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# Mammalian predator co-occurrence affected by prey and habitat more than competitor presence at multiple time scales

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**Abstract**

The behavior and abundance of sympatric predators can be affected by a complex dominance hierarchy. The strength of antagonistic interactions in predator communities is difficult to study and remains poorly understood for many predator assemblages. Predators directly and indirectly influence the broader ecosystem, so identifying the relative importance of competition, prey, and habitat in shaping predator interactions has broad conservation and management implications. We investigated space use among five predator species (black bear [*Ursus americanus*], bobcat [*Lynx rufus*], coyote [*Canis latrans*], mountain lion [*Puma concolor*], and gray wolf [*Canis lupus*]) across three temporal scales in northern Idaho, USA. We used camera trap data to test whether potentially subordinate predators spatially avoided dominant predators and how prey availability influenced those relationships. We found few instances of subordinate predators spatially avoiding dominant predators and only at the finest temporal scale of our analyses. Instead, habitat features generally influenced predator space use patterns at coarser scales whereas prey and competitor presence influenced space use patterns at finer scales. Co-occurrence was positively associated between coyotes and bobcats at coarser timescales and between mesopredators and apex predators at finer timescales. Bobcats and mountain lions temporarily delayed the use of sites recently visited by coyotes and black bears, respectively. And all predator species used sites sooner following the detection of a competitor in areas with higher relative abundances of prey (primarily white-tailed deer [*Odocoileus virginianus*]). Our results suggest attraction to shared habitats and prey resources influenced space use in the predator community more than avoidance of competitors. We propose that the effects of interspecific interactions on predator distributions were most evident for mesopredators because their trophic position requires balancing risks and rewards associated with prey, apex predators, and other mesopredators. In addition, relatively high densities of a common prey source likely facilitated the spatial coexistence in this predator community. Our study demonstrates the value

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of simultaneously assessing multiple interspecific interactions across different spatiotemporal scales to discern relationships within the predator guild.

**KEYWORDS**
apex predator, carnivore, competition, interspecific interactions, mesopredators, multispecies occupancy model, resource partitioning, space use

# INTRODUCTION

Competitive interactions among carnivores can shape the diversity and distribution of species within a wildlife community (Connell, 1983; Linnell & Strand, 2000). A change in the population of one carnivore species may influence populations of other sympatric carnivores and potentially alter predation on prey populations, resulting in community-wide effects of interspecific competition (e.g., mesopredator release; Crooks & Soule, 1999). Thus, management actions intended to manipulate one species may have unintended consequences for other species, highlighting the difficulty of managing and conserving communities without detailed information about interspecific competition among carnivores (Connell, 1983; Linnell & Strand, 2000; Penjor et al., 2022).

Numerous co-evolved life history traits and behavioral mechanisms facilitate coexistence among competing species (e.g., niche partitioning; MacArthur & Levins, 1967; Pianka, 1974). Segregation in space and/or time is one such process as it allows carnivores, particularly taxonomically related species with highly overlapping diets (Schoener, 1974), to use similar resources while minimizing potentially negative interactions (e.g., kleptoparasitism, intraguild killing; Palomares & Caro, 1999; Ramesh et al., 2017). Interspecific competition can therefore strongly influence the distribution and co-occurrence of predators, producing patterns of spatial avoidance across the entire carnivore guild in an ecosystem (Grassel et al., 2015; Ritchie & Johnson, 2009). For instance, Vanak et al. (2013) found that the home ranges of African wild dogs (*Lycaon pictus*) overlapped little with the home ranges of several larger competitors (African lions [*Panthera leo*], leopards [*Panthera pardus*], and cheetahs [*Acinonyx jubatus*]) and that wild dogs avoided areas recently used by larger competitors. Similarly, Ramesh et al. (2017) found that spotted hyenas (*Crocuta crocuta*) and leopards were less likely to be detected at the same sites, both were less likely to be detected at sites with lions, and smaller carnivores were less likely to be detected where leopards were observed. Challenges remain, however, in determining whether such patterns reflect functional responses to interspecific interactions or are simply due to differential habitat use (i.e., fundamental vs. realized Eltonian niche; Hutchinson, 1975; Soberón, 2007). Considering both habitat preferences and species interactions when assessing patterns of carnivore space use is therefore necessary to understand what factors structure a carnivore community (Blanchet et al., 2020; Gompper et al., 2016; Miller et al., 2018).

Prey availability is another important factor structuring carnivore communities (Karanth et al., 2017; Srivathsa et al., 2023) as it often governs the density and distribution of predators, and consequently their intensity of competition (Périquet et al., 2015; Shao et al., 2021). Dietary partitioning can facilitate coexistence among species (Pianka, 1974), but in areas of lower prey diversity, dietary overlap and thus competition are expected to increase among predators (Polis et al., 1989). Given that predators should differentiate along other niche dimensions when dietary overlap is high (e.g., spatial partitioning; Schoener, 1974), prey diversity has the potential to mediate spatial avoidance of competitors within a predator community. The abundance of a primary prey species can be an equally important factor influencing predator competition (Périquet et al., 2015; Shao et al., 2021; Wiens, 1977) and the extent of spatial avoidance (Srivathsa et al., 2023). For example, Grassel et al. (2015) found that black-footed ferrets (*Mustela nigripes*) avoided American badgers (*Taxidea taxus*) in areas with relatively low prairie dog (*Cynomys* spp.) densities, but avoidance decreased with increasing prey density. In this case, greater availability of a single shared prey likely reduced interference competition and facilitated coexistence between competitors (Grassel et al., 2015; Pianka, 1974; Polis & Holt, 1992; Srivathsa et al., 2023). In carnivore communities that compete over a more diverse prey base, identifying which prey species most strongly influence(s) coexistence could further clarify how competition influences carnivore space use and inform conservation efforts centered on species interactions.

Identifying an appropriate spatiotemporal scale of study further complicates the assessment of spatial partitioning between competing carnivores. If the spatiotemporal scale(s) at which carnivores respond to each other do not match the scales at which interactions are measured, evidence of competitive interactions, or lack thereof, may be overlooked or misinterpreted. Further, dominance hierarchies within a carnivore community influence the trade-offs that competitors make and the spatiotemporal scales at which they are observed. Human impacts aside, the spatial distributions of large carnivores are typically influenced by prey availability whereas the distributions of smaller subordinate carnivores reflect a trade-off between prey availability and safety from dominant carnivores (Polis & Holt, 1992; Prugh et al., 2023; Thompson & Gese, 2007; Vanak et al., 2013), where prioritization of food or safety may differ with scale (Broekhuis et al., 2013; Dröge et al., 2017; Vanak et al., 2013). For example, cheetahs in northern Botswana prioritized resource acquisition at larger spatial scales but avoided dominant predators (lions and hyenas) at finer scales (Broekhuis et al., 2013). The scale of observation further influences our ability to make inferences about competing carnivores (Blanchet et al., 2020; Cusack et al., 2017). Competition is assumed to be less important in structuring species distributions at broader scales (Godsoe et al., 2015; King et al., 2021; Soberón, 2007), and many interspecific interactions occur at fine scales that are challenging to detect with landscape-level sampling methods (Cusack et al., 2017). Despite these known sources of variation, studies of species interactions often focus on a single spatiotemporal scale, potentially overlooking important variation in the scales at which competitive interactions occur (King et al., 2021). Similarly, studies often consider interactions between only one pair of predators despite many terrestrial ecosystems comprising more than two interacting predators (Vanak et al., 2013). Assessing competitive interactions across a range of spatiotemporal scales and among the entire assemblage of carnivores in an ecosystem can therefore improve our understanding of how interspecific competition structures carnivore communities (Cusack et al., 2017; King et al., 2021; Levin, 1992).

In northern Idaho, USA, five predator species rely partially or almost entirely on large ungulate prey, creating the potential for exploitative and interference competition within the carnivore community. Wolves (*Canis lupus*), mountain lions (*Puma concolor*), black bears (*Ursus americanus*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*) are sympatric throughout this region and share multiple prey resources (Idaho Department of Fish and Game, 2002, 2019). Elk (*Cervus canadensis*) and deer (*Odocoileus* spp.) are particularly important resources for wolves, mountain lions, and black bears alike in northern Idaho (Husseman et al., 2003; Idaho Department of Fish and Game, 2014, 2019, 2021). Mountain lions and wolves are the dominant predators of elk (Horne et al., 2019) and white-tailed deer (Ganz et al., 2024) and black bears opportunistically prey on neonatal ungulates (Ganz et al., 2024; Idaho Department of Fish and Game, 2014, 2019; White et al., 2010). Coyotes are also an important predator of 0–6-month-old white-tailed deer young-of-year (Ganz et al., 2024) and both coyotes and bobcats prey on small mammals and avifauna (Idaho Department of Fish and Game, 2019; Koehler & Hornocker, 1991). Given the potential for competition over multiple shared prey species, subordinate predators in this system may rely on spatial partitioning to avoid dominant predators while maintaining access to these shared resources. Conversely, all five predators are also facultative scavengers and will scavenge from and kleptoparasitize the kills of other predators (Malesis et al., 2024; Prugh & Sivy, 2020; Ruprecht et al., 2021). Spatial avoidance may therefore decline in areas with greater access to carrion and in areas with higher prey availability.

We investigated patterns of spatial overlap among the large predator guild in northern Idaho, USA, to understand how prey availability mediates spatial partitioning of competing predators across temporal scales. Dominance hierarchies are often size- or socially structured (Polis et al., 1989), so we expected wolves were dominant over all other predators because they are a group-living species known to kill more solitary black bears, mountain lions, and coyotes (Ballard et al., 2003). Black bears are generally assumed to be dominant over mountain lions because bears usurp mountain lion kills, although research suggests mountain lions kill more black bears than the reverse, making their dominance hierarchy ambiguous (Elbroch & Kusler, 2018; Ruprecht et al., 2021). However, we expected black bears and mountain lions were dominant over bobcats and coyotes because both larger predators are much bigger than either mesopredator, mountain lions frequently kill coyotes (Brunet et al., 2022; Ruprecht et al., 2021), and coyote visitation rate increased in black bear core areas when bears were hibernating (i.e., temporarily absent; Moll et al., 2021). Finally, we expected coyotes were dominant over bobcats because of their larger size, more social behavior, and have been documented killing bobcats (Kamler & Gipson, 2004). Based on this dominance hierarchy, we hypothesized (H1) subordinate predators spatially avoid dominant predators to reduce antagonistic interactions (e.g., intraguild killing; Palomares & Caro, 1999). We therefore predicted the space use of dominant and subordinate predators to be negatively correlated. We further hypothesized (H2) that prey mediate this relationship, where areas of greater prey availability allow for greater spatial overlap among predators by reducing competition over shared resources (Grassel et al., 2015; Pianka, 1974; Srivathsa et al., 2023). Thus, we predicted spatial avoidance of competing predators to decrease with increasing abundance of their shared prey. We also expected to observe greater evidence of interspecific interactions at finer temporal scales than at coarser scales because species interactions can vary with scale (Levin, 1992) and are often more pronounced at fine spatiotemporal scales (Broekhuis et al., 2013; Cusack et al., 2017; Vanak et al., 2013). Finally, interference competition and lethal interactions are often strongest between taxonomically related species or ones with high dietary overlap (Palomares & Caro, 1999). We therefore expected interactions to be strongest between predators in the same family (i.e., Canidae: wolf–coyote or Felidae: mountain lion–bobcat) and predators that shared similar prey resources (i.e., wolf–mountain lion).

We fit multispecies occupancy models (Rota et al., 2016) and generalized linear models to camera trap data to test our hypotheses at three temporal scales (Cusack et al., 2017). At the coarsest scale, we estimated the effect of habitat, prey, and competitor presence on predator co-occupancy at an 11-week temporal scale. We then estimated co-detection between predators at a 1-week temporal scale, while accounting for broad-scale space-use patterns. And at the finest temporal scale, we estimated the effect of prey and recent competitor presence on the wait time between detections of sympatric predators at the scale of hours to days. Throughout our analyses, we focused on pairwise interactions between species that were taxonomically related, or species we expected would directly compete for food resources, resulting in seven dominant–subordinate predator dyads of interest: wolf–mountain lion, wolf–black bear, mountain lion–black bear, wolf–coyote, mountain lion–bobcat, black bear–coyote, and coyote–bobcat. We focused on the summer months (1 July–15 September) when hunting and trapping were generally not permitted in Idaho (Idaho Department of Fish and Game, 2020), ungulate prey were widely available and dispersed across summer range habitat, and most camera traps were operable.

# METHODS

## Study areas

We collected photo-captured data from 1 July to 15 September 2020 and 2021 within three study areas in northern Idaho, USA, comprising Idaho Department of Fish and Game (IDFG) game management units (GMUs) 1, 6, and 10A (Figure 1). The northern study area, GMU 1 (14,648.92 km$^2$, centered at −116.53973° E, 48.60161° N), was bounded by Canada, Washington, USA, and Montana, USA, and the Priest River, Idaho. This region is part of the Okanogan Highlands Ecological Section of the Canadian Rocky Mountain Ecoregion, with elevation ranging 518–2347m and annual precipitation averaging 86 cm (Idaho Department of Fish and Game, 2021). Dominant vegetation includes western hemlock (*Tsuga heterophylla*), subalpine fir (*Abies lasiocarpa*), western red cedar (*Thuja plicata*), Douglas fir (*Pseudotsuga menziesii*), and ponderosa pine (*Pinus ponderosa*) (Idaho Department of Fish and Game, 2021). We began sampling GMU 1 in July 2021. The central study area (GMU 6; 5905.44 km$^2$, centered at −116.20986° E, 47.20130° N) encompassed the lower St. Joe River Drainage. The southern study area (GMU 10A; 8527.31 km$^2$, centered at −115.88491° E, 46.58268° N) was immediately south of GMU 6 and bisected by the Dworshak Reservoir and North Fork Clearwater River. These two study areas are part of the Bitterroot Mountains Ecological Section, with annual precipitation averaging 84–97cm and elevation ranging 300–1920 m (Idaho Department of Fish and Game, 2021). Western red cedar, grand fir (*Abies grandis*), Douglas fir, and western hemlock forests dominate these areas (Idaho Department of Fish and Game, 2021). GMUs 6 and 10A were monitored in summer 2020 and 2021. All study areas were largely owned and managed by a mixture of private timber companies and the U.S. Forest Service, as well as some private landowners, the state of Idaho, and other federal agencies (Idaho Department of Fish and Game, 2021).

Black bears, bobcats, coyotes, mountain lions, and gray wolves were sympatric throughout northern Idaho, and a small population of grizzly bears (*Ursus arctos*) was present in only GMU 1 (Idaho Department of Fish and Game, 2021). Elk and white-tailed deer (*Odocoileus virginianus*) were the dominant wild ungulate species in northern Idaho, although moose (*Alces alces*) and mule deer (*Odocoileus hemionus*) were also present (Idaho Department of Fish and Game, 2021; Idaho Department of Fish and Game and Nez Perce Tribe, 2016). Wolves and mountain lions preyed on ungulates of all age classes whereas black bears, bobcats, and coyotes primarily preyed on neonatal ungulates in summer (Idaho Department of Fish and Game, 2014, 2019, 2021). In northern Idaho, white-tailed deer and mule deer parturition occurred throughout June (E. Painter-Flores, University of Montana, unpublished data). Our study did not include this peak period of ungulate parturition because many cameras were not active in June owing to deployment logistics. However, bear- and mesopredator-caused mortalities occurred up to 31 days post-parturition (E. Painter-Flores, University of Montana, unpublished data), meaning neonatal deer were available through July for all focal predators. And because carrion (e.g., adult ungulates killed by apex predators) and alternative prey were available all summer, we assumed the potential for

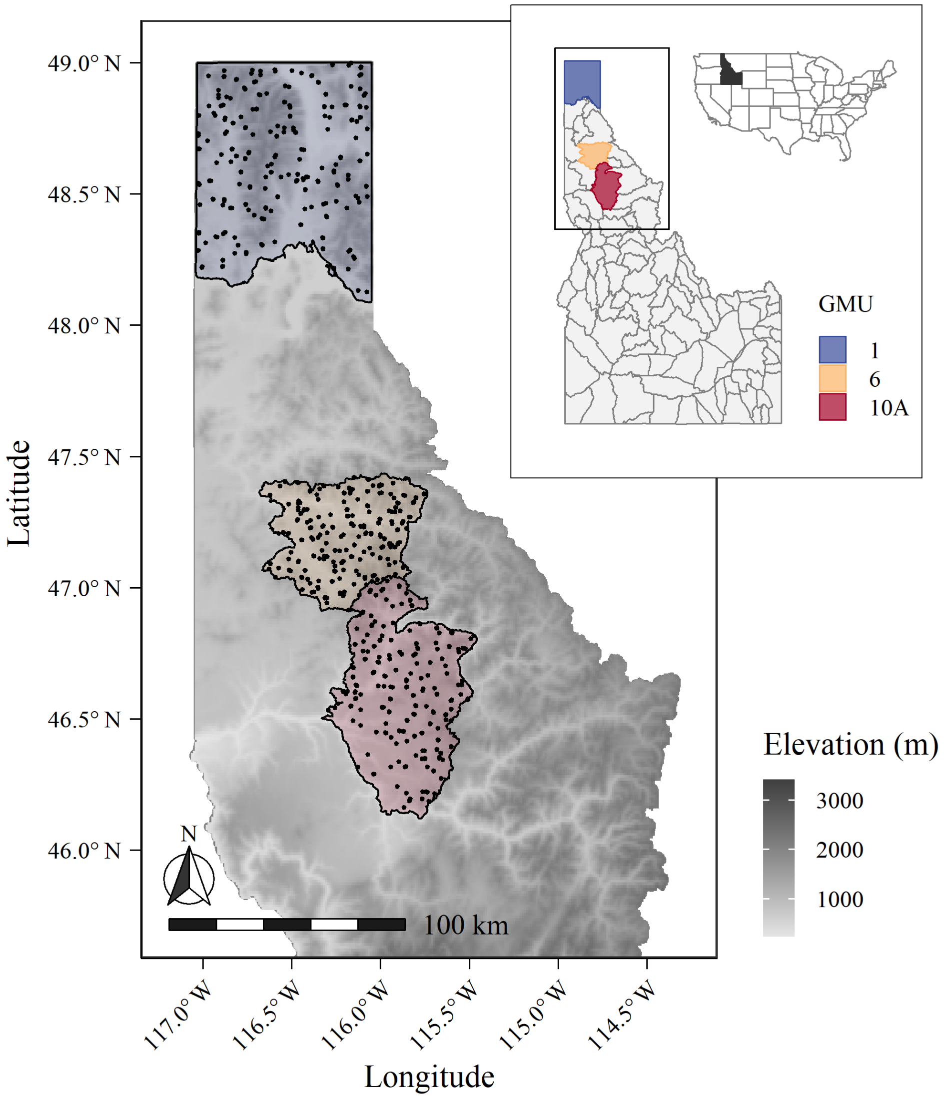

**FIGURE 1** Map of three study areas in northern Idaho, USA. Each study area was sampled using 250 camera traps (black points) from 1 July to 15 September. Sites in game management unit (GMU) 1 (blue) were surveyed in 2021, and sites in GMUs 6 (yellow) and 10A (red) were surveyed in 2020 and 2021. Idaho elevation base map generated from the U.S. Geological Survey Digital Elevation Model (U.S. Geological Survey, 2004).

resource competition occurred among all five predators even when neonates were unavailable.

Lagomorphs, particularly snowshoe hares (*Lepus americanus*), were also common in our study areas (Thornton et al., 2012) and were a common prey item for mesopredators in Idaho (Hurley et al., 2011; Koehler & Hornocker, 1991; E. Painter-Flores, University of Montana, unpublished data). Small mammals (e.g., mice) and avifauna were also important prey items for mesopredators (Koehler & Hornocker, 1991; E. Painter-Flores, University of Montana, unpublished data) but were not frequently detected on camera owing to their smaller size and camera deployment style. We therefore could not consider the effect of small mammals and birds on competition between mesopredators.

## Camera data

We used HyperFire2 (Reconyx, Holmen, Wisconsin, USA) trail cameras to monitor 750 randomly selected sites across our three study areas. We selected 150 locations per study area using a generalized random tessellation stratified (GRTS) spatially balanced sampling design (Stevens & Olsen, 2004) implemented with the spsurvey package version 4.1.1 (Dumelle et al., 2023). When necessary, we removed random sites that fell within large bodies of water, urban areas, or were inaccessible owing to private property. As a result, cameras were generally deployed on public land or timberlands where human development and activity were relatively low. We placed one un-baited camera within 30 m of each random location, ~1.5 m from the ground and pointing parallel to the ground in the direction that offered the least obstructed viewshed. This camera setup targeted the unbiased sampling of ungulates in our study areas (hereafter referred to as "random cameras"; Moeller et al., 2018). We paired 100 of the random cameras per study area with a second un-baited camera, each placed within 2 km and in the same habitat type as the paired random camera. We placed these cameras >2.5 m from the ground on the first dirt-bottomed linear feature (e.g., unpaved road, game trail) encountered from the random site, which targeted predator detections (hereafter "trail cameras"; Jacobs & Ausband, 2018). We programmed all cameras to both time-trigger, every 10 min, and motion-trigger, taking three images per trigger event with no delay between triggers. Cameras operated 1 July–15 September and monitored the same location both years in GMUs 6 and 10A. Cameras in GMU 1 were only deployed 1 July to 15 September 2021.

We used the Microsoft MegaDetector (Beery et al., 2019) to detect objects (i.e., animal, human, vehicle) in each image. The MegaDetector generates a value for every image, ranking how confident it is about a potential object detection in the image (Beery et al., 2019). Trained staff visually inspected all images in lower and lower confidence levels until we were no longer finding detections of animals. This process allowed us to focus our efforts on reviewing images that are most likely to contain animals and reduce the number of empty images reviewed by humans. To further reduce false negatives, we reviewed a random sample of unreviewed images to ensure we were unlikely to overlook animal detections at the lowest confidence levels. We recorded the species present, the number of individuals, and whether the camera was operational using Timeslapse2 software (S. Greenberg, University of Calgary, Alberta, Canada). We also extracted the date, time, and trigger mode from metadata tags. We used only motion-triggered images for subsequent analyses.

## Explanatory variables

We considered the effects of prey availability, habitat preferences, and sampling effort on predator space use and detectability. We calculated a relative abundance index (RAI) for each primary prey species from the camera data to represent prey availability. We grouped images into unique detection events, considering a detection to be independent when ≥30 min elapsed between images of the same species, or a different species was photographed (Sollmann, 2018). We summed the number of unique detection events within a summer study period (1 July–15 September) where ≥1 individual of a given species was detected. We then divided this sum by the number of days the camera was operable and multiplied by 100 to represent species-specific RAI (Bowkett et al., 2008; Rovero & Marshall, 2009). We used the RAI of four primary prey species in subsequent analyses: elk, moose, white-tailed deer, and lagomorphs. We assumed the RAI reflected differences in the relative abundance of each species (Tanwar et al., 2021) but recognized that RAI can also reflect animal movement and variation in detection probability (Broadley et al., 2019). We acknowledge that detection probability for lagomorphs was lower at random cameras than at road cameras owing to differences in camera angle. We did not calculate a RAI for small mammals or birds; we recognize that these taxa are important prey for mesopredators (Koehler & Hornocker, 1991) with the potential to influence competition and space use of coyotes and bobcats.

Predator space use is influenced by habitat and hunting strategy (e.g., stalking predators often prefer structurally complex habitats; Davidson et al., 2012), which should influence the distribution of predators regardless of competition. We therefore considered three habitat predictors—elevation, terrain ruggedness index (TRI), and percent forest cover—that we assumed captured broad-scale variation in terrain and vegetation across our study areas to account for differences in habitat selection. We extracted the elevation in meters at each camera location from a 10-m resolution Idaho Digital Elevation Model (DEM; U.S. Geological Survey, 2004) with the terra package version 1.6.17 (Hijmans, 2022) in Program R version 4.2.1 (R Core Team, 2022). We used the terra package to calculate TRI to represent variability in the terrain at each camera site (Hijmans, 2022). To calculate the percentage of forested habitat surrounding each site, we reclassified the 30-m resolution 2019 National Land Cover Database (NLCD; Dewitz, 2021) into two land cover types representing forested (deciduous, evergreen, and mixed forest cover classes) and non-forested (all other cover classes) habitat. We then used a moving window analysis in Program R (R Core Team, 2022) to calculate the percentage of forested habitat within a 100-m radius for every pixel and extracted values at each camera location (Ausband et al., 2023). Predators frequently use linear features (e.g., roads, trails) to facilitate movement, so we expected the probability of use, co-occupancy, and co-detection would differ between sites along linear features versus truly random locations (Iannarilli et al., 2021; Tanwar et al., 2021). We therefore used a binary variable (hereafter setup) to indicate whether cameras were deployed at random locations (i.e., random cameras = 0) or on linear features (i.e., trail cameras = 1). We tested for collinearity and z-transformed all continuous variables.

## Multispecies occupancy models

We used single-season, multispecies occupancy models for two or more interacting species (Rota et al., 2016) to test for effects of habitat, prey availability, and competitor presence on the co-occupancy of predator species. Occupancy models use detection/non-detection data to estimate the probability that $\geq$1 individual of a given species occupies a space when detection probability is less than perfect (MacKenzie et al., 2002). Multispecies occupancy models extend this general framework by incorporating detection/non-detection data of $\geq$2 species and testing whether their co-occupancy is statistically non-independent (Rota et al., 2016). Multispecies occupancy models can also estimate the effect of explanatory variables on each species' marginal occupancy (i.e., probability of occurring regardless of the presence of other species), their conditional occupancy (i.e., probability of occurring given other species is present or absent), and their marginal and conditional detection probabilities (Fidino et al., 2019; Kéry & Royle, 2021; Rota et al., 2016). Linear functions that relate to just one species are considered first-order parameters, and covariate effects are expressed as the log-odds change in occupancy for a species when other species are absent, given a one-unit change in the covariate (Kéry & Royle, 2021; Rota et al., 2016). For example, $f_1 = \log(\psi_{10}/\psi_{00}) = \alpha_0 + \alpha_1 x_1 + \alpha_2 x_2$ and $f_2 = \log(\psi_{01}/\psi_{00}) = \beta_0 + \beta_1 x_1 + \beta_2 x_2$ represent the first-order parameters for species 1 and species 2, conditional on the other being absent (Kéry & Royle, 2021). Second-order parameters are linear functions related to the interaction between two species, and covariates affecting these interactions reflect the difference between the log-odds change in occupancy of both species occurring together and the log-odds change in occupancy for each species when the other is absent, given a one-unit change in the covariate (Rota et al., 2016); for example, $f_{12} = \log(\psi_{11}\psi_{00}/\psi_{10}\psi_{01}) = \gamma_0 + \gamma_1 x_1 + \gamma_2 x_2$ (Kéry & Royle, 2021). Linear functions related to detection and co-detection probabilities follow a similar parameterization (Kéry & Royle, 2021; Rota et al., 2016).

We included detection data from two predator species in each multispecies occupancy model, resulting in seven pairwise combinations (wolf–black bear, wolf–coyote, wolf–mountain lion, mountain lion–black bear, mountain lion–bobcat, black bear–coyote, coyote–bobcat). In each dyad, we assumed the first species was dominant over the second species but allowed for symmetric interactions in the model in case the dominance hierarchy differed from expectations (e.g., relationship between black bears and mountain lions). We used the camtrapR package version 2.2.0 (Niedballa et al., 2016) in Program R (R Core Team, 2022) to reduce the independent detection events for each species into binary response variables based on whether a given species was detected (1) or not detected (0) at each site at least once during a 1-week (7-day) sampling occasion. This generated species-specific detection histories for 11 7-day sampling occasions per summer (1 July–15 September 2020 and 2021). We then combined species-specific detection histories for each predator dyad into two-species detection histories with four possible observation states: 1 = neither species detected, 2 = species 1 detected only, 3 = species 2 detected only, 4 = both species detected. Finally, because we were not interested in temporal dynamics in occurrence across years, we stacked the 2020 and 2021 detection histories to increase our sample size for each pairwise analysis (Rød-Eriksen et al., 2023). We initially included a random effect for site on the first-order parameter of each species ($f_1$ and $f_2$) to account for repeat measures at sites that were sampled both years (sites in GMU 6 and 10A). The inclusion of random effects resulted in unstable likelihoods and poor model convergence. We therefore treated observations from sites that were sampled both years as independent and included a binary variable for sampling year (year 1 = 0; year 2 = 1) to help account for repeat measures. We acknowledge that ignoring pseudo-replication in our data may result in overly precise estimates of variance.

We fit a set of nested occupancy models to each two-species detection history (Table 1). We developed a null model with only year as a first-order slope parameter on occupancy, and a baseline habitat model that included camera setup (random vs. trail), year, and habitat variables (percent forest cover, elevation, and terrain ruggedness) as first-order slope parameters on occupancy (Table 1). The habitat model tested whether basic habitat features influenced predator occurrence and assumed no dependency between species. In subsequent models, we then added the abundance index of different primary prey species as additional first-order slope parameters on occupancy (Table 1). The specific prey species included in the first-order parameters of the prey abundance model depended on the individual predator species $f_1$ and $f_2$. Based on the primary prey species of each predator in northern Idaho, we included the RAI for elk, moose, and white-tailed deer in the first-order parameter for wolves, elk and white-tailed deer in the first-order parameters for black bears and mountain lions, and white-tailed deer and lagomorphs in the first-order parameters for coyotes and bobcats. The prey abundance model tested whether the relative abundance of the primary prey for each predator influenced predator occurrence while accounting for habitat preferences, but still assumed no dependency between predator species.

**TABLE 1** Set of multispecies occupancy models used to test the influence of competitor presence and prey availability on the spatial overlap of predator species in a multi-predator community in northern Idaho, USA, from 1 July to 15 September 2020–2021 (covariates included in the first-order parameters [$f_1$ and $f_2$] and second-order parameter [$f_{12}$] are grouped into categories[a] for simplicity).

| Model | Linear predictors in first-order parameters[b] | Linear predictors in second-order parameter[b] |
|---|---|---|
| Null | Year | 0 |
| Habitat | Setup + year + habitat | 0 |
| Prey abundance | Setup + year + habitat + prey relative abundance | 0 |
| Interaction habitat[a] | Setup + year + habitat | Intercept |
| Interaction prey abundance[a] | Setup + year + habitat + prey relative abundance | Setup + prey relative abundance |

[a] Interaction models include a second-order parameter that estimates the effect the presence and absence of one species has on the probability of site use by another species.

[b] Covariate categories included in the first- and second-order parameters relate to sets of different covariates: Setup = binary variable for random (0) or trail (1) camera setup where random cameras represent the intercept; year = binary variable for year 1 (0) or year 2 (1) of sampling; habitat = percent forest cover, elevation, and terrain ruggedness; prey relative abundance = relative abundance index for elk, moose, white-tailed deer, and/or lagomorphs.

We then added second-order interactions to the habitat and prey abundance models (Table 1). The interaction habitat model was identical to the baseline habitat model but included a second-order interaction ($f_{12}$; intercept-only) to test whether predators aggregated or segregated more than would be expected by chance after accounting for their individual habitat use. The interaction prey abundance model was identical to the prey abundance model but included the second-order interaction and camera setup and RAI of different primary prey species as second-order slope parameters (Table 1). All primary prey species included in the first-order parameters ($f_1$ and $f_2$) were included in the second-order parameter ($f_{12}$) for a given predator pairing. The interaction prey abundance model tested whether the relative abundance of primary prey influenced the non-independent aggregation or segregation of co-occurring predators after accounting for predator-specific habitat use. Finally, we included camera setup and weekly sampling effort (i.e., number of days per 1-week sampling occasion that camera was operational) as first-order slope parameters on detection in all but the null model to account for species-specific variation in detection probability.

We fit models within a Bayesian framework, implemented in JAGS version 4.3.1 (Plummer, 2017) with the jagsUI package version 1.5.2 (Kellner & Meredith, 2021) and Program R version 4.2.1 (R Core Team, 2022). We used non-informative priors for all parameters (uniform between 0 and 1 for logit-transformed intercepts and normal with $\mu = 0$ and $\tau = 0.1$ for slopes) (Kéry & Royle, 2021). We ran three chains for each model, retaining every 10th observation for 75,000 iterations after an adaptation phase of 1000 and a burn-in phase of 15,000 iterations. We increased the number of iterations to 100,000 for the coyote–bobcat and mountain lion–bobcat models to improve model convergence. When necessary, we provided informed initial values based on estimates from each null model to improve the convergence of more complex models. We reviewed trace plots and the Gelman-Rubin convergence diagnostics (Gelman & Rubin, 1992) to assess adequate convergence. We compared candidate models for each predator pairing with the deviance information criterion (DIC; Spiegelhalter et al., 2002) to identify the best supported model from our candidate set and considered all models within 2 ΔDIC to be well supported by the data. We calculated ΔDIC and model weights with the R package AICcmodavg version 2.3.3 (Mazerolle, 2023). We assessed model goodness-of-fit for the detection sub-model of each best supported model by calculating a Bayesian *p*-value ($p_B$) from $\chi^2$ discrepancies using posterior predictive checks (Conn et al., 2018; Gelman et al., 1996). Bayesian *p*-values that equal 0.5 indicate a perfect fit whereas extreme values (e.g., $p_B < 0.1$ or $p_B > 0.90$) indicate the model does not adequately represent the data (Conn et al., 2018; Hobbs & Hooten, 2015). We considered slope parameters and the second-order intercept to be supported in these top models if the 95% credible intervals (CRI) of the posterior distribution excluded 0 (Kéry, 2010). We then predicted and plotted the marginal and conditional occupancy probabilities for each predator pairing across a range of values for each covariate while holding all other covariates at their mean value to visualize how competition, habitat, and prey influenced predator occurrence and co-occurrence.

We note that because the detection area of a camera is small relative to the movement and home range size of our focal species, camera data typically violate the occupancy model's assumption that sites (i.e., the camera viewshed) are closed to changes in the occupancy state during the sampling period (Burton et al., 2015; Cusack et al., 2017; Lonsinger, 2022; MacKenzie et al., 2006). Cameras in relatively close proximity (i.e., paired random and trail cameras) may also violate the spatial independence assumption of occupancy models (Cusack et al., 2017; MacKenzie et al., 2006). As a result, animals do not continuously occupy the area in front of a camera but are present more broadly (occupying an area of unknown size) and detection at one site may be correlated with detection at a nearby site. We therefore assumed animal movement in and out of a camera site was random and interpreted occupancy results as the probability of use (i.e., asymptotic occupancy where the probability a site was used approached 1.0 asymptotically over the 11-week sampling period; Burton et al., 2015; Efford & Dawson, 2012; Lonsinger, 2022). The probability an animal was available for detection is implied in the detection process because an animal must be available at the site to be detected, given the site is used/occupied (Burton et al., 2015).

Assuming interactions are "static" over an 11-week period ignores the dynamic nature of species interactions whereas evaluating the detection process can yield patterns more representative of the timescale at which interspecific interactions occur (Cusack et al., 2017). We therefore tested the dependency between predator detection probabilities on a weekly time scale in addition to the co-occupancy analysis. We added a second-order interaction term to the detection sub-model of the best supported occupancy model for each species pair and refit the model following the same JAGS specifications described above. This parameterization tested whether the probability of detecting both predators during a 1-week sampling occasion was statistically non-independent. We interpreted co-detection as evidence of a behavioral response between predators, as detection probability can reflect frequency of use (Popescu et al., 2014) and the magnitude of animal movement (Stewart et al., 2018), both of which we would expect to be affected by recent detection (within 1 week) of a heterospecific competitor.

## Wait times following competitor detection

Finally, we evaluated fine-scale spatiotemporal responses by estimating the wait time between the detections of different predator species. We retained the first and last image of every independent detection event and then filtered these images to only include series of images where one predator species was detected immediately after a different predator species. We required no other species (including humans) be detected between predator detections to ensure we only evaluated predator responses to predator presence and not other intervening non-predator animals (Karanth et al., 2017). We then calculated the number of hours between detections of different predator species. We excluded wait times ≥7 days from our analyses because we were interested in predator interactions at a timescale finer than a 1-week period (i.e., hourly- to daily-timescale).

We fit a set of exponential models to test the effects of recent competitor presence and local prey availability on the mean wait time for each predator species using the number of minutes between detections of different predator species as the response variable (Table 2). Specifically, we assumed observed wait times ($y$) followed the exponential distribution (Appendix S1: Figure S1) with rate parameter $\lambda$, that is, $y \sim \text{Exp}(\lambda)$, where $\lambda = e^{1/\boldsymbol{\beta}\mathbf{X}}$, $\boldsymbol{\beta}$ is a vector of coefficients, and $\mathbf{X}$ is a matrix of site-specific covariates (Bassing, 2022). We first fit a null model and two baseline models that included different variables representing either the identity of the competitor detected immediately prior to the focal predator or relative prey abundance (Table 2). The competitor model contained a categorical variable with four factor levels representing each of the previously detected competing predator species (competitor ID), whereas the prey abundance model included the RAI of different primary prey species based on the focal predator (e.g., the coyote model included white-tailed deer and lagomorph RAIs; Table 2). We then fit models using a combination of competitor ID and prey availability variables, allowing the covariates to have additive or interactive effects on wait time (Table 2). The global model combined all covariates and included interactions between competitor ID and RAI (Table 2).

We expected the wait times would be longer for a predator following the detection of a competitor compared with the wait times following a prey species if predators avoided competitors but were attracted to prey at a fine spatiotemporal scale. We therefore conducted a similar analysis, this time calculating the number of hours between detections of a prey species immediately followed

**TABLE 2** Set of exponential models used to test the effects of recent competitor presence and local prey availability on the mean wait time for each predator species in northern Idaho, USA, from 1 July to 15 September 2020–2021.

| Model | Linear predictors[a] |
|---|---|
| Null | Intercept only |
| Competitor | Competitor ID |
| Prey abundance | Prey relative abundance |
| Competitor–prey abundance | Competitor ID + prey relative abundance |
| Competitor × prey abundance | Competitor ID + prey relative abundance + (competitor ID × prey relative abundance) |

[a] Covariate groups relate to sets of different covariates used as linear predictors: Competitor ID = categorical variable with four levels indicating the predator species detected immediately prior to the focal predator species; prey relative abundance = relative abundance index for elk, moose, white-tailed deer, and/or lagomorphs.

by a predator. We replaced the categorical competitor ID variable with a categorical prey ID variable in the prey–predator models, using only the primary prey species of the predator in their respective models. We fit the wait times to only the null, two baseline, and global models, excluding interactions from the global model, because we were only interested in estimating the mean number of hours between detections of prey and predators as a comparison to the predator–predator models.

We fit models within a Bayesian framework, implemented in JAGS version 4.3.1 (Plummer, 2017) with the jagsUI package version 1.5.2 (Kellner & Meredith, 2021) and Program R version 4.2.1 (R Core Team, 2022). We used non-informative priors for all parameters (normal with $\mu = 0$ and $\tau = 0.01$). We ran 3 chains for each model, retaining every 10th observation for 30,000 iterations after an adaptation phase of 1000 and a burn-in phase of 5000 iterations. Following the same model selection and convergence diagnostics as described above, we then predicted and plotted the wait times across a range of values for each statistically supported covariate while holding all other covariates at their mean value to visualize how competition and prey influenced predator wait times. We assessed model goodness-of-fit for each best supported model by calculating a Bayesian $p$-value ($p_B$) from $\chi^2$ discrepancies using posterior predictive checks (Conn et al., 2018; Gelman et al., 1996).

# RESULTS

A total of 493 cameras were operable in 2020 and 710 cameras in 2021. Cameras generated on average 497.20 (SE = 150.27) independent detections per predator species per summer (Table 3) and were operable on average 67 days (SE = 0.49) of the 77-day study period per summer. Relative abundance indices (RAI; i.e., mean daily detection rate) of prey species detected on camera suggested white-tailed deer were the most abundant prey species whereas moose and mule deer were the least abundant prey species in our system (Appendix S1: Table S1).

## Multispecies occupancy models

Mean detection and marginal occupancy probabilities varied by species. Bobcats, mountain lions, and wolves had the lowest detection and marginal occupancy probabilities whereas coyotes had the highest detection probability and black bears had the highest marginal occupancy probability (Table 3). Marginal occupancy varied annually for wolves and black bears; wolf occupancy declined whereas black bear occupancy increased in summer 2021 when compared to summer 2020 (Table 3).

The most supported model identified by DIC varied by predator dyad. Most top models did not include a second-order interaction term, indicating predators generally co-occurred independently of one another (Table 4; Appendix S1: Table S2). Only the coyote–bobcat and black bear–coyote models included a second-order interaction between species (Table 4). The habitat model was most supported in the wolf–coyote analysis (Table 4). The null and habitat models were both supported (within 2 ΔDIC) in the wolf–black bear analysis; we interpreted results from the habitat model below (Table 4; Appendix S1: Table S2). The null model was considered the most supported model for any dyad that included

**TABLE 3** Summary of predator detection data and predicted mean marginal occupancy and detection probabilities and 95% credible intervals (CRI) for each species (using the null model in Table 1) using data collected from camera traps deployed in northern Idaho, USA, from 1 July to 15 September 2020 and 2021.

| Species | Year | Total detection events | Cameras with detections | Proportion cameras with detections | Mean occupancy (95% CRI) | Mean detection (95% CRI) |
|---|---|---|---|---|---|---|
| Black bear | 2020 | 425 | 220 | 0.48 | 0.64 (0.57, 0.71) | 0.19 (0.17, 0.20) |
| | 2021 | 929 | 413 | 0.61 | 0.77 (0.71, 0.82) | 0.19 (0.17, 0.20) |
| Bobcat | 2020 | 210 | 100 | 0.22 | 0.28 (0.23, 0.33) | 0.16 (0.15, 0.18) |
| | 2021 | 288 | 147 | 0.22 | 0.26 (0.23, 0.30) | 0.16 (0.15, 0.18) |
| Coyote | 2020 | 1125 | 241 | 0.52 | 0.83 (0.78, 0.87) | 0.19 (0.17, 0.21) |
| | 2021 | 1407 | 343 | 0.51 | 0.80 (0.76, 0.84) | 0.19 (0.17, 0.21) |
| Mountain lion | 2020 | 125 | 80 | 0.17 | 0.30 (0.24, 0.38) | 0.09 (0.08, 0.11) |
| | 2021 | 182 | 122 | 0.18 | 0.29 (0.24, 0.36) | 0.09 (0.08, 0.11) |
| Wolf | 2020 | 152 | 83 | 0.18 | 0.46 (0.37, 0.56) | 0.08 (0.05, 0.12) |
| | 2021 | 129 | 81 | 0.12 | 0.32 (0.25, 0.39) | 0.08 (0.05, 0.12) |

**TABLE 4** Best supported multispecies occupancy model for each predator dyad as indicated by model selection using deviance information criterion (DIC) using data collected from camera traps deployed in northern Idaho, USA, from 1 July to 15 September 2020 and 2021.

| Predator pair | Model | Linear predictors on first-order parameters[a] | Linear predictors on second-order parameters[b] |
|---|---|---|---|
| Wolf–black bear | Habitat | Setup + year + forest cover + elevation + ruggedness | 0 |
| Wolf–coyote | Habitat | Setup + year + forest cover + elevation + ruggedness | 0 |
| Black bear–coyote | Interaction habitat | Setup + year + forest cover + elevation + ruggedness | Intercept |
| Coyote–bobcat | Interaction habitat | Setup + year + forest cover + elevation + ruggedness | Intercept |
| Wolf–mountain lion | Null | Year | 0 |
| Mountain lion–black bear | Null | Year | 0 |
| Mountain lion–bobcat | Null | Year | 0 |

*Note*: Linear predictors included in the first-order parameters ($f_1$ and $f_2$) and second-order parameter ($f_{12}$) of each best supported model are provided. The full set of competing models, as well as their associated DIC model rankings, are reported for each predator dyad in Appendix S1: Table S2.

[a] Covariates included in the first-order parameters include: Setup = binary variable for random (0) or trail (1) camera setup, where random cameras represent the intercept; year = binary variable for year 1 (0) or year 2 (1) of sampling.

[b] Best supported models that included a second-order parameter included only an intercept (1) and no covariates.

mountain lions (Table 4). Aside from the wolf–black bear analysis, the top model for each dyad had a large difference in DIC compared with the next best model (ΔDIC ranged 17.56–445.66) and carried 100% of the weight in each model set (Appendix S1: Table S2). The null and habitat models carried 70% and 30% of the weight, respectively, in the wolf–black bear model set (Appendix S1: Table S2). Bayesian *p*-values ranged from 0.33 to 0.50, indicating reasonable fit. However, a closer examination of the $\chi^2$ discrepancy statistics showed the models tended to fit well for only the more detectable species. This likely indicates we failed to account for all sources of heterogeneity in the detection process (i.e., missing covariates) or that discretizing camera trap data induced some lack of fit (Kleiven et al., 2023).

Wolf and black bear co-occupancy was not related to the presence of the other predator, but their marginal use probabilities did differ in response to habitat features (Table 5). After accounting for annual differences in site use for each species, we found that wolves were more likely to use higher elevations but less likely to use more rugged terrain (Figure 2). We found weak evidence (95% CRI of posterior mean overlapped 0 slightly) that wolf site use also increased with the percentage of forest cover ($\widehat{\beta}_{\text{Forest}} = 0.20$, 95% CRI = −0.04 to 0.45; Table 5, Figure 2). Conversely, black bears were more likely to use more rugged terrain, areas with a higher percentage of forest cover, and higher elevations, although evidence supporting the elevation effect was weak ($\widehat{\beta}_{\text{Elevation}} = 0.13$, 95% CRI = −0.03 to 0.29; Table 5, Figure 2). Both predators were more likely to use sites along linear features (i.e., hiking trails, roads, game trails) than random sites (Table 5; Appendix S1: Figure S2). The probability of detecting wolves on camera during a 1-week sampling period increased with the number of days a camera was operable whereas black bear detection probability did not vary with sampling effort or camera placement (Appendix S1: Table S3).

Wolf and coyote co-occupancy was also not related to the presence of the other predator, and instead, variation in habitat use likely explained any spatial overlap at the 11-week temporal scale (Table 5). As in the wolf–black bear model, the probability of site use for wolves increased with elevation and forest cover and decreased in more rugged terrain (Table 5, Figure 2). Coyotes were less likely to use sites as the percentage of forest cover increased and as ruggedness increased (Table 5, Figure 2). Site use was higher for both canids along linear features compared with random sites (Table 5; Appendix S1: Figure S2) and their detection probabilities increased with sampling effort (Appendix S1: Table S3). Coyotes were also more detectable at trail sites than at random sites (Appendix S1: Table S3).

The coyote–bobcat pairing was one of the only predator dyads with evidence of dependent co-occupancy, where the conditional probability of use by either species increased if the other species also used that site (Table 5, Figure 3). However, the best supported model did not include covariates on the interaction term, suggesting co-occupancy did not vary with the relative abundance of white-tailed deer or lagomorphs. As in the wolf–coyote model, coyote site use declined with increasing forest cover and terrain ruggedness (Table 5, Figure 2). Bobcats were more likely to use a site as the percentage of forest cover increased, and we found weak support that bobcats used more rugged terrain, although the 95% CRI of the posterior mean overlapped 0 slightly ($\widehat{\beta}_{\text{TRI}} = 0.15$, 95% CRI = −0.06 to 0.35; Table 5, Figure 2). Both species were

**TABLE 5** Posterior means and 95% credible intervals (CRI) for coefficients included in the best supported multispecies occupancy model for pairs of predator species in northern Idaho, from 1 July to 15 September 2020–2021.

| Species 1 | Species 2 | Covariate[a] | Species 1 alone [mean (95% CRI)] | Species 2 alone [mean (95% CRI)] | Both species[b] [mean (95% CRI)] |
|---|---|---|---|---|---|
| Wolf | Black bear | Intercept | −2.26 (−2.78, −1.73) | 0.11 (−0.16, 0.39) | NA |
| **Wolf** | **Black bear** | **Trail setup** | **2.12 (1.55, 2.68)** | **0.46 (0.12, 0.81)** | NA |
| **Wolf** | **Black bear** | **Year 2** | **−0.63 (−1.06, −0.21)** | **0.62 (0.31, 0.94)** | NA |
| **Wolf** | **Black bear** | **Forest cover** | **0.20 (−0.04, 0.45)**[c] | **0.33 (0.18, 0.48)** | NA |
| **Wolf** | **Black bear** | **Elevation** | **0.29 (0.08, 0.50)** | **0.13 (−0.03, 0.29)**[c] | NA |
| **Wolf** | **Black bear** | **TRI** | **−0.31 (−0.56, −0.07)** | **0.20 (0.05, 0.37)** | NA |
| Wolf | Mountain lion | Intercept | −1.00 (−1.29, −0.71) | −0.84 (−1.15, −0.51) | NA |
| Wolf | Mountain lion | **Year 2** | **−0.60 (−0.96, −0.25)** | −0.04 (−0.40, 0.32) | NA |
| Wolf | Coyote | Intercept | −2.26 (−2.78, −1.73) | −0.46 (−0.72, −0.21) | NA |
| **Wolf** | **Coyote** | **Trail setup** | **2.12 (1.55, 2.67)** | **2.06 (1.75, 2.37)** | NA |
| **Wolf** | Coyote | **Year 2** | **−0.63 (−1.06, −0.22)** | −0.18 (−0.48, 0.12) | NA |
| Wolf | **Coyote** | **Forest cover** | **0.20 (−0.03, 0.45)**[c] | **−0.18 (−0.33, −0.03)** | NA |
| Wolf | Coyote | **Elevation** | **0.29 (0.07, 0.50)** | −0.06 (−0.21, 0.09) | NA |
| **Wolf** | **Coyote** | **TRI** | **−0.31 (−0.56, −0.07)** | **−0.36 (−0.51, −0.21)** | NA |
| Mountain lion | Black bear | Intercept | −0.84 (−1.15, −0.51) | 0.28 (0.06, 0.51) | NA |
| Mountain lion | **Black bear** | **Year 2** | −0.04 (−0.40, 0.32) | **0.58 (0.28, 0.88)** | NA |
| Mountain lion | Bobcat | Intercept | −0.84 (−1.15, −0.51) | −0.94 (−1.19, −0.70) | NA |
| Mountain lion | Bobcat | Year 2 | −0.05 (−0.41, 0.32) | −0.08 (−0.39, 0.23) | NA |
| Black bear | Coyote | Intercept | 0.13 (−0.17, 0.45) | −0.44 (−0.76, −0.12) | NA |
| **Black bear** | **Coyote** | **Trail setup** | **0.49 (0.12, 0.87)** | **2.07 (1.76, 2.38)** | NA |
| Black bear | Coyote | **Year 2** | **0.62 (0.31, 0.94)** | −0.17 (−0.47, 0.13) | NA |
| **Black bear** | **Coyote** | **Forest cover** | **0.33 (0.18, 0.48)** | **−0.17 (−0.33, −0.02)** | NA |
| Black bear | Coyote | **Elevation** | **0.13 (−0.03, 0.29)**[c] | −0.05 (−0.20, 0.10) | NA |
| Black bear | **Coyote** | **TRI** | **0.20 (0.04, 0.37)** | **−0.36 (−0.51, −0.21)** | NA |
| Black bear | Coyote | Interaction | … | … | −0.05 (−0.42, 0.31) |
| Coyote | Bobcat | Intercept | −0.66 (−0.94, −0.38) | −2.54 (−3.13, −1.94) | NA |
| Coyote | **Bobcat** | **Trail setup** | **1.71 (1.38, 2.05)** | **1.49 (0.93, 2.00)** | NA |
| Coyote | Bobcat | Year 2 | −0.18 (−0.48, 0.12) | 0.02 (−0.34, 0.40) | NA |
| Coyote | **Bobcat** | **Forest cover** | −0.24 (−0.40, −0.08) | **0.36 (0.16, 0.58)** | NA |
| Coyote | Bobcat | Elevation | −0.05 (−0.21, 0.10) | 0.01 (−0.18, 0.20) | NA |
| Coyote | **Bobcat** | **TRI** | **−0.40 (−0.56, −0.24)** | **0.15 (−0.06, 0.35)**[c] | NA |
| **Coyote** | **Bobcat** | **Interaction** | … | … | **1.30 (0.83, 1.78)** |

*Note*: Columns indicate the two species included in each analysis (species 1 and species 2), covariates included in the top model, coefficient estimates [mean (95% CRI)] influencing the conditional probability of site use for each species in the absence of the other (species 1 alone and species 2 alone), and coefficient estimates influencing the conditional probability of site use for each species given the other also uses the site (both species). Bold font indicates the species and covariates where the 95% CRIs excluded 0 and were considered statistically important relationships. NA indicates parameters not included in the best supported model; "…" indicates this column is not relevant.

[a] Random sites in year 1 represent the intercept for conditional site use for each species when the other is absent. Random sites represent the intercept for conditional site use for both species together.

[b] Species co-occurrence is considered non-independent if the 95% CRI of the interaction intercept (both species) excludes 0. NAs indicate the model did not include an interaction term and/or the covariate was not included in the interaction.

[c] Coefficient was interpreted as having marginal support because the 95% CRI of the posterior mean overlapped 0.

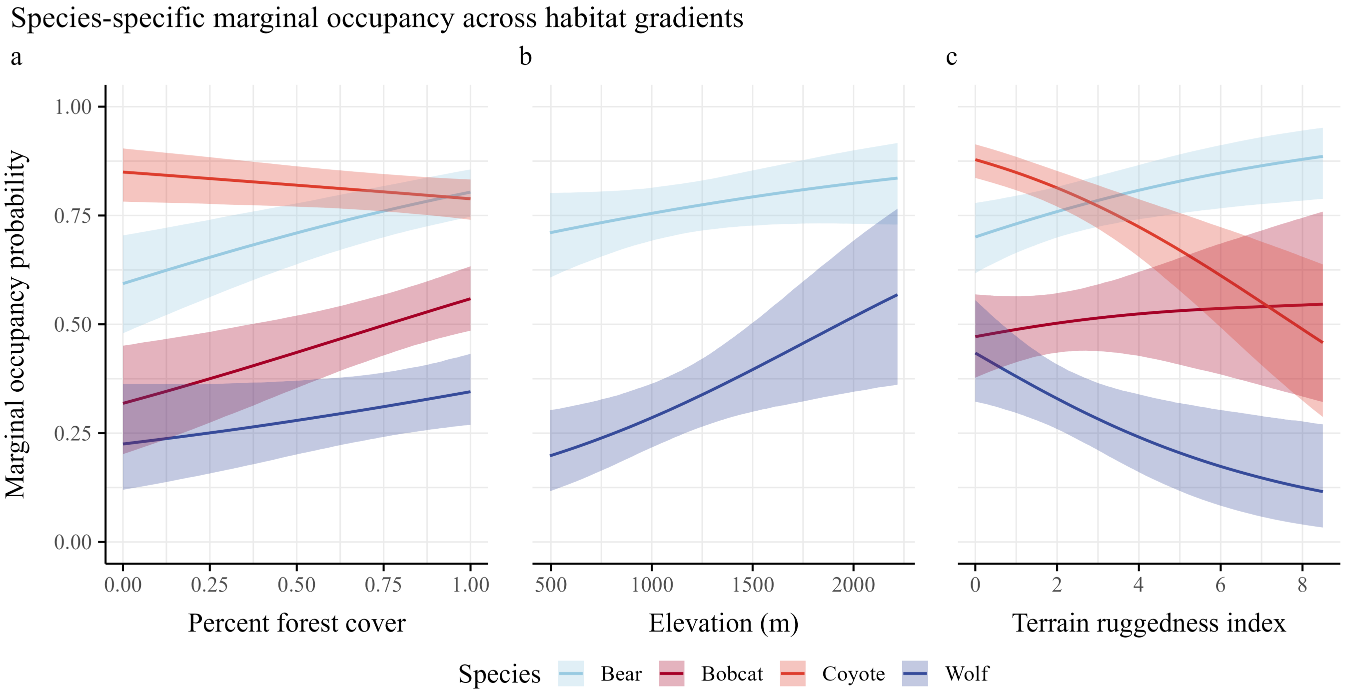

**FIGURE 2** Effect of (a) percent forest cover, (b) elevation, and (c) terrain ruggedness on the predicted marginal probability of site use for black bears, bobcats, coyotes, and wolves at trail sites in northern Idaho, 1 July–15 September 2020–2021. The posterior mean for each species and covariate relationship is represented by the dark line, and the 95% credible intervals (CRI) are represented by the semi-transparent ribbons. Only relationships where the 95% CRI did not include 0 are presented. The marginal probability of site use was lower at random sites; refer to Appendix S1: Figure S2.

more likely to use sites and be detected by cameras along linear features compared with random sites (Table 5; Appendix S1: Table S3, Figure S2). Finally, sampling effort did not influence weekly detection probability of bobcats whereas it positively influenced detection probability of coyotes (Appendix S1: Table S3).

The best supported model for black bear–coyote co-occupancy included a negative second-order interaction term (Table 5). However, the 95% CRI of the posterior distribution included 0 and the magnitude of the interaction was small (posterior mean $\widehat{\gamma}_0 = -0.05$, 95% CRI = −0.42 to 0.31), suggesting no statistical evidence of spatial avoidance between black bears and coyotes at the 11-week temporal scale. Instead, difference in habitat use likely explained any apparent spatial avoidance. As in the models described above, forest cover and terrain ruggedness had a positive effect on the marginal probability of black bear site use whereas they had a negative effect on coyote site use (Table 5, Figure 2). Elevation did not influence coyote site use, but we found weak evidence that black bears were more likely to use higher elevations ($\widehat{\beta}_{\text{Elevation}} = 0.13$, 95% CRI = −0.03 to 0.29; Table 5, Figure 2). Both species were more likely to use sites along linear features although the magnitude of the effect was much larger for coyotes (black bear $\widehat{\beta}_{\text{Setup}} = 0.49$ [95%CRI = 0.12 – 0.87] vs. coyote $\widehat{\beta}_{\text{Setup}} = 2.07$ [95%CRI = 1.76 – 2.38]; Table 5; Appendix S1: Figure S2). Coyotes were more detectable at trail sites compared with random sites and as sampling effort increased, whereas neither influenced the detection probability of black bears (Appendix S1: Table S3).

Finally, we found that detection probability was influenced by the detection of a competitor for three of the seven dyads once we included a second-order interaction in the detection sub-model. Wolves and coyotes, mountain lions and bobcats, and coyotes and bobcats were more likely to be detected within a 1-week sampling occasion if the other species was also detected at the same site within that same time period (Figure 4; Appendix S1: Table S4). Weekly detection probability was highest for coyotes, particularly when bobcats or wolves were also detected (Figure 4; Appendix S1: Table S4). Weekly detection probability was lowest for mountain lions and wolves and only increased marginally when bobcats or coyotes were also detected, respectively (Figure 4; Appendix S1: Table S4).

## Wait times

Model selection indicated that wait time models that included the type of competitor previously detected

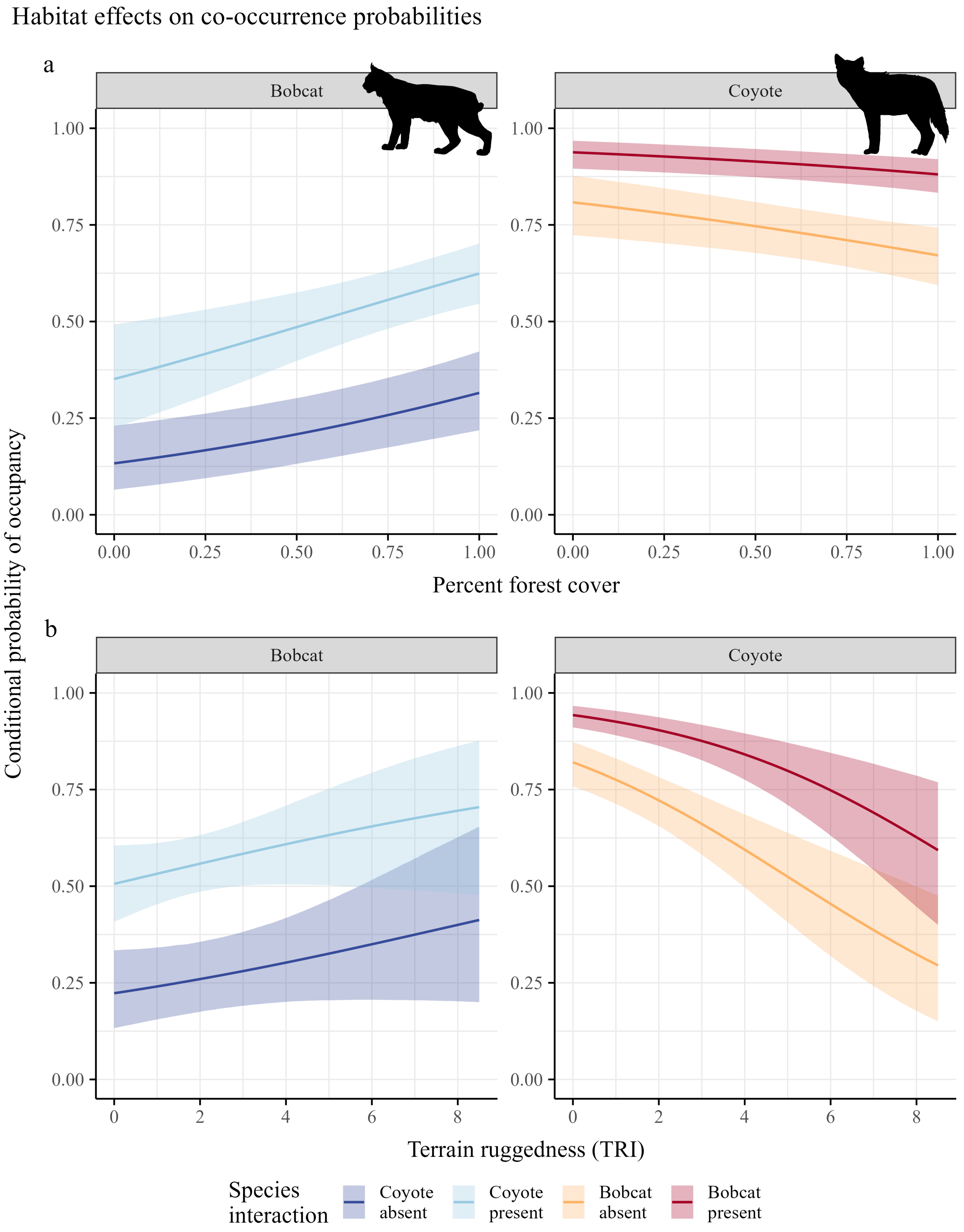

**FIGURE 3** Legend on next page.

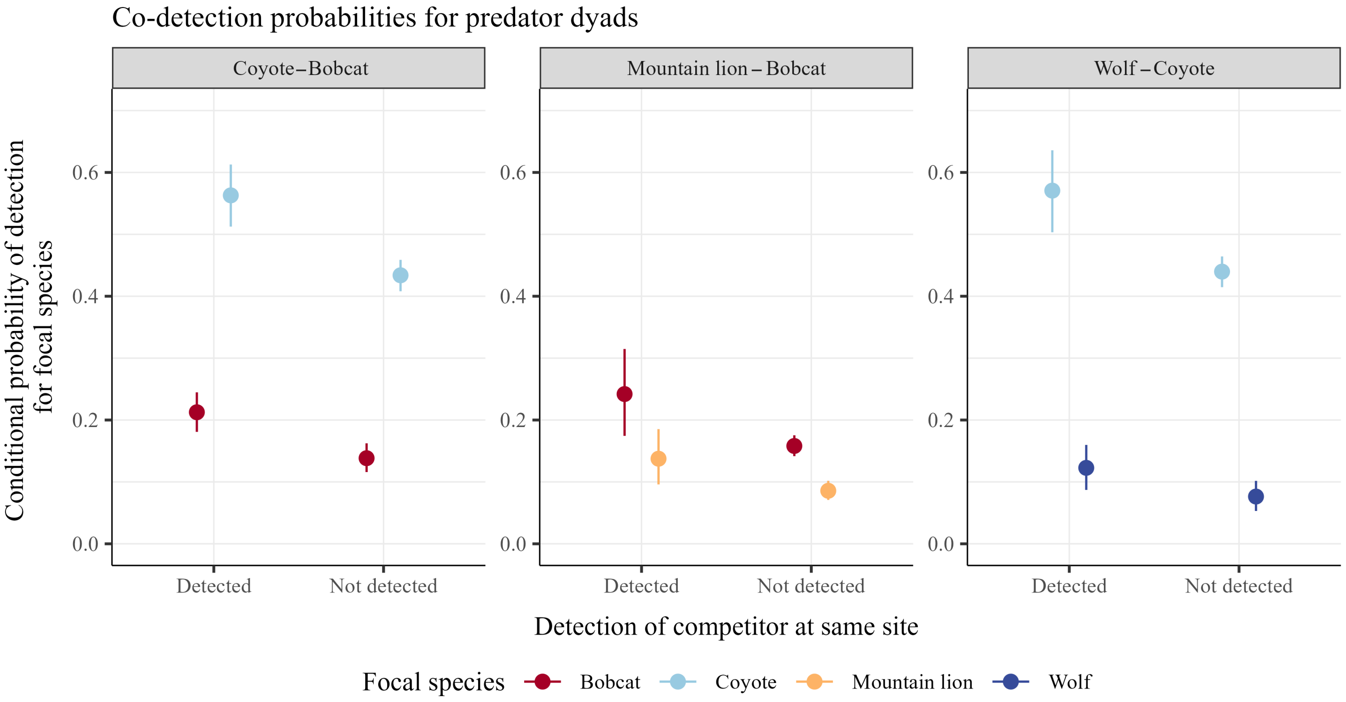

**FIGURE 4** Mean detection probability for bobcats, coyotes, mountain lions, and wolves, conditional on whether a competitor was also observed at the same site during a 1-week sampling occasion in northern Idaho, USA, 1 July–15 September 2020–2021. For each predator dyad, species-specific detection probability was higher when the competing species was also observed. Estimates represent the mean probability of detecting a predator along linear features (i.e., trail sites) with average sampling effort ($\bar{x} = 6.10$ days/week, SE = 0.02). Bars represent 95% credible intervals.

and/or the relative abundance of prey were most supported when estimating the mean wait time between detections of heterospecific predators. The prey abundance model was most supported in the bobcat, mountain lion, and wolf analyses (Appendix S1: Table S5). The competitor–prey abundance model, with additive effects for competitor ID and prey abundance, was the second most supported model (0.90 ΔDIC) in the bobcat analysis (Appendix S1: Table S5). The competitor × prey abundance model, with interactions between competitor ID and prey abundance, was most supported in the coyote analysis. The null and prey abundance models were both supported (≤2 ΔDIC) in the black bear analysis (Appendix S1: Table S5). Model selection further indicated that the mean wait time between detections of a prey species and a predator was best described by the relative abundance of primary prey but not the prey species most recently detected (Appendix S1: Table S6). Bayesian *p*-values ranged from 0.49 to 0.77 across analyses, indicating no lack of fit of our models to the data.

Predator wait times varied in response to the recent detection of a competitor species, whereas wait times were consistently shorter as the relative abundance of primary prey increased. Based on the posterior means from each of the most supported models, we found that bobcat wait times were shorter following the detection of a mountain lion ($\bar{x} = 13.55$ h, 95% CRI = 5.72–30.50 h) than wait times following the detection of any other competitor species (Figure 5). Bobcat wait times were longer following a coyote detection ($\bar{x} = 36.7$ h, 95% CRI = 21.75–62.07 h) than wait times following a black bear or mountain lion detection (Figure 5). Coyote wait times were shorter following the detection of a wolf ($\bar{x} = 20.20$ h, 95% CRI = 14.04–29.05 h) than wait times

**FIGURE 3** Influence of percent forest cover and terrain ruggedness on the predicted probability of use for coyotes and bobcats, conditional on whether the other predator was present or absent from sites in northern Idaho, USA, 1 July–15 September 2020–2021. Predictions include the effect of sites being on linear features (i.e., trail sites). Elevation did not influence coyote or bobcat site use and was not plotted here. Bobcat silhouette was created by Margot Michaud and is available for reuse under the CC0 1.0 Universal Public Domain Dedication license at https://www.phylopic.org/. Coyote silhouette was created by Gabriela Palomo-Munoz and is available for reuse under the Attribution-NonCommercial 3.0 Unported license at https://www.phylopic.org/.

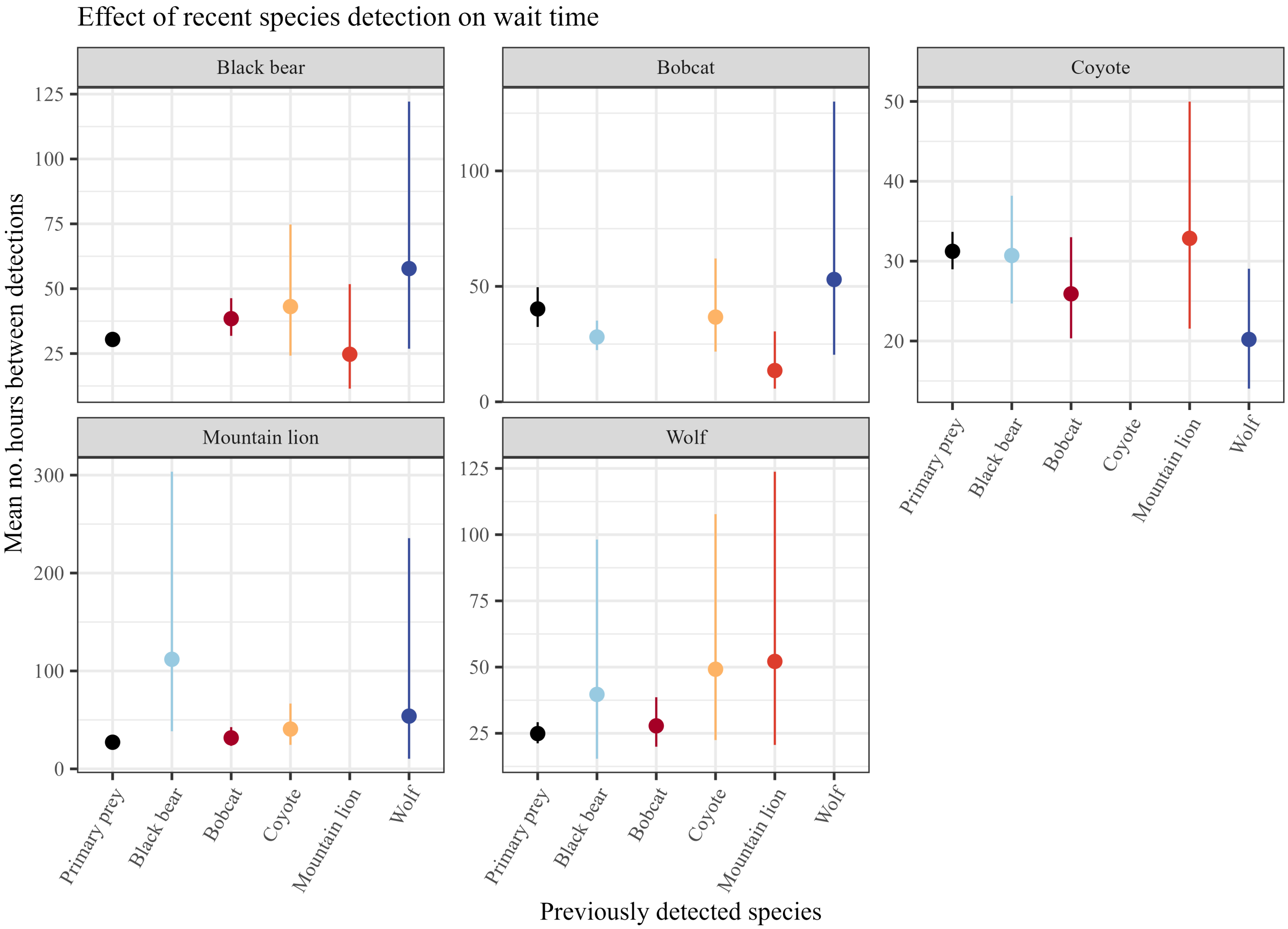

**FIGURE 5** Mean wait time before a black bear, bobcat, coyote, mountain lion, or wolf was detected following the recent detection of a different species. Bars represent 95% credible intervals sampled from their posterior distributions. Wait times following the detection of each predator's primary prey species (i.e., lagomorphs, elk, moose, or white-tailed deer) were estimated with a separate model; mean wait time following the detection of a primary prey animal is presented for comparison.

following any other competitor species (Figure 5). Wait times for black bears, mountain lions, and wolves did not differ with the competitor species previously detected (Figure 5; Appendix S1: Table S7). However, models with moderately less support (≤5 ΔDIC) that included the effect of competitor species indicated that mountain lion wait times were longer following the detection of a black bear than wait times following most other competitor species (Figure 5). We note these results are based on a limited sample size ($n = 16$ observations of a mountain lion detected immediately after a black bear). Black bear wait times were shorter following a mountain lion detection compared with a wolf detection (Figure 5). Wait times declined as the relative abundance of white-tailed deer increased across sites for bobcats, mountain lions, and wolves (Figure 6). Wait times also declined for mountain lions and black bears as the relative abundance of elk increased, although the upper limit of the 95% CRI for the elk effect on black bear wait times slightly overlapped 0 (Figure 6; Appendix S1: Table S7, Figure S3). Coyote wait times were affected by an interaction between the species of competing predator and prey relative abundance. Mean wait time for coyotes declined at a faster rate with increasing white-tailed deer relative abundance when wolves were most recently detected compared with other competitors (Figure 6; Appendix S1: Table S7, Figure S3).

## DISCUSSION

Interspecific interactions between competing predators have the potential to shape wildlife communities and are an important consideration when making conservation and management decisions (Connell, 1983; Linnell & Strand, 2000). Yet, the strength and type of interaction (e.g., competitive vs. facilitative) can vary across spatiotemporal scales and depend on the dominance hierarchy of sympatric species, complicating the study of

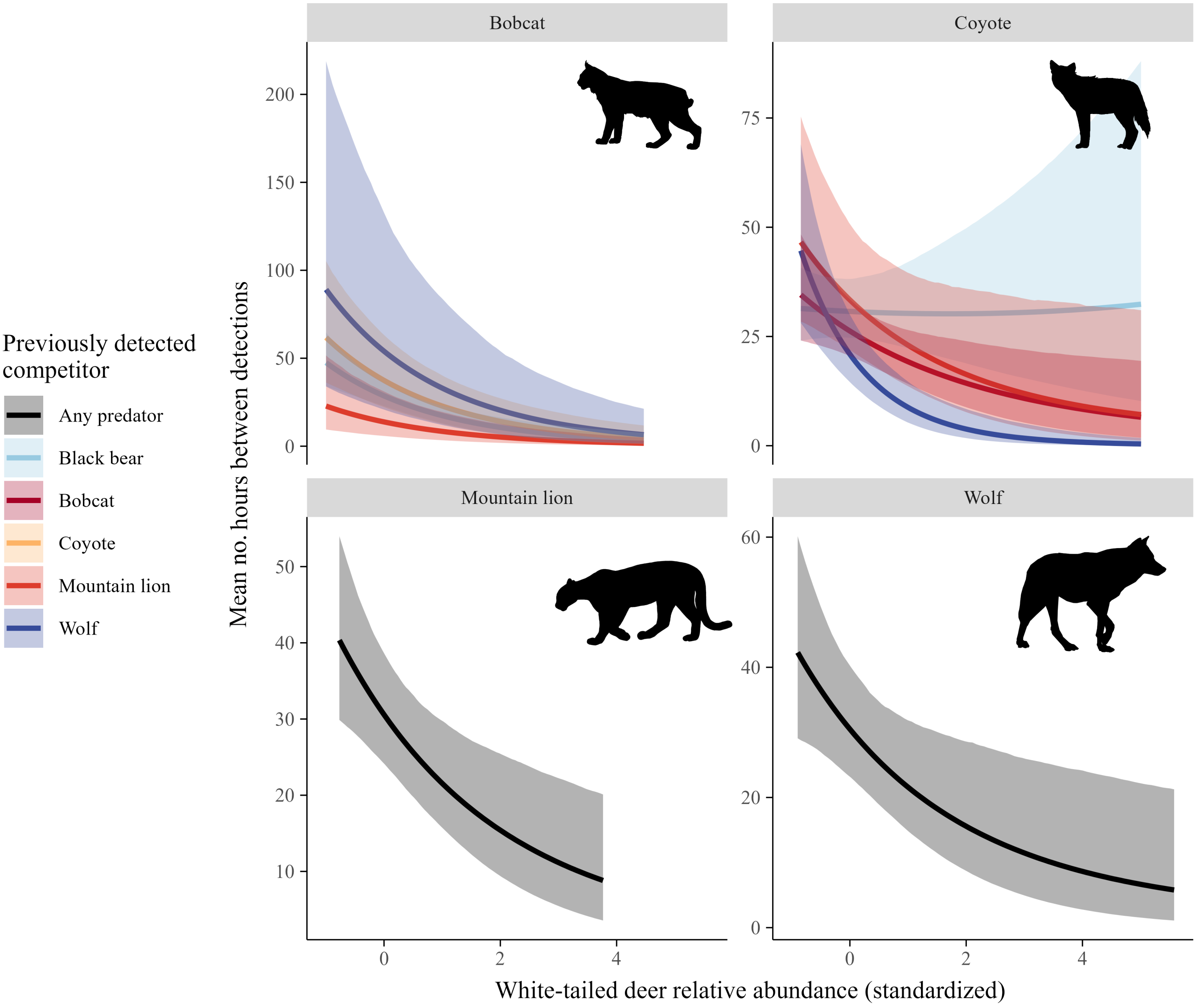

**FIGURE 6** Effect of relative abundance index of white-tailed deer on the predicted wait times (mean number of hours) before a bobcat, coyote, mountain lion, or wolf was detected following that of a competing predator species in northern Idaho, USA, 1 July–15 September 2020–2021. Wait times for bobcats were further influenced by an additive effect of the species of competing predator previously detected. Coyote wait times were affected by an interaction between the previously detected competing predator and the relative abundance of prey. Solid lines represent mean wait time predicted across a range of values for the relative abundance of prey; semi-transparent colors represent their 95% credible intervals. Bobcat and wolf silhouettes were created by Margot Michaud and are available for reuse under the CC0 1.0 Universal Public Domain Dedication license at https://www.phylopic.org/. Coyote and mountain lion silhouettes were created by Gabriela Palomo-Munoz and are available for reuse under the Attribution-NonCommercial 3.0 Unported license at https://www.phylopic.org/.

interspecific interactions (Broekhuis et al., 2013; Cusack et al., 2017; Prugh & Sivy, 2020). We investigated predator space use across three temporal scales, focusing on seven species dyads comprising five sympatric predators, to better understand how competition and prey availability influenced the co-occurrence and habitat use of predators in a multi-predator system. Our results were generally inconsistent with our spatial avoidance hypothesis (H1) as we detected few instances of negative co-occurrence between predators. When we observed significant co-occurrence, correlations were positive and often conserved between the same predator dyads at several temporal scales. We found moderate support for our prey mediation hypothesis (H2) as prey availability, especially the relative abundance of white-tailed deer, influenced predator space use at the finest temporal scale we examined. Dominance hierarchies and the temporal scale of observation further influenced whether we found evidence of predator interactions. Mesopredators demonstrated the strongest response to interspecific interactions and prey availability, likely because their position within the predator guild requires them to balance trade-offs between food acquisition and risk from other predators (De Satgé et al., 2017).

We found little evidence of spatial avoidance among predators across the three temporal scales we investigated. In general, predator occurrence, detection probabilities, and wait times were independent of other predator species. These results are consistent with numerous other studies that failed to find evidence of spatial avoidance within predator guilds at relatively coarse spatiotemporal scales (e.g., Gompper et al., 2016; Miller et al., 2018). In these studies, as with ours, species-specific variation in habitat preferences, predator hunting mode, or tolerance to human disturbance appeared to influence co-occurrence patterns as opposed to interspecific competition (Broekhuis et al., 2013; Gompper et al., 2016; Kachel et al., 2022; Krohner & Ausband, 2019; Miller et al., 2018). The effects of interspecific competition can manifest in other aspects of predator behavior or population dynamics, possibly explaining the lack of spatial avoidance in our study. Subordinate predators may reduce their visitation rates to sites used by dominant predators but not avoid them entirely (Moll et al., 2021). Dominant predators are also known to suppress the abundances of subordinate species, often through intraguild predation or exploitation competition (Bauder et al., 2022; Creel & Creel, 1996; Levi & Wilmers, 2012), but not completely exclude the subordinate species. And sympatric predators can temporally partition space as an alternative to spatially avoiding competitors (De Satgé et al., 2017; Schoener, 1974) as has been observed between black bears and wolves in our system already (Krohner & Ausband, 2019). Alternatively, dominant predators may not limit the abundances or space use of subordinate predators if the dominant predator's population density is relatively low (e.g., Crimmins & Van Deelen, 2019). Thus, competition may influence predator populations through other pathways that were challenging to detect through co-occurrence patterns in our study.

Habitat influenced the probability of site use for black bears, bobcats, coyotes, and wolves at the coarsest temporal scale of our study. This suggests that long-term patterns of predator space use are influenced by more predictable landscape features than relatively less predictable interspecific interactions (i.e., probability of competitor presence or the average daily detection rate of prey). Indeed, these habitat features may act as somewhat reliable cues of otherwise unpredictable processes. Predators often use habitats preferred by their prey or habitats that are advantageous to the predator's hunting strategies, presumably to increase the probability of encountering or capturing prey, even in areas where prey are less abundant (Atwood et al., 2007; Flaxman & Lou, 2009). We found that bobcats were likely to use sites with more structurally complex habitat (i.e., higher forest cover and ruggedness), consistent with a stalking hunting strategy where the predator relies on crypsis to approach and capture prey (Atwood et al., 2007). In comparison, coyotes and wolves, both coursing predators that chase prey over long distances, were more likely to use sites with less structural complexity (Atwood et al., 2007). Black bears and wolves were also more likely to use higher elevation sites, which was consistent with the general distribution of deer and elk on summer range in northern Idaho (Secord et al., 1999; Unsworth et al., 1998). At the 11-week temporal scale, predators may therefore use habitat features that predictably increase the possibility of encountering or capturing prey even if the frequency of use by prey (i.e., relative abundance) is less predictable.

Species-specific differences in habitat use likely contributed to why we did not find evidence of subordinate predators spatially avoiding dominant predators (i.e., negative co-occupancy). Namely, each species responded differently to the suite of habitat features we considered; as such, even if two species used the same site within the 11-week sampling period, the frequency at which they used the site differed. Landscape heterogeneity can reduce the chances of negative interactions between spatially overlapping predators (Müller et al., 2022). For instance, black bears, bobcats, and wolves were all more likely to use sites with higher forest cover, but their respective responses to terrain ruggedness were entirely different. Even for similar responses to a common habitat feature (e.g., forest cover), the relative importance of that variable in explaining marginal occupancy varied by species. Thus, any co-occupancy appears to have been driven largely by species-specific habitat use and not competitive interactions. This was perhaps most evident with the black bear–coyote dyad, where the best supported model indicated negative co-occupancy between the two predators, yet the interaction term was not statistically meaningful. Instead, the apparent spatial avoidance between black bears and coyotes likely arose owing to completely opposite responses to each habitat variable. Differences in habitat use may reflect the "ghost of competition past," where niche partitioning coevolved between competitors to reduce the effects of competition on fitness, but the patterns we observed more likely reflect differences in species-specific life-history traits (Connell, 1980). The results of our co-occupancy models therefore underscore the importance of considering habitat preferences when assessing interspecific interactions (Soberón, 2007).

We found positive spatial associations at finer temporal scales, suggesting that attraction or facilitation, but generally not avoidance, influenced space use for several predator dyads in our system. Coyotes and bobcats were more likely to be detected if the other species, or an apex predator (wolf or mountain lion, respectively), was also detected during a 1-week sampling occasion. Wait times were also shortest for mesopredators after an apex predator was most recently detected. These results are consistent with numerous studies that observed spatial overlap, or a lack of avoidance, between coyote–bobcat, wolf–coyote, and mountain lion–bobcat dyads (King et al., 2021; Koehler & Hornocker, 1991; Lombardi et al., 2020; Paquet, 1991). Although our co-detection analysis did not allow us to differentiate which species was detected first, our wait time analysis explicitly considered the sequential order of species detections, demonstrating at relatively fine spatiotemporal scales that mesopredators were attracted to sites recently used by apex predators. Dominant predators pose a threat to subordinate predators (Palomares & Caro, 1999), but it may be energetically profitable for mesopredators to visit sites recently used by an apex predator if the reward of potential scavenging opportunities outweighs the risk of antagonistic interactions (Malesis et al., 2024; Prugh & Sivy, 2020; Ruprecht et al., 2021; Sivy et al., 2017). Research in Oregon, USA, found that coyotes were strongly attracted to mountain lion kill sites despite mountain lions being a considerable source of mortality for coyotes (Ruprecht et al., 2021). Similarly, Paquet (1991) observed coyotes following wolves to kill sites even though wolves killed coyotes. It is possible that we detected a similar process occurring within the wolf–coyote and mountain lion–bobcat dyads in our system. However, without auxiliary information on predator movement and scavenging, we cannot determine if facilitation influenced these fine-scale spatial associations.

Prey availability strongly influenced space use for all predator species and, in some instances, increased the spatial overlap between predators at fine spatiotemporal scales. Notably, predators consistently visited a site sooner following the detection of a heterospecific where prey (elk or white-tailed deer) was relatively more abundant. Although predator responses varied by prey species, almost all predators responded to variation in the relative abundance of white-tailed deer at the finest temporal scale we investigated. Abundant prey is hypothesized to explain coexistence within predator guilds across continents (e.g., large carnivores in Africa and South and Southeast Asia, mesopredators in North America; Gese et al., 1996; Grassel et al., 2015; Lombardi et al., 2020; Périquet et al., 2015; Srivathsa et al., 2023). White-tailed deer densities were highest and the most evenly dispersed of the wild ungulates in our study areas (Idaho Department of Fish and Game, unpublished data). Given the positive associations between some predators and the general lack of spatial avoidance, it appears that relatively high densities of a shared prey facilitated spatial coexistence among northern Idaho's large predator community. In particular, we expected coyotes would avoid wolves, given their interactions are often highly antagonistic and can culminate in wolves killing coyotes (Merkle et al., 2009; Paquet, 1991). Yet, not only were wait times for coyotes lower following the detection of a wolf compared with other species, but wait times decreased at a faster rate as the relative abundance of white-tailed deer increased. Visiting sites with higher prey abundances that were recently used by a larger predator could be optimal for coyotes if the benefits from scavenging and encountering prey outweigh the risks from antagonistic interactions with dominant predators.

The dominance hierarchy of predators likely influenced which species were affected and the scales at which we observed interactions. Coyotes and bobcats were involved in spatial associations across all three scales whereas interactions involving the larger predators were only detected at finer temporal scales. Smaller predators face greater competition as dominant predators exert top-down pressures, and predators within the same trophic level overlap each other more closely across niche space (De Satgé et al., 2017). It is therefore not surprising that of all the predator dyads we considered, evidence of interspecific interactions frequently involved mesopredators. Interestingly, we found positive spatial associations between coyotes and bobcats at the seasonal and weekly timescales, but a negative effect of coyotes on bobcat space use at the hourly to daily timescale. Positive associations at the coarser scales may reflect common use of a shared (but unmodeled) resource, such as areas of higher small mammal densities. But longer wait times for bobcats following the detection of a coyote suggest bobcats avoided areas recently used by their larger competitor. Assuming coyotes are the dominant predator, these patterns likely reflect a balancing act for bobcats, where bobcats avoid sites only if there is an immediate risk of encountering a coyote but otherwise maintain access to shared resources (Broekhuis et al., 2013; Karanth et al., 2017). The dominance hierarchy between mountain lions and black bears also became more apparent at finer scales, as mountain lion wait times were longer following the detection of a black bear whereas black bear wait times were shorter following the detection of a mountain lion. Black bears often steal mountain lion kills or displace mountain lions at carcasses (Elbroch & Kusler, 2018). Mountain lions may therefore avoid areas recently used by black bears to minimize loss of kills whereas black bears may be attracted to areas recently used by mountain lions in search of carcasses they can kleptoparasitize. These findings are consistent with our expectation that competitive interactions would be most evident at finer scales and offer limited support for our first hypothesis that subordinate predators avoid dominant predators (H1).

Evidence of competitive effects on predator communities may vary with the temporal scale and response variable of interest. Theory suggests that interspecific competition manifests more strongly at fine scales (Godsoe et al., 2015; Vanak et al., 2013; Wiens, 1989). Consistent with this theory, we found that the space use of apex predators influenced weekly detection probabilities and wait times of subordinate predators but not their seasonal occupancy probabilities. Indeed, species interactions are often ephemeral and occur at relatively local scales (e.g., short-term encounters) that may not scale to broader patterns of space use within a predator community (Andrade-Ponce et al., 2022; Cusack et al., 2017; Godsoe et al., 2015). The effects of ephemeral antagonism on large-scale distribution or abundance are difficult to detect without landscape-scale replicated manipulation and are difficult to infer without detailed studies of individual energetics or survival. Spatial variation in abundance may be a more appropriate metric than co-occurrence to study the outcomes of competitive interactions between predators. The relationship between occupancy and abundance is non-linear (Emmet et al., 2021; Steenweg et al., 2018); densities of competing predators are often negatively correlated as dominant predators can suppress subordinate predator populations (Goodheart et al., 2022; Prugh & Sivy, 2020), yet patterns of spatial avoidance or competitive exclusion may go undetected depending on the occupancy–abundance relationship, scale, and strength of interactions (Blanchet et al., 2020; Godsoe et al., 2015; Steenweg et al., 2018). Studies of co-occurrence frequently find neutral or positive spatial associations between predators despite known antagonistic relationships (e.g., Davis et al., 2021; King et al., 2021; Lombardi et al., 2020), which begs the question of whether co-occurrence models can capture population-level effects of competition on predators (Blanchet et al., 2020). Co-abundance models may offer greater insight into both the spatial and demographic effects of competition on predator communities (e.g., Amir et al., 2022; Brodie et al., 2018) even when co-occurrence patterns are positive.

Our study focused on the effects of competition and prey availability on predator co-occurrence in mid- to late-summer. However, prey distributions and availability vary seasonally and likely influence predator competition and space use patterns. For instance, black bears, coyotes, and bobcats primarily prey on neonatal ungulates during the peak of deer and elk parturition (June) and shift their diets to other resources as neonates grow and become harder to catch (Kilgo et al., 2012; White et al., 2010). We were unable to consider predator co-occurrence patterns throughout the year owing to seasonal constraints of camera maintenance, and we acknowledge that our results apply to only a snapshot in time that may not reflect predator space use patterns at different times of year (Wiens, 1993). We also note that we did not account for anthropogenic effects in our system but recognize that humans can have a significant influence on predator populations and co-occurrence. For instance, Manlick et al. (2020) found that land-use change (i.e., development and agriculture) had negative effects on carnivore co-occurrence, likely owing to reduced habitat availability. We did not consider anthropogenic effects in our study because our cameras were deployed in relatively remote areas where human detections were infrequent on most cameras in summer and the human footprint (e.g., human density, development, and infrastructure) across camera sites was low (based on a global human footprint index; Gassert et al., 2023). Humans may strongly influence carnivore co-occurrence at other times of year however, particularly during the fall hunting season when hunter activity has been shown to influence predator space use and activity in nearby systems (e.g., Bassing et al., 2024).

Using camera trap data in multispecies occupancy models can provide insight into species interactions (Andrade-Ponce et al., 2022), but unknown and unmodeled variables could provide qualitatively different interpretations of co-occurrence patterns (Andrade-Ponce et al., 2022; Blanchet et al., 2020). Detection rates are influenced by animal movement (Broadley et al., 2019; Stewart et al., 2018), so animals that increase localized movement when dominant competitors are nearby (e.g., Goodheart et al., 2022) would generate positive co-detection under our study design. Multispecies occupancy models also require large amounts of data and can fail to detect interactions if sample sizes are too small (Kéry & Royle, 2021). Larger carnivores are particularly challenging to detect, which can limit robust inference about species interactions (Dröge et al., 2017). This, and violation of the closure assumption (Lonsinger, 2022), likely contributed to the limited evidence of interspecific interactions involving the larger predators in our system.

We demonstrated that space use among sympatric predators was largely structured by prey abundance and habitat, whereas the distribution of putative competitors generally did not influence predator co-occurrence in our system. Instead, some predator dyads appeared to be attracted to common sites, possibly owing to the availability of shared prey or scavenging opportunities. Space use by subordinate mesopredators was affected by the presence of multiple sympatric predators across temporal scales and sometimes with an interactive effect of prey availability. Our study highlights the importance of assessing multiple interspecific interactions simultaneously, as well as evaluating interactions across multiple spatiotemporal scales, to uncover nuanced relationships between competing predators, their prey, and space. Lastly, our results suggest that changes in space use by one predator species will generally have little impact on the distribution of sympatric predators in our system, which may have implications for predator conservation and management.

## AUTHOR CONTRIBUTIONS

Sarah B. Bassing developed the study design, conducted analyses, and wrote the initial draft of the manuscript. David E. Ausband and Matthew R. Falcy assisted with the study design and data analysis and contributed to manuscript revisions. Matthew A. Mumma and Mark A. Hurley developed the initial concept of the study, managed data collection, and contributed to study design and manuscript revisions. Sarah Thompson managed data collection and preparation and contributed to study design and manuscript revisions.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Code and anonymized data formatted for analyses (Bassing, 2025) are available in Zenodo at https://doi.org/10.5281/zenodo.14590225. Camera trap locations and images are sensitive and cannot be provided publicly; qualified researchers can contact the Data Management Lead, Idaho Department of Fish and Game, Idaho Fish and Wildlife Information System, Boise, Idaho, for full data requests by contacting idfgdatarequests@idfg.idaho.gov and using the following query details: camera trap data collected as part of the North Idaho Predator-Prey Project, collected from 1 July to 15 September 2020 and 1 July to 15 September 2021 in game management units (GMUs) 1, 6, and 10A, including camera ID and location coordinates, camera setup style, camera deployment and retrieval dates, and detections of black bears, bobcats, coyotes, mountain lions, wolves, elk, moose, rabbit-hare, and white-tailed deer, including date, time, and trigger method of individual images.

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## SUPPORTING INFORMATION

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

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