

Research Article

Large-scale overlap and fine-scale avoidance: assessing interactions between coyotes, bobcats, and cougars at multiple scales

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Abstract

In multi-carnivore systems individuals must forage and reproduce while also competing with other carnivores and avoiding intraguild predation. These interactions may vary by strength and scales across different ecosystems. We used occupancy analyses and attraction–avoidance indices to assess large- and fine-scale interactions, respectively, between Cougars (*Puma concolor*), Bobcats (*Lynx rufus*), and Coyotes (*Canis latrans*) in northeast Oregon based on data from camera traps set during the summer and fall of 2016 and 2017. To determine the importance of habitat preferences and spatial overlap, we compared occupancy (probability of use) models that included habitat covariates with and without species co-occurrence terms. Detection was different for all species and was influenced by roads, game trails, and canopy cover. Terrain ruggedness was important for all species; Bobcats showed the strongest preference for ruggedness, Cougars showed a weak preference, and Coyotes significantly but weakly avoided rugged areas. The top probability of use model showed that Bobcats and Coyotes were 1.88 times more likely to spatially overlap on roads. We also found evidence that interactions among carnivores were scale-dependent. At larger scales, habitat preference was more important than interactions with other carnivores, whereas at finer scales, most carnivores avoided each other. At fine spatiotemporal scales, our attraction–avoidance analyses showed that Bobcats avoided Coyotes and Coyotes avoided both Bobcats and Cougars. These findings suggest that carnivores in our study system were adept at minimizing conflict through fine-scale avoidance in space and time, that the human footprint can influence carnivore interactions, and that studying carnivore interactions at multiple scales is important for understanding the effects of spatial overlap and potential competition.

Key words: Bobcat, carnivores, communities, competition, Cougar, Coyote, habitat, interactions, occupancy modeling.

The impacts of historic carnivore extirpation and human land use have had rippling effects on carnivore communities. The decline of apex carnivores in North America is thought to have resulted in the range expansion of 60% of mesocarnivore species, including a 40% range expansion for Coyotes (*Canis latrans*) alone (Prugh et al. 2009). Mesocarnivore release can have trophic effects in many ecosystems, including impacts on human health. The expansion of Coyotes in the eastern United States and subsequent suppression of Red Fox (*Vulpes vulpes*) populations (Levi and Wilmsers 2012) has been linked to increased small mammal populations and Lyme's disease transmission to humans (Levi et al. 2012). Human suppression of other apex carnivores has also been linked to higher populations of invasive mesocarnivores (Brook et al. 2012) and changes in both forest structure and forest mammal assemblages (Colman et al. 2014). The recolonization of apex predators can have

opposite effects; for example, recolonizing Gray Wolves (*C. lupus*) in the Greater Yellowstone Ecosystem often suppress Coyote populations, which can lead to trophic effects such as lower rates of Coyote predation on Pronghorn (*Antilocapra americana*) fawns (Berger et al. 2008). However, strong competitive effects of this magnitude are relatively rare in carnivore communities across the globe (Davis et al. 2018), and it is important to carefully assess whether observed patterns in carnivore communities are a result of competitive effects or differences in habitat selection.

When competition does influence carnivore communities, it can have several cascading effects. Intraguild predation—a form of interference competition—can directly suppress subordinate carnivore populations (Case and Gilpin 1974; Polis et al. 1989; Palomares and Caro 1999), while exploitative competition can negatively affect the survival of individuals and populations of less

effective competitors despite high prey availability (Amarasekare 2008; Delong and Vasseur 2013; Lonsinger et al. 2017). When prey resources are limited, competition can have even greater consequences for both individuals (e.g., diminished body condition) and populations (e.g., reduced carrying capacity; Litvaitis and Harrison 1989; Caro and Stoner 2003).

One typical coexistence strategy of subordinate carnivores is avoiding dominant carnivores in space and time (Linnell and Strand 2000; Amarasekare 2008; Schuette et al. 2013). Even in multi-carnivore systems, subordinate competitors can avoid the risk of intraguild predation and interference competition through spatial and temporal avoidance even when habitat preferences overlap. Bobcats (*Lynx rufus*) have been shown to avoid den sites of Coyotes during the spring in an area where both species overlapped spatially and their populations were at high densities (Neale and Sacks 2001). Cheetahs (*Acinonyx jubatus*) and African Wild Dogs (*Lycaon pictus*) avoid more dominant predators like Lions (*Panthera leo*) and Spotted Hyenas (*Crocuta crocuta*) by shifting their daily activity patterns to reduce the risk of interference competition and kleptoparasitism (Hayward and Slotow 2009). In arid environments in the western United States, Kit Foxes (*Vulpes macrotis*) and Swift Foxes (*Vulpes velox*) spatially avoid shrubland habitats—which provide thermal cover and high prey availability for both species—due to the risk of intraguild predation from Coyotes (Thompson and Gese 2007; Lonsinger et al. 2017).

Identifying the driving causes behind behaviors such as habitat use and temporal activity patterns can be achieved by testing competing hypotheses in carnivore interaction research (Campbell 2004; Hayward and Slotow 2009; Gompfer et al. 2016). New analytical methods allow researchers to compare habitat preference models for single species and interaction models with multiple species in the same model set (Rota et al. 2016). These models also facilitate research on multispecies interactions at various spatial scales (Parsons et al. 2016). Analyzing habitat use and temporal activity at both large and fine scales can reveal the difference between underlying effects of competition (e.g., avoidance) and space use patterns (or lack thereof) that may appear to be competition on the surface. The difference between competition and habitat preferences may not be evident from studies focused primarily on differences in landscape-level habitat use alone (Gompfer et al. 2016; Lonsinger et al. 2017; Rich et al. 2018). Additionally, in multiuse landscapes, human disturbance (e.g., land use, recreation, hunting, cattle grazing, etc.) can have a significant impact on carnivore interactions (Elmhagen and Rushton 2007; Haswell et al. 2017). The cascading effects of apex carnivores on the carnivore community are likely to depend on the human context in which these interactions are occurring, namely the type of human disturbance and available prey (Sévéque et al. 2020).

Our objective was to evaluate patterns of spatial and temporal interactions between Cougars (*Puma concolor*), Bobcats, and Coyotes to ultimately test competing hypotheses of competition and habitat use among these species. We used camera trap data collected from 3 sites in northeastern Oregon to study species interactions and account for habitat features (including human impacts) in our study area to determine if they influenced species interactions. We considered a set of 4 competing hypotheses to explain if and how large-scale (e.g., landscape level) habitat preference, fine-scale (e.g., camera trap level) spatiotemporal activity, and species co-occurrence affected the space use of these carnivores. Our hypotheses were: (1) carnivores overlap on a large scale and segregate in space and time at fine scales; (2) carnivores overlap on a large scale and there are no detectable interactions at fine scales; (3) carnivores

segregate at large scales and there are no detectable interactions at fine scales; and (4) carnivores segregate at large scales and segregate in space and time at fine scales.

Materials and methods

Study area.

We surveyed carnivores in the Blue Mountains of northeastern Oregon (Fig. 1) where we placed 3 grids of heat- and motion-triggered trail cameras (hereafter, camera traps). One grid was located in the Starkey Experimental Forest (hereafter, Starkey), a 25,000-acre ungulate-proof enclosure located approximately 48 km southwest of La Grande, Oregon. This enclosure was created in 1989 by the U.S. Forest Service to research the long-term effects of land management practices on domestic cattle (*Bos taurus*), Elk (*Cervus canadensis*), and Mule Deer (*Odocoileus hemionus*). Data from GPS collars show that the ungulate-proof perimeter fence does not inhibit carnivore movements in and out of the fenced enclosure (Ruprecht et al. 2021). Two other camera grids, approximately 21 km from each other, were located in the Mt. Emily Wildlife Management Unit (hereafter, Mt. Emily) approximately 33 km northeast of Starkey.

Both areas were characterized by large flat ridges, steep canyons, and intermittent streams and water sources. The plant community was dominated by dry, Ponderosa Pine (*Pinus ponderosa*) forests with grassy south-facing slopes and north-facing slopes that contained thicker forests and mesic plants such as Douglas Fir (*Pseudotsuga menziesii*), Ocean Spray (*Holodiscus discolor*), Ninebark (*Physocarpus opulifolius*), and Common Snowberry (*Symphoricarpos albus*). The most abundant members of the mammal community in the study area included Elk, Mule Deer, White-tailed Deer (*Odocoileus virginianus*), Black Bears (*Ursus americanus*), Cougars, Coyotes, and Bobcats. Mt. Emily also had domestic Sheep (*Ovis aries*), low numbers of Moose (*Alces alces*), and low numbers of recolonizing Gray Wolves (*C. lupus*; Orning et al. 2021).

Camera trap surveys.

We used Bushnell Trophy Cams (Bushnell Outdoor Products, Overland Park, KS) in all camera trap grids. All cameras were equipped with invisible infrared flash to minimize disturbance to wildlife from night photos and were set to take photos with the minimum delay possible (approximately 1 s between photos). Camera traps were run from April to September in 2017 in Starkey, and from August to November in 2016 and 2017 in Mt. Emily. In Starkey we deployed 94 camera traps on a grid with 1-km spacing and a random starting point. In Mt. Emily we placed 54 cameras each year on a random subsample of grid points with a minimum spacing of 2 km to avoid clumping (which often results from random point selection) and cover more area (Fig. 1). Some camera sites in 2017 in Mt. Emily were the same sites as 2016 but most were not. We used different spacing between the grids because our 1-km Starkey camera grid was smaller than the average summer home range sizes of Cougars (87 km² for females, 314 km² for males; Ross and Jalkotzy 1992), Bobcats (2 to 11 km²; Witmer and DeCalesta 1986), and Coyotes (12 to 14 km²; Witmer and DeCalesta 1986; Ward et al. 2018). We had less available cameras for the Mt. Emily grids, so we subsampled grids with our spacing rule to ensure that cameras captured multiple carnivore home ranges.

Cameras were unbaited, placed approximately 40 cm off the ground, and deployed within 100 m of the original grid point in areas of animal traffic that included game trails, ridge tops, open and closed roads, and drainage bottoms. Field crews recorded whether a camera trap was set on a road, a game trail, or other

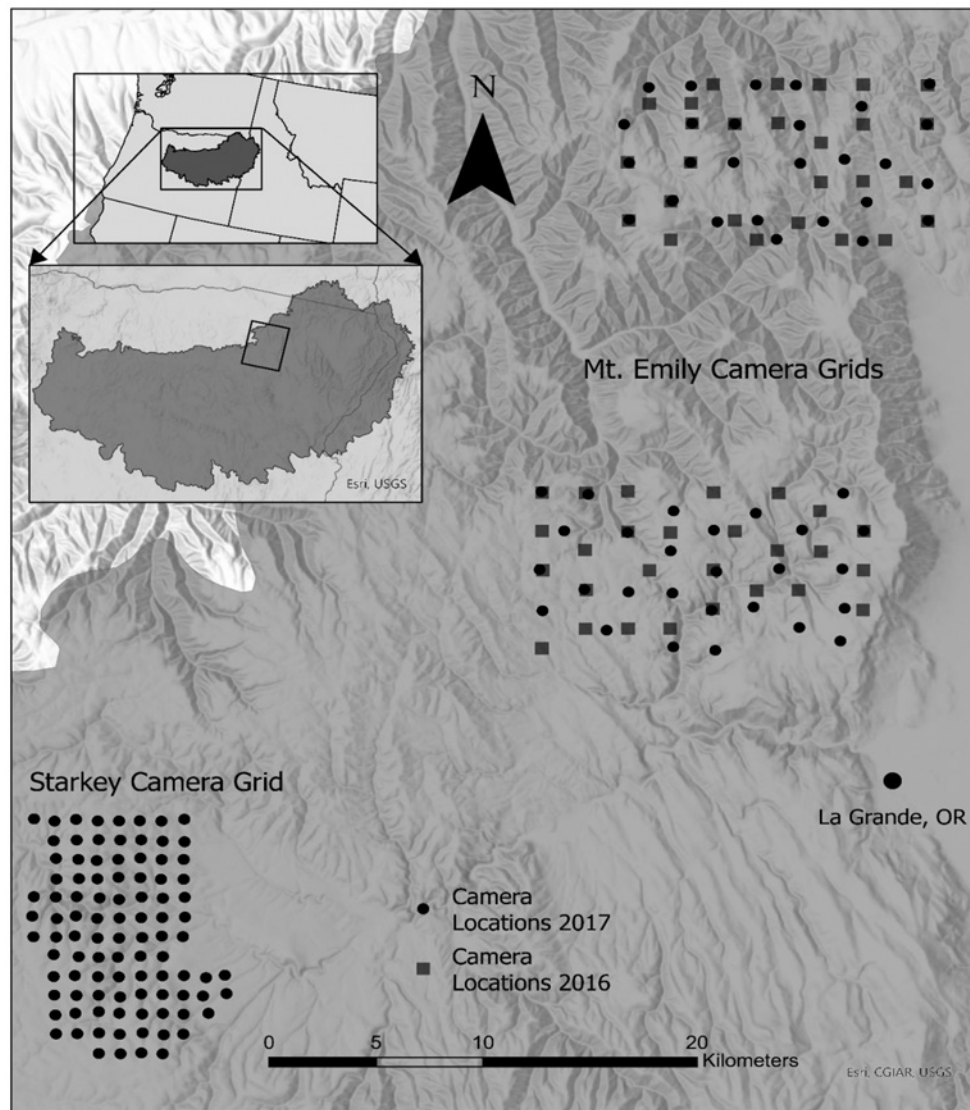


Fig. 1. Location of the 2 study sites (Starkey, located in the southwestern corner; and Mt. Emily, located in 2 grids in the northeastern corner) with camera trap locations in the Blue Mountains ecoregion (displayed on the map in the top left corner), Oregon, United States (map created with ESRI, USGS). In Starkey we placed a single camera every 1 km for a total of 94 camera traps. In Mt Emily there was a northern and southern camera grid, and we placed 54 cameras in each area on a random subsample of grid points that had a minimum spacing rule of 2 km to avoid clumping.

habitat features (e.g., spring, burrow, fruiting tree or shrub, etc.), the date of deployment, and all camera setting information. Once retrieved, camera trap photos were tagged with species identity by volunteers and project staff in *DigiKam* (version 5.9.0; [digiKam Team 2018](#)), then quality-checked by Oregon Department of Fish and Wildlife biologists for accuracy. We considered detections of the same species independent if they occurred more than 15 min apart and summarized these detections into daily and weekly detection/nondetection data for occupancy models.

Model covariates.

We generated 3 different covariate types, one using data recorded in the field while deploying camera traps (i.e., site characteristics), “detection” covariates derived from the detection rate from camera traps (i.e., the number of detections per species per camera night), and “occupancy” covariates derived from remote-sensed data. Large-scale (i.e., landscape level) effects were measured in terms of 10 to 100 km², fine-scale (i.e., camera trap level) spatial effects were measured in terms of meters away from the camera, and fine-scale

temporal effects were measured in minute-by-minute detections. Since cameras were deployed at a smaller scale than the average home range of our study species, detections represent the probability of use of a site rather than true occupancy ([MacKenzie et al. 2002](#); [Burton et al. 2015](#)). All covariates were expected to either influence detection of a species by our camera traps or influence the probability of use of a site by a species. We included 9 detection covariates and 8 occupancy covariates ([Table 1](#)). Year was included as a covariate to account for possible population changes between years, which would affect both detection probability and occupancy. All covariates were standardized to a mean of 0 for analysis and tested for covariance; any 2 covariates with a covariance >0.5 were not included in the same model. Descriptions of all covariates and how we analyzed them are in [Supplementary Appendix I](#).

Data analysis.

We used the multispecies occupancy model developed by [Rota et al. \(2016\)](#) to estimate occupancy and species interactions of Bobcats, Coyotes, and Cougars. This model is a generalization of the

Table 1. All habitat variables used in occupancy analyses derived from remote-sensed camera trap data for Cougars, Coyotes, and Bobcats in Starkey and Mt. Emily study areas in Oregon, 2016 to 2017. The “Model” column indicates whether variables were used as a covariate for detection (p), single-species occupancy (ψ), or species interactions (ψ_{11}). The “Metric” column indicates the calculation used to create model variable values. All covariates were calculated for each individual camera site, including detection rates.

Covariate category	Model	Metric	Model variable	Description
Time-varying	p	Mean	Precipitation	Mean of precipitation during sampling period (1 or 7 days)
	p	Mean	Temperature	Mean of daily temperature during sampling period (1 or 7 days)
	ψ	Binary	Year	Year (2016 or 2017) of camera deployment
Seasonal	p	Value	Julian Day	Julian day of camera deployment
Study area	p	Binary	Project Site	Project site camera was placed in (either Starkey or Mt. Emily)
Landscape features	p, ψ_{11}	Binary	Road	Camera placed on an open or closed road (yes/no)
	p	Binary	Game Trail	Camera placed on game trail (yes/no)
	p	Binary	Other Feature	Camera placed on other landscape feature (e.g., spring; yes/no)
	ψ	Count	Springs within 1 km	Number of springs with water for most or all of the year within 1 km of camera site
	ψ	Distance to	Forest Edge	Distance (m) to nearest forest edge
	ψ	Distance to	Open Road	Distance (m) to nearest road open to vehicular travel
	ψ	Distance to	Perennial Stream	Distance (m) to nearest stream with flow for most or all of year
	ψ	Distance to	Spring	Springs with water for most or all of year
	ψ, ψ_{11}	Mean	Ruggedness	Mean of terrain ruggedness (using a combination of slope, aspect, and elevation) within a 480-m radius of camera site
Topographic	p	Value	Elevation	Meters above sea level
Vegetation	p	Mean	Canopy Cover	Percentage of canopy cover derived from GNN averaged within a 480-m radius of camera site
	ψ	Maximum	Vegetation Greenness	Maximum NDVI of nonforested areas averaged within a 480-m radius of camera site
Human activity	ψ_{11}	Rate	Vehicle Detection	Number of vehicle detections divided by camera nights $\times$ 100
	ψ_{11}	Rate	Human Detection	Number of human detections divided by camera nights $\times$ 100

single-season occupancy model (Mackenzie et al. 2002) that allows for models of species co-occurrence that do not require initial assumptions of asymmetric species interactions. This model also enables the comparison of single-species occupancy models and co-occurrence models for species pairs (i.e., pairwise interactions) in a single model set (Rota et al. 2016). Constructing these co-occurrence models allowed us to test our hypotheses concerning large-scale habitat use.

The latent occupancy of each species at each site was modeled as a multivariate Bernoulli (MVB) random variable such that:

$$Z \sim \text{MVB}(\psi_{000}, \psi_{100}, \psi_{010}, \psi_{001}, \psi_{110}, \psi_{101}, \psi_{011}, \psi_{111})$$

where Z is a vector of 1s and 0s indicating the latent occupancy state of all species, ψ_{000} is the probability that no species occupy a site, ψ_{100} , ψ_{010} , and ψ_{001} are the probabilities that species 1, 2, and 3 occupy a site, respectively, ψ_{110} is the probability that both species 1 and 2 occupy a site, ψ_{101} is the probability that species 1 and 3 occupy a site, ψ_{011} is the probability that species 2 and 3 occupy a site, and ψ_{111} is the probability that all 3 species occupy a site. Beta values that quantify species interactions can be derived from log ratios of the appropriate ψ_{xxx} values (e.g., co-occurrence of species 1 and 2 = $f_{12} = \log(\psi_{110}/\psi_{010}\psi_{100})$; see Rota et al. 2016).

We ran occupancy models in program MARK and used Akaike's information criteria for small sample sizes (AICc) to rank models. The ΔAICc scores, number of parameters, AICc weights, and

log-likelihood were recorded for all top-ranking models. Models were ranked according to ΔAICc scores and AICc weights and were categorized based on single- or multispecies occupancy and the presence or absence of habitat covariates.

In all occupancy models we used 14 survey occasions of 7 days, which began on 1 July for Starkey and 5 August for Mt. Emily. We excluded survey data for occupancy models in Starkey during the Coyote denning period (April to June) to reduce potential detection bias because of behavioral differences and to increase temporal overlap in data between Starkey and Mt. Emily. Detection models were limited to 3 maximum detection covariates per species (from the set of 9) and occupancy models to a maximum of (from the set of 8) to maintain statistical power and make model results more interpretable. All covariates were centered and scaled.

We used a tiered approach to model construction and evaluation. In the first step, we determined whether detection probability was best explained by a single detection probability across all species or whether each species had unique detection probabilities. We evaluated all possible groups of up to 3 detection covariates and assessed time-varying detection models (28 total detection models). In the second step, we found the best focal-species occupancy models by combining the best detection model with a series of multispecies occupancy models wherein we evaluated all possible triads of hypothesized occupancy covariates for each focal species while using intercept-only models for the nonfocal species (25 single

focal-species models). We also evaluated a multispecies occupancy model in which the occupancy of all 3 focal species were modeled with occupancy covariates for each species (81 multispecies models). In the third step, we found the best species interaction model by evaluating whether the previously identified top focal-species occupancy models were improved by including a species interaction term (21 species interaction models). In the fourth step, we found the best species interaction-covariate models by evaluating whether the previously identified species interaction models could further be improved by including a covariate assessing whether species interactions were mediated by habitat or human detection rate (24 species interaction-covariate models). We additionally fit a null model that included no covariates on detection, occupancy, or species interactions. After determining the top models in the 6 categories described above, we then ranked the resulting 12 models (i.e., 1 null model, 1 detection model across all species, 3 focal-species occupancy models [1 model for each species], 1 multispecies occupancy model, 3 species interaction models, and 3 species interaction-covariate models).

Additionally, we used model averaging to estimate the species interaction terms for each pair of species (Bobcat–Cougar, Bobcat–Coyote, Coyote–Cougar) across all species interaction and species interaction-covariate models to determine large-scale patterns of co-occurrence. Model averaging calculates a weighted average of the values of interest (in this case, log odds of species co-occurrence) using the AICc weight of the model, so models with higher weight contribute more to the final average than models with less weight (Wagenmakers and Farrell 2004).

Lastly, we calculated attraction–avoidance ratios (AARs; Parsons et al. 2016) between each pair of carnivores to test our hypotheses concerning fine-scale temporal responses. Because cameras were deployed on a grid with a random starting point within each study area, camera locations encompassed a variety of microhabitats (e.g., terrain types, vegetation cover, canopy cover, etc.) and sampled these microhabitats in proportion to their availability. Microhabitats were thus unlikely to influence temporal behavioral patterns. These ratios measure the relative avoidance of a camera site by 1 carnivore after the passage of another carnivore species (Parsons et al. 2016). We calculated the T4/T3 ratios for each camera, where T3 is the median length of time between successive carnivore detections without a detection of another carnivore species in between, and T4 is the median length of time between carnivore detections with another carnivore species detection in between (Parsons et al. 2016). We then averaged these ratios across all cameras. For example, we calculated all Bobcat detections on a given camera that had a Cougar detection between the first and second Bobcat detection (T4) and divided that by the time between subsequent Bobcat detections with no other carnivore detected in between (T3). A T4/T3 ratio of 1 indicates no attraction or avoidance. A T4/T3 ratio > 1 indicates that the focal carnivore (e.g., Bobcats) avoid the secondary carnivore (e.g., Cougars), whereas T4/T3 ratios < 1 indicate attraction/co-occurrence. We used a 1-sided Wilcoxon rank sum test to determine if T4/T3 ratios of a pair of predators (i.e., Bobcats and Coyotes) were significantly greater than 1.

Results

During 15,829 camera trap nights we recorded 129 detections of Bobcats, 840 detections of Coyotes, and 152 Cougar detections. Coyotes had a relatively high marginal probability of use [$\psi = 0.74$; CI = (0.59, 0.87)] as did Bobcats [$\psi = 0.72$; CI = (0.30, 0.90)], while Cougars had a lower marginal probability of use [$\psi = 0.58$; CI =

(0.40, 0.71)]. The rankings of the 12 models from each of our 6 modeling categories described above are presented in Table 2. The 12 models included 1 null model (“Null Model”), 1 detection model (“Detection Only”), 3 single-species occupancy models (“Bobcat Occupancy,” “Coyote Occupancy,” and “Cougar Occupancy”), 1 multispecies occupancy model with the best focal-species covariate combinations (“Multi-Species Occupancy”), 3 species interaction models (“Bobcat–Coyote Interaction,” “Bobcat–Cougar Interaction,” and “Coyote–Cougar Interaction”), and 3 species interaction-covariate models (“Pairwise Interaction—Road,” “Pairwise Interaction—Human Detections,” and “Pairwise Interaction—Ruggedness”).

The best detection model (Table 2) included unique detection probabilities for each species and distinct landscape and vegetation covariates (Road, Trail, and Canopy Cover) that were not time-varying. While these 3 covariates had the greatest influence on the detection rates of all 3 species, there were varying responses across species. Both felines showed higher detection in areas with a higher percentage of canopy cover, while Coyotes showed the opposite. All species were more likely to be detected on roads and game trails, though the effect size varied (Table 3). No time-varying detection covariates were included in the best detection model (including varying detection among sample periods or months, as well as temperature and precipitation covariates).

The top focal-species occupancy models all included Ruggedness as a covariate. This was the single most important habitat feature for the “Coyote Occupancy” model, while the “Bobcat Occupancy” model included the Distance to Road covariate, and the “Cougar Occupancy” model contained a variable for Year. As expected, the multispecies model that contained covariates for each focal species together (“Single-Species Occupancy”) ranked much higher than the 3 focal-species models (which contained no covariates for the other 2 species) and was the third highest-ranked model in the final set of 12 (Table 2). The 3 highest-ranked species interaction models all included the same species-specific covariates as the top-ranked multispecies model and were ranked second (“Bobcat–Cougar Interaction”), fifth (“Bobcat–Coyote Interaction”), and sixth (“Coyote–Cougar Interaction”) in the final 12 model set (Table 2).

The highest-ranked model overall was a species interaction-covariate model that included Bobcat–Coyote interactions with a Road covariate (Table 2). The Ruggedness covariate was included in this model for all 3 carnivore species, with feline species trending toward using more rugged terrain (Fig. 2). Bobcats showed a preference for more rugged terrain [$\beta = 1.41$; CI = (−0.57, 3.39)] that was 3.7 times higher than Cougars [$\beta = 0.38$; CI = (−0.10, 0.86)], although the confidence interval for both beta estimates overlapped 0 (Table 3). Coyotes showed a significant preference for less rugged terrain [$\beta = -0.51$; CI = (−0.91, −0.1)] which was 2.7 times lower than the Bobcats preference for ruggedness and 1.3 times lower than the Cougars preference for ruggedness (Table 3). Bobcats were more likely to use areas near open roads, although the confidence interval for this beta estimate overlapped 0 (Table 3). Interestingly, this model included the Distance to Spring covariate for Coyote occupancy even though this covariate did not rank as highly in the single, multispecies, or species interaction model categories. Coyotes trended toward using areas closer to perennial springs, although this beta estimate also overlapped 0 (Table 3). Cougars were the only species that showed a trend toward differences in probability of use between years, although the beta value was not significant (Table 3). Finally, Bobcats and Coyotes were 1.88 times more likely to co-occur on roads than away from roads (Table 3).

The species interaction-covariate models for Bobcat–Cougar and Coyote–Cougar interactions that did not rank as highly were

Table 2. The 12 top models from each of 6 model categories (null model, top detection model, 1 top focal-species model for each species [3 total], the top multispecies occupancy model, the top model for each species interaction [3 total], and the top species interaction-covariate model for 3 different interaction covariates [3 total]). All models used the same data so AICc and AICc weight values can be directly compared. Under the “Model covariates” column, (1) the first row represents covariates used in the detection model indicated by $p()$; (2) the following 3 rows represent covariates used in the single-species occupancy models for each focal species indicated by ψ_{100} for bobcat, ψ_{010} for coyote, and ψ_{001} for cougar; and (3) the last row represents whether pairwise species interactions were included in the model indicated by the terms No Species Interaction, ψ_{110} Bobcat–Coyote(), ψ_{101} Bobcat–Cougar(), and ψ_{011} Coyote–Cougar(), followed by any covariates that were used as additional interaction parameters. The term “(.)” indicates that no covariates were used for a particular model component.

Model name	Model covariates	ΔAICc	No. par.	AICc wt.	-2LogL
Pairwise Interaction (Road)	p (Road, Trail, Canopy Cover) ψ_{100} Bobcat (Ruggedness, Distance to Road) ψ_{010} Coyote (Ruggedness, Distance to Spring) ψ_{001} Cougar (Ruggedness, Year) ψ_{110} Bobcat–Coyote (Road)	0.0	23	0.56	3,825.31
Bobcat–Cougar Interaction	p (Road, Trail, Canopy Cover) ψ_{100} Bobcat (Ruggedness, Distance to Road) ψ_{010} Coyote (Ruggedness) ψ_{001} Cougar (Ruggedness, Year) ψ_{101} Bobcat–Cougar (.)	3.82	21	0.08	3,834.20
Multi-Species Occupancy	p (Road, Trail, Canopy Cover) ψ_{100} Bobcat (Ruggedness, Distance to Road) ψ_{010} Coyote (Ruggedness) ψ_{001} Cougar (Ruggedness, Year) No Species Interaction	4.41	20	0.06	3,837.28
Pairwise Interaction (Human Detections)	p (Road, Trail, Canopy Cover) ψ_{100} Bobcat (Ruggedness, Distance to Road) ψ_{010} Coyote (Ruggedness) ψ_{001} Cougar (Ruggedness, Year) ψ_{101} Bobcat–Cougar (Human Detections)	4.91	22	0.05	3,832.77
Bobcat–Coyote Interaction	p (Road, Trail, Canopy Cover) ψ_{100} Bobcat (Ruggedness, Distance to Road) ψ_{010} Coyote (Ruggedness) ψ_{001} Cougar (Ruggedness, Year) ψ_{110} Bobcat–Coyote (.)	5.90	21	0.03	3,836.28
Coyote–Cougar Interaction	p (Road, Trail, Canopy Cover) ψ_{100} Bobcat (Ruggedness, Distance to Road) ψ_{010} Coyote (Ruggedness) ψ_{001} Cougar (Ruggedness, Year) ψ_{011} Coyote–Cougar (.)	6.75	21	0.02	3,837.13
Coyote Occupancy	p (Road, Trail, Canopy Cover) ψ_{100} Bobcat (.) ψ_{010} Coyote (Ruggedness) ψ_{001} Cougar (.) No Species Interaction	7.80	16	0.01	3,850.37
Pairwise Interaction (Ruggedness)	p (Road, Trail, Canopy Cover) ψ_{100} Bobcat (Ruggedness, Distance to Road) ψ_{010} Coyote (Ruggedness) ψ_{001} Cougar (Ruggedness, Year) ψ_{011} Coyote–Cougar (Ruggedness)	7.96	22	0.01	3,835.82
Bobcat Occupancy	p (Road, Trail, Canopy Cover) ψ_{100} Bobcat (Ruggedness, Distance to Road) ψ_{010} Coyote (.) ψ_{001} Cougar (.) No Species Interaction	21.30	17	<0.01	3,861.48
Cougar Occupancy	p (Road, Trail, Canopy Cover) ψ_{100} Bobcat (.) ψ_{010} Coyote (.) ψ_{001} Cougar (Ruggedness, Year) No Species Interaction	23.55	17	0.0	3,836.73
Detection Only	p (Road, Trail, Canopy Cover) ψ_{100} Bobcat (.) ψ_{010} Coyote (.) ψ_{001} Cougar (.) No Species Interaction	24.23	15	0.0	3,869.16
Null Model	p (.) ψ_{100} Bobcat (.) ψ_{010} Coyote (.) ψ_{001} Cougar (.) No Species Interaction	134.09	6	0.0	3,999.16

Table 3. Covariate beta values and confidence intervals for single-species occupancy and detection models, and the top multispecies co-occurrence model (ψ_{110}) for Bobcats, Coyotes, and Cougars within the highest-ranking model. Data were derived from remote-sensed camera trap data in the Starkey and Mt. Emily study areas in northeastern Oregon, USA, between 2016 and 2017. The first 2 covariates for each single-species model indicate occupancy covariates (ψ), and the following 3 (Road, Trail, and Canopy Cover) indicate detection covariates (p). Beta values over 0 indicate positive occupancy/co-occurrence while values under 0 indicate negative co-occurrence.

Species	Covariate type	Covariate	Beta	Standard error	95% confidence interval	
					Lower	Upper
Bobcat	ψ	Ruggedness	1.41	1.01	-0.57	3.39
	ψ	Distance to Open Road	-1.40	0.82	-3.02	0.21
	p	Road	1.50	0.26	0.99	2.01
	p	Trail	0.51	0.32	-0.12	1.15
	p	Canopy Cover	0.55	0.14	0.27	0.82
Coyote	ψ	Ruggedness	-0.51	0.21	-0.91	-0.1
	ψ	Distance to Spring	-0.35	0.20	-0.74	0.04
	p	Road	0.83	0.15	0.54	1.12
	p	Trail	0.57	0.16	0.26	0.89
	p	Canopy Cover	-0.24	0.06	-0.36	-0.12
Cougars	ψ	Ruggedness	0.38	0.25	-0.10	0.86
	ψ	Year	0.83	0.48	-0.12	1.77
	p	Road	1.11	0.29	0.54	1.68
	p	Trail	0.18	0.33	-0.46	0.82
	p	Canopy Cover	0.46	0.14	0.19	0.73
Bobcat-Coyote Interaction	ψ_{110}	Road	1.88	0.73	0.45	3.32

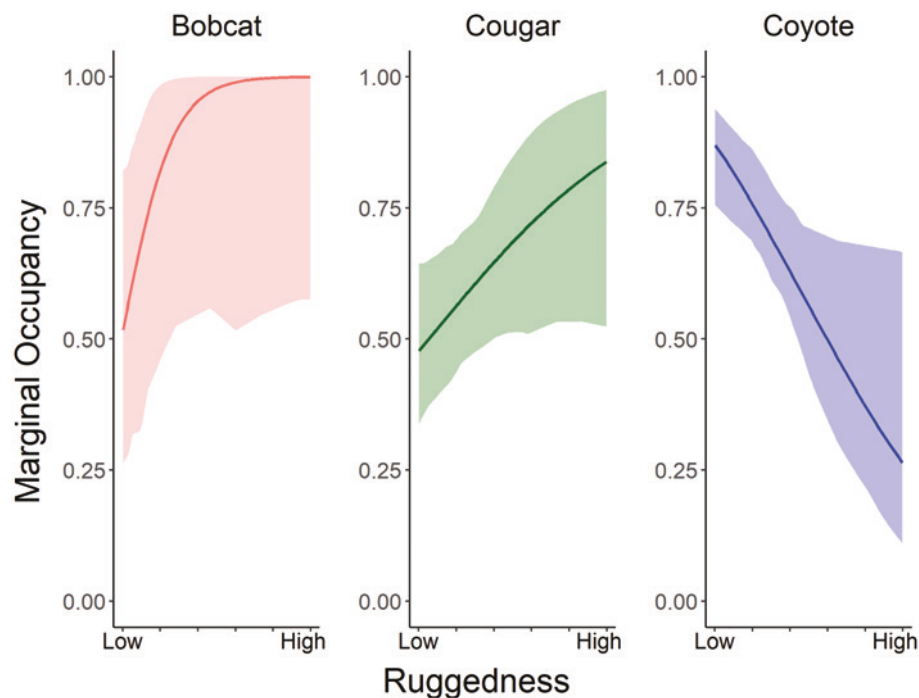


Fig. 2. Predicted occupancy values for Bobcats, Coyotes, and Cougars over the range of terrain ruggedness values (from lowest to highest value in the study area) found across 3 camera grids in northeastern Oregon in 2016 and 2017. Occupancy values for ruggedness were predicted from the top occupancy model with all other covariates held at their mean value.

“Pairwise Interaction (Human Detections)” and “Pairwise Interaction (Ruggedness),” respectively, which ranked fourth and eighth of 12. The first model resulted in a log odds species interaction value of 1.16 [CI = (-0.35, 2.67)] between Bobcats and Cougars and a beta

value for Human Detections of 0.24 [CI = (-0.19, 0.68)]. The second model resulted in a log odds species interaction value of 0.01 [CI = (-1.20, 1.21)] between Coyotes and Cougars and a beta value for Ruggedness of 0.56 [CI = (-0.41, 1.53); Table 2]. Ruggedness was

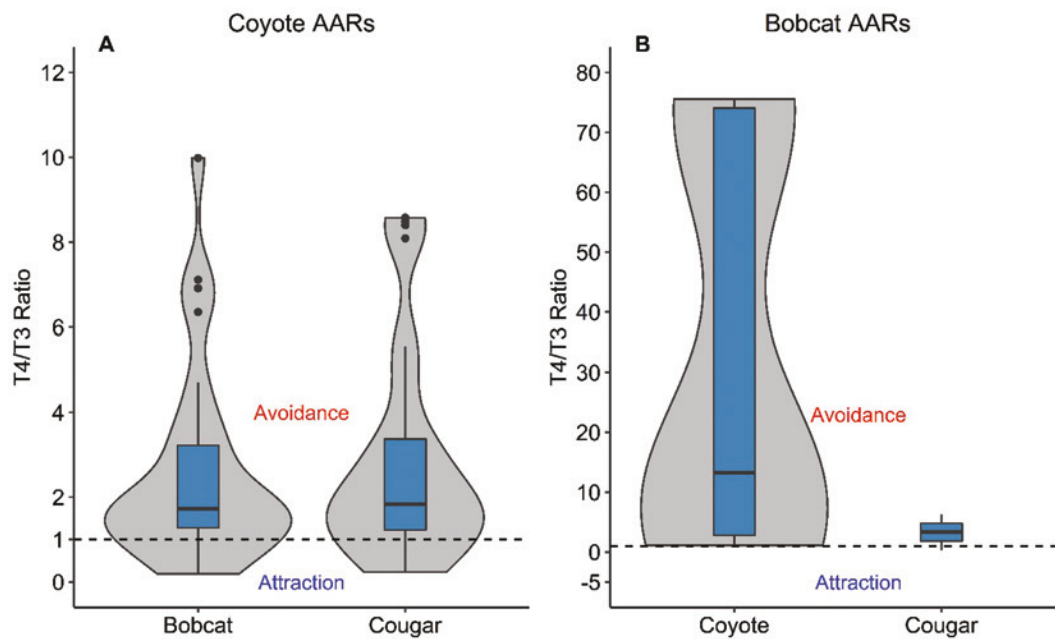


Fig. 3. Attraction-avoidance ratios (AARs) of Bobcats and Coyotes showing fine-scale temporal avoidance of an area after passage of a competing carnivore species. Data were derived from remote-sensed camera trap data in northeastern Oregon in 2016 and 2017. Panel A shows Coyote avoidance of Bobcats and Cougars while panel B shows Bobcat avoidance of Coyotes and Cougars. Boxplots show the median avoidance indicated by the black line, while violin plots are wider in areas with more data points and narrower in areas with fewer data points. Note the different scales on the plot y axes. Bobcats showed both small and large avoidance of Coyotes indicated by the 2 wide areas in the violin plot. Coyotes showed a significant but shorter avoidance of Bobcats and Cougars with some large outliers.

included as a covariate for species interactions post hoc after this covariate was included in the top models in the focal-species and multispecies categories.

Our model-averaged values for species interactions across all models showed varying trends for each pairwise species co-occurrence pattern. Bobcat–Coyote averaged co-occurrence varied widely with no significant pattern that was not explained by covariates [$\psi = -0.23$; $CI = (-1.80, 1.35)$]. Bobcat–Cougar averaged co-occurrence was significantly positive [$\psi = 0.75$; $CI = (8.03e^{-5}, 1.0)$], likely due to both species preferring rugged terrain. Coyote–Cougar averaged co-occurrence showed a weak but significantly positive trend [$\psi = 0.07$; $CI = (2.90e^{-6}, 1.0)$].

The results of the AARs showed that both Bobcats and Coyotes exhibited fine-scale temporal avoidance of other carnivores. Both species had increased passage time when other carnivores were detected between the focal species (i.e., when Coyotes were detected between Bobcat detections, the mean passage time between Bobcat detections increased). Bobcats significantly increased their passage time on cameras where Coyotes were detected (Wilcoxon Signed Rank Exact, $V = 91$, $P = <0.01$) with a median passage increase of 12 days. This avoidance also showed a second, nonsignificant, peak (Fig. 3) of longer avoidance (median passage time increase = 74 days). Bobcats only had enough passages with Cougars in between to calculate 2 $T4/T3$ ratios, which were not enough data to compare statistically. Coyotes avoided both Bobcats (Wilcoxon Signed Rank Exact, $V = 481$, $P = <0.001$; median passage time increase = 1.8 days) and Cougars (Wilcoxon Signed Rank Exact, $V = 615$, $P = <0.001$; median passage time increase = 2.2 days), with some outliers of larger avoidance (Fig. 3).

Discussion

While we found little evidence for large-scale spatial segregation between carnivores, interactions between Bobcats, Coyotes, and

Cougars varied at different spatiotemporal scales. Each of the 3 species showed unique detection rates and habitat use, and most species interactions occurred at fine spatiotemporal scales. These interactions demonstrated support for our first and fourth hypotheses depending on the species involved. The first hypothesis—which proposed that carnivores overlap on a large scale and segregate in space and time at fine scales—was exhibited in Cougar–Bobcat interactions and Cougar–Coyote interactions. Bobcats and Coyotes both showed positive co-occurrence with Cougars on a large scale, although Coyotes avoided the apex predator on a fine scale based on significant results from AARs. The fourth hypothesis—which proposed that carnivores segregate at large scales and segregate in space and time at fine scales—was exhibited in Bobcat–Coyote interactions. Bobcats and Coyotes showed no clear large-scale co-occurrence patterns and had opposing habitat preferences (i.e., Bobcats preferred more rugged terrain while Coyotes did not), although they overlapped on roads more than expected. AAR results also showed that Bobcats and Coyotes avoided each other on a fine spatiotemporal scale. Because we detected some level of interactions between all 3 species on a fine spatiotemporal scale, we found no support for our second and third hypotheses. We also found no evidence that the space use of Cougars was related to the presence of Coyotes at fine spatial scales, and limited support for Bobcats avoiding Cougars at fine spatial scales.

In general, habitat features explained more variation in the large-scale space use of all 3 carnivore species rather than the presence of other carnivores. Terrain ruggedness was important for all carnivore species, although preference for this habitat feature differed among species. Bobcats showed the strongest preference for areas with more rugged terrain, followed by Cougars, while Coyotes preferred more gentle terrain. Cougars likely showed less preference for rugged terrain in the single-species occupancy models than Bobcats because Cougars prey primarily on ungulates that occupy varied terrain, which could have diluted the strength of the

ruggedness covariate selection. Cougars typically use more diverse terrain each season as prey availability fluctuates (Elbroch et al. 2013), so this may have influenced weaker selection for ruggedness in our models. A third influence on Cougar habitat selection is conspecific territoriality (Elbroch et al. 2016), which we were unable to model without individual animal identification or GPS location data. Cougar models also included a year effect (i.e., probability of use differed slightly between 2016 and 2017), which is likely a factor of both fluctuations in their large home ranges and localized territory vacancies associated with hunter harvest, which was relatively high in our study area.

Other unique habitat features proved important for each species (Table 3)—Bobcats had a greater probability of use in areas closer to open roads, and Coyotes were more likely to use areas closer to perennial springs. Canids prefer denning sites close to water sources (Way et al. 2001; Person and Russell 2009) and while we avoided collecting data during the denning period to reduce bias, Coyote pairs still travel with pups to rendezvous sites and beyond throughout the summer. Their preference for less rugged terrain aligns with the location of perennial springs within our study area, which are typically found in ridge-top meadows and drainage bottoms. Past studies have indicated mixed responses by Bobcats to roads (Tigas et al. 2002; Young et al. 2019), although this may be dependent on the degree of urbanization and human use of roads in the areas they are inhabiting. For example, Bobcats in south Texas have been documented to use rural roads often (Bradley and Fagre 1988).

The importance of testing competing hypotheses regarding habitat preferences and species interactions is evident from our results. For example, it could be assumed that the presence of Bobcats and Cougars in more rugged landscapes would prompt Coyotes to avoid these areas and stick to more even terrain with less forest cover. However, our results showed no evidence of such large-scale avoidance behavior between all 3 carnivores, suggesting that interference competition was not the main driver behind large-scale space use patterns. One likely explanation for Coyote preferences for less rugged terrain is that areas such as valley bottoms and ridge-top meadows offer better hunting opportunities (Litvaitis and Shaw 1980; Toweill and Anthony 1988). Felids may prefer more rugged terrain because their ambush style of hunting is facilitated by features such as rocks, steeper slopes, and thicker vegetation (Logan and Irwin 1985; Riley and Malecki 2001; Rieth 2010). Without modeling terrain ruggedness as a covariate or model averaging species interactions (e.g., which showed no clear co-occurrence pattern between Bobcats and Coyotes), we might have concluded that Coyotes were avoiding Bobcats and Cougars due to competition (e.g., Fedriani et al. 2000; Rich et al. 2018).

When considering species interactions, Bobcats and Coyotes both showed positive trends toward large-scale spatial overlap with Cougars in our study area. The small but significant spatial overlap between Cougars and Coyotes is most likely due to an averaged value of strong attraction of Coyotes to Cougar kill sites (Ruprecht et al. 2021) despite divergent habitat preferences (e.g., rugged terrain) between the species. Coyotes scavenge carcasses provisioned by Cougars without large-scale spatial displacement (Ruprecht et al. 2021). Subordinate predator species occasionally demonstrate similar attraction behavior to larger carnivores if the resource reward is higher than the risk of intraguild predation (Paquet 1992; Wilmers et al. 2003; Lonsinger et al. 2017). In fact, carcasses are often such an important resource for scavenging mesocarnivores that apex predators can facilitate resource partitioning among mesocarnivore communities (Sivy et al. 2017) or indirectly suppress populations during resource-stressed years (Prugh and Sivy 2020). Large-scale

spatial overlap between Bobcats and Cougars, however, was more likely due to similar preferences for rugged terrain than scavenging. While Coyotes may heavily scavenge from kills provisioned by apex predators (Paquet 1992; Wilmers et al. 2003; Sivy et al. 2017; Ruprecht et al. 2021), there are fewer documented cases of Bobcats scavenging carcasses (Koehler and Hornocker 1991; Platt et al. 2010) and no Bobcats scavenged on cougar-killed animals in the Starkey study area (Ruprecht et al. 2021).

In contrast, on a fine spatiotemporal scale, Bobcats and Coyotes avoided each other and Cougars, despite Bobcats preferring the same habitat features as cougars. This fine-scale avoidance is not surprising given that Bobcats occasionally experience intraguild predation from both Cougars and Coyotes (Fedriani et al. 2000; Gipson and Kamler 2002). Other studies have found a lack of interference competition between Bobcats and Coyotes even with overlap in diet, home range, or activity patterns (Witmer and DeCalesta 1986; Major and Sherburne 1987; Litvaitis and Harrison 1989), suggesting some degree of segregation within 1 of these 3 categories (Neale and Sacks 2001). These variations show that Bobcat–Coyote interactions likely vary by region and/or habitat type and suggest that site-specific factors mediate the magnitude of their interactions.

In our study area, the interactions between Bobcats and Coyotes manifested in fine-scale avoidance overall but greater tolerance for each other on shared travel routes like roads, reflected in our highest-ranked model as the covariate for the species interaction term (Table 2). Roads are often used as efficient movement corridors by carnivores (Dickie et al. 2020) and a review of over 120 studies recording road use by mammals found that carnivores were the most common group of species to use roads (Hill et al. 2021). This finding also supports previous findings of Bobcats and Coyotes using roads as travel routes. In Michigan, they, along with other carnivore species, showed a preference for using roads, particularly at night (Kautz et al. 2021). While our top detection model showed that all 3 carnivores were more likely to be detected on roads, roads did not predict occupancy for Cougars in our top occupancy models (Table 2). This could be due to Cougars using different travel routes (e.g., ridgetops) more frequently than roads throughout their large home ranges, and thus they did not overlap with Bobcats and Coyotes as frequently in this regard. Additionally, Cougars regularly crossed drainages in our study area while roads did not.

The role of roads in explaining Bobcat–Coyote interactions highlights the importance of considering the impact of the human footprint (i.e., development) on species interactions. Without including roads as a covariate in species interaction models, it would have been easy to speculate that Bobcat–Coyote co-occurrence could be due to shared prey species given the documented diet overlap in these species (e.g., Witczuk et al. 2015). However, anthropogenic influences can affect the spatial distribution and daily activity patterns of carnivores (Díaz-Ruiz et al. 2016), particularly apex carnivores (Nickel et al. 2020). Subordinate competitors, on the other hand, may exploit the human footprint to use preferred habitat (Nickel et al. 2020). While human development in our study area was low, there were a large amount of forest roads built for logging.

We encourage future studies on species interactions to test hypotheses about differences in habitat use as well as competitive effects at multiple scales given that interactions could be interpreted inaccurately if both factors are not included. We found evidence that Bobcats, Cougars, and Coyotes in our study area coexist through fine-scale avoidance in space and time, but without accounting for habitat preferences (e.g., rugged terrain) we could have concluded that large-scale spatial segregation due to habitat preferences was also a result of competition. Conversely, if we

had not modeled fine scale spatiotemporal interactions (e.g., via attraction–avoidance ratios) we would have missed evidence of avoidance between carnivore species at this scale. Observational studies in particular should be mindful about accounting for habitat preferences and interactions at multiple spatiotemporal scales to fully investigate the effects of human-influenced landscapes on carnivore interactions, as these effects will have accelerating impacts on carnivore interactions in the Anthropocene (Haswell et al. 2017). Large-scale niche separation, fine-scale avoidance, and the exploitation or avoidance of manmade features on a landscape are likely common patterns among carnivore species in the increasingly managed landscapes of North America and the world.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

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Author contributions

Conceptualization—JR, TL, TDF; **data curation**—RJ, JR, EO, TDF; **formal analysis**—RJ, TDF; **funding acquisition**—TL, DEC; **investigation**—DEC, TDF; **methodology**—JR, EO, TL, TDF; **project administration**—JR, EO, TL, DEC, TDF; **resources**—DEC; **supervision**—TL, DEC, TDF; **validation**—TL; **visualization**—TDF; **writing, original draft**—RJ, TDF; **writing, review and editing**—RJ, JR, EO, TL, DEC, TDF.

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Conflict of interest

None declared.

Data availability

Data unavailable at this time, but will be made publicly available in the future by the U.S. Forest Service Pacific Northwest Research Station.

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