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Influence of landscape composition on spatiotemporal interactions between sympatric canids

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Abstract

Apex carnivores influence subordinate carnivores through intraguild competition. Landscape composition and configuration may mediate interactions between sympatric carnivores though intervening landscape-level effects on these interactions are relatively unknown. We used three years of detection data (2018–2020) from 381 sites in Kansas, USA, and Bayesian two-species occupancy models to evaluate how the proportion of Conservation Reserve Program (CRP) easements may influence spatial and temporal interactions between coyotes (*Canis latrans*), an apex carnivore, and swift foxes (*Vulpes velox*) in human-modified landscapes. Because both intraguild competition with, and predation by, coyotes may affect swift fox distributions, we also assessed how coyote presence influenced site occupancy, colonization, and persistence by swift fox at varying proportions of CRP around sites. Median site occupancy, colonization, and persistence by swift foxes was lower at sites where coyotes were present (0.013 [95% credible intervals {CrI} = 0.008–0.020]; 0.001 [95% CrI = 0.001–0.003]; 0.402 [95% CrI = 0.129–0.862]) than at sites where coyotes were absent (0.096 [95% CrI = 0.062–0.138]; 0.016 [95% CrI = 0.003–0.057]; 0.535 [95% CrI = 0.242–0.874]). The coefficient of temporal overlap between coyotes and swift foxes at sites where the proportion of CRP easements was ≥0.10 was significantly different (95% CIs did not overlap 95% CI of other measured activity) from the coefficient of overlap where CRP easements were <0.10. Swift foxes were influenced by coyotes through space and time only at sites surrounded by low proportions of CRP (≤0.04). Swift foxes and coyotes co-occurred more than would be expected by chance only when the proportion of CRP near a site was low (≤0.04). Swift foxes appear to avoid coyotes in areas where encounter risks are increased. Results from our study indicate that landscapes, and their inherent structure and composition, may influence intraguild interactions between canids in multiuse, agro-prairie ecosystems.

INTRODUCTION

Intraguild interactions among carnivores can influence species distributions, resource selection, and population dynamics (Brown et al., 1999; Chase et al., 2002; Vanak et al., 2013), and occur where multiple species vie for similar resources (Holt & Polis, 1997; Linnell & Strand, 2000; Polis et al., 1989; 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 & Humphries, 2019). Apex carnivores may restrict prey availability for subordinate species through interference competition, forcing subordinate carnivores to forage under threat of predation (Brown et al., 1999; Holt & Polis, 1997; Ritchie & Johnson, 2009). Intraguild predation among carnivores is common (Prugh & Sivy, 2020) and likely reduces densities and distributions of subordinate species, resulting in local extirpation or exclusion (Fedriani et al., 2000; Linnell & Strand, 2000; Mac Nally, 1983; Palomares & Caro, 1999).

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

Shortgrass prairie ecosystems throughout the North American Great Plains have undergone significant changes since colonization by Euro-Americans (Brockway et al., 2002; Hartnett et al., 1997; Licht, 1997). They have largely been converted to agriculture (Brockway et al., 2002; Hart & Hart, 1997) 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 provide habitat for native carnivores including swift foxes (*Vulpes velox*) and coyotes (*Canis latrans*). Coyotes (~50 cm tall, ~11 kg; Henke & Bryant, 1994) are the apex carnivore in the region (species ability to self-regulate their populations; Wallach et al., 2015) 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 & Keinath, 2003) prairie-obligate carnivores once extirpated from the region, though they have recolonized remnant prairie patches throughout their range. Because both canid species are primarily nocturnal and crepuscular (Andelt & Gipson, 1979; Lemons et al., 2003) and forage on similar prey (e.g., small mammals and insects; Kamler et al., 2007), there is potential for negative interactions. A previous study found swift foxes must balance predation risks by foraging in areas with reduced shrub densities while coyotes freely foraged in areas with increased prey availability (Thompson & Gese, 2007).

Given wide-ranging conversions to agriculture, native prairies are ongoing targets of landscape-level restoration efforts (Berger et al., 2020). The most common restoration effort in the United States is the Conservation Reserve Program (CRP; Baer et al., 2002); a voluntary program compensating farmers to remove marginal cropland from production and reestablish grassland vegetation (Reichelderfer & Boggess, 1988). Initially created to decrease soil erosion and commodity surpluses (Reichelderfer & Boggess, 1988), CRP may indirectly improve habitat for some native carnivores (e.g., coyotes; Kamler et al., 2005). Many CRP plantings, however, establish tallgrass species (e.g., big bluestem [*Andropogon gerardii*], switchgrass [*Panicum virgatum*]) in historically 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). Site occupancy and colonization probabilities of swift foxes also decreased with increasing proportions of CRP on the landscape in western Kansas (Werdel et al., 2022). Although coyotes and swift foxes co-occur, it is unclear if novel landscape compositions, specifically the landcover restoration efforts via CRP, mediate their spatiotemporal interactions.

We examined the influence of CRP composition on spatial and temporal interactions of swift foxes and coyotes using three years of camera-trap data from sites distributed across western Kansas. Additionally, we assessed the evidence for an effect of coyote presence on site occupancy, colonization, and persistence by swift fox in relation to the proportion of CRP. Because coyotes competitively suppress and kill small canids (Kitchen et al., 1999), we expected swift foxes to avoid land cover 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

Our study occurred within the westernmost counties of Kansas, USA (−100.81, 38.49; 7,160,077 ha; Figure 1). This region was historically shortgrass prairie but is now a heterogeneous 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 ha; wind turbines = 1429 ha). Remaining short- and mixed-grass prairie species include side-oats grama

(*Bouteloua curtipendula*), buffalo grass (*Bouteloua dactyloides*), big bluestem (*A. 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 overlapped completely within our study area. Other similar-sized sympatric carnivores occurring in this region included bobcat (*Lynx rufus*), striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), and American badger (*Taxidea taxus*)—none of which have reported associations with swift foxes. Western Kansas was characterized by low annual precipitation (31–107 cm), with temperatures ranging from −9 to 49°C (PRISM Group, 2019).

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). We established sites nearest
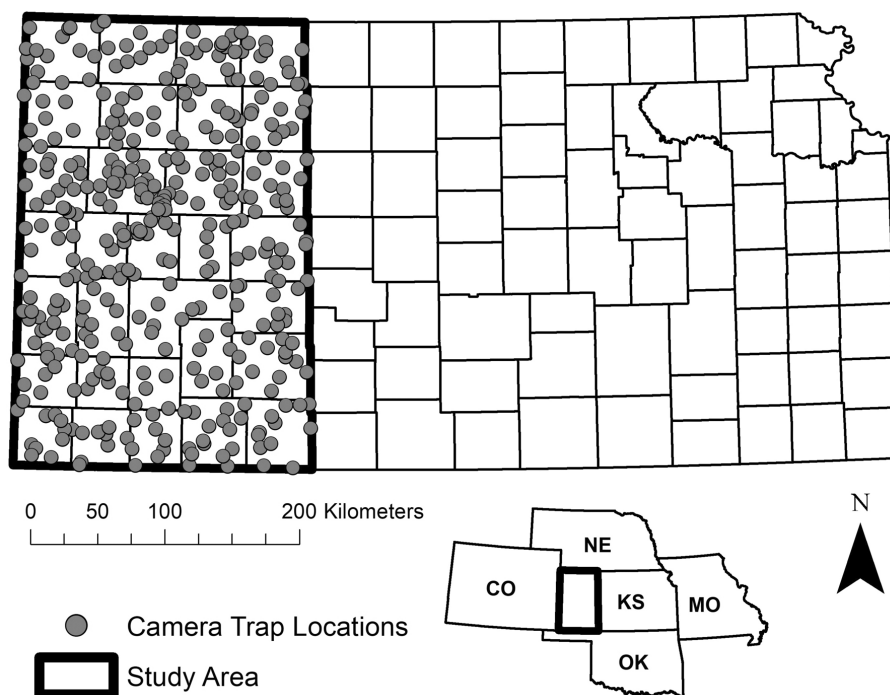

FIGURE 1 Study area in Kansas, USA (7,160,077 ha), where we sampled 381 camera-trap sites for detection of coyotes (*Canis latrans*) and swift foxes (*Vulpes velox*) for three years (2018–2020). Study area encompasses the furthest eastern extent of the contemporary swift fox range and is comprised of an agro-prairie landscape matrix.

randomly generated locations unless the likelihood of camera destruction was high (e.g., center of production agriculture, pasture, or fields). In these cases, we relocated cameras to the nearest fence line or field edge to avoid interference. We placed a wooden stake 3 m (40 cm high) in front of the camera and smeared it with an olfactory attractant (skunk essence and petroleum jelly [F&T Fur Harvester's Trading Post, Alepna, MI, USA]) to lure individuals into the camera field of view (Stratman & Apker, 2014). Vegetation in front of the camera was removed with a hand-held weed cutter to reduce visual obstruction. The 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; Kamler et al., 2003; Kitchen et al., 1999; Lebsock et al., 2012; Nicholson et al., 2007; Sovada et al., 2009), reducing the chances of violating model assumptions (e.g., independence among sites and closure). For a given deployment, cameras were in place for 28 days and we replaced lure, batteries, and digital memory cards every ~14 days (Wait et al., 2018).

Data collection

We sampled sites during spring and summer, as coyote and swift fox dispersal generally occurs late fall and early winter (Harrison, 1992; Nicholson et al., 2007). We attempted to sample the same sites throughout the entire study period (2018–2020), but due to changing landowner access issues, we 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. We established camera sites in three groups based on latitude (~1/3 of total sites within each of: ≥39° N; <39° N > 38° N; ≤38° N) 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 our sampling effort each year. We adjusted the timing of camera placement for all sites (~1/3 of camera traps in each latitudinal division that were nearest each other and then alternated sequence by year [e.g., west to east, east to west, north to south]), so they were not sampled during the same month each year ($\bar{x}$ difference in sampling per site = 82 days; Werdel, Piper, Ricketts, Peek, & Ahlers, 2023) in subsequent years. We archived images within a Microsoft Access database (Colorado Parks and Wildlife Photo Warehouse 4.0, Colorado Parks and Wildlife, Fort Collins, CO, USA). We tagged site and time-stamped specific images for detection (1) or non-detection (0) of swift foxes and coyotes each year. We considered a site occupied by a particular species if we detected ≥1 image of that species

during the 28-day sampling period for a given year. Detections were considered independent observations if >30 min elapsed between observations (Iannarilli et al., 2021).

Landscape characterization

We created a landcover raster (30 × 30 m) of our study area by merging information from 2018 CRP enrollments and CropScape (2018). From this raster, landcover was classified into two classes (CRP and agroprairie). We created 2-km radius buffers surrounding each site (Wait et al., 2018). We considered buffers at alternate scales (500-m, 1-km, and 5-km radii), but the proportion of landcover classes among buffer sizes was correlated ($r > 0.80$). We extracted landcover class proportions from circular buffers using R (v. 4.0.3) "landscapemetrics" package (Hesselbarth et al., 2019).

Spatial overlap

We quantified if coyote presence influenced swift fox site occupancy with a Bayesian dynamic occupancy model for interacting species adapted from Gallo et al. (2019) and Richmond et al. (2010). Briefly, this model assumes that site occupancy status of a subordinate species (i.e., swift fox) may vary due to the presence of a dominant species (species occupying higher trophic levels in comparison to another species; i.e., coyote). As a dynamic occupancy model, we 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 (see *Results*), we 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 we made each of these eleven probabilities a function of covariates. For all logit-linear predictors (i.e., initial site occupancy, colonization, persistence, and detection) we included proportion of CRP within a 2-km buffer. Doing so allowed us to evaluate whether coyote and swift fox interactions spatially varied across the landscape. All covariates were standardized prior to analyses.

To quantify whether coyote and swift fox co-occurred more or less than expected by chance, we derived species

interaction factors (SIFs) along a landcover gradient from the estimated probabilities of our model (Gallo et al., 2019; MacKenzie et al., 2004; Richmond et al., 2010). 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.

We followed Gallo et al.'s (2019) and Richmond et al. (2010) approach to calculate a SIF such that

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

where ψ^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, we 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 our occupancy model and to calculate SIFs between coyotes and swift foxes for each sampling season (Gallo et al., 2019).

We fitted this model in JAGS (v. 4.2.0; Plummer, 2003) using the "runjags" package (Denwood, 2016) in R. We sampled the posterior distribution 200,000 times across 12 chains following a 10,000-step adaptation and 10,000-step burn-in phase. Chains were thinned by two for a total of 100,008 posterior samples. Model convergence was assessed by visually inspecting trace plots and ensuring that Gelman-Rubin diagnostics were <1.1 (Gelman et al., 2013; Appendix S1). For logit-scale parameter estimates, we determined evidence of an effect and calculated 95% credible intervals (CrIs) for each parameter and checked whether or not they overlapped zero. Similarly, we calculated 95% CrI for the SIF, though we checked whether CrI for each SIF overlapped one.

Temporal overlap

We exported activity data (site and time of detections) specific to swift foxes and coyotes for use with the "activity" (Rowcliffe, 2016) and "overlap" (Meredith & Ridout, 2021) packages in R (v. 4.0.3; R Core Team, 2020). We 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 (Hardouin et al., 2021; Ridout & Linkie, 2009; Searle et al., 2021). We considered the proportion of CRP as a site-level landscape characteristic with the potential to mediate

temporal partitioning among swift foxes and coyotes. We 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 present that included CRP proportions $\geq$ the mean ($\bar{x} = 0.10$ [range = 0.00–0.62]), and (4) at sites where both species were present that included CRP proportions $\leq$ the mean. We estimated 95% CIs for each coefficient of overlap, and compared among overlap parameters, using smoothed bootstrapping with 10,000 resamples (Meredith & Ridout, 2021). We used the function compareCkern in the activity R package (Rowcliffe, 2016) to test for significant differences ($p < 0.05$) between species' temporal activity (Searle et al., 2021). These data and statistical code have been made publicly available (Werdel, 2025).

RESULTS

We documented 3624 independent detections (>30 min elapsed between images) of coyotes (2018 = 1307; 2019 = 988; 2020 = 1329) and 341 independent detections of swift foxes (2018 = 207; 2019 = 40; 2020 = 94) over 27,954 camera-trap days (2018 = 10,351; 2019 = 9478; 2020 = 8125).

Multi-species occupancy

Median detection-corrected initial occupancy for coyotes was 0.67 (95% CrI = 0.62–0.71; Table 1). Median site colonization by coyotes was 0.56 (95% CrI = 0.50–0.62), and persistence was 0.61 (95% CrI = 0.57–0.66; Table 1). CRP landcover had a minimal effect on coyote colonization (−0.09, 95% CrI = −0.32–0.14) and persistence (−0.08, 95% CrI = −0.27–0.12), suggesting that changes in CRP cover had little impact on coyote occurrence dynamics.

For swift foxes, detection and colonization rates were significantly lower at sites where coyotes were present compared to sites without coyotes. The probability of detecting swift foxes was significantly greater at coyote-absent sites, with a 95% CrI for the difference in detection ranging from 1.88 to 2.28. Similarly, swift foxes were more likely to colonize coyote-absent sites, with a 95% CrI for the difference in colonization ranging from 2.22 to 3.51. CRP landcover had a strong negative effect on swift fox colonization in coyote-occupied areas (−2.77, 95% CrI = −3.47 to −2.20) and on detection (−2.07, 95% CrI = −2.27 to −1.88). This indicates that swift foxes were less likely to colonize and harder to detect in areas with higher CRP cover when coyotes were present.

Additionally, swift foxes were more likely to initially occupy coyote-absent sites (0.10, 95% CrI = 0.06–0.14)

TABLE 1 Parameter summaries from our dynamic occupancy model which assumed that site occupancy of swift fox (*Vulpes velox*) varies due to the presence of coyotes (*Canis latrans*).

Species	Median	Lower–upper
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

Note: "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. We assessed presence/absence of swift foxes and coyotes using camera traps at sites (2018 = 375, 2019 = 361, 2020 = 360) distributed across western Kansas, USA.

than sites where coyotes were present (0.01, 95% CrI = 0.01–0.02; Table 1). For a summary of all parameter estimates and their explanation, see Appendix S1.

Spatial overlap

Credible Intervals (CrI; 95%) of spatial overlap and SIF were >1 between coyotes and swift foxes at sites where the proportion of CRP was low. Specifically, the proportion of CRP landcover where the SIF CrI did not overlap 1 ranged 0–0.04 (Figure 2), thus swift foxes were spatially associated with coyotes in areas with lower amounts of CRP landcover. However, at sites where the proportion of CRP landcover was >0.04, SIF trended negative, but the 95% CrI overlapped SIF = 1, indicating insufficient evidence to determine swift fox spatial dependence on coyotes (Figure 2).

Temporal overlap

When aggregating all coyote (independent observations [Obs] = 3624 and swift fox [Obs = 341]) activity, the
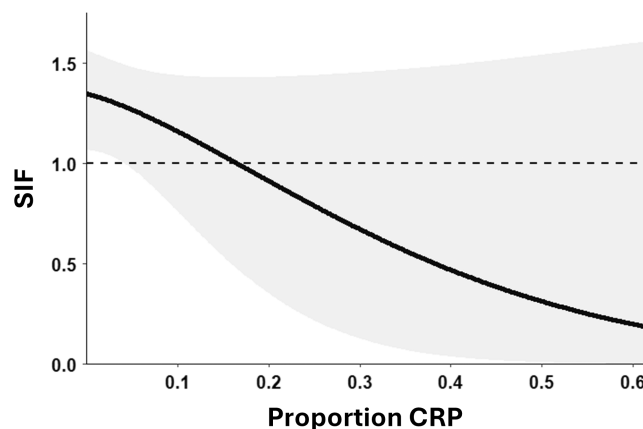

FIGURE 2 Species interaction factor (SIF) of swift foxes and coyotes in relation to the proportion of Conservation Reserve Program (CRP) landcover within 2 km buffers in Kansas, USA (2018–2020). An SIF of 1 indicates expected spatial overlap, while an SIF > 1 indicates the species interact more often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

coefficient of overlap (Δ_4) was 0.92 (95% CI = 0.87–0.94; Figure 3A), and it was 0.89 (95% CI = 0.84–0.93; Figure 3B) when both species were present at sites (coyote Obs = 379, swift fox Obs = 297). When both swift foxes and coyotes were present at sites where the proportion of CRP landcover was <0.10 (coyote Obs = 326, swift fox Obs = 261), the coefficient of overlap was 0.89 (95% CI = 0.86–0.95; Figure 3C), and at sites where both were present (coyote Obs = 53, swift fox Obs = 36) and CRP proportion was ≥0.10, the coefficient of overlap (Δ_1) was 0.67 (95% CI = 0.46–0.75; Figure 3D). The coefficient of overlap (Δ_1) at sites where the proportion of CRP landcover was ≥0.10 was significantly different (95% CI did not overlap) from all other landscape characteristics (Figure 4).

DISCUSSION

The primary objective of this study was to assess how the presence of coyotes and varying proportions of CRP landcover influenced the spatial and temporal dynamics of swift foxes. Specifically, we hypothesized that swift foxes would exhibit lower site occupancy and persistence at locations where coyotes were present, and that their activity patterns would shift in response to increased predation risk in landscapes with greater CRP landcover. As predicted, swift fox occupancy, colonization, and detection rates were significantly lower at sites with coyotes, suggesting that intraguild predation plays a key role in structuring their spatial distribution. Additionally, we
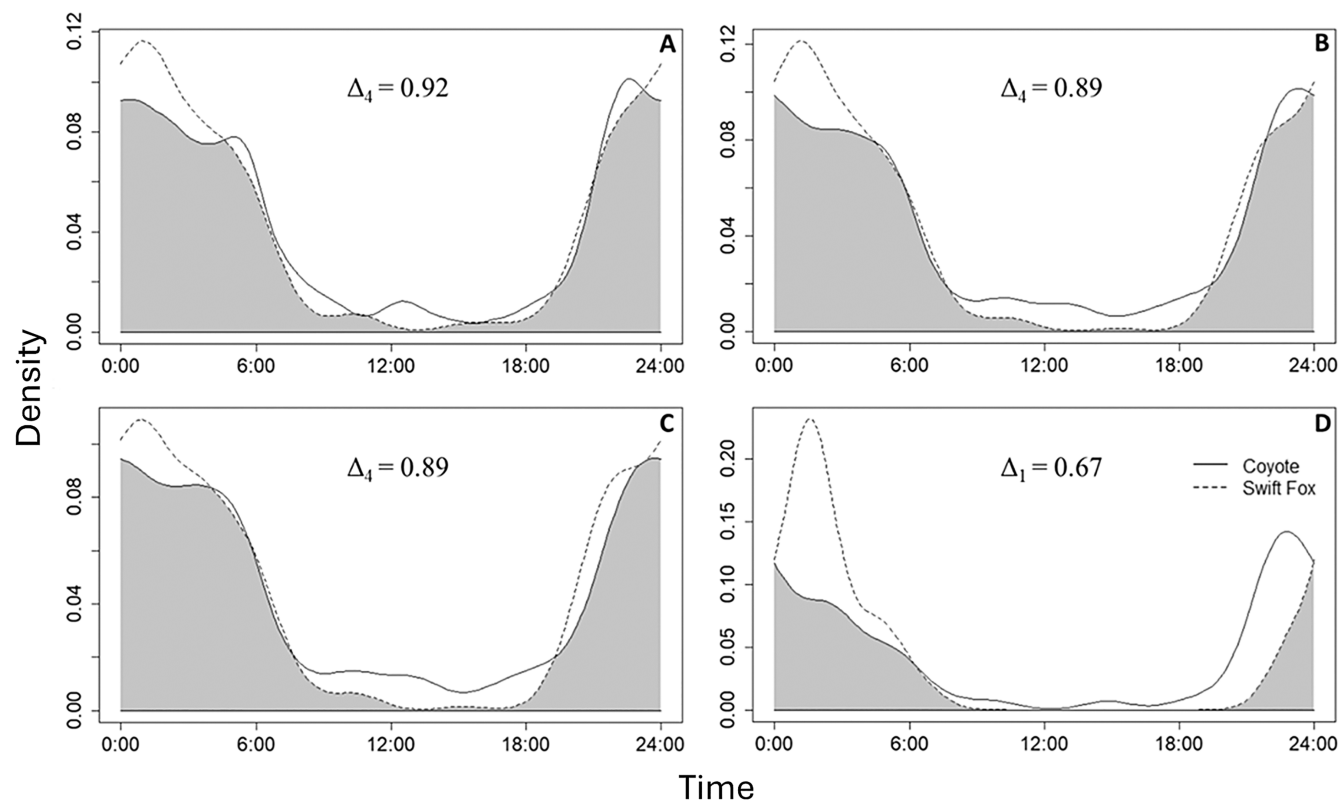
FIGURE 3 Kernel density function plots of coyote and swift fox activity in Kansas, USA (2018–2020). Kernel density functions and overlap estimation (Δ_1 if swift fox detections were <75, Δ_4 if swift fox detections at >75]) of (A) all coyote and swift fox activity, (B) coyote and swift fox activity when 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.

found that swift foxes adjusted their temporal activity at sites surrounded by greater proportions of CRP (≥0.10), likely to avoid interactions with coyotes. However, habitat use by swift foxes was generally independent of coyote presence, except in areas with low CRP cover (≤0.04), where co-occurrence was more frequent. These findings indicate that landscape composition, particularly CRP landcover, mediates the spatiotemporal interactions between these sympatric carnivores, with important implications for their coexistence in human-modified environments.

Swift foxes were less likely to initially occupy areas where coyotes were present at the start of our study, and this pattern extended to colonization and detection rates. The significant reduction in colonization and detection at coyote-occupied sites further supports our hypothesis that coyotes exert top-down pressure on swift fox distributions. These results suggest that the presence of coyotes not only influences swift fox habitat selection but also reduces their probability of successful colonization, reinforcing the role of intraguild predation. Subordinate carnivores either avoid landscapes where predation risk is greater (i.e., safety matching by avoiding tall

vegetation; Thompson & Gese, 2007), persist in areas where prey abundance is sufficient to support both subordinate and dominant carnivores (i.e., resource matching; Lonsinger et al., 2017), or exploit 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 occur not only when the abundance of the dominant carnivore is low enough to limit predation upon the subordinate species but also through other mechanisms, such as the availability of alternative prey, increased vigilance by the subordinate carnivore, or safety matching in areas of lower predation risk (Holt & Huxel, 2007; Kimbrell et al., 2007). These factors can help reduce direct encounters and competition, allowing the subordinate species to persist in landscapes where both species are present. Our results revealed significant reductions in swift fox colonization at coyote-occupied sites, suggesting that swift foxes may exhibit spatial niche partitioning by preferentially occupying areas with reduced coyote densities (Schuette et al., 2013). Alternatively, we may have failed to detect an effect on swift fox colonization rates due to spatial dependence occurring
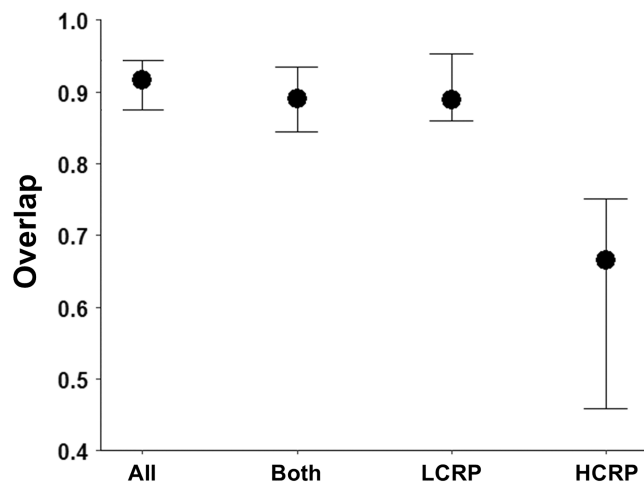
FIGURE 4 Bootstrapped means and 95% CIs of activity coefficient of overlap among swift foxes and coyotes in Kansas, USA (2018–2020). Coefficient of overlap means and CIs of (A) all coyote and swift fox activity (All), (B) coyote and swift fox activity when both are present at a site (Both), (C) coyote and swift fox activity when both are present at sites with proportions of Conservation Reserve Program (CRP) landcover <0.10 (LCRP), and (D) coyote and swift fox activity when both are present at sites with proportions of CRP landcover ≥0.10 (HCRP). LCRP, Low Conservation Reserve Program; HCPR, High Conservation Reserve Program.

on a finer timescale (<1 year), in which a dynamic occupancy model would fail to detect such a relationship. Because we 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 many CRP easements within our study area incorporated seeding mixtures producing taller vegetation communities (e.g., big bluestem [*A. gerardii*], switchgrass [*P. virgatum*]) that differed from native shortgrass prairie vegetation communities (Plumb et al., 2019; Sovada et al., 2003). This shift in vegetation structure to taller species likely enhances 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 & Gese, 2007). Our results support our hypothesis that swift foxes altered their temporal activity patterns, likely to reduce predation risk in landscapes with taller vegetation structure, such as CRP landcover. The 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 (*C. latrans*; Kamler et al., 2005). Because coyotes are the apex carnivore in our system, their densities likely correspond with prey (e.g., small mammals) densities which are expected to be greater in areas with more CRP landcover (Stanley, 2010;

Thompson & Gese, 2007). When coyotes and swift foxes both occur in areas with increased proportions of CRP landcover, our data suggest swift foxes will temporally segregate their activity patterns to avoid coyotes.

We expected CRP landcover proportion to influence spatial interactions between swift foxes and coyotes, and found that the amount of CRP surrounding sites mediated their spatial interactions. At sites with lower proportions of CRP (≤0.04), swift foxes were influenced by the presence of coyotes through space and time. This suggests that in landscapes with no or low amounts of CRP landcover, coyotes and swift foxes co-occur more often than expected by chance, possibly due to a combination of factors such as spatial and temporal avoidance, resource partitioning, and the availability of alternative prey, which together allow the two species to coexist despite the risk of predation (intraguild predation theory; Holt & Polis, 1997). Conversely, as the proportion of CRP landcover surrounding sites increased, SIF approached zero, suggesting that coyotes and swift foxes co-occur less often than expected by chance. However, the rarity of high CRP areas in our study region limited our sampling in these habitats, contributing to the uncertainty around this estimate. Although the 95% CrI of the estimated SIF overlapped zero, the general pattern aligns with 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 greater (Thompson & Gese, 2007). Coyotes may also be resource matching, leading to greater densities in landscapes with more CRP landcover, and swift fox may be actively avoiding these areas (Nelson et al., 2007). Additionally, the introduction of CRP onto the landscape may create landscape heterogeneity that allows coexistence of locally competing carnivores (Davies et al., 2021). We acknowledge that a multitude of landcover types may influence the spatiotemporal interactions of swift foxes and coyotes, as vegetation height (Dempsey et al., 2015; Kamler et al., 2003), prey (Robinson et al., 2014), and soil type (Lonsinger et al., 2017) influence the spatial dynamics of fox species. However, based on previous swift fox research conducted within this system (Werdel et al., 2022) we focused on the primary negative driver of decreased site occupancy probability of swift foxes (CRP).

Similar to previous studies documenting intraguild competition between sympatric carnivores (Kozlowski et al., 2008; Nelson et al., 2007; Robinson et al., 2014; Thompson & Gese, 2007), swift foxes likely practice spatiotemporal avoidance of coyotes in areas with increased predation risks. Our results suggest that CRP landcover, and its inherent structure and composition, may influence intraguild interactions between swift foxes and coyotes, but because of uncertainty of results at increased

proportions of CRP, future research should focus efforts on areas with greater than average proportions of CRP to further evaluate. Although agricultural land conversion is a known driver of habitat loss and fragmentation in prairie ecosystems (Di Minin, Slotow, et al., 2016; Foley et al., 2005, 2011; Woodroffe & Ginsberg, 1998), our study did not find a significant effect of row-crop agriculture on swift fox occupancy dynamics. Instead, our results underscore the important role of CRP landcover in shaping swift fox-coyote interactions. Current CRP practices often incorporate tallgrass species, which may increase predation risk for swift foxes. Future restoration efforts may benefit from incorporating more shortgrass species or maintaining lower proportions of CRP landcover to reduce the risk of coyote predation and improve habitat suitability for swift fox populations. Modifying CRP management strategies could help restore native prairie habitats while supporting swift fox conservation, providing a valuable approach for mitigating the negative effects of habitat loss and fragmentation.

Understanding how species interact within these novel landscapes may help managers identify and conserve important habitats or help us identify factors structuring trophic-level interactions among carnivores. Our findings offer valuable insights for the conservation and management of swift foxes and coyotes in multiuse landscapes like western Kansas. Given that over 95% of the land is privately owned (U.S. Bureau of the Census, 1991), conservation efforts must engage private landowners in habitat management decisions. Additionally, protecting areas with greater shortgrass prairie cover or incorporating corridors of shortgrass prairie may facilitate coexistence between the species (Werdel, Piper, Ricketts, Peek, Sullins, & Ahlers, 2023). These actions may help mitigate the impacts of land-use changes and support long-term conservation goals for both carnivores and their shared ecosystems (Foley et al., 2011; Ripple et al., 2014).

AUTHOR CONTRIBUTIONS

Ty J. Werdel, Adam A. Ahlers, Andrew M. Ricketts, and Matthew S. Peek conceived and designed the study. Ty J. Werdel and Colleen W. Piper conducted field data collection. Ty J. Werdel and Mason Fidino conducted data analyses. Ty J. Werdel, Colleen W. Piper, Mason Fidino, Matthew S. Peek, Andrew M. Ricketts and Adam A. Ahlers wrote the manuscript. Adam A. Ahlers, Andrew M. Ricketts and Matthew S. Peek secured funding.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Werdel, 2025) are available in Zenodo at https://doi.org/10.5281/zenodo.15191398. The Conservation Reserve Program spatial data parcels for 2018 were acquired by Ty J. Werdel through a request to the Kansas State Office of the Farm Service Agency (USDA Farm Service Agency, n.d.); these data are not publicly available online.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.