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Using multiple scales of movement to highlight risk–reward strategies of coyotes (*Canis latrans*) in mixed-use landscapes

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Abstract

Many wildlife species vary habitat selection across space, time, and behavior to maximize rewards and minimize risk. Multi-scale research approaches that identify variation in wildlife habitat selection can highlight not only habitat preferences and risk tolerance but also movement strategies that afford coexistence or cause conflict with humans. Here, we examined how anthropogenic and natural features influenced coyote (*Canis latrans*) habitat selection in a mixed-use, agricultural landscape in Mendocino County, California, USA. We used resource selection functions and hidden Markov models to test whether coyote selection for anthropogenic and natural features varied by time of day or by behavioral state (resting, foraging, and traveling). We found that coyotes avoided development, but, contrary to our expectations, coyotes selected for roads, agriculture, and areas with risk of human encounter and rifle use regardless of diel period or behavioral state. While traveling, coyotes increased selection for roads and avoided ruggedness, indicating that unpaved roads may enhance connectivity for coyotes in mixed-use landscapes. Finally, we found that coyotes selected for mountain lion habitat when resting and at night, signifying that risk from natural predators was not a factor in habitat selection at coarse scales. Coyote habitat selection for places and times associated with human activity, without variation across scales, signals a potential for conflict if coyotes are perceived by people as a nuisance.

KEYWORDS

behavioral partitioning, *Canis latrans*, habitat selection, hidden Markov model, humans, reward, risk, temporal partitioning

INTRODUCTION

Human activity has modified landscapes worldwide, contributing to wildlife range contractions and decline (Ceballos et al., 2017). Yet, some species successfully navigate human-modified environments by changing their behavior to exploit anthropogenic food resources (Geffroy et al., 2020; Newsome et al., 2015; Sih et al., 2011). Behaviorally flexible species can even achieve robust populations in human-modified landscapes

(Bateman & Fleming, 2012) inciting conflict with humans (i.e., crop damage, property damage, loss of livestock, and injury; Richardson et al., 2020; Treves et al., 2006) or causing outsized change to community structure via predation (Geffroy et al., 2015) or interference competition (Shochat et al., 2010). Efforts to understand how wildlife balance the use of anthropogenic and natural features remain critical to wildlife management and coexistence with people, especially as humans continue to alter landscapes around the world.

Animal survival depends on the ability to maximize reward, while reducing risk (Charnov, 1976; Lima & Bednekoff, 1999). Rewards are resources that increase animal fitness (e.g., forage, mates), while risk represents the challenges an animal faces (e.g., energy expenditure, predation; Sih, 1980). In human-modified landscapes, wildlife may encounter a novel portfolio of risks and rewards such as agriculture, food subsidies (Oro et al., 2013), infrastructure, and intensification of human activities such as hunting and recreation (Schell et al., 2021), in addition to the risks and rewards with which they evolved. This is especially true in mixed-use landscapes, characterized by mosaics of low-density development, agriculture, and wildlands. Because mixed-use landscapes experience a low to moderate level of disturbance, these areas can retain natural predators, competitors, and prey, alongside a variety of anthropogenic risks and foods (Ferreira et al., 2018; Gascon et al., 1999; Kremen & Merenlender, 2018). In mixed-use landscapes, the choice between anthropogenic and natural landscape features can reveal an animal's risk tolerance, habitat preferences, and potential constraints on an animal's behavior.

Analyzing animal movement by time and behavioral state have illuminated vast new understandings of how animals navigate landscapes. Animals that navigate human-modified landscapes have been found to alter diel activity, space use, behavior, or diet in response to cues, to take advantage of rewards and avoid spatial or temporal risks (Gaynor et al., 2018; Geffroy et al., 2020; Smith et al., 2015; Tucker et al., 2018). For example, lions (*Panthera leo*) avoided areas near livestock pens during the day, but selected for livestock areas at night to exploit prey when the risk of encountering humans was low (Suraci et al., 2019). Animals can also modify their behavior to navigate human-modified landscapes. For instance, African wild dogs (*Lycaon pictus*) selected for roads while running to maximize ease of travel, but avoided roads when walking, resting, and denning to minimize time spent in locations with vehicles (Abrahms et al., 2016). With the onset of the global COVID-19 pandemic in 2020, a decrease in diurnal human activity resulted in increased diurnal wildlife activity in both highly developed and undeveloped landscapes (Anderson et al., 2023; Gordo et al., 2021; Schofield et al., 2021). Thus, factors regulating fitness, like the risk of encountering humans, non-human predators, or food resources, should be important in shaping animal risk perception and habitat selection (Rettie & Messier, 2000).

Coyotes (*Canis latrans*) may display strategies of behavioral or temporal partitioning to manage risks and rewards posed by anthropogenic landscape features. Although coyotes are known to use spatial and temporal avoidance to successfully navigate landscapes with people (Atwood et al., 2004), including dense urban areas (Breck et al., 2019; Gehrt et al., 2011), coyote habitat selection in mixed-use agricultural landscapes where they predominantly occur is less understood. In some cases, food availability is the primary factor driving coyote habitat selection (Mills & Knowlton, 1991) and density (Fedriani et al., 2001). For instance, Youngmann et al. (2022) found that coyotes selected for agricultural fields while foraging. Others have found that coyotes only use agriculture during seasons of scarcity (Cherry et al., 2016), or that coyotes avoid agricultural fields and development altogether, instead selecting dense vegetation fragments (Atwood et al., 2004; Gehrt et al., 2011). Human-related risk factors, including vehicles, domestic dogs, and human presence (Breck et al., 2019), may drive how, when, or whether coyotes use anthropogenic features versus natural areas. For instance, in some mixed-use landscapes, landowners carry rifles to opportunistically remove coyotes in an effort to protect livestock and agricultural fields (T. McWilliams, personal communication, November 2020). Thus, while there are many lethal forms of coyote removal (i.e., trapping, poisoning), diurnal human encounter in open areas near roads or trails may pose a significant risk to coyotes. Last, natural predators may drive coyote habitat selection. For example, outsized fear of predation by mountain lions (*Puma concolor*) was found to drive coyote movement more than human presence, despite higher levels of human-caused mortality (Prugh et al., 2023). Ultimately, dissecting movement at multiple scales may reveal strategies for how coyotes can co-occur with humans, and highlight common risk responses associated with low to medium levels of development.

Here, we applied advances in GPS tracking and movement modeling to examine how anthropogenic and natural features influenced coyote (*C. latrans*) habitat selection across scales in a mixed-use, agricultural landscape in Mendocino County, California, USA. We hypothesized that coyotes would partition their use of anthropogenic features to maximize rewards while minimizing risk. Specifically, we expected that coyotes would avoid anthropogenic features during the day (including roads, development, agriculture, grasslands with livestock, and areas with risk of lethal removal by rifle) but select for these features at night to exploit food rewards and minimize human encounters. If coyote selection for anthropogenic features changed by diel period, it would indicate a behaviorally flexible response to a perceived risk of diurnal human activity. Additionally, we hypothesized coyotes would avoid anthropogenic features by behavioral state. We expected coyotes to avoid roads, development, agriculture, grasslands with livestock, areas with risk of lethal removal by rifle (hereafter "rifle encounter risk") while foraging and resting, but select for these features while traveling to minimize human encounters. If selection for anthropogenic features changed by behavioral state, it would reveal behavioral flexibility in response to constraints on when or how coyotes access anthropogenic features.

Finally, in addition to human-related risks, natural risks and rewards may drive aspects of coyote habitat selection. We anticipated that coyotes would avoid habitats with a high risk of encountering mountain lions (*P. concolor*) (hereafter "mountain lion encounter risk") because coyotes comprise 30% of mountain lion diet in this area (Sacks, 1996) and can exhibit outsized avoidance of mountain lions (Prugh et al., 2023). Specifically, we expected coyotes would avoid mountain lion encounter risk while resting, and at night when mountain lions in the area are most active (Gaynor et al., 2022). Vegetation and terrain may also influence coyote habitat selection. We expected coyotes would select woodlands for cover, and grasslands (with livestock resources) at night to avoid humans. We also expected coyotes would avoid rugged terrain during travel, but not while resting or foraging.

METHODS

Study area

We conducted this study in the Sanel Valley of Mendocino County, California (39°0′1.14 N, −123°4′45.86 W; Figure 1). The region is situated at the southern end of the Mayacamas mountains in the California Coast Range and is composed of a mosaic of rural agriculture, livestock pasture, residential areas, and wildlands dominated by oak savanna and chaparral habitat. The primary agricultural products in the valley are wine grapes and pears, while livestock operations for cattle and sheep are situated in grasslands in the surrounding hillsides. The valley is bisected by a major road corridor

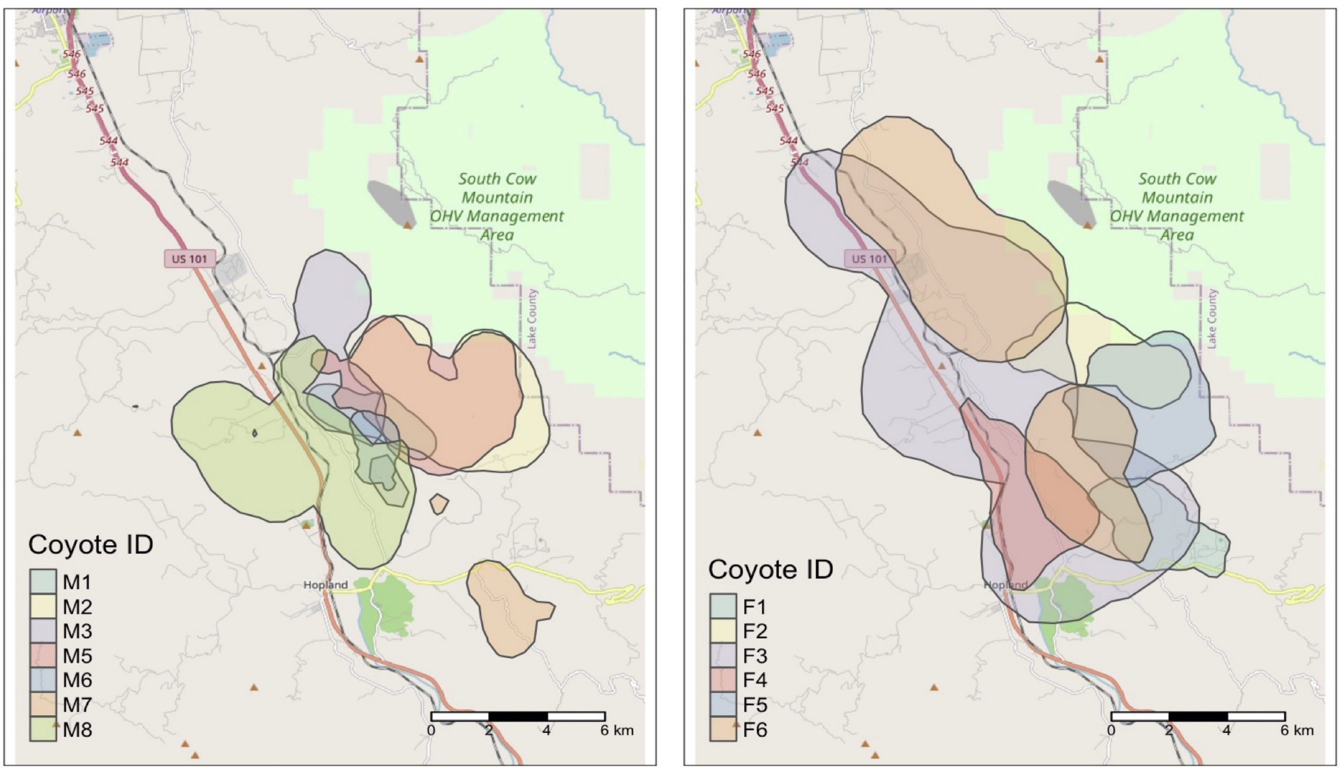

FIGURE 1 Study area in the Sanel Valley, Mendocino County, California, USA. Maps depict 95% kernel utilization home range for male (M) and female (F) coyotes (*Canis latrans*; $n = 13$) derived from hourly GPS locations for a total of 266 unique days (mean 60 days per individual) between late November and early March of 2020–2021, 2021–2022, and 2022–2023.

(US 101) on the banks of the Russian river and flanked by 25,000 ha of Bureau of Land Management land with Mendocino National Forest to the north. Coyote diet in the area consists of native prey species, including lagomorphs, rodents, birds, insects, reptiles, manzanita berries, as well as livestock and domestic fruit (Sacks, 1996). The region is also home to a host of potential coyote predators and competitors, including mountain lion (*P. concolor*), black bear (*Ursus americanus*), bobcat (*Lynx rufus*), and gray fox (*Urocyon cinereoargenteus*) (Gaynor et al., 2022). The climate is typically Mediterranean, with mild rainy winters and hot dry summers.

In this study area, humans often hunt and trap coyotes or use guardian dogs to prevent crop raiding and livestock depredation. While cattle are too large to be prey species to coyotes, coyotes pose the greatest threat to sheep and lambs (McInturff et al., 2021). One study on a Mendocino County sheep ranch estimated that up to 5% of lambs were killed annually by coyotes (Conner et al., 1998). Through Mendocino County's contract with the United States Department of Agriculture's (USDA) Wildlife Services, the county was called upon to conduct 4119 coyote removals between 1997 and 2017, using poison, leg hold traps, and snares (Blackwell, 2021). The County voted to end the Wildlife Services contract with the USDA in 2021, however, ranchers and landowners continue to protect livestock by trapping and opportunistically shooting coyotes on sight, from vehicles or trails. While individual statistics are not available, it is estimated that sheep ranches may kill 20–30 coyotes annually (T. McWilliams, personal communication, November 2020).

Data collection

All coyotes were live-captured at the University of California's 2169-ha Hopland Research and Extension Center, fitted with GPS collars (Vertex Lite 1C, Vectronic Aerospace, Iowa, USA), and released at the point of capture. All captures were conducted using cable snares and processed within a 30-min period in accordance with the protocol approved by the Institutional Animal Care and Use Committee at the University of California Berkeley (protocol number AUP-2016-04-8723-2) and a capture permit from the California Department of Fish and Wildlife. No complications were observed in any of the collared individuals.

The GPS collars recorded spatial locations hourly. Movement data were obtained for 14 coyotes (six females and eight males) across three field seasons from late November to early March of 2020–2021, 2021–2022, and 2022–2023. We excluded one adult male from the analysis due to death five days after capture, likely due to a vehicle collision. To reduce possible post-capture behavioral bias, we excluded the first three days of GPS data for all individuals. Ultimately, 13 coyotes were tracked for a total of 266 unique days (mean 60 days per individual).

Environmental data

We examined coyote habitat selection for anthropogenic and natural features, including development, roads, agriculture, rifle encounter risk, mountain lion encounter risk, terrain, and vegetation type (Table 1).

To obtain data on covariates, we used the 2016 National Land Cover Dataset (NLCD) to reclassify development, secondary and tertiary roads, and agriculture into distance rasters, and to obtain vegetation type at 30-m resolution (Dewitz, 2016). We chose the 2016 NLCD because it most closely resembled the vegetation cover of the study area in the 2020–2023 seasons. The 2019 NLCD (Dewitz, 2019) was not used because the 2018 River Fire burned large sections of chaparral and grassland, and the 2016 NLCD was more representative of the chaparral density in 3–4 years of post-fire

TABLE 1 Predicted relationship of coyote (*Canis latrans*) habitat selection with anthropogenic and natural features in the Sanel Valley, Mendocino County, California, USA.

Covariate	Description	Predicted relationship
Development	Distance to low, medium, high development; highway	Avoid
Road	Distance to secondary and tertiary roads	Select (night, travel)
Agriculture	Distance to agriculture	Select (night, forage)
Rifle encounter risk	Open viewshed, proximity to roads, ruggedness (intercepts from Gaynor et al., 2022)	Select (night, forage)
Mountain lion encounter risk	Shrubland, far from agriculture (intercepts from Gaynor et al., 2022)	Avoid (night)
Ruggedness	Terrain ruggedness index	Avoid (travel)
Vegetation type	Grassland Woodland Shrubland	Select (night) Select Avoid

vegetation growth. To measure terrain ruggedness, we used the NASA SRTM Digital Elevation 30 m (Farr et al., 2007), and calculated the topographic ruggedness index, which reflects the elevational difference between eight adjacent cells of a digital elevation model (Riley et al., 1999).

Our best approximation of mountain lion and human-related mortality risk was to estimate a risk map where mountain lions or human rifle use may occur. Landowners and ranchers that conduct coyote control typically carry rifles in their vehicles and shoot coyotes opportunistically when encountered. Thus, areas with the potential for visual detection by humans (i.e., close to roads or trails, and in open viewsheds) may elicit a coyote risk response. We modeled rifle encounter risk across the region using the spatial predictors of proximity to roads, open viewshed, and ruggedness, as informed by the coefficient values from a local study on hunter behavior (Gaynor et al., 2022). We excluded areas within 137 m of buildings to reflect local gun laws (Mendocino County Code of Ordinances, 1974). While other forms of coyote removal (e.g., trapping, poisoning) might also influence coyote habitat selection, these would present distinct risk cues (i.e., fencing, snares, chemical containers, smells). Similarly, we modeled the risk of mountain lion encounter in the study area with the results of a nearby camera trap study (Gaynor et al., 2022), using the top model coefficients (distance to agriculture and high elevation) as spatial predictors for mountain lions across our study region.

All environmental covariates were centered and scaled (Appendix S1: Figure S1). We ensured that there was no pairwise collinearity ($|r| < 0.7$; Dormann et al., 2013) among environmental covariates using Pearson correlation coefficients (Appendix S1: Table S1). We extracted covariates to coyote spatial locations using the "raster" package in R (Hijmans et al., 2013).

Behavioral segmentation

To determine whether coyote habitat selection varied by behavioral state, we used hidden Markov models (HMMs) to label GPS data with three ecologically relevant behavioral states: resting, foraging, and traveling (e.g., Abrahms et al., 2016). HMMs are a class of sequence-dependent models that use an observed process to infer an unobserved, underlying state process (Langrock et al., 2012). We developed HMMs using turning angle (the angle between locations) and step length (the distance between locations) between GPS fixes within the "moveHMM" package in R (Michelot & Langrock, 2016). To maximize the likelihood of the data fit, we iterated 25 models from a randomized set of plausible parameters for each behavioral state (Appendix S1: Table S2). We chose the model with the smallest negative log-likelihood and assigned the most likely sequence of states to each individual track using the Viterbi algorithm (Zucchini et al., 2017). GPS points were then segmented into resting, foraging, and traveling datasets to examine differences in habitat selection by behavior.

Habitat selection modeling

To estimate the influence of environmental variables on coyote habitat selection, we fit single-season resource selection functions (RSFs) to each individual's home range (i.e., third-order selection; Johnson, 1980). We fit three types of RSFs for each coyote home range to directly compare habitat selection using (1) the full dataset, (2) behavioral state datasets, and (3) diel period datasets. Behavioral state (i.e., resting, foraging, and traveling datasets) was derived from aforementioned HMMs, while day-night datasets were segmented using the local, daily sunset and sunrise times with the "lubridate" package in R (Grolemund & Wickham, 2013). To generate the RSFs, we obtained used points and available points from within 95% kernel home range polygons of each individual, using the "kernelUD" function in the "adehabitatHR" package in R (Calenge, 2006; R Core Team, 2022). For each RSF, we randomly generated five times as many available points as used points to reduce bias (Appendix S1: Table S3; Northrup et al., 2013; Stears et al., 2019).

We used generalized linear mixed effects models with a binomial error distribution and log-link function to model coyote habitat selection for development, roads, terrain ruggedness, agriculture, rifle encounter risk, and mountain lion encounter risk. We included random intercepts of coyote ID in the models to account for individual differences in sample size and resource availability within animal home ranges (Hebblewhite & Merrill, 2007). We estimated beta coefficients and calculated odds ratios (OR) for each model and estimated 95% CIs. We identified differences in habitat selection between models as being estimates with non-overlapping 95% CIs. This modeling approach allowed us to compare how selection for covariates differed between resting, foraging, and traveling datasets and the full model, as well as how selection differed between day and night datasets and the full model. We fit a separate generalized linear mixed effects model (logistic) to examine coyote habitat selection for vegetation type, given that shrubland was correlated with mountain lion encounter risk (see Appendix S1). We ensured that there was no multicollinearity among the predictor variables within each model by conducting a variance inflation factor analysis (Appendix S1: Table S4). Finally, to validate whether it was appropriate to include all seasons of collared coyotes in the same model, we tested the influence of collaring year on the covariates in the full model, by using collaring year as a nested random effect.

RESULTS

Behavioral state allocation

We found that the top HMM adequately estimated three state distributions for coyote foraging, resting, and traveling, using the step length and turning angle distributions of GPS points (Appendix S1: Figure S2). The traveling state was associated with longer step lengths and turning angles centered on 0 (i.e., directed movement), whereas resting was associated with shorter step lengths and wide turning angles (i.e., undirected movement) and foraging step lengths and turning angles were inbetween (Appendix S1: Figure S2). All iterated models converged with little variation between models (maximum log likelihood = 152,963.6, mean = 149,767.4, SD = 2259.1, $n = 25$). We found that, on average, coyotes spent 41% of time resting, 33% foraging, and 26% traveling each day (Figure 2). There was little variation in activity budget between collaring years, except that in 2022–2023 coyotes exhibited significantly more resting than foraging or traveling (ANOVA; $F_{2,10} = 19.04$, $p < 0.001$; post hoc Tukey test; $p < 0.01$). This variation in resting was due to an individual difference in activity budget for a single coyote in 2022–2023. Overall, there was a tendency to increase resting behavior at night (18:00–0:00),

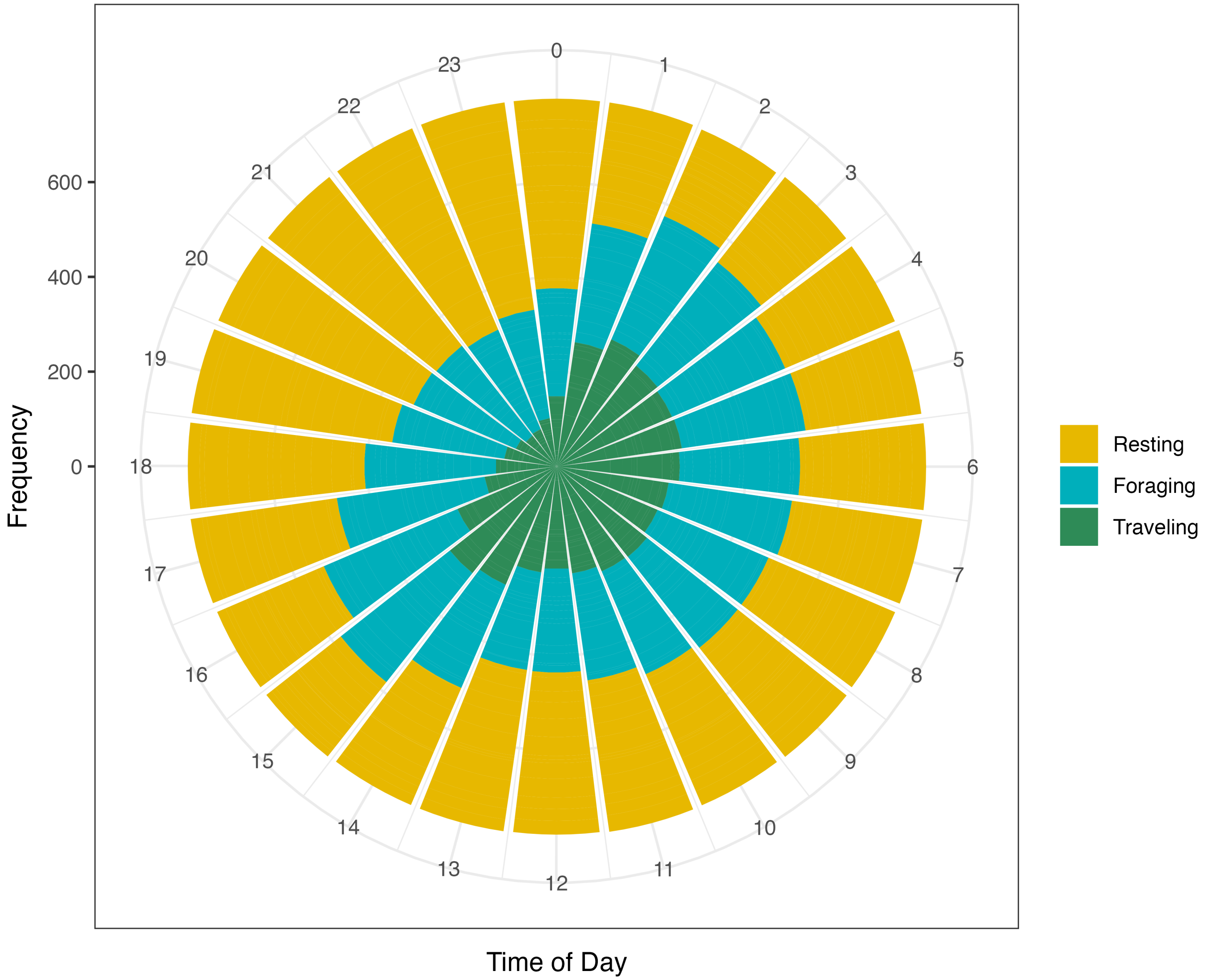

FIGURE 2 Diel state-activity budget for resting, foraging, and traveling behavior for coyotes (*Canis latrans*; $n = 13$) from the Sanel Valley, Mendocino County, California, USA, from November–March of 2020–2023. The diel state-activity budget was estimated by the top hidden Markov model (maximum log likelihood = 152,963.6, mean = 149,767.4, SD = 2259.1, $n = 25$). Frequency indicates the number of GPS points over a period of 266 unique days (mean 60 days per individual).

and foraging and traveling behavior at pre-dawn (01:00–07:00) and in the late afternoon (14:00–16:00), which was consistent among years.

Coyote habitat selection

Overall, the full dataset showed that coyotes avoided development, but selected for roads, agriculture, rifle encounter risk, mountain lion encounter risk, and ruggedness (Figure 3). Coyotes also avoided shrubland and woodland relative to grassland (Appendix S1: Figure S3). We found no difference in the results of the full model across collaring years, when using collaring year as a nested random effect.

Behavioral partitioning of habitat selection

We found that models partitioned by behavioral state differed from the full model and each other in several

FIGURE 3 Estimates of coyote (*Canis latrans*; $n = 13$) habitat selection in the Sanel Valley, Mendocino County, California, USA, using a full model with all GPS locations, and three models partitioned by resting, foraging, and traveling behavior estimated by the top hidden Markov model. All covariates were standardized prior to modeling. For covariates corresponding to the distance to a feature (Dist.), a negative estimate means that selection was higher closer to that feature. Error bars indicate 95% confidence interval.

ways (Figure 3; Appendix S1: Table S5). By visualizing model estimates and comparing OR of covariates we found that coyotes avoided ruggedness while traveling ($OR_{full} = 1.02$, 95% CI [1.00, 1.04]; $OR_{travel} = 0.84$, 95% CI [0.81, 0.87]). Coyotes also had significantly stronger selection for roads while traveling and foraging than resting ($OR_{travel} = 0.82$, 95% CI [0.78, 0.85], $OR_{forage} = 0.82$, 95% CI [0.79, 0.85], $OR_{rest} = 0.92$, 95% CI [0.89, 0.95]). We found that coyotes avoided development overall, but significantly more while foraging than resting or traveling ($OR_{forage} = 1.17$, 95% CI [1.12, 1.21], $OR_{rest} = 1.06$, 95% CI [1.02, 1.09], $OR_{travel} = 1.06$, 95% CI [1.02, 1.11]). Coyote selection for agriculture was stronger while resting and foraging than traveling ($OR_{rest} = 0.73$, 95% CI [0.69, 0.77], $OR_{forage} = 0.83$, 95% CI [0.80, 0.87], $OR_{travel} = 0.94$, 95% CI [0.89, 0.98]). Coyote selection for rifle encounter risk was weaker while traveling ($OR_{full} = 1.11$, 95% CI [1.09, 1.13]; $OR_{travel} = 1.05$, 95% CI [1.02, 1.08]). Selection for mountain lion encounter risk was strongest while resting ($OR_{full} = 1.20$, 95% CI [1.18, 1.22]; $OR_{rest} = 1.38$, 95% CI [1.34, 1.43]). Finally, coyotes avoided shrublands in the full model, but selected for shrublands while resting ($OR_{full} = 0.93$, 95% CI [0.90, 0.97]; $OR_{rest} = 1.25$, 95% CI [1.17, 1.33]; Appendix S1: Figure S3, Table S6).

Diel partitioning of habitat selection

We found that models partitioned by diel period did not significantly differ from the full model (Figure 4). Additionally, there was no significant difference in coyote selection for roads, development, rifle encounter risk, and mountain lion encounter risk by day or night (Figure 4; Appendix S1: Table S5). However, coyotes selected for agriculture significantly more during the day than at night ($OR_{day} = 0.80$, 95% CI [0.77, 0.84], $OR_{night} = 0.87$, 95% CI [0.84, 0.90]). Coyotes avoided shrublands during the day, with no effect at night ($OR_{day} = 0.86$, 95% CI [0.80, 0.90], $OR_{night} = 1.00$, 95% CI [0.95, 1.05]; Appendix S1: Figure S4, Table S6). Additionally, coyotes avoided woodlands significantly more during the day ($OR_{day} = 0.45$, 95% CI [0.41, 0.50], $OR_{full} = 0.56$, 95% CI [0.52, 0.59]; Appendix S1: Figure S4, Table S6). Finally, coyotes selected for ruggedness at night, with no effect during the day ($OR_{night} = 1.05$, 95% CI [1.03, 1.08]; $OR_{day} = 0.98$, 95% CI [0.95, 1.00]).

DISCUSSION

Using RSFs, we found that coyotes have a complex response to natural and anthropogenic features in mixed-use landscapes. Our results indicate that coyotes avoided development, shrubland, and woodland, but selected for roads, agriculture, and areas with mountain lion and rifle encounter risk regardless of diel period or behavioral state. While the strength of habitat selection clearly varied by behavioral state and diel period, coyotes continued to select for habitats that we anticipated to be associated with mortality and persecution by humans (i.e., agriculture, roads, and areas with rifle encounter risk).

Opposite our expectations, coyotes selected for agriculture significantly more while resting, foraging, and during the day. This suggests that coyotes moved slowly through agricultural fields for foraging, and perceived low risk from diurnal human activity in open spaces. Coyotes also selected for rifle encounter risk, which was parameterized using locally informed coefficients for open viewsheds, roads, and rugged terrain. It is possible that the health, age, or social rank of coyotes in our study influenced risk perception of agriculture and open space. For instance, one study found that resident coyotes selected for cropland and pasture more than transients (Mitchell et al., 2015). The lure of associated food rewards, particularly in early winter with available grape crops and young livestock in pasture, may also have outweighed perceived risks. Previous research suggests coyotes supplement their diets with remnant crops during food-scarce periods in fall and winter (Cherry et al., 2016; Youngmann et al., 2022). A limitation lies in disentangling whether habitat selection was a response to low risk, high reward, or both. Fine-scale telemetry data could provide insights into coyote movement relative to predators (i.e., humans, livestock, guardian dogs; Buderman et al., 2018), while diet studies might clarify whether coyotes use agricultural and pasture lands for food. Ultimately, increased diurnal use of human-protected resources may raise human-caused mortality unless humans choose to tolerate coyote use.

We observed a significant preference among coyotes for secondary and tertiary roads, during travel and foraging. This contrasts with findings from other studies suggesting that coyotes either avoid roads (Youngmann et al., 2022) or limit road use to transient individuals (Hinton et al., 2015). The volume of vehicle traffic on roads may impact wildlife use (Anton et al., 2020; Barrueto et al., 2014; Kautz et al., 2021). Thus, it is plausible that coyotes in our study area did not perceive vehicle traffic as a risk on the secondary and tertiary roads. Coyotes may also select road edges for various rewards, including hunting burrowing rodents in disturbed roadside soils (Latham et al., 2011), scavenging roadkill (Youngmann et al., 2022), scent-marking (Barja & List, 2014), or facilitating movement between foraging

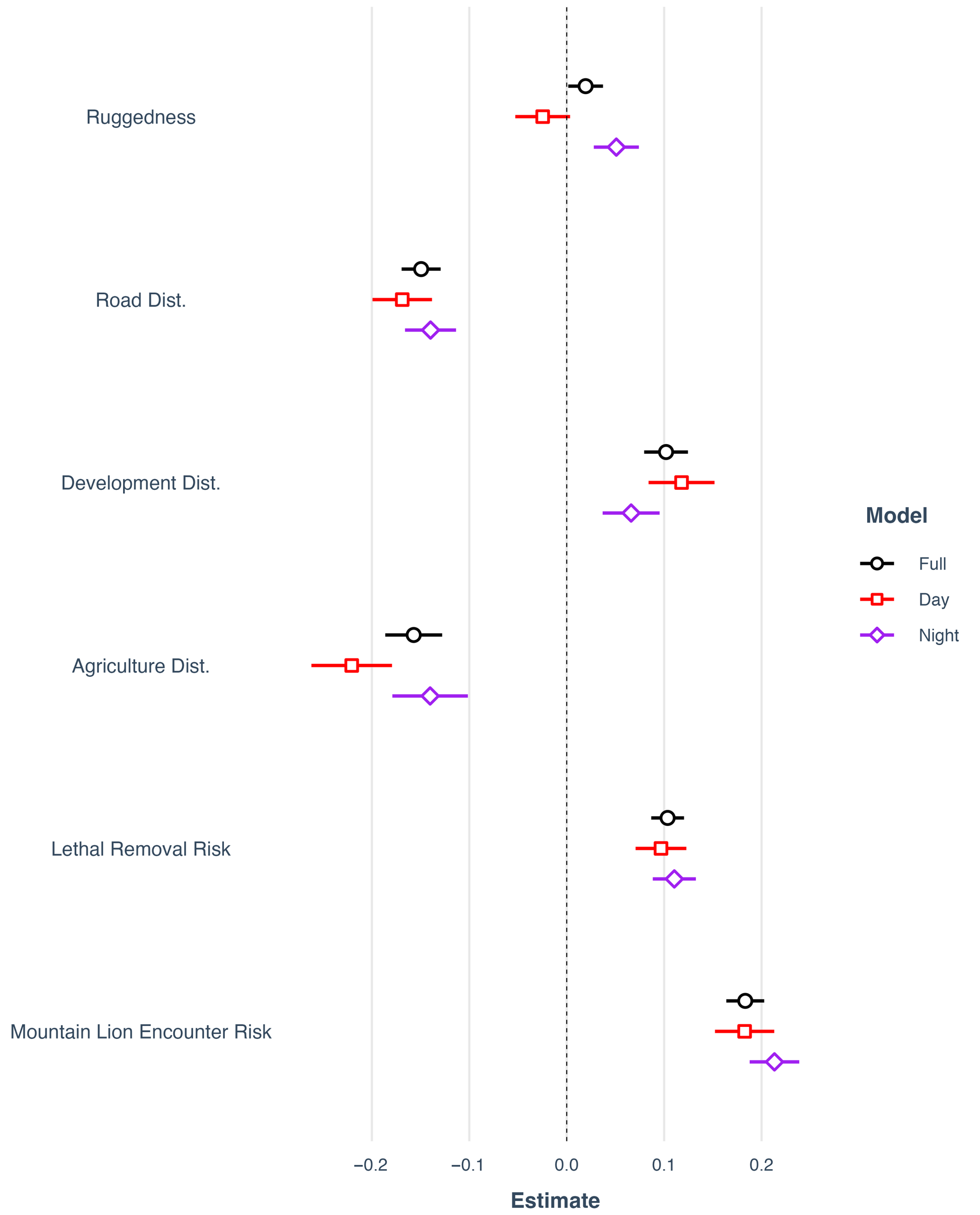

FIGURE 4 Estimates of coyote (*Canis latrans*; $n = 13$) habitat selection in the Sanel Valley, Mendocino County, California, USA, using a full model with all GPS locations, and two models partitioned by day and night. All covariates were standardized prior to modeling. For covariates corresponding to the distance to a feature (Dist.), a negative estimate means that selection was higher closer to that feature. Error bars indicate 95% confidence interval.

territories (Abrahms et al., 2016; Andersen et al., 2017; Latham et al., 2011). Our results indicated that coyotes avoided rugged terrain while traveling; therefore, unpaved roads may provide a means for coyotes to bypass rugged terrain, thus enhancing landscape connectivity for coyotes in mixed-use landscapes.

While there is ample research suggesting that coyotes can thrive in developed areas (Poessel et al., 2017), even surpassing survival and density in rural areas (Gehrt et al., 2011), development itself may constrain coyote behavior and dietary patterns (Gehrt et al., 2011). We found that coyotes avoided development (composed of low, medium, and high-intensity development and highways), in support of previous work (Gehrt et al., 2009; Riley et al., 2003). Coyotes are known to use behavioral partitioning to access urban environments, moving farther and faster to acquire food, than in non-urban environments (Riley et al., 2003). Thus, we expected coyotes might be more willing to approach development at night or while traveling to access food resources (i.e., house pets, anthropogenic food). However, we found no evidence to suggest that coyotes adjust behavior or diel patterns to select for development. Coyotes may have disproportionately avoided development because of lethal risks (e.g., humans, highways, or domestic dogs) or unfamiliar features (e.g., infrastructure, noise, or lighting). It is also possible that coyotes avoided development because it had fewer food rewards, instead preferring agriculture and grassland habitats. Future research could explore whether coyotes favor development during other seasons or investigate how demographic parameters, such as age, social rank, or health, influence their willingness to risk exposure to human activity (Hinton et al., 2015; Mitchell et al., 2015).

In addition to anthropogenic features, we expected natural features to drive aspects of coyote habitat selection. Contrary to our expectations, coyotes selected for mountain lion encounter risk across diel periods, including at night when mountain lions at this study site were most active (Gaynor et al., 2022). As a result, coarse-scale predator risk did not appear to be a factor in coyote habitat selection at our site. In fact, coyotes had an overall positive association with mountain lion encounter risk, which was predicted using distance to agriculture and high elevation as described by Gaynor et al. (2022). While coyotes have, at times, composed a large fraction of mountain lion diet (Sacks, 1996), coyotes are not obligate prey of mountain lions, as mountain lions can exhibit diet flexibility in response to prey availability (Karandikar et al., 2022). Reduced mountain lion detections following the 2018 River Fire near the study area, may also have allowed further coyote expansion into these habitats undeterred (Calhoun et al., 2023). However, it is still possible that coyotes continue to avoid mountain lions at fine scales, as was found in other studies (Prugh et al., 2023), by avoiding habitat features or other cues that coyotes associate with mountain lions (Brunet et al., 2022). Ultimately, coyotes may be using mountain lion habitat to hunt for similar prey species, scavenge on the kills of larger predators, or to seek dense cover. Follow-up studies on the diet composition of coyotes will help to disentangle whether coyotes co-occur in areas with large predators for food, vegetation cover, or perceived safety.

Finally, we found that coyotes avoided woodlands and shrublands relative to grassland. Open, high-visibility habitats are advantageous for cursorial hunters, like coyotes, and previous research has found coyotes readily use open habitat in other parts of their range (Cherry et al., 2017; Stevenson et al., 2019). Interestingly, our finding that coyotes selected grasslands more than expected (based on availability) is the opposite of what Sacks and Neale (2002) found at this study site 28 years prior. Renewed coyote use of grasslands may be the result of lower livestock densities and corresponding mortality factors, such as humans or livestock guardian dogs, at this site (McInturff et al., 2021; Sacks, 1996). Likewise, grasslands may be attractive habitats in that they have higher prey densities and allow for high-visibility, giving coyotes an advantage in detecting risk from afar while hunting small mammals and lagomorphs (Aben et al., 2018; Stevenson et al., 2019). Reduced ability to detect risk, travel in dense understory, and lower prey densities may equally explain why coyotes avoided dense vegetation cover and low-visibility habitats (i.e., shrublands and woodlands) relative to grasslands. However, dense vegetation cover can also provide a refuge, and is perhaps why coyotes tended to avoid woodlands less at night or while resting.

Incorporating behavior patterns explicitly into habitat selection can illuminate the tradeoffs of mixed-use landscapes natural and anthropogenic risks and rewards (Ferreira et al., 2018; Gascon et al., 1999; Kremen & Merenlender, 2018). However, a significant limitation of this study, and many habitat selection studies, lies in the inability to distinguish between risk and reward as the underlying drivers of habitat selection. Experimentally manipulating risk cues or reward features within each habitat feature would help identify the risk–reward thresholds influencing coyote behavior. The addition of empirical data on coyote mortality or local prey availability could further highlight why coyotes select or avoid anthropogenic features. Our closest approximation of mountain lion and human-related mortality risk was to estimate a risk map where mountain lions or human rifle use typically occur. Thus, our habitat selection models could not capture coyote response to fine-scale risks, such as the presence or absence of mountain lions, humans, livestock guardian dogs, or vehicles. Collecting higher resolution movement data for coyotes and their predators will enhance our understanding of coyote risk responses and movement near anthropogenic features in agricultural landscapes.

Overall, coyotes generally selected for places and times associated with human activity, without significant behavioral variation. While this may suggest that coyotes are resilient to low levels of anthropogenic risk in mixed-use landscapes, critically, it may also suggest that coyotes are not equipped to evaluate the risk posed by modern humans, who can equally appear as facilitators, neutral actors, or threats. In certain mixed-use landscapes, human-related coyote mortality surpasses coyote risk responses to humans (Prugh et al., 2023). Consequently, safeguarding livestock and crop resources with non-lethal tools may enable coyotes to learn to avoid humans, triggering coyote risk responses and mitigating long-term conflict (Treves et al., 2023; Young et al., 2019). Continued integration of research on coyote habitat preferences, mortality, and diet, into landscape-level monitoring and connectivity planning is crucial, particularly in the face of any intensification of road or residential development. Key questions remain about how coyotes will adjust their habitat preferences amid growing disturbances such as drought or fire. Exploring these research directions could provide valuable insights or future management strategies, given the potential for escalated human–wildlife conflict and increased wildlife use of agriculture in response to declining wild prey, drought, and extreme climatic events (Abrahms, 2021).

CONCLUSION

This research supports a growing body of literature indicating that carnivores navigate human-modified landscapes to use anthropogenic and natural features (Geffroy et al., 2020; Newsome et al., 2015). Our finding that coyotes avoided development, but disproportionately selected for low-density anthropogenic features, without spatiotemporal partitioning, may suggest that coyote are resilient in mixed-use landscapes. However, without information on how coyote habitat selection influences survival, it is possible that coyote use of anthropogenic features (such as roads, grasslands, and agricultural areas) also results in higher mortality. These findings underscore the importance of managing livestock and crop resources by considering the use of non-lethal tools to avoid coyote conflict. Further studies on seasonal or disturbance-related shifts in coyote diet and risk perception may help to disentangle how coyotes interact with predators, livestock, and agriculture. Ultimately, advancing multi-scale models of animal habitat selection to uncover local risks and rewards can help to improve the fate of adaptable predators in altered environments.

AUTHOR CONTRIBUTIONS

Amy Van Scoyoc, Kendall L. Calhoun, and Justin S. Brashares conducted animal captures and fieldwork. Amy Van Scoyoc analyzed the data and led the writing of the manuscript. Kendall L. Calhoun and Justin S. Brashares contributed critically to the interpretation of results, 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

All data, code, and materials used in the analysis (Van Scoyoc et al., 2023) are available from Dryad: https://doi.org/10.6078/D1TH99.

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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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