significance of an effect within an SEM does not preclude the importance of a variable (Kline 2018). Water availability is an important factor affecting carnivore richness (Schuette et al. 2013), with carnivores dependent on water sources for maintenance, as well as greater prey abundances in water-associated riparian areas (Matos et al. 2009). Semi-permanent prairie water sources (e.g., creeks, ponds, and wetlands) are sensitive to future climate change (Johnson and Poiani 2016) and their losses may result in sensitive species extirpation.

My results provide the first evidence of how landscape change affects a carnivore guild in a rapidly changing shortgrass prairie ecosystem. This research has important management implications for the conservation of remaining carnivore species. Contemporary agro-prairie mosaics may act as filters for carnivores' agricultural tolerance, with species more vulnerable to native prairie loss becoming locally extirpated (Gascon et al. 1999, Acosta-Jamett and Simonetti 2004, Henle et al. 2004, Ferreira et al. 2018).

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Table 4.1 Naïve Occupancy (number of sites occupied divided by total sites) results sampled from camera-trap sites (2018 = 375, 2019 = 361, 2020 = 360) for detection of carnivore[a] and lagomorph[b] species for 3 years (2018-2020) in western Kansas, USA.

Species	Naïve Occupancy
Carnivora	
American Badger	0.66
Bobcat	0.10
Coyote	0.91
Long-Tailed Weasel	0.01
Raccoon	0.61
Striped Skunk	0.67
Swift Fox	0.14
Lagomorpha	
Black-tailed Jackrabbit	0.45
Eastern Cottontail Rabbit	0.38

[a] Carnivore species include: American badger (*Taxidea taxus*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), long-tailed weasel (*Mustela frenata*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), and swift fox (*Vulpes velox*).

[b] Lagomorph species include: Black-tailed jackrabbits (*Lepus californicus*) and eastern cottontail rabbit (*Sylvilagus floridanus*).

Table 4.2 Standardized coefficients (Std. coef.), standard errors (SE), and P-values (P) for latent variables and structural equation model (SEM) regressions of carnivore richness in western Kansas, USA. Within an SEM, unobserved hypothetical constructs (latent variables) are summarized by one or more observed indicator variables. Indicator variables were derived from a 2-km buffer surrounding each site sampled using camera-traps over 3 years (2018 = 375, 2019 = 361, 2020 = 360) in western Kansas, USA (7,160,077 ha). Source material for indicator variables can be found in Table D.1.

Latent Variable	Indicator	Std. coef.	SE	P
Agriculture				
	Rowcrop Proportion	1.00		
	Rowcrop Total Edge	0.91	0.05	<0.00
CRP				
	CRP Proportion	1.00		
	CRP Total Edge	0.92	0.04	<0.00
Water				
	Stream Density	1.00		
	Distance to Streams	-1.12	0.12	<0.00
Response	**Explanatory**	**Std. coef.**	**SE**	**P**
CRP				
	Water	-0.38	0.09	<0.00
Native Prairie				
	CRP	-0.49	0.03	<0.00
	Agriculture	-0.92	0.05	<0.00
	Loamy Tableland Soil	-0.11	0.05	0.02
Landcover Diversity				
	Native Prairie	-1.11	0.26	<0.00

	CRP	-0.27	0.15	0.07
	Agriculture	-1.36	0.30	<0.00
	Loamy Tableland Soil	-0.40	0.06	<0.00
	Water	0.30	0.07	<0.00
Agriculture				
	Loamy Tableland Soil	0.35	0.06	<0.00
	CRP	-0.21	0.05	<0.00
	Water	-0.45	0.08	<0.00
Lagomorph				
	Agriculture	0.22	0.10	0.03
	Days Camera Active	0.09	0.05	0.07
	Native Prairie	0.01	0.09	0.87
Richness				
	Agriculture	0.88	0.27	0.00
	Native Prairie	0.54	0.22	0.01
	Days Camera Active	0.20	0.05	<0.00
	Water	0.38	0.10	<0.00
	Lagomorph	0.17	0.05	<0.00
	CRP	0.12	0.11	0.29
	Landcover Heterogeneity	0.11	0.08	0.19

Figure 4.1 Conceptual flow of structural equation metamodel for the hypothesized effects of soil type, water availability, landscape composition, landscape structure, landcover diversity, prey abundance and sampling effort on carnivore richness in agro-prairie landscapes.

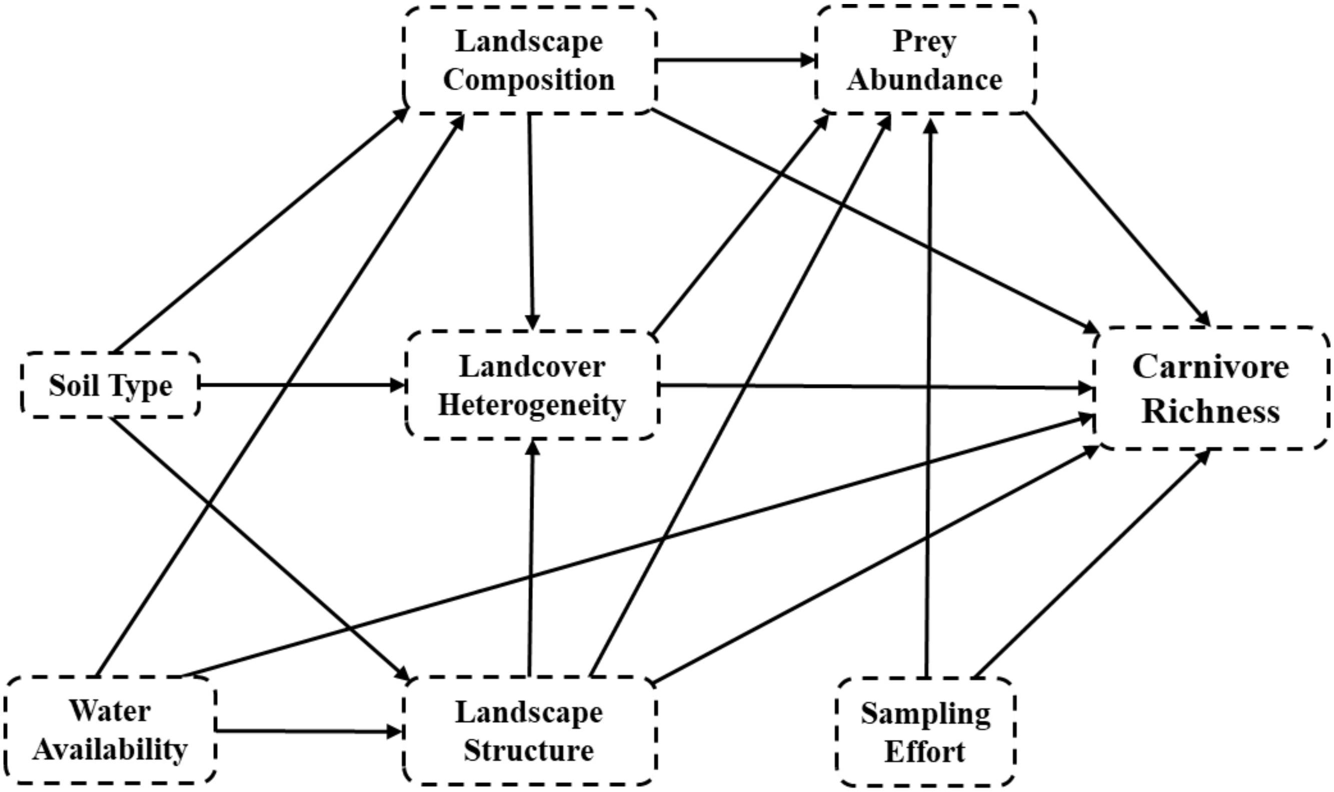


Figure 4.2 Study area in western Kansas, USA (KS; 7,160,077 ha) where I sampled camera-trap sites (2018 = 375, 2019 = 361, 2020 = 360) for carnivore community richness and lagomorph (Black-tailed jackrabbits [*Lepus californicus*] and eastern cottontail rabbit [*Sylvilagus floridanus*]) abundances over three years (2018-2020). Surrounding states included Nebraska (NE), Missouri (MO), Oklahoma (OK), and Colorado (CO).

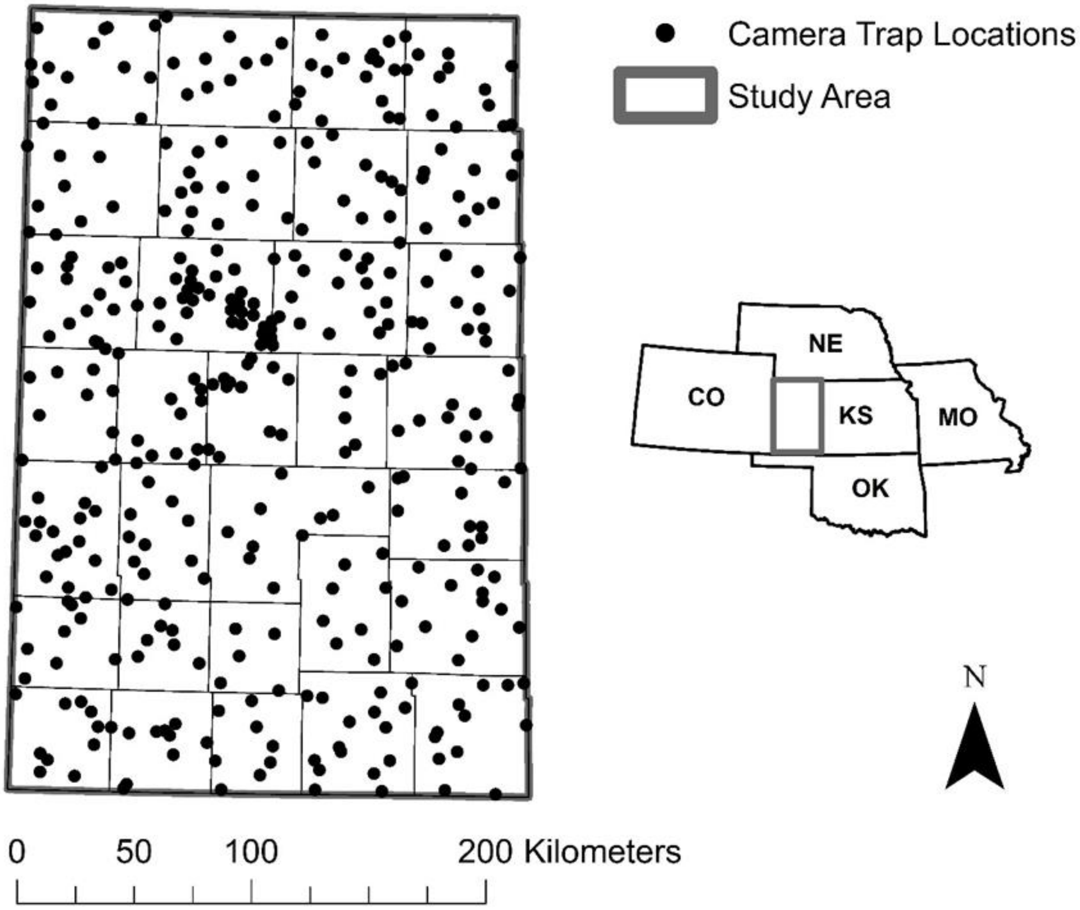
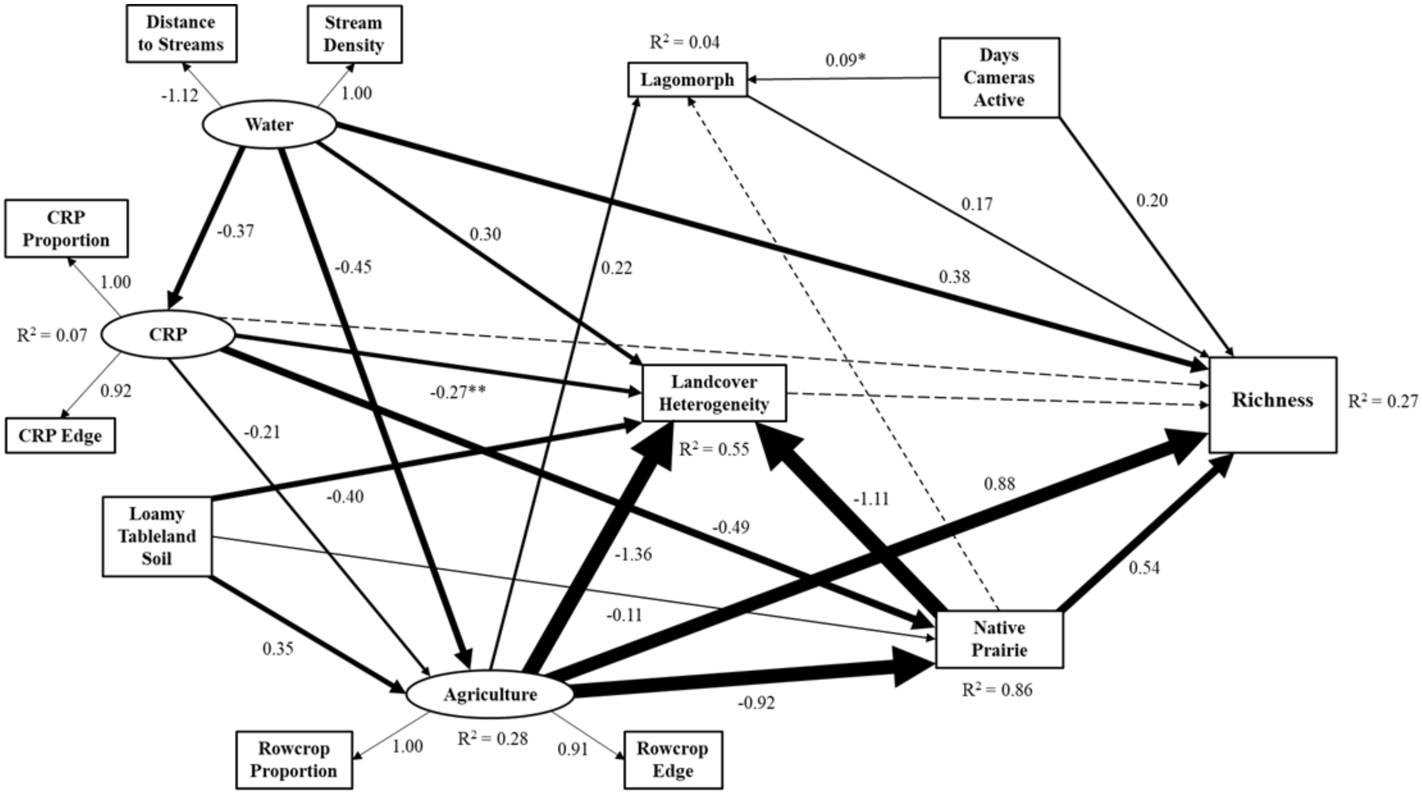


Figure 4.3 Structural equation model describing effects of loamy tableland soils, Conservation Reserve Program, water, agriculture, native prairie proportion, lagomorph total observations, landcover diversity, and days cameras were active on carnivore richness in western Kansas, USA. The model includes latent (ovals) and observed (rectangles) variables. Solid lines represent significant pathways at P<0.05 (thicker lines represent stronger effects), and dashed lines represent not-significant pathways. Standardized coefficients are shown for significant pathways. *P = 0.068, **P = 0.065



Appendix D - Chapter 4 Supplemental Material

Table D.1 Variables used within latent and structural equation model coefficients and regressions of carnivore richness. Each variable, and its associated scale, is in reference to sampled camera-trap sites (2018 = 375, 2019 = 361, 2020 = 360) within my study area in western Kansas, USA (KS; 7,160,077 ha).

Variable	Source	Range	Description
Rowcrop Proportion	CropScape 2018	0.00 - 0.90	Proportion of rowcrop landcover within 2km
Rowcrop Total Edge	CropScape 2018	0 - 110490	Total distance (m) of row crop edges within 2km
CRP Proportion	CropScape 2018	0.00 0.62	Proportion of CRP landcover within 2km
CRP Total Edge	CropScape 2018	0 - 51810	Total distance (m) of CRP edges within 2km
Stream Density	U.S. Census Bureau 2018	0.00 - 152.26	Density of streams within 2km
Distance to Streams	U.S. Census Bureau 2018	2 - 15808	Distance to the nearest stream (m)
Native Prairie	PRAIRIEMAP 2003	0.00 - 0.98	Proportion of native prairie landcover within 2km
Loamy Tableland Soil	Web Soil Survey 2018	0.00 - 1.00	Proportion of loamy tableland soil within 2km
Landcover Heterogeneity	CropScape 2018, PRAIRIEMAP 2003	0.91 - 2.19	Shannon Diversity Index within 2km

Days Camera Active	Direct Sampling 2018-2020	27 - 84	Total days camera was active
Lagomorph	Direct Sampling 2018-2020	0 - 371	Independent Observations
Carnivore Richness	Direct Sampling 2018-2020	0 - 6	Total number of carnivore species at sites

Summary

Temperate grasslands (hereafter prairies) are the most imperiled terrestrial ecosystem on Earth (Suttie et al. 2005, Carbutt et al. 2017). Unfortunately, prairies have relatively little state, federal, or international protection, resulting in increased anthropogenic pressures (e.g., urbanization, agriculture, energy production) that are driving global landscape change (Newbold et al. 2016, Carbutt et al. 2017). Systematic conversion of native prairies to production agriculture has resulted in a 70% loss of historical prairie landcover in the Great Plains of North America alone (DeLuca and Zabinski 2011). Native prairies provide important ecosystem services including livestock forage, water quality, flood mitigation, wildlife habitat, and carbon sequestration that mitigates the effects of climate change (Bakker and Higgins 2009, Chang et al. 2021). Nevertheless, demand for biofuels and increases in crop prices (e.g., corn [*Zea mays*]) will likely continue to drive conversion of remaining native prairies to cropland (Lark et al. 2019, 2020). Current and future prairie ecosystems have been or will likely be modified (e.g., grazing, fire suppression, cultivation, invasive species), affecting the integrity of ecosystem processes (Askins et al. 2007). Prairie conservation attempts do exist however, and in the United States the Conservation Reserve Program (CRP) is the most widespread restoration effort. CRP was enacted in the United States in the 1985 Food Security Act, and was initially created to decrease soil erosion and crop surpluses (Reichelderfer and Boggess 1988), but may indirectly improve habitat for native wildlife species (coyotes [*Canis latrans*; Kamler et al. 2005], lesser prairie-chickens [*Tympanuchus pallidicinctus*; Sullins et al. 2019]). Due to the extensive conversion of native prairies of the Great Plains, and subsequent restoration efforts, research investigating how the contemporary composition of an agro-prairie landscape mosaic influences wildlife species distributions was timely and warranted.

The overarching goal of my dissertation research was to determine if landscape composition and configuration (at informative scales for management) had an influence on the structure and distribution of native carnivore species within an agriculturally dominated mosaic of historical shortgrass prairie in western Kansas, USA. Specifically, I was interested in how the distribution of swift foxes (*Vulpes velox*) is affected by intraguild competition and landscape characteristics at the edge of their eastern range, and how to prioritize prairie patches for future conservation. Major results of my study indicated that 1) swift foxes were more likely to occupy sites with greater proportions of shortgrass prairie and loamy tableland soil, and less likely to occupy sites with greater proportions of CRP, 2) swift foxes were less likely to occupy sites where coyotes were also present, 3) swift foxes adjusted their temporal activity patterns at sites surrounded by greater proportions of CRP, likely to avoid interactions with coyotes, 4) strategic conservation of native prairie patches for swift foxes overwhelmingly identified privately owned lands (98%), and 5) I documented seven species of native carnivores species with evidence that carnivore richness in a contemporary agro-prairie mosaic was influenced through multiple variable pathways.

CRP has been a successful conservation tool for prairie-obligate species including lesser prairie chickens (Dahlgren et al. 2016; Sullins et al. 2019), with other species indirectly benefitting from increased habitat (grasshopper sparrows [*Ammodramus savannarum*; Herkert 1998], and coyotes [Kamler et al. 2005]). However, these efforts may be indirectly constraining distributions of swift foxes on the edge of their range (Chapter 1 and Chapter 3). Seeding mixtures associated with CRP focus on creating vegetation communities not associated with Indigenous short grass prairie communities (Sovada et al. 2003, Plumb et al. 2019), resulting in taller, more dense vegetation (e.g., big bluestem [*Andropogon gerardii*], switchgrass [*Panicum* *virgatum*]). CRP seeding mixtures that shift vegetation composition to taller species (>30 cm) may inhibit the visual range of swift foxes and increase predation risk in these areas (Chapter 2). Carnivore richness likely corresponds with prey (e.g., small mammals) densities which are expected to be greater in areas with increased CRP landcover (Chapter 4; Thompson and Gese 2007, Stanley 2010). When coyotes and swift foxes both occur in areas with increased proportions of CRP landcover, my data suggests swift foxes have lower occupancy rates and alter temporal overlap with coyotes (Chapter 2).

The amount of loamy soil coverage was positively associated with the distribution of swift foxes (Chapter 1 and Chapter 3). Swift fox dens in my study area occur across both agriculture and grassland areas, but are uniformly present in loamy soil types (Jackson and Choate 2000). Loamy soil types are friable enough for digging and cohesive enough to not result in den structural failure (Jackson and Choate 2000, Weil and Brady 2016), providing an adequate substrate for swift fox dens. Small mammals also utilize loamy soils for burrowing (e.g., black-tailed prairie dog [*Cynomys ludovicianus*; (Desmond et al. 2000, Kretzer and Cully 2001] and kangaroo rats [*Dipodomys spp.*; Sjoberg et al. 1984]) and may provide an indirect indication of prey availability, thus, increasing carnivore richness (Chapter 4).

Within my study area, swift foxes use areas with less diverse landcover types (Chapter 1 and Chapter 3), likely because greater landcover diversity reduces the amount, or modifies the configuration or patch size, of shortgrass prairie present on the landscape. As landcover diversity increases, shortgrass prairie patch sizes may also decrease, further reducing good-quality swift fox habitat or connections between good-quality habitats (Kamler et al. 2003, Martin et al. 2007, Butler et al. 2020). Traversing non-shortgrass prairie landcover types may expose swift foxes to predation or human conflict (Sovada et al. 2003, Thompson and Gese 2007). Re-establishing connectivity between shortgrass prairie patches may be necessary to facilitate recolonization of swift foxes at the edge of their range (Cushman et al. 2013, Schwalm et al. 2014). However, landcover diversity may have a positive influence on overall carnivore richness (Chapter 4).

Surprisingly, swift fox distributions were insensitive to the amount of row-crop agriculture surrounding sites (Chapter 1 and Chapter 3). Small mammals can be most abundant within tall vegetation that provides more food and cover resources (Benedek and Sîrbu 2018), and grassy row-crop field borders (i.e., fencerows, roadsides, and crop edges) may provide refugia (Bilenca et al. 2007). For instance, deer mice (*Peromyscus maniculatus*) can be more abundant in landscapes dominated by row-crop landcover (Heisler et al. 2013) and small mammal abundance may be greatest in post-harvested fields (Kaufman et al. 2000). Carnivore richness was positively influenced by agricultural landscapes (Chapter 4) and carnivores may be exploiting prey resources available in these field edges.

Swift foxes were more likely to occur in areas with greater proportions of shortgrass prairie (Chapter 1 and Chapter 3). Within my study area on the eastern edge of their range, my results suggest that swift foxes are occupying and using the remaining small patches of shortgrass prairie embedded in the agro-prairie ecosystem. By using smaller patches of shortgrass prairie embedded within other landcover types, swift foxes may be minimizing intraspecific or interspecific resource competition and maximizing population fitness in contemporary landscapes (Durrett and Levin 1998, Thompson and Gese 2007, Kozlowski et al. 2008). Native shortgrass prairie is likely the greatest in habitat quality for specialist, prairie-obligate carnivores (e.g., swift fox; Ferreira et al. 2018, Chapter 1 and Chapter 3), and reasonably has a direct positive influence on overall carnivore richness (Chapter 4), as native carnivore species evolved to survive within this semi-arid landscape (Küchler 1972).

In a semi-arid environment such as the shortgrass prairie region, water availability has a direct impact on carnivore richness (Chapter 4). My SEM determined that water (stream density and distance to water [negative]) not only increases carnivore richness, but also is the primary driver of landcover diversity within my study area (Chapter 4). Landcover diversity (i.e., heterogeneity) was hypothesized to be important for carnivore richness due to spatial partitioning and increased carnivore species coexistence (Davies et al. 2021). Landcover diversity had a weak positive effect on carnivore richness, but was important nonetheless, as it helped explain additional variance within the model (Chapter 4)

My results provide the first evidence of landscape effects on an entire carnivore guild in a historically shortgrass prairie ecosystem. This research has important management implications and outlines the importance of native shortgrass prairies to the conservation of remaining, and possible restoration, of native carnivore species, particularly swift fox. Native prairies identified as areas of priority conservation importance were overwhelmingly owned and managed by private landowners (98%; Chapter 3). Beef cattle production was the major enterprise on privately owned grasslands (i.e., rangelands) within my study area (Boyer et al. 2004). Rangelands have experienced increasing recognition for their value to provide ecosystem services, with ecological stewardship becoming part of their management framework (Havstad et al. 2007, Chapin III et al. 2009). However, it is important to acknowledge that wildlife can act as both actual and perceived competition and risk to livestock production, especially when landowners derive no tangible benefits from wildlife (Ranglack and Toit 2016). For strategic native prairie conservation to promote the sustainability of carnivores in my study area, it is important for wildlife managers to provide incentives (e.g., monetary or social) to landowners who contribute to conservation management, such as conservation easements (easements are granted to conservation entities, reducing property value, but landowners may recoup costs through tax deductions [Ward and Benfield 1988]); of note, the most intact temperate grassland in the world (Sand Hills of Nebraska) has no mandated conservation strategy, but production as a rangeland for grazing cattle and membership in local conservation groups acts as incentive (Scholtz and Twidwell 2022).

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