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ARTICLE

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Mesopredators have differing influences on prey habitat use and diel activity in a multipredator landscape

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Abstract

Resource distribution, habitat structure, and predators greatly influence spatial and temporal landscape use by prey species. The "risky places" hypothesis establishes prey will proactively respond to predators' presence based on habitat cues, whereas the "risky times" hypothesis predicts prey will reactively respond by increasing vigilance in the presence of predators regardless of habitat cues. We fit a multiscale, Bayesian species interaction occupancy model with detection/non-detection data to evaluate black-tailed jackrabbit (*Lepus californicus*) and eastern cottontail rabbit (*Sylvilagus floridanus*) habitat use in the presence and absence of coyotes (*Canis latrans*), American badgers (*Taxidea taxus*), and swift foxes (*Vulpes velox*). We also evaluated how species-specific predator presence modified temporal activity patterns of prey. Jackrabbits decreased habitat use in areas with greater forage and opted to use areas with greater visibility when coyotes or swift foxes were present. However, cottontails used habitat in open areas with greater visibility when American badgers were present and all other predators absent, suggesting dissimilar habitat-use patterns dictated by predator-specific risks. Both lagomorph species are nocturnal with segregated peaks of activity compared with predators, suggesting fine-scale temporal use partitioning. Our results provide insights into predator–prey dynamics across heterogenous landscapes in a multi-predator system.

KEYWORDS

Bayesian occupancy model, black-tailed jackrabbit, eastern cottontail rabbit, multispecies occupancy, predator–prey, short-grass prairie

INTRODUCTION

Prey species must consider predation risks in decisions regarding foraging activity and habitat use. However, predator presence may impose varying levels of risk, according to the landscape of fear (Laundré et al., 2009). As a result, a landscape can have spatial and temporal "peaks and valleys" of risk which prey use nonuniformly

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across their home ranges (Arias-Del Razo et al., 2012; Laundré et al., 2001, 2009). Prey species, for example, will use less risky foraging areas (e.g., increased vegetation cover) even when food opportunities are not ideal (Laundré et al., 2001, 2009). At a temporal scale, prey can reduce predation risk by segregating activity overlap with predators, though predators attempt to match temporal activity of their prey (Lima, 2002; Monterroso et al., 2013). Thus, the distribution of resources and the presence of predators greatly influence when and where prey species use the landscape (Svoboda et al., 2019; Willems & Hill, 2009).

Avoidance behavior plays an important role in habitat selection (Frank, 2008; Lazenby & Dickman, 2013). The landscape of fear model suggests prey will exhibit antipredator behavior in response to risk (Gehr et al., 2018; Moll et al., 2017). For example, perceived risks may drive prey toward less risky, but less ideal habitats (Sand et al., 2021; Thaker et al., 2011) or prey may use riskier but more resource-rich areas during certain times considered safe (Gallo et al., 2019; Palmer et al., 2022; Smith et al., 2019). By understanding predation risk in both space and time, we can better understand the effects of predators on prey distributions and prey behaviors (Palmer et al., 2022).

Two hypothesis help explain how prey may respond to temporal and spatial variation in predation risk (Creel et al., 2008). The risky places hypothesis posits that prey use the long-term risk levels of their location to assess spatial and temporal variation in predation risk based on habitat characteristics and adjust their behavior proactively (i.e., vigilance; Creel et al., 2008; Gehr et al., 2018). However, the risky times hypothesis states that prey will increase vigilance in the presence of predators (i.e., reactive), regardless of environmental cues and prior assessment of risks (Creel et al., 2008; Moll et al., 2017).

The landscape of fear suggests that prey will respond to both risky places and risky times with observable antipredator behaviors (Moll et al., 2017). The way risk is characterized depends on the study species and the methods used to study them. Researchers have characterized predation risk differently, including wolf-pack (*Canis lupus*) presence and absence (Moll et al., 2016), measure of habitat openness (Christianson & Creel, 2014), and distance between elk (*Cervus canadensis*) and wolves at a given time (Middleton et al., 2013; Moll et al., 2017). The risky places hypothesis is usually informed by long-term metrics, whereas the risky times hypothesis uses short-term metrics (Moll et al., 2017). The risky places hypothesis can be informed by habitat characteristics that may be correlated with long-term risk (Moll et al., 2017). For example, vegetation structure can affect how individuals perceive predation risk. In certain landscapes, prey may not perceive dense cover as refugia because complex vegetation structure can also provide ambush cover for predators (Camp et al., 2012; LaManna et al., 2015). Additionally, the risky times hypothesis can be informed by local predator presence and absence during a short time frame (e.g., 24-h period) (Creel & Winnie, 2005), chemical, auditory, or visual cues that simulate predator presence (Kuijper et al., 2014).

The risky times hypothesis establishes that prey will behave reactively to temporal variation in predation risk as a function of direct cues of predator presence or absence (Gehr et al., 2018). For example, prey have been found to respond to temporal variation in predators' visibility at night when visual detection is decreased (Lynch et al., 2015; Palmer et al., 2017; Smith et al., 2019). Risky habitats with low vegetation structure may create a temporal refuge for prey during the day where predators cannot rely on the landscape to remain concealed. Further, prey may track their predators daily activity pattern over a large physical landscape and use risky places during "predator downtimes" (Kohl et al., 2018). However, prey will often use behavioral strategies to avoid predation because they have a higher mortality risk while active (Lima & Dill, 1990), like reducing their own activity during predator's peak activity hours (Arias-Del Razo et al., 2011).

Lagomorph species (i.e., rabbits and hares) are common prey species with many predators, and investigations regarding their habitat use may give us insight into how prey balance foraging activity and predator avoidance (Owen-Smith, 2014; Tambling et al., 2015). In semiarid environments, lagomorphs tend to rest more during the day to avoid greater daytime temperatures, and as such must balance predator avoidance (risk) and thermoregulation (resource) (Arias-Del Razo et al., 2011). Black-tailed jackrabbit (*Lepus californicus*, "jackrabbits" henceforth) and eastern cottontail rabbits (*Sylvilagus floridanus*, "cottontails" henceforth) are sympatric species throughout the southwestern United States, Great Plains, and northern Mexico (Best, 1996; Chapman & Litvaitis, 2003). Both species show similar preferences for habitat and food resources (Arias-Del Razo et al., 2012; Best, 1996; Chapman & Litvaitis, 2003; Marín et al., 2003). However, jackrabbits and cottontails differ in body size and predator escape tactics (Harrison, 2019; Wagnon et al., 2020). Jackrabbits usually outrun their predators (Simes et al., 2015) whereas, cottontails tend to seek refugia (Harrison, 2019; Orr, 1940). Both lagomorphs have been documented as a major food source for coyotes (*Canis latrans*; Brown et al., 2018), American badgers (*Taxidea taxus*, badgers henceforth; Messick & Hornocker, 1981), and swift foxes (*Vulpes velox*; Cutter, 1958), although swift foxes consume relatively few jackrabbits and rely mostly on cottontails as an important food resource (Schauster et al., 2002).

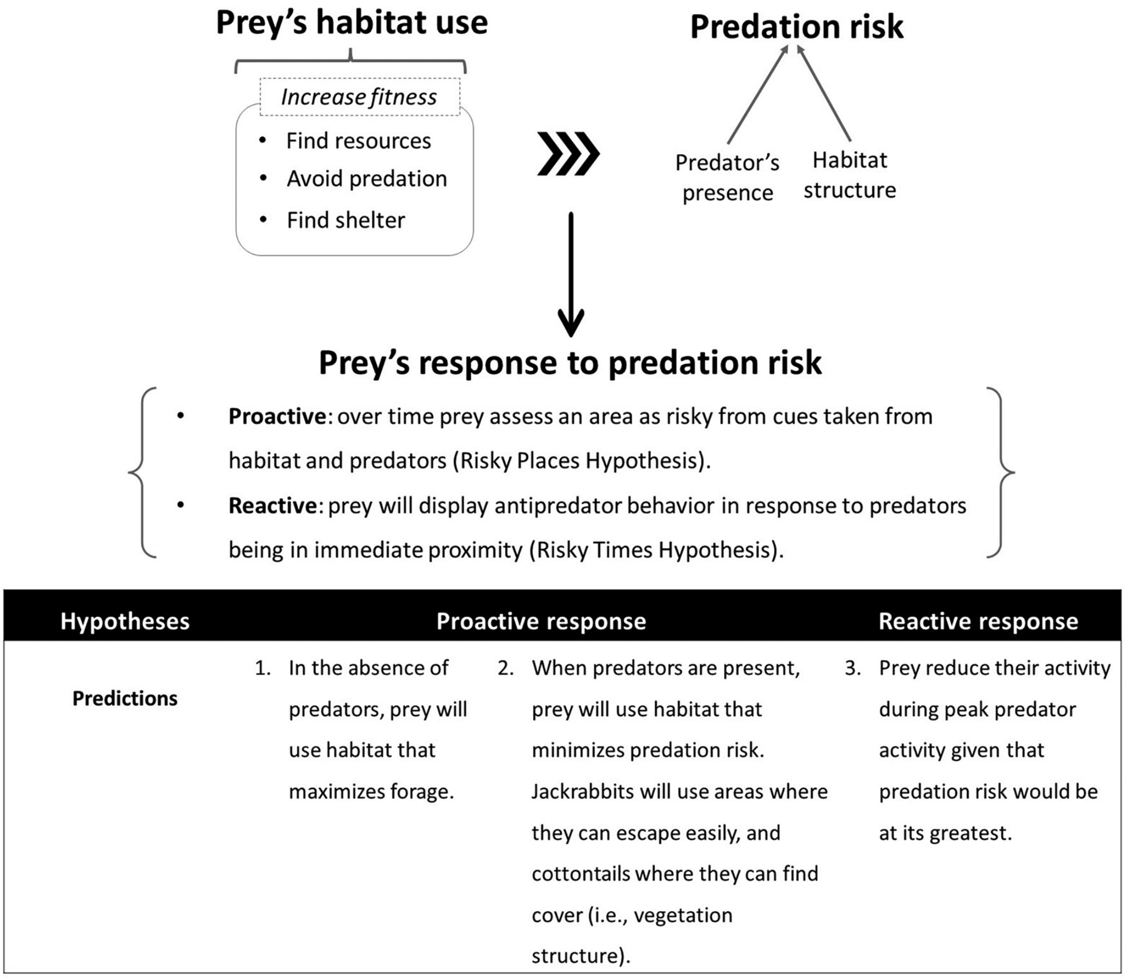
Here we investigated how habitat use by jackrabbits and cottontails vary in response to both risky times and risky places. We used a Bayesian multispecies occupancy model that included interactions among mesopredators and lagomorph species to determine how local- and landscape-scale habitat characteristics influenced their co-occurrence (Waddle et al., 2010). Specifically, we investigated co-occurrence between cottontails and jackrabbits with coyotes (*C. latrans*), American badgers (*T. taxus*), and swift foxes (*V. velox*) using detection/non-detection camera trap data from 2018 to 2020 in western Kansas, USA. Additionally, we studied temporal avoidance between lagomorphs and predators on a short time scale (24-h).

Following the risky places hypothesis (Figure 1), we expected that when predators are absent, prey will use habitat that maximizes forage, and, in the presence of predators, prey will use habitat that minimizes predation. Therefore, we predicted that lagomorphs will occur in areas where forbs and grasses are more abundant when predators are absent. Conversely, when the presence of predators creates a constant risk of predation, jackrabbits would use areas with less cover where they can spot predators more easily and rely on their mobility to escape, whereas cottontails would occur in areas with more cover because they rely more heavily on vegetation structure to avoid predation. Following the risky times hypothesis and to explore temporal avoidance of predators, we also quantified temporal overlap between lagomorphs and each predator. We hypothesized prey would reduce their activity when predator activity is greatest (Figure 1).

MATERIALS AND METHODS

Study area

This study was conducted in western Kansas, USA (~71,600.77 km^2, centered on 38.54 N, 100.68 W; Figure 2).



- **Proactive**: over time prey assess an area as risky from cues taken from habitat and predators (Risky Places Hypothesis).
- **Reactive**: prey will display antipredator behavior in response to predators being in immediate proximity (Risky Times Hypothesis).

Hypotheses	Proactive response		Reactive response
Predictions	1. In the absence of predators, prey will use habitat that maximizes forage.	2. When predators are present, prey will use habitat that minimizes predation risk. Jackrabbits will use areas where they can escape easily, and cottontails where they can find cover (i.e., vegetation structure).	3. Prey reduce their activity during peak predator activity given that predation risk would be at its greatest.

FIGURE 1 Prey use habitat to find resources, avoid predation, and find shelter (i.e., increase fitness). The landscape of fear states that prey will make decisions based on predation risk and availability of resources, and consequently modify their behavior in response to perceived risk. The risk allocation model suggests that two hypotheses can help explain prey's antipredator response to risk: Proactive and reactive behavior.

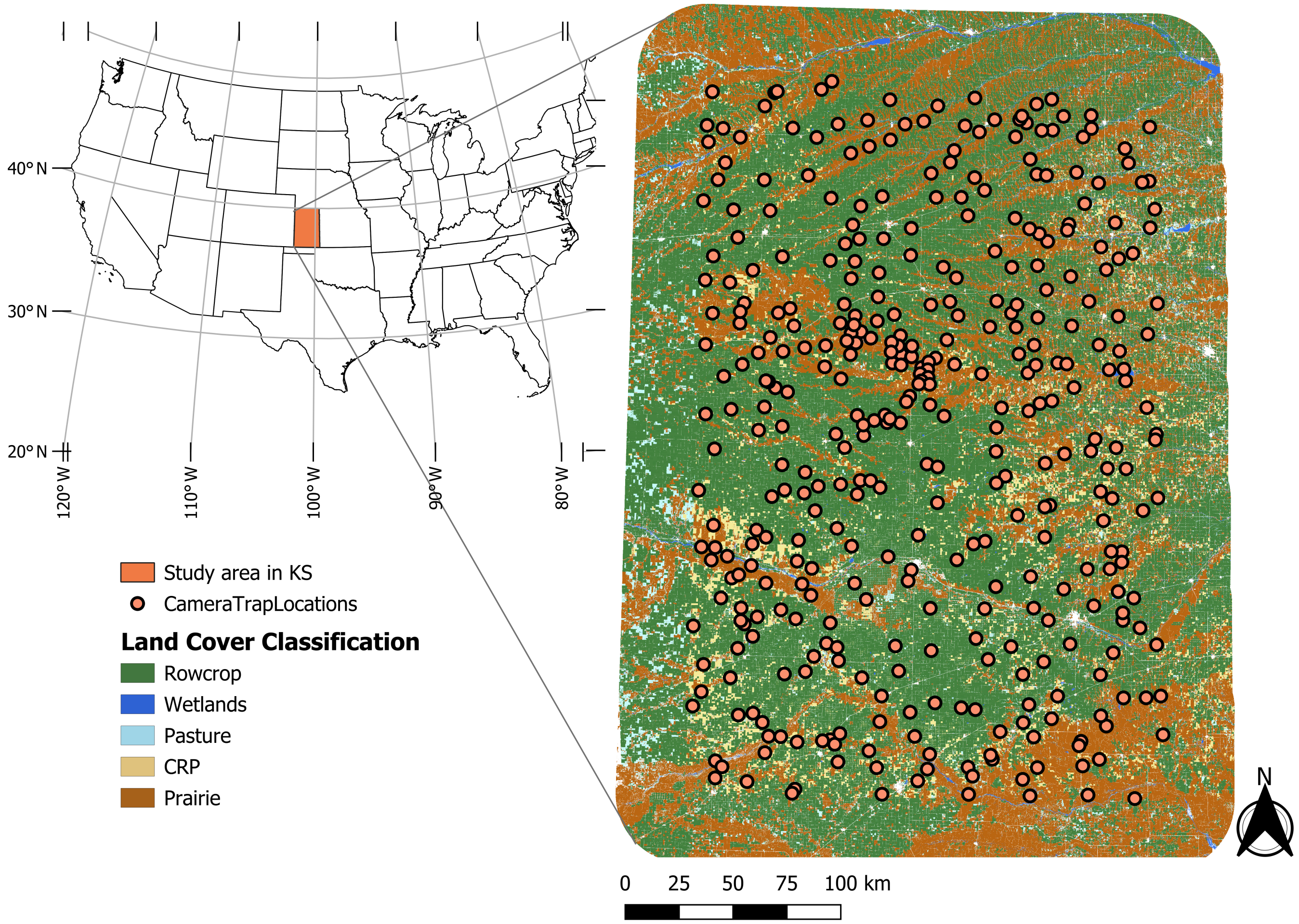


FIGURE 2 Study area in Kansas, USA (~71,600 km^2). The map shows all camera sites (2018: $N = 375, 291$; $n = 361$, 2020: $N = 360$). The land classes represent the most common landcover across the region: Row crop, wetlands, pasture, Conservation Reserve Program (CRP), and prairie aggregates tall, short, and mixed prairie.

This area was historically characterized by short grass, mixed, and sage-prairies, but row-crop agriculture expansion and cattle (*Bos taurus*) ranching have transitioned this region to an agro-prairie ecosystem. Average annual precipitation ranged from 31 to 107 cm and average temperature from 10 to 14°C (PRISM Climate Group, 2021). Our study area consisted mainly of grama-buffalograss prairie which is dominated by buffalo grass (*Buchloe dactyloides*) and blue grama (*Boutelousa gracilis*) to the west, and to the east, mixed prairie with tall, medium tall, and short grasses (Kuchler, 1974; Lacey, 1942).

Camera surveys

We deployed camera traps in our study area from 2018 to 2020 at randomly selected sites during three annual surveys—5 May to 2 November 2018 ($n = 375$), 20 May to 2 October 2019 ($n = 361$), and 22 April to 28 September 2020 ($n = 360$). Camera sites were spatially separated by a minimum of 2 km ($\bar{x} = 8.16, \mathrm{SD} = 3.61$). We initially selected sites using a random-point generator in ArcMap (v. 10.8). If sites could not be accessed or located where cameras were likely to be destroyed (e.g., in a row-crop agriculture field), we chose a site in the nearest suitable location. All sites remained at the same location for each annual survey.

Each site included a single motion-sensing camera trap (Bushnell Trophy Cam, Bushnell, Overland, KS, USA) anchored to a metal post 40 cm above ground. Because of varying access on private property, we were unable to sample all sites in 2019 and 2020. We removed any herbaceous material within the field of view of each camera trap using a hand-held weed cutter. We used an olfactory attractant to maximize the chances of photo capturing cryptic or elusive species (i.e., swift fox). The attractant was a mixture of skunk essence (F&T Fur Harvester's Trading Post, Alepna, MI, USA) and petroleum jelly applied to the top of a wooden stick positioned ~3 m in front of the camera.

Olfactory attractants do not introduce significant biases regarding carnivore spatial ecology, however, they can increase detection of certain species and photograph quality (du Preez et al., 2014; Fidino et al., 2020; Gerber et al., 2012). For each camera deployment we reapplied skunk essence, changed batteries, and replaced digital memory cards at ~14 days. Each camera was active 28 consecutive days during a study period, but camera traps were not all active simultaneously. We processed photographs manually and used Colorado Parks and Wildlife Photo Warehouse to tag and organize photographs (Ivan & Newkirk, 2016). For more details on survey design see Werdel et al. (2022) and Palomo-Munoz et al. (2023).

Local-scale habitat composition

Each sampling year, we measured local-scale habitat characteristics at each site prior to deploying camera traps. At each site we created a sampling grid (50 × 50 m) centered on the camera site. From 15 evenly spaced sampling sites within each grid, we measured proportion of cover for grasses and forbs, and vegetation height (in centimeters) using a meter stick and a Daubenmire square (1/4 m^2). We then averaged each variable across all measuring sites to include as a single site-level covariate (Palomo-Munoz et al., 2023).

Landscape characterization

To characterize landscape cover in our study area, we merged and reclassified three raster datasets: area enrolled in Conservation Reserve Program (CRP; USDA, 2021), CropScape (NASS CDL Program, 2021), and PRAIRIEMAP (United States Bureau of Land Management, 2018; Figure 2). Our final custom landcover raster had a 30 × 30 m resolution and extended up to 10 km beyond the study area extent. For each site, we created a circular buffer (radius = 1 km) and extracted proportions of short-, tall-, and mixed-grass prairie, and sandsage prairie using the landscape metrics package (Hesselbarth et al., 2019) in R 4.0.3 (R Core Team, 2020). We summed the proportions of every class of prairie to estimate proportion of prairie landcover around each site. We assessed different scales (0.5, 2, 5 km) and found a strong positive correlation among our measured covariates across all scales. We chose to use 1 km scale as it encompassed home range extents of cottontail (0.047 km^2) (Bond et al., 2001; Trent & Rongstad, 1974) and jackrabbit (<1–3 km^2) (Smith, 1990).

Risky places hypothesis: Predator–prey co-occurrence model

To estimate how predator presence affected the spatial distribution of both lagomorphs we extended a hierarchical occupancy model for potentially interacting species (Waddle et al., 2010). Specifically, we (1) allowed for multiple "dominant" predator species that may influence occupancy of their prey, (2) allowed for multiple "subordinate" prey species, (3) added a first-order autologistic term to account for temporal correlation between primary sampling periods (Royle & Dorazio, 2008) and (4) used a Bayesian framework to parameterize the model. With this model we estimated occupancy and detection probabilities for all species across the entire study area and assessed the effect of three predator species on cottontail and jackrabbit occupancy across varying local- and landscape-scale covariates.

Our model included the number of days predators and prey were detected, y_{kit} and y_{mit} for predator k and prey m at site i and time t, which informs the latent true occupancy states z_{kit} and z_{mit} ($z = 1$ where a species is present, otherwise it is zero). We conducted three surveys in the years 2018–2020 which is represented by t, and at each site $j_{i,t}$ observation days occurred. The probability of detection for predators and prey was respectively ρ_{kit} and ρ_{mit} (MacKenzie et al., 2017). Our hierarchical model stated that the observed detection/non-detection data was conditional on the true occupancy state such that:

$$z_{kit} \sim \text{Bernoulli}(\psi_{kit}), \tag{1}$$

$$z_{mit} \sim \text{Bernoulli}(\psi_{mit}), \tag{2}$$

$$y_{kit} | z_{kit} \sim \text{Binomial}(j_{it}, z_{kit}\rho_{kit}), \tag{3}$$

$$y_{mit} | z_{mit} \sim \text{Binomial}(j_{it}, z_{mit}\rho_{mit}), \tag{4}$$

where ψ_{kit} and ψ_{mit} represented the occupancy probability for predator k and prey m at site i at time t. Both detection and occupancy probabilities can be modeled as linear functions of predictor variables. We made the detection probabilities of predators and prey a function of average vegetation height at a site (VegH) and proportion of prairie (prairie) within a 1-km buffer, such that:

$$\text{logit}(\rho_{kit}) = \alpha_{0k} + \alpha_{1k}\text{VegH}_i + \alpha_{2k}\text{prairie}_{i,} \tag{5}$$

The prey model was identical to Equation (5) except the k subscripts are replaced with m, so we do not repeat here. We used an intercept-only model for predators, save for the inclusion of the autologistic term, θ_k, when $t > 1$.

We used an intercept-only model because we did not expect occupancy patterns to vary from survey to survey (2018–2020), since all species were established in the area (Kass et al., 2020).

$$\mathrm{logit}\left(\psi_{k,t=1}\right) = \beta_{0k}, \tag{6}$$

$$\mathrm{logit}\left(\psi_{kit>1}\right) = \beta_{0k} + \theta_k z_{kit-1}, \tag{7}$$

Given this model specification, the expected occupancy of the K predators is:

$$\overline{\psi}_k = \mathrm{expit}(\beta_{0k}) / (\mathrm{expit}(\beta_{0k}) + (1 - \mathrm{expit}(\beta_{0k} + \theta_k))), \tag{8}$$

where expit is the inverse logit link function. In the event of site-specific covariates influences on occupancy, Equation (6) could easily be extended by adding covariates and their associated slope terms. Similarly, replacing the k subscripts with m in Equation (8) would then estimate the expected occupancy of a given prey species.

We estimated the occupancy of a prey species as a function of four covariates, predator presence, and their interaction. Thus, let $\boldsymbol{X}$ represent the prey design matrix which has number of rows equal to number of sites monitored and five columns. The first column is a vector of 1's for the model intercept, while the remaining four columns contained scaled covariates associated to proportion of forbs, proportion of grass, vegetation height, and proportion of prairie within a 1-km buffer. At $t = 1$, the logit linear predictor was.

$$\mathrm{logit}\left(\psi_{m,i,t=1}\right) = x_i \beta_m^T + \sum_{k=1}^{K} x_i \boldsymbol{\delta}_{km}^T z_{kit}, \tag{9}$$

where β_m^T is a vector of conformable of intercept and slope terms for prey species m, and $\boldsymbol{\delta}_{km}^T$ is a vector of conformable parameters that are related to how occupancy pattern of prey m varies by the interaction of predator presence and presence of predator k. For example, the first element of $\boldsymbol{\delta}_{km}^T$ (i.e., δ_{1km}) is the log-odds difference in occupancy of prey m given the presence of predator k, while the remaining parameters represent how prey occupancy may differ along the four covariates given the presence of predator k. For the remaining two surveys, we added an autologistic term to Equation (9) such that

$$\mathrm{logit}\left(\psi_{m,i,t>1}\right) = x_i \beta_m^T + \theta_m z_{mit-1} + \sum_{k=1}^{K} x_i \boldsymbol{\delta}_{km}^T z_{kit}, \tag{10}$$

Model implementation

We calculated Pearson's correlation coefficient between all covariates and did not include variables with $r > 0.6$ in the model. We used vague logistic (0, 1) priors for all parameters. We ran the model with 3 chains and 50,000 iterations per chain, with a burn-in of 30,000, and a thinning of 10. We assessed convergence using the Brooks–Gelman–Rubin convergence ($\widehat{R} < 1.1$) and visually inspected stability of all chains in the posterior predictions for each parameter using traceplots. To provide evidence for the direction of a given parameter estimate, we calculated the proportion of the posterior distribution that was greater than or less than zero, given the direction of the effect. To provide some additional information about parametric uncertainty, we also estimated 95% Bayesian credible intervals for each one of our parameters from their posterior distributions. We used an MCMC algorithm implemented in JAGS v. 4.3.0 (Plummer, 2003) using jagsUI v. 1.5.2 (Kellner, 2021) R package in R 4.1.3 (R Core Team, 2022). Graphs and other visualization packages used are ggplot2 v. 3.3.6 (Wickham, 2016), MCMCvis v. 0.15.5 (Youngflesh, 2018), kableExtra v. 1.3.4.9000 (Zhu, 2019).

Advice on interpretation of interaction terms

The interaction terms in our model (second term in Equation 9) represent log-odds differences from either a species baseline occupancy (e.g., the change in a species intercept given the presence of a predator) or in a species response to a given environmental feature (e.g., the change in a species slope term given the presence of a predator). With respect to the latter, slope interaction terms could be positive, but the overall effect is still negative. For example, jackrabbits, no predators, grass $\beta = -1.42$ and jackrabbits, coyotes, grass $\beta = 0.94$. So, when predators are absent, the effect is negative ($-1.42 + 0.94 \times 0 = -1.42$). However, the prey response to this covariate would still be negative but to a lesser magnitude ($-1.42 + 0.94 \times 1 = -0.48$; Appendix S1: Table S4). The first term is the median estimate of jackrabbits' response to grass given the absence of all predators. The latter term is the median estimate of jackrabbits' response to grass given the presence of coyote, hence the 1. The estimated association between jackrabbits, coyote presence, and grass is not strong enough to flip the direction of the effect. Additionally, we provide a figure on Appendix S1: Figure S1 in which we summarize the direction of the effect for each covariate and predator–prey pairing.

Risky times hypothesis: Temporal activity

We assessed differences in diel activity between lagomorph and predators using circular plots and estimating the proportion of the circles that overlap (overlap coefficient Δ_4). We used independent photo capture events for each species (photos separated by ≥60 min) at each site each year. To create diel activity circular plots, we collapsed all encounters by hour in a circular 24 h period disregarding calendar date. We estimated the activity of each species using kernel density estimates using package Activity v. 1.3.2 (Rowcliffe, 2022) in R. The kernel density curve was fitted to the original data and then simulated observations were drawn from that distribution, resulting in most of the simulated observations to fall near the original data (Rovero & Zimmerman, 2016). We plotted kernel density functions of temporal data of each species in a circular graph using ggplot2 3.3.6 (Wickham, 2016).Using overlap package 0.3.4 (Ridout & Linkie, 2009) in R 4.2.1 (R Core Team, 2022), we estimated overlap in activity patterns between species using the $\widehat{D}_4$ coefficient which ranges from 0 (no overlap) to 1 (complete overlap) and is recommended with large sample sizes ($n \geq 75$).

RESULTS

We deployed camera traps across 383 sites that operated a total of 24,571 camera days (2018 = 8984, 2019 = 8594, 2020 = 6993). Cameras were active for an average of 21 days across all years (SE = 0.25, range = 2–28). We detected cottontail rabbits at 0.23 of sites in 2018, 0.20 in 2019, and 0.17 in 2020; jackrabbits at 0.34 of sites, 0.15, and 0.24 of sites in 2018–2020 respectively, coyotes at 0.67 in 2018, 0.54 in 2019, and 0.63 in 2020; swift foxes at 0.08, 0.04, and 0.06 and badgers at 0.35, 0.42, and 0.33 sites in 2018–2020, respectively. Overall, coyote and badger probability of expected occupancy was moderately high across our study area, but swift foxes had moderately lower occupancy and detection probabilities (Appendix S1: Table S2).

Risky places: Effects of predator–prey co-occurrence across habitat gradients

If prey species use forage-rich habitats in the absence of predators, then we would expect that, in the absence of predators, lagomorphs will occur in areas where forbs and grasses are more abundant (Hypothesis 1, Figure 1). Our data suggest lagomorph occupancy varied as a function of predator presence in areas considered rich in food resources. Here, we report the value of the overall effect of the presence or absence of a predator and the species response to a particular environmental feature (Equation 9). In the absence of predators, jackrabbits showed a slight negative effect in their habitat use with proportion of forbs present at each site (jackrabbit, no predators, forbs, $\beta = -0.66$, 95% CI = −1.51, 0.03; Figure 3; Appendix S1: Table S4). However, when coyotes were present, the magnitude of the negative effect increases (jackrabbit, coyote, forbs, $\beta = 0.14$, 95% CI = −0.56, 0.96) but not enough to change the direction of the effect. Similarly, when badgers are present (jackrabbit, badger, forbs, $\beta = 0.0$, 95% CI = −0.67, 0.64), the effect of forbs on jackrabbits' occupancy is negative (jackrabbit, badger, forbs, $\beta = 0.0$, 95% CI = −0.67, 0.64). However, in the presence of swift foxes, there is no change in jackrabbits' response to variation in forbs (jackrabbit, swift fox, forbs, $\beta = 0.76$, 95% CI = −0.80, 2.28). Jackrabbits' response to grass in the absence of predators is slightly negative (jackrabbit, no predators, grass, $\beta = -1.42$, 95% CI = −1.51, 0.03; Figure 4; Appendix S1: Table S4). However, jackrabbits were less likely (i.e., magnitude of the effect increases) to use sites with greater grass cover when coyotes (jackrabbit, coyotes, grass, $\beta = 0.64$, 95% CI = 0.05, 2.04), badgers (jackrabbit, badger, grass, $\beta = -0.02$, 95% CI = −0.74, 0.73), and swift foxes (jackrabbit, swift fox, grass, $\beta = 0.07$, 95% CI = −1.40, 1.35) were present.

If prey use habitat that minimizes predation risk in the presence of predators, then we would expect jackrabbits to use areas with less visual obstruction to detect predators more easily and rely on their speed to avoid predation (Hypothesis 2, Figure 1). Jackrabbit occupancy negatively covaried with vegetation height when all three predators were absent (jackrabbit, no predators, vegHeight, $\beta = -1.16$, 95% CI = −2.29, −0.18; Figure 5; Appendix S1: Table S4). In the presence of coyotes, the effect of vegetation height on jackrabbit occupancy remained negative (jackrabbit, coyote, vegHeight, $\beta = 0.04$, 95% CI = −0.78, 0.94), and similarly with swift foxes (jackrabbit, swift fox, vegHeight, $\beta = -0.45$, 95% CI = −1.41, 0.44) but not with badgers (jackrabbit, badger, vegHeight, $\beta = 1.06$, 95% CI = 0.25, 2.03). There was no landscape-scale effect of prairie landcover on jackrabbit occupancy probabilities when all three predators were absent (jackrabbit, no predator, prairie, $\beta = 0.26$, 95% CI = −0.53, 1.05; Figure 6; Appendix S1: Table S4). However, when coyotes (jackrabbit, coyote, prairie, $\beta = 0.11$, 95% CI = −0.63, 0.86) and badgers (jackrabbit, badger, prairie, $\beta = 0.46$, 95% CI = −0.18, 1.07) were present, the proportion of prairie had a positive effect on jackrabbit's occupancy. Interestingly, there was no effect of proportion of prairie on jackrabbit's habitat use when swift foxes were present.

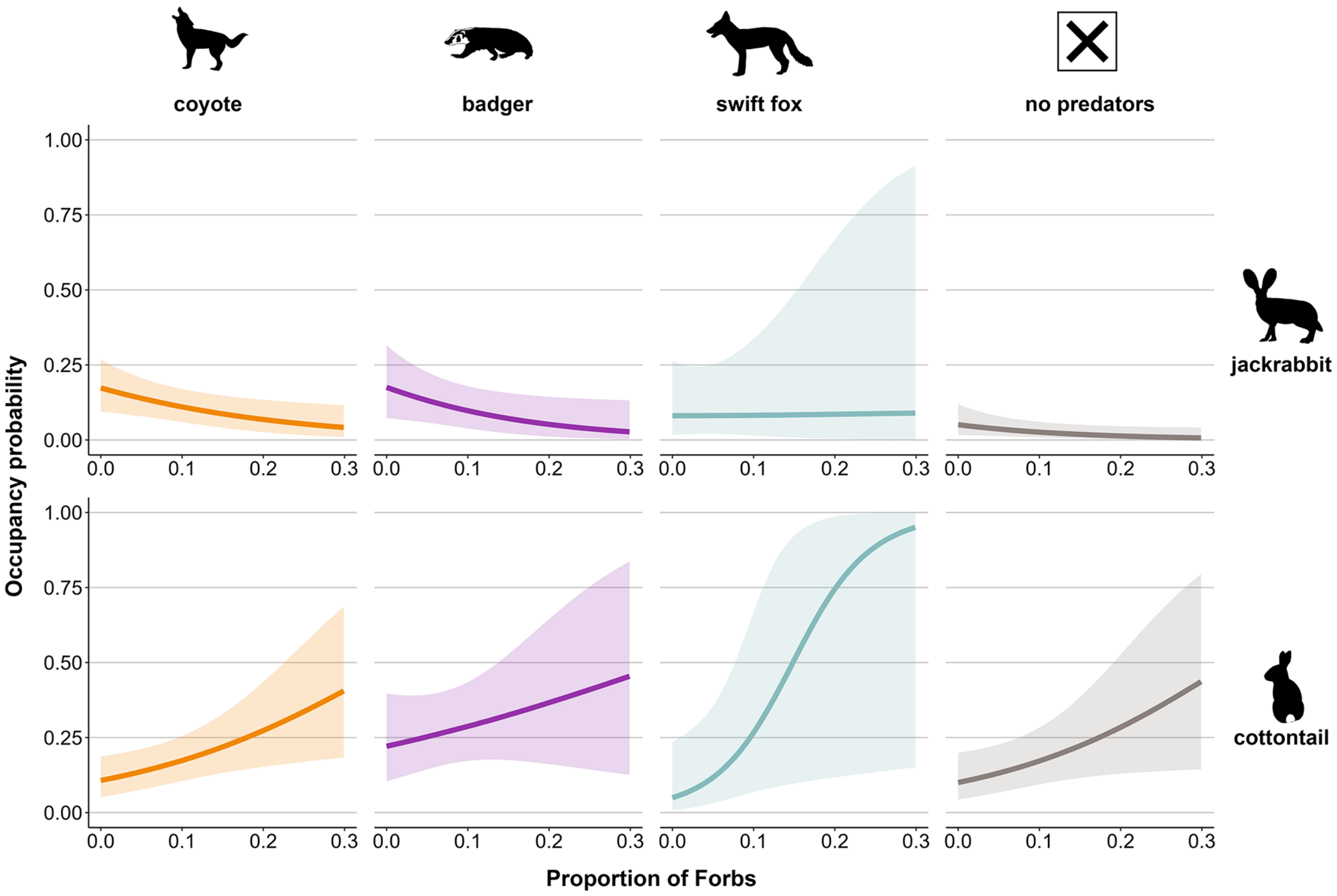


FIGURE 3 Response curves for lagomorph (top row, black-tailed jackrabbit; bottom row, eastern cottontail rabbit) occupancy probability when coyote, American badger, and swift fox are present, and when predators are absent (right), over the proportion of forbs (local-scale covariate).

For cottontails, the effect of forbs on their habitat use was positive (cottontail, no predator, forbs, $\beta = 0.51$, 95% CI $= 0.02, 1.05$; Figure 3, Appendix S1: Table S4) and there was no change in the effect when coyotes (cottontail, coyote, forbs, $\beta = -0.05$, 95% CI $= -0.63, 0.50$), badgers (cottontail, badger, forbs, $\beta = -0.23$, 95% CI $= -0.81, 0.30$), or swift foxes (cottontail, swift fox, forbs, $\beta = 1.05$, 95% CI $= -0.32, 2.89$) were present. We failed to detect a relationship between cottontail habitat use and the proportion of grass when all predators were absent (cottontail, no predator, grass, $\beta = 0.18$, 95% CI $= -0.36, 0.76$; Figure 4; Appendix S1: Table S4) or any predator was present (cottontail, coyote, grass, $\beta = -0.10$, 95% CI $= -0.69, 0.45$; cottontail, badger, grass, $\beta = -0.05$, 95% CI $= -0.54, 0.44$; cottontail, swift fox, grass, $\beta = -0.61$, 95% CI $= -1.90, 0.53$).

We expected cottontails to occupy areas with more cover and rely more on vegetation structure to hide from predators, though failed to detect a relationship between cottontail occupancy and vegetation height when predators were present (cottontail, coyote, vegHeight, $\beta = 0.02$, 95% CI $= -0.63, 0.72$; cottontail, badger, vegHeight, $\beta = -0.07$, 95% CI $= -0.67, 0.52$; cottontail, swift fox, vegHeight, $\beta = 0.58$, 95% CI $= -0.31, 1.53$) or absent (cottontail, no predator, vegHeight, $\beta = 0.01$, 95% CI $= -0.71, 0.68$). The proportion of prairie landcover surrounding sites had a similar positive effect for cottontails when all three predators were absent (cottontail, no predator, prairie, $\beta = 0.43$, 95% CI $= -0.11, 0.99$; Figure 6, Appendix S1: Table S4), and with coyotes (cottontail, coyote, prairie, $\beta = -0.30$, 95% CI $= -0.86, 0.23$) and badgers (cottontail, badger, prairie, $\beta = -0.08$, 95% CI $= -0.60, 0.45$). However, there was no effect when swift foxes were present (cottontail, swift fox, prairie, $\beta = 0.03$, 95% CI $= -0.66, 0.74$).

Overall, detection probabilities of jackrabbits ($p = 0.47$, 95% CI $= 0.43, 0.51$) and cottontails ($p = 0.52$, 95% CI $= 0.48, 0.56$) where greater than detection probabilities of all predators (Appendix S1: Table S2). We estimated the effect of vegetation height on detection and found a strong negative association across all predators (coyote: $p = -0.24$, 95% CI $= -0.33, -0.16$, swift fox: $p = -0.80$, 95% CI $= -1.12, -0.48$) and prey species

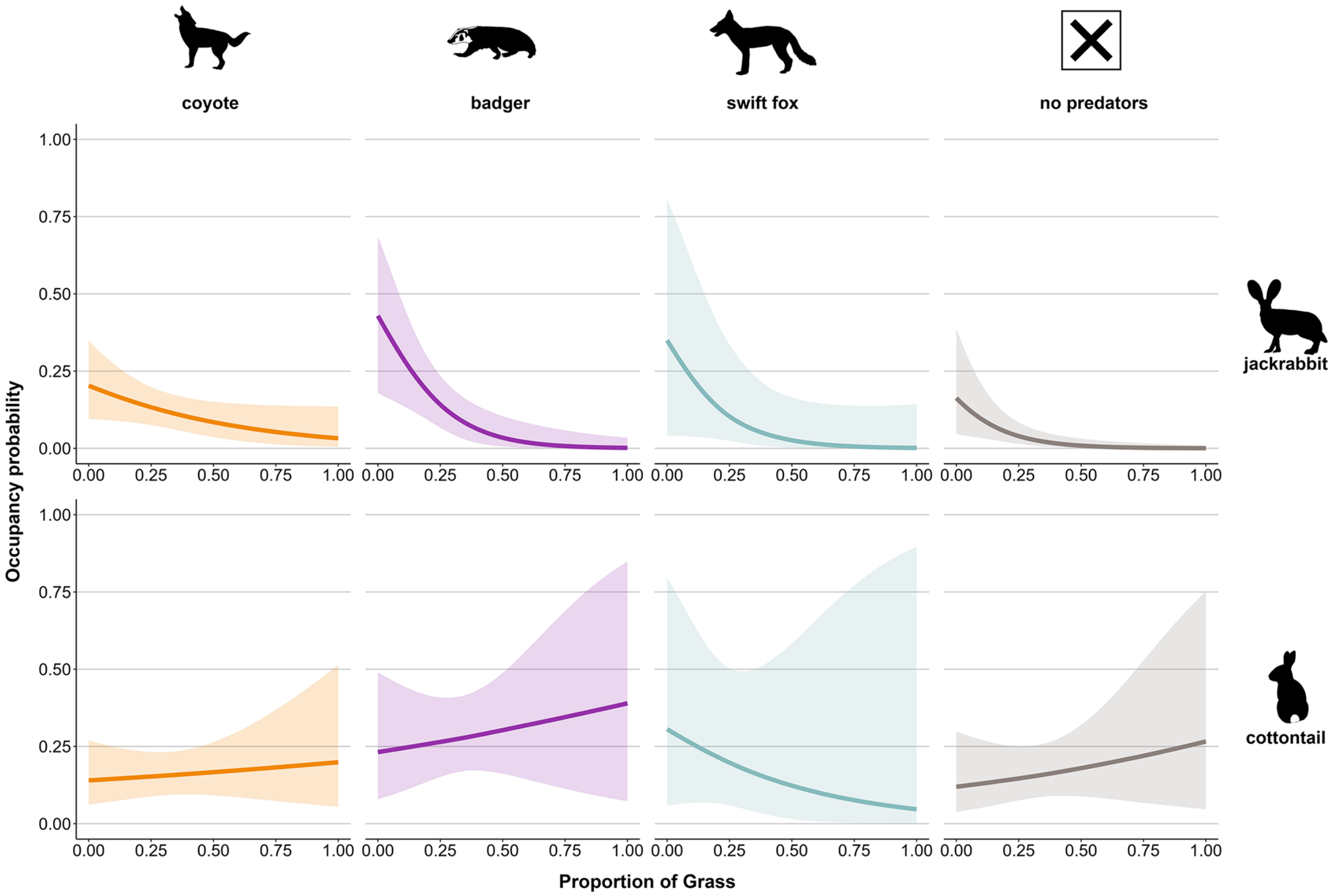


FIGURE 4 Response curves for lagomorph (top row, black-tailed jackrabbit; bottom row, eastern cottontail rabbit) occupancy probability when coyote, American badger, and swift fox, and when predators are absent (right), over the proportion of grasses (local-scale covariate).

(jackrabbits: $p = -0.29$, 95% CI $= -0.46$, -0.12, cottontail rabbits: $p = -0.17$, 95% CI $= -0.34$, 0.00), except for badgers (badger: $p = -0.02$, 95% CI $= -0.13$, 0.09) where we failed to find an effect (Figure 7). Proportion of prairie had a negative effect on cottontail and badger detection probability ($p = -0.22$, 95% CI $= -0.41$, -0.05, $p = -0.51$, 95% CI $= -0.63$, -0.38, respectively) and a slight negative effect for swift foxes ($p = -0.26$, 95% CI $= -0.50$, -0.03). However, we failed to detect a relationship between proportion of prairie and jackrabbits ($p = -0.06$, 95% CI $= -0.20$, 0.07) or coyotes ($p = -0.04$, 95% CI $= -0.12$, 0.05; Figure 7). A full account of the model's parameter distributions can be found in Appendix S1: Table S4 and Figure S2.

Risky times: Predator–prey temporal activity partitioning

Our third hypothesis posits prey reduce activity during peak predator times where predation risk would likely be at its greatest (Hypothesis 3, Figure 1). All species were predominantly nocturnal (Figure 8) except cottontail rabbits which displayed a peak of activity around 1000. Predators had different nocturnal activity peaks with coyotes and badgers having increased activity around 2200, and swift foxes at 0100. Generally, predators and prey had a high overlap of temporal activity ($\Delta_4 > 0.7$; Appendix S1: Table S3). The greatest overlap in activity between jackrabbits and a predator was coyotes ($\Delta_4 = 0.911$, 95% CI $= 0.886$, 0.928) and badgers ($\Delta_4 = 0.923$, 95% CI $= 0.898$, 0.951), and similarly for cottontails and coyotes ($\Delta_4 = 0.829$, 95% CI $= 0.792$, 0.840) and badgers ($\Delta_4 = 0.846$, 95% CI $= 0.808$, 0.866). The lowest overlap in activity between jackrabbits and a predator was swift foxes ($\Delta_4 = 0.797$, 95% CI $= 0.724$, 0.823), and similarly for cottontails and swift foxes ($\Delta_4 = 0.846$, 95% CI $= 0.808$, 0.866).

DISCUSSION

We assessed the relative influences of predator presence and habitat structure on habitat and time use by prey

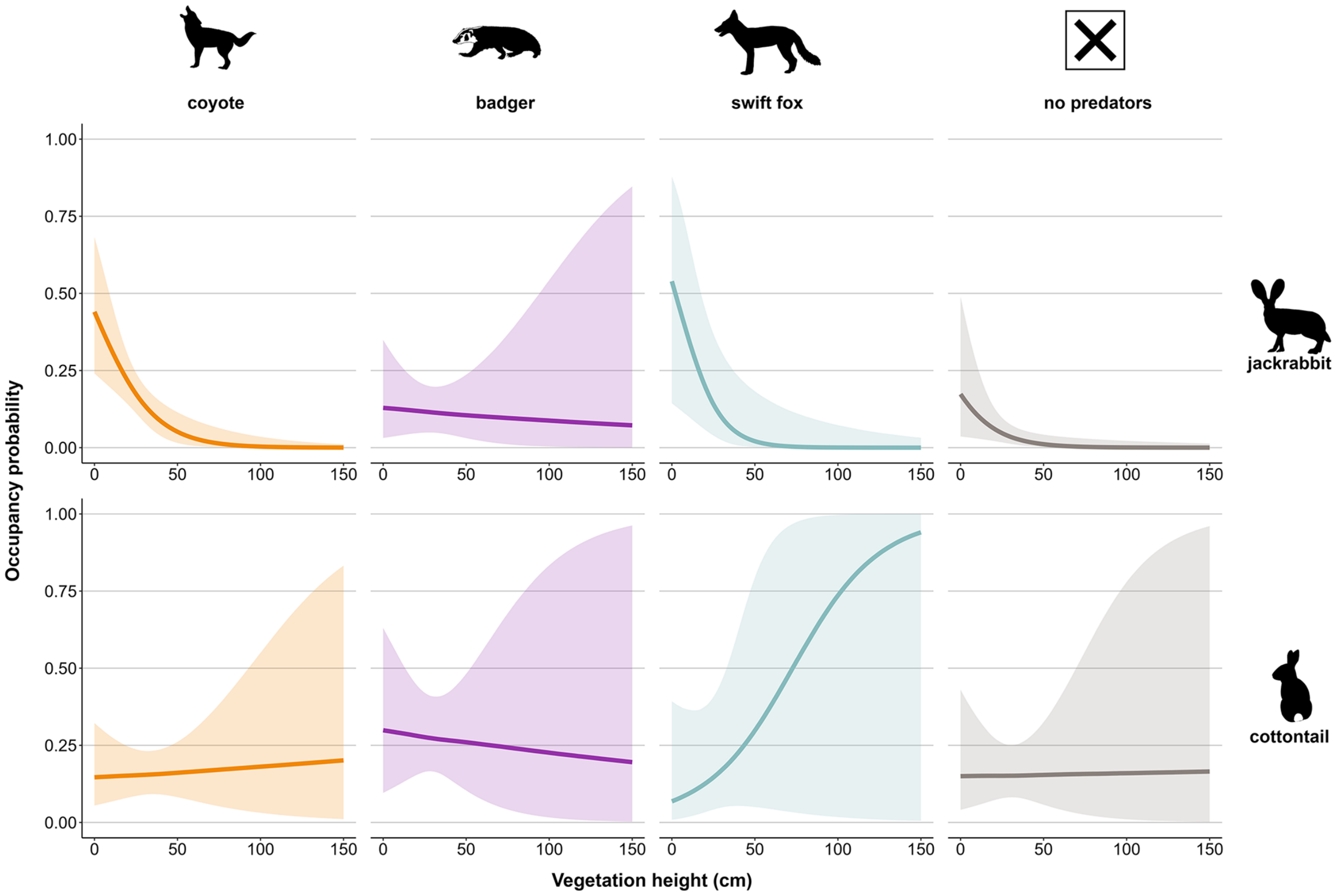


FIGURE 5 Response curves for lagomorph (top row, black-tailed jackrabbit; bottom row, eastern cottontail rabbit) occupancy probability when coyote, American badger, and swift fox are present, and when predators are absent (right), over vegetation height (in centimeters; local-scale covariate).

in a multi-predator and human-dominated landscape. We found that co-occurrence patterns between prey and predators vary spatially such that jackrabbits decreased habitat use in forb-rich areas regardless of predators being absent or coyotes or badgers being present, but cottontails increased use of areas rich in forbs regardless of predator presence. Jackrabbits decreased their use of areas with limited visibility (i.e., high vegetation height) when no predator was present or with coyotes or swift foxes being present and increased their use of areas of open areas (i.e., prairies) with and without predators being present. Similarly, cottontails, used open areas regardless of predators' presence or absence. Prey and predators were nocturnal, and their activity overlapped considerably. Taken together, these results provide compelling evidence that in a predator-rich system, lagomorphs show a proactive response to predation risk where jackrabbits use habitat to reduce predation risks and cottontails will use habitat that maximizes forage access regardless of predator activity.

Risky places: Lagomorph space use under constant predation risk

Areas with greater proportions of forbs/grasses are rich in forage for lagomorphs (Bond et al., 2001; Boyd & Henry, 1991; Flinders & Crawford, 1977; Marín et al., 2003; Sparks, 1968) but our results reveal the importance of these areas are different for each prey species. Interestingly, jackrabbits and cottontails used areas rich in food resources despite the presence of coyotes and badgers which would likely be risky. Jackrabbit habitat use decreased in areas rich in forbs and grasses regardless of predator presence indicating they may be relying on other food resources in this agro-prairie ecosystem. For example, in southern Idaho cultivated crops are a large part of the spring and summer diet for jackrabbits (e.g., wheatgrass, barley; Fagerstone et al., 1980). Cottontails increased their use of forb-rich areas despite predators being present or absent, which suggests that cottontails will forage similarly in areas where food opportunities are ideal despite the risk

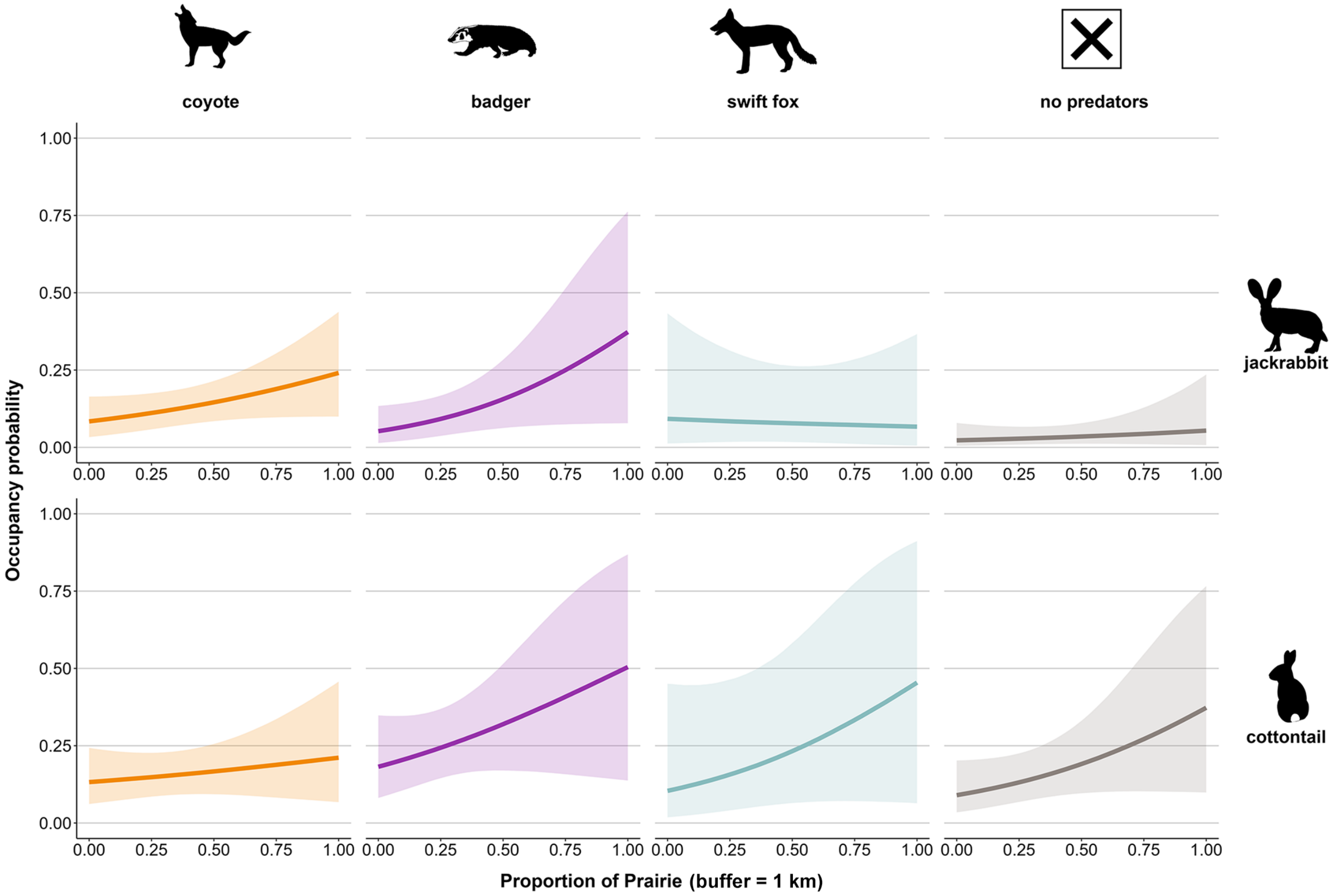


FIGURE 6 Response curves for lagomorph top row, black-tailed jackrabbit; bottom row, eastern cottontail rabbit) occupancy probability when coyote, American badger, and swift fox are present, and when predators are absent (right), over the proportion of prairie inside a 1-km buffer (landscape covariate).

of predators' presence. Our results contradict the landscape of fear hypothesis which states that prey species will avoid risky foraging areas. However, occupancy is a relatively coarse metric and lagomorphs in our study area are likely responding to richer sources of information, such as the local abundance of predators. Future studies assessing fine-scale habitat selection decisions by lagomorphs across gradients of predator activity and abundance would be helpful to address the influence of predations risks on habitat selection.

We used vegetation height at the local scale and amount of prairie landcover at the landscape scale as proxies for shelter and open areas (habitat structure) which may be used by lagomorphs to avoid predators. As expected, jackrabbit occupancy was lower in areas where vegetation height was greater when coyotes or swift foxes were present. There was a slight negative effect when predators were absent, but the effect was not as strong as with both predators. This result is likely because prey species like jackrabbits, who often flee from predators to avoid predation (Arias-Del Razo et al., 2012; Hoffmeister, 1986), will avoid riskier landscapes where vegetation may restrict line-of-sight (Lechleitner, 1958). Therefore, jackrabbits are likely to use areas with better visibility to detect predators more easily. Jackrabbits likely make trade-offs regarding habitat use at multiple scales. At a local scale, jackrabbits are using areas with greater visibility because they are perceived as less risky, but at a larger scale their response may be different.

For both lagomorphs, the amount of prairie landcover at a landscape scale positively affected habitat use but the magnitude of this relationship changed due to the presence of predators. Jackrabbits are increasingly using open areas (i.e., increased amount of prairie) when coyotes and badgers are present but when all predators are absent jackrabbits use of open areas does not vary. Just as jackrabbits avoided areas with greater vegetation cover, these results provide further evidence that jackrabbits may be selecting areas where it is easier to escape from predators because there is increased visibility and openness. Coyotes, for example, are coursing predators with a high movement ability that often forage in flat open

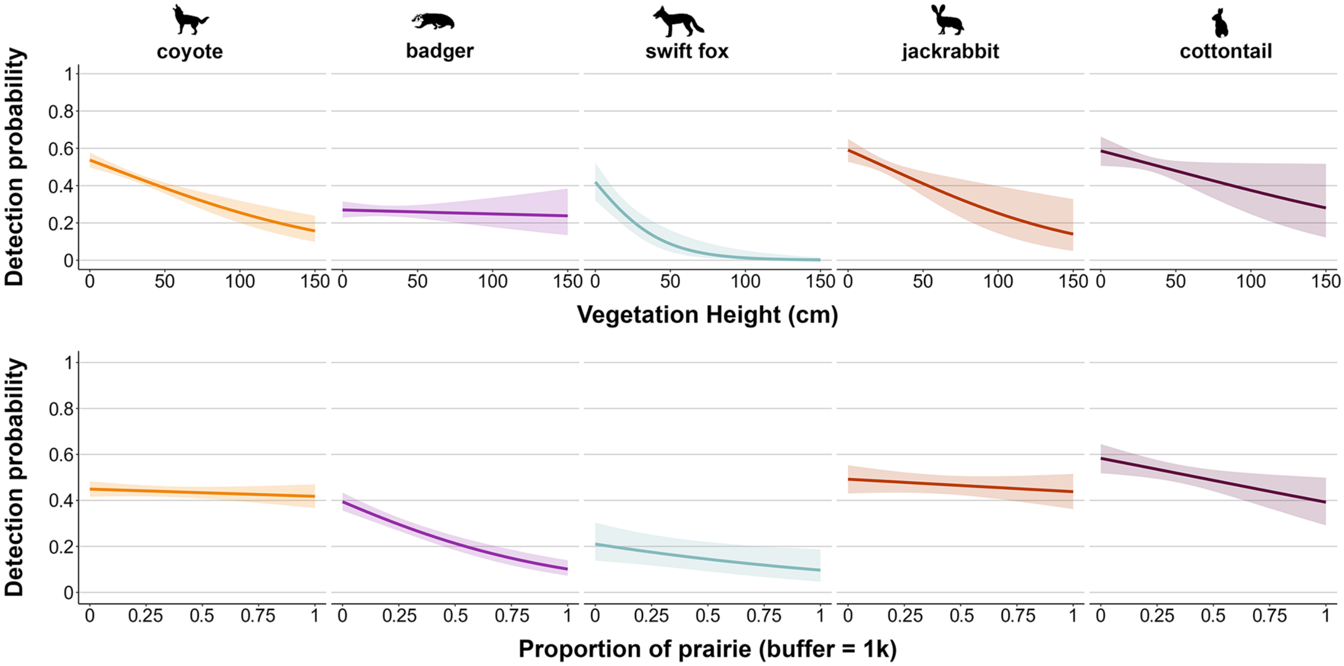


FIGURE 7 Response curves for species detection probability with varying levels of vegetation height and proportion of prairie inside a 1-km buffer. Species shown in order are coyote, American badger, swift fox, black-tailed jackrabbit, cottontail rabbit.

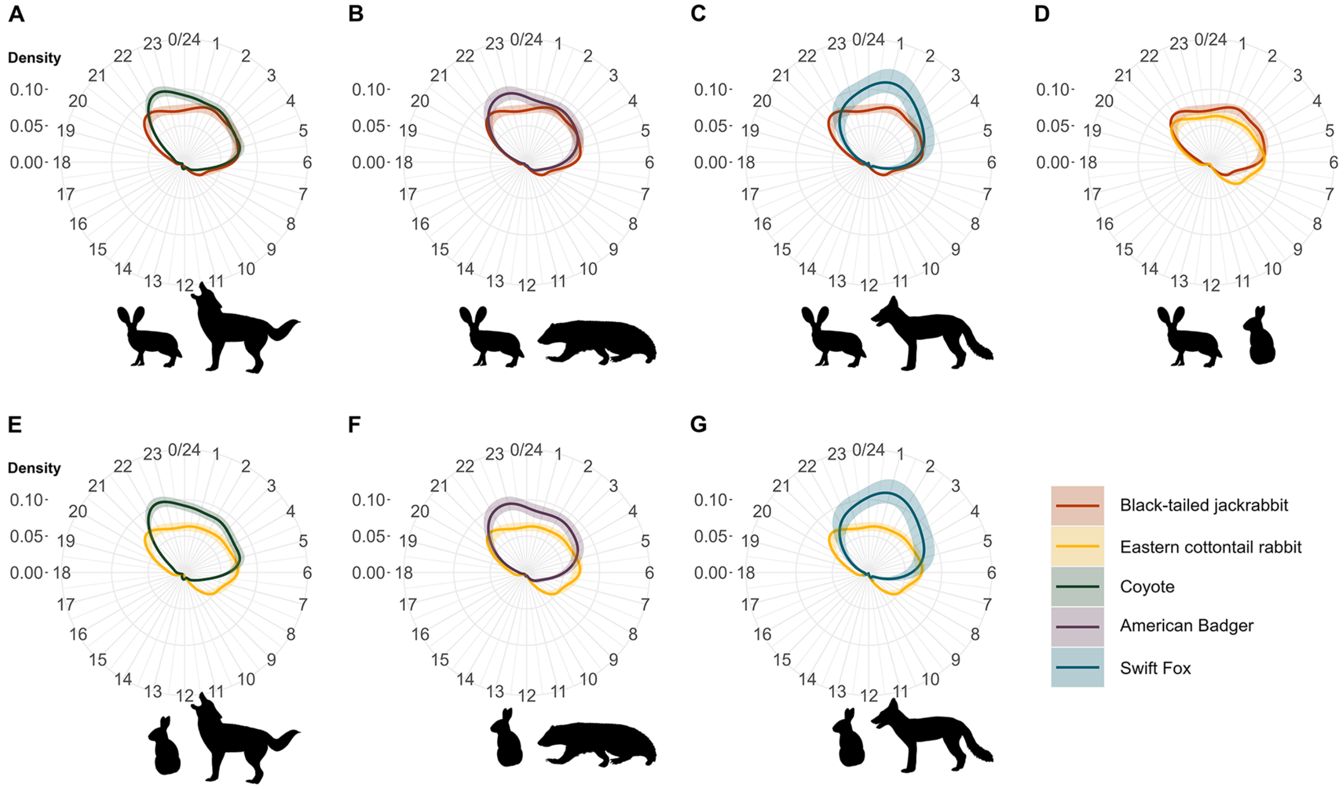


FIGURE 8 Daily activity patterns between lagomorphs and predators. (A) Black-tailed jackrabbit and coyote. (B) Black-tailed jackrabbit and American badger. (C) Black-tailed jackrabbit and swift fox. (D) Black-tailed jackrabbit and Eastern cottontail rabbits. (E) Eastern cottontail rabbits and coyote. (F) Eastern cottontail rabbits and badger. (G) Eastern cottontail rabbits and swift fox. The time of day is shown from 0000 to 2359 around each circle, and activity is measured by kernel density (shaded areas are 95% confidence intervals).

terrain (Bender et al., 2017; Bleich, 1999; Reddell et al., 2021), so areas surrounded by prairie (i.e., open areas) may be considered less risky by jackrabbits where they can rely on their speed and agility to escape predators. Vegetation height had no effect on cottontail habitat use regardless of the presence or absence of predators. However, cottontail's response to open areas (i.e., prairies) was positive when predators were absent or with coyotes or badgers present which suggest that cottontails are using open areas similarly in the absence of risk by the presence of predators or under constant predation risk. Cottontails may perceive prairies as rich in food resources and accessing with heightened vigilance when predators are present (Lima & Dill, 1990), and the non-consumptive effects predators have on prey may not be explained by fear alone. Additionally, cottontails escape tactics rely heavily on crypsis, concealment, and escape refuge where they remain immobile until predators leave the area, and only rely on running or speed as a last resort (Harrison, 2019; Wagnon et al., 2020) so they might increase vigilance and caution and rely on speed to avoid predators when navigating open areas under constant predation risk. Additionally, they may rely on being active in risky areas during predators' "down time" (Kohl et al., 2018).

Prairie ecosystems are the most altered biome worldwide (Samson & Knopf, 1994) and land conversion and agricultural practices are creating a variety of consequences including overall loss of prairie and isolation of prairie patches (Pogue & Schnell, 2001). While we did not assess the impact that human disturbance may have on predator–prey interactions, future research could assess whether co-occurrence patterns between predators and prey vary across agricultural systems. Such research could further elucidate the effects of humans on lagomorph's habitat use and therefore provide further information on ways in which human activities and human presence may be affecting lagomorphs' response to predation risk. We observed reduced habitat use by jackrabbits in areas rich in food resources which may be an indication that they are using other abundantly available areas as food resources, such as agricultural subsidies. The use of agriculture areas could lead to a potential ecological trap (Hale & Swearer, 2016) in which lagomorphs are forced to find alternative food resources in modified landscapes, especially in areas where predation risk may be constant. Such areas could alter lagomorphs predator avoidance ability and create an ecological trap (see Nawrocki et al., 2019). Additionally, areas that may seem rich in forage and safe from predators may offer other risks including human-wildlife conflict and pesticides.

Risky times: Predator–prey temporal activity

We hypothesized that prey would reduce their activity during peak predator activity given that predation risk would likely be at its greatest. We found all predators were mostly nocturnal, with coyotes and badgers having similar temporal activity with peaks of activity between 2200 and 2300. Similarly, lagomorphs were mainly nocturnal. However, our data partially supported our hypothesis of potential temporal disconnect between predators and prey during nocturnal hours. Jackrabbits increased activity at 2100, whereas coyotes and badgers had an initial peak of activity around 2200 and swift foxes around 0100. Cottontail rabbits increased activity at 2000 and then show another peak between 0600 and 1000, whereas coyotes decrease activity after 0500. Lagomorphs seem to be reducing predation risk by remaining active before or after peaks in predator activity. Similarly, coyotes throughout the Chihuahuan Desert in Mexico showed an early morning peak of activity (0700–1000), but lagomorphs had peaks of activity much earlier (0400–0700) (Arias-Del Razo et al., 2011). However, the full 24-h period is not likely available for lagomorphs in some areas. For example, in semiarid environments, lagomorphs tend to remain inactive during the day to avoid high daytime temperatures (Arias-Del Razo et al., 2011; Villafuerte et al., 1993). Therefore, lagomorphs must try their best to temporally avoid predators at night-time during their active hours.

The risky times hypothesis states that local predator presence/absence during a short time frame (e.g., 24-h period) can provide an insight into anti-predator behavior but can underestimate risk due to non-detection (Moll et al., 2017). Therefore, our results should be interpreted with caution regarding immediate prey responses to predation risk. However, given that risky times metrics are recommended to be measured at finer scales (i.e., daily periods), our results offer a general view of both prey and predators 24-h diel patterns, where despite being nocturnal there are fine-scale avoidances as listed above.

While we did observe variation in co-occurrence patterns between predators and prey, it is important to recognize that the patterns we estimated may or may not correspond with a true ecological biotic interaction (Blanchet et al., 2020). Further, other environmental variables not included in the model may be important, for example, if species covaried along an unmodelled environmental gradient (Fidino et al., 2019). In our study, there could be an effect from an anthropogenic activity on both predators' and species' habitat use that we did not account for in the model. It is worth noting that some of the variables included in the model likely negatively covary with standard anthropogenic features (e.g., impervious cover), but nevertheless, additional research is needed to determine if the presence of humans could modulate co-occurrence (Berger, 2007; Muhly et al., 2011). Another limitation of our study is that we did not consider other predators for lagomorphs (i.e., raptors). Open areas (i.e., prairies) offer increased visibility for aerial predators like owls and raptors, which could influence the way lagomorphs perceive risk (Nawrocki et al., 2019). Unfortunately, camera traps are not an ideal method to survey aerial predators, and as such our study design made it impossible to investigate such patterns. Nevertheless, our model furthers our understanding of lagomorph habitat use in a rapidly changing landscape under constant mammalian predation rate.

CONCLUSIONS

Our results suggest that in predator-rich landscapes, lagomorphs tend to respond proactively assessing risk over time and using habitat to maximize forage (cottontails), and minimize predation risk (jackrabbits). Further, habitat use is species specific and modulated by the presence of different predators and we found most support for coyote and badger influencing lagomorph habitat use than swift fox. We found lagomorph-reactive responses to predators at a fine scale at night by alternating their peaks of activity, but we recommend using activity data at an even finer scale (i.e., instantaneous observations). Additionally, we presented here a hierarchical occupancy model for potentially interacting species with multiple dominant predators (coyote, badger, swift fox) and their influence on two subordinate prey species (jackrabbit and cottontail) across environmental gradients. While Waddle et al. (2010) developed a hierarchical occupancy model for interacting species, our model adds multiple dominant and subordinate species and includes an autologistic term to account for temporal correlation between sampling periods (2018–2020). However, even though our results are clear, we encourage future studies to incorporate other covariates (i.e., effects of crops) and include effects of other potential known predators in the system (e.g., raptors).

AUTHOR CONTRIBUTIONS

Gabriela Palomo-Munoz and Adam A. Ahlers conceived the framework. Adam A. Ahlers and Ty J. Werdel designed the sampling study. Ty J. Werdel and Colleen W. Piper collected the data. Gabriela Palomo-Munoz and Mason Fidino designed the model and analyzed the data. Gabriela Palomo-Munoz and Mason Fidino led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Palomo-Munoz, 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.11110386.

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SUPPORTING INFORMATION

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

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