Space use and temporal relationships among western spotted skunks (*Spilogale gracilis*) and two competing mesocarnivores on the Olympic Peninsula of Washington

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Abstract

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Among sympatric carnivores, acts of interference competition range in intensity from the threat of attack to interspecific killing (IK). If IK is a regular outcome of encounters between two carnivores, the subordinate species may be forced to avoid the other in space and/or time. Carnivores are at the greatest risk of becoming victims of IK if they are 2–4 times smaller than their potential attacker. Thus, the spatial distributions and activity patterns of small carnivores may be dictated by the presence of larger competitors. However, many species rely on constitutive defenses—those that are always present and provide continuous protection—to reduce the risk of mortality during encounters with predators, and thus small, but constitutively defended, carnivores such as skunks may not respond to the threat of IK through spatial or temporal avoidance. To explore the hypothesis that the risk of predation and IK by larger competitors is mitigated by constitutive defenses, we used multispecies occupancy models and detection/non-detection data from baited camera stations and collocated hair snares to test for pairwise interaction effects on the space use of western spotted skunks (*Spilogale gracilis*), coyotes (*Canis latrans*), and bobcats (*Felis rufus*) on the Olympic Peninsula of Washington, USA. Use of a multispecies occupancy model simultaneously allowed us to examine the spatial relationship between coyotes and bobcats and thus we also tested a secondary hypothesis that the slight body size disparity between the coyotes and bobcats and high dietary overlap between the two species promotes IK, which is dominated by coyotes. We also used timestamp data taken from camera detections to analyze the temporal overlap of daily activity patterns of all three species. We found no evidence of spatial or temporal avoidance among the three focal species. Our best supported occupancy model indicated that these species use space independently of one another, and we found high levels of temporal overlap among all three species. Our findings suggest that neither western spotted skunks nor bobcats fall victim to IK at a great enough rate to promote avoidance of their respective potential attacker(s). The decision to engage in IK is influenced by many risk and reward factors and the constitutive defense of western spotted skunks is likely a strong deterrent. Likewise, bobcats may be too formidable of an opponent—armed with sharp claws in addition to teeth—for coyotes to attack with regularity.

Acknowledgements

My masters research was originally focused on the Pacific marten (*Martes caurina*) population on the Olympic Peninsula. Due to the local rarity of the species, after two field seasons of hard work, we detected martens in only five study sites. While I believe our findings concerning the marten will have meaningful impact on the species' conservation, they didn't provide me with opportunity to conduct an in-depth analysis worthy of a master's degree. To that end, I am very pleased to have been able to transition my focus to another small carnivore residing on the Olympic Peninsula: the western spotted skunk (*Spilogale gracilis*). Data used in this thesis originates from a collaboration of tribal, state, and federal agencies, and I am very grateful to have been brought on as a collaborator. These agencies include: The Port Gamble S'Klallam Tribe, Lower Elwha Klallam Tribe, Makah Tribe, Point-no-Point Treaty Council, Quileute Tribe, Quinault Indian Nation, Skokomish Tribe, Jefferson Land Trust, Washington Department of Fish and Wildlife, Washington Department of Natural Resources, Olympic National Park, Olympic National Forest, and the United States Geological Survey. I would like to thank all of the people from these agencies who helped collect this data and especially the Olympic Fisher Field Crew members for their hard work.

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Introduction

Competition among sympatric carnivores can have considerable impacts on the subordinate competitor's abundance and distribution (Soulé et al. 1988, Crooks and Soulé 1999, Linnell and Strand 2000, Prugh et al. 2009, Ripple et al. 2013, Newsome et al. 2017). The outcomes of interference competition among carnivores, which range from displacement from shared resources to interspecific killing (IK) (Palomares and Caro 1999, Donadio and Buskirk 2006), are driven primarily by relative body size, with smaller-bodied guild members generally being subordinate (Palomares and Caro 1999, Prugh et al. 2009, Prugh and Sivy 2020). Interspecific killing has been found to account for the majority of mortality suffered by subordinate species in some systems (Cypher and Spencer 1998, Palomares and Caro 1999, Fedriani et al. 2000, Breck et al. 2006). Carnivores are most likely to be a victim of IK when they are 2–4 times smaller than their attacker (Palomares and Caro 1999, Prugh and Sivy 2020) and have a high degree of dietary overlap with (Donadio and Buskirk 2006) the would-be perpetrator.

To avoid being killed, prey species and subordinate competitors within carnivore guilds are expected to alter their behavior to reduce exposure to potential attackers (Lima and Dill 1990). These behavioral changes can manifest as spatial or temporal avoidance (Amarasekare 2003). However, constitutive defenses allow many species to reduce their risk of mortality during encounters with predators or dominant competitors (Wirsing et al. 2021). Constitutive defenses are defensive traits that are constantly present and provide continuous protection for a species. For example, some insects (Sloggett et al. 2009, Dowdy and Conner 2016, Decker et al. 2019) and amphibians (Hague et al. 2016, Kaczmarek et al. 2022) synthesize or sequester toxins from their food to make themselves unpalatable to predators. These species often forgo attempting to hide from predators and instead advertise their unpalatability through conspicuous aposematic coloring (Caro and Ruxton 2019). Species such as the North American porcupine (*Erethizon dorsatum*), nine-banded armadillo (*Dasypus novemcinctus*), and Western long-beaked echidna (*Zaglossus bruijnii*) instead use quills, dermal plates, and spines to prevent or withstand attacks from predators (Stankowich and Campbell 2016), and various members of the families Viverridae (e.g., common genet [*Genetta genetta*]), Ailuridae (red panda [*Ailurus fulgens*]), Mustelidae (e.g., zorilla [*Ictonyx striatus*]), and Mephitidae (e.g., striped skunk [*Mephitis mephitis*]) use noxious secretions or sprays in defense against attackers (Stankowich et al. 2014). By reducing the risk of predation or IK, effective constitutive defenses may reduce the need for subordinate members of carnivore guilds to avoid these threats through spatial or temporal avoidance.

However, even the most potent constitutive defenses may be overcome by predators or larger competitors. For instance, the quills of the North American porcupine can maim or even kill attackers (Katzner et al. 2015) and yet this species is subject to predation by fishers (*Pekania pennanti*), considered to be porcupine specialists, mountain lions (*Puma concolor*), and coyotes (*Canis latrans*) (Sweitzer 1996, Sweitzer et al. 1997, Mabille et al. 2010, Pokallus and Pauli 2015). Defenses may also only be effective against some of the predators or competitors that a species may encounter. The noxious spray defense of skunks, for example, is effective against mammalian predators but avian predators that lack highly developed olfactory senses are known to depredate skunks (Lesmeister et al. 2010, Hassler et al. 2021*a*, Tosa et al. 2022). Additionally, environmental factors may reduce the efficacy of defensive adaptations. For instance, porcupine predation rates have been linked to winter precipitation rates as deep snow inhibits this already slow-moving animal's ability to reach escape cover (Sweitzer 1996, Mabille et al. 2010).

Pokallus and Pauli (2016) found that porcupines increased energy expenditures by taking longer routes, despite being nutritionally stressed during the winter, to avoid open habitats that were perceived to be more risky and were more likely to use areas with refuge trees. Accordingly, responses to the risk of predation or IK by constitutively defended taxa may vary as a function of the enemy posing the threat and changing environmental factors.

In a review of the order Carnivora, Hunter and Caro (2008) found that the skunks of the family Mephitidae are sympatric with the greatest number of larger carnivores with which they also overlap in habitat type, habitat strata, and temporal activity pattern. This high degree of overlap with multiple higher-order carnivores potentially exposes them to considerable risk of IK (Hunter and Caro 2008). However, all members of Mephitidae are capable of accurately directing a noxious spray at attackers, and they signal their defensive capabilities to would-be attackers through black and white aposematic coloration (Stankowich et al. 2014, Caro and Ruxton 2019). Predators exposed to skunk spray are at risk of temporary blindness, disorientation, vomiting, and, in rare cases, death (Garcelon 1981, Zaks et al. 2005, Fierro et al. 2013, Means 2013, Harris et al. 2019). This advanced predator defense likely contributes to the low observed predation rates of skunks; striped skunks tracked via radio telemetry in North Dakota and Illinois, USA were rarely preyed upon (Sargeant et al. 1982, Gehrt 2005, Prange and Gehrt 2007). Dietary analyses of bobcats (reviewed by Tewes et al. 2017) and an analysis of the stomach contents of ~14,000 coyotes (Sperry 1941) from across the continental USA found that skunks typically constituted <2% of samples. Furthermore, skunk behavioral responses to potential predators and/or sources of IK in carnivore guilds have been found to be muted. Striped skunks did not shift or alter the size of their home ranges (Prange and Gehrt 2007) or alter their foraging behavior at bait sites (Fisher and Stankowich 2018) in response to an artificial increase in perceived coyote activity (accomplished by spreading coyote urine or playing recordings of howls), and furthermore did not flee from coyotes that were also attracted to bait sites (Fisher and Stankowich 2018). In fact, Fisher and Stankowich (2018) report that skunks in their study area frequently charged at approaching coyotes and caused them to retreat. Yet, skunks are sometimes subject to high rates of predation or IK. For instance, Lesmeister et al. (2010) found that 26% of eastern spotted skunk (*Spilogale putorius*) mortalities were attributable to mammalian predators. Thus, the behavioral responses of skunks to the risks of predation and IK may vary across ecosystems and potential perpetrators.

Here, we examine the spatial and temporal responses of western spotted skunks (*Spilogale gracilis*) to the risk of predation and IK in the Pacific Northwest of the USA where they are sympatric with coyotes and bobcats (*Lynx rufus*). The western spotted skunk (WSS) is thought to be common throughout its range along the west coast of the USA (Verts et al. 2001, Zielinski et al. 2005, Tosa et al. 2024). On Washington State's Olympic Peninsula, the species was the most commonly detected forest carnivore during winter surveys in the Olympic National Park (Happe et al. 2005). Nevertheless, its ecology is poorly understood (Carey and Kershner 1996, Tosa et al. 2023). WSS are dietary generalists and have been found to consume a wide variety of food items including plants, amphibians, small mammals, birds, insects, and carrion (Tosa et al. 2023). However, in the Pacific Northwest they primarily consume insects during the dry season and increase their consumption of small mammals during the wet season (Tosa et al. 2023). While bobcats are native to the Olympic Peninsula, coyotes invaded the region in the early 1900s, facilitated by the extirpation of gray wolves (*Canis lupus*) and the conversion of forests to pasture and cropland (Bailey 1930, Dalquest 1948). Coyotes and bobcats in Washington, USA, weigh approximately 13.6 and 9.1 kg, respectively (Dalquest 1948). By contrast, the average weight of male and female WSS, captured in Oregon, USA, was 595 and 392 g, respectively (Tosa et al. 2024). Thus, coyotes and bobcats are approximately 22 and 15 times larger than male WSS, respectively. A diet analysis of coyotes and bobcats conducted in Olympic National Park found that, although mountain beavers (*Aplodontia rufa*) and snowshoe hares (*Lepus americanus*) were the primary prey of both species, small mammals were also frequently consumed (Witczuk et al. 2013). The large body size disparity between WSS and coyotes and bobcats would suggest that the risk of IK may be low, but overlapping use of small mammals may promote IK. Furthermore, WSS are of similar body size to mountain beavers (0.40–1.29 kg; Verts and Carraway 1998), a primary prey item of both coyotes and bobcats on the Olympic Peninsula, which could position WSS as a valuable prey item as well if its defenses could be overcome. Here, using a multispecies occupancy model and temporal overlap analysis, our primary goal was to test the hypothesis that the risk of predation and IK by larger competitors is mitigated by the constitutive defenses of smaller competitors. This hypothesis leads to the prediction that WSS will not avoid spatial or temporal overlap with coyotes and bobcats. The framework of the multispecies occupancy model also allows us to simultaneously examine the spatial relationship between bobcats and coyotes. Thus, we also test the hypothesis that the body size advantage of coyotes and high dietary overlap with bobcats, which lack specialized constitutive defenses, promotes interference competition and IK. This hypothesis leads to the prediction that bobcats will avoid spatial or temporal overlap with coyotes.

Methods

Study Area

Survey sites that yielded the detection/non-detection data used in this investigation were established as part of the Olympic Fisher Monitoring Program (OFMP), which used baited camera trap stations to evaluate the success of fisher reintroductions on the Olympic Peninsula of Washington state, USA from 2013–2016 (Happe et al. 2015, 2020). The Olympic Peninsula is characterized by a rapid transition from sea level to the peaks of the Olympic Mountain Range, resulting in a rain shadow effect and thus a marked precipitation gradient from west to east. The west side of the peninsula receives 300–500 cm of precipitation per year whereas the eastern side receives approximately 100 cm per year (Nielsen et al. 2021). Precipitation falls primarily as rain at elevations below 300 m and as snow at elevations above 900 m (Nielsen et al. 2021). Forests on the peninsula are predominately coniferous, with broadleaf forests located in low elevation riparian zones (Nielsen et al. 2021). The Olympic National Park (ONP) and designated wilderness areas of the Olympic National Forest (ONF) lie in the center of the Olympic Peninsula and along its western coast. The ONP and ONF wilderness areas support old-growth forests that are protected from development and timber harvest. Much of the private and public lands surrounding the ONP and ONF wilderness areas are managed for timber production.

Data Sources and Preparation

The methods used to select survey locations and deploy and maintain camera traps are described in Happe et al. (2020). Briefly, a grid of 24 km^2 hexagonal cells was overlaid on the Olympic Peninsula and every other cell was selected as a potential sample unit; sample units in which the elevation of the centroid exceeded 1,425 m were rejected, resulting in 150 sample units. The sampling frame was divided into two panels and each panel was surveyed every other year from 2013–2016 with the goal of surveying every sample unit twice with a 2-year interval between surveys. In 2015 and 2016, survey efforts were focused on repeating surveys conducted in 2013 and 2014, respectively, but additional sample units were also added and surveyed for the first time, resulting in a total of 180 sample units (Fig. 1). Sample units were surveyed from late

May to early November each year. Within each sample unit, three survey stations were deployed in forested stands with trees ≥20 cm in diameter at breast height; stations were separated by at least 800 m when possible. Each survey station consisted of a motion-sensing camera (Bushnell Trophy Cam HD, Overland Park, KS) and a hair snaring device (Schwartz et al. 2006) to collect DNA samples. Each station was baited by affixing a piece of raw chicken and applying ~10 ml of a scent lure (Caven's Gusto, Minnesota Trapline Products, Pennock, MN) and lanolin mixture to the base of a tree. Each hair snare device was equipped with metallic brushes and was also baited with chicken to encourage fishers to enter the cubby and, in doing so, deposit hair samples on the brushes. Hair snare devices were placed on the ground at the base of the bait tree, and the camera was positioned to capture both the hair snare device and the bait tree in its field of view. Three consecutive 14-day surveys were attempted at each station with a researcher visit at the start of each survey to replenish bait, and to collect camera data and hair samples from the previous survey period. The survey period was defined as the number of days between researcher visits and sometimes varied across surveys due to field logistics. If survey stations were disturbed by American black bears (*Ursus americanus*), the station was moved at least 50 m to attempt to avoid habituated responses to bait. Similarly, WSS were often found to spend considerable time at survey stations, consuming all available bait, and thus some survey stations were moved to avoid baits being consumed early in a survey period by a species the monitoring program was not targeting. At the conclusion of each survey period, all detected species were identified from the camera data, and hair samples were sent to the National Genomics Center for Wildlife and Fish Conservation (Rocky Mountain Research Station, Fort Collins, CO, USA) for identification to the species level. Because cameras and hair snare devices were collocated at survey stations, detections from each were combined to determine what species were detected

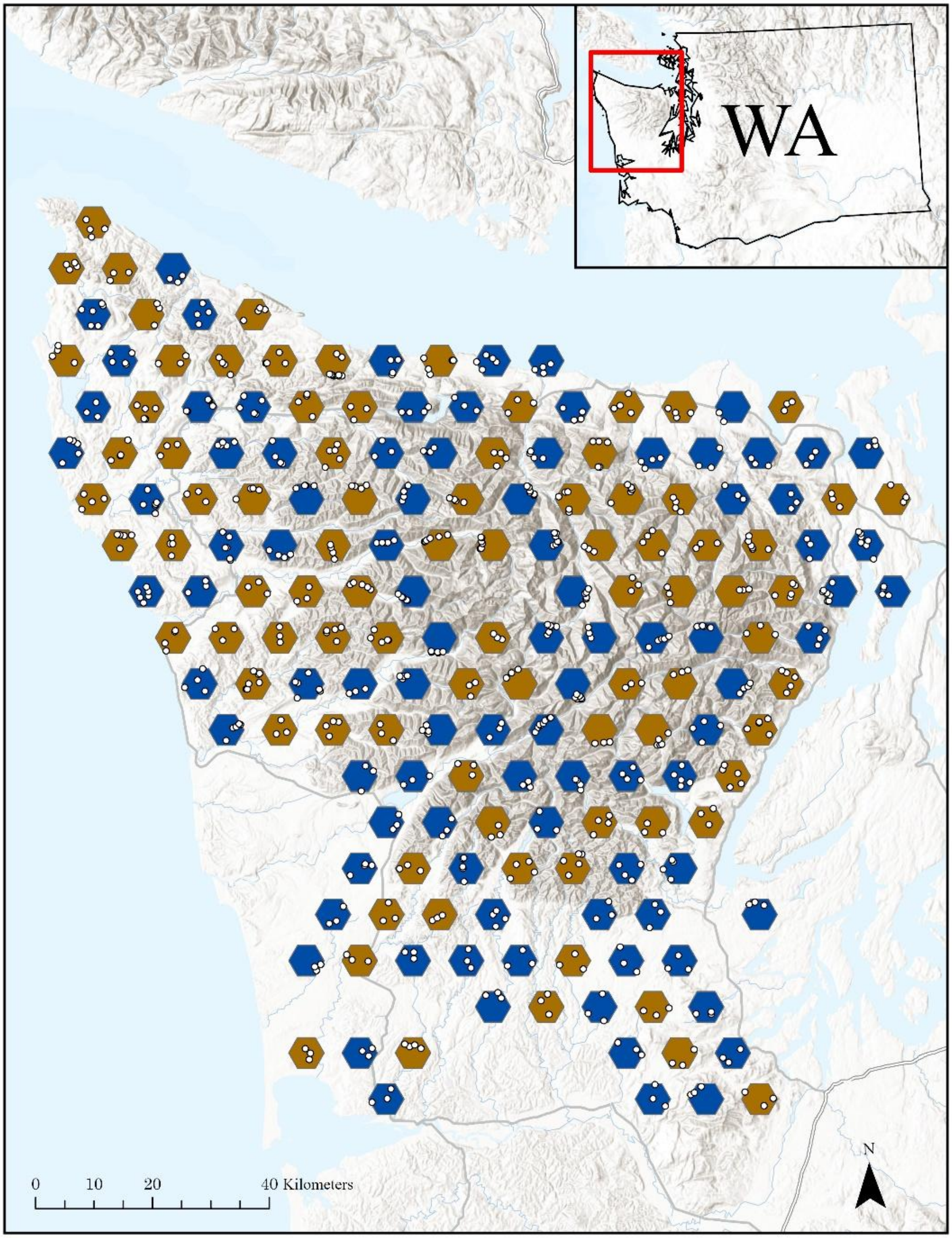

Figure 1. Layout of the Olympic Fisher Monitoring Program sample units (blue and brown hexagons) and the locations of survey sites (white dots) on the Olympic Peninsula. The sample frame was divided into halves and each panel was surveyed every other year. Brown hexagons were surveyed in 2013 and/or 2015 and blue hexagons were surveyed in 2014 and/or 2016.

during each survey period.

To derive biologically relevant occupancy estimates and avoid “grid saturation,” where occupancy probability tends toward 1 as the size of the sample unit increases (Kunin et al. 2000), the home range size of the focal species is typically used as the sample unit size (Steenweg et al. 2018). Accordingly, OFMP sample units (24 km^2) were selected to correspond to the size of home range core areas used by female fishers in the study area (Happe et al. 2015) and the distances between concurrently deployed survey stations within a sample unit ranged up to 5,080 m. Few studies have analyzed the home range size of WSS, but annual home ranges of *Spilogale* spp. range from 0.52–5.72 km^2 (Jones et al. 2008, Thorne 2020, Harris et al. 2023, but see Tosa et al. 2024) and seasonal home ranges of eastern spotted skunks have been found to range from 0.76–8.66 km^2 (Lesmeister et al. 2009). Owing to the mismatch in size between OFMP sample units and the reported home ranges of *Spilogale* spp., we elected to not use the OFMP sample units.

Because of the highly variable distances among survey stations, when attempting to generate new sample units based on WSS home ranges, we consistently encountered overlapping sample units that shared survey stations. Rather than arbitrarily assigning survey stations to a sample unit when overlaps occurred, we instead treated the survey stations themselves as sample units (hereafter: sites). To improve the degree of independence between sites, we considered any survey stations within 150 m of each other to be sampling the same site. Thus, all survey stations established >150 m from any neighboring station were considered unique sites. Sites contained at most two survey stations and in sites with two stations, we considered the first station established (i.e., the older station) to be the center of the site. We selected 150 m as a cutoff as there was a natural break in the data when examining the distances to nearest neighbor for all stations.

We created detection histories of WSS, coyotes, and bobcats for each site. Each value in a detection history corresponds to a survey conducted at the site, and indicates whether the focal species was detected during that survey, with a "1" indicating a detection and a "0" indicating a non-detection. We then combined the three focal species' detection histories into a single community state detection history for each site. With three species, there are eight possible community states that can be observed. We arbitrarily numbered each community state (Table 1) and used those values to assemble community state detection histories according to which combination of species had been detected in each survey. As an example, if three surveys were conducted at site j and the following detection histories were generated for the three focal species:

$$H_{j,WSS} = 110$$

$$H_{j,coyote} = 100$$

$$H_{j,bobcat} = 100$$

the resulting community state detection history for site j would be:

$$H_{j,community} = 821$$

Table 1. Community state labels and descriptions

Community State	Description
1	No WSS, coyotes, or bobcats present
2	Only WSS present
3	Only coyotes present
4	Only bobcats present
5	WSS and coyotes present
6	WSS and bobcats present
7	Coyotes and bobcats present
8	WSS, coyotes, and bobcats present

The community state detection histories (hereafter: detection histories) were unequal in length across sites due to 1) the number of survey stations in each site, 2) the number of surveys completed at each survey station, and 3) whether the site was sampled in one year or two. While the goal was to conduct three surveys at each station within a sampling year, some stations did not reach that goal if they were relocated due to American black bear or WSS activity and, conversely, at a limited number of stations a fourth survey was opportunistically conducted. Thus, within a single year, detection histories ranged in length from 1–4 occasions. To ease model implementation, we added dummy occasions so that each site's detection history contained eight occasions. We then set detection probabilities to 0 for these dummy occasions (more details below). We followed a robust design (Pollock 1982, MacKenzie et al. 2003) and split the detection histories into two primary sampling periods, representing two years of sampling, with four secondary sampling periods each, representing four surveys conducted in the site each year. By assuming that the state of the site can change between, but not within, years, we can reasonably meet the assumption of temporal closure necessary for occupancy modeling. Finally, we treated the primary sampling periods as generic "season 1" and "season 2" regardless of the actual year in which the sampling occurred by using a "stacked data" approach (Kery and Royle 2020).

Statistical Analysis

We used a Bayesian multispecies occupancy model (Miller et al. 2012, MacKenzie et al. 2018) similar to that described by Rota et al. (2016) to test for interactions among the focal species. A multispecies model modifies the single-species occupancy model put forth by MacKenzie et al. (2002) to accommodate two or more species. Importantly, the imperfect detection of each of the focal species is accounted for while estimating the latent community state of the sites. This step is accomplished by pairing a detection process model with a latent state process model (MacKenzie et al. 2002, Rota et al. 2016). For those sites that were surveyed in two years, we also incorporated an autoregressive function to allow the estimated latent community state of a site in season 1 to inform its season 2 estimate (MacKenzie et al. 2018, Sipe et al. 2023, Larson et al. 2024). Because some of the distances between sites were less than the radii of the average estimated home ranges of WSS, coyotes, and bobcats, the assumption of independence between sites is likely violated and therefore we interpret the results of our analysis as use rather than occupancy (MacKenzie 2005).

State Process Model

The latent community state of each site was treated as a categorical random variable with eight potential outcomes:

$$Z_{\mathrm{j,t}} \sim \mathrm{Categorical}\left(\Psi_{j,t}^{1}, \Psi_{j,t}^{2}, \Psi_{j,t}^{3}, \Psi_{j,t}^{4}, \Psi_{j,t}^{5}, \Psi_{j,t}^{6}, \Psi_{j,t}^{7}, \Psi_{j,t}^{8}\right)$$

where $Z_{\mathrm{j,t}}$ is the latent state of site *j* during season *t* and $\Psi_{j,t}^{s}$ is the probability that site *j* will take community state *s* during season *t*. The community state probabilities ($\Psi_{j,t}^{s}$) were then modelled as a function of covariates using the multinomial-logit link (Rota et al. 2016, Fidino et al. 2019):

$$\psi_{j,t}^{1}=\frac{1}{1+\exp\left(f_{j,t}^{1}\right)+\exp\left(f_{j,t}^{2}\right)+\exp\left(f_{j,t}^{3}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{12}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{3}+f_{j,t}^{13}\right)+\exp\left(f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{23}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{12}+f_{j,t}^{13}+f_{j,t}^{23}\right)}$$

$$\psi_{j,t}^{2}=\frac{\exp\left(f_{j,t}^{1}\right)}{1+\exp\left(f_{j,t}^{1}\right)+\exp\left(f_{j,t}^{2}\right)+\exp\left(f_{j,t}^{3}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{12}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{3}+f_{j,t}^{13}\right)+\exp\left(f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{23}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{12}+f_{j,t}^{13}+f_{j,t}^{23}\right)}$$

$$\psi_{j,t}^{3}=\frac{\exp\left(f_{j,t}^{2}\right)}{1+\exp\left(f_{j,t}^{1}\right)+\exp\left(f_{j,t}^{2}\right)+\exp\left(f_{j,t}^{3}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{12}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{3}+f_{j,t}^{13}\right)+\exp\left(f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{23}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{12}+f_{j,t}^{13}+f_{j,t}^{23}\right)}$$

$$\psi_{j,t}^{4}=\frac{\exp\left(f_{j,t}^{3}\right)}{1+\exp\left(f_{j,t}^{1}\right)+\exp\left(f_{j,t}^{2}\right)+\exp\left(f_{j,t}^{3}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{12}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{3}+f_{j,t}^{13}\right)+\exp\left(f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{23}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{12}+f_{j,t}^{13}+f_{j,t}^{23}\right)}$$

$$\psi_{j,t}^{5}=\frac{\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{12}\right)}{1+\exp\left(f_{j,t}^{1}\right)+\exp\left(f_{j,t}^{2}\right)+\exp\left(f_{j,t}^{3}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{12}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{3}+f_{j,t}^{13}\right)+\exp\left(f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{23}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{12}+f_{j,t}^{13}+f_{j,t}^{23}\right)}$$

$$\psi_{j,t}^{6}=\frac{\exp\left(f_{j,t}^{1}+f_{j,t}^{3}+f_{j,t}^{13}\right)}{1+\exp\left(f_{j,t}^{1}\right)+\exp\left(f_{j,t}^{2}\right)+\exp\left(f_{j,t}^{3}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{12}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{3}+f_{j,t}^{13}\right)+\exp\left(f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{23}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{12}+f_{j,t}^{13}+f_{j,t}^{23}\right)}$$

$$\psi_{j,t}^{7}=\frac{\exp\left(f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{23}\right)}{1+\exp\left(f_{j,t}^{1}\right)+\exp\left(f_{j,t}^{2}\right)+\exp\left(f_{j,t}^{3}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{12}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{3}+f_{j,t}^{13}\right)+\exp\left(f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{23}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{12}+f_{j,t}^{13}+f_{j,t}^{23}\right)}$$

$$\psi_{j,t}^{8}=\frac{\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{12}+f_{j,t}^{13}+f_{j,t}^{23}\right)}{1+\exp\left(f_{j,t}^{1}\right)+\exp\left(f_{j,t}^{2}\right)+\exp\left(f_{j,t}^{3}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{12}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{3}+f_{j,t}^{13}\right)+\exp\left(f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{23}\right)+\exp\left(f_{j,t}^{1}+f_{j,t}^{2}+f_{j,t}^{3}+f_{j,t}^{12}+f_{j,t}^{13}+f_{j,t}^{23}\right)}$$

The use of the multinomial-logit link constrains the probability of $\Psi_{j,t}^{s}$ such that $\sum_{s=1}^{8}\Psi_{j,t}^{s}=1$. The first-order natural parameters, $f_{j,t}^{1},\ f_{j,t}^{2},\ f_{j,t}^{3}$, are logit-linear predictors of the log odds that WSS, coyotes, and bobcats, respectively, will use site *j* during season *t* (Rota et al. 2016, Fidino et al. 2019). Additionally, the second-order natural parameters, $f_{j,t}^{12}$, $f_{j,t}^{13}$, $f_{j,t}^{23}$, are logit-linear predictors that represent how the interaction effect between the members of a dyad modifies the probability that both species will use a site in the same season. The species will occur independently of one another if their corresponding second-order parameter is equal to zero (Rota et al. 2016). We assumed that the potential third-order natural parameter was equivalent to zero (i.e., there is no additional interaction effect modifying the probability of all three species occurring together; Rota et al. 2016, Fidino et al. 2019). During season $t = 1$, the natural parameters are modeled solely as functions of covariates:

$$f_{j,1}^{n} = x_j^T \beta_n$$

where *n* denotes the specific natural parameter, x_j is a vector of site-specific covariates (described below), and β_n is a natural parameter-specific vector of regression coefficients.

To model the "persistence" of each species, or its probability of continuing to use a site in season 2 if it had used the site in season 1, we incorporated an autoregressive parameter, following Larson et al. (2024), into the models of the first-order natural parameters during season $t = 2$:

$$f_{j,2}^{n} = x_j^T \beta_n + (S_{n,j,t=1}\, \theta_n)$$

where *n* can take the values 1, 2, or 3 to represent WSS, coyotes, or bobcats, respectively. $S_{n,j,t=1}$ takes the value of 1 if the species used site *j* during season $t = 1$ or a 0 if not and θ_n is the autoregressive parameter for species *n*. Traditionally, multi-season occupancy models incorporate information regarding the persistence of the focal species by estimating site extinction and colonization parameters (MacKenzie et al. 2003, Fidino et al. 2019). We elected to use the simpler autoregressive parameter approach given the already considerable model complexity and because our interest was primarily in the species interactions. Additionally, the two-year interval between primary sampling periods would complicate interpretation of the colonization and extinction parameters.

We used minimally informative normal priors, normal(0, SD = 1), on the intercepts of all logit-linear predictors and on each species' autoregressive parameter. We used shrinkage priors on all other regression coefficients. Shrinkage priors are a method of model regularization that balances model fit with model parsimony by shrinking coefficients associated with less influential covariates toward zero while having little effect on coefficients associated with more influential covariates (Hooten and Hobbs 2015, Van Erp et al. 2019). This approach in effect acts as a method of model-based model selection by only retaining covariate effects that have a detectable effect on the response variable while shrinking others toward zero (Hooten and Hobbs 2015). Each of g coefficients was given a prior of normal(0, σ_g) and σ_g was given a prior of exponential(1). Although this method does shrink coefficients toward zero, it is not capable of reducing them to exactly zero (Van Erp et al. 2019).

Observation Process Model

The observations, $y_{k,j,t}$, resulting from each survey k of site j during season t (i.e., the survey results comprising the detection history of each site) were treated as imperfect observations of the site's true community state, and we modeled them as categorical random variables:

$$y_{k,j,t} \mid Z_{j,t} \sim Categorical(p^1_{k,j,t}, p^2_{k,j,t}, p^3_{k,j,t}, p^4_{k,j,t}, p^5_{k,j,t}, p^6_{k,j,t}, p^7_{k,j,t}, p^8_{k,j,t})$$

where $p^n_{k,j,t}$ is the probability of observing community state n during survey k of site j in season t, conditional on the true community state of the site, $Z_{j,t}$. We assumed there can be no false positive detections of any species. Therefore, the true community state of the site constrains which community states can potentially be observed by each survey conducted in the site. For instance, if a site is occupied by skunks and coyotes (true community state = 5), a survey could potentially observe neither species, just skunks, just coyotes, or both skunks and coyotes (community states 1, 2, 3, or 5, respectively) but could never observe a community state containing bobcats (community states 4, 6, 7, or 8). Thus, the probabilities in the above equation are taken from the rows of a single column, dictated by the site's true community state, in the probability matrix:

$$z_{j,t}$$

$$y_{k,j,t}\quad \begin{array}{c|cccccccc}
 & \mathbf{1} & \mathbf{2} & \mathbf{3} & \mathbf{4} & \mathbf{5} & \mathbf{6} & \mathbf{7} & \mathbf{8} \\
\hline
\mathbf{1} & 1 & 1-p^s_{k,j,t} & 1-p^c_{k,j,t} & 1-p^b_{k,j,t} & (1-p^s_{k,j,t})\ast(1-p^c_{k,j,t}) & (1-p^s_{k,j,t})\ast(1-p^b_{k,j,t}) & (1-p^c_{k,j,t})\ast(1-p^b_{k,j,t}) & (1-p^s_{k,j,t})\ast(1-p^c_{k,j,t})\ast(1-p^b_{k,j,t}) \\
\mathbf{2} & 0 & p^s_{k,j,t} & 0 & 0 & p^s_{k,j,t}\ast(1-p^c_{k,j,t}) & p^s_{k,j,t}\ast(1-p^b_{k,j,t}) & 0 & p^s_{k,j,t}\ast(1-p^c_{k,j,t})\ast(1-p^b_{k,j,t}) \\
\mathbf{3} & 0 & 0 & p^c_{k,j,t} & 0 & (1-p^s_{k,j,t})\ast p^c_{k,j,t} & 0 & p^c_{k,j,t}\ast(1-p^b_{k,j,t}) & (1-p^s_{k,j,t})\ast p^c_{k,j,t}\ast(1-p^b_{k,j,t}) \\
\mathbf{4} & 0 & 0 & 0 & p^b_{k,j,t} & 0 & (1-p^s_{k,j,t})\ast p^b_{k,j,t} & (1-p^c_{k,j,t})\ast p^b_{k,j,t} & (1-p^s_{k,j,t})\ast(1-p^c_{k,j,t})\ast p^b_{k,j,t} \\
\mathbf{5} & 0 & 0 & 0 & 0 & p^s_{k,j,t}\ast p^c_{k,j,t} & 0 & 0 & p^s_{k,j,t}\ast p^c_{k,j,t}\ast(1-p^b_{k,j,t}) \\
\mathbf{6} & 0 & 0 & 0 & 0 & 0 & p^s_{k,j,t}\ast p^b_{k,j,t} & 0 & p^s_{k,j,t}\ast(1-p^c_{k,j,t})\ast p^b_{k,j,t} \\
\mathbf{7} & 0 & 0 & 0 & 0 & 0 & 0 & p^c_{k,j,t}\ast p^b_{k,j,t} & (1-p^s_{k,j,t})\ast p^c_{k,j,t}\ast p^b_{k,j,t} \\
\mathbf{8} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p^s_{k,j,t}\ast p^c_{k,j,t}\ast p^b_{k,j,t}
\end{array}$$

In each true community state column, the probabilities of observing each community state (represented by the rows) are composed of different combinations of the detection probabilities of WSS ($p^s_{k,j,t}$), coyotes ($p^c_{k,j,t}$), and bobcats ($p^b_{k,j,t}$) in survey k of site j during season t. Because the probabilities in each column naturally sum to one, the multinomial-logit link is not needed. Each species' detection probability was estimated as a function of survey specific covariates:

$$p^{s}_{k,j,t} = logit^{-1}(x^{T}_{k,j,t}\alpha_{s})$$
$$p^{c}_{k,j,t} = logit^{-1}(x^{T}_{k,j,t}\alpha_{c})$$
$$p^{b}_{k,j,t} = logit^{-1}(x^{T}_{k,j,t}\alpha_{b})$$

where $x_{k,j,t}$ is a vector of survey-specific covariates (described below) and α_s, α_c, and α_b are species-specific vectors of regression coefficients. To accommodate dummy occasions in the detection histories, we used a survey effort matrix to ensure that each species' detection probability was fixed to zero when there was no survey effort (MacKenzie et al. 2004). We assumed the detection of one species was not affected by the presence or detection of the other focal species. Again, we specified priors of normal(0, SD = 1) for the logit-linear intercepts and shrinkage priors for all other regression coefficients, as described above.

Detection and Use Covariates

To model heterogeneity in detection and use probabilities as functions of landscape, habitat, or survey-specific conditions, we extracted covariate data from either the point of the site itself or from a 2.28 km radius buffer surrounding the site using ArcGIS Pro (Esri, Remond, CA). We selected this buffer size to match the estimated annual home range of male WSS, estimated in Oregon, USA (Tosa et al. 2024). It also aligned with the upper range of estimates of annual and seasonal home ranges of *Spilogale* spp. across North America (Jones et al. 2008, Thorne 2020, Harris et al. 2023). Tosa et al. (2024) similarly used a 2.5 km radius buffer to model the effects of landscape-level covariates on WSS occupancy in similar forested habitat in Oregon. Additionally, this home range size is within the bounds of home ranges estimated for coyotes and bobcats elsewhere, which have been found to vary widely based on location, age, social status, and prey availability (e.g., Knowles 1985, Knick 1990, Chamberlain et al. 2000, Gantz and

Knowlton 2005). We clipped buffers along shorelines and removed patches of standing, fresh water (i.e., ponds and lakes) to exclude unavailable habitat (with respect to our terrestrial focal species) from the buffers. We identified standing, fresh water bodies by comparing the "Open Water" land cover category of the LEMMA GNN Structure Map data (LEMMA; https://lemma.forestry.oregonstate.edu/data/structure-maps) to satellite imagery. The removal of unavailable habitats resulted in non-uniform site buffers across the study area and thus, when appropriate, we divided covariate values by the area of the buffer from which they were extracted.

To model heterogeneity in the detection process, we selected three survey-specific covariates: the number of days the camera was active, the number of days bait was present, as evidenced by the camera data, and the average nightly moon illuminance. Because surveys used two independent detection devices—cameras and hair snares—they were considered active even if one device malfunctioned. However, we assumed a species present at the site was more likely to be detected via the camera than the hair snare and thus we considered the camera to be the primary detection device. Hence, we elected to use the number of days the camera was active rather than the number of days in the survey period. We calculated the average nightly moon illuminance for the survey period by scaling the number of minutes the moon was above the horizon, between sunset and sunrise, by the illuminated fraction of the moon each night of the survey using the 'suncalc' package (Thieurmel and Elmarhraoui 2022) in R v.4.4.2 (R Core Team 2024). The scaled number of minutes was summed over the survey period and then divided by the total number of nights. Marneweck et al. (2022) found that eastern spotted skunks and bobcats exhibited altered activity patterns when comparing dark and moonlit nights and thus the detection probabilities of these species, especially the primarily nocturnal WSS (Verts et al. 2001), may change with differing levels of illumination.

We found that correlations were <0.60 for all three detection process covariates. However, after initial model runs, we found that the estimated effect of the number of days bait was present was consistently negative for the detection probability of WSS. This result would be interpreted to mean that the longer bait was available at the site, the less likely it was that WSS would be detected during the survey. Because bait was replenished at the beginning of each survey, this negative effect represents a circular relationship in which bait only remained at sites that were not visited by WSS as they were likely the cause of bait disappearing early in the survey period. Because of this circular relationship, we removed the bait covariate from the detection models.

To model heterogeneity in occupancy (interpreted as the probability of use) we selected eight covariates that broadly described forest conditions, landscape conditions, and levels of human disturbance. To avoid the model becoming overly complex, we limited the number of covariates we included and selected parameters that were likely to affect use by all three focal species. We used the 2012 LEMMA GNN structure map data to describe the forest conditions surrounding each site (Happe et al. 2020). We classified all areas with >40% canopy cover as forested habitat and all other areas as open habitat. We then calculated the proportion of each site's buffer that consisted of forested habitat. Next, we measured the cumulative length of borders (edges) between forested and open habitats in each site buffer. The removal of standing, open water bodies (fresh and salt) ensured that transitions from forested habitat to open water were not included in calculating the length of forest edge. We determined the edge density of each site by dividing the cumulative length of forest edge by the area of the site's buffer. Finally, we calculated the average tree density of the forested habitat in each site's buffer. We used a 10 x 10 m resolution digital elevation model (University of Washington's State-GIS Data; https://wagda.lib.washington.edu) and annual precipitation data (PRISM Climate Group; https://prism.oregonstate.edu) to identify the elevation and average annual precipitation of each site. We also used the 2013 National Land Cover Database (NLCD) (USGS; https://www.usgs.gov/centers/eros/science/national-land-cover-database) to describe human disturbances in the study area. We combined all NLCD Science Products Land Cover categories describing human development (Open Spaces and Low–High Development Intensities) into a "developed land" category. Additionally, we combined the Hay/Pasture and Cropland categories into an "agricultural land" category. We used the NLCD Urban Impervious Descriptor data to identify roads in the developed land and separated them into their own category. We then determined the proportion of each site's buffer composed of developed land and agricultural land as well as its road density.

We checked for correlations >0.60 between each of the covariates. We found that the proportion of forested habitat was correlated with forest edge density (r = -0.86) and the proportion of agricultural land was correlated with the proportion of developed land (r = 0.68). We elected to retain the forest edge density covariate as increased edge habitat can reduce the functional size of habitat patches for prey species that avoid habitat edges in an attempt to reduce predation risk (Bowers and Dooley 1993, Fagan et al. 1999, Moriarty et al. 2015) and, conversely, some predators can be drawn to edges owing to increased foraging success or ease of movement (Dijak and Thompson 2000, Svobodová et al. 2011). We also retained the developed land covariate as only 309 sites (43%) consisted of any amount of agricultural land and thus the developed land category was a more representative metric of human disturbance.

We scaled each of the covariates in the detection and state processes. By scaling the covariates, the magnitude and direction of individual coefficient estimates can be directly compared to determine which covariates were the most influential on species' use and detection probabilities or to compare the effects of covariates between species. The 95% credible interval (CI) associated with each estimated coefficient can be used to infer uncertainty in the estimate's magnitude and direction of effect based on whether the interval contains zero and, if so, how much of the interval lies on each side of zero. We interpreted coefficient estimates with an absolute value <0.05 as having no effect due to their small size.

Model Fitting and Selection

All models were fit using the 'NIMBLE' package (de Valpine et al. 2017, 2024) in R. To evaluate support for our hypotheses, we constructed three separate models. Within each model, we used the same set of covariates in the logit-linear equations describing the first-order natural parameters ($f_{j,t}^{1},\ f_{j,t}^{2},\ f_{j,t}^{3}$): site elevation, annual precipitation, forest edge density, tree density, precent of developed land, road density, and the autoregressive "persistence" parameters. We also used the same set of covariates in the detection process of each model: the number of days the camera was active during the survey and the average nightly moon illuminance. However, we altered the parameterization of the second-order natural parameters ($f_{j,t}^{12},\ f_{j,t}^{13},\ f_{j,t}^{23}$) to induce different interaction relationships in each model. In the first model (M1) we allowed the effects of interactions between species to vary depending on site-specific conditions by modeling the second-order natural parameters as functions of the same site-level covariates as the first-order natural parameters. This would allow site conditions to amplify or mute interspecific interactions. In the second model (M2) we implemented a constant interaction effect between species by only including the intercept in the logit linear equations of the second-order natural parameters. Finally, in the third model (M3), we removed the interaction effects and allowed each species to occur independently of the others by setting the second-order natural parameters to zero.

For each of the three models, we ran three Markov chains for 100,000 iterations and discarded a burn-in of 10,000 samples. Thus, we made inference from 270,000 samples from the posterior distributions of parameters. Evidence of model convergence was assessed using trace plots generated with the 'MCMCvis' package (Youngflesh 2018) and Gelman-Rubin diagnostics ($\hat{R}$) < 1.1 (Gelman and Rubin 1992) generated with the 'coda' package (Plummer et al. 2006). We performed a goodness-of-fit test on the global model, M1, using a Bayesian p-value, by comparing the deviance residuals of our observations to those of model-predicted observations (Broms et al. 2016). Bayesian p-values near 0 or 1 would indicate a substantial lack of fit (Broms et al. 2016). The top model was then selected using Watanabe-Akaike information criterion (WAIC) scoring. There is no clear consensus on what model selection method is the most appropriate for Bayesian hierarchical models, but WAIC has been identified as a suitable tool (Hooten and Hobbs 2015, Broms et al. 2016) and has been used in conjunction with the same multispecies occupancy model used here (Rota et al. 2016, Parsons et al. 2019).

Temporal Overlap Analysis

Temporal partitioning of resources (i.e., accessing prey or habitat at different times) represents another means by which competing species may avoid encounters. Thus, to examine the temporal relationships among the focal species, we measured the extent of overlap in activity patterns through time. To do so, we used time-stamped camera data to determine the time of day that each detection occurred for WSS, coyotes, and bobcats. For each species, we removed any detections that occurred within 30 minutes of an initial detection as we assumed they were not independent detections (Ridout and Linkie 2009). We used the R package ‘overlap’ (Meredith et al. 2024) to construct average daily activity patterns for each species and then estimated the coefficient of overlapping (Δ; Ridout and Linkie 2009) for each species pairing. Because WSS are nocturnal, we also estimated Δ using only the detections of each species that occurred during the period in which WSS were active, as determined by the average daily activity pattern constructed in the initial analysis. Because our smallest sample size had more than 50 observations, in both iterations of the analysis, we report the package’s $\hat{\Delta}_4$ estimator value which was found to be the most reliable estimator for relatively large sample sizes (Ridout and Linkie 2009, Meredith et al. 2024). Confidence intervals were calculated within the package using 500 bootstrap samples. The value of Δ can range from 0–1, with 0 indicating no overlap in activity patterns and 1 indicating complete overlap (Ridout and Linkie 2009).

Results

In total, 976 sampling stations were assigned to 712 sites. Across all sites and years, 2,709 surveys were conducted. Additionally, 239 of the 712 sites were re-sampled in season 2. Cameras were active during survey periods for an average of 13.8 days and were operational for the full survey period in 95.6% of surveys. Western spotted skunks were detected via DNA only (i.e., not also detected by camera) in 27 surveys. At 11 sites, DNA accounted for the only WSS detections in the site across all surveys. No coyotes or bobcats were detected via DNA. During season 1, WSS were detected in 218 sites (naïve use: 30.6%) and coyotes and bobcats were each detected in 118 sites (naïve use: 16.6%). During season 2, of the 239 sites resampled, WSS were detected in 100 sites (naïve use: 41.8%), coyotes were detected in 32 sites (naïve use: 13.4%), and bobcats were detected in 52 sites (naïve use: 21.8%).

All three models achieved convergence and the goodness-of-fit test indicated the global model (M1) fit our observations well (p = 0.497). The model assuming all three species use space independently of one another (M3) was selected as the top model via WAIC scoring (Table 2). There was separation between M3 and the models containing species interactions as indicated by respective ΔWAIC values of 11 and 94 for the other candidate models.

Table 2. Model ranking via WAIC. ΔWAIC is the difference in WAIC score from the top model.

Model	Description	WAIC	ΔWAIC
M3	Second-order natural parameters set to 0	3441	0
M2	Second-order natural parameters modeled as intercept only	3452	11
M1	Second-order natural parameters modeled as functions of site-level covariates	3535	94

Model estimates of the marginal probability of use differed between the two seasons. During season 1, the marginal probabilities of use for WSS, coyotes, and bobcats were 33.1% [95% credible interval = 32.0%, 34.6%], 27.8% [24.3%, 32.4%], and 60.0% [42.4%, 83.0%], respectively. During season 2, the marginal probabilities of use for WSS, coyotes, and bobcats were 44.7% [42.7%, 46.9%], 23.0% [18.4%, 29.3%], and 72.4% [52.7%, 91.2%], respectively. The autoregressive parameter was positive for WSS ($\theta = 1.47$ [0.91, 2.06]). For bobcats it was also positive, but the credible interval included 0 ($\theta = 1.07$ [-0.16, 2.47]). For coyotes, it was essentially 0 ($\theta = -0.10$ [-1.03, 0.80]). This indicates that WSS and possibly bobcats were more likely to continue to use a site in season 2 if they had used it in season 1, while use in a previous season had no discernible effect on coyote use of a site.

The average detection probability for WSS, coyotes, and bobcats was 64.3% [95% credible interval = 60.7%, 67.8%], 28.3% [23.4%, 33.8%], and 11.1% [8.0%, 15.7%], respectively (Fig. 2). The number of days the camera operated during a survey had a weak positive effect on bobcat ($\beta = 0.08$ [-0.06, 0.26]) detection probability and strong positive effects on WSS (β = 0.20 [0.07, 0.34]) and coyote (β = 0.43 [0.18, 0.70]) detection probability. Moon illumination had a weak positive effect on WSS (β = 0.08 [-0.03, 0.21]) and coyote (β = 0.07 [-0.06, 0.24]) detection probability, whereas the effect was nearly zero for bobcat detection probability (β = 0.04 [-0.08, 0.19]).

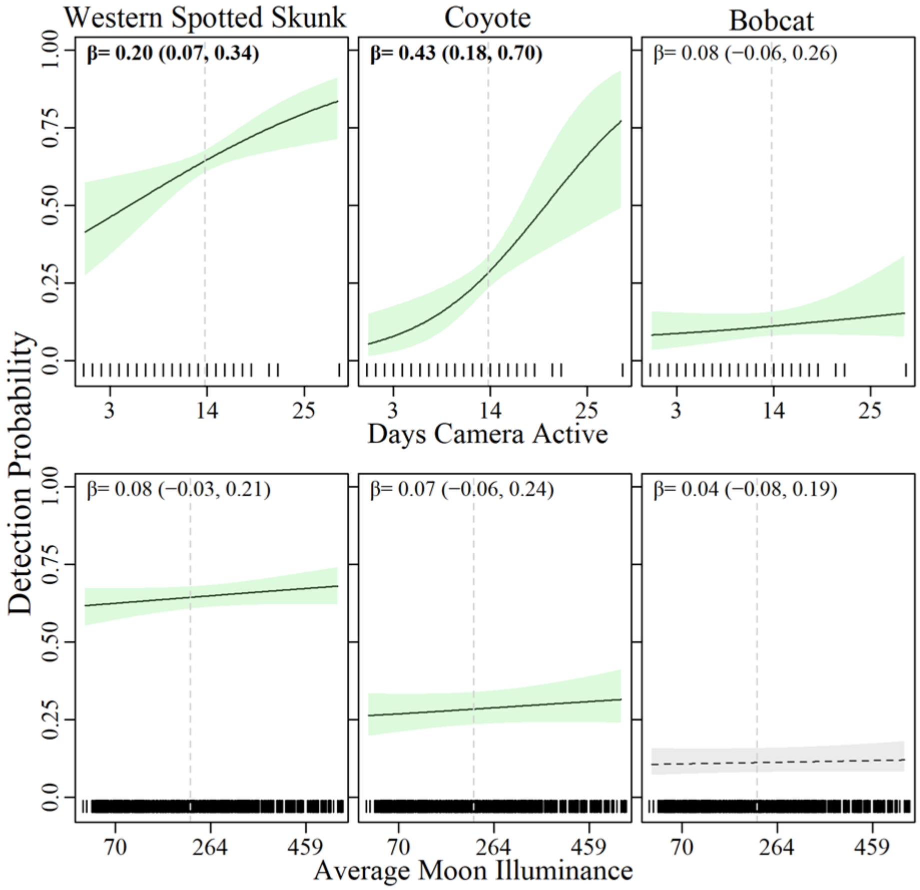

Figure 2. Detection probability estimates (line) and 95% credible interval (CI, shaded area) for western spotted skunks, coyotes, and bobcats in relation to the number of days the camera was active during the survey and the average nightly moon illuminance during the survey. Species-specific beta estimates and accompanying CI are labeled and estimates with a CI that does not overlap zero have been bolded. Green shaded areas indicate positive beta estimates. Beta estimates with absolute values <0.05 are represented by dashed lines and gray shaded CI areas to indicate non-effect. Black line segments (n = 2,709) represent the covariate values for every survey period. The gray, dashed line represents the mean value of the covariate across all surveys. The x-axis units of each graph have been back-transformed to the original units of the respective covariate.

Forest density had a strong positive effect on WSS (β = 0.42 [95% credible interval = 0.24, 0.60]) space use and had weak positive effects on coyote (β = 0.11 [-0.09, 0.37]) and bobcat (β = 0.15 [-0.13, 0.54]) space use (Fig. 3). Western spotted skunks and bobcats were negatively associated with forest edge density (WSS β = -0.35 [-0.55, -0.14]; bobcats β = -0.16 [-0.68, 0.19]), whereas the effect was near zero for coyotes (β = -0.01 [-0.25, 0.22]). Road density had a strong positive effect on WSS use (β = 0.24 [0.05, 0.44]) but the effect was near zero for bobcats (β = 0.04 [-0.29, 0.44]) and coyotes (β = 0.00 [-0.20, 0.21]). Coyotes had a strong positive association with the percent of developed land around the site (β = 3.92 [1.83, 6.67]), whereas the effect was near zero for bobcats (β = 0.03 [-0.51, 1.01]) and WSS were negatively associated with developed land (β = -0.21 [-0.52, 0.01]). Western spotted skunks (β = -1.26 [-1.55, -1.00]) and coyotes (β = -0.45 [-0.74, -0.16]) exhibited strong negative associations with elevation while the effect was near zero for bobcats (β = -0.03 [-0.41, 0.41]). Coyotes (β = 0.46 [0.18, 0.75]) had a strong positive association with the average annual precipitation at sites and WSS (β = 0.10 [-0.05, 0.27]) and bobcats (β = 0.28 [-0.06, 0.77]) had weak positive associations with annual precipitation.

Time stamp data, taken from camera detections, corresponded to 4,471 WSS detection events, 416 coyote detections events, and 221 bobcat detections events. Western spotted skunks were primarily nocturnal with a peak in their activity at approximately 0400 followed by a steep decline; activity was suppressed during the day (Fig. 4). Coyotes were more active during the night and early morning but did not cease activity during the day. Bobcats exhibited the least amount of variability in their activity patterns but were the least active around 1200. When considering all detection events, coyotes and bobcats had the greatest amount of activity overlap

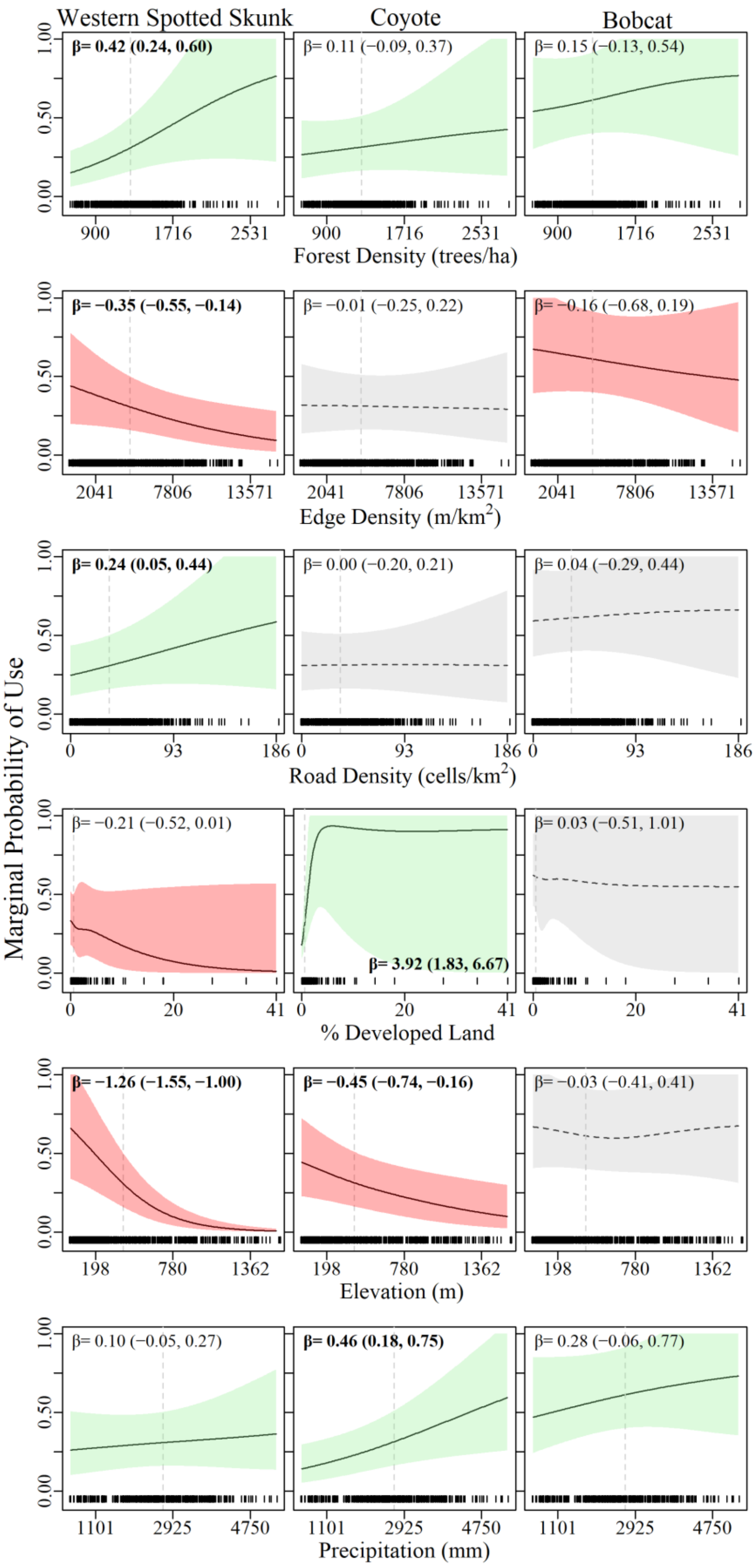

Figure 3. Marginal probability of use estimates (line) and 95% credible interval (CI, shaded area) for western spotted skunks, coyotes, and bobcats in relation to six site-specific covariates. Species-specific beta estimates and accompanying CI are labeled and estimates with a CI that does not overlap zero have been bolded. Green and red shaded areas indicate positive and negative beta estimates, respectively. Beta estimates with absolute values <0.05 are represented by dashed lines and gray shaded CI areas to indicate non-effect. Black line segments (n = 712) along the x-axis represent the covariate value of every site. The gray, dashed line represents the mean value of the covariate across all sites. The x-axis units of each graph have been back-transformed to the original units of the respective covariate.

(Δ = 0.88, 95% confidence interval (CI) = 0.82, 0.94), followed by WSS and coyotes (Δ = 0.64, 95% CI = 0.59, 0.68) and then WSS and bobcats (Δ = 0.59, 95% CI = 0.53, 0.65).When considering only detections that occurred between 1800 and 0730 (i.e., the period during which WSS were active), the estimated extent of overlap between WSS and coyotes and bobcats increased (WSS/coyotes: Δ = 0.87, 95% CI: 0.82, 0.91; WSS/bobcats: Δ = 0.80, 95% CI: 0.73, 0.87).

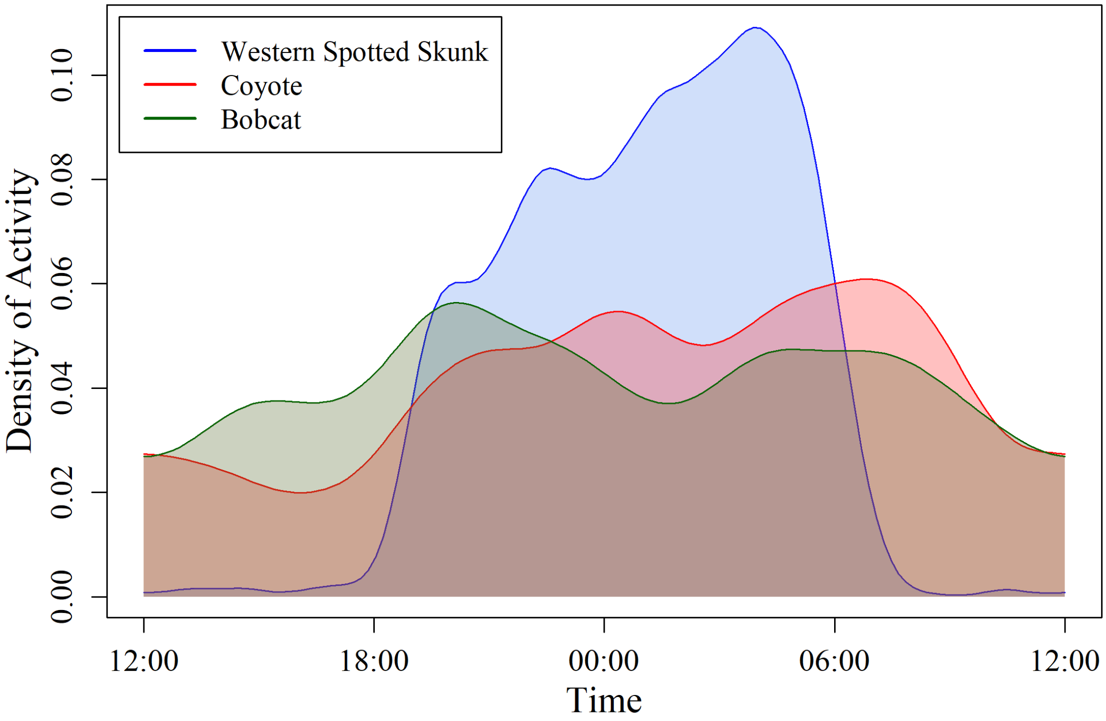

Figure 4. Daily activity patterns representing when WSS, coyotes, and bobcats are active throughout the day on the Olympic Peninsula. Note that the x-axis begins and ends at noon with midnight centered.

Discussion

Species Interactions

Our best supported model indicated that all three species use space independently of one another, aligning with our prediction that WSS do not avoid coyotes and bobcats. Furthermore, when considering only the nocturnal period during which WSS are active, their activity overlapped extensively with coyotes and bobcats (Δ = 0.87 and 0.80, respectively). These findings, taken together, lend support to our first hypothesis that the constitutive defense of skunks mitigates the risk of IK during encounters with larger bodied carnivores. However, the model results do not support our second hypothesis that the body size advantage of coyotes and high dietary overlap with bobcats promotes IK, which predicts that bobcats should avoid coyotes. Likewise, the lack of temporal avoidance between bobcats and coyotes, indicated by a high coefficient of overlapping (Δ = 0.88), suggests a high probability for encounters between the two species if they are using the same sites and therefore does not support our second hypothesis.

Our findings that indicate that WSS do not avoid coyotes and bobcats are in agreeance with other multispecies occupancy studies that have found no evidence that eastern spotted skunks or striped skunks avoid those larger carnivores spatially (Lesmeister et al. 2015, Avrin et al. 2023). Furthermore, studies investigating interactions between skunks and coyotes and bobcats using methods other than occupancy analysis have found that skunk species, across North America, are rarely depredated by larger mammalian carnivores (Sperry 1941, Sargeant et al. 1982, Gehrt 2005, Prange and Gehrt 2007, Tewes et al. 2017), and that they do not exhibit a behavioral or spatial response to increased carnivore activity (Prange and Gehrt 2007, Fisher and Stankowich 2018). Observations of coyotes, and other large carnivores, avoiding agonistic interactions with skunks demonstrate the potency of their noxious defense. Striped skunks forced coyotes to flee from experimental bait stations (Fisher and Stankowich 2018) and WSS, in California, were able to usurp and defend carrion resources from larger carnivores including a mountain lion (Allen et al. 2013, 2016). Although our findings indicate that WSS use space independently of these larger carnivores, they do not imply that attacks on WSS by coyotes and bobcats do not occur on the Olympic Peninsula but rather suggest that the risk of mortality from IK is not great enough to result in a population-level spatial response by WSS to the presence of these larger carnivores.

When examining the full daily activity patterns of all three species, the nocturnal activity of WSS does appear to result in reduced exposure to coyotes and bobcats as evidenced by moderate coefficients of overlapping (WSS/coyote: $\Delta = 0.64$; WSS/bobcat: $\Delta = 0.59$), however coyotes and bobcats were primarily active during the same condensed period in which WSS were active. Indeed, we found that the activity patterns of coyotes and bobcats overlapped extensively with that of WSS when only nocturnal detections were considered (WSS/coyotes: $\Delta = 0.87$; WSS/bobcats: $\Delta = 0.80$). Marneweck et al. (2022) found very similar levels of temporal overlap with coyotes and bobcats when examining the nocturnal activity of eastern spotted skunks. Considerable temporal overlap with these larger carnivores during the period in which WSS have concentrated their activity suggests that the nocturnal activity of WSS is not driven by temporal avoidance of coyotes and bobcats. Nocturnality is a shared trait among *Spilogale* spp. (Crabb 1948, Verts et al. 2001) and may be influenced by a variety of factors other than predation and IK risk, such as prey activity patterns and foraging efficiency (Theuerkauf et al. 2003). Coyotes and bobcats displayed a relatively uniform activity pattern and thus the opportunity to temporally avoid these species may be limited. However, mid-afternoon represents the greatest opportunity for temporal avoidance for WSS. In fact, if we assumed that all WSS detections happened exactly 12 hours later than they actually occurred, the coefficients of overlapping would be decreased (WSS/coyote: $\Delta = 0.41$, 95% CI: 0.37, 0.45; WSS/bobcat: $\Delta = 0.46$, 95% CI: 0.40, 0.52). Thus, if predation and IK were exerting significant pressure, WSS could reduce the probability of encountering coyotes and bobcats by shifting their activity to midday. We recognize that other constraints, such as a high risk of predation by avian predators during the day (Stankowich et al. 2014), could prevent WSS from shifting their activity period even if predation and IK from coyotes and bobcats was a significant threat. However, if predation and IK from coyotes and bobcats were significant threats and WSS were unable to respond through temporal avoidance, we would expect spatial avoidance to be their main recourse. Therefore, the observed lack of temporal avoidance, when coupled with a lack of spatial avoidance as indicated by our top model, further supports our hypothesis that the constitutive defense of skunks mitigates the risk of IK by larger predators.

The finding that bobcats do not spatially or temporally avoid coyotes is surprising, as the pairing of these two species ranks highly in regard to the greatest predictors for IK; namely, high dietary overlap and slight body size disparity. Dietary analyses have revealed nearly identical diets for coyotes and bobcats in our study area (Witczuk et al. 2015). Additionally, coyotes are 1.5 times larger than bobcats (Dalquest 1948), which approaches the highest risk body size disparities of 2–4 (Prugh and Sivy 2020). Based on these conditions, we would expect intense interference competition and high likelihoods of IK, with coyotes being the dominant species. Yet, a review of studies investigating interactions between coyotes and bobcats found that only approximately 25% have found evidence of interference competition (Dyck et al. 2022). Coyotes have been found to engage in IK against bobcats (Litvaitis and Harrison 1989, Fedriani et al. 2000, Kamler and Gipson 2004) but observations of killings are relatively rare (Dyck et al. 2022). Coyotes may avoid engaging in IK of bobcats because although bobcats do not have potent chemical defenses like WSS, they are more heavily armed than coyotes, with sharp claws, which may nullify the coyote's slight body size advantage (Allen et al. 2016). In direct confrontations between the two species, bobcats were found to successfully displace coyotes from carrion resources in the majority of encounters (Allen et al. 2016). This lack of evidence for IK between coyotes and bobcats is another departure from the predicted relationship between carnivores based on body size and dietary overlap. This alternative result could be explained by an advantage owing to increased physical defenses (i.e., claws in addition to teeth).

For any predator, the decision to engage in IK is influenced by many risk and reward factors (Palomares and Caro 1999, Donadio and Buskirk 2006, Prugh and Sivy 2020). Although the constitutive defense of WSS is likely a considerable deterrence, it is likely not the only mitigating circumstance benefiting WSS. The large body size disparities between WSS and coyotes and bobcats fall well outside of the range of body size ratios most likely to promote IK (Prugh and Sivy 2020). Furthermore, although the diets of these three species overlap with respect to small mammals, they use different primary prey, as WSS are primarily insectivorous and coyotes and bobcats in our study system heavily rely on mountain beavers and snowshoe hares (Witczuk et al. 2015, Tosa et al. 2023). The core motives for IK are thought to be reductions of exploitative competition or the risk of reciprocal killing or killing of offspring (Palomares and Caro 1999). Western spotted skunks do not pose an IK risk to coyotes or bobcats, nor their offspring, and exploitative competition is likely low because of low dietary overlap. Therefore, the non-consumptive motives of IK against WSS may be lacking in this system. By contrast, coyotes and bobcats should exert considerable exploitative competition pressure on each other. However, abundant prey resources are thought to mediate the effects of exploitative competition between these species in other systems (Witmer and deCalesta 1986, Neale and Sacks 2001), and in turn reduce the incentive for direct agonistic interactions. This could potentially be the case on the Olympic Peninsula, but we currently lack data on prey abundance.

Additionally, as noted above, although coyotes are larger, bobcats are more heavily armed and thus the risk of injury to a coyote may outweigh the potential rewards of engaging in IK.

Although our finding that these three species do not spatially avoid one another gives us reason to infer that IK does not have a strong effect on the populations of WSS or bobcats, the consequences of IK could manifest in a variety of ways that may be obscured by detection/non-detection data. The binary nature of detection/non-detection data means that only a single detection of a species is required to confirm that it is using a site. Thus, if WSS or bobcat populations were being reduced in abundance through IK by their respective dominant competitor(s) but not completely excluded from shared habitats, we may still find no evidence of spatial avoidance. Additionally, detection/non-detection data cannot relay information regarding the fitness of individuals that are detected in shared habitats with predators or dominant competitors. For instance, juvenile American marten (*Martes americana*) that are forced to disperse from natal territories into habitats shared with larger-bodied fishers suffer increased rates of mortality (Jensen and Humphries 2019). Thus, although a subordinate competitor may be detected in shared habitats, IK may still have negative consequences for its population. We currently do not know how the abundances of our focal species or individual fitness varies across environmental gradients or in the presence of one another in our study area. Future studies using capture-mark-recapture techniques or GPS/telemetry tracking would be better suited to collect data regarding abundances and demographic rates of these populations to further investigate the effects of interactions within this carnivore community.

Species-specific Detection

Western spotted skunk detection probability, under the average survey conditions, was high (64.3%). Similar detection probabilities were reported for WSS in Oregon, after accounting for differences in survey length (1 week vs 2 weeks; Tosa et al. 2024), suggesting this species is highly detectable in the Pacific Northwest. By contrast, the detection probabilities of coyotes and bobcats were low; 28.3% and 11.1%, respectively. Low detection probabilities (~25–32%) have been reported elsewhere for these species (Long et al. 2011, Robinson et al. 2014, Lesmeister et al. 2015) and trap-shyness has been attributed to both species (Harris and Knowlton 2001, Séquin et al. 2003, Larrucea et al. 2007, Lesmeister et al. 2015). A tendency to avoid novel stimuli such as the cameras, hair snare cubbies, and scent lures used in this study may have contributed to the low detection probabilities of coyotes and bobcats. The probability that the focal species will be detected in a site after k surveys is $1 - (1 - p)^k$, where p is the detection probability during a single survey. MacKenzie and Royle (2005) suggest that studies should be planned with enough surveys to attain site detection probabilities >0.85. With three surveys conducted at each site, on average, the site detection probability of WSS was 0.95. However, site detection probabilities for coyotes and bobcats in our study were 0.63 and 0.30, respectively. These low detection probabilities likely impacted the precision of parameter estimates in our model. Coefficient estimates related to the number of days the camera was active during a survey indicate that coyote detection probability would have benefited from longer survey intervals but gains in bobcat detection probability would be limited. Therefore, we suggest that future camera trap studies focused on coyotes and bobcats on the Olympic Peninsula should increase the number of surveys rather than the length of survey intervals.

Contrary to studies focused on eastern spotted skunks (Thorne et al. 2017, Benson et al. 2019, Marneweck et al. 2022), we did not find that moon illumination negatively affected the detection probability of WSS. Our model results indicated that average moon illumination may have had a weak positive effect on WSS and coyote detection probabilities and no effect on bobcat detection probability. Increased predation risk from mammalian and avian predators such as great-horned owls (*Bubo virginianus*) and barred owls (*Strix varia*) on brightly lit nights has been suggested as the mechanism driving reduced eastern spotted skunk nightly activity. Indeed, a study focused on the Florida spotted skunk (*S. p. ambarvalis*) found that in habitats with low avian predator activity, moon illumination did not affect nightly activity (Harris et al. 2023). Barred owls are known predators of WSS (Tosa et al. 2022) and are present in our study area (Yackulic et al. 2019). Thus, WSS in our study are exposed to the full suite of predators, which eastern spotted skunks appear to avoid by restricting activity during brightly lit nights. The length of our survey periods required us to use an average moon illuminance value encompassing 13 nights on average whereas studies examining the effect of moon illumination on eastern spotted skunk activity modeled detection probability or activity rates on a nightly basis (Thorne et al. 2017, Benson et al. 2019, Marneweck et al. 2022). The use of an average moon illuminance value rather than a nightly value may have obscured the effect of moon illuminance on WSS detection probability. Additionally, we did not directly measure light values at survey stations and true moon illuminance values were very likely affected by cloud and canopy cover, which we were unable to account for.

Species-specific Habitat Use

Like many small forest carnivores, *Spilogale* spp. have been found to select habitats with dense understories and closed canopies (Lesmeister et al. 2008, 2009, Hassler et al. 2021*b*). The use of protective habitat types may be an important reason WSS are able to coexist with coyotes and bobcats. Indeed, other mesocarnivores have been found to make use of habitat features to allow them to evade agonistic encounters while spatially overlapping with coyotes. For instance, the arboreal abilities of raccoons (*Procyon lotor*) and the use of prairie dog tunnels by kit foxes

(*Vulpes macrotis*) have been suggested as the primary means by which they avoid IK by sympatric coyotes (Gehrt and Prange 2007, Moehrenschlager et al. 2007). Perhaps most importantly, though, dense forests and closed canopies provide protection from avian predators (Lesmeister et al. 2013), such as the barred owl, as avian predators have been found to be the greatest source of mortality for *Spilogale* spp. (Lesmeister et al. 2010, Butler et al. 2021, Tosa et al. 2022). Although we were unable to directly evaluate the relationship between WSS space use and avian predation risk, our results align with avian predator avoidance being a key factor in habitat selection for WSS. Namely, in our study area WSS were more likely to use dense forests and to avoid areas with high edge density. Lesmeister et al. (2010) found that 92% of the avian-caused mortalities of eastern spotted skunks in their study occurred in forests characterized by open canopies and sparse understories highlighting the importance of dense escape cover for *Spilogale* spp. Additionally, we found that edge density was characterized by a strong negative correlation (r = -0.86) with the proportion of forested habitat surrounding a site. Thus, the strong negative response to edge density is also a response to decreasing proportions of forested habitat in the surrounding area. Similarly, the occupancy probability of eastern spotted skunks in Arkansas, USA was found to be positively associated with forest stand size (Lesmeister et al. 2013). Large, contiguous forest patches likely reduce the need to traverse open habitats, and thus risk exposure to avian predators, as they are more likely to contain sufficient resources, such as prey, within their boundaries than small forest patches. The strong positive effect of road density seems to oppose their avoidance of edge habitats and the idea that WSS are selecting habitat based on avian predator avoidance, as use of roads would inherently mean moving without cover. Nevertheless, WSS in Oregon were also more likely to use areas within their home ranges that were close to roads (Tosa et al. 2024). Tosa et al. (2024) reported extremely large annual home ranges for WSS (10.93–35.83 km^2) in Oregon and if annual home range sizes are similar in our study area, perhaps the energetic savings of moving on smooth road surfaces is worth the risk of exposure to avian predators.

Human presence may also present a risk of mortality, as WSS appeared to avoid developed land ($\beta_{developed} = -0.21[-0.52, 0.01]$). Incentives for associating with human development include food subsidies and, for some mesocarnivores, potentially reduced exposure to larger carnivores that avoid humans (Prugh et al. 2023). However, associating with human presence may result in increased mortality via hunting, trapping, or vehicle collisions (e.g., Hinton et al. 2015). The majority of sites in our study were surrounded by very little developed land (mean = 0.6%), but a few sites were surrounded by high amounts of developed land (max = 41.0%). These sites may have affected the precision of our estimates of the effect of developed land for all three species.

Previous research on the Olympic Peninsula found that WSS were generally associated with low elevation riparian habitats (Carey and Kershner 1996) and our model results support those habitat associations. Carey and Kershner (1996) reported that WSS had been trapped on the Olympic Peninsula at elevations of up to 880 m, but they did not capture any above 500 m. In this study, 90% of sites where WSS were detected were located below 500 m but one detection did occur at 1,168 m. Elevation was the most important covariate in determining WSS space use and had a strong negative effect. Tosa et al. (2024) found that WSS in Oregon also avoided high-elevation areas. Avoidance of high elevations seems to be common amongst *Spilogale* spp., as eastern spotted skunk occupancy studies have also reported similar results (Hackett et al. 2007, Thorne et al. 2017, Eng and Jachowski 2019). This strong avoidance of high elevations has been attributed to the need to avoid deep snow accumulations (Carey and Kershner 1996, Tosa et al.

2024). Finally, WSS showed a weak, positive relationship with annual precipitation. Greater amounts of precipitation support mesic forest types and may sustain a higher density of wetlands, streams, and rivers than drier areas. For instance broadleaf riparian forest types occur mostly on the west side of the Peninsula where precipitation is greater due to the rain shadow effect (Nielsen et al. 2021). Thus, increased use of areas with high precipitation may suggest greater use of wet riparian areas, which provide abundant foraging opportunities, and generally have dense understories, which provide important cover from avian predators (Carey and Kershner 1996).

Coyote space use was most influenced by a strong positive association with the proportion of developed land surrounding a site. This result is not surprising as coyotes generally show positive associations to developed lands across their range (Poessel et al. 2017). Developed areas provide coyotes with anthropogenic food subsidies and can act as “human shields” (Prugh et al. 2023), whereby coyotes reduce their exposure to larger carnivores, such as wolves (*Canis lupus*) and cougars (*Puma concolor*), by taking advantage of their tendency to avoid areas with human activity. In our study area, coyotes may be making use of the “human shield” to avoid sympatric cougars or their tolerance for disturbance may simply allow them to make use of open habitats and food sources that may be inaccessible to other competitors. The estimated effect of developed land on coyote space use was the largest effect estimated for all species across all covariates. This was likely caused by the majority of sites having very low percentages of developed land in their surrounding areas and coyotes being detected at the limited number of sites that had high proportions of developed land in the area. Coyotes were also strongly associated with low elevation habitats. This finding is interesting as coyotes have been implicated as the main cause of decline in the Olympic marmot (*Marmota olympus*) population, which exclusively occupies high elevation alpine meadows (Witczuk et al. 2013). Alpine meadows generally occur at and above 1,350 m in elevation (Nielsen et al. 2021). Only 19 sites in this study were situated at or above 1,350 m and thus we are unable to rigorously evaluate if coyotes use high elevation areas, but with a small sample size and low detection probability, coyotes using high elevation areas may have gone undetected.

As a coursing predator, coyotes are often associated with open habitats (Arjo and Peltscher 2004, Hinton et al. 2015), but as habitat generalists they make use of forested habitats as well (Crête et al. 2001). Coyote populations residing in forests may be limited by bottom-up trophic factors, as they may have difficulty foraging in dense vegetation (Crête et al. 2001). Thus, habitat use in forests may be heavily dictated by prey availability. Coyote space use in the forested habitats of our study area may be tracking the habitat preferences of their primary prey: snowshoe hares and mountain beavers. Snowshoe hares are known to have a strong affinity for dense forest cover, which they use to evade predators (Litvaitis et al. 1985, Feierabend and Kielland 2014). Mountain beavers use forests of all seral stages but show preference for forest openings with dense forb and herbaceous growth such as recently regenerated clear cuts (Arjo et al. 2007). Mountain beavers are also highly reliant on freshwater streams as their kidneys do not efficiently concentrate urine (Schmidt-Nielsen and Pfeiffer 1970). These habitat associations may be driving the weak positive association with forest density and the strong positive association with increased annual precipitation rates that we observed for coyotes.

The lack of strong predictors of bobcat space use may stem from their low detection probability in this study. The small sample size of bobcat detections limited our ability to accurately assess their habitat associations. The effects of the percentage of developed land surrounding the site, road density, and elevation were near zero and there was considerable uncertainty in the magnitudes and directions of effects for the remaining predictors. Witczuk et al. (2015) found evidence, using the distribution of scats across forested and open habitats, that bobcats on the Olympic Peninsula select for forested habitats, and selection for forested habitats has also been documented elsewhere (Clare et al. 2015). Our results also show weak evidence for a positive association with forest density and a negative association with edge density. Again, negative associations with edge density are also negative responses to a decreasing amount of forested habitat surrounding a site. Thus, a negative association with edge density may also be connected to the species' general selection for forested habitats. It would also be reasonable to assume that bobcat space use may be dependent on prey availability. Indeed, evidence that bobcat space use may be driven by prey availability has been found elsewhere in its range (Litvaitis et al. 1986, Bled et al. 2015, Morin et al. 2020). Thus, similarly to coyotes which bobcats mirror in diet, positive associations with forest density and sites that receive more annual precipitation may be driven by access to snowshoe hares and mountain beavers.

Future Research

Little is known about WSS in the Pacific Northwest, but a small body of literature is growing (Carey and Kershner 1996, Tosa et al. 2022, 2023, 2024). With so little known about the species, there is risk that this species will suffer the same fate as the eastern spotted skunk, which experienced a precipitous decline that went largely unnoticed for 50 years (Gompper and Hackett 2005). Moreover, a lack of basic knowledge of the eastern spotted skunk hindered monitoring and management efforts after its decline was recognized. For instance, Gompper and Hackett (2005) note that, at the time, researchers did not have a clear understanding of basic ecological information such as the species' habitat preferences. Studies were required to identify optimal monitoring methods (e.g., cameras vs track plates (Hackett et al. 2007) and bait types (Eng and

Jachowski 2019)) to reliably detect the species before large scale monitoring could be implemented. Considerable effort has been invested into research on the eastern spotted skunk (Jachowski and Edelman 2021) and has led to the formation of the Eastern Spotted Skunk Cooperative Study Group. This group has identified key knowledge gaps in eastern spotted skunk research and management (Eastern Spotted Skunk Cooperative Study Group 2020) many of which are applicable to WSS in the Pacific Northwest, such as understanding how forestry practices affect local populations; estimating survival, mortality, and reproductive rates; and investigating the genetic health of the population. Fortunately, WSS currently appear to be common on the Olympic Peninsula, allowing researchers to collect robust datasets on which to base management decisions to ensure that this species remains common (Tosa et al. 2024).

We used broad habitat covariates that offer insights into the large-scale habitat requirements of WSS, but a single-species occupancy model could allow for a much more in-depth examination of habitat associations. Results from such a study could be compared to the findings of the WSS single-species occupancy analysis conducted using data from Oregon’s Cascade Mountain Range (Tosa et al. 2024) to determine how consistent the habitat associations of the species are throughout the Pacific Northwest. Telemetry or GPS tracking of the species could provide information on survival and direct evidence of which species, if any, are responsible for WSS mortalities. The unique pelage patterns of the species may also provide the means to estimate abundance and density using non-invasive monitoring techniques (Karanth and Nichols 1998). Estimating baselines for these demographic parameters would be important to identifying changes to the abundance of the local population should they occur.

Finally, continued exploration of interactions among WSS and the wider predator community of the Olympic Peninsula is warranted. In particular, how WSS respond to the presence of avian predators such as the invasive barred owl should be examined. Avian predators have been identified as the greatest source of mortality for *Spilogale* spp. (Lesmeister et al. 2010), likely because the constitutive defenses of skunks are unlikely to be as effective against these aerial predators, which do not have strong olfactory senses (Stankowich et al. 2014). If paired with data on owl presence, the framework presented in this study could serve as a starting point for testing the prediction that, unlike bobcats and coyotes, owls may elicit avoidance by WSS. Additionally, the recovering fisher population on the Olympic Peninsula presents another potential source of IK for WSS. Fishers and WSS exhibit a body size disparity of 3.3–9 (fishers: 2–5.5 kg; Pauli et al. 2022) and share use of small mammal and insect prey (Zielinski et al. 1999, Weir et al. 2005), which may promote IK of WSS by fishers. The fisher is well known for overcoming the constitutive defense of porcupines (Earle and Kramm 1982, Weir et al. 2005) and a dietary analysis of fishers in California's Sierra Nevada Mountains found evidence of WSS predation (Zielinski et al. 1999). Thus, fishers may be a more likely threat to WSS on the Olympic Peninsula than coyotes and bobcats. Examining the interactions of these forest carnivores may provide important insights into how the WSS population will respond to the continued growth and expansion of the recovering fisher population on the Olympic Peninsula.

Conclusion

In this study we investigated how the constitutive defense of a small carnivore, the WSS, may mitigate the risk of mortality during encounters with two larger sympatric carnivores and thus obviate the need for avoidance. Using a multispecies occupancy model and temporal overlap analyses, we found no evidence that WSS avoid coyotes or bobcats. Nor did we find evidence that bobcats avoid coyotes. The decision to engage in IK is clearly complex and the instigator must weigh the reward of removing a competitor or potential predator from the landscape or the procurement of a meal, if the victim is consumed, against the risk of sustaining potentially life-threatening injuries during a struggle with their would-be victim. The constitutive defense of WSS is very likely a potent mitigating defense against IK. Likewise, although bobcats do not have a sophisticated defense, their sharp claws in addition to teeth may make them a formidable opponent that coyotes are hesitant to attack. Notably, however, the high dietary overlap of coyotes and bobcats places them into exploitative competition with one another. Bobcats may not have suffered an outright loss of access to habitats and therefore prey resources with the invasion of coyotes on the Olympic Peninsula, but they must now share access to the carrying capacity of the landscape and as a result may be at lower abundances and densities than prior to the coyote invasion (Litvaitis and Harrison 1989).

The noxious spray of skunks has a clear defensive function, but, interestingly, some anecdotal observations have reported skunks, including WSS, acting aggressively toward larger carnivores to usurp food sources (Allen et al. 2013, Fisher and Stankowich 2018). Allen et al. (2013), for example, recorded a WSS charging an adult mountain lion at a kill site to successfully gain access to a carcass. At artificially created “feeding arenas,” WSS regularly displaced gray foxes (*Urocyon cinereoargenteus*) from carrion but no encounters were recorded with larger carnivores (Allen et al. 2016). Carrion resources represent an ecological trap for many mesocarnivores around the world as they may be killed quite often by larger carnivores while attempting to access the resource (Prugh and Sivy 2020). If the constitutive defense of WSS can truly mitigate the risk of IK while accessing high value food sources such as carrion, the species may actually benefit from sharing the landscape with an intact and healthy community of large carnivores.

References

Allen, M. L., L. M. Elbroch, and H. U. Wittmer. 2013. Encounter Competition between a Cougar, Puma concolor, and a Western Spotted Skunk, Spilogale gracilis. The Canadian Field-Naturalist 127:64–66.

Allen, M. L., C. C. Wilmers, L. M. Elbroch, J. M. Golla, and H. U. Wittmer. 2016. The importance of motivation, weapons, and foul odors in driving encounter competition in carnivores. Ecology 97:1905–1912.

Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. Ecology Letters 6:1109–1122.

Arjo, W. M., R. E. Huenefeld, and D. L. Nolte. 2007. Mountain beaver home ranges, habitat use, and population dynamics in Washington. Canadian Journal of Zoology 85:328–337.

Arjo, W. M., and D. H. Peltscher. 2004. Coyote and Wolf Habitat Use in Northwestern Montana. Northwest Science 78:24–32.

Avrin, A. C., C. E. Pekins, C. C. Wilmers, J. H. Sperry, and M. L. Allen. 2023. Can a mesocarnivore fill the functional role of an apex predator? Ecosphere 14:e4383.

Bailey, V. 1930. Predatory animal control in Washington. US Biological Survey.

Benson, I. W., T. L. Sprayberry, W. C. Cornelison, and A. J. Edelman. 2019. Rest-Site Activity Patterns of Eastern Spotted Skunks in Alabama. Southeastern Naturalist 18:165.

Bled, F., S. Summers, D. Martell, T. R. Petroelje, D. E. Beyer, and J. L. Belant. 2015. Effects of Prey Presence and Scale on Bobcat Resource Selection during Winter. M. S. Crowther, editor. PLOS ONE 10:e0143347.

Bowers, M. A., and J. L. Dooley. 1993. Predation Hazard and Seed Removal by Small Mammals: Microhabitat versus Patch Scale Effects. Oecologia 94:247–254.

Breck, S. W., D. E. Biggins, T. M. Livieri, M. R. Matchett, and V. Kopcso. 2006. Does predator management enhance survival of reintroduced black-footed ferrets? Pages 203–209 *in* J. E. Roelle, B. J. Miller, J. L. Godbey, and D. E. Biggins, editors. Recovery of the black-footed ferret: Progress and continuing challenges. United States Geological Survey, Scientific Investigations Report 2005-5293.

Broms, K. M., M. B. Hooten, and R. M. Fitzpatrick. 2016. Model selection and assessment for multi-species occupancy models. Ecology 97:1759–1770.

Butler, A. R., A. J. Edelman, R. Y. Y. Eng, S. N. Harris, C. Olfenbuttel, E. D. Thorne, W. M. Ford, and D. S. Jachowski. 2021. Demography of the Appalachian Spotted Skunk (Spilogale putorius putorius). Southeastern Naturalist 20.

Carey, A. B., and J. E. Kershner. 1996. Spilogale gracilis in Upland Forests of Western Washington and Oregon. Northwestern Naturalist 77:29–34.

Caro, T., and G. Ruxton. 2019. Aposematism: Unpacking the Defences. Trends in Ecology & Evolution 34:595–604.

Chamberlain, M. J., C. D. Lovell, and B. D. Leopold. 2000. Spatial-use patterns, movements, and interactions among adult coyotes in central Mississippi. Canadian Journal of Zoology 78:2087–2095.

Clare, J. D. J., E. M. Anderson, and D. M. MacFarland. 2015. Predicting bobcat abundance at a landscape scale and evaluating occupancy as a density index in central Wisconsin. The Journal of Wildlife Management 79:469–480.

Crabb, W. D. 1948. The Ecology and Management of the Prairie Spotted Skunk in Iowa. Ecological Monographs 18:201–232.

Crête, M., J.-P. Ouellet, J.-P. Tremblay, and R. Arsenault. 2001. Suitability of the forest landscape for coyotes in northeastern North America and its implications for coexistence with other carnivores. Écoscience 8:311–319.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Cypher, B. L., and K. A. Spencer. 1998. Competitive Interactions between Coyotes and San Joaquin Kit Foxes. Journal of Mammalogy 79:204–214.

Dalquest, W. W. 1948. Mammals of Washington. University of Kansas.

Decker, L. E., A. J. Soule, J. C. de Roode, and M. D. Hunter. 2019. Phytochemical changes in milkweed induced by elevated CO2 alter wing morphology but not toxin sequestration in monarch butterflies. Functional Ecology 33:411–421.

Dijak, W. D., and F. R. Thompson. 2000. Landscape and Edge Effects on the Distribution of Mammalian Predators in Missouri. The Journal of Wildlife Management 64:209–216.

Donadio, E., and S. W. Buskirk. 2006. Diet, Morphology, and Interspecific Killing in Carnivora. The American Naturalist 167:524–536.

Dowdy, N. J., and W. E. Conner. 2016. Acoustic Aposematism and Evasive Action in Select Chemically Defended Arctiine (Lepidoptera: Erebidae) Species: Nonchalant or Not? M. Renou, editor. PLOS ONE 11:e0152981.

Dyck, M. A., E. Wyza, and V. D. Popescu. 2022. When carnivores collide: a review of studies exploring the competitive interactions between bobcats Lynx rufus and coyotes Canis latrans. Mammal Review 52:52–66.

Earle, R. D., and K. R. Kramm. 1982. Correlation Between Fisher and Porcupine Abundance in Upper Michigan. The American Midland Naturalist 107:244–249.

Eastern Spotted Skunk Cooperative Study Group. 2020. Eastern Spotted Skunk Conservation Plan. <https://easternspottedskunk.weebly.com/uploads/3/9/7/0/39709790/ess_conservation_plan_dec92020.pdf>. Accessed 25 Apr 2024.

Eng, R. Y. Y., and D. S. Jachowski. 2019. Evaluating detection and occupancy probabilities of eastern spotted skunks. The Journal of Wildlife Management 83:1244–1253.

Fagan, W. F., R. S. Cantrell, and C. Cosner. 1999. How Habitat Edges Change Species Interactions. The American Naturalist 153:165–182.

Fedriani, J. M., T. K. Fuller, R. M. Sauvajot, and E. C. York. 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258–270.

Feierabend, D., and K. Kielland. 2014. Movements, activity patterns, and habitat use of snowshoe hares (Lepus americanus) in interior Alaska. Journal of Mammalogy 95:525–533.

Fidino, M., J. L. Simonis, and S. B. Magle. 2019. A multistate dynamic occupancy model to estimate local colonization–extinction rates and patterns of co-occurrence between two or more interacting species. Methods in Ecology and Evolution 10:233–244.

Fierro, B. R., D. W. Agnew, A. E. Duncan, A. F. Lehner, and M. A. Scott. 2013. Skunk musk causes methemoglobin and Heinz body formation in vitro. Veterinary Clinical Pathology 42:291–300.

Fisher, K. A., and T. Stankowich. 2018. Antipredator strategies of striped skunks in response to cues of aerial and terrestrial predators. Animal Behaviour 143:25–34.

Gantz, G. F., and F. F. Knowlton. 2005. Seasonal Activity Areas of Coyotes in the Bear River Mountains of Utah and Idaho. The Journal of Wildlife Management 69:1652–1659.

Garcelon, D. K. 1981. Mortality of Great Horned Owls Associated with Skunks. The Murrelet 62:26–26.

Gehrt, S. D. 2005. Seasonal Survival and Cause-Specific Mortality of Urban and Rural Striped Skunks in the Absence of Rabies. Journal of Mammalogy 86:1164–1170.

Gehrt, S. D., and S. Prange. 2007. Interference competition between coyotes and raccoons: a test of the mesopredator release hypothesis. Behavioral Ecology 18:204–214.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–511.

Gompper, M. E., and H. M. Hackett. 2005. The long-term, range-wide decline of a once common carnivore: the eastern spotted skunk (Spilogale putorius). Animal Conservation 8:195–201.

Hackett, H. M., D. B. Lesmeister, J. Desanty-Combes, W. G. Montague, J. J. Millspaugh, and M. E. Gompper. 2007. Detection Rates of Eastern Spotted Skunks (Spilogale putorius) in Missouri and Arkansas Using Live-Capture and Non-Invasive Techniques. The American Midland Naturalist 158:123–131.

Hague, M. T. J., L. A. Avila, C. T. Hanifin, W. A. Snedden, A. N. Stokes, E. D. Brodie Jr., and E. D. Brodie III. 2016. Toxicity and population structure of the Rough-Skinned Newt (Taricha granulosa) outside the range of an arms race with resistant predators. Ecology and Evolution 6:2714–2724.

Happe, P. J., K. F. Beirne, C. E. Cantway, D. J. Manson, and D. W. Smith. 2005. Forest Carnivore Inventory, Olympic National Park. NPS/PWR-NCCN/INV-2005-001, Natural Resource Technical Report, Olympic National Park, Port Angeles, WA.

Happe, P. J., K. J. Jenkins, T. J. Kay, K. Pilgrim, M. K. Schwartz, C. Lewis, and K. B. Aubry. 2015. Evaluation of Fisher (Pekania pennanti) restoration in Olympic National Park and the Olympic Recovery Area. Natural Resource Data Series NPS/OLYM/NRDS--2015/804, National Park Service, Fort Collins, Colorado.

Happe, P. J., K. J. Jenkins, R. M. Mccaffery, J. C. Lewis, K. L. Pilgrim, and M. K. Schwartz. 2020. Occupancy Patterns in a Reintroduced Fisher Population during Reestablishment. The Journal of Wildlife Management 84:344–358.

Harris, C. E., and F. F. Knowlton. 2001. Differential responses of coyotes to novel stimuli in familiar and unfamiliar settings. Canadian Journal of Zoology 79:2005.

Harris, S. N., T. J. Doonan, E. L. H. Ragheb, and D. S. Jachowski. 2023. Home range, movement, and activity patterns of the Florida spotted skunk (Spilogale putorius ambarvalis) in prairie habitat. Mammalian Biology 103:613–621.

Harris, S. N., J. B. Holmes, and D. S. Jachowski. 2019. First Record of Consumption of a Spilogale putorius (Eastern Spotted Skunk) by an Alligator mississippiensis (American Alligator). Southeastern Naturalist 18.

Hassler, K. N., B. E. Kessinger, C. E. Harms, L. E. Price, E. P. Barton, K. J. Oxenrider, R. E. Rogers, K. J. Pearce, T. L. Serfass, and A. B. Welsh. 2021*a*. Genetic Confirmation of Predation of an Adult Female Eastern Spotted Skunk by a Barred Owl. Southeastern Naturalist 20:110–118.

Hassler, K. N., C. D. Waggy, R. M. Spínola, K. J. Oxenrider, R. E. Rogers, K. J. Pearce, and T. L. Serfass. 2021*b*. Den-Site Selection by Eastern Spotted Skunks in the Central Appalachian Mountains of West Virginia. Southeastern Naturalist 20:209–224.

Hinton, J. W., F. T. Van Manen, and M. J. Chamberlain. 2015. Space Use and Habitat Selection by Resident and Transient Coyotes (Canis latrans). M. Apollonio, editor. PLOS ONE 10:e0132203.

Hooten, M. B., and N. T. Hobbs. 2015. A guide to Bayesian model selection for ecologists. Ecological Monographs 85:3–28.

Hunter, J., and T. Caro. 2008. Interspecific competition and predation in American carnivore families. Ethology Ecology & Evolution 20:295–324.

Jachowski, D. S., and A. J. Edelman. 2021. Advancing Small Carnivore Research and Conservation: The Eastern Spotted Skunk Cooperative Study Group Model. Southeastern Naturalist 20.

Jensen, P. G., and M. M. Humphries. 2019. Abiotic conditions mediate intraguild interactions between mammalian carnivores. Journal of Animal Ecology 88:1305–1318.

Jones, K. L., D. H. Van Vuren, and K. R. Crooks. 2008. Sudden Increase in a Rare Endemic Carnivore: Ecology of the Island Spotted Skunk. Journal of Mammalogy 89:75–86.

Kaczmarek, J. M., M. Kaczmarski, J. Mazurkiewicz, and J. Kloskowski. 2022. Forget the toad and eat the frog: no associational protection against fish from a chemically defended toad to a later-breeding anuran species. Ethology Ecology & Evolution 34:485–495.

Kamler, J. F., and P. S. Gipson. 2004. Survival and Cause-Specific Mortality among Furbearers in a Protected Area. The American Midland Naturalist 151:27–34.

Karanth, K. U., and J. D. Nichols. 1998. Estimation of Tiger Density in India Using Photographic Captures and Recaptures. Ecology 79:2852–2862.

Katzner, T., T. A. Miller, J. Rodrigue, and S. Shaffer. 2015. A Most Dangerous Game: Death and Injury to Birds from Porcupine Quills. The Wilson Journal of Ornithology 127:102–108.

Kery, M., and J. A. Royle. 2020. Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS. Volume 2: Dynamic and Advanced Models. Elsevier Science and Technology.

Knick, S. T. 1990. Ecology of Bobcats Relative to Exploitation and a Prey Decline in Southeastern Idaho. Wildlife Monographs 3–42.

Knowles, P. R. 1985. Home range size and habitat selection of bobcats, Lynx rufus, in North-Central Montana. Canadian Field-Naturalist 99:6–12.

Kunin, W. E., S. Hartley, and J. J. Lennon. 2000. Scaling Down: On the Challenge of Estimating Abundance from Occurrence Patterns. The American Naturalist 156:560–566.

Larrucea, E. S., G. Serra, M. M. Jaeger, and R. H. Barrett. 2007. Censusing Bobcats using Remote Cameras. Western North American Naturalist 67:538–548.

Larson, R. N., H. A. Sander, M. Fidino, J. L. Angstmann, S. Hayes Hursh, S. B. Magle, K. Moore, C. M. Salsbury, T. Stankowich, K. Tombs, L. Barczak, A. M. Davidge, D. Drake, L. Hartley, P. Reed Sanchez, A. Robey, T. Snyder, J. Williamson, and A. J. Zellmer. 2024. Patterns in tree squirrel co-occurrence vary with responses to local land cover in US cities. Urban Ecosystems. https://doi.org/10.1007/s11252-024-01581-7.

Lesmeister, D. B., R. S. Crowhurst, J. J. Millspaugh, and M. E. Gompper. 2013. Landscape Ecology of Eastern Spotted Skunks in Habitats Restored for Red-Cockaded Woodpeckers. Restoration Ecology 21:267–275.

Lesmeister, D. B., M. E. Gompper, and J. J. Millspaugh. 2008. Summer Resting and Den Site Selection by Eastern Spotted Skunks (Spilogale putorius) in Arkansas. Journal of Mammalogy 89:1512–1520.

Lesmeister, D. B., M. E. Gompper, and J. J. Millspaugh. 2009. Habitat Selection and Home Range Dynamics of Eastern Spotted Skunks in the Ouachita Mountains, Arkansas, USA. The Journal of Wildlife Management 73:18–25.

Lesmeister, D. B., J. J. Millspaugh, M. E. Gompper, and T. W. Mong. 2010. Eastern Spotted Skunk (Spilogale putorius) Survival and Cause-specific Mortality in the Ouachita Mountains, Arkansas. The American Midland Naturalist 164:52–60.

Lesmeister, D. B., C. K. Nielsen, E. M. Schauber, and E. C. Hellgren. 2015. Spatial and temporal structure of a mesocarnivore guild in midwestern north America. Wildlife Monographs 191:1–61.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Linnell, J. D. C., and O. Strand. 2000. Interference interactions, co-existence and conservation of mammalian carnivores. Diversity and Distributions 6:169–176.

Litvaitis, J. A., and D. J. Harrison. 1989. Bobcat–coyote niche relationships during a period of coyote population increase. Canadian Journal of Zoology 67:1180–1188.

Litvaitis, J. A., J. A. Sherburne, and J. A. Bissonette. 1985. Influence of Understory Characteristics on Snowshoe Hare Habitat Use and Density. The Journal of Wildlife Management 49:866–873.

Litvaitis, J. A., J. A. Sherburne, and J. A. Bissonette. 1986. Bobcat Habitat Use and Home Range Size in Relation to Prey Density. The Journal of Wildlife Management 50:110–117.

Long, R. A., T. M. Donovan, P. MacKay, W. J. Zielinski, and J. S. Buzas. 2011. Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. Landscape Ecology 26:327–340.

Mabille, G., S. Descamps, and D. Berteaux. 2010. Predation as a probable mechanism relating winter weather to population dynamics in a North American porcupine population. Population Ecology 52:537–546.

MacKenzie, D. I. 2005. What Are the Issues with Presence-Absence Data for Wildlife Managers? The Journal of Wildlife Management 69:849–860.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. Bailey, and J. E. Hines. 2018. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurence. Second edition. Elsevier Science and Technology, San Diego, CA.

MacKenzie, D. I., J. D. Nichols, and USGS Patuxent Wildlife Research Center, Laurel, USA. 2004. Occupancy as a surrogate for abundance estimation. Animal Biodiversity and Conservation 27:461–467.

MacKenzie, D. I., and J. A. Royle. 2005. Designing Occupancy Studies: General Advice and Allocating Survey Effort. Journal of Applied Ecology 42:1105–1114.

Marneweck, C. J., C. R. Forehand, C. D. Waggy, S. N. Harris, T. E. Katzner, and D. S. Jachowski. 2022. Nocturnal light-specific temporal partitioning facilitates coexistence for a small mesopredator, the eastern spotted skunk. Journal of Ethology 40:193–198.

Means, C. 2013. Skunk spray toxicosis: an odiferous tale. Veterinary Medicine 108:172–178.

Meredith, M., M. Ridout, and L. A. D. Campbell. 2024. Package “overlap”: Estimates of Coefficient of Overlapping for animal activity patterns.

Miller, D. A. W., C. S. Brehme, J. E. Hines, J. D. Nichols, and R. N. Fisher. 2012. Joint estimation of habitat dynamics and species interactions: disturbance reduces co-occurrence of non-native predators with an endangered toad. Journal of Animal Ecology 81:1288–1297.

Moehrenschlager, A., R. List, and D. W. Macdonald. 2007. Escaping Intraguild Predation: Mexican Kit Foxes Survive While Coyotes and Golden Eagles Kill Canadian Swift Foxes. Journal of Mammalogy 88:1029–1039.

Moriarty, K. M., C. W. Epps, M. G. Betts, D. J. Hance, J. D. Bailey, and W. J. Zielinski. 2015. Experimental evidence that simplified forest structure interacts with snow cover to influence functional connectivity for Pacific martens. Landscape Ecology 30:1865–1877.

Morin, S. J., J. Bowman, R. R. Marrotte, and M.-J. Fortin. 2020. Fine-scale habitat selection by sympatric Canada lynx and bobcat. Ecology and Evolution 10:9396–9409.

Neale, J. C. C., and B. N. Sacks. 2001. Resource utilization and interspecific relations of sympatric bobcats and coyotes. Oikos 94:236–249.

Newsome, T. M., A. C. Greenville, D. Ćirović, C. R. Dickman, C. N. Johnson, M. Krofel, M. Letnic, W. J. Ripple, E. G. Ritchie, S. Stoyanov, and A. J. Wirsing. 2017. Top predators constrain mesopredator distributions. Nature Communications 8:15469.

Nielsen, E., C. Copass, R. Brunner, and L. Wise. 2021. Olympic National Park vegetation classification and mapping project report. National Park Service.

Palomares, F., and T. M. Caro. 1999. Interspecific Killing among Mammalian Carnivores. The American Naturalist 153:492–508.

Parsons, A. W., C. T. Rota, T. Forrester, M. C. Baker-Whatton, W. J. McShea, S. G. Schuttler, J. J. Millspaugh, and R. Kays. 2019. Urbanization focuses carnivore activity in remaining natural habitats, increasing species interactions. H. Wheeler, editor. Journal of Applied Ecology 56:1894–1904.

Pauli, J. N., P. J. Manlick, J. M. Tucker, G. B. Smith, P. G. Jensen, and J. T. Fisher. 2022. Competitive overlap between martens (Martes americana) and (Martes caurina) and fishers (Pekania pennanti) : a rangewide perspective and synthesis. Mammal Review 52:392–409.

Plummer, M., N. Best, K. Cowles, and K. Vines. 2006. CODA: Convergence Diagnosis and Output Analysis for MCMC. R News 6:7–11.

Poessel, S. A., E. M. Gese, and J. K. Young. 2017. Environmental factors influencing the occurrence of coyotes and conflicts in urban areas. Landscape and Urban Planning 157:259–269.

Pokallus, J. W., and J. . N. Pauli. 2015. Population dynamics of a northern-adapted mammal: disentangling the influence of predation and climate change. Ecological Applications 25:1546–1556.

Pokallus, J. W., and J. N. Pauli. 2016. Predation shapes the movement of a well-defended species, the North American porcupine, even when nutritionally stressed. Behavioral Ecology 27:470–475.

Pollock, K. H. 1982. A Capture-Recapture Design Robust to Unequal Probability of Capture. The Journal of Wildlife Management 46:752.

Prange, S., and S. D. Gehrt. 2007. Response of Skunks to a Simulated Increase in Coyote Activity. Journal of Mammalogy 88:1040–1049.

Prugh, L. R., C. X. Cunningham, R. M. Windell, B. N. Kertson, T. R. Ganz, S. L. Walker, and A. J. Wirsing. 2023. Fear of large carnivores amplifies human-caused mortality for mesopredators. Science 380:754–758.

Prugh, L. R., and K. J. Sivy. 2020. Enemies with benefits: integrating positive and negative interactions among terrestrial carnivores. Ecology Letters 23:902–918.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The Rise of the Mesopredator. BioScience 59:779–791.

Ridout, M. S., and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14:322–337.

Ripple, W. J., A. J. Wirsing, C. C. Wilmers, and M. Letnic. 2013. Widespread mesopredator effects after wolf extirpation. Biological Conservation 160:70–79.

Robinson, Q. H., D. Bustos, and G. W. Roemer. 2014. The application of occupancy modeling to evaluate intraguild predation in a model carnivore system. Ecology 95:3112–3123.

Rota, C. T., M. A. R. Ferreira, R. W. Kays, T. D. Forrester, E. L. Kalies, W. J. McShea, A. W. Parsons, and J. J. Millspaugh. 2016. A multispecies occupancy model for two or more interacting species. Methods in Ecology and Evolution 7:1164–1173.

Sargeant, R. J., R. J. Greenwood, J. L. Pehl, and W. B. Bicknell. 1982. Recurrence, mortality, and dispersal of prairie Striped Skunks, Mephitis mephitis, and implications to rabies epizootiology. The Canadian field-naturalist 96:312–316.

Schmidt-Nielsen, B., and E. Pfeiffer. 1970. Urea and urinary concentrating ability in the mountain beaver Aplodontia rufa. American Journal of Physiology-Legacy Content 218:1370–1375.

Schwartz, M. K., T. Ulizio, and B. Jimenez. 2006. U.S. Rocky Mountain Fisher Survey Protocol. Rocky Mountain Research Station, Missoula, MT.

Séquin, E. S., M. M. Jaeger, P. F. Brussard, and R. H. Barrett. 2003. Wariness of coyotes to camera traps relative to social status and territory boundaries. Canadian Journal of Zoology 81:2015–2025.

Sipe, H. A., I. N. Keren, and S. J. Converse. 2023. Integrating community science and agency-collected monitoring data to expand monitoring capacity at large spatial scales. Ecosphere 14:e4585.

Sloggett, J. J., K. F. Haynes, and J. J. Obrycki. 2009. Hidden costs to an invasive intraguild predator from chemically defended native prey. Oikos 118:1396–1404.

Soulé, M. E., D. T. Bolger, A. C. Alberts, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed Dynamics of Rapid Extinctions of Chaparral-Requiring Birds in Urban Habitat Islands. Conservation Biology 2:75–92.

Sperry, C. C. 1941. Food habits of the coyote. Wildlife Research Bulletin 4, United States Fish and Wildlife Service.

Stankowich, T., and L. A. Campbell. 2016. Living in the danger zone: Exposure to predators and the evolution of spines and body armor in mammals. Evolution 70:1501–1511.

Stankowich, T., P. J. Haverkamp, and T. Caro. 2014. Ecological drivers of antipredator defenses in carnivores: Evolution of noxious weaponry. Evolution 68:1415–1425.

Steenweg, R., M. Hebblewhite, J. Whittington, P. Lukacs, and K. McKelvey. 2018. Sampling scales define occupancy and underlying occupancy–abundance relationships in animals. Ecology 99:172–183.

Svobodová, J., J. Kreisinger, M. Šálek, M. Koubová, and T. Albrecht. 2011. Testing mechanistic explanations for mammalian predator responses to habitat edges. European Journal of Wildlife Research 57:467–474.

Sweitzer, R. A. 1996. Predation or Starvation: Consequences of Foraging Decisions by Porcupines (Erethizon dorsatum). Journal of Mammalogy 77:1068–1077.

Sweitzer, R. A., S. H. Jenkins, and J. Berger. 1997. Near-Extinction of Porcupines by Mountain Lions and Consequences of Ecosystem Change in the Great Basin Desert. Conservation Biology 11:1407–1417.

Tewes, M. E., J. M. Mock, and J. H. Young. 2017. Bobcat Predation on Quail, Birds, and Mesomammals. National Quail Symposium Proceedings 5.

Theuerkauf, J., W. Jędrzejewski, K. Schmidt, H. Okarma, I. Ruczyński, S. Śnieżko, and R. Gula. 2003. Daily Patterns and Duration of Wolf Activity in the Białowieża Forest, Poland. Journal of Mammalogy 84:243–253.

Thieurmel, B., and A. Elmarhraoui. 2022. Package "suncalc": Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase.

Thorne, E. D. 2020. Spatial ecology of a vulnerable species: home range dynamics, resource use, and genetic differentiation of easter spotted skunks in central Appalachia. Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, VA.

Thorne, E. D., C. Waggy, D. S. Jachowski, M. J. Kelly, and W. M. Ford. 2017. Winter Habitat Associations of Eastern Spotted Skunks in Virginia. The Journal of Wildlife Management 81:1042–1050.

Tosa, M. I., D. B. Lesmeister, J. M. Allen, and T. Levi. 2023. Multi-locus DNA metabarcoding reveals seasonality of foraging ecology of western spotted skunks in the Pacific Northwest. Ecosphere 14:e4386.

Tosa, M. I., D. B. Lesmeister, and T. Levi. 2022. Barred owl predation of western spotted skunks. Northwestern Naturalist 103:250–256.

Tosa, M. I., D. B. Lesmeister, and T. Levi. 2024. Western spotted skunk spatial ecology in the temperate rainforests of the Pacific Northwest. Ecosphere 15:e4981.

de Valpine, P., C. Paciorek, D. Turek, N. Michaud, C. Anderson-Bergman, F. Obermeyer, C. Wehrhahn Cortes, A. Rodriguez, D. Temple Lang, and S. Paganin. 2024. NIMBLE: MCMC, Particle Filtering, and Programmable Hierarchical Modeling. <https://cran.r-project.org/package=nimble>.

de Valpine, P., D. Turek, C. J. Paciorek, C. Anderson-Bergman, D. Temple Lang, and R. Bodik. 2017. Programming with models: writing statistical algorithms for general model structures with NIMBLE. Journal of Computational and Graphical Statistics 26:403–413.

Van Erp, S., D. L. Oberski, and J. Mulder. 2019. Shrinkage priors for Bayesian penalized regression. Journal of Mathematical Psychology 89:31–50.

Verts, B. J., and L. N. Carraway. 1998. Aplodontia rufa. Land Mammals Of Oregon. University of California Press.

Verts, B. J., L. N. Carraway, and A. Kinlaw. 2001. Spilogale gracilis. Mammalian Species 2001:1–10.

Weir, R. D., A. S. Harestad, and R. C. Wright. 2005. WINTER DIET OF FISHERS IN BRITISH COLUMBIA. J. C. Lewis, editor. Northwestern Naturalist 86:12–19.

Wirsing, A. J., M. R. Heithaus, J. S. Brown, B. P. Kotler, and O. J. Schmitz. 2021. The context dependence of non-consumptive predator effects. Ecology Letters 24:113–129.

Witczuk, J., S. Pagacz, J. Gliwicz, and L. S. Mills. 2015. Niche overlap between sympatric coyotes and bobcats in highland zones of Olympic Mountains, Washington. Journal of Zoology 297:176–183.

Witczuk, J., S. Pagacz, and L. S. Mills. 2013. Disproportionate predation on endemic marmots by invasive coyotes. Journal of Mammalogy 94:702–713.

Witmer, G. W., and D. S. deCalesta. 1986. Resource use by unexploited sympatric bobcats and coyotes in Oregon. Canadian Journal of Zoology 64:2333–2338.

Yackulic, C. B., L. L. Bailey, K. M. Dugger, R. J. Davis, A. B. Franklin, E. D. Forsman, S. H. Ackers, L. S. Andrews, L. V. Diller, S. A. Gremel, K. A. Hamm, D. R. Herter, J. M. Higley, R. B. Horn, C. McCafferty, J. A. Reid, J. T. Rockweit, and S. G. Sovern. 2019. The past and future roles of competition and habitat in the range-wide occupancy dynamics of Northern Spotted Owls. Ecological Applications 29:e01861.

Youngflesh, C. 2018. Tools to visualize, manipulate, and summarize MCMC output. Journal of Open Source Software 3:640.

Zaks, K. L., E. O. Tan, and M. A. Thrall. 2005. Heinz body anemia in a dog that had been sprayed with skunk musk. Journal of the American Veterinary Medical Association 226:1516–1518.

Zielinski, W. J., N. P. Duncan, E. C. Farmer, R. L. Truex, A. P. Clevenger, and R. H. Barrett. 1999. Diet of Fishers (Martes pennanti) at the Southernmost Extent of Their Range. Journal of Mammalogy 80:961–971.

Zielinski, W. J., R. L. Truex, F. V. Schlexer, L. A. Campbell, and C. Carroll. 2005. Historical and Contemporary Distributions of Carnivores in Forests of the Sierra Nevada, California, USA. Journal of Biogeography 32:1385–1407.