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Spatial and temporal patterns of predator-prey interactions in a large mammal
community in eastern Washington

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Abstract

Spatial and temporal patterns of predator-prey interactions in a large mammal community in eastern Washington

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Non-consumptive predator-prey interactions (NCEs) take numerous forms and occur over a broad range of spatial and temporal scales. In this dissertation, I assessed the spatial and temporal patterns of NCEs as they arose across the human-dominated landscape of eastern Washington, USA. Using data collected by myself and collaborators with the Washington Predator-Prey Project, I 1) evaluated the influence of sampling design on the inferences we draw about wildlife populations, particularly when monitoring predators and prey, 2) assessed how predator hunting mode influenced predator-prey movements, 3) considered the interactive effects of background and immediate levels of predation risk on the temporal activity of prey, and 4) evaluated the influence of livestock grazing and hunting on predator-prey co-occurrence and

temporal overlap. Together, these studies demonstrate the complex nature of NCEs in a multi-predator, multi-prey system, particularly when they occur across mixed-use landscapes. Results from this research can advance our general understanding of multi-species interactions, predator-prey dynamics, and inform wildlife monitoring and conservation decisions.

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DEDICATION

*To the librarians, artists, and entrepreneurs in my life who showed me the value of curiosity,
creativity, and hard work.*



Chapter 1. INTRODUCTION

1.1 BACKGROUND

Gray wolves (*Canis lupus*) have been naturally recolonizing Washington State since 2008 (Washington Department of Fish and Wildlife et al. 2022). Their continued population expansion will generate heightened stakeholder interest in the effects of wolf recolonization on ungulate populations in a state already occupied by several large predator species (e.g., cougars [*Puma concolor*]) and heavily influenced by anthropogenic activities (Washington Department of Fish and Wildlife et al. 2022). In response to these interests, Washington State legislatively mandated that the Washington Department of Fish and Wildlife partner with the University of Washington to evaluate the impact of wolves on mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*) and elk (*Cervus canadensis*) populations in Washington, USA. Thus, the Washington Predator-Prey Project (<https://predatorpreyproject.weebly.com/>) was initiated in 2016 to evaluate wolf – wild ungulate interactions, while recognizing that these species are part of a larger wildlife community coexisting in a human-dominated landscape where a multitude of species interactions and anthropogenic factors likely influence predator-prey dynamics. This collaborative study generated data from >460 Global Positioning System (GPS) - collared animals and 360 camera trap stations, among other data streams, and drew on partnerships across multiple universities, state and federal agencies, tribes, non-government organizations, timber and agriculture producers, and dozens of private landowners. My dissertation was one part of this collaboration.

Understanding predator-prey relationships requires examining species interactions through multiple lenses given the number of potential interactions that may occur in a multi-

predator, multi-prey system. Whereas the consumptive effects of predator-prey interactions have the most obvious consequences for prey species (i.e., mortality), non-consumptive effects of predation can widely influence prey populations as well (Say-Sallaz et al. 2019). Prey may engage in a number of antipredator behaviors to reduce predation risk, such as allocating time to vigilance (Kuijper et al. 2015) or using habitats that facilitate their escape (e.g., Forshee et al. 2022). Conversely, predators engage in behaviors to increase encounter and capture success, often tracking areas of higher prey density or prey's resources (Flaxman and Lou 2009), or using habitats that provide an advantage when hunting (Balme et al. 2007, Cresswell et al. 2010). This dance between predators and prey influences their space-use (Dickie et al. 2020), daily activity (Higdon et al. 2019), and interactions with other species (Schmitz et al. 2004), all of which can affect encounter or capture rates (Guiden et al. 2019, Suraci et al. 2022) and risk effects (i.e., incurred costs associated with antipredator responses, CITE), with potential demographic consequences for both predators and prey (Say-Sallaz et al. 2019).

1.2 RESEARCH OBJECTIVES

The goal of my dissertation was to evaluate patterns of space-use and temporal activity within the wildlife community of eastern Washington to better understand the non-consumptive effects of predator-prey interactions in a multi-predator, multi-prey system. Although there are numerous approaches to studying predator-prey dynamics (Prugh et al. 2019, Suraci et al. 2022), one commonality across studies is that data are either collected at the individual level (by monitoring specific individuals as they navigate their environment) or at the population level (by sampling many individuals as they use a common space; Phillips et al. 2019). Although we often assume data collected from both perspectives can provide similar inferences about wildlife, few studies have explicitly evaluated this assumption (Phillips et al. 2019). I therefore leveraged the

GPS collar and camera trap data collected on seven species from across the Washington Predator-Prey Project to ask whether information from individual- versus population-level survey perspectives yielded similar inferences about wildlife-habitat associations and space-use patterns (Chapter 2).

I then used these datasets to evaluate different spatial and temporal patterns of predator-prey interactions among a suite of wild ungulates, apex predators, and mesopredators. How animals move through space has the potential to alter predator-prey interactions (Avgar et al. 2008, Scharf et al. 2008), and prey may adjust their movement behaviors to minimize predation risk based on the hunting strategies of different predator species (Miller et al. 2014). In Chapter 3, I therefore focused on evaluating how predator hunting mode (i.e., the foraging behaviors predators use to encounter and catch prey; Mclaughlin 1989, Schmitz 2005) and habitats associated with predation risk (e.g., structurally complex habitats; Atwood et al. 2009) influenced animal movement using telemetry data from GPS-collared animals and hidden Markov movement models (McClintock et al. 2020).

The antipredator behaviors of prey are also influenced by the predictability of predation risk (Creel et al. 2008) and prey responses to different levels of risk may vary depending on the interaction between predictably risky places and unpredictable risky times (Dröge et al. 2017). I therefore used photo-capture data of nine species in Chapter 4 to assess the temporal scales at which prey avoided predation risk based on varying levels of background risk (i.e., risky places) and immediate risk (i.e., risky times).

Finally, predator-prey interactions play out across human-dominated landscapes in much of the world (Dorresteijn et al. 2015), including in eastern Washington, USA. Anthropogenic activities and land use can provide refuge from predation risk (Muhly et al. 2011) or push

predators and prey into closer spatiotemporal proximity (Gaynor et al. 2018), both of which have the potential to alter species interactions within wildlife communities (Dorresteijn et al. 2015). I therefore used camera trap data to evaluate the influence of two common anthropogenic disturbances in the western US – livestock grazing and hunting by humans – on the spatiotemporal overlap of predators and prey in Chapter 5.

1.3 BROADER IMPACTS

Together, these chapters demonstrate the complexity of multi-predator, multi-prey interactions across space in time and highlight important considerations when monitoring wildlife communities. Chapter 2 provides a comparison of two common but disparate wildlife monitoring tools which decision makers can use when designing future monitoring plans and research. Chapters 3 and 4 explore multiple facets of predator-prey theory within a multi-predator, multi-prey framework. These studies advance our understanding of animal movement, temporal partitioning, and the “response race” that predators and prey are engaged in. Finally, Chapter 5 offers new insight to how anthropogenic activities influence predator-prey interactions, highlighting the importance of incorporating humans in predator-prey studies.

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Chapter 2. ARE WE TELLING THE SAME STORY? COMPARING INFERENCES MADE FROM CAMERA TRAP AND TELEMETRY DATA FOR WILDLIFE MONITORING

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Dedicated to the late Dr. John Pierce who supported and helped develop the Washington Predator-Prey Project.

Abstract: Estimating habitat and spatial associations for wildlife is common across ecological studies, and it is well known that individual traits can drive population dynamics and vice versa. Thus, it is commonly assumed that individual- and population-level data should represent the same underlying processes, but few studies have directly compared contemporaneous data representing these different perspectives. We evaluated the circumstances under which data collected from Lagrangian (individual-level) and Eulerian (population-level) perspectives could yield comparable inference to understand how scalable information is from the individual to the population. We used Global Positioning System (GPS) collar (Lagrangian) and camera trap (Eularian) data for seven

species collected simultaneously in eastern Washington (2018 – 2020) to compare inferences made from different survey perspectives. We fit the respective data streams to resource selection functions (RSFs) and occupancy models and compared estimated habitat- and space-use patterns for each species. Although previous studies have considered whether individual- and population-level data generated comparable information, ours is the first to make this comparison for multiple species simultaneously and to specifically ask whether inferences from the two perspectives differed depending on the focal species. We found general agreement between the predicted spatial distributions for most paired analyses, though specific habitat relationships differed. We hypothesized the discrepancies arose due to differences in statistical power associated with camera and GPS-collar sampling, as well as spatial mismatches in the data. Our research suggests data collected from individual-based sampling methods can capture coarse population-wide patterns for a diversity of species, but results differ when interpreting specific wildlife-habitat relationships.

Keywords: Ecological scaling, Eulerian, individual-based sampling, Lagrangian, location-based sampling, multiple-species, occupancy model, resource selection function, study design

2.1 INTRODUCTION

Understanding the habitat and spatial associations of species is fundamental to the study of ecology (Strickland and McDonald 2006, Mayor et al. 2009) and increasingly important as human land use and climate change push more species to the limits of their ranges (Lenoir and Svenning 2015, Williams and Newbold 2021). Within management and conservation contexts, these relationships are evaluated at the population level to make predictions about how species will respond to environmental perturbations and to assess the efficacy of management actions (Martin 1998, Merrick and Koprowski 2017). However, the data collected to inform these population level parameters may vary from individual- to population-level, necessitating an

evaluation of how consistently different survey types scale when making inference. In addition, researchers and decision makers must evaluate trade-offs between costs, technology, multiple objectives, feasibility, animal welfare, and human safety when considering how to design and implement wildlife surveys.

Wildlife surveys are typically either individual-based, following a Lagrangian survey perspective where sampling equipment moves with the individual (e.g., Global Positioning System (GPS) collars), or location-based, following a Eulerian survey perspective in which observations are taken at predetermined locations where animals may occur over time, thus collecting population-level data (e.g., transect surveys; Aarts et al. 2008, Tremblay et al. 2009, Baratchi et al. 2013, Phillips et al. 2019). Individual-level traits and decisions scale up to population-level patterns (Mueller and Fagan 2008), so data collected under either survey perspective can be used to answer similar ecological questions despite sampling different hierarchical levels of a wildlife population or community (Phillips et al. 2019). However, few studies have explicitly considered whether Lagrangian and Eulerian surveys capture the same population-level patterns equally well, partly because studies rarely collect concurrent and spatially overlapping data from both survey perspectives (Phillips et al. 2019, Del Bosco 2021). Previous studies that did collect contemporaneous datasets often used one data source to validate the other. For example, Popescu et al. (2014) evaluated how well the detection probability of Pacific fisher (*Pekania pennanti*), estimated from camera trap data, was predicted by the number of fisher telemetry locations near camera traps within telemetry-based utilization distributions. Gould et al. (2019) took this approach a step further and used telemetry locations from collared American black bears (*Ursus americanus*) as a spatially independent data source to assess the fit and performance of occupancy models constructed from photo-capture data of black bears. Both

studies found the different data sources provided complimentary information, but they did not evaluate whether information from each perspective scaled up to make similar population-level inferences. This is an important missing step because each sampling method has inherent biases associated with their respective survey perspectives that can propagate through analyses to influence the final estimates, inferences, and conservation decisions. Phillips et al. (2019) addressed this knowledge gap by comparing the estimated utilization distributions of common murre (*Uria aalge*) derived from satellite-tagged individuals (i.e., Lagrangian perspective) and ship-based and aerial transect surveys (i.e., Eulerian perspective). They found close agreement between survey perspectives and sampling methods early in the breeding season but observed divergent space-use patterns estimated from the different survey perspectives as the breeding season progressed (Phillips et al. 2019). Their work demonstrated that although data from different survey perspectives can yield similar inferences, exceptions exist, underscoring the need for further research evaluating the prevalence of these discrepancies.

Animal-borne GPS collars and camera traps are two common tools for wildlife monitoring (O'Connell et al. 2011, Latham et al. 2015) that fall under the respective Lagrangian and Eulerian perspectives (Baratchi et al. 2013, Phillips et al. 2019, Del Bosco 2021). Both technologies generate large amounts of data that can be used to assess habitat associations and species distributions (Aarts et al. 2008, O'Connell et al. 2011, McClintock et al. 2020). Animal-borne technologies, such as GPS collars, can generate high-resolution location data for individual animals (Hebblewhite and Haydon 2010), whereas camera traps can collect detections of many individuals within a population non-invasively and are ideal for monitoring multiple species simultaneously (O'Connell et al. 2011, Burton et al. 2015, Iannarilli et al. 2021). Yet, each technology presents its own set of challenges (Hebblewhite and Haydon 2010, Burton et al.

2015). Lagrangian-based studies using GPS collars are limited by the number of animals they can monitor because they are expensive and labor intensive to deploy (Shimada et al. 2021), which can result in a relatively small, non-random sample of the population (Fieberg et al. 2010, Hebblewhite and Haydon 2010). Sequential animal locations are often autocorrelated (Boyce et al. 2010, Fieberg et al. 2010), which can also introduce bias when scaling up from the individual to the population (Aarts et al. 2008, Watanuki et al. 2016, Phillips et al. 2019). Conversely, camera trap and other Eulerian-based studies monitor finite space and locations, thus limiting the spatial extent and resolution of inference while potentially failing to account for important individual-level variation that influences broader patterns (Wakefield et al. 2011, Watanuki et al. 2016, Phillips et al. 2019). Camera placement greatly influences the habitats, species, and ecological phenomena that are sampled, which may inadvertently bias photo-capture data (Burton et al. 2015, Hofmeester et al. 2019, Iannarilli et al. 2021, Tanwar et al. 2021). In particular, many large carnivores prefer to travel on roads whereas prey species often avoid linear features (Dickie et al. 2020, Hofmeester et al. 2021), which can greatly influence their detectability and thus our inferences when cameras are placed non-randomly on these features (Iannarilli et al. 2021). Consequently, survey-specific biases and limitations that arise may make information gained from one method incomparable to that of the other (Popescu et al. 2014).

It is increasingly important that we evaluate how survey perspective and study design influence population-level inferences, particularly as we continue to adopt new technologies, integrate data across methods, and try to relate trends and relationships observed in one data set to that of another (Priddel et al. 2014, Phillips et al. 2019). For example, Phillips et al. (2019) hypothesized that their common murre population comprised both resident and non-resident individuals and that the various sampling methods captured breeding, foraging, and transient

behaviors differently, resulting in the divergent spatial distributions estimated from the individual- and location-based perspectives. If this is the case, then we might expect to see divergent patterns of space-use in other species where individual-based and population-level approaches sample different portions of the same population or capture different movement behaviors. For instance, collar-based studies focused on cervid species often only collar adult females (Gaillard et al. 1998, Forrester and Wittmer 2013) whereas many carnivore-focused studies collar a more demographically random sample of the population. Camera traps typically capture a more random sample of the entire population regardless of the species, but when deployed to increase detections of rare or elusive species (e.g., carnivores), they may disproportionately sample certain movement or foraging behaviors depending on the species (Cusack et al. 2015, Kolowski and Forrester 2017). As a result, population-level inferences may be more or less consistent depending on the movement and foraging strategies of the species of interest (e.g., predator or prey) and the demographics sampled by each perspective. Comparing habitat- and space-use patterns estimated from Lagrangian and Eulerian sampling approaches for a diversity of species should provide further insight about the circumstances under which inferences about wildlife populations may differ with survey perspective.

We used camera trap and telemetry data from seven species (bobcat [*Lynx rufus*], cougar [*Puma concolor*], coyote [*Canis latrans*], elk [*Cervus canadensis*], gray wolf [*C. lupus*], mule deer [*Odocoileus hemionus*], and white-tailed deer [*O. virginianus*]) collected simultaneously in eastern Washington, USA, and evaluated how survey perspective influenced inferences about wildlife-habitat associations and space use. We deployed camera traps under a multiple-species monitoring framework where camera sites were chosen randomly across the landscape but placed non-randomly along linear features to increase the probability of detecting more elusive

species in the wildlife community (Meek et al. 2014, Mann et al. 2015). Accordingly, we hypothesized that inferences from our Eulerian and Lagrangian perspectives would be less consistent for species whose detections were low or for species that move along linear features and thus their detections could be strongly influenced by camera placement on roads (e.g., wolves). GPS collars were deployed on both sexes for all carnivore species but only on adult females of the cervid species, so we also hypothesized that inferences would be less consistent between sampling approaches for species where the GPS-collaring efforts targeted only one demographic group. Because camera traps and GPS collars collect different types of data (i.e., detection/non-detection versus presence-only; Aarts et al. 2008), we applied different, but commonly used and appropriate methods to the photo-capture and telemetry data to estimate habitat and spatial relationships in wildlife science (i.e., occupancy models and resource selection functions [RSF], respectively). If the two survey perspectives capture similar ecological relationships and patterns despite sampling different aspects of a wildlife population, we expected the results from these two analyses to produce similar inferences about habitat- and space-use patterns. We therefore compared the estimated habitat associations and predicted space-use derived from the two perspectives for each species, expecting to see different habitat predictors and probability of use for a given species when the two perspectives were least consistent.

2.2 METHODS

2.2.1 *Study areas*

Photo-capture and telemetry data were collected across two study areas in eastern Washington, USA, from June 2018 – March 2020 (Fig. 2.1). The Northeast study area (4,535 km²; centered at -117.7193° W, 48.28302° N) was defined by two Washington Department of Fish and Wildlife

Game Management Units (GMU) and was bordered by the Pend Oreille River and Columbia River. White-tailed deer and elk occurred in relatively high densities in this study area along with smaller sympatric populations of mule deer and moose (*Alces alces*). Common carnivore species included cougars, coyotes, bobcats, and black bears, as well as four documented gray wolf packs (Washington Department of Fish and Wildlife et al. 2019). This region was characterized by mixed conifer forests of varying seral stages following climatic and topographic gradients of the southern Selkirk and Huckleberry Mountains (elevation ranging 378 – 2079 m; Williams et al. 1995). Mean annual temperatures in Chewelah, WA ranged -2.4° C in January to 19.2° C in July with a mean annual precipitation of 52.3 cm (Western Regional Climate Center 2016, National Oceanic and Atmospheric Administration 2021). Forests were dominated by Douglas fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), ponderosa pine (*Pinus ponderosa*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*; Williams et al. 1995). The Okanogan study area (5,300 km²; centered at -120.1096° W, 48.42966° N) was defined by six Washington Department of Fish and Wildlife GMUs and was bordered by the Okanogan River and North Cascade Range, overlaying a topographically rugged and mountainous region characterized by deep valleys and steep slopes (elevation ranging 225 – 2790 m; Williams and Lillybridge 1983). A large, partially migratory mule deer herd made up the predominant ungulate species in this region, although white-tailed deer, moose, and elk also occurred in the study area. The carnivore community was similar to that of the Northeast but also includes a small population of Canada lynx (*L. canadensis*) and two documented wolf packs during the study (Washington Department of Fish and Wildlife et al. 2019). Mean annual temperatures in Winthrop, WA ranged -3.2° C in January to 20.3° C in July with a mean annual precipitation of 36.1 cm (National Oceanic and Atmospheric Administration 2021). Mixed conifer forests were

dominated by stands of Douglas fir, Engelmann spruce (*Picea engelmannii*), lodgepole pine (*P. contorta*), ponderosa pine, and subalpine fir (*A. lasiocarpa*; Williams and Lillybridge 1983), and open regions were dominated by big sagebrush (*Artemisia tridentata*) and antelope bitterbrush (*Purshia tridentata*).

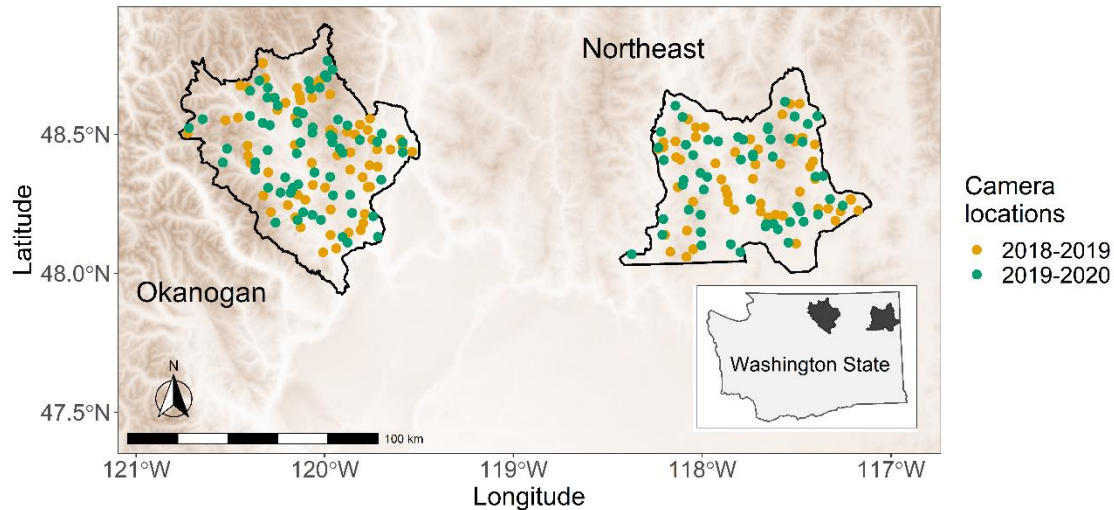


Figure 2.1. Locations of 240 camera stations that sampled the Okanogan and Northeast study areas in eastern Washington, USA from 2018 – 2020, plotted against the elevational gradient where darker shades represent higher elevations.

2.2.2 Camera data

We used motion-sensing trail cameras (Model HyperFire2 Pro; Reconyx, Holmen, WI, USA) to monitor 120 randomly selected sites in the Northeast ($n = 55$) and Okanogan ($n = 65$) study areas each year. We deployed and maintained cameras from June 2018 to June 2019 and redeployed them to new random locations from June 2019 through June 2020 to monitor a total of 240 unique sites, each for one year. We used a stratified random sampling design to select camera trap locations (O’Connell and Bailey 2011) by stratifying each study area into 4 elevation bands.

We excluded locations above ~2,100 m elevation in the Okanogan to avoid sampling alpine habitat that was both logistically difficult to access and not frequently used by the animal community of interest. We overlaid a 1 km² grid across each study area and randomly selected grid cells within each elevation strata by area-weighting each stratum and selecting the number of cells proportional to the amount of land area within each stratum per study area. We deployed a single, un-baited, camera within 250 m of the centroid of each selected cell. We placed cameras on secondary (unpaved) roads, human-use trails, or game trails to target linear features that would funnel animal movement and increase the likelihood of detecting rarer species that occur at low densities (e.g., large carnivores; Cusack et al. 2015). The cameras were motion- and temperature- triggered and programmed to record 5 images per trigger. They operated day and night for an entire year and recorded the date and time when each photo was taken (camera programming reported in Appendix A. S1).

We processed the photo-capture data using the Microsoft AI for Earth machine learning algorithm (“MegaDetector”; Beery et al. 2019) and program Timelapse2 (Greenberg 2019). The MegaDetector indicated whether an animal, human, or vehicle was present in each image. Two technicians independently reviewed images based on the MegaDetector predictions and recorded the species for all animals detected in each image using Timelapse2. A third technician compared the independent data sets to ensure images were labeled correctly and generated the final image set used for analysis.

2.2.3 *Telemetry data*

We monitored a total of 469 individuals of seven species between January 2017 and March 2020 using Global Positioning System (GPS) collars (Fig. 2.2). We captured and collared adult male and female carnivores in both study areas. Bobcats were captured and collared (n = 37; Model

Gen4 GPS-Iridium, Telonics, Mesa, Arizona, USA) using cage traps baited with grouse wings, beaver or road-killed deer (Koehler and Hornocker 1991). Cougars were captured and collared (n = 60; Model Vertex Lite, Vectronic Aerospace and GPS-enabled accelerometer collars, Advanced Telemetry Systems, Inc., Isanti Minnesota, USA) using trained dogs or large, steel cage traps baited with cougar-killed or road-killed deer and elk (Kertson et al. 2011). Coyotes were captured and collared (n = 23; Model Gen4 GPS-Iridium, Telonics) using rubber-padded foothold traps (Victor #3 soft-catch offset 4x4 foothold traps; Linhart 1983). Similarly, wolves were captured and collared (n = 14; Models Vertex Lite and Vertex Plus, Vectronic Aerospace) using rubber-padded foothold traps (#7 EZ Grip foothold traps, Livestock Protection Company, Alpine, Texas, USA) and aerial darting (Jessup 1982, Frame and Meier 2007). We captured and collared only adult female cervids in one study area per species owing to their higher densities and broader distributions within their respective study areas. Specifically, adult female elk were captured and collared (n = 63; Model Survey, Vectronic Aerospace, Berlin, Germany) by aerial darting (Jessup 1982) in the Northeast study area. Adult female mule deer were captured and collared (n = 138; Model Survey, Vectronic Aerospace) by drive netting and aerial net-gunning (Kock et al. 1987) in the Okanogan study area. And adult female white-tailed deer were captured and collared (n = 131; Models Survey and Vertex Plus, Vectronic Aerospace) using clover traps, suspended net-guns (Wildlife Capture Services, Flagstaff, Arizona, USA), and ground darting (Clover 1954, Hawkins et al. 1968, VerCauteren et al. 1997, Haulton et al. 2001) in the Northeast study area. All collars were programmed to attempt a GPS fix every 4 hours for 180 seconds. All animal captures and handling were performed in accordance with University of Washington Institutional Animal Care and Use Committee guidelines under IACUC Protocols #4226-01, #4381-01, Washington Department of Fish and Wildlife scientific collection permits #20-290,

#17-162 and renewals, and adhered to standards promulgated by the American Society of Mammologists (Sikes 2016).

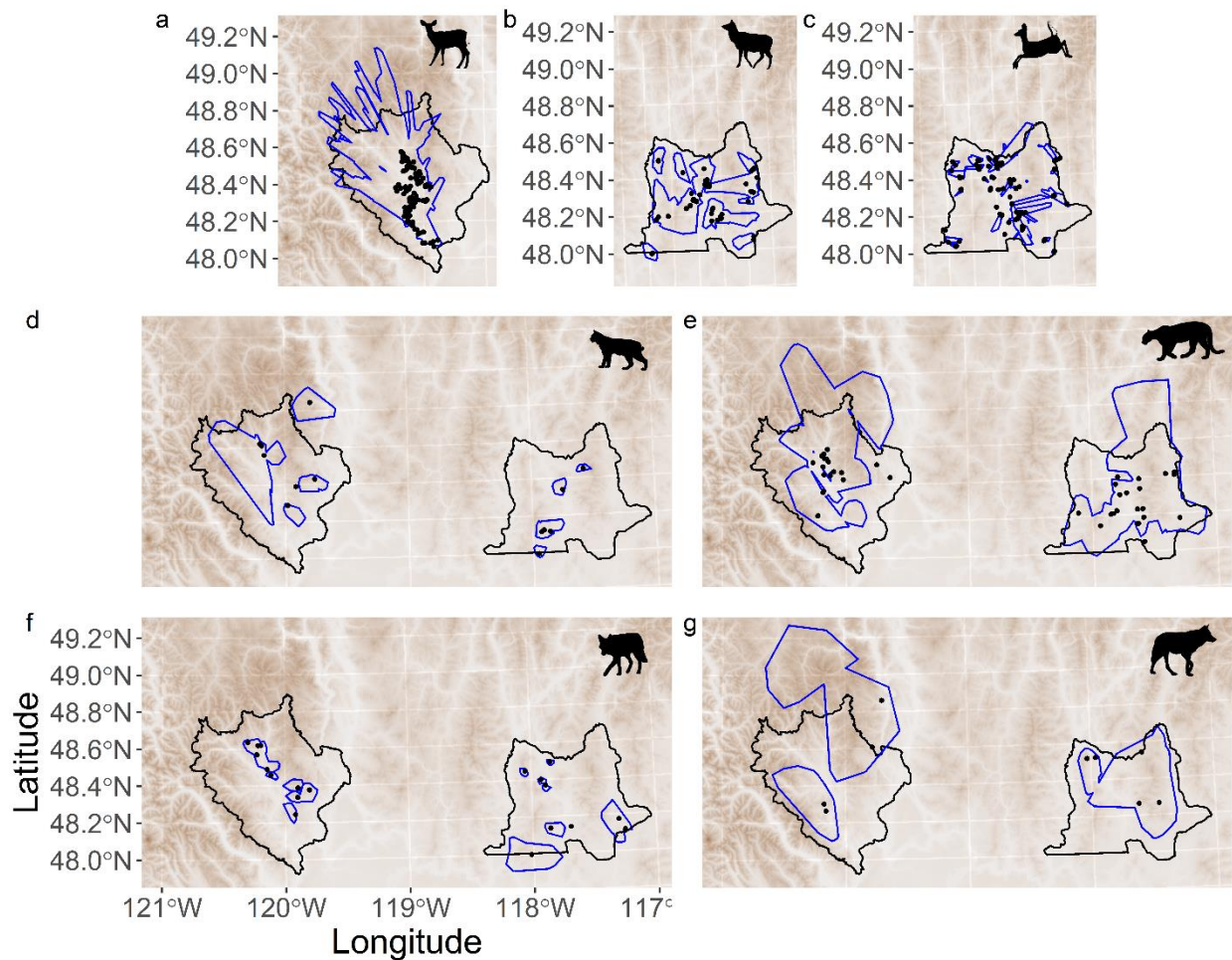


Figure 2.2. Maps of approximate capture locations (black points) for seven species in two study areas in eastern Washington, 2018 – 2020 and the outline of species- and study area-specific home ranges (blue lines) of all individuals used for resource selection function (RSF) analyses. We used individual home ranges (100% minimum convex polygons) to define the area “available” for each collared individual but they were too numerous to show so the outermost outline of all home ranges combined are shown here. (a) Mule deer were only captured and collared in the Okanogan study area; (b) elk and (c) white-tailed deer were only captured and collared in the Northeast study area. (d) Bobcats, (e) cougars, (f) coyotes, and (g) wolves were captured and collared in both study areas. Approximate capture locations that fall outside the blue polygon correspond to animals that were captured and dispersed to new areas (within the blue polygon) prior to the start of the focal period of this study. Approximate capture locations

and home range polygons plotted against the elevational gradient in each study area where darker shades represent higher elevations.

2.2.4 *Habitat predictors*

We included seven habitat-related covariates in our models that are commonly used in studies to evaluate wildlife-habitat associations and represented variation in terrain, vegetation, and anthropogenic impacts across our study areas. We extracted elevation and slope data for each camera site and telemetry location from the Shuttle Radar Topography Mission (SRTM) 30 m resolution digital elevation model (DEM; Farr et al. 2007). We used annual land cover data from the Cascadia Biodiversity Watch TerrAdapt:Cascadia tool (30 m resolution; <https://cascadiapartnerforum.org/terradapt>) to classify the dominant vegetation around each camera site and telemetry location. We reclassified the land cover data into six land cover types (forest, xeric shrub, xeric grass, mesic grass, developed, and water) and used a moving window analysis in Program R version 4.0.2 (R Core Team 2020) to calculate the percent of each land cover classification within a 250 m radius of each observation. We included percent forest, percent xeric grass, and percent xeric shrub in our analyses because these made up the bulk of the land cover types in our study areas. We calculated the density of roads per 1 km pixel (road length/1 km²) in Program R (R Core Team 2020) based on the Cascadia Biodiversity Watch TerrAdapt:Cascadia tool roads layer, which included highways, residential roads, and service roads (primarily logging roads). Finally, we included the study area in which each camera was deployed.

We also incorporated site-specific information collected at each camera trap in the occupancy models only. Specifically, we recorded the type of linear feature each camera trap monitored, hereafter referred to as trail type (game trail, decommissioned road, or open road), the

height of the camera from the ground, and the distance of the camera to the closest point of the linear feature it monitored, measured at the center of the camera's viewshed. We also included an interaction between camera height and distance to account for the angle of the camera because the angle varied greatly depending on the terrain, directionality of the linear feature, and the location of the object the camera was affixed to relative to the linear feature. We expected these variables associated with camera placement would influence the probability of detecting different species on camera (Hofmeester et al. 2019, Iannarilli et al. 2021). In addition, given that ambient temperature can affect animal activity patterns (Van Beest et al. 2012, Hofmann et al. 2016), and affect a camera's ability to differentiate background surface temperatures from that of an animal (Jacobs and Ausband 2018), we used the North American Regional Reanalysis (NARR; 32 km resolution) weather data to characterize the weekly mean temperature at each camera site for every day the camera was deployed (Mesinger et al. 2006).

We centered and scaled all continuous variables to allow for direct comparison among covariate effects. We checked for collinearity among continuous variables and excluded those that were highly correlated ($r \geq |0.6|$) in species- and season-specific models (discussed below).

2.2.5 *Occupancy models*

We used the photo-capture data from each camera trap to create detection histories for each species for two 13-week time periods, summer (July 1 – Sept 29) and winter (December 1 – March 1). We considered two different seasons because the life-histories of these species and environmental pressures they experience vary over the annual cycle, thus their behaviors and associated habitat use may differ from summer to winter. Each seasonal and species-specific detection history consisted of 13 seven-day sampling occasions where each species was either detected (1) or not detected (0) at a given camera trap site during each sampling occasion. We

considered a detection event to be independent when the first detection of a given species followed a ≥ 30 -minute interval between photographs of the same species (O'Brien et al. 2003, Burton et al. 2015, Sollmann 2018). We combined data from both years of sampling into a single detection history for each season and species (summer [2018 and 2019] and winter [2018 – 2019 and 2019 – 2020]).

We fit single-season, single-species occupancy models (MacKenzie et al. 2002) with the unmarked package (Fiske and Chandler 2011) in Program R version 4.0.2 (R Core Team 2020) to estimate the probability of use at each camera site. Occupancy models use detection/non-detection data to estimate the probability a species will occur in a given area while accounting for imperfect detection during repeat surveys (MacKenzie et al. 2002). Although sometimes referred to as species distribution models (e.g., Lahoz-Monfort et al. 2014, Koshkina et al. 2017), occupancy models are more commonly used to estimate the probability of occurrence within a pre-defined region while assessing environmental factors associated with the occurrence patterns, making them an ideal statistical framework when estimating habitat- and space-use patterns with camera trap data (O'Connell and Bailey 2011). Because camera traps sample a small area relative to the average home range of any of our focal species occurring across a continuous habitat, we interpreted our results as asymptotic occupancy, or the probability that a species would use a given camera site at some point during our study period (Efford and Dawson 2012).

We included the same seven covariates on the probability of occupancy (elevation, slope, percent forest, percent grass, percent shrub, road density, and study area) and same five covariates on the probability of detection (trail type, camera height, camera distance to trail, height*distance interaction, and weekly mean temperature) for each season- and species-specific

occupancy model. We chose to fit an identical model to all detection histories to allow for more direct comparison across species and sampling methods (camera traps and GPS collars).

However, we excluded percent grass and/or percent shrub from various species- and season-specific occupancy models when they were highly correlated with other variables or due to poor model convergence. Given that sample size can influence power to detect significant relationships in the data, and the GPS collars generated an order of magnitude more observations than the camera traps, using a common set of habitat predictors allowed us to reduce the chance that data volume drove differences between significant relationships identified by the two different types of models. We considered any coefficients in the occupancy models with a p -value ≤ 0.1 as “significant” for the purposes of this analysis. We considered a species difficult to detect if the mean probability of detecting that species during a one-week sampling occasion was ≤ 0.3 and rare in our study areas during a given season if the mean probability it used a camera site was ≤ 0.3 (Specht et al. 2017).

2.2.6 *Resource selection functions*

Telemetry data provide information on “used” locations only, so unlike the photo-capture data, we could not identify locations that were “unused” by an animal and therefore could not estimate the probability of use from these data. A resource selection function (RSF), however, allows us to compare “used” resource units to a random sample of resource units that were “available” to the animal within a specified area, thus allowing us to estimate habitat selection (Manly et al. 2002, Johnson et al. 2006). RSFs are proportional to the probability of selecting a resource unit and estimate the relative probability that a resource unit will be selected when it is encountered (Boyce et al. 2002, Lele et al. 2013).

We defined used locations as any telemetry location generated by a GPS-collared animal during the same seasonal time periods included in the occupancy models (summer [2018 and 2019] and winter [2018 – 2019 and 2019 – 2020]). We sampled available resource units based on 2nd-order habitat selection (i.e., what determines the placement of an individual's home range; Johnson 1980) because we assumed this level of selection was most comparable to that of our occupancy models, which estimate species habitat use across the study areas, not within individual home ranges (Aarts et al. 2008). We defined the spatial extent of what was available to each collared individual by calculating a 100% minimum convex polygon (MCP) using the telemetry locations of the collared individual and buffering that MCP by its diameter with the *adehabitatHR* package (Calenge 2006) in Program R (R Core Team 2020; Fig. 2). This allowed us to center the geographic area available to each animal around its current home range and avoid the often-unrealistic assumption that the entire study area is equally available to every collared individual. We then randomly sampled locations within each collared animal's respective buffered MCP at a 1:20 ratio of used to available points (Fieberg et al. 2021). We note that other studies should compare the ratio of used to available points to assess how sample size influences study-specific coefficient estimates (Fieberg et al. 2021). We assigned a weight of 5,000 to the available locations and a weight of 1 to the used locations (Fieberg et al. 2021). We extracted covariate values at each used (1) and available (0) location and populated RSFs with these data.

We fit species-specific used and available data for each season (summer and winter) to mixed-effects logistic regression models using the *lme4* package (Bates et al. 2015) in Program R (R Core Team 2020) to estimate the coefficients in the resource selection function (RSF) for each species and season (Fieberg et al. 2021). We included all habitat-related covariates

(elevation, slope, percent forest, percent grass, percent shrub, and road density) as fixed effects in our models. We excluded percent grass and/or percent shrub from species- and season-specific RSFs when these variables were excluded from the corresponding occupancy model for easier comparison between models. We excluded study area from all RSFs because GPS-collared animals could not select between study areas based on what was available to them. We included a random effect for unique animal ID to account for individual variation and pseudo-replication (Gillies et al. 2006). We removed the random effect from the summer elk RSF due to issues of singularity. We considered any coefficients with a p-value ≤ 0.05 for interpretation owing to the larger sample sizes in the RSFs compared to the occupancy models.

2.2.7 *Comparing habitat associations and space-use*

We compared individual model coefficients, as well as broadscale predictions of space use, to determine if the different data types yielded similar inferences for a given species and season when estimated using two common habitat analyses. We recognized that the occupancy and RSF coefficient values were not directly comparable due to their methodological differences (Lele et al. 2013), but we assumed both analyses would capture similar habitat relationships and spatial patterns if the data from camera traps and GPS collars scaled to similar patterns at the population level. To make these comparisons, we first inspected the estimated model coefficients from each pair of occupancy and RSF analyses, specifically evaluating the magnitude of the covariate effects in each model and whether the directionality (+/-) of those effects agreed. We then predicted the species- and season-specific probability of use and relative probability of selection across each study area from the respective occupancy models and RSFs. We plotted predictions within each study area and visually compared the predicted space-use patterns for each species and season. Finally, as a more quantitative comparison, we rescaled the predicted values of

relative probability of selection to range 0 – 1 and calculated the mean correlation between predicted pixel values for each pair of maps using Pearson’s correlation coefficient.

2.3 RESULTS

2.3.1 *Camera data*

A total of 233 and 218 camera traps were active over the course of our summer and winter sampling seasons, yielding 18,377 and 19,262 trapping nights, respectively. We collected on average 954 (SE = 462) independent detections per focal species across active cameras during the summer sampling seasons and on average 524 (SE = 263) independent detections per focal species in the winter sampling seasons (Table 2.1).

Table 2.1. Summary of species detected by semi-randomly placed camera traps and GPS collared animals in the Northeast and Okanogan study areas, eastern Washington, USA 2018 – 2020. Camera trap detections were considered independent when a ≥ 30 -minute interval elapsed between photographs of the same species at a given camera site.

Species	Season	Independent detections	Proportion of cameras [*]	Collared animals [†]	Used locations	Tracking days
Bobcat	Summer	198	0.30	10	3043	815
Bobcat	Winter	74	0.17	12	2673	821
Cougar	Summer	159	0.35	34	21721	3968
Cougar	Winter	72	0.16	34	16597	3039
Coyote	Summer	1140	0.62	16	6962	1367
Coyote	Winter	777	0.53	18	9376	1847
Elk	Summer	151	0.38	46	44384	7714

Elk	Winter	33	0.13	50	45059	7546
Mule Deer	Summer	1582	0.86	82	76811	13192
Mule Deer	Winter	794	0.58	108	80373	13296
White-tailed Deer	Summer	3385	0.93	58	27744	4947
White-tailed Deer	Winter	1896	0.34	74	29569	5147
Wolf	Summer	63	0.12	9	5078	909
Wolf	Winter	27	0.08	7	3437	598

*Proportions were calculated based on the number of active cameras in that season. Only active cameras within the Northeast study area were used to calculate proportions for elk and white-tailed deer; only active cameras in the Okanogan study area were used for mule deer proportions.

†Elk and white-tailed deer were only collared in the Northeast study area; mule deer were only collared in the Okanogan study area.

2.3.2 *Telemetry data*

Of the 469 animals fitted with GPS collars during our study, we included telemetry relocation data from 255 collared animals in the summer sampling seasons and 303 animals in the winter sampling seasons, respectively (Table 2.1). These collars generated an average of 26,535 (SE = 10,079) used locations per focal species across the two summer sampling seasons and an average of 16,726 (SE = 10,631) used locations across the two winter sampling seasons, resulting in over 65,206 tracking days across all species and seasons (Table 2.1).

2.3.3 *Occupancy models*

We fit 14 occupancy models, i.e., one per species and season, to the photo-capture data. The probability of site use and detection varied by species and season but in general carnivores were less likely than ungulates to use camera sites or be detected by a camera trap within a one-week

sampling occasion (Table 2.2, Appendix S1: Table S1). Bobcats, elk, and wolves were the rarest species in our study areas (mean occurrence probability ≤ 0.3). These species also had the lowest detection probabilities, along with cougars and coyotes (mean detection probability ≤ 0.3). Mule deer and white-tailed deer had the highest probability of site use (0.63 – 0.92) and detection (0.35 – 0.67).

Habitat predictors that significantly ($p\text{-value} \leq 0.1$) affected the probability of occurrence varied by species and season (Table 2.2). Elevation had a negative effect on the probability coyotes and white-tailed deer would use a camera site in either season. Conversely, elevation had a positive effect on wolf and cougar site use in the summer but a negative effect on cougar site use in the winter, suggesting seasonal variation in their habitat use. Slope had a negative effect on the probability of coyote site use in summer (Table 2.2). Cougars in either season, and bobcats, mule deer, and white-tailed deer in summer, were more likely to use a camera site as the percentage of forested habitat increased, whereas mule deer site use increased in winter as the percent of grassland and shrubland habitat increased. We also found there was a higher probability that a camera site was used by cougars and wolves in the Northeast compared to the Okanogan study area, consistent with known density and distribution of wolf packs between the two study areas (i.e., four documented packs in the Northeast and two documented packs in the Okanogan; Washington Department of Fish and Wildlife et al. 2019). Coyotes were more likely to use camera sites in the Okanogan study area. Road density had no effect on probability of site use for any species (Table 2.2). We found no significant relationships between any habitat predictors and bobcat, elk, or wolf occupancy in winter or elk occupancy in summer (Table 2.2).

Covariate effects on detection probability also varied by species and season in the occupancy models (Appendix A. S1: Table S1). Trail type significantly influencing detection

probability ($p\text{-value} \leq 0.1$) for most species, but with notable differences between predators and prey (Appendix A. S1: Table S1). We were more likely to detect carnivores at camera sites monitoring an open or decommissioned road compared to a trail. Conversely, we were less likely to detect deer and elk at camera sites monitoring open or decommissioned roads compared to sites monitoring trails (Appendix A. S1: Table S1). The probability of detecting most species was also significantly influenced by camera height, distance to the linear feature it monitored, or an interaction between the two, though the strength and directionality of those effects varied by species and season (Appendix A. S1: Table S1). Finally, coyotes and white-tailed deer were more likely to be detected in winter as temperature increased (Appendix A. S1: Table S1).

Table 2.2. Estimated coefficients and standard errors (SE) for the effect of habitat predictors on the probability a camera site was used by a species of interest (estimated using occupancy models [Occ]) and the relative probability of 2nd-order resource selection for GPS-collared animals (estimated with resource selection functions [RSF]) in eastern Washington, summer and winter 2018 – 2020. Habitat predictors included study area (occupancy models only; Northeast study area representing the intercept), elevation, percent of forest, percent of xeric grass, and percent of xeric shrub landcover within 250 meters of an observation, respectively, road density (road length/1 km²), and slope. Individual ID was included as a random effect in the RSFs. Bolded estimates and standard errors indicate the predictor was significant (p-value ≤ 0.1 for occupancy models, p-value ≤ 0.05 for RSFs).

Type of analysis	Species	Season	Intercept (SE)	Study Area (SE)*	Elevation (SE)	Percent Forest (SE)	Percent Grass (SE)†	Percent Shrub (SE)†	Road Density (SE)	Slope (SE)
Occ	Bobcat	Summer	0.11 (0.45)	-0.46 (0.6)	0.49 (0.37)	0.81 (0.39)	-0.19 (0.44)	-0.01 (0.42)	0.06 (0.25)	0.4 (0.27)
RSF	Bobcat	Summer	-12.17 (0.09)	NA	0.06 (0.03)	0.62 (0.03)	-0.61 (0.11)	-0.9 (0.14)	-0.13 (0.02)	0.18 (0.02)
Occ	Bobcat	Winter	-1.23 (0.42)	-0.07 (0.61)	-0.28 (0.31)	0.61 (0.38)	0.2 (0.31)	NA	0.32 (0.23)	0.11 (0.23)
RSF	Bobcat	Winter	-11.71 (0.11)	NA	-0.89 (0.03)	0.5 (0.03)	-0.04 (0.03)	NA	-0.11 (0.02)	0.16 (0.02)
Occ	Cougar	Summer	0.87 (0.54)	-1.18 (0.7)	0.8 (0.4)	0.73 (0.44)	0.26 (0.35)	-0.08 (0.5)	-0.29 (0.31)	-0.23 (0.26)
RSF	Cougar	Summer	-11.58 (0.03)	NA	0.11 (0.01)	0.2 (0.01)	-0.41 (0.02)	-0.02 (0.01)	-0.08 (0.01)	-0.13 (0.01)
Occ	Cougar	Winter	-1.42 (0.61)	0.91 (0.86)	-1.76 (0.7)	1.41 (0.55)	NA	-0.09 (0.4)	-0.35 (0.35)	0.46 (0.34)
RSF	Cougar	Winter	-11.71 (0.05)	NA	-0.83 (0.01)	0.41 (0.01)	NA	0.08 (0.01)	-0.08 (0.01)	0.44 (0.01)

Occ	Coyote	Summer	0.14 (0.3)	1.06 (0.47)	-0.79 (0.24)	-0.29 (0.29)	0.03 (0.31)	0.07 (0.36)	0.13 (0.2)	-0.59 (0.18)
RSF	Coyote	Summer	-11.61 (0.04)	NA	0.18 (0.02)	0.1 (0.02)	-0.04 (0.02)	-0.12 (0.02)	0.06 (0.01)	-0.55 (0.02)
Occ	Coyote	Winter	-0.13 (0.31)	0.6 (0.48)	-1.53 (0.28)	-0.2 (0.27)	NA	0.12 (0.33)	-0.07 (0.22)	-0.16 (0.19)
RSF	Coyote	Winter	-11.56 (0.07)	NA	-0.17 (0.02)	0.26 (0.01)	NA	-0.15 (0.02)	0.14 (0.01)	-0.23 (0.01)
Occ	Elk	Summer	-0.39 (0.42)	NA	0.03 (0.42)	0.27 (0.49)	NA	NA	0.32 (0.28)	0.34 (0.27)
RSF	Elk	Summer	-11.58 (0.01)	NA	-0.15 (0.01)	0.26 (0.01)	NA	NA	-0.35 (0.01)	-0.1 (0.01)
Occ	Elk	Winter	-1.67 (0.65)	NA	-0.93 (0.75)	-0.26 (0.66)	NA	NA	-0.14 (0.43)	0.52 (0.35)
RSF	Elk	Winter	-11.55 (0.01)	NA	-0.26 (0.01)	-0.01 (0)	NA	NA	-0.14 (0.01)	-0.04 (0.01)
Occ	Mule Deer	Summer	2.23 (0.43)	NA	-0.01 (0.3)	0.67 (0.38)	-0.03 (0.24)	NA	-0.23 (0.23)	0.15 (0.28)
RSF	Mule Deer	Summer	-11.63 (0.04)	NA	0.6 (0.01)	0.13 (0)	-0.09 (0.01)	NA	0.13 (0)	-0.04 (0)
Occ	Mule Deer	Winter	0.21 (0.27)	NA	0.01 (0.27)	0.25 (0.3)	0.74 (0.32)	0.6 (0.32)	0.12 (0.27)	0.14 (0.21)
RSF	Mule Deer	Winter	-12.54 (0.07)	NA	-0.88 (0.01)	-0.74 (0.01)	0.29 (0.01)	0.25 (0)	-0.15 (0)	0.46 (0)
Occ	White-tailed Deer	Summer	1.74 (0.5)	NA	-1.5 (0.72)	1.12 (0.67)	NA	NA	0.01 (0.46)	0.57 (0.57)
RSF	White-tailed Deer	Summer	-11.63 (0.03)	NA	0.23 (0.01)	0.28 (0.01)	NA	NA	0.2 (0)	-0.54 (0.01)

Occ	White-tailed Deer	Winter	0.13 (0.44)	NA	-2.29 (0.56)	0.74 (0.56)	NA	NA	-0.1 (0.34)	-0.05 (0.31)
RSF	White-tailed Deer	Winter	-11.65 (0.03)	NA	-0.26 (0.01)	0.57 (0.01)	NA	NA	0.14 (0.01)	-0.27 (0.01)
Occ	Wolf	Summer	-1.15 (0.47)	-1.65 (0.77)	1.41 (0.42)	0.32 (0.49)	0.27 (0.55)	NA	-0.26 (0.33)	-0.06 (0.28)
RSF	Wolf	Summer	-11.78 (0.06)	NA	0.61 (0.02)	0.37 (0.02)	-0.03 (0.03)	NA	-0.07 (0.02)	-0.82 (0.02)
Occ	Wolf	Winter	-0.42 (0.65)	-1.42 (0.88)	0.12 (0.53)	0.2 (0.51)	NA	NA	-0.05 (0.42)	0.16 (0.37)
RSF	Wolf	Winter	-11.59 (0.11)	NA	-0.3 (0.02)	0.36 (0.02)	NA	NA	-0.28 (0.02)	-0.15 (0.02)

*Study area was excluded from deer and elk models because detection data were only used from one study area per species to be consistent with the distribution of GPS collared ungulates (Northeast study area for elk and white-tailed deer occupancy models; Okanogan study area for mule deer occupancy models).

†NA indicates the predictor was excluded from the model due to poor convergence or high collinearity with other predictors.

2.3.4 *Resource selection function models*

We fit 14 RSFs, i.e., one per species and season, to the used and available resource data. Almost all habitat predictors had a significant ($p\text{-value} \leq 0.05$) effect on 2nd-order resource selection for all species, although the strength and directionality of the effects varied by species and season (Table 2.2). All species but bobcats and elk selected for higher elevation areas in the summer whereas all species selected for lower elevation areas in the winter. Elk selected for lower elevation in summer whereas elevation was not significantly correlated with bobcat resource selection in summer (Table 2.2). Slope had a positive effect on resource selection for bobcats in both seasons, and cougars and mule deer in winter. Conversely, slope had a negative effect on resource selection for all other species across seasons (Table 2.2). The percentage of forested habitat had a significant positive effect on resource selection for most species in both seasons (Table 2.2). However, mule deer and elk avoided forested areas in winter. Mule deer selected for areas with increasing percent grass in winter, whereas bobcats, cougars, coyotes, and mule deer avoided areas with increasing percent grass in summer (Table 2.2). Bobcats and cougars avoided areas with increasing shrub habitat in summer, and coyotes avoided increasing shrub habitat in both seasons, but mule deer and cougars selected for shrub habitat in winter (Table 2.2). Finally, road density generally had a negative effect on 2nd-order resource selection for most species, although coyotes and white-tailed deer selected for areas with higher road densities in both seasons and mule deer selected for these areas in summer (Table 2.2).

Table 2.3. Comparison of wildlife-habitat relationships estimated by occupancy models using camera trap data and resource selection functions (RSFs) using GPS collar data for seven species in eastern Washington, 2018 – 2020. Estimated mean probability of occupancy and mean probability of detection for each species and season from the occupancy models are reported to distinguish which species were considered rare (mean occupancy probability ≤ 0.3) and which are more difficult to detect (mean detection probability ≤ 0.3). Road effect indicates whether the placement of camera traps on open roads (compared to game trails) had a positive (+), negative (-), or non-significant (ns) effect on detection probability. Collared sex indicates whether males and females (MF) or only females (F) were GPS-collared and included when estimating RSFs. We report the positive, negative, or non-significant effect of each habitat predictor included in the species- and season-specific occupancy models and RSFs. The first position corresponds to the occupancy model estimates and the second corresponds to RSF estimates. Finally, we present the mean correlation (r) between predicted pixel values for each pair of analyses once extrapolated across the study areas as a measure of consistency between estimated distributions from the paired analyses.

		Mean	Mean	Road	Collared		Percent	Percent	Percent	Road		Correlation
Species	Season	Detection	Occupancy	Effect	Sex	Elevation	Forest	Grass [†]	Shrub [†]	Density	Slope	(<i>r</i>)
Bobcat	Summer	0.12	0.50	1.36	MF	ns/ns	+ / +	ns/ -	ns/ -	ns/ -	ns/ +	0.91
Cougar	Summer	0.08	0.57	1.06	MF	+ / +	+ / +	ns/ -	ns/ -	ns/ -	ns/ -	0.86
Coyote	Summer	0.32	0.63	0.59	MF	- / +	ns/ +	ns/ -	ns/ -	ns/ +	- / -	0.25
Elk	Summer	0.19	0.44	ns	F	ns/ -	ns/ +	NA	NA	ns/ -	ns/ -	-0.46*
Mule Deer	Summer	0.50	0.85	ns	F	ns/ +	+ / +	ns/ -	NA	ns/ +	ns/ -	0.58

White-tailed Deer	Summer	0.67	0.92	-0.46	F	- / +	+ / +	NA	NA	ns/ +	ns/ -	-0.1
Wolf	Summer	0.09	0.18	1.02	MF	+ / +	ns/ +	ns/ns	NA	ns/ -	ns/ -	0.52
Bobcat	Winter	0.09	0.24	ns	MF	ns/ -	ns/ +	ns/ns	NA	ns/ -	ns/ +	0.66*
Cougar	Winter	0.04	0.36	1.09	MF	- / -	+ / +	NA	ns/ +	ns/ -	ns/ +	0.83
Coyote	Winter	0.27	0.54	0.35	MF	- / -	ns/ +	NA	ns/ -	ns/ +	ns/ -	0.36
Elk	Winter	0.12	0.18	ns	F	ns/ -	ns/ -	NA	NA	ns/ -	ns/ -	0.51*
Mule Deer	Winter	0.35	0.58	-0.71	F	ns/ -	ns/ -	+ / +	+ / +	ns/ +	ns/ +	0.79
White-tailed Deer	Winter	0.50	0.75	-0.59	F	- / -	ns/ +	NA	NA	ns/ +	ns/ -	0.63
Wolf	Winter	0.03	0.26	2.27	MF	ns/ -	ns/ +	NA	NA	ns/ -	ns/ -	0.53*

†NA indicates the habitat predictor was excluded from the occupancy model and RSF so no comparison was made.

*Estimated effects were non-significant for all habitat predictors in the bobcat (winter), elk (summer and winter), and wolf (winter) occupancy models so the correlation between predicted probability of use and relative probability of selection were not included in our comparisons.

2.3.5 *Comparing habitat associations and space-use*

We were unable to detect a significant effect on the probability a species would use a camera site for most habitat predictors in either season whereas we observed almost all had a significant effect on resource selection. As a result, the occupancy models and RSFs differed in terms of which covariates significantly influenced wildlife-habitat associations for any given species (Table 2.2, Fig. 2.3). For instance, occupancy models indicated that elevation did not influence mule deer occurrence in either season in the Okanogan study area but the corresponding RSFs showed mule deer resource selection was influenced by elevation in both seasons. However, of the 15 habitat predictors that were significant in the occupancy models (excluding the 3 significant study area effects; Table 2.2), 13 of the estimated coefficients shared a consistent directionality with the corresponding coefficients in the RSFs (i.e., the effects were both positive or both negative; Table 2.3, Fig. 2.3). For example, occupancy models indicated white-tailed deer in the Northeast study area were less likely to use camera sites as elevation increased and the corresponding RSFs indicated white-tailed deer selected against areas of higher elevation. These consistent habitat associations were spread among the various paired occupancy and RSF analyses, where 10 of the 14 species- and season-specific comparisons contained at least one habitat predictor that shared consistent directionality and significance (Table 2.3, Fig. 2.3). We observed two cases where significant habitat predictors in the occupancy models and RSFs had opposing effects on the probability of use and resource selection (Table 2.3, Fig. 2.3). The occupancy models estimated that coyotes and white-tailed deer were less likely to use camera sites at higher elevations in summer, whereas the RSFs indicated both species selected for higher elevation areas in summer (Table 2.3, Fig. 2.3). Lastly, we found the coefficient with the largest magnitude in the RSF differed from the coefficient with the largest magnitude in the occupancy

model for all paired analyses (Table 2.2). The one exception was that elevation has the largest effect size, compared to all other covariates, on relative selection and probability of use for cougars in winter (Table 2.2).

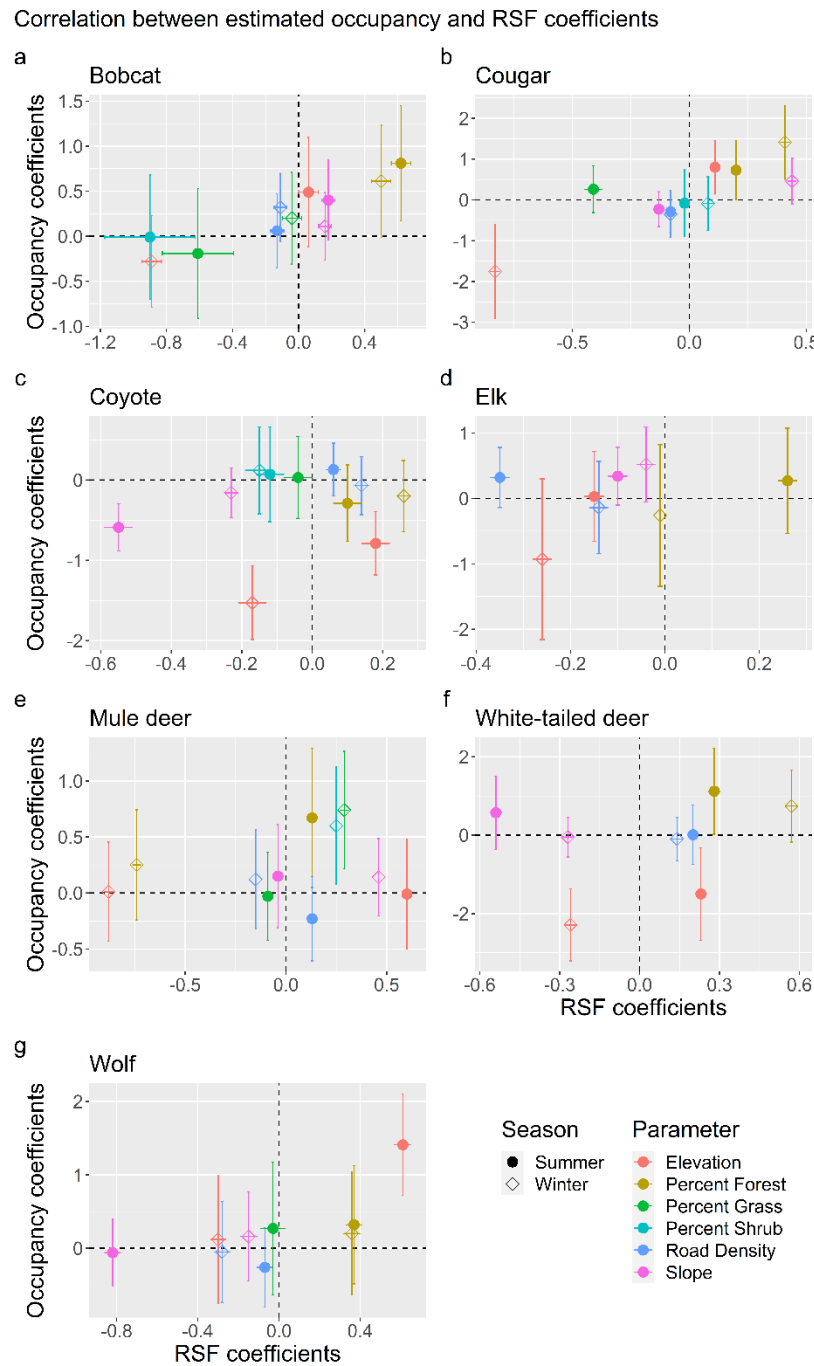


Figure 2.3. Correlation plots comparing the estimated coefficients and confidence intervals of (a) elevation, (b) percent forest, (c) percent grass, (d) percent shrub, and (e) road density included in

single-species, single-season occupancy models and corresponding species-and season-specific resource selection functions (RSFs) from eastern Washington, 2018 – 2020. Horizontal dashed lines indicate no effect of habitat predictors on a species' probability of site use (occupancy model); vertical dashed lines indicate no effect of habitat predictors on a species' relative probability of resource selection (RSF). Ninety percent confidence intervals are depicted for coefficient estimates from occupancy models and 95% confidence intervals are depicted for coefficient estimates from RSFs, indicating a significant effect if they do not overlap a dashed line. Paired significant coefficients in the lower left or upper right quadrant indicate agreement between models in the directionality of the habitat effect for a given species and season; paired significant coefficients in the upper left or lower right quadrant indicate disagreement between paired analyses.

We found no clear pattern with regard to whether sex-biased collaring efforts or camera trap placement influenced whether we saw agreement or disagreement between corresponding coefficients from the paired occupancy models and RSFs (Table 2.3). Most instances of agreement (8 of the 13 pairs of corresponding coefficients) and half the instances of disagreement ($n = 1$) between the two analyses were associated with species where both sexes were GPS-collared, whereas fewer instances of agreement ($n = 5$) arose from species where only females were collared. Approximately half of the instances of agreement ($n = 7$) were associated with species that were difficult to detect (detection probability ≤ 0.30) whereas both instances of disagreement were associated with species with higher detection probabilities. We saw more instances of agreement ($n = 8$) and one instance of disagreement between the two analyses for species that were more likely to be detected by camera traps on open roads compared to game trails, whereas fewer instances of agreement ($n = 4$) and one instance of disagreement arose for species that were less likely to be detected on open roads. We were unable to detect an effect of camera placement on open roads for mule deer in summer, which accounted for one instance of agreement between the occupancy model and RSF results. Finally, we saw one instance of

agreement for a rare species (wolves; occupancy probability ≤ 0.30); whereas all other instances of agreement ($n = 12$) and disagreement ($n = 2$) between the two models were for species that had a moderate to high probability of using a camera site (occupancy probability > 0.30 ; Table 2.3).

Consistent predicted space use

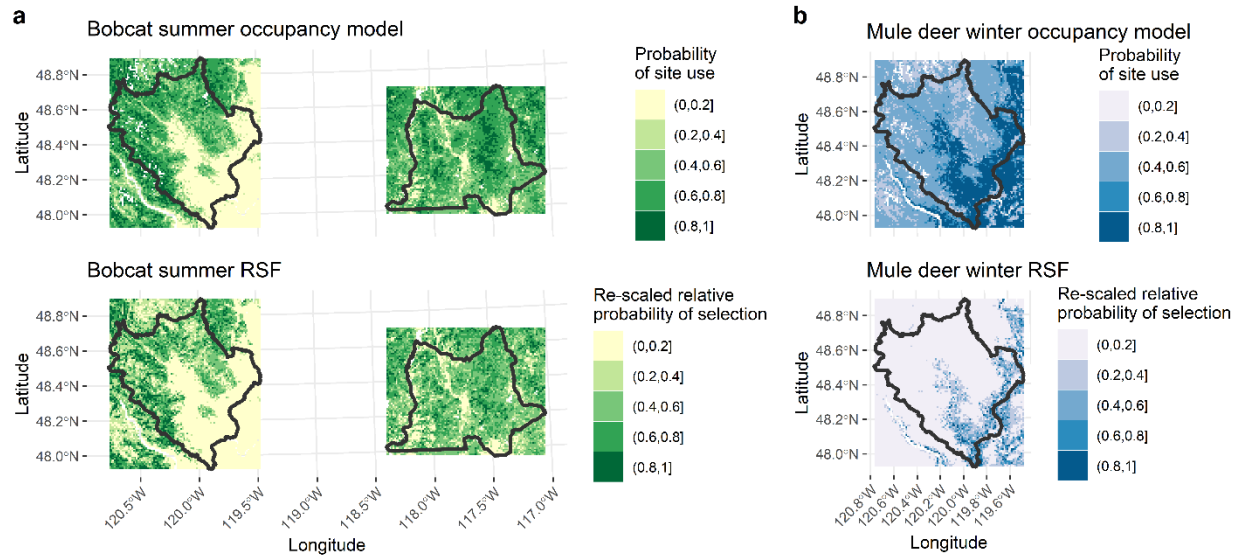


Figure 2.4. Consistent distribution maps from predicted probability of use and relative probability of selection for (a) bobcats in summer (green) across two study areas and (b) mule deer in winter (blue) in the Okanogan study area in eastern Washington, 2018 – 2020, based on paired occupancy models and resource selection functions (RSF). RSF values have been rescaled to range from 0 – 1 to be more comparable with occupancy model estimates. Darker shades correspond to higher probabilities of use and relative probabilities of selection. Sampling and analyses for mule deer were restricted to only the Okanogan study area..

Correlation between the probability of use and relative probability of selection as predicted by the respective occupancy models and RSFs varied by species and season. Seven of the paired analyses showed general similarities in the probability of use and relative probability of selection once predictions were mapped across the study areas (i.e., bobcats, cougars, and mule deer in summer, cougars, coyotes, mule deer, and white-tailed deer in winter; Fig. 2.4 and

Appendix A. S1: Figure S1). Except for the winter coyote analyses, the mean correlation between predicted values for any given pixel was also relatively high for most of these paired analyses (mean Pearson's correlation coefficient (r) ranged 0.58 – 0.91; Table 2.3). For example, the distribution maps yielded similar patterns of predicted use and relative selection across the study areas for bobcats in summer, and mule deer in winter, and cougars in both seasons (Fig. 2.4 and Appendix A. S1: Figure S1). Conversely, the paired predictions for coyotes, white-tailed deer, and wolves in summer showed conflicting patterns of space use and low correlation between predicted pixel values (mean r ranged -0.01 – 0.52; Table 2.3, Fig. 2.5 and Appendix A. S1: Figure S1). Finally, we observed four instances where predictions from the occupancy models could not be adequately compared to the RSFs owing to there being no significant habitat predictors included in the models (i.e., bobcats and wolves in winter and elk in both summer and winter; Appendix A. S1: Figure S2).

Inconsistent predicted space use

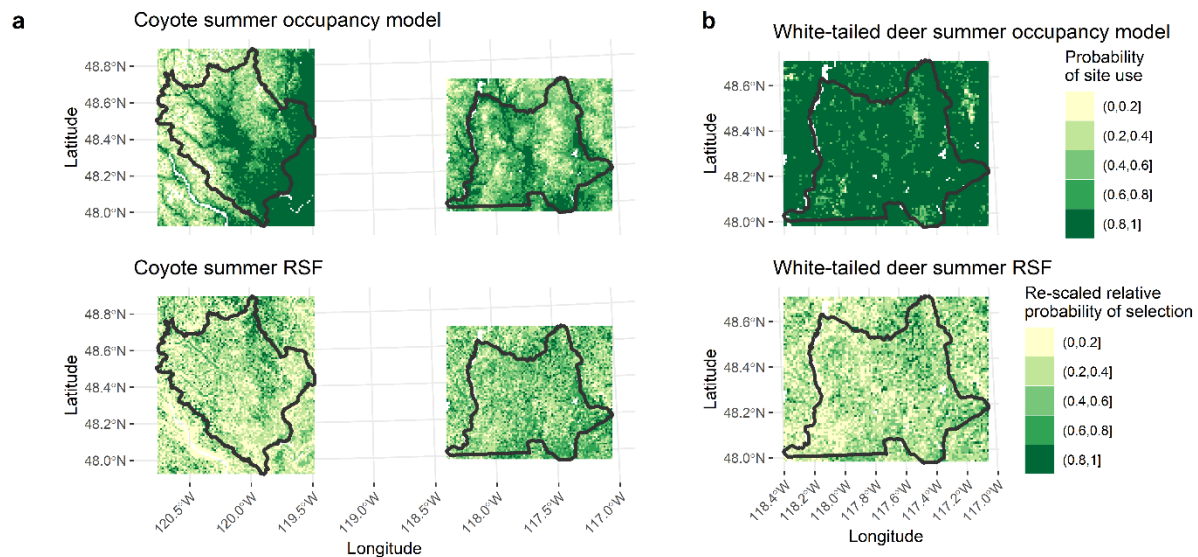


Figure 2.5. Inconsistent distribution maps from predicted probability of use and relative probability of selection for (a) coyotes in summer across two study areas and (b) white-tailed deer in summer in the Northeast study area in eastern Washington, 2018 – 2020, based on paired occupancy models and resource selection functions (RSF). RSF values have been rescaled to

range from 0 – 1 to be more comparable with occupancy model estimates. Darker shades correspond to higher probabilities of use and relative probabilities of selection. Sampling and analyses for white-tailed deer were restricted to only the Northeast study area.

2.4 DISCUSSION

Wildlife science is often faced with the challenge of scaling data from sampled individuals to population-level patterns to understand ecological relationships and make informed decisions. Understanding the limitations and inferential power associated with different sampling methods, particularly when deciding between individual- versus location-based survey perspectives, is a key component to scaling that information. In this study, we assessed whether data collected from a Lagrangian (GPS collars) and Eulerian (camera traps) perspective could be used to make comparable inferences about habitat associations and space-use patterns for seven wildlife species over multiple seasons. We found little support for our hypotheses that comparability between the survey perspectives would vary with camera placement, species detectability, or demographically biased collaring efforts. Instead, we found discrepancies arose among all paired analysis with respect to the magnitude of significant habitat relationships within each model. However, the paired analyses generally agreed on the directionality of specific wildlife-habitat relationships and at a broader scale, predicted similar distribution patterns. These results demonstrate that the different perspectives can yield comparable inferences, but these data types are not equivalent and fundamental differences between survey perspectives can lead to divergent inferences about specific habitat and spatial associations.

When comparing individual covariate effects, we found large differences between the paired analyses when assessing the magnitude of effect sizes relative to other covariates in each model. Specifically, the habitat predictor(s) with the largest absolute effect size(s) on habitat use

differed from those on relative selection for a given species and season. For example, in summer, elevation had the largest absolute effect size in the white-tailed deer occupancy model, whereas slope had the largest absolute effect size in the RSF. If inferences are being made about the magnitude of specific wildlife-habitat relationships, our results indicate the use of Lagrangian- and Eulerian-based surveys would yield very different interpretations of specific habitat predictors. We expected to find discrepancies between the analyses of species with a low probability of being detected, species where camera placement influenced their detection probability, or species where only females were collared. Yet the variation in absolute effect size among covariates of paired analyses occurred across all species. We suspect these inconsistencies arose due to differences in statistical power associated with the two survey perspectives instead. The occupancy models had much smaller sample sizes compared to the RSFs due to the finite number of camera sites and infrequent detections of many of the focal species, which limited the power to estimate the effects of multiple habitat predictors at once (Bailey et al. 2007). In addition, changes in elevation and forested habitat characterized much of the spatial variation across our camera sites, likely making them the most predictive covariates given the low power of the occupancy models. In comparison, the RSFs had power to estimate more nuanced habitat relationships more precisely because the GPS-collars generated a large (though not independent) sample of relocation data for each collared-individual (Street et al. 2021). As a result, differences in sample size and statistical power associated with our location- versus individual-based sampling methods limited how comparable the more nuanced inferences were with respect to the significance and magnitude of specific habitat predictors.

Despite differences in the magnitude of specific habitat predictors across analyses, we found the directionality of most wildlife-habitat relationships and the broad-scale predicted

space-use were generally similar between the individual- and location-based perspectives. In particular, the paired analyses for cougars, coyotes, mule deer, and white-tailed deer agreed on the directionality of several significant habitat predictors in both summer and winter analyses, suggesting that both perspectives can yield consistent, albeit coarse, inferences about wildlife-habitat relationships regardless of seasonal variation in species-specific life-histories. In addition, once we predicted the probability of use and relative selection across the study areas, the prediction maps derived from the two survey perspectives were highly correlated for many of the species, especially the predicted distributions of bobcats and cougars in summer and mule deer in winter. Even when we found only moderate pixel-by-pixel correlation for some species (i.e., mule deer in summer, coyote and white-tailed deer in winter), the respective maps still highlighted qualitatively consistent areas of high and low probability of use and relative selection. Furthermore, these prediction maps were relatively correlated despite the underlying differences in covariate-specific effects in the occupancy models and RSFs. These findings suggest that from a qualitative perspective, data collected from individual-based sampling methods can capture broad-scale patterns consistent with those observed from location-based sampling methods for a diversity of species.

Our results also captured ecological patterns that we would expect to see given our understanding of the ecology of these different species, suggesting that the consistencies we observed between models were not simply spurious results but reflected the biology of the individual species. This is a particularly powerful finding given we did not test species-specific biological hypotheses but instead applied a suite of common but very general habitat predictors to all species. For instance, both the occupancy models and RSFs found a positive relationship between percent forest habitat and the probability of site use and relative selection, respectively,

for bobcats and cougars. The RSFs further estimated that both species selected for steeper slopes and avoided areas with increasing grass habitat for at least part of the year. These results are fairly consistent with habitat features that benefit stalking predators, like bobcats and cougars, that use more structurally complex habitats to stalk and quickly subdue prey (Atwood et al. 2007). As another example, both analyses found a positive relationship between mule deer and percent grass and shrub habitat in winter. The RSF further indicated mule deer selected for steeper slopes at lower elevations and areas with increasing road densities in winter but avoided forested habitats. These results reflect the migratory nature of the Okanogan mule deer herd, where most individuals congregate in open, shrub-steppe habitats at lower elevations (which overlap with areas of greater anthropogenic impact, including higher road densities) where mule deer rely on the antelope bitterbrush for winter forage (Washington Department of Fish and Wildlife 2003, 2016). When model predictions were mapped across the study areas, both distribution maps highlighted the Okanogan mule deer herd's winter range as having a high probability of use and relative selection. Thus, not only can these disparate data sources provide complimentary information, but the inferences gained are ecologically relevant across a number of species and time periods, further suggesting that data collected at the individual level can scale to the population.

We found two instances of disagreement regarding the directionality of covariate effects, where elevation had opposing effects on the probability of use versus relative selection for coyotes and white-tailed deer in summer. These differences scaled up to produce opposite predictions in the distribution maps for both species as well. We hypothesize these discrepancies were related to differences in the range of elevations sampled by the cameras and collars. Our camera trap sampling design allowed us to sample the full elevational gradient across our study

areas (up to 2,100 m), whereas the “used” and “available” locations included in the RSFs were limited to the general areas where animals were captured and collared. For example, white-tailed deer were only GPS-collared at mid- to low-elevations in the Northeast, resulting in few high elevation areas being available to them in the RSFs. Fitting linear models over different covariate ranges can result in different patterns, which likely led to the conflicting effects of elevation on site-use and relative-selection. These inconsistencies reflect a fundamental difference between Lagrangian and Eulerian survey perspectives where one samples the movement of specific individuals and the other samples many individuals as they use specific locations (Aarts et al. 2008, Tremblay et al. 2009). Due to where coyotes and white-tailed deer were captured relative to the distribution of camera traps, the cameras and collars sampled different components of the same population. As a result, the habitat- and predicted space-use patterns observed with the collared individuals did not scale to the patterns we observed at the population-level within the study area. These discrepancies are consistent with findings reported in Priddel et al. (2014) and Phillips et al. (2019), who both hypothesized their Lagrangian- and Eulerian-based surveys sampled different subsets of the respective seabird populations they studied, which led to different distribution patterns. Our results may offer support for this hypothesis or simply demonstrate that the behaviors of a few sampled individuals may not be representative of broader population-level patterns and ecological relationships (Aarts et al. 2008). However, given we know we sampled different ranges of habitat values for the summer coyote and white-tailed deer analyses, we suspect the observed discrepancies were owed to spatially mismatched comparisons and not an outright inability to scale from the individual to the population.

In addition to the differences in statistical power that limited our comparisons, we made several assumptions that may have influenced our findings. We assumed that occupancy models

and 2nd order resource selection functions would capture similar wildlife-habitat associations, namely, that habitat features influencing species occurrence within our study areas were similar to those that animals used when selecting their home ranges. Habitat use and selection are different processes, however, so even where we saw agreement between paired analyses, the interpretations of the results are not fully interchangeable (Lele et al. 2013), and some discrepancies may have partially been due to estimating different aspects or scales of wildlife-habitat associations. That said, our goal was not to compare occupancy models and RSFs per se, but to compare the inferences gained from different survey perspectives when the disparate data types were used to estimate similar ecological relationships. There are other ways to evaluate animal space-use not considered here (e.g., utilization distributions and camera detection rates) which may have resulted in different levels of agreement between survey perspectives if used to evaluate whether individual-level data can predict population-level patterns. In addition, we applied the same suite of covariates to all species, seasons, and models to make for easier comparison. But some models may have been overparameterized for species with very low detection probability or lacked additional complexity that was important for some but not all species (e.g., missing quadratic effect on elevation). Thus, how we structured the models may also explain some of the differences we observed. Lastly, while we sampled both areas simultaneously, population density can impact inference from both methods in different ways. For example, spatial variation in population density can create abundance-induced heterogeneity in detection probability (Royle and Nichols 2003, MacKenzie et al. 2017), leading to negatively biased estimates in occupancy (MacKenzie et al. 2017). Similarly, population density can affect resource selection when intraspecific competition changes resource availability (Matthiopoulos et al. 2015). Finally, density-dependent variation in animal movement and home-range size can

affect camera detection rates (Broadley et al. 2019), as well as influence the spatial extent of what is considered “available” in an RSF context. Thus, density-dependent detection and habitat selection make extrapolating wildlife-habitat relationships to different study areas or over time challenging (Fieberg et al. 2021) and may further add to the inconsistencies we observed.

Our findings demonstrate that data from camera traps and GPS-collars yield inconsistent inferences about covariate-specific estimates of wildlife-habitat associations, but inferences are more consistent at broad-scales and from a more qualitative perspective. This knowledge is particularly valuable if data from different survey perspectives are integrated under a single analysis (Priddel et al. 2014, Watanuki et al. 2016, Phillips et al. 2019). Integrating the two should allow practitioners to overcome inherent limitations of each data type while leveraging their benefits (Fletcher et al. 2019, Miller et al. 2019). For instance, telemetry data would allow more nuanced wildlife-habitat relationships to be estimated while randomly deployed cameras could fill spatial gaps where no collars were deployed and provide information about habitats that animals truly do not use (i.e., non-detection data) with a higher degree of confidence compared to randomly sampling “available” resources. Sample sizes from telemetry are generally much larger than camera traps, thus integrating the two in a formal model would require a way to weight the data sources appropriately so that larger-sized telemetry data do not mask the information provided by the camera data (Fletcher et al. 2019). Our results suggest, however, formal data integration will require careful consideration if inference is focused on specific wildlife-habitat relationships, particularly if the different survey perspectives yield conflicting results in stand-alone analyses.

Decision makers must often evaluate trade-offs when designing wildlife studies and monitoring programs, including whether to use more or less costly sampling methods to collect

sufficient data. Our study highlights how camera traps can generate reliable information about broad-scale habitat associations and space-use for multiple species at once, even without the more nuanced species-specific information that comes with more expensive individual-based monitoring devices. The non-invasive nature of camera-based monitoring adds to their appeal, particularly when compared to individual-based monitoring approaches which necessitate the physical capture and handling of wild animals. Wildlife captures bring risks for both wildlife (Soulsbury et al. 2020) and human researchers (Caulkett and Shury 2014), and thus researchers should carefully consider if the information gained is worth the cost to those involved or if non-invasive techniques can provide adequate information. That said, the density, distribution, and site selection of location-based surveys could limit the ability to collect a sufficiently large sample, which can limit statistical power and ecological inference (Phillips et al. 2019). In addition, if animals move outside the study area, location-based sampling methods can miss important ecological patterns. Individual-based sampling can capture these patterns even if animals leave the study area, but this monitoring approach can fail to sample the actual population of interest if a non-random sample of individuals was monitored (Aarts et al. 2008, Priddel et al. 2014, Watanuki et al. 2016) or if the monitoring was intended to focus on ecological processes within a defined area. Ultimately, whether to collect data following a Lagrangian- or Eulerian-based perspective comes down to the monitoring objectives. If the goal is to make inference and decisions about a species (or multiple species) within a pre-defined area or understand broad-scale patterns and relationships, then Eulerian-focused methods provide sufficient data for making robust, population-wide inferences. Conversely, Lagrangian-focused methods may be better suited if the goal is to draw inference and make decisions about very specific wildlife-habitat relationships, a species without a pre-defined focal area, for species that

are prone to long-distance movements or dispersal, or if monitoring objectives also include collecting information on animal movement, survival, and reproduction.

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Chapter 3. PREDATOR-PREY INTERACTIONS AND LANDSCAPE FEATURES INFLUENCE MOVEMENT BEHAVIORS IN A LARGE-MAMMAL COMMUNITY

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Abstract: Predator hunting strategies, such as stalking versus coursing behaviors, are hypothesized to influence antipredator behaviors of prey and can describe the movement behaviors of predators themselves. Predators and prey may alter their movement in relation to predator hunting strategies, yet few studies have evaluated how these strategies influence movement behaviors of free-ranging animals in a multiple-predator, multiple-prey system. To this end, we fit hidden Markov models (HMM) with movement data derived from >450 GPS collared ungulates, mesopredators, and large predators in eastern Washington, USA. We used these models to test our hypotheses that stalking (e.g., cougars [*Puma concolor*]) and coursing (e.g., gray wolves [*Canis lupus*]) predators would exhibit different movement behaviors consistent with their respective hunting strategies in areas that increased the likelihood of encountering or capturing ungulate prey (e.g., mule deer [*Odocoileus hemionus*]), whereas the movement behaviors of prey would change in response to each predator's hunting strategy to reduce encounter rates with stalking versus coursing predators. We found that predators and ungulate prey adjusted their movement behaviors in response to one another but not based on differences in predator hunting strategies. Predators

changed their movement behaviors based on the type of prey, whereas ungulates consistently moved less in response to large predators, regardless of the predator's hunting strategy. Both predator and prey movements varied in response to landscape features but not necessarily based on habitat complexity that would facilitate specific hunting behaviors. Our results suggest that predators and prey adjust their movements in relation to each other, likely influencing their encounter rates with one another. Habitat may further mediate these interactions, resulting in a complex combination of movement behaviors in multiple-predator, multiple-prey systems.

Keywords: Animal movement, antipredator behavior, hidden Markov model, landscape permeability, predator hunting mode, predation risk

3.1 INTRODUCTION

Understanding animal space use is central to ecology because it can structure populations, species interactions, and community dynamics, particularly with respect to predator-prey interactions (Mitchell and Lima 2002, Sih 2005, Schlägel et al. 2020). Predator space use is generally associated with areas that increase the likelihood of locating and killing prey (Sih 2005), whereas prey typically balance trade-offs between the need to acquire resources and avoid predation (Lima 1998). Consequently, how predators and prey respond to each other can strongly influence habitat use, movement, and foraging behaviors of species in a community (Sih 2005, Cresswell et al. 2010).

Predator hunting strategies encompass a spectrum of behaviors that predators use to encounter and catch prey, including stalking (i.e., relying on concealment to approach close enough to quickly attack) and coursing (i.e., roaming widely and openly pursuing over long distances; Makin et al. 2017, Dröge et al. 2019). Predator space use is often associated with habitats that facilitate the efficacy of these hunting strategies (e.g., structural complexity;

Atwood et al. 2009) and track the distribution of prey or the prey's resources (Flaxman and Lou 2009). Hunting strategies can also inherently describe a predator's mobility and movement traits (Schlägel et al. 2020). For example, stalking predators typically concentrate their movements when intensively searching for prey, resulting in shorter distances moved and more torturous movement paths compared to cursorial hunters (Barker et al. 2022). In addition, predators will change their movements in response to habitat complexity and food availability, consistent with different hunting behaviors (Michel and Adams 2009, Sims et al. 2012, Říha et al. 2021). Accordingly, predator movements should reflect their respective hunting strategies, particularly in areas where predators are more likely to encounter or capture prey. For instance, if capture success varies for a given hunting strategy based on specific habitat features, we might expect stalking predators to have slower, less directed movements in structurally complex habitats where stalking behaviors are most advantageous versus faster, more directed movements in open habitats where a stalking strategy is less profitable.

Predator hunting behaviors are also hypothesized to influence the antipredator behaviors of prey, with prey responding more strongly to stalking predators compared to coursing predators (Schmitz 2005, Preisser et al. 2007). This is presumably because more sedentary predators provide more reliable cues (e.g., scent) of predation risk compared to more active predators (Schmitz 2005, Preisser et al. 2007). Predator habitat use is also often tied to their hunting strategies (Hopcraft et al. 2005, Gorini et al. 2012), making habitats associated with a predator's hunting strategy a predictable signal of predation risk, particularly for stalking predators who are more spatially anchored to habitats that provide stalking cover (Thaker et al. 2011, Smith et al. 2019). Prey often show stronger avoidance of habitats used by stalking predators (Thaker et al.

2011) and will alter their movement behaviors in response to predation risk (Miller et al. 2014, Dröge et al. 2019).

Encounter success should be highest for active predators when prey move slower or with less directionality than the predator and highest for more sedentary predators when prey move faster than the predator (Scharf et al. 2006, Avgar et al. 2008). Hence, it would benefit prey to counter predator movement behaviors by moving in a manner that reduces encounters based on the predator's hunting strategy (Schlägel et al. 2020). Experiments using spiders and grasshoppers provide evidence of this phenomenon, with grasshoppers reducing activity and space use in response to more sedentary spider species but increasing their activity in response to highly mobile spiders (Miller et al. 2014). Field-based studies have been less conclusive and more limited. Dröge et al. (2019) found that although wildebeest (*Connochaetes taurinus*) reduced their speed and increased turning angles in areas with higher long-term predation risk, this response was consistent across predator species regardless of hunting strategy. Frair et al. (2005) and Ditmer et al. (2018) studied elk (*Cervus canadensis*) and moose (*Alces alces*) movements, respectively, in response to predation risk from wolves (*Canis lupus*) and found that both species moved faster in areas predicted to have higher probability of wolf presence. However, neither study considered prey movements in response to stalking predators so the effect of different hunting strategies on prey movements in natural settings is unclear.

Previous studies that investigated predator-prey movement typically used simulations (e.g., Scharf et al. 2006, Avgar et al. 2008) or metrics describing changes to prey movement in response to predation risk (e.g., first passage time or expected squared displacement; e.g., Avgar et al. 2013, Ditmer et al. 2018, Dröge et al. 2019, Merrill et al. 2020). However, few considered predator and prey movements simultaneously (but see Miller et al. 2014) and none explicitly

incorporated the effect of predation risk on behavioral states. Hidden Markov models (HMM) bridge this gap by providing a statistically rigorous framework for incorporating habitat and predation risk data into movement analyses and behavioral classification, allowing for a more mechanistic approach to understanding animal movement (Langrock et al. 2012). Animal movements change with habitat and behavior (Forester et al. 2007, Morales et al. 2010) and although an animal's true behavioral states are unknown without auxiliary information, HMMs allow for inferences of these states by estimating the probability an animal will transition from one (unknown) state to another using movement data and relevant variables (McClintock et al. 2012, 2020). Thus, HMMs allow formal inclusion of variables hypothesized to influence movement behaviors and more confident classification of behavioral states associated with different movement patterns than other methods previously used to study predator-prey movements.

Here, we used HMMs and telemetry relocation data from two stalking (bobcats [*Lynx rufus*] and cougars [*Puma concolor*]) and two coursing (coyotes [*C. latrans*] and gray wolves) predator species and three ungulate prey species (elk, mule deer [*Odocoileus hemionus*], and white-tailed deer [*O. virginianus*]) in eastern Washington, USA to test two hypotheses regarding how predator hunting strategies influence animal movement in a heterogeneous landscape. First, we hypothesized that predator movements would reflect their respective hunting strategies in areas that prey were more likely to use or in habitats that facilitated the capture of prey. If true, we expected 1) stalking predators would transition to their hunting behavioral state (i.e., a more “encamped” state characterized by shorter, less directed movements) and coursing predators would transition to their hunting state (i.e., a more “exploratory” state, with longer, more directed movements) in areas that prey were more likely to use. We expected 2) stalking

predators would transition to their hunting state in more complex habitats and coursing predators would transition to their hunting state in less complex habitats. Under both predictions, these movements should reflect behaviors that increase encounter rates with prey or capture success, given the predators' respective hunting strategies. Second, we hypothesized that prey movement would change in response to predator hunting strategy as an antipredator response to reduce the probability of encountering different types of predators. If true, we expected 1) prey would transition to an evasive behavioral state in areas that predators were more likely to use, but that the evasive behavioral state would look different depending on the predator's hunting strategy (i.e., a more "encamped" state characterized by shorter, less directed movements in response to stalking predators; a more "exploratory" state with longer, more directed movements in response to coursing predators; Miller et al. 2014). Similarly, we expected 2) prey would transition to an evasive state in response to habitat complexity, moving less and more randomly in complex habitats associated with stalking predators and moving more and with greater directionality in less complex habitats associated with coursing predators.

3.2 METHODS

3.2.1 *Study areas*

We conducted our study across two regions in eastern Washington, USA, from July 2018 – March 2021 (Fig. 3.1). White-tailed deer and elk were the most common cervid species in the Northeast study area (4,535 km²; -117.7193° W, 48.28302° N), although smaller populations of moose and mule deer also occurred in the region. Black bears (*Ursus americanus*), bobcats, cougars, coyotes, and wolves occurred throughout this study area (Washington Department of Fish and Wildlife et al. 2019). Mule deer were the predominant cervid species in the Okanogan study area (5,300 km²; -120.1096° W, 48.42966° N), although white-tailed deer, moose, and elk

also occurred in the study area. The carnivore community was similar to that of the Northeast but also included a small population of Canada lynx (*L. canadensis*; Washington Department of Fish and Wildlife et al. 2019). Detailed study area characteristics are described in length in Bassing et al. (2022) and Ganz et al. (2022a, b).

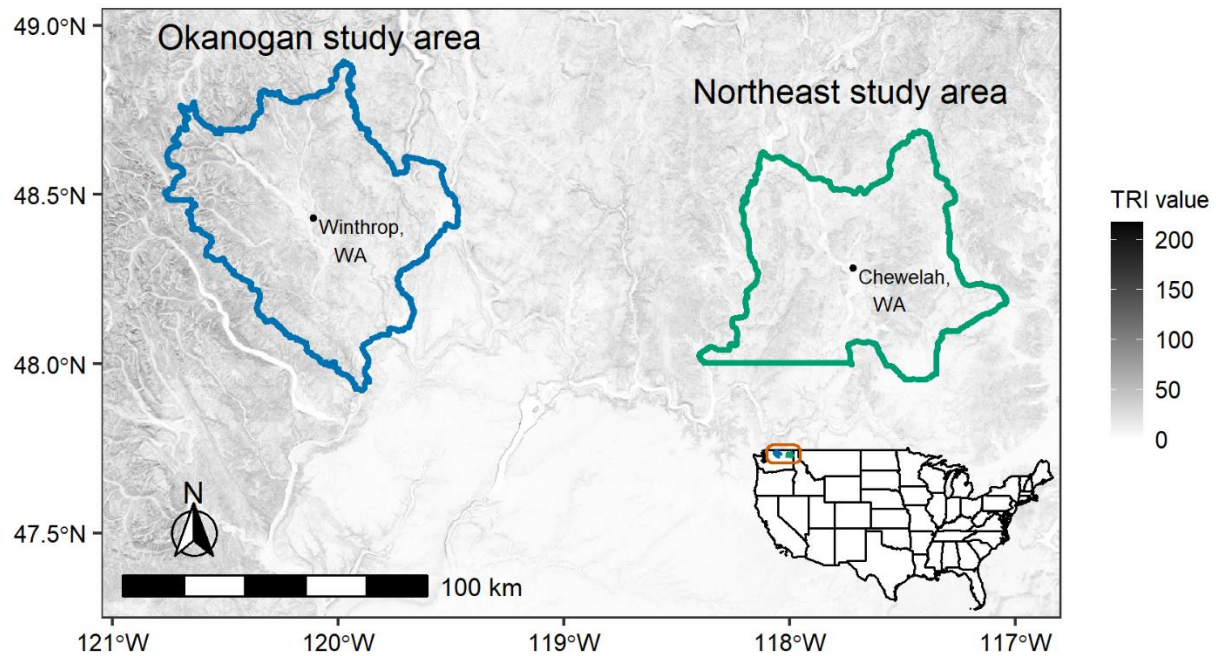


Figure 3.1. Map of Okanogan (blue) and Northeast (green) study areas in eastern Washington, USA. From 2017 – 2021, bobcats, cougars, coyotes, and wolves were GPS collared and monitored in both study areas, mule deer were GPS collared and monitored in the Okanogan study area, and elk and white-tailed deer were GPS collared monitored in the Northeast study area. Higher TRI values represented more rugged terrain.

3.2.2 Telemetry data

We monitored 469 individuals of seven species between January 2017 and March 2021 using Global Positioning System (GPS) collars. We collared elk and white-tailed deer only in the

Northeast study area and mule deer in the Okanogan study area because they occurred at higher densities and were more evenly distributed within those regions. We captured and collared adult female elk ($n = 63$; Model Survey, Vectronic Aerospace, Berlin, Germany) by aerial darting (Jessup 1982) and adult female white-tailed deer ($n = 131$; Models Survey and Vertex Plus, Vectronic Aerospace) using clover traps, suspended net-guns (Wildlife Capture Services, Flagstaff, Arizona, USA), and ground darting (Clover 1954, Hawkins et al. 1968, VerCauteren et al. 1997). We captured adult female mule deer ($n = 138$; Model Survey, Vectronic Aerospace) by drive netting and aerial net-gunning (Kock et al. 1987).

We captured and collared adult female and male carnivores in both study areas owing to their broad distributions across both regions. We captured and collared bobcats ($n = 37$; Model Gen4 GPS-Iridium, Telonics, Mesa, Arizona, USA) using cage traps baited with grouse (*Bonasa umbellus* or *Dendragapus* spp.) wings, beaver (*Castor canadensis*), or road-killed deer (Koehler and Hornocker 1991). We captured and collared cougars ($n = 60$; Model Vertex Lite, Vectronic Aerospace, Berlin, DE and GPS-enabled accelerometer collars, Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) using trained dogs or large, steel cage traps baited with cougar-killed or road-killed deer and elk (Kertson et al. 2011). We captured and collared coyotes ($n = 23$; Model Gen4 GPS-Iridium, Telonics) using rubber-padded foothold traps (Victor #3 soft-catch offset 4x4 foothold traps; Linhart 1983). Similarly, we captured and collared wolves ($n = 14$; Models Vertex Lite and Vertex Plus, Vectronic Aerospace) using rubber-padded foothold traps (#7 EZ Grip foothold traps, Livestock Protection Company, Alpine, Texas, USA) and aerial darting (Jessup 1982, Frame and Meier 2007). We programmed all collars to attempt a GPS fix every 4 hours for 180 seconds. We censored telemetry data for 3 weeks post capture to avoid the inclusion of capture-related movements in subsequent analyses (Northrup et al. 2014).

3.2.3 *Predator and prey presence*

We used resource selection functions (RSF) to approximate the spatial distribution of each predator and prey species. Although spatial overlap with a predator or prey species does not automatically equate to increased predator-prey encounters or predation risk (Suraci et al. 2022), previous studies found predator space-use can influence patterns of animal movement (Frair et al. 2005, Ditmer et al. 2018). Using the same GPS collar data described above, we constructed species- and season-specific RSFs at the 3rd order of selection (i.e., habitat selection within a home range; Johnson 1980, Boyce et al. 2002) for each species in summer and winter, respectively (Appendix B. S1: Table S1.1). We ran a single global model for each data set, which included covariates for elevation, slope, distance to nearest water, road density, canopy cover, landcover type, distance to nearest forested to non-forested edge, and an index for human modified landscape in the RSFs, as well as a random effect for individual (Appendix B. S1: Table S1.2). We chose environmental and anthropogenic variables that we expected would influence habitat selection for these species but that differed from the landscape variables included in the HMMs. We followed the Boyce et al. (2002) approach to K-fold cross-validation for RSFs to test the predictive capacity of each model. Five-fold cross-validation indicated our models were highly predictive (Spearman's rank-order correlation coefficient ρ ranged 0.86 – 1.00; Appendix B. S1: Table S1.3) so we predicted the annual relative probability of resource selection for each species across the landscape. We predicted bobcat, cougar, coyote, and wolf resource selection across both study areas, whereas we restricted the elk, mule deer, and white-tailed deer predictions to only the study area where each species was collared (Appendix B. S1: Figure S1.1). We assumed the prey RSFs reflected habitat that predators would use to track prey densities or prey resources (Flaxman and Lou 2009). We assumed the predator RSFs reflected

habitat conditions associated with predators and thus reflected “risky places” where prey could perceive varying levels of vulnerability (Merrill et al. 2020). We used these predicted surfaces as covariates in the HMMs to represent the relative probability of use for each species across the landscape in summer and winter. We note that although K-fold cross-validation indicated the RSFs were highly predictive, we did not account for uncertainty in the prediction surfaces when using them as covariates; consequently, the estimated effects of these covariates on animal movement may be overly precise.

3.2.4 *Habitat features*

We included a measure of terrain variability (Wilson et al. 2007) and the percentage of open habitat within 250m of each animal location in the HMMs to represent landscape features expected to be associated with predator hunting modes (Atwood et al. 2009). We derived the terrain ruggedness index from the Shuttle Radar Topography Mission (SRTM) 30m resolution digital elevation model (DEM; Farr et al. 2007) in Program R (R Core Team 2020). We created the open habitat variable by reclassifying annual landcover type from the Cascadia Partner Forum TerrAdapt:Cascadia tool (30m resolution) landcover data into 2 categories (forested and non-forested) and used a moving window analysis to calculate the percentage of open (non-forested) habitat within 250 of each 30m pixel. We also included distance to nearest road and a categorical variable of whether snow cover was (1) or was not (0) present at each animal location (winter models only) to represent landscape permeability (Avgar et al. 2013), which we expected would influence animal movement regardless of predator hunting mode. We calculated distance to nearest road in ArcGIS using the Euclidean Distance tool (ESRI 2020) and the Cascadia Partner Forum TerrAdapt:Cascadia tool (<https://cascadiapartnerforum.org/terradapt>) roads layer. We identified the first day without snow looking backwards from 31 Dec and the annual snow

disappearance date (Nolin et al. 2021) at each animal location using Google Earth Engine (Gorelick et al. 2017) and the MODIS Terra Snow Cover Daily Global 500m product (Hall and Riggs 2016) to create a temporally dynamic covariate for snow cover.

3.2.5 *Hidden Markov movement models*

We fit hidden Markov models (HMM) to the movement data derived from the GPS collars to evaluate whether predictors of predator and prey presence influenced animal movement behaviors. Hidden Markov movement models comprise a hidden state process, where the probability of being in the current behavioral state depends on the animal's most recent state, and a state-dependent observation process that arises at each point in time from one of the underlying behavioral states (Langrock et al. 2012, McClintock et al. 2020). Animal movement changes with behavior (Morales et al. 2010) and although an animal's true behavioral states are unknown without auxiliary information, we can use movement data to infer these states by estimating the probability an animal will transition from one (unknown) state to another (McClintock et al. 2020).

Hidden Markov movement models assume temporally regular location data (Langrock et al. 2012). Therefore, we interpolated missing locations following a regular 4-hr time step. To minimize interpolating over large gaps in relocation data (often due to collar malfunctions) we only interpolated up to 6 consecutive missing locations (i.e., up to 24-hour gaps in the collar data) and included only movement data from GPS collars that generated at least 90 successful fixes and were deployed for ≥ 20 days within a given time period of interest. We then calculated the step length and turning angle between sequential telemetry relocations for each collared individual and assumed variation in these bivariate observation data corresponded with different

unknown behavioral states. GPS locations had a high accuracy rate so we assumed negligible location measurement error in the GPS data (McClintock and Michelot 2018).

We separated the GPS collar data by summer (July 1 – Sept 30) and winter (December 1 – February 28/29) for each year. We considered movement behavior in different seasons because the life-histories of these species and environmental pressures they experience vary over the annual cycle but did not consider spring or fall to avoid the confounding effects of ungulate migration and human hunting activity. We pooled all movement data across years for a given species and season and fit the data to a 2-state HMM (where State 1 = “encamped” and State 2 = “exploratory” behavioral states; Langrock et al. 2012, McClintock et al. 2020) using a likelihood-based approach with the *momentuHMM* package (McClintock and Michelot 2018) in Program R (R Core Team 2020). We assumed each animal moved according to a correlated random walk where the observed step lengths were gamma distributed and turning angles followed a von Mises distribution (Langrock et al. 2012). We included a zero-mass parameterization on the step length distribution for the deer, elk, and cougar models when zeros were present in the distance dataset.

We built two baseline movement models (one for predators and one for prey) using different sets of covariates on the transition probabilities that we adjusted based on the species, season, and study area. The baseline predator movement model included terrain ruggedness, percent open habitat, distance to nearest road, and the relative probability of use for one or more prey species (Table 3.1). The predator movement models varied by study area in that the Okanogan predator models included the mule deer RSF layer whereas the Northeast predator models included the elk and white-tailed deer RSF layers. The prey movement model included terrain ruggedness, percent open habitat, distance to nearest road, and the relative probability of

use for each predator species (Table 3.1). We added snow cover to the winter models only. In addition, we included an effect for time-of-day with sine and cosine transformations and a binary covariate representing whether it was day (1) or night (0) at the time of each location on the step length parameters in all models to help account for circadian patterns in daily animal activity (Forester et al. 2007).

Table 3.1. Predicted covariate effects on the probability that a prey species (elk, mule deer, white-tailed deer), a stalking predator (bobcat, cougar), and a coursing predator (coyote, wolf) would transition from one behavioral state to the other, where State 1 represents an “encamped” behavioral state and State 2 represents an “exploratory” behavioral state. We predicted rugged terrain, the percentage of open habitat, distance to nearest road, the presence of snow cover, and the predicted presence of prey, stalking predators, and coursing predators would influence state transition probabilities.

Explanatory variable	Expected effect on probability of transitioning states					
	Prey		Stalking predator		Coursing predator	
	1 → 2	2 → 1	1 → 2	2 → 1	1 → 2	2 → 1
Terrain ruggedness index	-	+	-	+	-	+
Habitat openness	+	-	+	-	+	-
Distance to nearest road	+	-	+	-	+	-
Snow cover (winter only)	-	+	-	+	-	+
Prey presence [†]	NA	NA	-	+	+	-
Stalking predator presence [†]	-	+	NA	NA	NA	NA
Cursorial predator presence [†]	+	-	NA	NA	NA	NA

[†]Prey presence represents 3 separate covariates: relative probability of use by mule deer in the Okanogan, elk in the Northeast, and white-tailed deer in the Northeast. Stalking predator presence represent 2 separate covariates: relative probability of use by bobcats and relative probability of use by cougars across both study areas. Cursorial predator presence represents 2

separate covariates: relative probability of use by coyotes and relative probability of use by wolves across both study areas.

We checked for collinearity among all covariates within each model and found terrain ruggedness was highly correlated ($r \geq |0.7|$) with predicted coyote presence for the summer mule deer model and terrain ruggedness was highly correlated with predicted mule deer presence (Okanogan study area only) for the winter cougar and coyote models. In these cases, we fit a pair of identical models to the data but excluded one correlated variable from each and used AIC to select the best supported model for interpretation. We considered variables with a p-value ≤ 0.05 as significant in our interpretation. Based on the transition probabilities, we calculated the stationary-state probabilities (i.e., the probability an animal was in a given state) over a range of covariate values for each significant variable. We used the estimated covariate coefficients on transition probability and the plotted stationary-state probabilities to interpret how animal movement behaviors varied in response to the significant variables. We evaluated model performance by reviewing QQ-plots of model pseudo-residuals and autocorrelation plots (McClintock et al. 2020).

3.3 RESULTS

3.3.1 *Telemetry data*

Of the 469 telemetered animals in our study, we included GPS location data from 333 animals in the summer sampling period and 313 animals in the winter sampling period (Table 3.2). These yielded an average of 32 (SE = 6) individual movement tracks per species per summer and 42 (SE = 10) movement tracks per species per winter. The proportion of interpolated locations included in the HMMs varied by species, ranging from 1% (SE = 0.2%; mule deer) to 46% (SE = 0.2%; bobcat; Table 3.2). We chose to not analyze the bobcat movement data owing to the large

percentage of interpolated locations in the bobcat datasets, which could strongly influence model estimates.

Table 3.2. Summary table of GPS collar data used to fit hidden Markov models (HMM) for animal movement. The average number of GPS-collared animals, the average number of movement tracks generated by the GPS collars, the average number of relocations generated by individually GPS-collared animals, the average proportion of locations interpolated for the HMM analyses, and their standard errors (SE) over the three years of study are reported for seven species across two study areas in eastern Washington, USA, 2018 – 2021.

Species	Study Area	Season	Mean Collars (SE)	Mean Tracks (SE)	Mean Locations (SE)	Mean Proportion Interpolated Locations (SE)
Mule Deer	Okanogan	Summer	76 (6)	80 (8)	39356 (2999)	0.03 (0.004)
Mule Deer	Okanogan	Winter	86 (6)	158 (44)	37945 (94)	0.01 (0.002)
Elk	Northeast	Summer	41 (2)	62 (14)	20209 (1647)	0.05 (0.002)
Elk	Northeast	Winter	39 (5)	64 (10)	18847 (2609)	0.02 (0.003)
White-tailed Deer	Northeast	Summer	43 (15)	78 (26)	20042 (7742)	0.07 (0.003)
White-tailed Deer	Northeast	Winter	41 (15)	85 (37)	17619 (6948)	0.04 (0.004)
Cougar	Okanogan	Summer	6 (3)	9 (4)	2734 (1152)	0.09 (0.005)
Cougar	Okanogan	Winter	6 (2)	10 (4)	1598 (720)	0.16 (0.037)
Cougar	Northeast	Summer	14 (2)	22 (3)	6297 (1135)	0.07 (0.007)
Cougar	Northeast	Winter	11 (2)	18 (7)	4606 (714)	0.07 (0.008)
Wolf	Okanogan	Summer	2 (1)	3 (1)	1018 (294)	0.07 (0.01)

Wolf	Okanogan	Winter	2 (1)	7 (5)	1002 (293)	0.16 (0.121)
Wolf	Northeast	Summer	3 (0)	3 (0)	1351 (184)	0.05 (0.024)
Wolf	Northeast	Winter	2 (1)	2 (1)	950 (412)	0.02 (0.016)
Bobcat	Okanogan	Summer	6 (3)	30 (21)	1695 (675)	0.36 (0.054)
Bobcat	Okanogan	Winter	5 (1)	37 (18)	982 (101)	0.43 (0.046)
Bobcat	Northeast	Summer	8 (3)	61 (24)	1798 (662)	0.45 (0.007)
Bobcat	Northeast	Winter	6 (0)	44 (4)	1096 (14)	0.46 (0.002)
Coyote	Okanogan	Summer	7 (3)	8 (4)	2317 (1179)	0.16 (0.021)
Coyote	Okanogan	Winter	7 (3)	9 (4)	2541 (1064)	0.16 (0.014)
Coyote	Northeast	Summer	6 (1)	7 (2)	1892 (587)	0.17 (0.04)
Coyote	Northeast	Winter	6 (1)	12 (5)	2259 (494)	0.19 (0.053)

3.3.2 *Hidden Markov movement models*

We fit 18 hidden Markov models for movement to the interpolated location data, i.e., one per species, season, and study area. In all models, we were able to differentiate the estimated state-dependent distributions associated with our two defined behavioral states (encamped and exploratory). In general, the estimated parameters for the von Mises distributions describing turning angles were consistent with our expectations for each behavioral state. The concentration parameter was smaller (often equal or very close to 0) when species were in an encamped state and larger when in an exploratory state. The reciprocal of the concentration parameter is analogous to the variance of a normal distribution, meaning the larger the concentration parameter, the more the distribution is concentrated about the turning angle (Mardia and Jupp 2000). The estimated concentration parameters therefore indicated an animal's direction change

was more variable when encamped and more directed and consistent when exploratory (Appendix B. S2: Table S2.1). The only exceptions were mule deer turning angles in summer in the Okanogan and coyote and elk turning angles in summer in the Northeast. In these instances, the concentration parameters were larger when in an encamped state and smaller when exploratory (Appendix B. S2: Table S2.1). Across all species, mean step length was consistently shorter when in an encamped state (mean step length ranged 9.52 – 166.84 m) and longer when in an exploratory state (mean step length ranged 230.50 – 2607.44 m; Appendix B. S2: Table S2.2). Mean step lengths were typically shorter in winter compared to summer for all species and study areas (Appendix B. S2: Table S2.2). Model performance checks indicated relatively good fit for the turning angle parameters but moderate temporal autocorrelation in step length across models (Appendix B. S2).

3.3.3 *Predator hypothesis*

Although the magnitude and shape of the relationships varied by species and season, the effect of prey RSFs on predator movements tended to vary by prey species instead of predator hunting strategy. Conditional on their current behavioral state, all three predator species were more likely to transition to an encamped behavioral state as mule deer RSF values increased across the Okanogan study area in summer, whereas cougars and wolves were less likely to transition into an encamped state as elk RSF values increased in the Northeast study area, particularly in the summer (Table 3.3, Appendix B. S3: Table S3.1, Fig. 3.2). Predator responses to white-tailed deer were more variable, with cougars (in summer) and coyotes (in winter) being more likely to switch between behavioral states as white-tailed deer RSF values increased in the Northeast study area, although coyotes were almost twice as likely to transition to an exploratory state

compared to an encamped state (Appendix B. S3: Table S3.1, Fig. 3.2). Wolves were also more likely to transition to an exploratory state in winter as white-tailed deer RSF values increased.

Table 3.3. Example of estimated probabilities of transitioning from the encamped behavioral state to the exploratory behavioral state (Trans. 1→2) and from the exploratory behavioral state to the encamped behavioral state (Trans. 2→1) for cougars and wolves in the Northeast study area in summer. Transition probabilities were estimated in response to covariates representing the relative probability of use by ungulate prey species [RSF(Elk) and RSF(White-tailed Deer)], habitat features associated with predator hunting mode [terrain ruggedness index and percentage of open habitat], and habitat features associated with landscape permeability (distance to nearest road). Bolded coefficient estimates and standard errors (SE) indicate the 95% confidence intervals did not overlap 0 and were considered significant. See Appendix Table S4.2 for complete table of results.

Species	Transition	Parameter*	Estimate	SE
Cougar	Trans.1→2	Intercept	-1.37	0.04
		Terrain ruggedness	0.15	0.04
		Percent Open	-0.05	0.03
		Nearest Road	-0.11	0.03
		RSF(Elk)	0.03	0.04
		RSF(White-tailed Deer)	0.12	0.04
	Trans.2→1	Intercept	-1.90	0.04
		TRI	0.09	0.04
		Percent Open	0.13	0.03
		Nearest Road	-0.07	0.04
		RSF(Elk)	-0.16	0.04

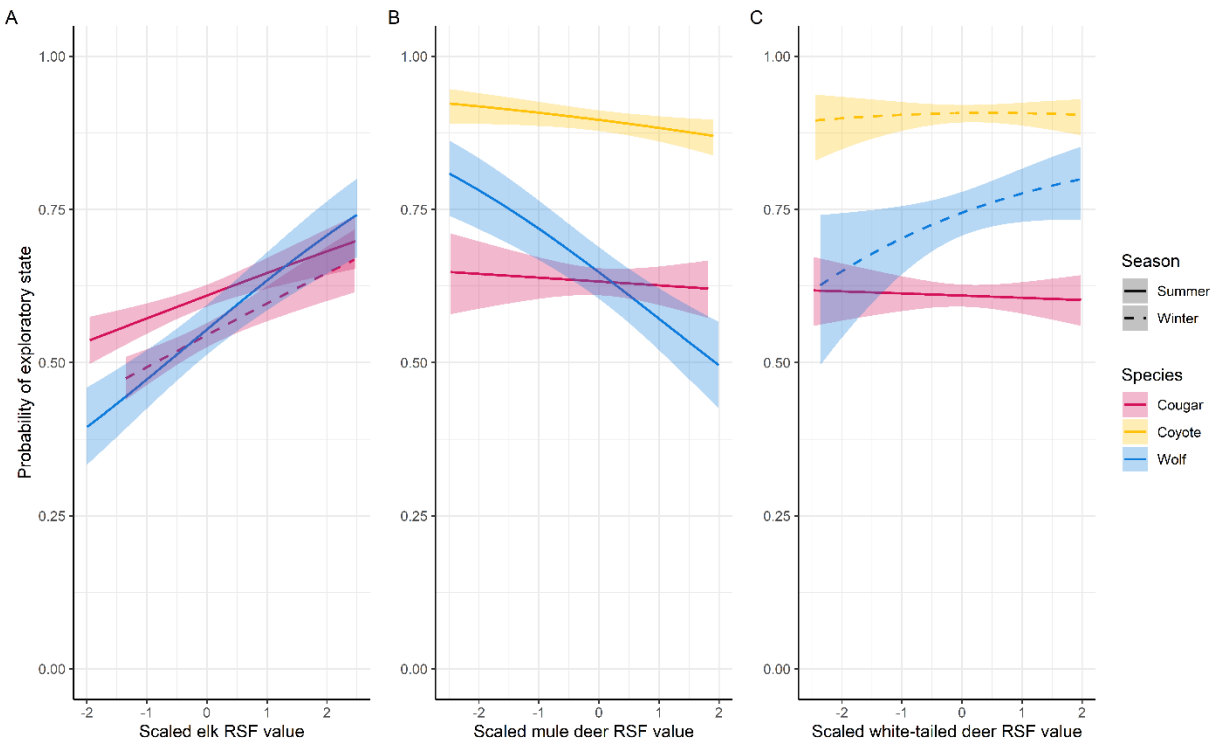
		RSF(White-tailed Deer)	0.13	0.04
Wolf	Trans.1→2	Intercept	-0.57	0.07
		Terrain ruggedness	-0.07	0.07
		Percent Open	0.05	0.06
		Nearest Road	-0.18	0.06
		RSF(Elk)	0.21	0.07
		RSF(White-tailed Deer)	-0.11	0.08
	Trans.2→1	Intercept	-0.89	0.08
		Terrain ruggedness	-0.15	0.07
		Percent Open	-0.06	0.06
		Nearest Road	0.15	0.06
		RSF(Elk)	-0.28	0.06
		RSF(White-tailed Deer)	0.13	0.07

*Covariate representing RSF(Mule Deer) was not included in predator models fitted with movement data from the Northeast study area owing to no mule deer were GPS-collared in the Northeast study area.

Predator movements were only moderately consistent with our expectations with respect to habitats associated with their hunting strategies. All three predators were more likely to transition to an exploratory state or less likely to transition to an encamped state as terrain ruggedness increased across the two study areas, except for coyotes in winter in the Okanogan study area (Table 3.3, Appendix B. S3: Table S3.1, Fig. 3.3). Coyotes and wolves were less likely to transition to an encamped state as habitat became more open whereas cougar

movements varied by season and study area with respect to habitat openness (Appendix B. S3: Table S3.1, Fig. S3.1). In addition, cougars and wolves were generally less likely to transition to an exploratory state as distance to nearest road increased, particularly in the Northeast study area (Table 3.3, Appendix B. S3: Table S3.1, Fig. S3.1). Cougars and coyotes in the Northeast study area transitioned to an encamped state when snow cover was present, whereas cougars in the Okanogan transitioned to an exploratory state (Appendix B. S3: Table S3.1).

Predator stationary state probabilities in response to relative probability of use by ungulate prey



Ungulate stationary state probabilities in response to relative probability of use by predators

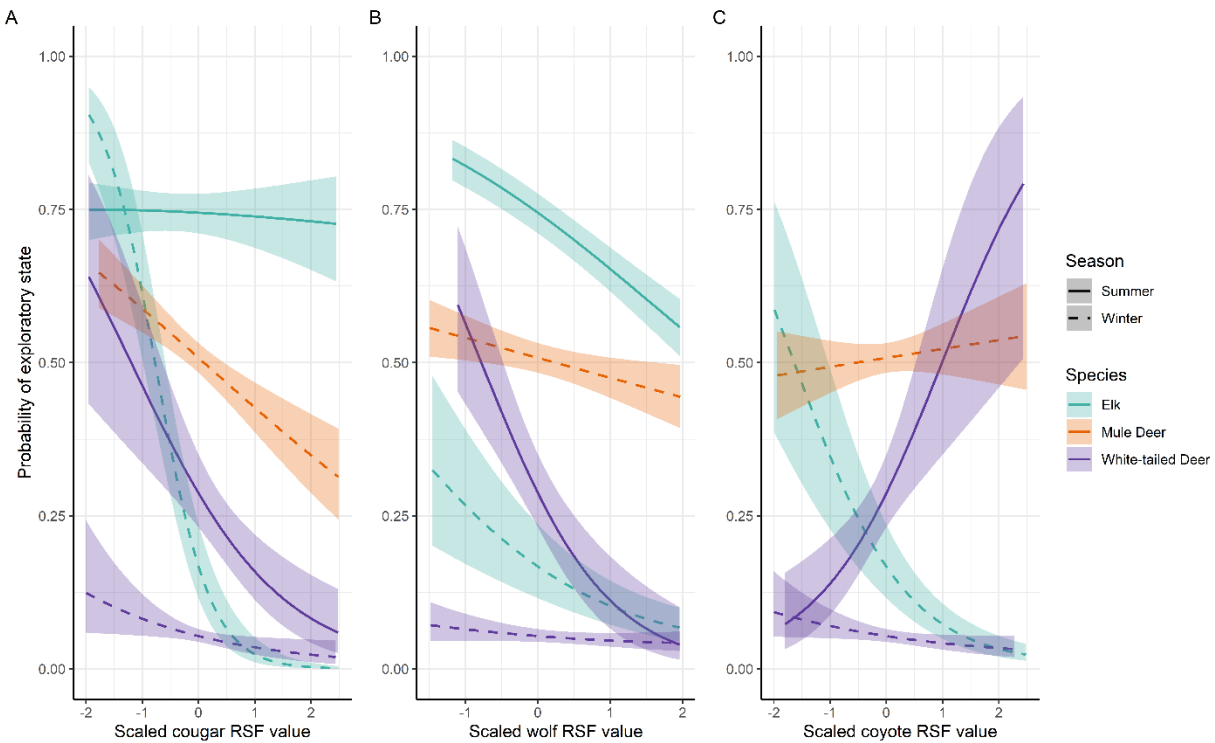


Figure 3.2. Statistically significant ($p\text{-value} \leq 0.05$) estimated probability of being in an “exploratory” behavioral state in summer (solid line) and winter (dashed line) across the Okanogan and Northeast study areas. Top: The probability of a predator (cougar, coyote, wolf) being in the exploratory state in relation to the relative probability of use (based on the species-specific RSF values) by A) elk, B) mule deer, and C) white-tailed deer. Bottom: The probability of an ungulate being in the exploratory state with respect to the relative probability of use (based on the species-specific RSF values) by A) cougars, B) coyotes, and C) wolves. Plotted relationships are based on covariate values that have been centered and scaled and all other covariates held at their mean value (0); the binary snow cover covariate was held at 1 in the winter results. The range of scaled RSF values on the x-axis varied in each species-specific analysis because the mean and standard deviation differed by species. The probability of a species being in an “encamped” behavioral state is 1 minus the probability of being in an “exploratory” state.

3.3.4 *Prey hypothesis*

Ungulate responses to predator RSFs did not vary by predator hunting strategy as expected. In general, all three ungulates were less likely to transition to an exploratory state or more likely to transition to an encamped state as cougar and wolf RSF values increased (Table 3.4, Fig. 3.2, Appendix B. S3: Table S3.2). Elk and white-tailed deer were likely to switch between behavioral states in winter as wolf RSF values increased but were 2 to 3 times more likely to switch into an encamped state compared to an exploratory state (Fig. 3.2, Appendix B. S3: Table S3.2). Elk were likely to stay in their current state as cougar RSF values increased in summer, but overall were less likely to switch to an exploratory state compared to an encamped state (Fig. 3.2, Appendix B. S3: Table S3.2). Ungulate responses to bobcat and coyote RSFs were more variable but in general, deer were generally more likely to transition to an exploratory state as bobcat RSF values increased (Table 3.4, Fig. 2, Appendix B. S3: Table S3.2, Fig. S3.2). Predator RSFs had a greater effect on white-tailed deer movement behaviors in the summer compared to the winter, whereas the effect of the cougar RSF was greater on elk movement in the winter compared to the summer (Fig. 3.2, Appendix B. S3: Fig. S3.2).

Table 3.4. Example of estimated probabilities of transitioning from the encamped behavioral state to the exploratory behavioral state (Trans. 1→2) and from the exploratory behavioral state to the encamped behavioral state (Trans. 2→1) for elk and mule deer in summer in the Northeast and Okanogan study areas, respectively. Transition probabilities were estimated in response to covariates representing the relative probability of use by stalking predators [RSF(Bobcat) and RSF(Cougar)] with a sit-and-pursue hunting mode, relative probability of use by cursorial predators [RSF(Coyote) and RSF(Wolf)] with an active hunting mode, habitat features associated with predator hunting mode [terrain ruggedness index and percentage of open habitat], and habitat features associated with landscape permeability (distance to nearest road and presence of snow cover where No snow cover represents the intercept). Bolded coefficient

estimates and standard errors (SE) indicate the 95% confidence intervals did not overlap 0 and were considered significant. See Appendix Table S4.1 for complete table of results.

Species	Study Area	Transition	Parameter	Estimate	SE
Elk	Northeast	Trans.1→2	Intercept	-1.79	0.11
			Terrain ruggedness	0.07	0.09
			Percent Open	-0.20	0.07
			Nearest Road	-0.23	0.06
			RSF(Cougar)	-0.35	0.10
			RSF(Wolf)	0.12	0.08
			RSF(Coyote)	0.13	0.10
		Trans.2→1	Intercept	-2.97	0.14
			TRI	1.15	0.10
			Percent Open	-0.29	0.09
			Nearest Road	-0.22	0.07
			RSF(Cougar)	-0.29	0.09
			RSF(Wolf)	0.58	0.08
			RSF(Coyote)	-0.04	0.14
Mule Deer	Okanogan	Trans.1→2	Intercept	-4.02	0.06
			Terrain ruggedness	-0.58	0.08
			Percent Open	0.08	0.07
			Nearest Road	0.16	0.06
			RSF(Cougar)	0.03	0.06
			RSF(Wolf)	-0.13	0.07

	RSF(Bobcat)	0.35	0.09
Trans.2→1	Intercept	-3.75	0.07
	Terrain ruggedness	0.45	0.07
	Percent Open	0.02	0.07
	Nearest Road	0.03	0.05
	RSF(Cougar)	0.08	0.07
	RSF(Wolf)	0.11	0.06
	RSF(Bobcat)	0.55	0.10

With respect to habitat features associated with predator hunting strategies, ungulates were consistently more likely to transition to an encamped behavioral state as terrain ruggedness increased (Table 3.4, Fig. 3.3, Appendix B. S3: Table S3.2). Habitat openness, however, had relatively little effect on ungulate movement. Only mule deer in winter were more likely to transition to an exploratory state as habitat became more open whereas elk in summer were likely to stay in their current state with increasing habitat openness (Appendix B. S3: Table S3.2, Fig. S3.1). The effect of distance to nearest road was variable but deer were generally less likely to transition to an encamped behavioral state as distance to nearest road increased. Conversely, elk were more likely to transition to an encamped state in winter but, conditional on their current state, likely to stay in that state in summer as distance to nearest road increased (Table 3.4, Appendix B. S3: Table S3.2, Fig. S3.1). Elk and mule deer were less likely to transition to an exploratory state in winter when snow cover was present (Appendix B. S3: Table S3.2).

Stationary state probabilities for ungulates and predators in response to Terrain Ruggedness Index (TRI)

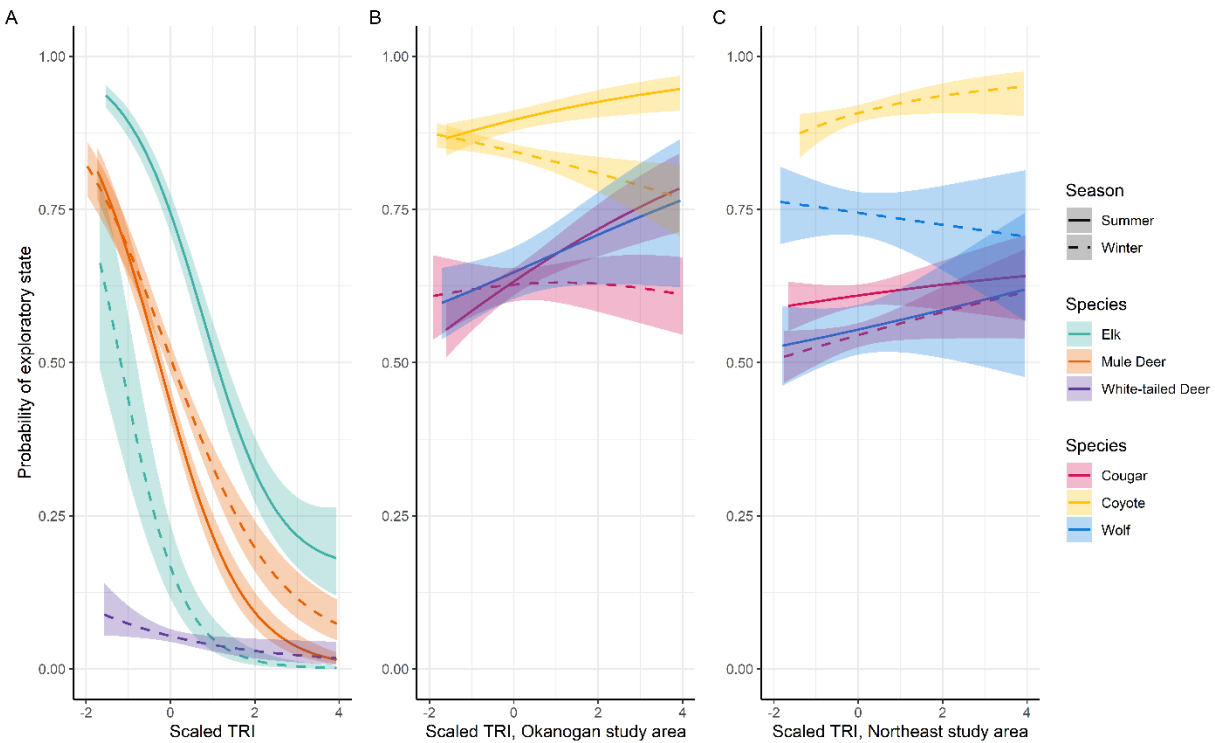


Figure 3.3. The estimated probability that cougars, coyotes, and wolves, and elk, mule deer, and white-tailed deer will be in an “exploratory” behavioral state in relation to terrain ruggedness index (TRI) in summer (solid line) and winter (dashed line). Plots depict significant A) ungulate responses to TRI and predator responses to TRI in the B) Okanogan and C) Northeast study areas, respectively. Plotted relationships are based on covariate values that have been centered and scaled and all other covariates held at their mean value (0); the binary snow cover covariate was held at 1 in the winter results. The range of scaled RSF values on the x-axis varied in each species-specific analysis because the mean and standard deviation differed by species. The probability of these species being in an “encamped” behavioral state is the inverse of these plotted relationships.

3.4 DISCUSSION

Identifying how predator hunting mode influences animal movement can improve our understanding of predator-prey encounter rates, predation risk, and how predator-prey interactions shape species distributions in wildlife communities. We found that cougar, coyote,

and wolf movements changed in response to prey and habitat complexity, but their movement behaviors did not strictly align with our expectations for stalking and coursing predators. Similarly, we found that elk, mule deer, and white-tailed deer adjusted their movement behaviors in response to predators and landscape features that may be associated with predator hunting mode, but these behaviors were likely tied to general predation risk and mobility instead of responses to specific hunting strategies. Although our results demonstrate that predators and prey do adjust their movements in response to one another and various landscape features, these movement behaviors may suggest prey are relying on alternative antipredator behaviors, such as increased vigilance or reduced activity, to minimize predation risk.

We expected the movement behaviors of predators to reflect their hunting strategies, where stalking predators would be more encamped and cursorial predators would be more exploratory in areas where the relative probability of use increased for prey. Instead, our results suggested that predator movement behaviors differed in response to specific prey species more so than the predator's respective hunting mode. Specifically, cougars and wolves were more likely to be in an exploratory state around elk whereas all three predators were more likely to be in an encamped state around mule deer, although the magnitude and shape of these relationships varied by predator species. Predator responses were less consistent in response to white-tailed deer, but coyotes and wolves were much more likely to transition into an exploratory state as the relative probability of use increased for white-tailed deer. This pattern may speak to the fact that cougars, coyotes, and wolves are generalist predators that can adjust their hunting and movement behaviors based on prey type (e.g., Gable et al. 2018) or prey escape tactics (Dellinger et al. 2019). Our study areas are relatively forested compared to other regions where studies have contrasted cougar and wolf hunting behaviors (e.g., Atwood et al. 2007) and all three predators

may converge on similar broad-scale movement patterns as a result. The predictability of prey, and whether they exhibit uniform or clumped distributions across the landscape, can also influence predator movement behaviors (Sims et al. 2012). In our system, elk distributions appeared patchier whereas deer were more uniformly dispersed across the landscape. Under this scenario, directed (i.e., exploratory) predator foraging movements should be more effective for encountering clumped resources and more localized (i.e., encamped or area-restricted) foraging movements should be more effective for encountering uniformly dispersed resources (Huey and Pianka 1981), consistent with the predator movements in response to elk and mule deer RSFs.

We found that ungulates responded to large predators in a similar manner regardless of their hunting behaviors, which was not what we expected based on our hypotheses. Ungulates appeared to apply the same antipredator behavior (becoming more encamped) to all large predators, presumably to improve the assessment of short-term risk (e.g., direct encounters with predators) in areas with elevated long-term risk (e.g., areas with higher predator RSF values; Dröge et al. 2019). Prey may reduce their movements in response to all large predators to increase vigilance (Forester et al. 2007) and because more active prey tend to be killed by predators (Sih 2005). Alternatively, ungulates may adjust their behavioral responses to the more predictable predator. Stalking predators leave more cues of their presence and are more consistently associated with certain habitat features, which should allow prey to respond more “appropriately” to perceived risk from these predators (Schmitz 2005). In our system, cougars occurred at higher densities compared to wolves and were never extirpated whereas wolves are recolonizing Washington State (Washington Department of Fish and Wildlife et al. 2019). Ungulates may be responding to the more predictable and common predator while applying the same antipredator movement behaviors to the less predictable, lower density predator. If

ungulates reduce their movements in response to large predators, increasing predators on the landscape may have a cascading effect on ungulate populations to alter their risk to other sources of mortality such as harvest, disease, or vehicle collisions that can be associated with increased movement (Raynor et al. 2021). While the ungulate responses to large predators was consistent, their movement behaviors were more variable in response to bobcats and coyotes. In the study area, mesopredators are not the primary predator of adult ungulates (Ganz et al. 2022b), which may explain why there is less of a clear response from the different ungulates.

After accounting for the effect of snow cover, prey/predator presence had the largest effect size for three paired models (wolf/white-tailed deer, coyote/white-tailed deer, and cougar/elk in the Northeast in winter), indicating the presence of the reciprocal species had the greatest influence on animal movement (Table S3.1, Table S3.2). In these examples, prey were more likely to be in an encamped state as predator RSF values increased whereas predators were more likely to be in an exploratory state as prey RSF values increased. These movement behaviors should theoretically increase encounter rates between these species (Huey and Pianka 1981, Scharf et al. 2006). As a result, predators may win the “space-race” by not only spatially overlapping with prey (Sih 2005) but also moving in a manner that should increase encounter rates with prey (Scharf et al. 2006, Miller et al. 2014, Suraci et al. 2022). Testing the outcomes of these movement behaviors requires data on actual encounter or capture rates that are difficult to collect.

Landscape features appeared to mediate the potential for encounters as our analyses also indicated that predator and prey movements changed in response to common habitat variables. For example, mule deer, coyotes, and wolves were more likely to be in an exploratory state as the percentage of open habitat increased. This trend is consistent with our expectations that

coursing predators would be more exploratory in less complex habitats and that prey would be more exploratory in habitats where coursing predators have an advantage. Open habitat is also easier to move through so these exploratory behaviors may simply reflect increased mobility among species (Avgar et al. 2013). Regardless, the movement behaviors of mule deer and cursorial predators in open habitat should reduce encounter rates (Sih 2005, Miller et al. 2014). Conversely, movement behaviors were different for predators and prey as terrain ruggedness increased. Ungulates were consistently more likely to be encamped whereas carnivores were generally more likely to be in an exploratory state as terrain became more rugged. This more encamped behavioral state may reflect ungulates responding to perceived risk in complex habitats as we expected, or simply reflect reduced mobility when traversing challenging terrain (Avgar et al. 2013). The increased probability of predators transitioning to an exploratory state as terrain ruggedness increased was inconsistent with our expectations. Transitioning to an exploratory state may reflect predators adjusting their movements to account for reduced prey movements in rugged terrain, which would theoretically increase encounter rates between predators and prey. Alternatively, predators may be traversing relatively unprofitable, challenging terrain quickly (Avgar et al. 2013), regardless of prey movement behaviors. This latter explanation may apply particularly to coursing predators that rely on chasing down prey and are at a disadvantage when hunting in more complex habitats (Gorini et al. 2012). Although we cannot definitively say whether changes in movement behavior due to habitat complexity were associated with predator hunting mode or simply tied to mobility, our results do suggest these habitat features mediate interactions between predators and prey, potentially by influencing encounter rates through altered movement.

The effects of landscape permeability on animal movement may also alter predator-prey interactions. Large carnivores were more likely to be in an encamped state as the distance to nearest road increased, consistent with prevailing knowledge of carnivores exploiting linear features (Zimmermann et al. 2014). Similarly, elk were more likely to be encamped farther from roads. Mule deer, however, were more likely to be exploratory as distance to road increased. By implication, more exploratory movements closer to roads for both large predators and elk may reduce encounters between these species, whereas the more encamped behavior of mule deer near roads may increase encounters with large predators closer to roads. Road development has the potential to alter predator-prey interactions and potentially increase encounters between large predators and some ungulate prey species (Mumma et al. 2017, Dickie et al. 2020). Similarly, decommissioning or obstructing linear features can significantly reduce predator-prey encounter rates by increasing the cost of travel for predators (Keim et al. 2021). Our findings add further weight that how predators and prey move with respect to roads contributes to predation risk for some ungulate species (Dickie et al. 2020) and is an important consideration in informing landscape planning and habitat restoration decisions in human dominated landscapes (Vanlandeghem et al. 2021). Lastly, elk and mule deer were less likely to transition to an exploratory behavioral state where snow cover was present in winter, presumably because moving in snow is energetically costly and hinders mobility for ungulates (Parker et al. 1984). We found that snow cover generally did not influence movement behaviors for coursing predators which, in combination with more encamped ungulates, should benefit wolves and coyotes when searching for and pursuing ungulate prey in winter (Penczykowski et al. 2017).

Without knowing encounter rates or capture success in relation to these movement behaviors, our interpretations of the outcome of predator-prey movements are speculative. Future

studies of predator-prey movement would benefit from using accelerometer data or proximity collars to estimate encounter rates or pairing movement data with kill-site investigations to understand the outcomes of predator-prey movements (Suraci et al. 2022). Moreover, the temporal scale of our telemetry relocation data (4-hour fix interval) may have limited our ability to detect fine-scale changes in movement associated with predator hunting strategies, particularly if prey movement behaviors differ when stalking and coursing predators are immediately present (Dröge et al. 2019). We also assumed the “encamped” and “exploratory” behavioral states could capture typical stalking and coursing hunting strategies. Although cougars are considered a stalking predator and we assumed this was representative of a more sedentary hunting mode, their hunting behaviors are more consistent with a search-and-stalk behavior where cougars wait for relatively short periods of time before relocating (Beier et al. 1995). Thus, since the behavioral states are unknown in the HMM, the encamped behavioral state may not be as consistent with the cougar hunting mode as we assumed owing to the temporal resolution of our data and the temporal scale of how cougars hunt. Finally, inter- and intra-specific interactions (e.g., density of competitors or conspecifics) also influence movement behaviors (Merrill et al. 2020, Grenier-Potvin et al. 2021). The influence of competitive interactions on animal movement were not considered here but could have masked or mediated the effects of predator-prey interactions on movement.

By investigating the movement behaviors of multiple predators and prey simultaneously, we demonstrated that these species may not move as expected in response to predator hunting strategy, but they do adjust their movements in response to one another in ways that likely alter encounter rates. We also showed that habitat features may influence predator-prey interactions based on how different species alter their movements in relation to various landscape features. In

addition to improving our general understanding of predator-prey interactions, our findings add evidence that predators and prey are engaged in a game where their movements and spatial distributions are a product of their joint behavioral responses (Sih 2005). Thus, our study highlights the importance of the reciprocal responses of both predator and prey movements in structuring patterns of space use (Mitchell and Lima 2002). Finally, HMMs provide a unique approach to understanding predator-prey dynamics by separating movements into latent states as a function of covariates. Based on our findings, we expect that integrating data collected at a finer temporal resolution with auxiliary data, such as accelerometers, should provide further insight to how interspecific interactions influence animal movement.

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Chapter 4. TEMPORAL RESPONSES TO RISKY PLACES AND RISKY TIMES IN A MULTI-PREDATOR, MULTI- PREY SYSTEM

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Abstract: Antipredator behaviors are partially influenced by the predictability of predation risk and whether prey perceive and respond to different levels of (predictable) background risk and (unpredictable) immediate risk. Prey may therefore reduce predation risk by avoiding areas with predictable patterns of predator activity (i.e., risky places hypothesis), responding reactively to times when death from predation may be imminent (i.e., risky times hypothesis), or a combination of both. The spatial outcomes of predator-prey interactions are well studied, particularly with

respect to the effect of predator hunting mode, but the temporal activity responses of prey to risky places and times are less understood. We evaluated the temporal patterns of four ungulate species (elk [*Cervus canadensis*], moose [*Alces alces*], mule deer [*Odocoileus hemionus*], and white-tailed deer [*O. virginianus*]) under varying levels of background and immediate risk of predation from five predator species (black bear [*Ursus americanus*], bobcat [*Lynx rufus*], cougar [*Puma concolor*], coyote [*Canis latrans*], and gray wolf [*C. lupus*]) to understand the temporal scales at which prey respond to predation risk in a multi-predator system in eastern Washington, USA. We tested the effect of background risk on diel activity patterns of ungulates using camera trap data and estimated the differences in activity curves of predators and ungulates with respect to varying levels of habitat complexity and predator presence. We then tested whether prey avoided immediate predation risk at sites where predators were recently present by modeling the time between detections of predators and ungulates at each camera site. We found moderate support for the risky places and risky times hypothesis, respectively. In general, deer shifted activity to avoid peaks in background activity patterns of predators, especially in winter, but the effect of habitat complexity on daily activity varied by species and season. In addition, deer and moose delayed their use of cameras sites after a predator was recently present, where the latency of site-use varied by predator species and/or season. Our results demonstrated the complex nature of predator-prey interactions in a multi-predator, multi-prey system and highlight the importance of considering the responses of multiple ungulate species to a diversity of predators across spatiotemporal scales simultaneously. *Keywords:* Antipredator, avoidance, cervid, non-consumptive, predator hunting mode, predator-prey interactions, predation risk, temporal overlap, time-between-detections, ungulate

4.1 INTRODUCTION

Antipredator behaviors vary depending on background levels of predation risk as well as the level of immediate predation risk in a given location (Lima and Bednekoff 1999, Creel et al. 2008, Dröge et al. 2017). Background levels of risk are determined by the long-term, predictable patterns of habitat selection by predators, temporal patterns of predator activity, and habitat features that influence attack or escape success (Gehr et al. 2018). Immediate predation risk is less predictable, reflects short time periods, and is influenced by the direct presence or absence of a predator rather than long-term patterns of predator activity (Dröge et al. 2017, Gehr et al. 2018). Although animals lack perfect knowledge of their environment, prey species perceive and respond to both types of predation risk based on information gained through past encounters with predators and various cues of current or recent predator presence (Lima and Steury 2005, Weissburg et al. 2014).

There is ample evidence that prey proactively avoid “risky places” (Creel et al. 2008) that exhibit high levels of background risk (e.g., Lone et al. 2017, Kohl et al. 2018), and separately, that prey reactively respond to “risky times” (Creel et al. 2008) when immediate predation risk is high (e.g., Courbin et al. 2016). Yet, despite the long-held recognition that predation risk is temporally dynamic, and that prey responses vary depending on both the immediate level of predation risk and the background context within which it arises (i.e., risk allocation hypothesis; Lima and Bednekoff 1999), few studies have considered the combined effect of both forms of risk on antipredator behaviors (Dröge et al. 2017). However, recent research demonstrates that different cues of predation risk may interact across spatiotemporal scales to shape antipredator behaviors (i.e., risky places – risky times hypothesis; Dröge et al. 2017, Moll et al. 2017, Gehr et al. 2018). For instance, Dröge et al. (2017) found that prey vigilance was strongest in areas

where both immediate and background predation risk were high, but not when immediate risk was low, and that this response was greatest when the predator species posing the immediate threat was detected in an area heavily used by that predator species (i.e., high background risk). This suggests that the interactive effects are strongest when prey can anticipate predation risk and thus responses to immediate risk levels are better informed (Lima and Bednekoff 1999, Dröge et al. 2017).

Antipredator responses to background and immediate predation risk also depend on the cues prey use to assess risk level and how reliable those cues are at representing risk (Lima and Steury 2005, Luttbeg and Trussell 2013). Cues associated with risk of predation from ambush and stalking predators are presumably more reliable than those of cursorial predators because ambush and stalking predators use predictable habitats for hunting (e.g., hiding cover at night) and spend more time in a given location as they wait for prey (Preisser et al. 2007, Gaynor et al. 2018, Smith et al. 2019a). Indeed, Thaker et al. (2011) found that three different prey species avoided habitats that were heavily used by ambush predators but did not avoid habitats frequently used by cursorial predators. Similarly, Wikenros et al. (2015) observed that ungulates reduced visitation time in areas when presented with cues of immediate risk from stalking predators, but not from cursorial predators. More sedentary predators may elicit stronger antipredator responses from prey because they provide reliable cues of both background and immediate risk levels (Preisser et al. 2007) and thus, we might expect the interactive effects to be even stronger in response to some predator species compared to others (Dröge et al. 2017). Yet, most tests of the “risky places” and “risky times” hypotheses overlook the complexity of multi-predator, multi-prey systems, typically relying on laboratory experiments or simpler predator-prey systems to test their predictions (Dröge et al. 2017). It is therefore imperative to evaluate

prey responses to multiple predators simultaneously to test how well predictions from simpler systems hold up under more complicated species interactions and field settings (Montgomery et al. 2019).

The spatial proximity of predators to prey is often used as a proxy for immediate predation risk in studies of antipredator behaviors in wild populations (Gehr et al. 2018), but temporal proximity may also be an important measure of immediate risk. Given that prey can respond to varying background levels of predation risk by temporally partitioning their use of risky places when predators are less active (Kohl et al. 2018, Smith et al. 2019b), it is likely that prey also alter their activity patterns at finer temporal scales in response to varying levels of immediate predation risk. In addition to altering vigilance, foraging, visitation duration, and other behaviors (Kuijper et al. 2014, Wikenros et al. 2015), prey animals may respond to the recent presence of a predator by simply delaying their use of that location. Recent predator presence may therefore produce a lag in when prey animals would otherwise use a specific area, leading to latency between the presence of a predator and the presence of prey at a given location. The effect of temporal proximity of predators on prey site-use has rarely been explored, however.

The multi-predator, multi-prey system in eastern Washington, USA provided an opportunity to investigate the temporal scales at which prey respond to predation risk, where several ungulate prey species (elk [*Cervus canadensis*], moose [*Alces alces*], mule deer [*Odocoileus hemionus*] and white-tailed deer [*O. virginianus*]) navigated predation risk from both stalking predators (bobcats [*Lynx rufus*] and cougars [*Puma concolor*]) and cursorial predators (coyotes [*Canis latrans*] and wolves [*C. lupus*]), as well as American black bears (*Ursus americanus*). Using camera trap detections of these species, we tested three hypotheses

regarding spatiotemporal responses to background and immediate predation risk. Under the *risky places hypothesis*, prey should temporally avoid areas with high levels of background risk (Creel et al. 2008), so we expected the daily activity patterns of prey species to differ between locations that were predictably used by predators or in habitats associated with a predator's hunting mode compared to those that were not. Under the *risky times hypothesis*, prey should react to immediate risk by avoiding locations where predators were recently present (Creel et al. 2008), so we expected greater latency between detections of prey following a predator detection than would be expected if predator presence had no effect. Finally, under the *risky places – risky times hypothesis*, prey responses should be greatest when and where immediate risk is high in areas and at times when background levels of predation risk are also high (Dröge et al. 2017). We therefore expected similar activity patterns in response to background risk as in the risky places hypothesis, but that the latency between detections of predators and prey would be greatest in habitats that are predictably used by the same predator species that posed the immediate risk of predation. Lastly, we expected any evidence of temporal partitioning (regardless of the hypothesis) to be strongest in response to stalking predators, owing to their more predictable use of habitat and times of day.

4.2 METHODS

4.2.1 Study areas

We deployed camera traps across two study areas in eastern Washington, USA, from June 2018 – May 2021 (Fig. 4.1). The Northeast study area (4,535 km²; -117.7193, 48.28302) was characterized by climatic and topographic gradients of the southern Selkirk and Huckleberry Mountains (elevation ranging 378 – 2079 m; Williams et al. 1995). The vegetative community was dominated by Douglas fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), ponderosa

pine (*Pinus ponderosa*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*; Williams et al. 1995). White-tailed deer and elk were the most common cervid species, although smaller populations of moose and mule deer were also present. Black bears, bobcats, cougars, coyotes, and wolves occurred in this study area (Washington Department of Fish and Wildlife et al. 2019). The Okanogan study area (5,300 km²; -120.1096, 48.42966) was characterized by topographically rugged and mountainous terrain with deep valleys and steep slopes (elevation ranging 225 – 2790 m; Williams and Lillybridge 1983). Forests were dominated by mixtures of Douglas fir, Engelmann spruce (*Picea engelmannii*), lodgepole pine (*P. contorta*), ponderosa pine, and subalpine fir (*A. lasiocarpa*; Williams and Lillybridge 1983), whereas open regions were dominated by big sagebrush (*Artemisia tridentata*) and antelope bitterbrush (*Purshia tridentata*). Mule deer were the predominant cervid species in the Okanogan study area, although white-tailed deer, moose, and elk also occurred in the study area. The carnivore community was similar to that of the Northeast but also included a small population of Canada lynx (*L. canadensis*; Washington Department of Fish and Wildlife et al. 2019).

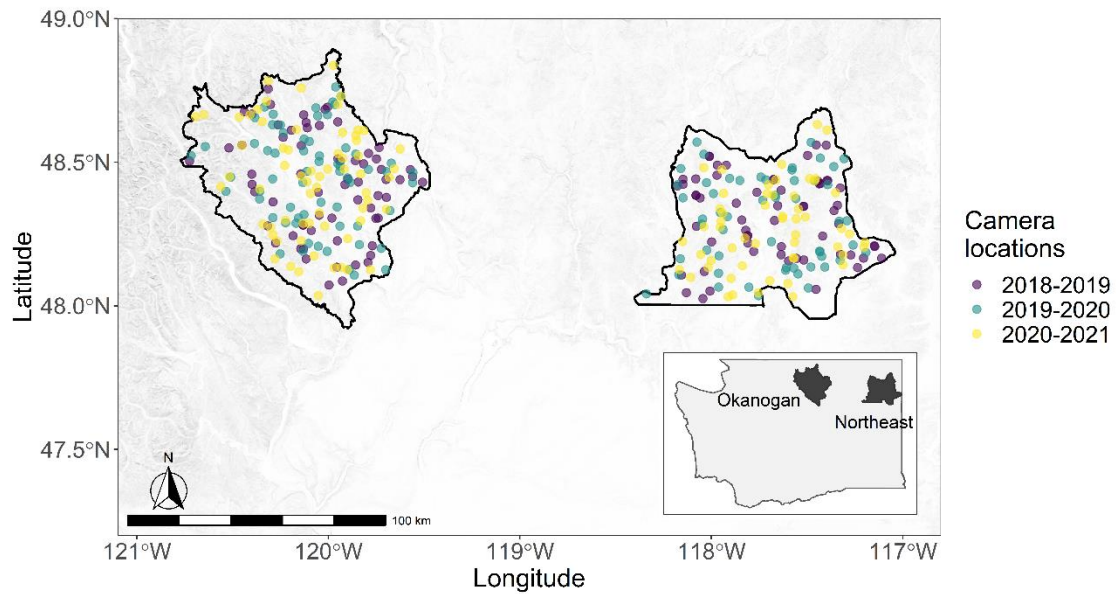


Figure 4.1. Locations of 350 camera stations that sampled the Okanogan and Northeast study areas in eastern Washington, USA from 2018 – 2021, plotted against an index of terrain ruggedness (TRI) where darker shades represent more rugged terrain.

4.2.2 Camera data

We used temperature and motion-sensing trail cameras (Model HyperFire2 Pro; Reconyx, Holmen, WI, USA) to monitor 120 randomly selected sites annually in the Northeast ($n = 55$) and Okanogan ($n = 65$) study areas (Fig. 4.1). We deployed and maintained cameras from June 2018 – May 2019, at which point we redeployed cameras to new random locations in June 2019 and again in June 2020. We followed a stratified random sampling design to guide camera site selection (O’Connell and Bailey 2011) by stratifying each study area into 4 elevational bands and overlaying a 1 km^2 grid across each study area. We then randomly selected grid cells within each elevation stratum by area-weighting each stratum and selecting the number of cells proportional to the amount of land area within each stratum per study area. We excluded locations above $\sim 2,100 \text{ m}$ elevation to avoid sampling alpine habitat that was both logistically difficult to access

and not frequently used by the animal community of interest. We deployed one camera within 250 m of the center of each selected cell. We placed un-baited cameras on secondary (unpaved) roads, decommissioned roads, human-use trails, or game trails to target linear features that would funnel animal movement and increase the likelihood of detecting rarer species that occur at low densities (e.g., large carnivores; Cusack et al. 2015, Tanwar et al. 2021). Cameras recorded the date and time when each photo was taken (full programming reported in Bassing et al. 2022).

We labeled photo-capture data using the Microsoft AI for Earth machine learning algorithm (“MegaDetector”; Beery et al. 2019) and program Timelapse2 (Greenberg 2019). The MegaDetector probabilistically identified objects in each image as animal, human, or vehicle with confidence 0 – 1.0. Two technicians independently verified the presence of ≥ 1 animal in images classified by the MegaDetector and recorded the species of each animal using Timelapse2. A third expert reviewer compared the independent data sets to ensure consistency and generated the final image set used for analysis. We grouped images by season for all analyses: summer = 1 June – 30 Sept, fall = 1 Oct – 30 Nov, winter = 1 Dec – 31 Mar, spring = 1 April – 31 May. We recognize that detection probability can vary by species (Bassing et al. 2022), but we assumed the detection rates were relatively constant within a given season and represented activity across the 24-hour cycle.

4.2.3 *Classification of background risk level*

Habitats associated with predator hunting mode represent predictable spatial cues of risk from different predator species and daily peaks in predatory activity represent predictable temporal cues of risk (Kohl et al. 2018, 2019). General predator occurrence (i.e., if a predator was ever detected at a site) can also represent a predictable cue of predation risk (Creel et al. 2008, Tambling et al. 2015). We therefore determined the level of background risk at each camera

based on two different classifications: habitat complexity and whether predators were detected at a camera site. For habitat complexity, we classified cameras as having high or low background risk based on a measure of terrain variability (Wilson et al. 2007), assuming this represented one aspect of habitat complexity in our system. We derived terrain ruggedness index (TRI) from the Shuttle Radar Topography Mission (SRTM) 30m resolution digital elevation model (Farr et al. 2007) for each camera site in Program R 4.2.1 (R Core Team 2022).

We considered background risk of predation from stalking predators (bobcats and cougars) to be relatively high at a camera if the TRI value was greater than the mean TRI when averaged across all camera sites, owing to stalking predators relying on structural complexity for hunting (Atwood et al. 2009). Conversely, we considered background risk of predation from a coursing predator (coyotes and wolves) to be relatively high at a camera if the TRI value was less than the mean TRI, owing to coursing predators relying on gentler terrain when pursuing prey over long distances (Atwood et al. 2009, Makin et al. 2017). Black bears are omnivores and do not fit within either predator hunting mode classification, but we considered predation risk from black bears to be higher in areas of higher habitat complexity given bears generally do not chase prey over long distances like coursing predators (Mumma et al. 2019). We also classified camera locations as having high or low background risk based on whether a predator was detected at the site in each season. For instance, background risk of predation from cougars in summer was low if no cougar was detected at a camera from 1 June – 30 Sept and high if ≥ 1 cougar was detected at the camera in this time.

4.2.4 *Temporal overlap*

We used the Overlap package (Meredith and Ridout 2017) in Program R 4.2.1 (R Core Team 2022) to test our first hypothesis and assess how background predation risk influenced the

temporal activity patterns of predators and prey in each season. We considered sequential images of the same species to be a single detection event and required ≥ 30 -minutes to have elapsed between the last image of a species and the next image of that same species for detections to be considered independent events at the same camera (O'Brien et al. 2003, Sollmann 2018). We retained only the first image of each detection event and grouped all images based on whether the detections came from camera sites with low or high background risk according to the TRI and species-specific predator detections per season. Detection times over the 24-hr cycle are circular and their underlying density may be bimodal for species with multiple activity peaks in a day (Ridout and Linkie 2009). We therefore converted the clock time of each image to radial time and adjusted for changes in day length over the course of the year by scaling the time of day to sunrise and sunset (Nouvellet et al. 2012, Meredith and Ridout 2017).

We estimated each species' daily activity curve per season using nonparametric kernel density estimators quantifying the density of detections of a given species over the 24-hour cycle (Ridout and Linkie 2009). We used these species- and season-specific activity curves to estimate the coefficient of overlapping ($\bar{\Delta}$), i.e., the proportion of the area where two kernel density curves overlap, to compare how activity patterns differed in areas with high and low levels of background predation risk (Ridout and Linkie 2009, Tambling et al. 2015). We used the Δ_1 estimator to measure the coefficient of overlapping when the sample size of the smaller of the two curves was < 50 detections and the Δ_4 estimator when the sample size was ≥ 50 detections (Meredith and Ridout 2017). When $\bar{\Delta} = 0$, the coefficient indicates no overlap in activity curves whereas $\bar{\Delta} = 1$ indicates complete overlap in activity curves (Ridout and Linkie 2009). We used 10,000 smoothed bootstrapped samples to estimate the 95% confidence interval (CI) for each

overlap estimate and reported the 95% CI adjusted for bootstrap bias (“basic0”; Meredith and Ridout 2017).

We first estimated the coefficient of overlapping for each prey species by overlapping season- and species-specific activity curves from camera sites with low versus high measures of habitat complexity, as well as sites where each predator was and was not detected, to evaluate how prey activity changed with different levels and types of background predation risk (e.g., overlap between summer mule deer activity curves at sites where cougars were and were not detected). We then estimated the coefficient of overlapping for each pairwise predator-prey combination for cameras with low habitat complexity and for cameras with high habitat complexity to compare the times when predator and prey activity overlapped under varying levels of habitat complexity (e.g., the temporal overlap between cougar and mule deer activity curves at cameras with low TRI values vs. cameras with high TRI values). We considered estimates of predator-prey temporal overlap under low and high levels of habitat complexity to be significantly different if the 95% bootstrapped CIs did not overlap the mean of the other and trending towards significant if the 95% bootstrapped CI of only one estimate did not overlap the mean of the other. We excluded black bears from all winter analyses and did not compare the temporal overlap of mesopredators, elk, and moose. We excluded overlap analyses if the sample size for at least one species was extremely low ($n < 20$ detections; Niedballa et al. 2019).

4.2.5 *Latency of site-use*

Assuming photo-capture data represent a random sample of animals moving independently across the landscape, individual detections of a species should follow a Poisson point process and the time between detections of that species should follow an exponential distribution (Moeller et al. 2018). If species are moving randomly with respect to one another, detections of

two species on a single camera should also be Poisson distributed and thus, the time between detections of those two species exponentially distributed. We therefore re-filtered the independent detection events by retaining only the last image from each predator detection event and the first image from each prey detection event at each camera. We further filtered these images to only pairs of images where a detection of a predator species was immediately followed by detection of a prey species so that we only evaluated prey responses to the animal that was most recently present at a given camera site. We calculated the time between these detections in minutes and used this measure to represent the latency between detections of predators and prey. We excluded latency observations for elk in the Okanogan study area owing to few elk detections from this region. We excluded latency observations above the 97th quantile for moose, mule deer, and white-tailed deer owing to large time lags between detections of a predator and prey which would not be biologically relevant, e.g., one observation was 244 days. Predator scent typically does not last in the environment longer than 20 days (Galindo-Aguilar et al. 2022), and we assumed any cues ungulates would perceive and respond to would not persist beyond this time. This adjustment limited the observations to no more than 8 – 12 days between detections of a predator followed by an ungulate.

We tested our second and third hypotheses using the latency measurements as an exponentially distributed response variable in a series of ungulate-specific generalized linear mixed models (GLMM; Appendix C. S1). For each ungulate-specific GLMM, we included continuous variables representing habitat complexity (TRI), categorical variables representing season (summer, fall, winter, spring) and predator species (bobcat, coyote, black bear, cougar, wolf), and interactions between predator species and habitat complexity (predator*TRI) as explanatory variables and the ungulate-specific predator-prey latency measurements as the

response variable. We also included a random effect for camera site to account for repeat measures of latency at cameras. We excluded wolves from the elk model owing to very few wolf-elk latency observations ($n = 1$). Lastly, we derived the mean time-between-detections from each model to evaluate how latency in site-use varied under different levels of immediate (specific predator species) and background (habitat complexity) risk of predation.

We conducted a similar analysis using the time-between-detections of different ungulate species. We assumed that if prey actively avoided a camera site after a predator was most recently present, latency of site-use would be greater if the previous species was a predator compared to a different ungulate prey species. Comparing latency after a detection of the same ungulate species (conspecific) may be a more appropriate comparison to the latency following a detection of a predator but differentiating unmarked individuals of the same species made it challenging to accurately estimate the time-between-detections of unique individuals. Therefore, we calculated the time-between-detections of different ungulate species, requiring the detection immediately before that of an ungulate to be of a different ungulate species (e.g., mule deer detection followed immediately by a white-tailed deer detection). We excluded latency observations above the 95th quantile for the moose data set and the 97th quantile for the elk and deer data sets to be consistent with the predator-prey observations. We then fit the ungulate latency measurements for each species with a GLMM similar to that of the predator-prey analyses described above but used a variable representing the previously detected ungulate species instead of the predator species (Appendix C. S1). We compared the mean time-between-detections of different ungulates to those of predators and ungulates to assess whether any predator effects on latency of site-use were biologically meaningful.

We fit all GLMMs in a Bayesian framework within program JAGS 4.3.1 (Plummer 2017) using the jagsUI package (Kellner and Meredith 2021) in Program R 4.2.1 (R Core Team 2022). We ran 3 independent chains of 75,000 Markov chain Monte Carlo (MCMC) iterations, discarding the first 25,000 iterations after an adaptation period of 5,000 iterations, and did not thin the chains. We inspected traceplots and used the Gelman-Rubin diagnostic to check for convergence (Gelman and Rubin 1992). We considered covariates to be supported by the model if the 95% Credible Interval (CRI) of the posterior distributions did not overlap 0 (Kéry 2010) and the mean time-between-detections to be different from one another if the 95% CRI did not overlap the mean of other latency estimates.

4.3 RESULTS

4.3.1 *Camera data*

A total of 350 unique sites were monitored for one year each, with an average of 114 cameras being active each season annually, yielding 36,347.17 (SE = 65.63) trap nights per year on average. Cameras generated on average 1,031.36 (SE = 474.61) independent detection events per species, with white-tailed deer generating the most detections per season and wolves generating the least (Appendix C. S2: Table S2.1). We identified 2,759 instances where an ungulate prey species was detected immediately following the detection of a predator species across seasons, resulting in 689.75 (SE = 318.69) observations per ungulate species on average (Appendix S2: Table S2.2). We identified 1,809 instances where ungulates of different species were detected immediately after one another across seasons, resulting in 436.75 (SE = 119.61) observations per ungulate species on average (Appendix C. S2: Table S2.2). The time between detections of a predator and prey species ranged 0.02 – 21,138.20 minutes, averaging 2,512.87 (SE = 60.41) minutes across species and seasons after extreme observations were removed. The time between

detections of different ungulates ranged 0.02 – 20,163.05 minutes, averaging 2,191.26 (SE = 66.89) minutes across species and seasons after extreme observations were removed.

4.3.2 *Risky-places hypothesis: Temporal overlap*

Ungulates were generally crepuscular with activity peaking around dawn and dusk (Appendix C. S3: Fig. S3.1). Mule deer tended to be moderately more active near dawn compared to dusk whereas white-tailed deer activity was generally similar at dawn and dusk (Appendix C. S3: Fig. S3.1). Elk and moose activity curves were more variable (Appendix C. S3: Fig. S3.1).

Mean temporal overlap ($\bar{\Delta}$) of ungulate activity at camera sites with high versus low levels of background risk (habitat complexity or predator detections) was high, averaging 0.89 (SE = 0.006) overlap of temporal activity curves across ungulate species, seasons, and types of background risk (Fig. 4.2, Appendix C. S3: Table S3.1 and Fig. S3.1). Ungulate activity patterns were relatively consistent across seasons, regardless of the type or level of background risk (Fig. 4.2, Appendix C. S3: Table S3.1 and Fig. S3.1). That said, the coefficient of overlapping estimates for mule deer in winter were relatively low compared to other seasons, indicating mule deer activity differed with the level of background risk at a camera site (i.e., low versus high TRI and whether bobcats, cougars, coyotes, or wolves were detected) in the winter (Fig. 4.2). The effect of background risk on white-tailed deer activity was more variable with respect to season, but relatively low coefficients of overlapping indicated that the level of TRI influenced white-tailed deer activity in winter, cougar detections influenced white-tailed deer activity in spring, coyote detections influenced white-tailed deer activity in winter, and wolf detections influenced white-tailed deer activity in fall, winter, and spring (Fig. 4.2). Elk activity differed with respect to TRI levels in spring and whether cougars were present in fall, winter, and spring (Fig. 4.2),

whereas moose activity only moderately differed with respect to TRI in the winter and spring, and with cougar detections in the winter (Fig. 4.2).

Temporal overlap of ungulate activity patterns at camera sites with low vs. high background risk of predation

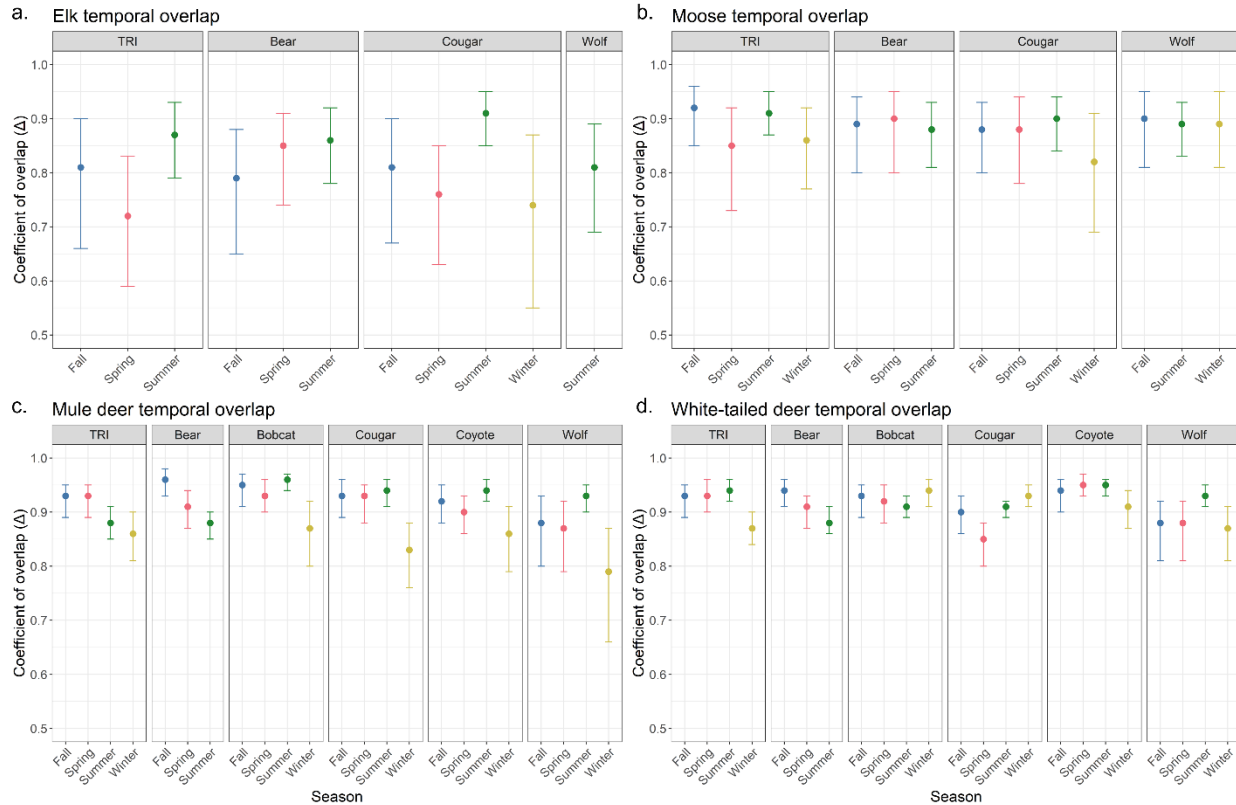


Figure 4.2. Coefficient of overlapping estimates ($\bar{\Delta}$) and bootstrapped 95% confidence intervals measuring the amount of overlap in diel activity curves for each ungulate species at camera sites with low versus high terrain ruggedness (TRI) or risk of predator occurrence. Risk of predator occurrence was determined by whether a given predator species was detected at least once (high risk) or never detected (low risk) at a camera site. Temporal overlap was estimated seasonally for elk (a), moose (b), mule deer (c), and white-tailed deer (d) at each level and type of background risk, seasonally. Detections of mesopredators (bobcats and coyotes) were not considered for elk or moose analyses and bears were excluded from all winter analyses. Overlap estimates based on small sample sizes ($n < 20$ independent detections) were not considered for interpretation and excluded from plots.

The specific differences in diel activity related to these lower overlap estimates varied with the type of background risk, season, and ungulate species. Mule deer were moderately more

diurnal at camera sites with higher TRI values and where cougars were detected in winter (Fig. 4.3, Appendix C. S3: Fig. S3.1). Conversely, mule deer activity peaked at dusk or was generally more nocturnal where bobcats, coyotes, or wolves were detected in winter (Fig. 4.3, Appendix C. S3: Fig. S3.1). White-tailed deer were moderately more nocturnal at camera sites with higher TRI in winter, whereas they increased their dawn and dusk activity at sites where coyotes were detected in winter (Fig. 4.3). White-tailed deer responses to wolves varied seasonally but their crepuscular activity generally shifted to after dawn and dusk, or they were overall less active during the day where wolves were detected (Fig. 4.3). White-tailed deer were more diurnal where cougars were detected in spring (Fig. 4.3). The lower overlap estimates for elk and moose activity were generally driven by increased activity near dawn or dusk, although the exact shifts in activity varied with season and type of background risk (Appendix C. S3: Fig. S3.1).

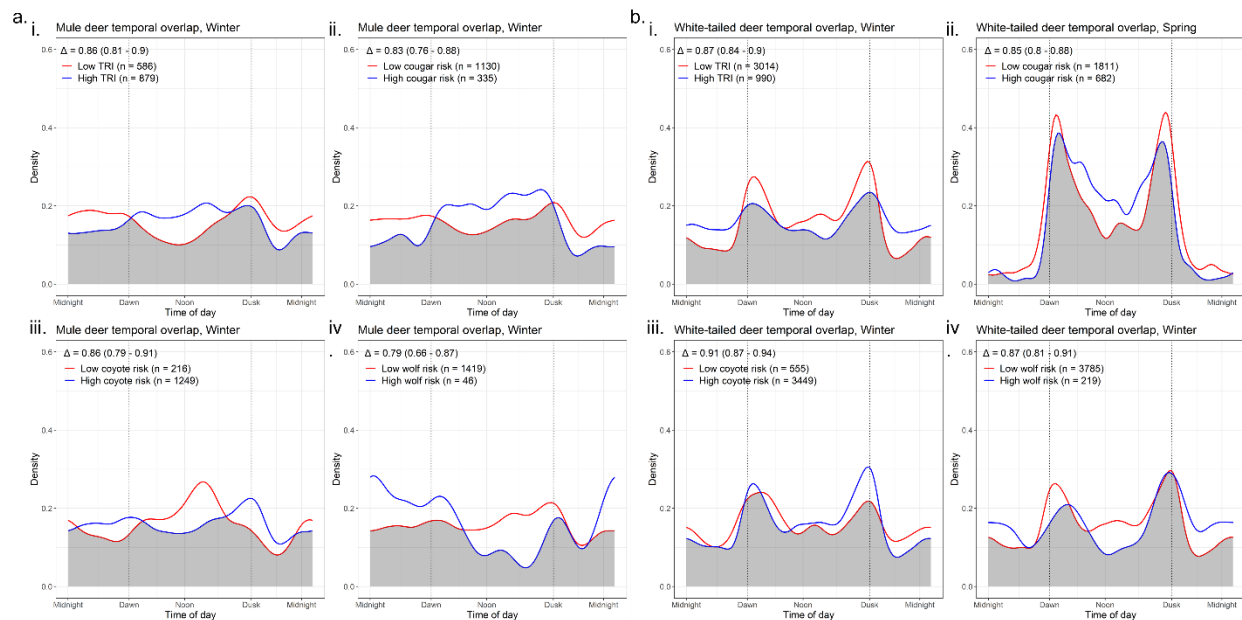


Figure 4.3. Example of overlap plots of differences in diel activity curves for mule deer (a) and white-tailed deer (b) at camera sites with low versus high levels of terrain ruggedness index values (TRI; i) and whether cougars (ii), coyotes (iii) or wolves (iv) were detected at least once (high risk) or never detected (low risk) at a camera site. Differences in activity with respect to cougar detections are presented for white-tailed deer in spring; all other differences are based on

deer activity in winter. The estimated coefficient of overlapping ($\bar{\Delta}$), bootstrapped 95% confidence intervals, and the number of detections (n) per level are reported in each analysis. See Appendix C. S2. Fig. S2.1 for complete set of plots.

Mean predator-prey temporal overlap ($\bar{\Delta}$) varied by species-pair and season (Fig. 4.4; Appendix C. S3: Table S3.2). In general, predator-prey overlap estimates were >0.50 , indicating relatively high overlap of activity curves between species. Temporal overlap between predators and prey did not statistically differ (bootstrapped 95% CIs overlapped) between cameras in areas of low versus high TRI for most pairings, although we note we could not confidently compare temporal overlap estimates for many pairings owing to small sample sizes (Fig. 4.4). When sample size permitted comparison, predator-prey temporal overlap did differ, or trended towards differing, with varying levels of terrain ruggedness for 33% ($n = 11$) of the comparisons made (Appendix C. S3: Table S3.2). Notably, the temporal activity curves of mule deer and black bears, mule deer and coyotes, moose and black bears, and moose and cougars overlapped less where terrain ruggedness was high (Fig. 4.4). The overlap between predators and white-tailed deer activity was more variable with respect to predator species and season (Fig. 4.4). Temporal activity curves for white-tailed deer and bobcats, cougars, and coyotes overlapped less in areas with higher terrain ruggedness in summer (Fig. 4.4). Conversely, temporal activity curves for white-tailed deer and coyotes, and white-tailed deer and cougars, overlapped more in areas with higher terrain ruggedness in fall and winter (Fig. 4.4). Of the overlap estimates that differed by habitat complexity, approximately two thirds (63.6%, $n = 7$) were consistent with our expectation that ungulates would adjust their temporal activity to avoid predators in risky places based on predator hunting mode (e.g., lower temporal overlap between stalking predators and ungulates in more complex habitat; Fig. 4.4). The other third (36.4%, $n = 4$) were inconsistent with our

expectations (e.g., higher temporal overlap between stalking predators and ungulates in more complex habitat). See Appendix C. S3 (Table S2.3) for complete results.

Effect of terrain ruggedness on predator-prey temporal overlap

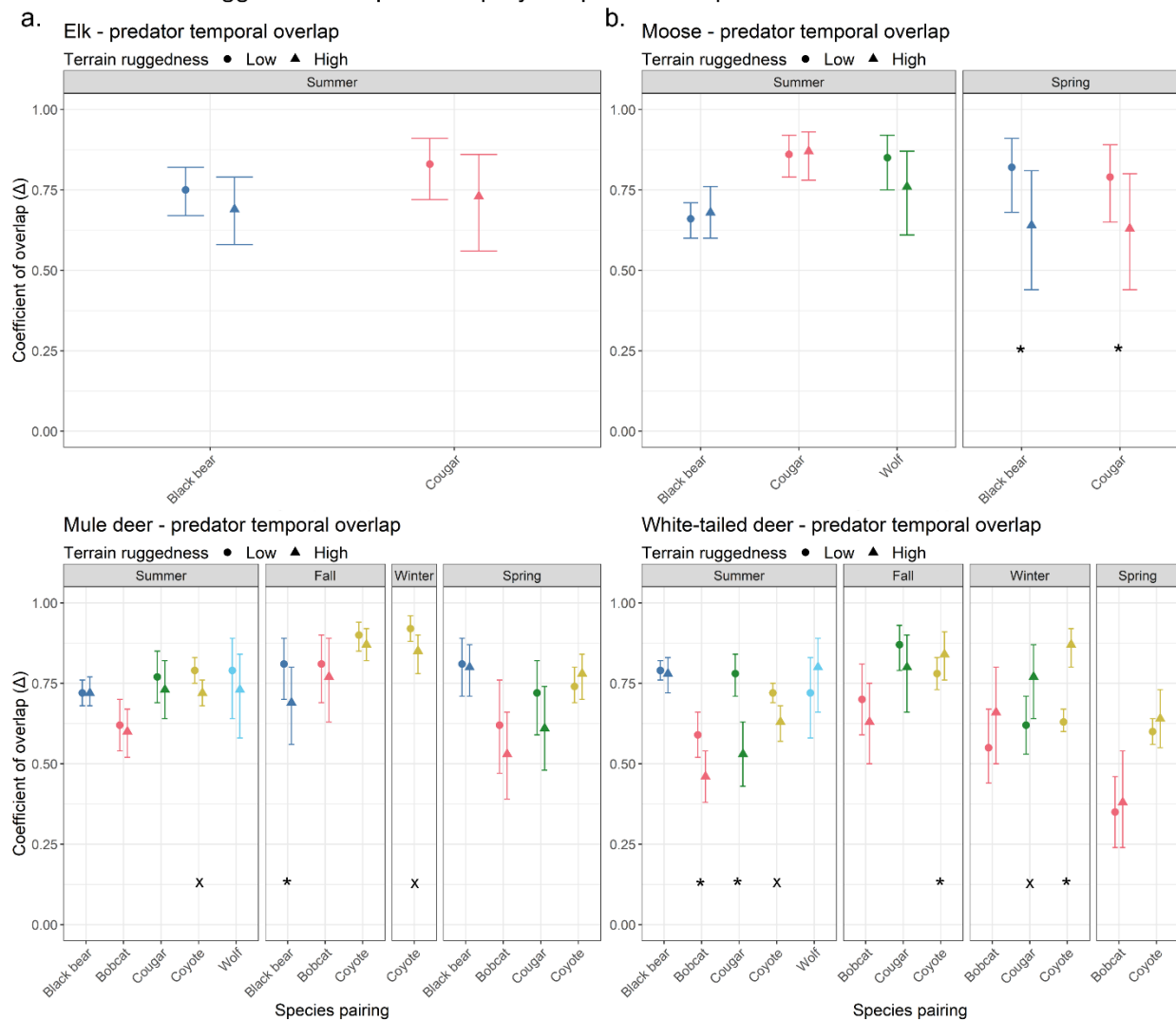


Figure 4.4. Coefficient of overlapping estimates ($\bar{\Delta}$) and bootstrapped 95% confidence intervals (CI) measuring the amount of overlap in diel activity curves between pairs of predators and ungulate prey at camera sites with a low index of terrain ruggedness (TRI) compared to camera sites with a high index of terrain ruggedness in eastern Washington, USA, 2018 – 2021. Temporal overlap was estimated seasonally between predators and elk (a), moose (b), mule deer (c), white-tailed deer (d), respectively, at low and high TRI. Black bears were excluded from winter analyses. The temporal overlap between predators and prey was considered different in areas with low vs high TRI if the bootstrapped 95% CIs did not overlap the coefficient of

overlapping between the two levels of TRI for a given pair of species. Asterisks (*) indicate the differences in temporal overlap were consistent with our expectation that predator-prey overlap would be lower where background risk was higher given the predator's hunting mode; "x" indicates the differences were inconsistent with our expectations.

The differences in predator-prey temporal overlap between areas with low versus high terrain ruggedness were influenced by shifts in both predator and prey diel activity (Fig. 4.5, Appendix C. S3: Fig. S3.2). For example, spring moose activity increased near dawn whereas black bear and cougar activity increased near dusk in areas with higher TRI values, resulting in moose and predators being less active together during the spring where terrain ruggedness was higher (Fig. 4.5). Similarly, summer white-tailed deer activity increased near dawn whereas bobcat, cougar, and coyote activity increased at night in areas with higher TRI values, leading to less temporal overlap between white-tailed deer and predators where terrain was more rugged (Fig. 4.5). In other cases, differences in ungulate activity appeared to more strongly influence whether predators and prey temporally overlapped. For example, white-tailed deer were less crepuscular and more active at night during the winter in areas with higher TRI. Although cougar activity also differed with terrain ruggedness, increased nocturnal activity from white-tailed deer led to greater temporal overlap between white-tailed deer and cougars where terrain was more rugged (Fig. 4.5). Differences in coyote activity were relatively subtle between areas with low and high TRI across seasons, whereas changes in mule deer and white-tailed deer activity (increased diurnal and nocturnal activity, respectively) influenced the extent to which deer and coyotes temporally overlapped with varying levels of terrain ruggedness (Fig. 4.5). See Appendix C. S3 (Fig. S3.2) for complete results.

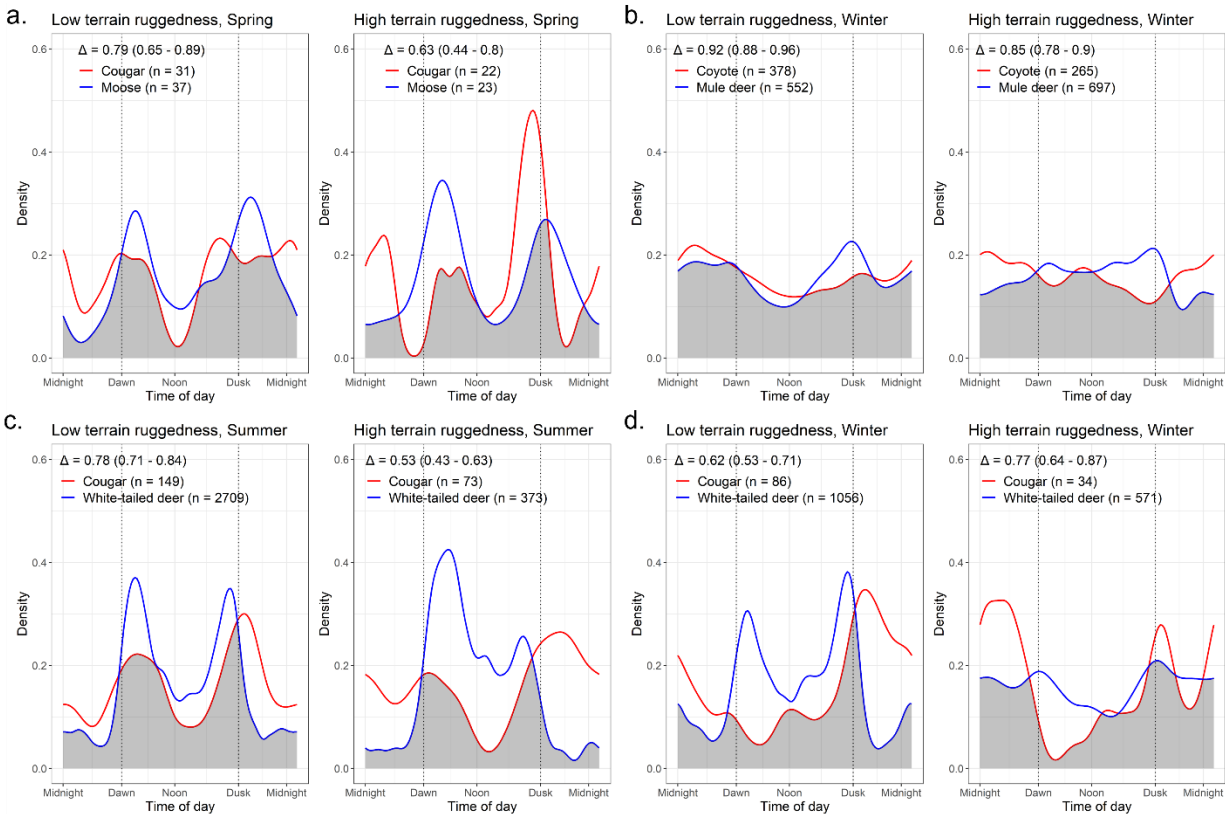


Figure 4.5. Example of temporal overlap plots of paired predator and prey diel activity curves at camera sites with low terrain ruggedness index values (TRI) compared to camera sites with high TRI in eastern Washington, USA, 2018 – 2021. The estimated coefficient of overlapping ($\bar{\Delta}$), bootstrapped 95% confidence intervals, and sample sizes for number of detections of each species (n) are reported for moose – cougar activity in spring (a), mule deer – coyote activity in winter (b), white-tailed deer – cougar activity in summer (c), and white-tailed deer – cougar activity in winter (d) in areas with low and high habitat complexity. See Appendix S2 Fig. S2.2 for complete set of plots.

4.3.3 Risky-times hypothesis: Latency of site-use

The time-between-detections of a predator and ungulate were affected by season and/or predator species for moose, mule deer, and white-tailed deer (see Appendix C. S4: Table S4.1 for full results). Season had the greatest effect on moose latency, most notably the time-between-detections were longer in the winter compared to summer. Mule deer latency was longer

following the detection of a black bear or cougar when compared to that of a bobcat, with cougars having the greatest effect on mule deer latency. The time-between-detections of predators and mule deer were also longer in the winter and spring compared to summer. White-tailed deer latency was longer in the winter and fall compared to summer and positively affected by an interaction between black bears and terrain ruggedness. We did not find an effect of terrain ruggedness, predator species, or season on elk latency.

Species-specific latency of site use at camera traps

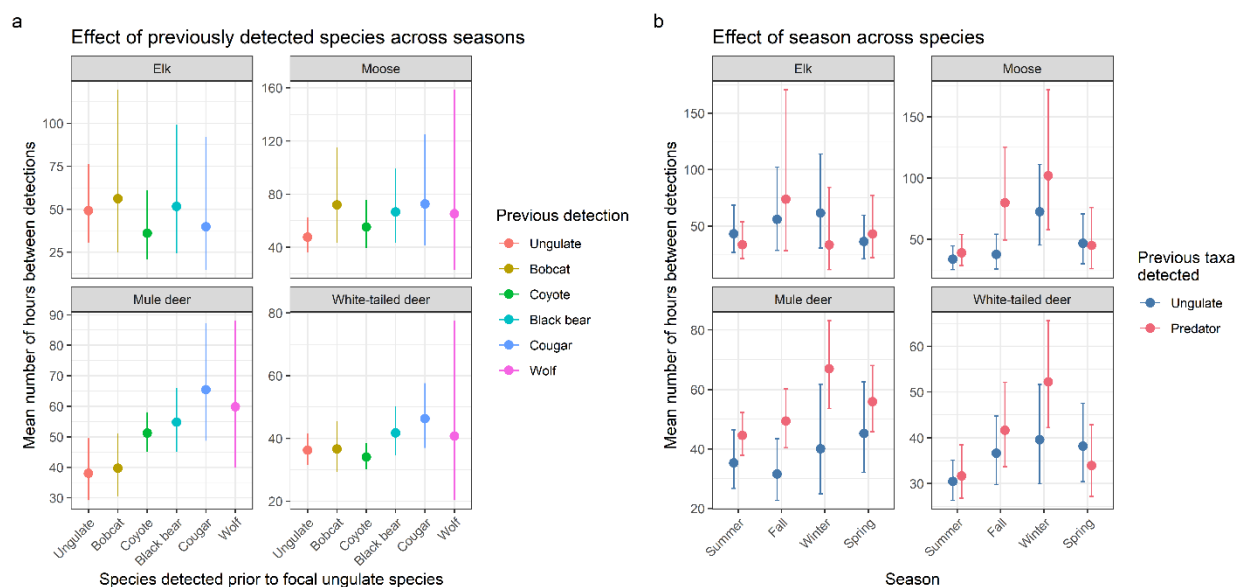


Figure 4.6. Effect of species and season on latency of ungulate detections at camera sites in eastern Washington, USA, 2018 – 2020. Plot panels depict the estimated mean (and 95% Bayesian credible intervals) number of hours between detections of the focal ungulate species (elk, moose, mule deer, or white-tailed deer) following the detection of a different ungulate species or predator species (bobcat, coyote, black bear, cougar, or wolf) when averaged across seasons (a) and the seasonal mean number of hours between detections of predators and ungulate prey or between detections of different ungulate species (b).

The time-between-detections of an ungulate following that of a different ungulate species was affected mostly strongly by the recent presence of another ungulate (see Appendix C. S4: Table S4.2, Fig. S4.1 for full results). Elk latency increased with terrain ruggedness and was

longer following the detection of a moose compared to mule deer. Moose latency was shorter following detections of elk and white-tailed deer compared to mule deer and longer in the winter compared to summer. Mule deer latency was shorter following the detection of moose compared to white-tailed deer. Finally, white-tailed deer latency increased with terrain ruggedness, but declined when moose were most recently detected in more rugged terrain and was longer after elk were detected compared to mule deer.

When averaged across seasons and species, the mean number of minutes between detections of a predator followed by an ungulate prey species were longer than the mean number of minutes between detections of different ungulate species for both moose and mule deer (Appendix C. S4: Table S4.3 and S4.4). Specifically, on average, 3984.13 minutes (95% CRI = 2885.05 - 5589.89 min) elapsed between detections of a moose following that of a predator compared to 2859.95 minutes (95% CRI = 2162.01 - 3763.53 min) between detections of a moose following that of another ungulate species (Appendix C. S4: Table S4.3 and S4.4). On average, 3251.91 minutes (95% CRI = 2800.05 - 3786.39 min) elapsed between detections of a mule deer following that of a predator compared to 2282.31 minutes (95% CRI = 1749.1 - 2970.84 min) between detections of a mule deer following the detection of another ungulate species (Appendix C. S4: Table S4.3 and S4.4). The mean number of minutes between detections of a predator and ungulate did not differ from those between detections of different ungulates for elk and white-tailed deer (Appendix C. S4: Table S4.3 and S4.4). The seasonal mean number of minutes between detections of predators and prey were longer than that of detections between different ungulates for moose and mule deer in the fall and winter, and for white-tailed deer in the winter (Fig. 4.6)

The mean number of minutes between detections of predators and ungulate prey differed by predator species for mule deer and white-tailed deer (Fig. 4.6). Specifically, the mean times between detections of bobcats and mule deer was shorter than that of any other predator and the mean time between detections of cougars or wolves and mule deer trended towards being longer than that of coyotes (Fig. 4.6). The overall mean number of minutes between detections of any ungulate and mule deer were also shorter than that of detections between apex predators, coyotes, and mule deer (Fig. 4.6,). The mean number of minutes between detections of cougars and white-tailed deer was longer than that of bobcats or coyotes and the mean time between detections of black bears was longer than that of coyotes (Fig. 4.6). The overall mean number of minutes between detections of any ungulate and white-tailed deer were shorter, or trending towards shorter, than between cougars and white-tailed deer or black bears and white-tailed deer, respectively (Fig. 4.6). There was no difference in the mean number of minutes between detections of any predator species and elk or moose, although the overall mean number of minutes between detections of any ungulate and moose trended towards being shorter than between detections of apex predators, bobcats, and moose (Fig. 4.6). See Appendix S4 (Tables S4.3, S4.4, and Fig. S4.1) for complete results.

4.4 DISCUSSION

We evaluated the temporal activity patterns of four ungulate species with respect to varying levels of background and immediate risk of predation from five predator species to understand the temporal scales at which prey attempt to reduce predation risk. We found moderate support for the *risky places hypothesis* (Creel et al. 2008), with some ungulates shifting their activity to times when predators were less active at sites where background risk was high. We further found support for the *risky times hypothesis* (Creel et al. 2008), where the recent presence of a predator

influenced the latency of site-use for some ungulates species but the strength of the response varied with season and predator identity. However, the *risky places – risky times hypothesis* (Dröge et al. 2017) was not well supported as we found little evidence of an interaction between habitat complexity and recent predator presence on the time-between-detections of predators and prey. Our results demonstrate extensive interspecific variation in antipredator responses across temporal scales, underscoring the value of considering context dependence and multiple prey species simultaneously when evaluating the non-consumptive effects of predator-prey interactions in multi-predator, multi-prey systems.

4.4.1 *Risky-places*

We expected ungulates to shift their diel activity to reduce exposure to predation risk at camera sites with higher background risk, consistent with the risky places hypothesis. In general, we found little evidence that ungulates adjusted their diel activity in response to habitat complexity or predator site-use alone. When we did find support for this hypothesis, it was due to ungulates shifting their activity in response to predator presence more so than terrain ruggedness. Most notably, we found mule deer becoming more diurnal where cougars were detected and more nocturnal where wolves were detected in winter. Elk in Yellowstone National Park, Wyoming, USA, used risky places at times of day when wolves and cougars were less active, exploiting vacant hunting domains (i.e., the spatiotemporal extent of where and when predators kill prey) over the diel cycle (Kohl et al. 2019). Our definition of “risky places” differed from Kohl et al. (2018, 2019) but our results are consistent with their findings; mule deer were more active during lulls in cougar activity at sites where predation risk from cougars was higher and mule deer were more active when wolves were less active at sites where predation risk from wolves was higher. Adjusting activity patterns according to different predator hunting domains may allow prey to

reduce predation risk while still exploiting risky places in a multi-predator system (Kohl et al. 2019). However, it is difficult to tease apart shifts in prey activity in a multi-predator system, particularly if different predators have divergent but partially overlapping activity patterns, which may explain why we did not see a consistent shift in ungulate activity patterns.

The interactive effect of habitat complexity on predator-prey temporal overlap lent moderate support for the risky places hypothesis. Approximately two thirds of the significant differences in predator-prey overlap were consistent with our expectation that prey would reduce activity in riskier habitats based on a predator's hunting mode. For example, the temporal overlap between white-tailed deer and bobcats or cougars in summer was lower at sites with high levels of habitat complexity (i.e., higher risk from stalking predators) and white-tailed deer – coyote overlap was lower in less complex habitats in fall and winter (i.e., higher risk from coursing predators). In these cases, ungulates reduced their exposure to predation risk by shifting their activity to times when a specific predator was less active in the habitat where that predator's hunting mode was most effective (Kohl et al. 2019, Smith et al. 2019b). Several of the relationships that lent support for the risky places hypothesis involved bobcats or cougars, consistent with our prediction that prey would respond more strongly to stalking predators owing to their more predictable use of specific habitats at predictable times (Preisser et al. 2007, Smith et al. 2019b). In addition, black bear and bobcat predation of adult deer was rare whereas they contributed more substantially to fawn mortalities in our study areas (Ganz et al. 2022). Deer may therefore temporally avoid black bears and bobcats in risky places at times of year when neonates are most vulnerable and these predators pose a more predictable level of risk. Finally, the dual response of white-tailed deer to both cougars and coyotes based on the level of habitat complexity suggests deer are not only responding to risky places, but they are using temporal

avoidance to balance predation risk from multiple predators (Kohl et al. 2019). In combination, these results suggest ungulates temporally respond to the predictability of risky places (Creel et al. 2008) but what constitutes predictable risk appears to be species- and season-specific.

Of the significant differences in predator-prey overlap, ~30% failed to support the risky places hypothesis. In these cases, deer activity tended to be “mismatched” and higher in riskier places. We posit these mismatches may have arisen owing to deer responding to predation risk from multiple predators simultaneously and temporally avoiding the predator that posed the greatest risk (Kautz et al. 2022). For example, white-tailed deer and coyotes were more likely to temporally overlap during the summer in areas of low terrain ruggedness where coursing predators typically have an advantage, inconsistent with our expectations. Yet, at the same time temporal overlap between white-tailed deer, bobcats, and cougars was lower in areas of high terrain ruggedness where stalking predators may be more dangerous. White-tailed deer may have prioritized temporally avoiding stalking predators during the summer, especially cougars who are their primary predator in our system (Ganz 2022), which increased their temporal overlap with predators that posed less of a risk (Dröge et al. 2017). Mule deer – coyote overlap in summer and winter were also inconsistent with our expectations. Yet, mule deer also shifted their activity in winter based on where apex predators (cougars and wolves) were detected, further suggesting deer prioritized temporal avoidance of predators that posed the greatest risk. These results suggest nonintuitive responses to one predator may be related to antipredator responses to another.

4.4.2 *Risky-times*

We found species-specific support for the risky times hypothesis based on our expectation that ungulates would respond to immediate predation risk by increasing the latency of site-use

following a predator detection. Not only was the mean number of minutes between detections of an ungulate following a predator longer than that between detections of an ungulate following another ungulate species, latency of site-use was also affected by the type of predator most recently detected in some cases. Mule deer had the clearest response to recent predator presence with longer latency of site-use after apex predators and coyotes were detected compared to bobcats or other ungulate species. Most notably, it took an average of 25.72 hours longer for mule deer to be detected at a camera site after a cougar detection compared to a bobcat detection. And although the effect was weaker, white-tailed deer were also slower to use a camera site after a cougar was detected compared to other species, taking 9.73 hours longer on average to be detected after a cougar compared to a bobcat. Finally, latency of site use was longer for moose following a predator detection compared to other ungulate species but did not vary by the predator species.

Although these findings generally support our hypothesis that prey would avoid camera sites after a predator was recently present, we expected variation in latency would arise due to differences in predator hunting mode. While latency of site-use for both deer species was longest in response to a stalking predator (cougars) as expected (Preisser et al. 2007), latency was least affected by the other stalking predator (bobcats) in the system, and mule deer avoided wolves almost as much as cougars. Instead, our results suggest that trophic level may have influenced the latency of site-use for deer more than the predator's hunting mode. Mesopredators were not the primary predator of ungulates in our study system (Ganz 2022) whereas deer comprised a large portion of cougar and wolf diets year-round (Satterfield et al. *In prep*). Prey may show stronger antipredator behaviors towards the predator(s) that are the highest risk to them (Thaker et al. 2011, Cremona et al. 2014) which likely explains the stronger avoidance of apex predators

over mesopredators in our study. Dröge et al. (2017) only considered the immediate presence of large predators in their evaluation of prey responses to short- and long-term predation risk so it is unclear whether trophic level influenced prey behavior in their study. However, they found relatively weak support for their prediction that antipredator behaviors would be strongest when in areas frequently used by stalking versus coursing predators (Dröge et al. 2017), consistent with our findings that predator hunting mode was not a strong predictor of delayed site-use.

We failed to find any support for the risky times hypothesis in our elk analysis. Elk may have relied on other antipredator behaviors (e.g., changes in group size; Mao et al. 2005) in response to varying levels of immediate risk as opposed to delaying their use of sites where predators were recently present. Sample size may have further limited our ability to detect an effect of predator presence on the latency of site use by elk. Finally, the time between detections of a predator and any of the ungulate species was on the order of days to weeks. Although we can only speculate on the cues ungulates used to assess the level of immediate predation risk at a camera site (Weissburg et al. 2014), any immediate risk from a predator that was most recently present was on average 1.5 – 2.7 days old by the time an ungulate was detected. Predator scent from urine can persist in the environment for several weeks (Galindo-Aguilar et al. 2022) and can elicit shifts in daily activity patterns (Palmer et al. 2021) and vigilance (Eccard et al. 2017); however, olfactory cues may not be sufficient for ungulates to delay their use of a camera site when the cue is relatively old. Previous studies evaluating ungulate responses to immediate predation risk typically used spatial proximity (e.g., Dröge et al. 2017, Oates et al. 2019), observations of direct encounters with predators (e.g., Dröge et al. 2019), or experimentally manipulated visual or olfactory cues of risk (e.g., Kuijper et al. 2014, Eccard et al. 2017, Palmer

et al. 2021) which are likely better signals of immediate risk than the time since a predator was most recently present.

4.4.3 *Risky places – risky times*

We found little support for the risky places – risky times hypothesis. White-tailed deer were the only species whose latency of site use was influenced by an interaction between habitat complexity and predator species, which we expected if prey responded most strongly to immediate risk in areas with higher background risk of predation (Dröge et al. 2017). However, the mean number of minutes between detections of a white-tailed deer following another ungulate also increased with terrain ruggedness, suggesting the detection rate of white-tailed deer declined with increasing terrain ruggedness regardless of the previous species detected. Instead, both analyses likely reflected reduced white-tailed deer movement in response to increasingly rugged terrain (Chapter 3) and not evidence of background levels of risk mediating antipredator responses to immediate risk.

We defined of background risk based on terrain ruggedness, a habitat feature that we assumed was associated with predator hunting mode and a relatively predictable signal of risk (Atwood et al. 2009). However, others have represented long-term predation risk with utilization distributions for each predator species (e.g., Dröge et al. 2017). Our findings may have differed if we had used a measure of background risk associated with actual predator space-use (e.g., probability of occupancy) and not habitat features associated with hunting behavior.

4.4.4 *Seasonal variation*

Although there was substantial variation in ungulate activity patterns in response to different levels of background and immediate predation risk, we found relatively consistent seasonal

patterns in their responses. Ungulate activity was generally similar between sites with high and low background risk in summer whereas they were more dissimilar in other seasons, especially in winter. This signal may be a product of ungulates temporally avoiding predators at a time of year when ungulates in temperate latitudes are in poorer body condition (i.e., winter) and more vulnerable to predation (Kautz et al. 2020, Olson et al. 2021). Ungulates are more constrained in their ability to spatially avoid predators during nutritionally stressful times (Oates et al. 2019) and may emphasize temporal segregation from predators if they are spatially anchored by access to food or other resources (Smith et al. 2019b).

Season also affected the latency of site-use but in different ways depending on whether an ungulate detection followed that of a predator or a different ungulate species. Latency of site-use increased in winter for moose, regardless of whether a predator or other ungulate species was detected previously. Ungulate movement is typically lower in winter because of reduced mobility in snow and is a strategy to conserve energy during a physiologically stressful time of year (Parker et al. 1984), which may explain this seasonal effect. Immediate predation risk influenced latency of site-use for deer in winter, as the mean number of minutes between detections of a predator and deer were longer than those between different ungulate species. Thus, ungulates appear to avoid predation risk at multiple temporal scales at times of year when they are most vulnerable to predation.

4.4.5 *Conclusion*

Our method of assessing latency of site-use offers a new approach to evaluating avoidance and attraction between different species. Using a generalized linear mixed-effects model to estimate the mean time between detections of species on camera offers a flexible approach for simultaneously testing the effects of multiple variables on the latency of site-use and can be

paired with various model selection techniques to test competing hypotheses. Unlike similar methods (i.e., Parsons et al. 2016, Karanth et al. 2017, Galindo-Aguilar et al. 2022), ours did not require nonparametric approaches to identify statistically significant results. By comparing the mean time between detections of predators and prey to those of different ungulates, we were able to parametrically compare across a combination of biologically meaningful interspecific interactions simultaneously.

Our results provide context-dependent support for the risky places and risky times hypotheses. The strength of the temporal responses to background and immediate risk levels varied by ungulate species, predator species, predator hunting mode, and season. Although we found most ungulates responded to risky places and risky times to varying degrees, white-tailed deer responded more consistently to risky places, mule deer responded most strongly to risky times, moose responded seasonally, and we found little evidence that elk responded temporally at all. In addition, ungulate responses to risky places were generally influenced by habitats or times of day associated with a predator's hunting mode whereas responses to risky times appeared more related to trophic level and the predator species that were most dangerous. These results add further weight to the risky places and risky times hypotheses (Creel et al. 2008); ungulates shifted daily activity in response to predictable cues of risk associated with predator hunting mode whereas they responded more strongly to the more dangerous predators when risk was less predictable risk. In sum, interspecific variation in ungulate responses to varying levels of background and immediate predation risk resulted a complex combination, and seemingly inconsistent, suite of antipredator behaviors (Wirsing et al. 2021), making it challenging to predict behavioral responses to risk in our multi-predator, multi-prey system. Our study demonstrates the importance of incorporating the full predator guild (Montgomery et al. 2019,

Prugh et al. 2019) and multiple prey species at once to more accurately capture the complexity and context-dependence of predator-prey interactions in natural systems (Wirsing et al. 2021).

Our results demonstrate that ungulates adjusted their activity patterns in response to a combination of habitat variability and predator species. Terrain ruggedness is not the only way to represent habitat complexity, however, and considering other measures of habitat (e.g., vegetation structure) would create a more complete picture of the temporal responses to background and immediate risk of predation. Lastly, humans often pose real or perceived threats to ungulates, potentially altering predator-prey relationships and antipredator behaviors (Lone et al. 2017). Human activity may push predators and prey into closer spatiotemporal overlap, potentially limiting prey's ability to temporally avoid predators in human-dominated landscapes (Gaynor et al. 2018). Thus, considering anthropogenic influences on predator-prey interactions can shed further light on how prey balance predation risk from multiple sources.

4.5 BIBLIOGRAPHY

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Chapter 5. ANTHROPOGENIC IMPACTS ON SPATIAL AND TEMPORAL OVERLAP OF PREDATORS AND PREY IN EASTERN WASHINGTON, USA

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Abstract: Livestock grazing and hunting by humans occur across large tracks of land in western North America but whereas their impacts on individual species are well studied, their effects on predator-prey interactions are less understood. We evaluated how cattle and hunter activity influenced the co-occurrence and daily activity patterns of five large predator (black bear [*Ursus americanus*], bobcat [*Lynx rufus*], cougar [*Puma concolor*], coyote [*Canis latrans*], and gray wolf [*C. lupus*]) and four ungulate prey species (elk [*Cervus canadensis*], moose [*Alces alces*], mule deer [*Odocoileus hemionus*], and white-tailed deer [*O. virginianus*]) in eastern Washington, USA, from 2018 – 2020. We hypothesized anthropogenic activities would influence predator-prey co-occurrence patterns depending on whether predators and ungulates avoided anthropogenic disturbance and mortality risk or were attracted to potential food subsidies. And we further hypothesized that both predators and prey would shift their diel activity patterns to temporally avoid anthropogenic activity. We fit multi-species occupancy models and kernel density estimators to photo-capture data collected during the grazing (July – Sept) and hunting (Oct – Nov) seasons to test our spatial and temporal hypotheses, respectively. We found cattle activity, hunter activity,

and land use associated with grazing and hunting influenced many species-specific occurrence probabilities and activity patterns but few co-occurrence probabilities. When anthropogenic activities did influence patterns of spatiotemporal overlap, ungulates were generally more likely to use areas associated with cattle grazing whereas predator responses varied. Ungulates generally avoided public land during the hunting season but were also more likely to co-occur with predators on public land. Finally, predators increased nocturnal activity where anthropogenic activity occurred whereas ungulate temporal responses were less marked. Our results demonstrate that species-specific responses to anthropogenic activities are diverse and create nuanced patterns of spatiotemporal overlap between predators and prey. And in some cases, cattle and hunter activity may help prey win the predator-prey response race, underscoring the importance of considering anthropogenic effects on predator-prey interactions. *Keywords:* Activity patterns, cattle, co-occurrence, grazing allotments, hunting, predator-prey, public access, public land, refugia, response race

5.1 INTRODUCTION

The non-consumptive effects of predator-prey interactions can structure food webs through varying behavioral responses that occur across a range of spatial and temporal scales (Wirsing et al. 2021). Predators engage in behaviors to increase the likelihood of encountering and catching prey (Balme et al. 2007, Cresswell et al. 2010) and prey, in turn, may engage in antipredator behaviors to avoid detection or capture by predators (Gorini et al. 2012). These behaviors lead to a “response race” that can shape the spatiotemporal distribution of an entire community of species in ways that depend on whether predator or prey responses dominate the interaction (Sih 1984, 2005).

Where predation risk is relatively predictable across space or time, prey may proactively shift their space use or timing of activity to minimize overlapping with predators (Kohl et al. 2018, Wirsing et al. 2021). For instance, buffalo (*Syncerus caffer*) and kudu (*Tragelaphus strepsiceros*) in Addo Elephant National Park, South Africa, were more diurnal when they spatially co-occurred with nocturnal predators (e.g., African lion; *Panthera leo*; Tambling et al. 2015). Conversely, predator space use often mirrors areas of higher prey densities or patches of resources preferred by prey, particularly when prey are mobile and relatively unpredictable in space (Flaxman and Lou 2009). Predators can also match their daily activity patterns to those of their main prey, likely to reduce energy expenditure while hunting (Foster et al. 2013, Azevedo et al. 2018). Behavioral responses in this “race” between predators and prey are often species-specific and interacting species may segregate on one niche axis (space or time) when high overlap occurs on the other (Kohl et al. 2019, Galindo-Aguilar et al. 2022). Understanding the non-consumptive effects of predator-prey interactions therefore requires careful consideration of both spatial and temporal overlap among interacting species.

Predator-prey interactions do not exist in a vacuum, however, and many wildlife live in human-dominated landscapes where anthropogenic land use and activities have the potential to affect species interactions through bottom-up and top-down processes (Muhly et al. 2013, Dorresteijn et al. 2015). In some systems, human activity alters predator space-use or activity patterns, creating spatiotemporal refuges for prey where and when human activity is high (e.g., human shield; Berger 2007, Muhly et al. 2011, Kautz et al. 2022). But anthropogenic disturbances can also impact the space-use and temporal activities of prey (Gaynor et al. 2018), sometimes increasing their spatiotemporal overlap with nocturnal predators (Bonnot et al. 2020) and altering predation risk (Lendrum et al. 2018). The spatiotemporal responses of wildlife to

humans are often species-specific and vary with the type of disturbance (Harris et al. 2019), creating complex patterns of predator-prey overlap among wildlife communities in human-dominated landscapes.

Livestock grazing and outdoor recreation, especially hunting, are two economically, environmentally, and socially important anthropogenic activities that occur globally and impact wildlife (Arnett and Southwick 2015, Erb et al. 2016). In the western United States, summer grazing activities are typically concentrated on public lands when cattle (*Bos taurus*), sheep (*Ovis aries*), and other domestic animals are turned out on public grazing allotments and leases for several months (Morehouse and Boyce 2011). The U.S. Forest Service (USFS) alone manages livestock grazing on more than 102 million acres of national grasslands and forest for over 2 million head of livestock nationally (United States Forest Service 2017). Conversely, hunting activities are concentrated during the fall where public and private lands are hunted to varying degrees (U.S. Department of the Interior et al. 2018). For instance, 90% of hunters in Washington State reported hunting on public lands in the past 3 years, 66% of whom hunted on lands managed by the USFS (Responsive Management 2022). As a result, grazing and hunting both occur at varying intensities on public and private lands within seasonally restricted time periods, creating spatiotemporally predictable patterns of anthropogenic disturbance that may affect wildlife communities and species interactions.

The effects of livestock grazing on wildlife communities have long been debated but the ultimate outcomes are often specific to the ecosystem, species, and grazing regime (Schieltz and Rubenstein 2016). In general, livestock grazing tends to have the strongest effects on species that rely on the vegetation consumed or trampled by livestock (Schieltz and Rubenstein 2016, Filazzola et al. 2020). Studies of livestock-wild ungulate interactions, for example, have

generally found wild ungulates spatially or temporally avoid areas grazed by livestock, particularly when livestock are currently present and the species compete for shared resources (Coe et al. 2004, Feng et al. 2021, Liu et al. 2022). Livestock grazing can also affect higher trophic levels directly, when livestock become prey for predators (Morehouse and Boyce 2011, Ciucci et al. 2020), or indirectly, when predators are displaced due to altered habitat, loss of native prey, or human-carnivore conflict (Filazzola et al. 2020). Thus, if both predators and prey avoid areas where livestock are present, or if predators track the distribution of their prey (Laundré et al. 2010) when prey avoid livestock, we might expect the spatial overlap of predators and prey to increase in areas where less grazing occurs. However, if predators are attracted to livestock, predator and prey distributions may be less correlated or even inversely related.

The effects of human hunters on predators and prey are equally complex. Hunted species respond to perceived mortality risk from hunters with a number of antipredator behaviors (Marantz et al. 2016) that have the potential to influence interspecific interactions. For example, wild ungulates appear to respond to human hunters more strongly than to wild predators (Lone et al. 2017, Bonnot et al. 2020, Gaynor et al. 2022), and often use spatial refugia created by variation in land ownership (e.g., public versus private lands) to spatially avoid risky places during the hunting season (Proffitt et al. 2016, Visscher et al. 2017, Sergeyev et al. 2022). Similarly, hunted species may increase their activity at times when hunting is prohibited (e.g., nighttime) to minimize hunting risk (Oriol-Cotterill et al. 2015, Gaynor et al. 2022). As a result, spatiotemporal overlap between predators and prey may increase if they employ similar strategies to avoid hunters. Alternatively, food subsidies provided by human hunters (i.e., gut piles and wounding loss) may attract predators to areas where hunting occurs (Rodewald et al.

2011, Singh et al. 2021), which may result in spatial decoupling of predators and prey during the hunting season.

Although the effects of grazing and hunting have been studied extensively with respect to individual species responses and some community dynamics (e.g., Madsen and Fox 1995, Vavra 2005), their effects on predator-prey interactions are less understood. Patterns of spatial and temporal overlap between predators and prey influence risk effects, encounter rates, and capture success, all of which influence predator-prey population dynamics (Sih 2005). When wildlife adjust their space-use or diel activity in response to anthropogenic activities, such as livestock grazing or hunting, they have the potential to alter the non-consumptive effects of predator-prey interactions or the predation sequence itself, both of which can scale to demographic consequences for predator-prey communities (Suraci et al. 2022). Thus, understanding the effects of grazing and hunting on spatial and temporal patterns of predator-prey interactions may help decision makers manipulate predator-prey dynamics through anthropogenic activities, which can be more easily managed than the wildlife populations themselves.

The relatively intact wildlife community in eastern Washington, USA, provides an opportunity to explore how patterns of predator-prey overlap are affected by livestock and hunting. Eastern Washington is a human-dominated, mixed-used landscape characterized by a matrix of publicly managed and privately-owned lands. Using camera trap data collected over three summer grazing and fall hunting seasons (2018 – 2020), we assessed the effects of cattle and hunter activity on predator-prey co-occurrence and activity patterns among five predator species (black bear [*Ursus americanus*], bobcat [*Lynx rufus*], cougar [*Puma concolor*], coyote [*Canis latrans*], and wolf [*C. lupus*]) and four wild ungulate species (elk [*Cervus canadensis*], moose [*Alces alces*], mule deer [*Odocoileus hemionus*], and white-tailed deer [*O. virginianus*]).

We tested three hypotheses related to how these anthropogenic activities influence spatiotemporal overlap of predators and prey. First, hypothesized that predator-prey co-occurrence patterns are affected by human-mediated effects on prey distributions. Under this hypothesis, we expected the co-occurrence of predators and prey to decline in areas with anthropogenic activities and associated land uses owing to ungulate competition with cattle and mortality risk from hunters. Alternatively, we hypothesized that predator-prey co-occurrence patterns might be affected by predator responses to anthropogenic food subsidies (e.g., calves in the grazing season, remains of harvested ungulates in the hunting season). In this case, we expected predators and prey to positively co-occur and for their co-occurrence to increase where predators were attracted to anthropogenic activities, though we still expected ungulates to generally avoid anthropogenic activities. Lastly, we hypothesized that predators and prey would temporally avoid cattle or hunters if they could not spatially avoid them. This hypothesis predicts the diel activity patterns of both predators and prey to shift to times when cattle and human hunters are less active, resulting in greater overlap of predator-prey activity patterns where these anthropogenic activities occur.

5.2 METHODS

5.2.1 *Study areas*

We collected data across two study areas in eastern Washington, USA, from June 2018 – May 2021 (Fig. 5.1). The Northeast study area (4,535 km²; -117.7193, 48.28302) lay between the Pend Oreille and Columbia Rivers and was characterized by climatic and topographic gradients of the southern Selkirk and Huckleberry Mountains (elevation ranging 378 – 2079 m; Williams et al. 1995). Mean annual temperatures ranged -2.4° C in January to 19.2° C in July in Chewelah, WA; mean annual precipitation was 52.3 cm (Western Regional Climate Center 2016, National

Oceanic and Atmospheric Administration 2021). The vegetative community was dominated by Douglas fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), ponderosa pine (*Pinus ponderosa*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*; Williams et al. 1995). The Northeast study area comprised Washington Department of Fish and Wildlife (WDFW) Game Management Units (GMU) 117 and 121 and was predominantly owned and managed by individual property owners and industrial timber companies (77%), although about 23% of the study area fell within the Colville National Forest, the Little Pend Oreille National Wildlife Refuge, and other federally and state managed lands (Esri 2018). The spatial configuration of property ownership resulted in a mosaic of smaller parcels of intermixing public and private properties.

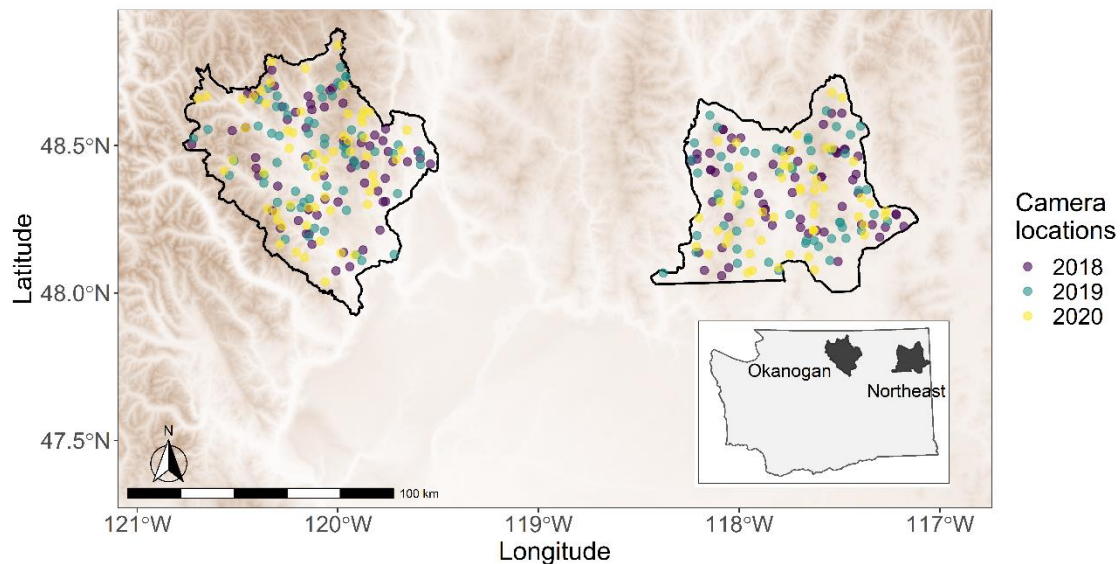


Figure 5.1. Locations of camera traps randomly deployed each year across the Okanogan and Northeast study areas in eastern Washington, USA, 2018 – 2020, plotted against the elevational gradient where darker shades represent higher elevations.

The Okanogan study area (5,300 km²; -120.1096, 48.42966) lay between the Okanogan River and the North Cascade Range and was characterized by topographically rugged and mountainous terrain with deep valleys and steep slopes (elevation ranging 225 – 2790 m; Williams and Lillybridge 1983). Mean annual temperatures ranged -3.2° C in January to 20.3° C in July in Winthrop, WA; mean annual precipitation of 36.1 cm (National Oceanic and Atmospheric Administration 2021). Forests were dominated by mixtures of Douglas fir, Engelmann spruce (*Picea engelmannii*), lodgepole pine (*P. contorta*), ponderosa pine, and subalpine fir (*A. lasiocarpa*; Williams and Lillybridge 1983), whereas open regions were dominated by big sagebrush (*Artemisia tridentata*) and antelope bitterbrush (*Purshia tridentata*). The Okanogan study area was comprised of WDFW GMUs 218, 231, 224, 233, 242, and 239 and was predominantly managed by the U.S. Forest Service (USFS; 64%), although approximately one-third was privately owned and managed by individual landowners (32%; Esri 2018). Private property was concentrated in the lower elevation valleys, resulting in relatively large tracks of unbroken public and private land in the Okanogan study area.

Public grazing of cattle and hunting activities were generally confined to specific annual time periods and parcels of land. Cattle grazing on public land occurred April – October, although the duration and number of cattle present varied over the course of the grazing season as cattle were rotated through grazing allotments (J. Rohrer, U.S. Forest Service, *pers. comm.*). Most public grazing occurred in the Okanogan study area on grazing permits managed by the USFS, the Washington Department of Natural Resources (WDNR), and the WDFW (WDNR 2019, WDFW 2021, USFS2022). Grazing permits are typically issued for 10 years where grazing re-occurred on an annual basis (USFS 2005) so we assumed grazing allotments represented long-term forage quality associated with grazing. The fall hunting season occurred

September – mid-December, although species-specific hunting seasons varied by study area and GMU (WDFW 2021b). The majority of deer and elk harvest occurred during modern firearm hunting seasons, mid-October through mid-November (WDFW 2018, 2021b). Moose were harvested October – November with a special permit in the Northeast study area (WDFW 2021b). Black bears, bobcats, cougars, and coyotes were harvested with any weapon throughout the fall hunting season (WDFW 2021b). Wolves were protected by state and federal law and could not be harvested at any time (WDFW et al. 2022). Hunter participation was highest during the modern firearm seasons whereas participation was lower and more diffuse during fall archery and muzzleloader seasons (WDFW 2018). Hunting was generally allowed across public lands and lands owned by private timber companies whereas public hunting access was prohibited on most private properties (although landowners could hunt their own properties and allow access to individual hunters who requested permission).

5.2.2 *Camera data*

We deployed 120 motion-sensing trail cameras (Model HyperFire2 Pro; Reconyx, Holmen, WI, USA) to monitor randomly selected sites in the Northeast ($n = 55$) and Okanogan ($n = 65$) study areas annually (Fig. 5.1). Cameras were first deployed in June 2018 and were maintained for one year, at which point they were redeployed to new random locations in June 2019 and again in June 2020, resulting in a total of 360 unique sites being monitored for one year each. We used a stratified random sampling design based on elevation to select camera trap locations (O’Connell and Bailey 2011). We created 4 elevation bands, excluding areas above 2,100m to avoid sampling difficult to access alpine habitat which is used less by the study species. We overlaid a 1 km² grid across each study area and randomly selected grid cells within each elevation strata by selecting the number of cells proportional to the amount of land area within each stratum per

study area. Within 250 m of the centroid of each selected cell, we placed one un-baited camera, targeting linear features that would funnel animal movement and increase the likelihood of detecting lower density species (e.g., large carnivores; Cusack et al. 2015, Tanwar et al. 2021). We recorded the type of linear feature being monitored (i.e., unpaved road, decommissioned road, human-use trail, or game trail), whether the camera was deployed on publicly accessible land (e.g., state or federally managed land), and which study area the camera was deployed in. All camera programming details reported in Bassing et al. (2022).

We labeled photo-capture data using the Microsoft AI for Earth machine learning algorithm (“MegaDetector”; Beery et al. 2019) and program Timelapse2 (Greenberg 2019). The MegaDetector indicated whether an animal, human, or vehicle was present in each image. Two technicians then independently reviewed images and recorded the species of all individual animals detected in each image; a third technician reconciled the independent datasets and reconciled any differences. We also recorded if cattle or humans were detected and whether humans on-foot were rifle hunting or bow hunting (i.e., carrying a rifle or bow) in each image. We then reduced the image set to a series of independent detection events for each species of interest. We considered a detection event to be independent when ≥ 30 -minutes had elapsed between the last image of a species and the next image of that same species at a camera (O’Brien et al. 2003, Sollmann 2018).

5.2.3 *Anthropogenic activity and environmental variables*

We tested the effects of four anthropogenic variables on predator-prey spatiotemporal overlap: cattle activity, hunter activity, camera placement on public grazing allotments, and camera placement on publicly accessible land. Because cattle and hunter activity can be represented numerous ways in camera trap data, we generated 4 metrics of activity and evaluated the

correlation among these metrics before choosing which to include in our analyses. For each week during the grazing and hunting seasons we recorded 1) the sum of individual images of cattle or hunters generated at a camera site, 2) the sum of independent detection events of cattle or hunters at a camera site, 3) the sum of the maximum number of individuals counted in a single image per independent detection event at a camera site, and 4) the sum of minutes that elapsed during independent detection events at a camera site. We tested the correlation among the 4 measures of weekly activity using a Pearson's correlation test and considered 5, 10, 30, and 60-minute intervals to define an independent detection event. We found all metrics were highly correlated (correlation coefficient ranged $\rho = 0.95 - 0.98$) when we used 5-minute intervals and the correlation decreased as the elapsed time between detection events increased. We therefore used the weekly sum of independent detection events (metric #2) based on 5-minute intervals to represent weekly cattle and hunter activity at each camera to be consistent with our overall definition of independent detection events. We then summed across weekly cattle and hunter activity, respectively, to generate a single, site-level, measure of cattle and hunter activity for each camera site. We standardized the site-level activity metrics by the number of days each camera was operable to account for sampling effort, resulting in an average number of cattle or hunter detections per day at each site. Lastly, we used the USFS livestock grazing allotment layer (USFS 2022) and maps of grazing leases and permits on Washington State lands (WDNR 2019, WDFW 2021a) to identify whether each camera was deployed on an active USFS, WDFW, or WDNR grazing allotment. We used this binary variable to represent recurring annual grazing that occurred at a broader spatial scale than the immediate vicinity of each camera (i.e., "long-term" cattle activity). Similarly, we used the binary classification of whether cameras were deployed on private (0) or public (1) land to represent broad-scale hunter activity. Although

parcels owned by timber companies were privately owned, most companies allowed public access during the hunting season, so we considered cameras on timberlands to be on “public” land for the purposes of our analyses.

We accounted for spatial variation in habitat features that are known to influence species occurrence patterns in our study system (Bassing et al. 2022). We extracted the elevation in meters at each camera site from the Shuttle Radar Topography Mission (SRTM) 30 m resolution digital elevation model (DEM; Farr et al. 2007). We calculated the percentage of forest habitat within 250 m of each camera site using annual landcover data from the Cascadia Biodiversity Watch TerrAdapt:Cascadia tool (30 m resolution; <https://cascadiapartnerforum.org/terradapt>). We reclassified annual landcover raster data into two landcover types (forest and not forest) and used a moving window analysis in Program R version 4.2.1 (R Core Team 2022) to calculate the percent of landcover classified as forest within a 250 m radius of each camera site. Lastly, we included binary variables representing whether each camera was deployed in the Northeast (0) or Okanogan (1) study area and whether each camera was deployed on a trail (0; game or human-use) or road (1; open or decommissioned). We checked for collinearity and centered and scaled all continuous variables before including them in our analyses.

5.2.4 *Multispecies occupancy models*

We used a single-season, multispecies occupancy model for two or more interacting species (Rota et al. 2016) to assess the effects of cattle and hunter activity on predator-prey co-occurrence. In its simplest form, an occupancy model uses detection/non-detection data to estimate the probability that ≥ 1 individuals of a species occurs at a site while accounting for imperfect detection of that species (MacKenzie et al. 2002). Multispecies occupancy models build on this original model by including detection data of two or more species and explicitly

modelling the dependence between them (Rota et al. 2016). Although numerous two-species and multispecies occupancy models are available (briefly reviewed by Kéry and Royle 2021:457-459), the Rota et al. (2016) multispecies occupancy model offers several advantages that make it well suited for estimating the effects of anthropogenic activity on co-occurrence patterns of multiple species in a wildlife community. Namely, it can accommodate more than two interacting species in a single model, does not assume asymmetric interactions (e.g., a dominant and subordinate species), does not require the estimation of additional parameters (e.g., “Species Interaction Factor” [SIF]; Mackenzie et al. 2004), and can incorporate the effects of covariates on the probability of co-occurrence (Rota et al. 2016). To this last point, covariate effects are expressed in terms of first-order conditional occupancy probabilities (e.g., the probability of species 1 occurring, given species 2 is absent) and higher order interactions between species (e.g., the non-independent pairwise probability of occupancy for two species; Rota et al. 2016, Kéry and Royle 2021). It should also be noted that despite modeling “interactions” among ≥ 2 species, this model can only estimate statistical associations or non-independence among species, not true biotic interactions. As a result, while we tested a priori hypotheses about possible biological mechanisms underlying predator-prey co-occurrence patterns, these models do not demonstrate causation (Sells et al. 2018, Kéry and Royle 2021).

We included $S = 2$ species in each multispecies occupancy model. We considered all pairwise predator-prey combinations for the three large carnivores (black bear, cougar, wolf) and four ungulates (elk, mule deer, moose, white-tailed deer). We paired the two mesocarnivores with the two deer species only because bobcats and coyotes were not common predators of elk or moose in our system (T. Ganz, University of Washington, *pers. comm.*). This resulted in 16 pairwise predator-prey combinations. We consolidated all independent detection events (based

on ≥ 30 -minute intervals) for each of the 2 species into binary response variables where each species was either detected (1) or not detected (0) at a given camera site during each 7-day sampling period. We focused our grazing season analyses between July and September after plotting histograms to identify the peak timeframe when cattle were detected on camera. We focused our hunting season analyses between October and November because hunter participation was at its highest and most species were legally harvestable within this timeframe (WDFW 2018, 2021b). This generated 13 7-day sampling occasions for the grazing season (1 July – 29 Sept) and eight 7-day sampling occasions for the hunting season (1 Oct – 30 Nov). We combined data from all years of sampling into a single detection history for each species and season (grazing and hunting season [2018, 2019, 2020], respectively). We then reduced the two single-species detection histories into one 2-species detection history representing the 4 different possible states: 00, 10, 01, 11. This parameterization of the multispecies occupancy model is conceptually similar to a multi-state occupancy model where states are classified by the presence or absence of each species (Kéry and Royle 2021). Thus, the probability of occupancy corresponds to 2^S possible latent occupancy states (i.e., whether species were truly present or absent).

We modeled the 16 pairwise species interactions during two different time periods – the summer grazing season and the fall hunting season. We started with a separate global model for each seasonal analysis. For the grazing season model, we included the effect of trail type, weekly cattle activity, and the binary variable representing whether public grazing was permitted on detection probability. We included the effects of study area, elevation, elevation-squared, percent forested habitat, site-level cattle activity, and the public grazing variable on the first-order conditional occupancy parameters. We also allowed the second-order interaction term to differ

from 0 (i.e., assumed co-occurrence was non-independent) and let this interaction vary with site-level cattle activity and public grazing (Table 5.1). This model tested species-specific responses to immediate (cattle activity) and broad-scale (public grazing allotments) impacts of cattle, as well as how these variables influence predator-prey co-occurrence. We followed a similar global model structure for the hunting season analysis but applied hunter activity and whether public hunter access was permitted to the detection, occurrence, and co-occurrence parts of the model instead of cattle activity and public grazing allotments (Table 5.1). The global model failed to converge for some species pairs, owing to the lower detection probabilities for the large carnivores or because most predator detections occurred on public land during the hunting season (except black bears). When this occurred, we used a piecewise approach to reducing model complexity. When the binary public land variable failed to converge, we removed it from the predator occurrence part of the model first, then from the prey occurrence part of the model. We followed the same procedure if the mean daily hunter activity variable converged poorly. Last, we removed variables from the second order interaction, and then set the interaction to 0 (essentially assuming co-occurrence was independent), if necessary.

Table 5.1. The linear predictors fit to the detection and occurrence parameters for each multispecies occupancy model using detection/non-detection data for $S = 2$ species (1 predator, 1 prey) collected during the grazing season (1 July – 29 Sept) and hunting season (1 Oct – 30 Nov) in eastern Washington, 2018 – 2020. Variables used to estimate species-specific detection probability (p_1 , p_2) included trail type (trail = 0; road = 1), weekly cattle activity, weekly hunter activity, whether each camera was deployed on a public grazing allotment (no public grazing permitted = 0; public grazing permitted = 1), and whether each camera was deployed on public land (private land = 0; publicly accessible land = 1). Variables used to estimate the log odds of the probability that only species s occurred at a camera site (or 1st-order interactions: f_1 , f_2) included study area (Northeast = 0; Okanogan = 1), elevation, percentage of forest habitat within 250 m of the camera, site-level cattle activity and hunter activity (average number of cattle or

hunter detections per day over the entire grazing/hunting season, respectively), and whether cameras were on grazing allotments during the grazing season and public land during the hunting season. Variables used to estimate the log odds of the probability that both species occurred together (or 2nd-order interactions; f_{12}) included site-level cattle activity, grazing allotments, site-level hunter activity, and public land.

Season	Sub-model	Parameters	Linear model [†]
Grazing	Detection	p_1, p_2	$\alpha_{0s} + \alpha_{1s} * \text{Trail} + \alpha_{2s} * \text{WeeklyCattleActivity} + \alpha_{3s} * \text{GrazingAllotment}$
Grazing	Conditional occupancy	f_1, f_2	$\beta_{0s} + \beta_{1s} * \text{StudyArea} + \beta_{2s} * \text{Elevation} + \beta_{3s} * \text{Elevation}^2 + \beta_{4s} * \text{Forest} + \beta_{5s} * \text{CattleActivity} + \beta_{6s} * \text{GrazingAllotment}$
Grazing	2 nd -order interaction	f_{12}	$\gamma_{0s} + \gamma_{1s} * \text{CattleActivity} + \gamma_{2s} * \text{GrazingAllotment}$
Hunting	Detection	p_1, p_2	$\alpha_{0s} + \alpha_{1s} * \text{Trail} + \alpha_{2s} * \text{WeeklyHunterActivity} + \alpha_{3s} * \text{PublicLand}$
Hunting	Conditional occupancy	f_1, f_2	$\beta_{0s} + \beta_{1s} * \text{StudyArea} + \beta_{2s} * \text{Elevation} + \beta_{3s} * \text{Elevation}^2 + \beta_{4s} * \text{Forest} + \beta_{5s} * \text{HunterActivity} + \beta_{6s} * \text{PublicLand}$
Hunting	2nd order interaction	f_{12}	$\gamma_{0s} + \gamma_{1s} * \text{HunterActivity} + \gamma_{2s} * \text{PublicLand}$

[†]HunterActivity and PublicLand covariates were excluded from models for select species pairs when they could not be estimated owing to most predator detections occurring on public land where most hunting activity was detected on camera.

We fit all models with the unmarked package (Fiske and Chandler 2011) in Program R 4.2.1 (R Core Team 2022). We considered covariates that were significant (p-value ≤ 0.05) and trending towards significant (p-value ≤ 0.1) for interpretation. Lastly, because camera traps

sample a small area across continuous space, we interpreted our results as asymptotic occupancy, or the probability that species would *use* a camera site at some point during our study period (Efford and Dawson 2012).

5.2.5 *Temporal analyses*

We used the *Overlap* package (Meredith and Ridout 2017) in Program R 4.2.1 (R Core Team 2022) to assess how cattle and hunter activity influenced the temporal co-occurrence of predators and prey. Detection times over the 24-hr cycle are circular and their underlying density may be bimodal (e.g., for crepuscular species; Ridout and Linkie 2009). We therefore converted the clock time of each detection to radial time, while accounting for changes in day length by scaling the time of day to sunrise and sunset (Nouvellet et al. 2012, Meredith and Ridout 2017). We then sorted all independent detection events (based on ≥ 30 -minute intervals) from the grazing season into groups based on whether the detections came from camera sites where cattle were or were not detected and whether public grazing was permitted. Similarly, we grouped detections from the hunting season based on whether hunters were detected at the site and whether detections occurred at cameras on publicly accessible land. Pooling data can bias overlap estimates high so caution is needed when combining data across study areas (Ridout and Linkie 2009, Meredith and Ridout 2017). Whereas hunting activity and publicly accessible lands were distributed across both study areas, most of the grazing activity occurred in the Okanogan study area (82% of cameras with cattle detections were in the Okanogan). We therefore considered the effects of cattle activity and public grazing allotments on predator-prey temporal overlap using only data from the Okanogan study area.

We used nonparametric kernel density estimates to quantify the density of detections of a given species over a 24-hour cycle, thus estimating their diel activity curves (Ridout and Linkie

2009). We estimated the coefficient of overlapping ($\bar{\Delta}$), i.e., the proportion of the area where two kernel density curves overlap, for each of the 16 pairwise predator-prey combinations for each type of anthropogenic activity where it was and was not detected (e.g., overlap between cougar and elk activity curves at cameras where hunters were detected vs. where hunters were not detected). To gain a better understanding of how individual species influenced these temporal overlap patterns in response to different anthropogenic activities, we also estimated the coefficient of overlapping for each species by comparing species-specific activity curves at camera sites where an anthropogenic activity did and did not occur (e.g., overlap between cougar activity curves at sites where hunters were and were not detected). We used the Δ_1 estimator to measure the coefficient of overlapping when the sample size of the smaller of the two curves was <50 detections and the Δ_4 estimator when the sample size was ≥ 50 detections (Meredith and Ridout 2017). An overlap value of 0 indicated no overlap in activity curves whereas a value of 1 indicated complete overlap in activity curves (Ridout and Linkie 2009). We used 10,000 smoothed bootstrapped samples to estimate the 95% confidence interval (CI) for each overlap estimate and reported the basic 95% CI, which adjusts the CI for bootstrap bias (Meredith and Ridout 2017). We repeated these analyses using detection data from sites where public grazing and public hunting were permitted vs not permitted, respectively. We considered the predator-prey overlap estimates under varying levels of anthropogenic activity to be significantly different if the 95% bootstrapped CIs did not overlap each other and interpreted these when evaluating anthropogenic impacts on predator-prey activity patterns.

5.3 RESULTS

5.3.1 *Camera data*

A total of 349 and 342 camera traps were active during the grazing and hunting seasons, yielding 27,359 and 18,432 trap nights, respectively. During the grazing season, the cameras generated on average 494.46 (SE = 120.60) independent detection events (≥ 30 -minute intervals) per wildlife species and 794.67 (SE = 223.26) detections (≥ 5 -minute intervals) of cattle (Appendix S1: Table S1.1). During the hunting season, the cameras generated on average 281.04 (SE = 76.59) independent detection events per wildlife species and 267.67 (SE = 77.50) detections (≥ 5 -minute intervals) of hunters on foot (Appendix D. S1: Table S1.1). Weekly cattle activity ranged 0 – 101 independent detections per week during the grazing season, whereas weekly hunter activity ranged 0 – 52 independent detections per week during the hunting season.

5.3.2 *Multi-species occupancy models*

We found little evidence that cattle activity or grazing allotments influenced spatial co-occurrence of predators and prey during the summer grazing season. Namely, the only second-order interactions influenced by mean daily cattle activity were between cougars and white-tailed deer and between coyotes and white-tailed deer (Table 5.2). For the cougar-white-tailed deer interaction, cattle activity positively influenced co-occurrence but had a moderately negative effect on cougar occurrence when deer were absent (p-value = 0.06; Table 5.2). As a result, cougars and white-tailed deer were more likely to occur together as cattle activity increased at a camera site, whereas cougars were less likely to use a site as cattle activity increased when white-tailed deer were absent (Fig. 5.2a). Mean daily cattle activity had a negative effect on second-order coyote-white-tailed deer interactions but had an even greater positive effect on

coyote and white-tailed deer occurrence conditional on the other being absent (Table 5.2). Thus, coyotes and white-tailed deer were less likely to use a site together as cattle activity increased but had a higher probability of using a camera site with increasing cattle activity when the other species was absent (Fig. 5.2b). Bobcats and mule deer, and coyotes and mule deer, were also more likely to occur at sites together as cattle activity increased, although these relationships were weaker (p -values = 0.09 and 0.08, respectively; Table 5.2). We found no difference in co-occurrence patterns between sites where public grazing was and was not permitted (Table 5.2).

Table 5.2. Subset of estimated coefficients and standard errors (SE) for the effects of grazing predictors on the log odds of the probability that a predator (1st-order natural parameters: f_1) or prey (1st-order interactions: f_2) species used a camera site in the absence of the other and on the log odds of the probability that both species used a camera site together (2nd-order interactions: f_{12}) during the grazing season in eastern Washington, USA (1 July – 29 Sept, 2018 – 2020). The mean number of weekly cattle detections (cattle activity) and whether cameras were deployed on public grazing allotments were included in all natural parameters to evaluate how cattle grazing influenced occurrence and co-occurrence of predators and prey. Bolded estimates and SE indicate the predictor was significant (p-value ≤ 0.05) or trending towards significant (p-value ≤ 0.1)[†]. Significant 2nd-order intercepts (f_{12}) indicate predator-prey co-occurrence was non-independent. The intercepts and habitat predictors included in the 1st-order natural parameters are not shown for simplicity, but complete model results are presented in the supplemental materials (Appendix D. S2: Table S2.2). Lands where public grazing was not permitted in the Okanogan study area represent the intercepts. NAs indicate the predictor was excluded owing to poor convergence.

	f_1 : Grazing		f_2 : Grazing		f_{12} :	f_{12} : Grazing	
	f_1 : Cattle	allotment	f_2 : Cattle	allotment	Intercept	f_{12} : Cattle	allotment
Predator: prey pairing	activity (SE)	(SE)	activity (SE)	(SE)	(SE)	activity (SE)	(SE)
Black Bear: Elk	0.58 (0.51)	0.91 (0.46)	-3.17 (7.94)	1.62 (1.55)	1.75 (2.00)	2.99 (7.95)	-1.22 (1.62)
Black Bear: Moose	0.64 (0.53)	0.86 (0.46) [†]	0.44 (0.33)	1.41 (0.57)	0.12 (0.46)	NA	NA
Black Bear: Mule Deer	0.64 (0.81)	-0.31 (0.82)	-0.05 (1.01)	-0.79 (0.69)	0.48 (0.52)	0.06 (1.01)	1.30 (0.86)
Black Bear: White-tailed Deer	0.26 (0.72)	0.93 (0.49) [†]	0.50 (1.06)	-0.08 (0.89)	0.67 (0.53)	0.55 (1.08)	-0.06 (0.98)
Bobcat: Mule Deer	-0.16 (0.34)	-0.13 (0.81)	-0.55 (0.40)	-0.07 (0.55)	0.06 (0.53)	0.85 (0.50) [†]	0.54 (0.83)

Bobcat: White-tailed Deer	0.99 (0.57)[†]	0.26 (0.53)	1.60 (0.56)	-0.07 (0.47)	0.81 (0.59)	-0.89 (0.59)	-0.12 (0.70)
Cougar: Elk	0.25 (0.31)	0.49 (0.72)	0.12 (0.34)	2.02 (1.05)	0.77 (0.95)	-1.56 (1.41)	-2.05 (1.26)
Cougar: Moose	0.43 (0.40)	0.51 (0.73)	0.24 (0.40)	1.78 (0.80)	0.66 (0.64)	-0.34 (0.46)	-0.60 (0.94)
Cougar: Mule Deer	0.51 (0.80)	0.60 (1.24)	0.56 (0.79)	0.25 (0.84)	-0.16 (0.65)	-0.54 (0.82)	-0.16 (1.10)
Cougar: White-tailed Deer	-1.37 (0.72)[†]	0.78 (0.73)	0.48 (0.38)	0.27 (0.57)	0.82 (0.71)	1.77 (0.78)	-0.82 (0.95)
Coyote: Mule Deer	-0.05 (0.25)	0.18 (0.57)	-0.59 (0.40)	-0.01 (0.55)	0.82 (0.40)	0.76 (0.44)[†]	0.26 (0.64)
Coyote: White-tailed Deer	1.80 (0.83)	0.22 (0.38)	2.50 (0.86)	-0.31 (0.58)	0.70 (0.50)	-1.75 (0.84)	0.24 (0.61)
Wolf: Elk	-0.65 (0.61)	-0.58 (0.66)	-0.18 (0.20)	0.56 (0.60)	-0.25 (0.63)	NA	NA
Wolf: Moose	-0.66 (0.61)	-0.61 (0.66)	0.45 (0.33)	1.44 (0.57)	0.18 (0.60)	NA	NA
Wolf: Mule Deer	-0.33 (0.80)	-0.99 (1.10)	0.07 (0.18)	-0.07 (0.56)	-1.62 (1.21)	-0.67 (1.17)	0.28 (1.13)
Wolf: White-tailed Deer	-0.82 (0.96)	-0.35 (0.81)	1.00 (0.32)	0.00 (0.42)	-0.03 (0.89)	0.36 (1.19)	-0.59 (1.11)

[†]Indicates p-value between 0.05 and 0.1.

Although cattle activity and grazing allotments did not appear to influence co-occurrence between most species, they did affect conditional occupancy and detection probability for some species. The probability that white-tailed deer used a site increased with increasing cattle activity, conditional on predators (bobcats, coyotes, and wolves) being absent (Table 5.2). Cattle activity also trended toward having a positive effect on bobcat occurrence when white-tailed deer were absent (p-value = 0.09; Table 5.2). In addition, moose were more likely to use public grazing allotments, conditional on predators (black bears, cougars, and wolves) being absent from the site, elk were more likely to use public grazing allotments where cougars were absent, and black bears were more likely to use public grazing allotments where ungulates (elk, moose, and white-tailed deer) were absent, although the effect was only moderate in the bear-moose and bear-white-tailed deer models (p-values = 0.06; Table 5.2). The probability of detecting coyotes increased with increasing weekly cattle activity whereas detection probability for moose decreased as weekly cattle activity increased (Appendix D. S2: Table S2.1). Where public grazing was permitted, bobcats were more likely to be detected whereas deer were less likely to be detected (Appendix D. S2: Table S2.1). Effects of the environmental predictors on species-specific conditional occupancy and detection probabilities were variable but generally consistent with expected wildlife-habitat associations for this region (Appendix D. S2). Study area and elevation were the most commonly significant predictors of species-specific occurrence and trail type influenced detection probability; predators and moose were more detectable on roads whereas mule deer were more detectable on trails (Appendix D. S2: Table S2.1, S2.2).

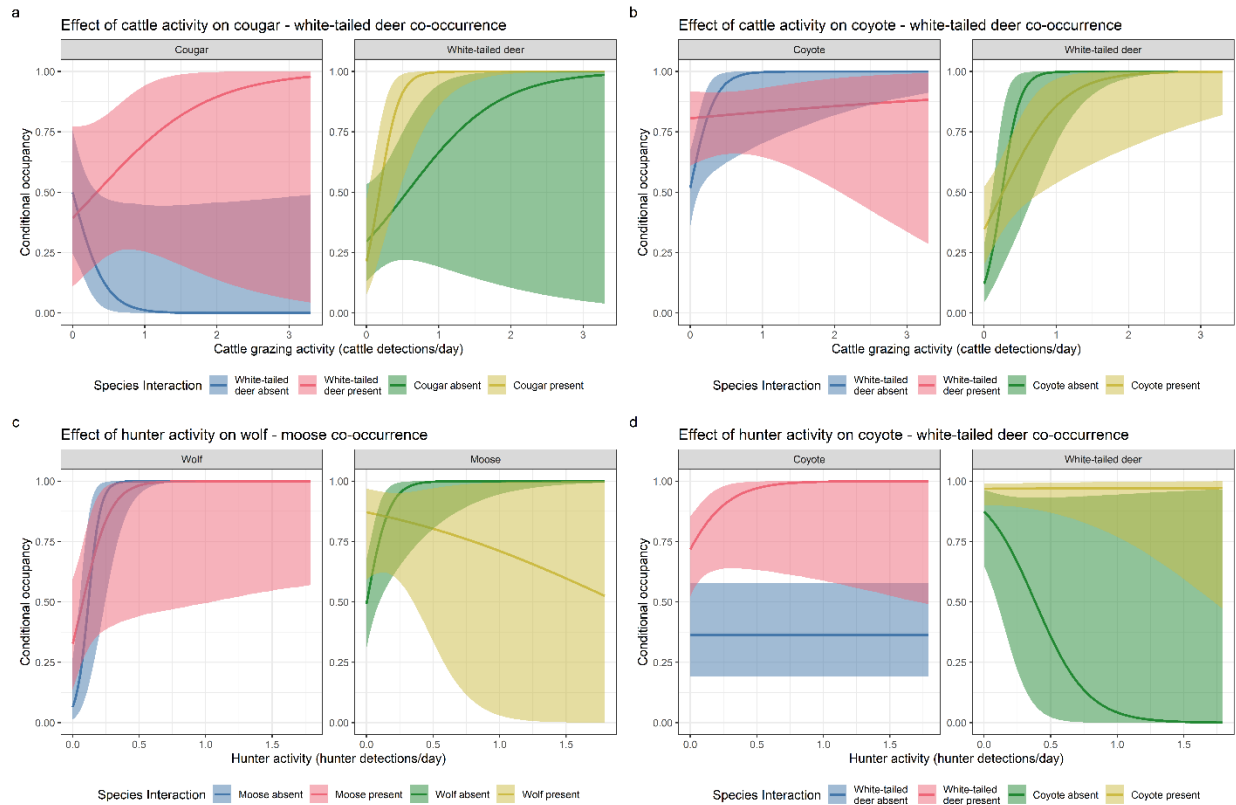


Figure 5.2. Conditional occupancy plots for predator-prey interactions during the summer grazing and fall hunting seasons in eastern Washington, USA, 2018 – 2022. Top: cougar and white-tailed deer (a) and coyote and white-tailed deer responses (b) to cattle activity when the interacting species was present (pink/yellow) and absent (blue/green) at a camera site. Bottom: wolf and moose (c) and coyote and white-tailed deer (d) responses to hunter activity (mean hunter detections per day at a camera site) when the interacting species was present (pink/yellow) and absent (blue/green) at a camera site.

We found evidence of dependent co-occurrence between predators and prey during the fall hunting season for several species-pairings, primarily with respect to landownership. Public land had a significant, positive, effect on the co-occurrence of bobcats and mule deer, cougars and mule deer, and cougars and white-tailed deer, indicating positive dependency between these species on public land, although white-tailed deer were less likely to use public land conditional on predators being absent (Table 5.3). Mule deer were also less likely to use public land when

cougars were absent, although the effect was weak (p -value = 0.09; Table 5.3). Public land trended towards having a significant negative effect on coyote – white-tailed deer co-occurrence (p -value = 0.06), but after accounting for the large positive intercept, our results indicated coyotes and white-tailed deer did co-occur on public land, but the strength of the effect was relatively weak compared to other species-pairings (Table 5.3).

Hunter activity further influenced the spatial overlap of two predator-prey pairings during the fall hunting season. Mean daily hunter activity had a negative effect on the second-order interaction between wolves and moose, but it positively influenced wolf and moose site use when the other species was absent (Table 5.3). As a result, wolves and moose were less likely to occur together as hunter activity increased but both were more likely to use a camera site with increasing hunter activity when the other species was absent (Table 5.3; Fig. 5.2c). In addition, hunter activity trended towards having a positive effect on the second-order interaction between coyotes and white-tailed deer (p -value = 0.08), which was further influenced by whether coyotes and white-tailed deer were on public land (p -value = 0.06; Table 5.3). Coyotes and white-tailed deer were more likely to occur together as mean daily hunter activity increased (Fig. 5.2d), although their co-occurrence was lower on publicly accessible land (Table 5.3). White-tailed deer were less likely to use a site with increasing hunter activity when coyotes were absent (Table 5.3; Fig. 5.2d).

Table 5.3. Subset of estimated coefficients and standard errors (SE) for the effects of hunting predictors on the log odds of the probability that a predator (1st-order interactions: f_1) or prey (1st-order interactions: f_2) species used a camera site in the absence of the other and on the log odds of the probability that both species used a camera site together (2nd-order interactions: f_{12}) during the hunting season in eastern Washington, USA (1 Oct – 30 Nov, 2018 – 2020). The mean number of weekly hunter detections (hunter activity) and whether a camera was deployed on public land were included in all natural parameters to evaluate how hunting influenced occurrence and co-occurrence of predators and prey. Bolded estimates and SE indicate the predictor was significant (p-value ≤ 0.05) or trending towards significant (p-value ≤ 0.1)[†]. Significant 2nd-order intercepts (f_{12}) indicate predator-prey co-occurrence was non-independent. The intercepts and habitat predictors included in the 1st-order natural parameters are not shown for simplicity, but complete model results are presented in the supplemental materials (Appendix D. S2: Table S2.4). Public land in the Okanogan study area represented the intercepts. NAs indicate the predictor was excluded owing to poor convergence.

	f_{12} :						
	f_1 : Hunter	f_1 : Public	f_2 : Hunter	f_2 : Public	Intercept	f_{12} : Hunter	f_{12} : Public
Predator: prey pairing	activity (SE)	land (SE)	activity (SE)	land (SE)	(SE)	activity (SE)	land (SE)
Black Bear: Elk	0.16 (0.18)	NA	0.14 (0.45)	NA	1.9 (1.07)	-0.14 (0.52)	NA
Black Bear: Moose	NA	0.37 (0.86)	NA	0.85 (0.73)	0.35 (0.63)	NA	NA
Black Bear: Mule Deer	-0.29 (0.43)	0.13 (1.27)	-0.35 (0.30)	-0.31 (0.76)	0.5 (1.14)	0.55 (0.50)	0.52 (1.15)
Black Bear: White-tailed							
Deer	0.23 (0.26)	0.11 (1.05)	0.13 (0.28)	-1.13 (0.66)[†]	-0.71 (1.03)	-0.25 (0.38)	0.46 (1.10)

Bobcat: Mule Deer	1.88 (0.94)	1.19 (0.68)[†]	0.04 (1.30)	0.30 (0.63)	-0.26 (1.02)	-0.06 (1.33)	-0.73 (1.00)
Bobcat: White-tailed Deer	NA	NA	0.01 (0.20)	-1.68 (0.65)	-0.16 (0.70)	-0.09 (0.28)	1.75 (0.70)
Cougar: Elk	-0.08 (0.19)	NA	0.06 (0.22)	NA	NA	NA	NA
Cougar: Moose	-0.08 (0.19)	NA	0.32 (0.16)	NA	NA	NA	NA
Cougar: Mule Deer	NA	NA	-0.01 (0.2)	-1.47 (0.87)[†]	-1.63 (1.33)	-0.2 (0.22)	3.16 (1.30)
Cougar: White-tailed Deer	NA	NA	-0.02 (0.19)	-1.6 (0.62)	-1.16 (1.06)	-0.03 (0.29)	2.06 (0.81)
Coyote: Mule Deer	1.22 (0.45)	NA	-0.12 (0.18)	NA	0.16 (0.45)	NA	NA
Coyote: White-tailed Deer	NA	NA	-0.69 (0.40)[†]	-0.23 (0.64)	1.7 (0.59)	0.69 (0.39)[†]	-0.85 (0.46)[†]
Wolf: Elk	1.13 (0.46)	NA	0.06 (0.44)	NA	-0.03 (0.90)	0.00 (0.50)	NA
Wolf: Moose	3.04 (0.85)	NA	1.62 (0.63)	NA	1.42 (0.78)	-1.76 (0.72)	NA
Wolf: Mule Deer	1.02 (0.42)	NA	-0.37 (0.33)	NA	1.94 (0.83)	0.13 (0.38)	NA
Wolf: White-tailed Deer	1.16 (0.45)	NA	0.07 (0.28)	NA	-0.22 (0.91)	-0.19 (0.37)	NA

[†]Indicates p-value between 0.05 and 0.1.

Hunter activity and land ownership also influenced conditional occupancy and detection probability for many species. When mean daily hunter activity was included in the model, the probability that bobcats, coyotes, and wolves used a site increased with increasing hunter activity, conditional on ungulates being absent (Table 5.3). Similarly, hunter activity was positively associated with moose occurrence when predators (cougars and wolves) were absent (Table 5.3). The effect of land ownership was excluded from conditional occupancy for most predator species, though public land had a moderately positive effect on bobcat occurrence when mule deer were absent (p -value = 0.08) and a moderately negative effect on mule deer and white-tailed deer occurrence when black bears and cougars were absent, respectively (p -values = 0.09; Table 5.3). We found no evidence that weekly hunter activity affected detection probability for any species (Appendix D. S2: Table S2.3). Conversely, bobcats, coyotes, cougars, mule deer, and white-tailed deer all had lower detection probability on public land compared to private land during the hunting season (Appendix D. S2: Table S2.3). In the cases where we could not fit the public land effect to conditional occupancy owing to few detections on private land, these results suggest predators were unlikely to use private land but when they did use private land, they were more detectable. Only moose had higher detection probability on public land during the hunting season (Appendix D. S2: Table S2.3). Finally, the effects of the environmental predictors on species-specific conditional occupancy and detection probabilities during the hunting season were generally consistent with those in the grazing season (Appendix D. S2: Table S2.3, S2.4).

Livestock grazing and hunting effects on predator-prey diel activity overlap

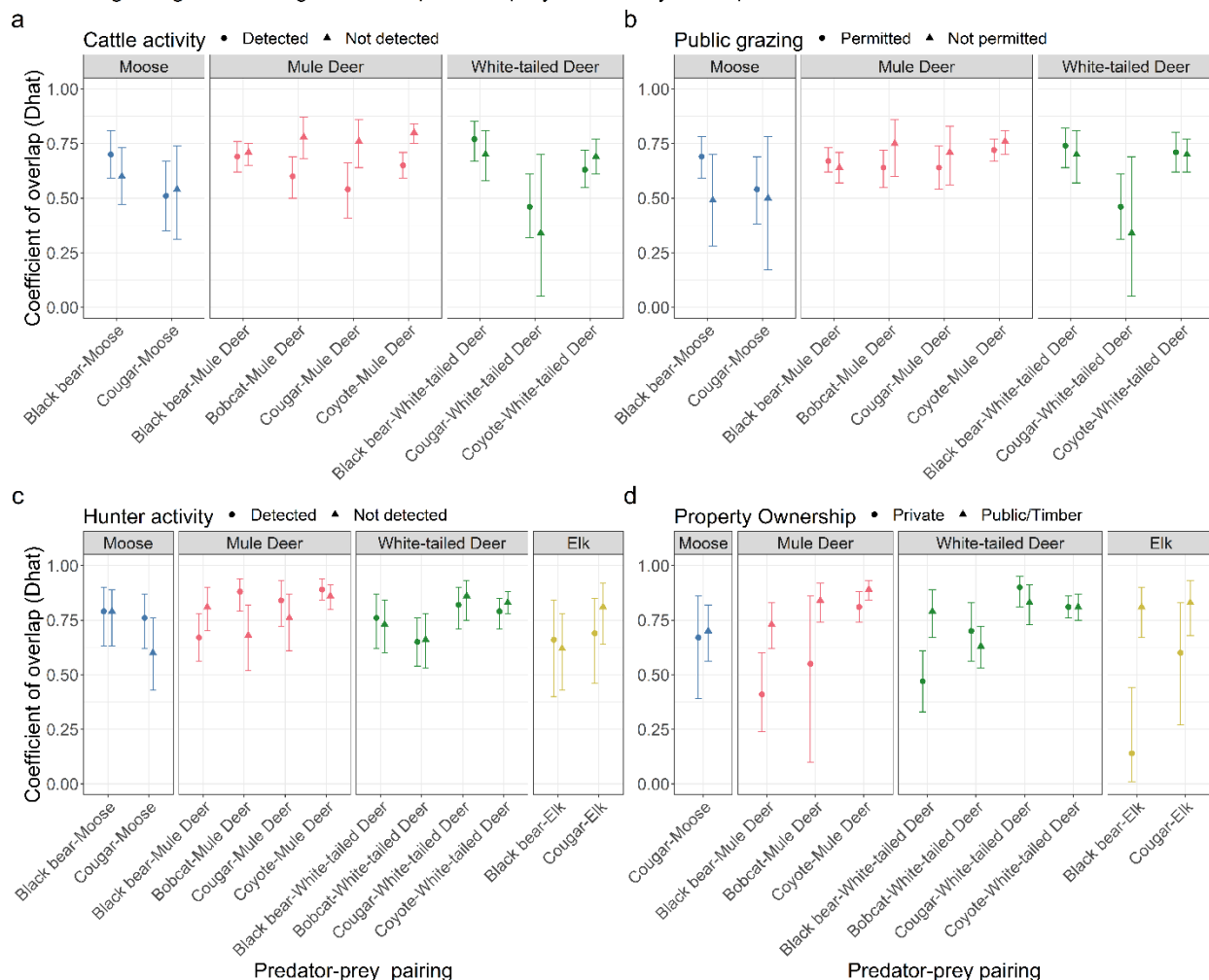


Figure 5.3. Coefficient of overlapping estimates ($\bar{D}_{hat}$) and bootstrapped 95% confidence intervals (CI) measuring the amount of overlap in diel activity curves between pairs of predators and ungulate prey at camera sites with contrasting levels of anthropogenic activity or land use in the grazing season (1 July – 29 Sept) and hunting season (1 Oct – 30 Nov) in eastern Washington, USA, 2018 – 2021. Figure panels show $\bar{D}_{hat}$ and 95% CIs for each predator-prey pairing comparing the temporal overlap of predator and prey activity curves at sites where cattle were detected to temporal overlap at sites where cattle were not detected (a), predator-prey overlap at sites on grazing allotments compared to sites where public grazing is not permitted (b), predator-prey overlap at sites where hunters were detected compared to sites where hunters were not detected (c), and predator-prey overlap on public land compared to private land (d). Some coefficients of overlapping could not be estimated owing to too few detections of some species under different levels of anthropogenic activity.

5.3.3 *Temporal analyses*

During the grazing season, mean predator-prey temporal overlap ($\bar{\Delta}$) was 0.63, ranging $\bar{\Delta} = 0.34 - 0.80$. Mule deer were the only prey species for which estimates of predator-prey temporal overlap were statistically different in response to whether cattle activity was detected at a camera site (Fig. 5.3). For mule deer and bobcats, cougars, and coyotes, all three pairings had higher measures of temporal overlap at camera sites where cattle were not detected compared to sites where cattle were detected, indicating predator and prey activity patterns were more similar where cattle were not present (Fig. 5.3 and 5.4, Appendix D. S3: Fig. S3.1). Most estimates of species-specific temporal overlap were also relatively high with respect to cattle activity (Appendix D. S3: Fig. S3.2), although bobcat ($\bar{\Delta} = 0.77$ [95% CI = 0.62 – 0.87]), cougar ($\bar{\Delta} = 0.78$ [95% CI = 0.63 – 0.89]), and white-tailed deer ($\bar{\Delta} = 0.76$ [95% CI = 0.67 – 0.83]) coefficients of overlap suggested greater changes in activity patterns at sites where cattle were detected (Appendix D. S3: Fig. S3.2). Notably, bobcats became more nocturnal, cougars increased activity at dusk, and white-tailed deer became more diurnal at sites where cattle were detected compared to where they were not (Fig. 5.5, Appendix D. S3: Fig. S3.3). In comparison, none of the estimates were statistically different when comparing predator-prey temporal overlap at sites where public grazing was and was not permitted (Fig. 5.3, Appendix D. S3: Fig. S3.1, S3.3). Estimates of species-specific temporal overlap were relatively similar across species and indicated only moderate differences ($\bar{\Delta}$ ranged 0.59 – 0.92) in species-specific activity patterns where public grazing was permitted compared to where it was not (Appendix D. S3: Fig. S3.2). Moose and wolf activity differed the most where public grazing was permitted, although the temporal overlap estimates for wolves were based on relatively small sample size ($n = 25$). Moose activity shifted from a single peak post-dawn to a more crepuscular activity pattern ($\bar{\Delta} =$

0.73 [95% CI = 0.55 – 0.85]) and wolf activity increased in the morning and decreased in the evening at sites where public grazing was permitted ($\bar{\Delta} = 0.59$ [95% CI = 0.32 – 0.81]; Appendix D. S3: Fig. S3.3).

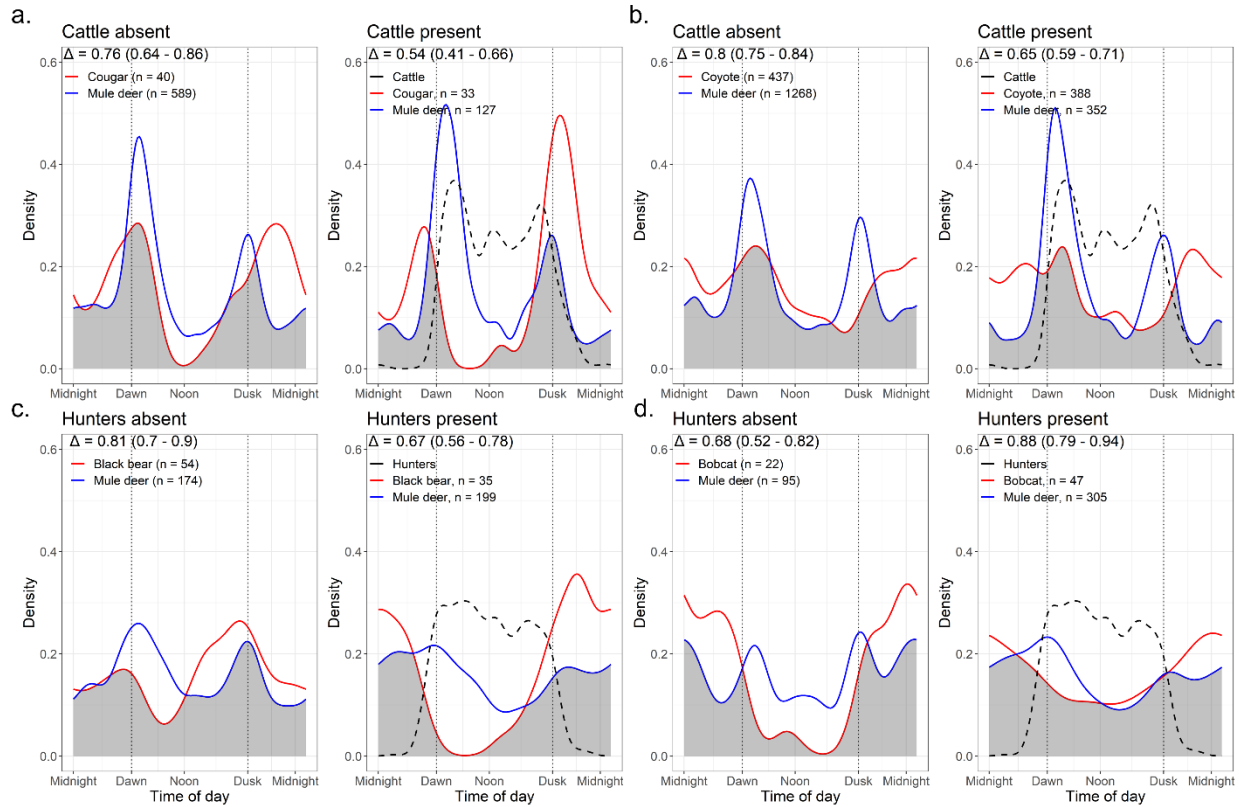


Figure 5.4. Examples of diel activity curves, coefficient of overlapping estimates ($\bar{\Delta}$), and 95% bootstrapped confidence intervals (95% CI) measuring the percentage of overlap between diel activity patterns of predators and prey in response to cattle and hunter activity in eastern Washington, USA, 2018 – 2020. Figure panels compare temporal overlap of predators and prey at camera sites where cattle were and were not detected during the grazing season (1 July – 29 Sept) for cougars and mule deer (a) and coyotes and mule deer (b) and temporal overlap of predators and prey at camera sites where hunters were and were not detected during the hunting season (1 Oct – 30 Nov) for black bear and mule deer (c) and bobcat and mule deer (d). Complete set of predator-prey overlap curves are presented in Appendix D. S3: Fig. S3.1, S3.2.

During the hunting season, mean predator-prey temporal overlap ($\bar{\Delta}$) was 0.72, ranging $\bar{\Delta} = 0.14 – 0.90$. We found little evidence that hunter activity at a camera site influenced temporal

overlap between predators and prey. Again, mule deer were the only prey species for which we saw a statistical difference; black bear and mule deer activity patterns overlapped less whereas bobcat and mule deer activity patterns overlapped more where hunters were detected compared to where they were not (Fig. 5.3 and 5.4, Appendix D. S3: Fig. S3.4). Cougar and moose temporal overlap trended towards being higher where hunters were detected (Fig. 5.3, Appendix D. S3: Fig. S3.4). Most estimates of species-specific temporal overlap were relatively high regardless of hunter activity, although coefficients of overlap for elk ($\bar{\Delta} = 0.68$ [95% CI = 0.50 – 0.81]) and wolves ($\bar{\Delta} = 0.55$ [95% CI = 0.35 – 0.74]) indicated notable changes in activity patterns in response to hunter activity (Appendix D. S3: Fig. S3.2). Namely, elk activity shifted from crepuscular activity to a single peak at dusk whereas wolf activity appeared to shift from peaks at dawn and dusk to peaking pre-dawn and post-dusk, as well as increased nocturnal activity overall where hunter activity was detected (Fig. 5.5, Appendix D. S3: Fig. S3.3). Conversely, estimated temporal overlap between predators and prey was statistically different for black bear and mule deer, black bear and white-tailed deer, and black bear and elk when comparing detections on publicly accessible land versus inaccessible land (Fig. 5.3). All three pairings had higher measures of temporal overlap at camera sites on public land compared to private land (Fig. 5.3, Appendix D. S3: Fig. S3.4). The temporal overlap estimate for black bear-elk was particularly low on private land ($\bar{\Delta} = 0.14$ [95% CI = 0.10 – 0.44]), indicating bear and elk activity patterns were very different from each other in these areas, although the sample size was small. In all cases, differences in bear-prey activity on public and private land were predominantly driven by changes in black bear activity. Coyote and mule deer overlap were also higher on public land (Fig. 5.3, Appendix D. S3: Fig. S3.4). Estimates of species-specific temporal overlap were relatively high for most species, except for black bears where the

coefficient of overlap ($\bar{\Delta} = 0.54$ [95% CI = 0.44 – 0.65]) indicated bear activity patterns differed on public versus private land (Appendix D. S3: Fig. S3.2). Black bears were nocturnal with two activity peaks before dawn and after dusk on private land whereas black bear activity increased during the day and peaked at dusk on public land (Appendix D. S3: Fig. S3.3). Elk were crepuscular on private land whereas elk activity declined at dawn and shifted to just after dusk on public land (Appendix D. S3: Fig. S3.3). Mule deer were less active at dawn but more active during the day on public land whereas white-tailed deer activity patterns were only moderately lower on public land than private land (Appendix D. S3: Fig. S3.3).

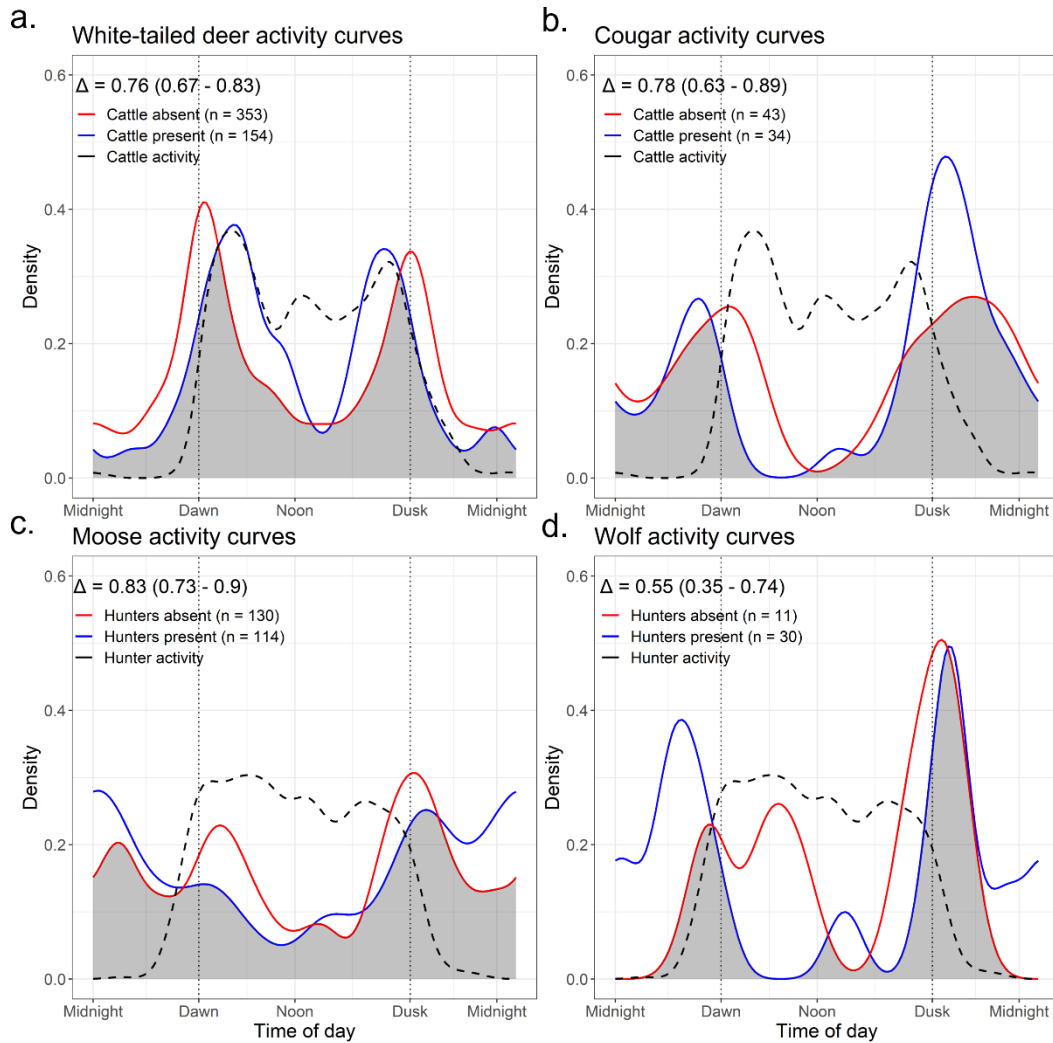


Figure 5.5. Examples of activity curves, coefficient of overlapping estimates ($\bar{\Delta}$), and 95% bootstrapped confidence intervals (95% CI) measuring the percentage of temporal overlap for white-tailed deer (a) and cougars (b) at cameras where cattle were (blue) and were not (red) detected during the grazing season, and for moose (c) and wolves (d) at cameras where hunters were (blue) and were not (red) detected during the hunting season in eastern Washington, 2018 – 2020. Cattle and hunter activity curves (black dashed lines) plotted for reference. Complete set of overlap curves are presented in Appendix D. S3: Fig. S3.3.

5.4 DISCUSSION

We evaluated how patterns of spatiotemporal overlap of large predators and their ungulate prey were influenced by two common anthropogenic activities – cattle grazing and hunting. We found

predators and prey responded to activities and land uses associated with grazing and hunting, but the specific patterns of spatial and temporal overlap offered mixed support for our hypotheses. Ungulate occurrence generally increased where grazing occurred or was permitted, whereas predator responses varied. We found moderate support for our second hypothesis in the hunting season, where deer generally avoided public land but were also more likely to co-occur with predators on public land. Predators also temporally avoided daily peaks in hunter activity, lending support for our temporal avoidance hypothesis. The influence of cattle grazing and hunting on the spatiotemporal overlap of predators and prey were more nuanced than we originally predicted but may suggest some anthropogenic activities help prey win the predator-prey response race.

Livestock grazing influenced the co-occurrence patterns of some predators and prey, yet the species-specific responses underlying these patterns were generally inconsistent with our expectations. We predicted wild ungulates would avoid areas associated with cattle grazing due to interspecific competition, yet the conditional probability that white-tailed deer used a site increased with cattle activity and elk and moose were more likely to use sites where public grazing was permitted. Cattle grazing can improve forage quality (Ganskopp et al. 2004, Vavra 2005) and wild ungulates may preferentially use areas previously grazed by cattle (Yeo et al. 1993, Crane et al. 2016). Proximity to cattle may further benefit wild ungulates if cattle provide added vigilance against predators. Alternatively, competition can increase over the course of the grazing season as forage resources are depleted, potentially increasing spatial overlap between wild ungulates and cattle where they would otherwise spatially avoid each other (Coe et al. 2004). Regardless of the underlying mechanism, ungulates in our system did not spatially avoid areas associated with cattle grazing, refuting our first hypothesis. Ungulates were less likely to be

detected in these same areas, however, potentially indicating some level of temporal avoidance. Conversely, predator responses to livestock grazing were mixed and generally did not support our second hypothesis. Mesopredators were conditionally more likely to use sites with greater cattle activity, yet mesopredators rarely depredate cattle (Mitchell et al. 2004). Thus, under our hypothesis, any “food subsidies” that could have increased mesopredator occurrence in these areas were likely associated with the disturbance grazing can have on small mammal communities, making small mammals more vulnerable to predation (Torre et al. 2007). Lastly, cougars strongly avoided cattle activity when white-tailed deer were absent, suggesting cattle were more of a disturbance than an attractant to this apex predator.

Co-occurrence increased with hunter activity and on public land for several predator-prey pairings despite ungulates avoiding public land, lending support for our second hypothesis that predator responses to anthropogenic activities would drive predator-prey co-occurrence patterns. Deer were less likely to use or be detected on public land in the absence of predators, consistent with a growing body of literature demonstrating ungulates use private lands as refuge from hunters (Proffitt et al. 2016, Sergeyev et al. 2022). But deer were also more likely to occur with bobcats and cougars on public land. At this courser spatial scale, predators appeared to be attracted to public lands despite these areas posing increased mortality risk from hunters and reduced hunting opportunities of wild ungulates. We posit scavenging opportunities provided by hunter-harvested animals attract some predators to public land during the hunting season. Bears and canids are known for their scavenging behavior during the hunting season (Lafferty et al. 2016), but bobcats and cougars will also scavenge carcasses, including hunter-killed ungulates (Nowak et al. 2000). Although we were unable to explicitly test the effect of public land on predator occurrence owing to poor convergence of this variable, we would expect higher co-

occurrence on private land if predator site-use simply mirrored ungulate distributions during the hunting season (i.e., our first hypothesis). Given we found the opposite, our results suggest there is a spatial mismatch between their occurrence patterns, particularly for bobcats, cougars, and deer. And unlike previous research that found hunters may facilitate predators (Gehr et al. 2018), our results suggest deer using private lands may experience a reprieve from mortality risk from both hunters and natural predators in cases where hunter and predator distributions are predominantly tied to public lands. Similar to our findings, (Gaynor et al. 2022) found predation risk from both human hunters and mountain lions was lowest for deer in areas near human settlements. Thus, depending on the spatial configuration of private lands, predator responses to hunting, and hunting intensity, private lands may have the potential to strongly modify predator-prey interactions. Spatial overlap is not a perfect proxy for predation risk, however (Suraci et al. 2022), and data on hunter- vs. predator- encounter and mortality rates for ungulates during the hunting season would provide further insight regarding the relationship between predators, prey, and hunters.

Temporal responses to anthropogenic activity were relatively clear cut, with most changes in temporal overlap between predators and prey arising due to predators avoiding peaks in cattle and hunter activity. Ungulate activity shifted minimally (i.e., deer) or to times when both predators and humans were less active (i.e., moose). Evidence continues to mount that wildlife shift diel activity to times when humans and related disturbances are less active to minimize exposure to real or perceived anthropogenic-related risks (Gaynor et al. 2018, Kautz et al. 2022), but whether that increases exposure to predators or competitors depends on the interacting species, the type of anthropogenic disturbance, and the species-specific responses to that disturbance (Frey et al. 2020, Sévêque et al. 2020, Suraci et al. 2021). We found that where

cattle or hunters were detected, predators consistently avoided the anthropogenic disturbances that reduced the amount of time they and ungulate prey were both active. As a result, cattle and hunter activity may help ungulates win the predator-prey “response race” (Sih 1984) by decoupling predator diel activity patterns from that of their prey or even creating vacant times in the 24-hour cycle that act as temporal refugia from both anthropogenic disturbance and predation risk (Muhly et al. 2011, Kohl et al. 2019, Kautz et al. 2022).

We found notable differences in whether predators or prey adjusted spatially or temporally to anthropogenic activities, particularly during the hunting season. The probability a deer used public land was lower than that on private land, but temporally we only found moderate shifts in activity with respect to land ownership or hunter activity. In comparison, predator responses were almost the complete opposite. The probability a predator (namely, bobcats, coyotes, and wolves) used a camera site increased with hunter activity but temporally, almost all predators were more nocturnal on public land and where hunters were detected. The axis (spatial or temporal) on which species respond to anthropogenic activities may be influenced by the level of disturbance or risk posed to the individual species. Hunters are a large source of mortality for deer in our study areas, with almost 5,000 deer harvested from our study areas in 2020 (Washington Department of Fish and Wildlife 2022). Although temporal avoidance can reduce the probability of encountering a hunter, spatial segregation should be a more effective strategy for minimizing mortality risk and may point to the stronger spatial response for some ungulate species. Conversely, if hunters simultaneously provide food subsidies and pose a mortality risk to predators, temporally avoiding hunters while spatially overlapping with them would allow predators to balance the risks and rewards of the hunting season.

Anthropogenic activities may also influence the trade-offs ungulates make under predation risk and the strategies used to mitigate that risk. For example, regardless of cougar presence, white-tailed deer were more likely to use sites as cattle activity increased, suggesting white-tailed deer prioritized resource acquisition over predator avoidance in these areas. Nutritional value of forage tends to decline through summer whereas nutritional demands are high for lactating females (Fryxell 1991, Tollefson et al. 2011), potentially limiting deer's ability to invest in antipredator behaviors if they are competing for limited resources with cattle. The positive association between white-tailed deer and cattle may have made deer relatively predictable across space, making them more vulnerable to predation risk from cougars. However, cattle presence may have also allowed white-tailed deer to mitigate this risk. Both white-tailed deer and cougars adjusted their activity patterns in response to cattle, but white-tailed deer increased their temporal overlap with cattle whereas cougars avoided cattle activity by being more nocturnal. As a result, cattle activity may have helped cougars anticipate deer distributions and win the "space race", but cattle activity also provided a temporal refuge for white-tailed deer to minimize their exposure to cougars in these risky places.

Wolf-moose co-occurrence patterns in the hunting season provide a different example of the strategies ungulates used to balance anthropogenic and predation risks. We found a negative effect of hunter activity on wolf-moose co-occurrence, yet both species were positively associated with hunter activity when the other was absent. Wolves and moose were almost exclusively detected on public land where most hunter activity occurred so this positive correlation with hunters is not necessarily surprising. However, the negative effect on co-occurrence was largely driven by moose, which only avoided hunter activity when wolves were present, suggesting it was wolves and not hunters that moose were spatially avoiding. Yet both

species shifted their daily activity where hunters were detected on camera. Moose were more nocturnal whereas wolf activity peaked just before dawn and after dusk, likely allowing moose to reduce encounters with wolves and human hunters simultaneously. The different spatiotemporal responses to wolves and hunters likely reflected the strategies moose used to balance risk from two different sources of mortality. Wolves were the dominant predator of moose in the Northeast study area (Harris et al. 2021), and likely the Okanogan, whereas human hunters could harvest ~60 moose per hunting season in the Northeast study area only (Washington Department of Fish and Wildlife 2019). Moose appeared to prioritize spatially avoiding of their primary, year-round predator, but temporally avoided of their second largest source of mortality (hunters) during the hunting season.

Although we found numerous examples of anthropogenic influences on the spatial and temporal overlap of predators and prey, the second-order interactions were non-significant for many species-pairings, indicating these species occurred independently of each other. This was surprising given predator distributions are often closely linked to the distributions of their prey (Laundré 2010). Multispecies occupancy models require large sample sizes to estimate co-occurrence and associated covariate relationships (Kéry and Royle 2021) but the rarity of some species in our study areas (e.g., wolves) likely limited our ability to estimate their co-occurrence with other species. In addition, single-season occupancy models assume sites are closed to changes in occupancy over the course of the sampling season (MacKenzie et al. 2002). Violation of this closure assumption can lead to overestimated occupancy probabilities and the model incorrectly identify species co-occurring as independent (Lonsinger 2022). Occupancy models using camera trap data inherently violate the closure assumption owing to most species having home ranges much larger than the cameras' viewshed (Efford and Dawson 2012, Lonsinger

2022), further impacting our models' ability to estimate pairwise dependencies between species. Misidentifying dependent interactions likely affected our interpretation of whether predators and prey responded to one another but should not have affected our interpretation of their responses to anthropogenic activities or the ultimate patterns of their co-occurrence.

Our results demonstrate that the effects of cattle grazing and hunting on predator-prey interactions make for complex patterns of spatiotemporal overlap across a mixed-used landscape. All study species responded either spatially or temporally to varying levels of cattle and hunter activity or the broad-scale land uses associated with these anthropogenic activities, but the strength, directionality, and axes on which they responded varied greatly. Cattle grazing and hunting tipped the scale in favor predators or prey on one axis but when the spatial and temporal response were considered across species prey were often able to segregate from predation risk to some degree by using spatiotemporal refuges created by land use, the anthropogenic activities themselves (e.g., cattle activity), or predator responses to cattle grazing and hunting. Thus, anthropogenic activities may help prey win the “response race” under specific circumstances (Muhly et al. 2011). Our results also suggest that decision makers may be able to manipulate predator-prey interactions, or at least their spatiotemporal overlap, by modifying cattle or hunter activity levels across the landscape, as well as by altering public access for hunting, offering alternatives to the more common practices of manipulating habitat or predator population. Finally, livestock grazing and hunting may have implications for food web interactions and, by extension, community dynamics, even when grazing and hunting-related management decisions were not aimed at predators or prey.

5.5 BIBLIOGRAPHY

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APPENDIX A

Supplemental Materials for Chapter 2

Are we telling the same story? Comparing inferences made from camera trap and telemetry data for wildlife monitoring

Reconyx HyperFire2 Pro Camera Settings

< Motion >

- Motion Pictures: **ON**
- Number of Pics: **5**
- Time between Pic: **Rapidfire** (up to 2 frames per second, 0.2 second trigger speed)
- Motion Video: **OFF**
- Quiet Period: **No Delay**
- Sensitivity: **High** (Reduced to **medium-high** if false triggers were an issue)
- Motion Schedules: **24 hour**

< Time Lapse > **OFF**

< Day/Night >

- Take Pictures: **Day/Night**
- Flash Output: **High**
- Shutter: **1/30th** (default)
- Max ISO: **ISO 1600** (default)

< Data Bands >

- Time Format: **24 hour**
- Temperature: **Fahrenheit**
- Show Logo: **Yes**

< Location >

- Location: **USA**
- State: **WA**
- Daylight Savings: **auto adjust**

< Resolution >

Resolution: **4:3 standard**

< Other >

- PIR Type: **HF Legacy** (up to 30m detection range)
- Loop Recording: **OFF**
- Record audio: **ON**
- Delay start: **OFF**
- External Trigger: **OFF**
- Export Config: **NO**

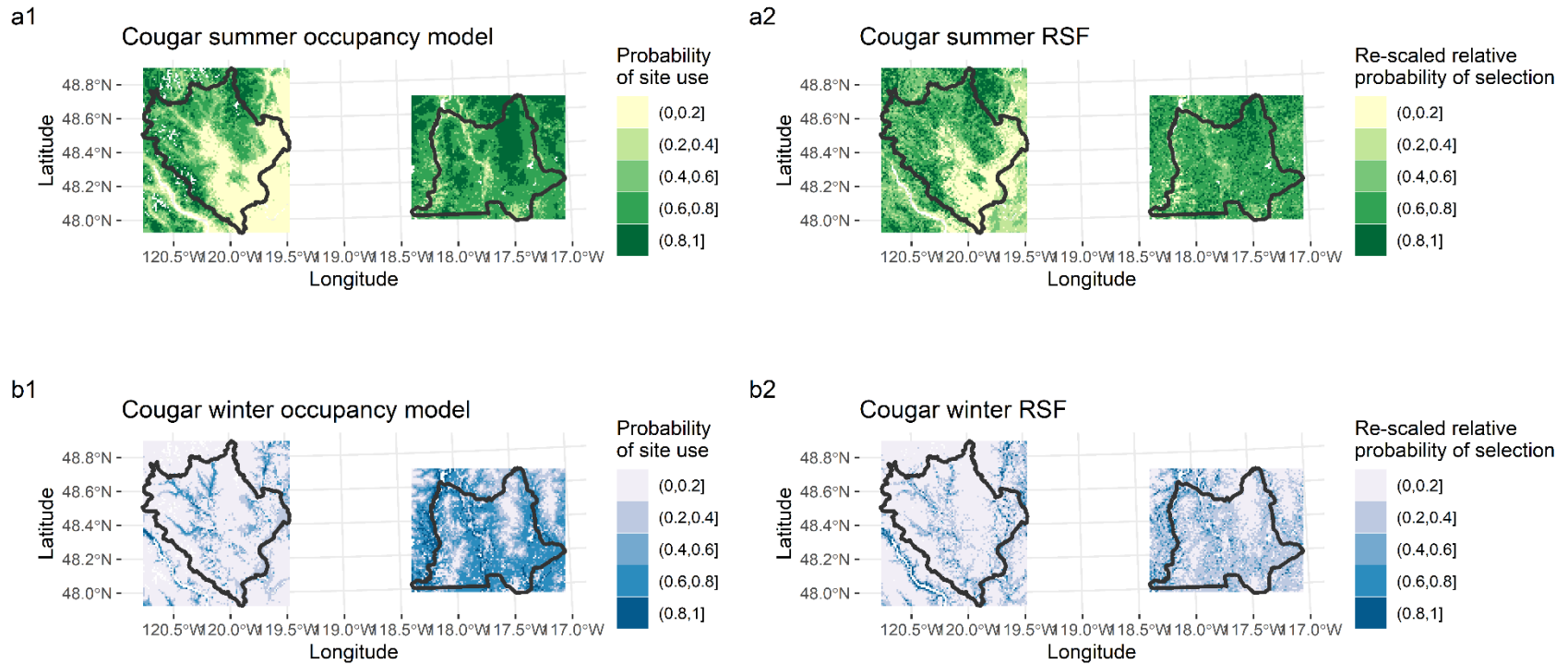
< Battery type > **Lithium**

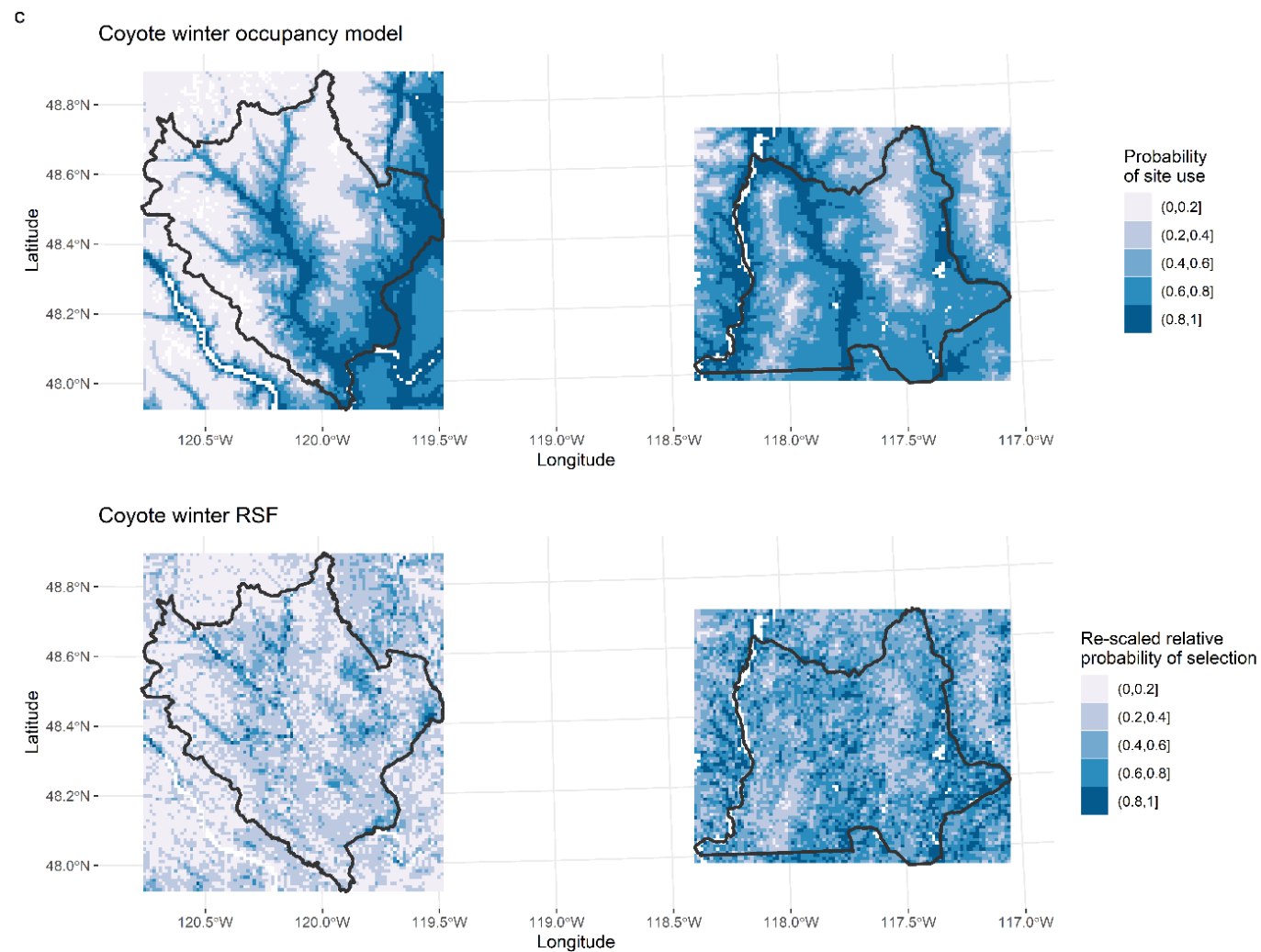
Table S1. Estimated coefficients and standard errors (SE) for the effect of site- and survey-specific predictors on the probability of detecting a species of interest at a camera site during a one-week sampling occasion in eastern Washington, 2018 – 2020, based on photo-capture data from randomly deployed camera traps. Predictors included distance of camera to linear feature (m), height of camera from ground (m), an interaction between camera height and distance, weekly mean temperature (for summer and winter models, respectively), and whether the camera trap was monitoring a decommissioned road or open road (relative to game trails). Bolded estimates and standard errors indicate the predictor was significant (p-value ≤ 0.1).

Species	Season	Intercept (SE)	Distance (SE)	Height (SE)	Height x Distance (SE)	Summer Temp (SE)	Winter Temp (SE)	Decommed Road (SE)	Open Road (SE)
Bobcat	Summer	-2.8 (0.26)	0.28 (0.09)	-0.14 (0.09)	0.32 (0.1)	-0.08 (0.09)	NA	1.01 (0.32)	1.36 (0.29)
Cougar	Summer	-2.89 (0.2)	-0.16 (0.11)	0.13 (0.11)	0.02 (0.08)	-0.01 (0.1)	NA	0.8 (0.28)	1.06 (0.26)
Wolf	Summer	-2.9 (0.37)	0.05 (0.17)	0.25 (0.2)	0.18 (0.18)	0.02 (0.18)	NA	1.16 (0.58)	1.02 (0.48)
Coyote	Summer	-0.88 (0.08)	-0.04 (0.05)	0.12 (0.06)	-0.02 (0.05)	-0.03 (0.05)	NA	-0.04 (0.16)	0.59 (0.12)
Mule Deer	Summer	0.02 (0.07)	-0.15 (0.07)	0.1 (0.06)	-0.11 (0.07)	-0.02 (0.06)	NA	0.07 (0.18)	-0.01 (0.15)
Elk	Summer	-1.41 (0.28)	0.3 (0.16)	0.24 (0.15)	0.05 (0.18)	-0.1 (0.11)	NA	-0.77 (0.38)	0.32 (0.33)
White-tailed Deer	Summer	1.02 (0.1)	0.04 (0.06)	-0.16 (0.08)	-0.07 (0.06)	0.02 (0.06)	NA	-0.66 (0.16)	-0.46 (0.15)
Bobcat	Winter	-2.36 (0.28)	-0.28 (0.21)	-0.07 (0.17)	0.02 (0.17)	NA	0.14 (0.15)	-0.68 (0.57)	0.49 (0.41)
Cougar	Winter	-3.51 (0.36)	-0.14 (0.2)	-0.29 (0.19)	0.03 (0.17)	NA	0.03 (0.17)	0.46 (0.55)	1.09 (0.41)
Wolf	Winter	-4.62 (0.65)	0.48 (0.37)	-0.1 (0.23)	-0.25 (0.27)	NA	-0.15 (0.25)	1.06 (0.81)	2.27 (0.67)
Coyote	Winter	-1.09 (0.09)	-0.07 (0.06)	-0.21 (0.07)	-0.13 (0.05)	NA	0.28 (0.06)	0.11 (0.19)	0.35 (0.13)
Mule Deer	Winter	-0.43 (0.09)	-0.4 (0.1)	0 (0.09)	-0.49 (0.1)	NA	0.12 (0.08)	-0.29 (0.25)	-0.72 (0.22)
Elk	Winter	-2.22 (0.51)	-0.28 (0.43)	0.35 (0.32)	-0.02 (0.39)	NA	0.26 (0.23)	-0.65 (1.1)	0.8 (0.67)
White-tailed Deer	Winter	0.28 (0.09)	0 (0.07)	0.17 (0.09)	0.11 (0.06)	NA	0.26 (0.07)	-0.56 (0.18)	-0.59 (0.16)

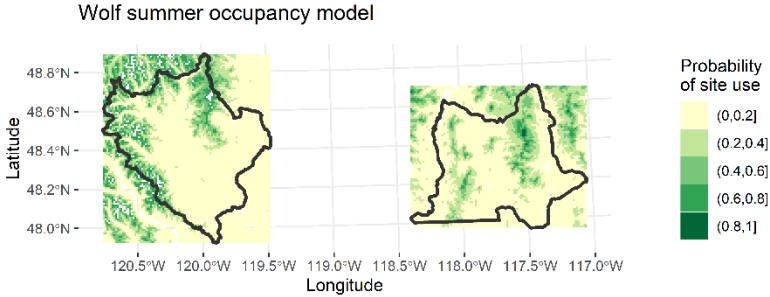
Figure S1. Predicted probability of use and relative probability of selection for (a) cougars in summer, (b) coyotes in winter, (c) mule deer in summer, (d) mule deer in winter, (e) white-tailed deer in winter, and (f) wolves in summer across two study areas in eastern Washington, 2018 – 2020, based on paired occupancy models and resource selection functions (RSF).

Seasonal predicted space use

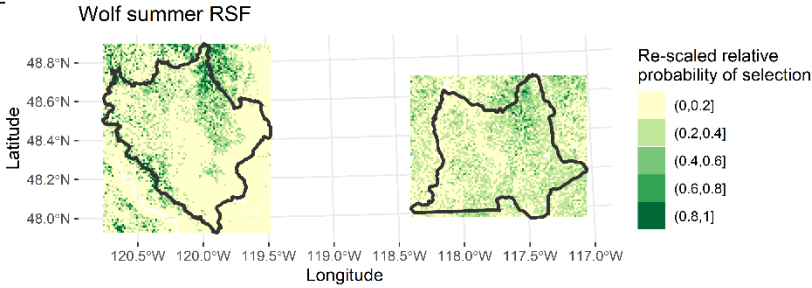




d1

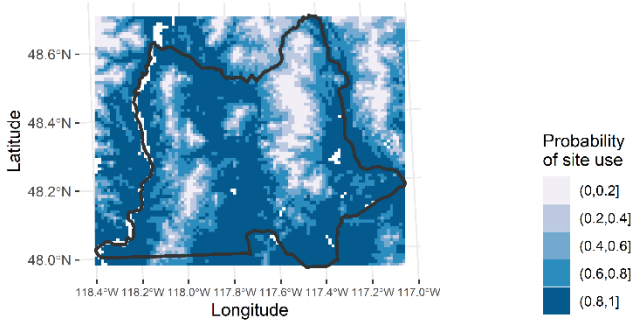


d2



e1

White-tailed deer
summer occupancy model



e2

White-tailed deer winter RSF

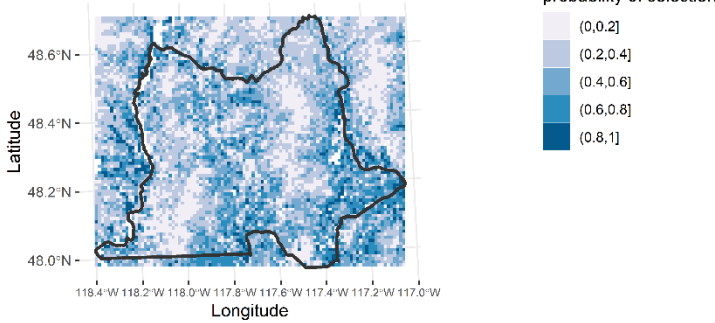
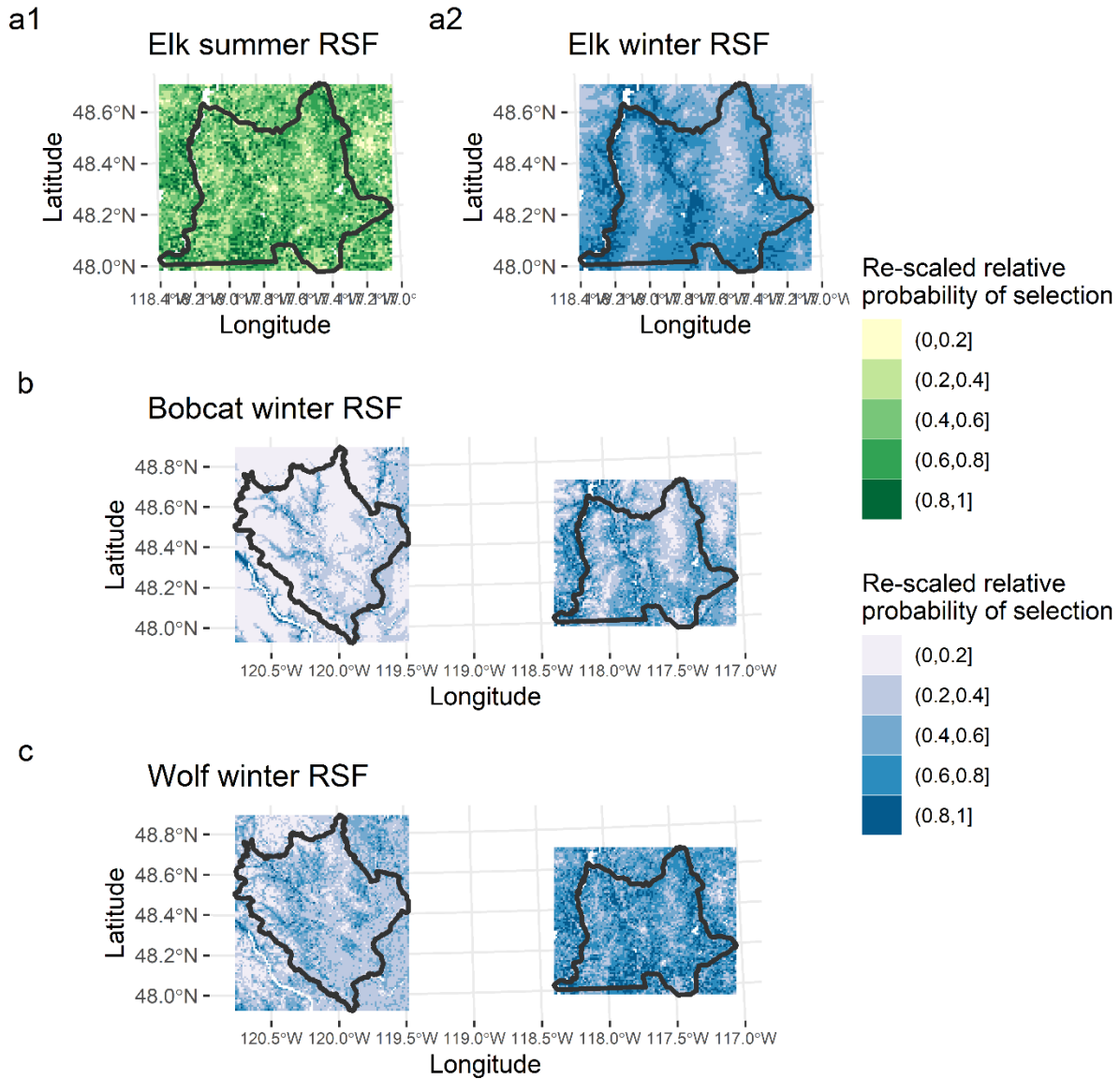


Figure S2. Predicted relative probability of selection for (a) elk in summer (green) and winter (blue), (b) bobcats in winter, and (c) wolves in winter across two study areas in eastern Washington, 2018 – 2020, based on resource selection functions (RSF). The estimated effects of all habitat predictors in the corresponding occupancy models were non-significant in these species and seasons so comparisons with the RSF predictions were uninformative.

Predicted resource selection functions



APPENDIX B

Supplemental Materials for Chapter 3

Predator-prey interactions and landscape features influence movement behaviors in a large-mammal community

Appendix S1: Resource Selection Function (RSF) analysis as covariates representing the relative probability of species presence

Methods

We fit resource selection functions (RSFs) to the GPS collar data for mule deer, elk, white-tailed deer, bobcats, cougars, coyotes, and wolves to predict the relative probability of each species' presence across the study areas. We censored telemetry relocation data for 3 weeks post capture (Northrup et al. 2014, van de Kerk et al. 2020) and excluded relocations associated with dispersal events (predators only; L. Satterfield and R. Wendell, University of Washington, *pers. comm.*) and seasonal migrations (mule deer only; Ganz et al. *in prep*). We then pooled all remaining location data for a given species across years (2018 – 2021) to create seasonal RSFs (summer: 1 July – 30 Sept; winter: 1 Dec – 28/29 Feb) for each species.

We defined the spatial extent of what was used and available to each collared individual based on 3rd-order resource selection (i.e., resources used within an animal's home range; Johnson, 1980). We created utilization distributions for each collared individual's annual home range using a 95% kernel density estimator (KDE; Worton 1989, Hooten et al. 2017), with the *adehabitatHR* package (Calenge 2006) in Program R (R Core Team 2020). We masked water bodies as unavailable, then randomly sampled 20 available resources units per 1 used location within the 95% KDE (Fieberg et al. 2021) and extracted covariate values at each used (1) and available (0) location.

We considered eight covariates to represent environmental features and human impacts that we expected would influence habitat selection. This included elevation, slope, an index for human-modified landscape, distance to nearest water, road density, canopy cover, landcover type, and distance to nearest habitat edge (Koehler and Hornocker 1991, Long et al. 2009, Smereka et al. 2020, Peterson et al. 2021, Staudenmaier et al. 2021). We extracted elevation and slope from the Shuttle Radar Topography Mission (SRTM) 30 m resolution digital elevation model (DEM; Farr et al. 2007) in Program R (R Core Team 2020). We extracted an index of human modification to the landscape from the Global Human Modification map (Kennedy et al. 2019) in Program R (R Core Team 2020). We calculated distance to nearest water in ArcGIS using the Euclidean Distance tool (ESRI 2020) and the National Hydrology Dataset for Washington (Washington State Department of Ecology 2019). We calculated road density (road length/1 km²) in Program R (R Core Team 2020) using the Cascadia Partner Forum TerrAdapt:Cascadia tool (<https://cascadiapartnerforum.org/terradapt>) roads layer. We calculated percent canopy cover for each year (2018, 2019, 2020) from the Global Forest Change data (Hansen et al. 2013) in Program R (R Core Team 2020). We reclassified annual landcover data from the Cascadia Partner Forum TerrAdapt:Cascadia tool (30 m resolution) into 6 landcover types (developed, forest, open grass, shrub mix, wetlands, and other). Due to few observations in the developed landcover classes for some species, we further reclassified the developed category

into the other category for white-tailed deer, elk, and cougar winter models, and for bobcat, coyote, and wolf summer and winter models. Finally, we derived distance to nearest edge by reclassifying the annual Cascadia landcover data into binary forested and non-forested categories and calculated the distance from each pixel to the edge of forested and non-forested habitat for each year in ArcGIS using the Euclidean Distance tool (ESRI 2020). Because percent canopy cover, landcover type, and distance to edge varied annually, we extracted these covariate values from annual data sets that matched the year each used and available location arose. We centered and scaled all continuous variables and checked for collinearity, excluding human-modified landscape when correlated ($r \geq 0.60$) with elevation. We used the remaining variables to create a global model, including a quadratic term on elevation, for each season and species-specific RSF. We included a random effect for individual in all models to account for pseudo-replication of non-independent GPS locations. Each model followed the same structure but varied in how landcover was categorized and whether the effect of human-modified landscape was excluded (excluded from cougar, coyote, elk, and mule deer summer models; coyote and mule deer winter models): $\text{Used} \sim 1 + \text{Elevation} + \text{Elevation}^2 + \text{Slope} + \text{Road Density} + \text{Distance to Water} + \text{Human Modified} + \text{Canopy Cover} + \text{Distance to Edge} + \text{Landcover Type} + (1|\text{ID})$. Finally, we assigned a weight of 1 to the used locations and a weight of 5,000 to the available locations (Fieberg et al. 2021).

We fit the species and season specific RSFs using mixed-effect logistic regression models and the lme4 package (Bates et al. 2015). We then predicted annual RSFs across the extent of each study area at 30m pixel resolution (Figure S1.1). We scaled the predicted relative probability of resource selection between 0 and 1 by subtracting each predicted value from the maximum predicted value. To minimize the effect of large outliers skewing the scaled predictions, we considered all predicted RSF values above the 99% percentile to be outliers and forced these values to the RSF value at the 99th percentile. Because mule deer were only collared in the Okanogan study area and elk and white-tailed deer were only collared in the Northeast study area, we restricted the predicted ungulate RSFs to the respective study area where they were collared (Figure S1). We used these annual season- and species-specific predictions as covariates in the movement analyses to represent the relative probability of species presence across the landscape.

Lastly, we used the Boyce et al. (2002) method for K-fold cross-validation to evaluate the predictive capacity of the RSFs to ensure they were predictive of animal presence throughout the study areas. To do this, we reclassified the landcover data and standardized the continuous covariates for all used and available locations as described above. We then randomly partitioned each season- and species-specific dataset into 5 folds in Program R (R Core Team 2020), balancing each fold proportional to the number of used and available locations in the original dataset with the groupdata2 package (Olsen 2021). Each fold comprised 4/5th of the data for model training and 1/5th of the data for model testing. We fit the season- and species-specific RSFs to each of the 5 training datasets, withholding the corresponding testing data from each model run. We then predicted the RSF results from each training model across the study areas for each year, adjusted for outliers, and rescaled the RSF values between 0 and 1 as described above. For each trained RSF, we then reclassified the scaled RSF predictions into 10 ranked bins based on its quantiles (Boyce et al. 2002, Morris et al. 2016). To cross-validate the binned predictions, we plotted the used locations from the testing datasets and extracted the binned RSF values from these locations and area-weighted the frequency of each bin by the number of pixels representing that bin (Boyce et al. 2002, Morris et al. 2016). Finally, we calculated the

Spearman's rank-order correlation (ρ) between each bin rank and the area-weighted frequency of used locations to evaluate the predictive ability of the RSFs (Boyce et al. 2002, Morris et al. 2016). Although Morris et al. (2016) suggests mapping RSF results following the same binning approach used to test model accuracy, we used the non-binned predictions, scaled 0 – 1 (Figure S1.1), as covariates in the movement analyses given their more intuitive linear relationship when used as an explanatory variable compared to when the predictions were binned based on quantiles.

Results

In total, we included location data from 381 GPS collared animals in the RSF analyses. The number of unique individuals included in each seasonal RSF varied by species, ranging from 9 to 119 individuals (Table S1.1). On average, 41,653.57 (SE = 15,437.87) used locations were included in the summer RSFs and 38,172.57 (SE = 15,172.28) used locations were included in the winter RSFs, but this varied greatly by species (Table S1.1). The mule deer RSFs included the most GPS location data whereas the bobcat and wolf RSFs included the least (Table S1.1).

We found all covariates were statistically significant in at least one RSF (p -value ≤ 0.05), although the strength and directionality of the effects varied by species and season (Table S1.2). In general, distance to water, elevation, road density, slope, and landcover type were significant in most or all models. Landcover class had the strongest effect on resource selection for most species, where the “Other” and “Developed” landcover classes were strongly avoided relative to the “Forest” landcover class by almost all species (Table S1.2). Conversely, most species were more likely to select for the “Shrub mix” and “Wetland” landcover classes relative to the “Forest” landcover class, although not as strongly compared to their avoidance of “Other” and “Developed” landcover classes (Table S1.2). The effect of the “Open grass” landcover class and road density varied by species and season (Table S1.2). Most species selected for flatter slopes and mid-elevations within each study area (Table S1.2). In addition, most species avoided areas with increasing distance to nearest edge, canopy cover, and human modification to the landscape but selected for areas as distance to water increased (Table S1.2).

We found that the testing data withheld during the K-fold process were highly correlated with the binned RSF predictions in the K-fold cross-validation analyses (Table S1.3), indicating the RSFs were predictive of the relative probability of resource selection for each species. The mean Spearman's rank-order correlation coefficient (ρ) for each species, season, and year-specific RSF ranged 0.86 – 1.00 (SE ranged 0.00 – 0.02; Table S1.3). The summer bobcat RSFs had the lowest mean rank-order correlations (mean ρ ranged 0.86 – 0.90; Table S1.3) but were still considered highly correlated and thus predictive of their space use.

Table S1.1. Summary of GPS collar data included in the seasons and species-specific resource selection functions for seven species in eastern Washington, USA, 2018 – 2021. Mule deer were only GPS-collared in the Okanogan study area; elk and white-tailed deer were only GPS-collared in the Northeast study area. Bobcats, cougars, coyotes and wolves were GPS-collared in both study areas.

Species	Season	Individuals (n)	Used locations (n)
Bobcat	Summer	27	7698
Bobcat	Winter	24	4803
Cougar	Summer	38	27094
Cougar	Winter	32	18611
Coyote	Summer	24	11272
Coyote	Winter	25	13954
Elk	Summer	52	61209
Elk	Winter	49	57136
Mule Deer	Summer	114	118079
Mule Deer	Winter	119	115053
White-tailed Deer	Summer	87	59117
White-tailed Deer	Winter	79	52707
Wolf	Summer	12	7106
Wolf	Winter	9	4944

Table S1.2. Estimated coefficients from the season- and species-specific resource selection functions (RSFs) used to predict the relative probability of resource use across the Okanogan and Northeast study areas in eastern Washington, USA, 2018 – 2021. The species, season, parameter type, estimated coefficient, standard error, and p-value are provided. Covariates included elevation and elevation², slope, road density (road length/km²), distance to nearest water (Distance to Water), index for human modified landscape (Human Modified), percent canopy cover, distance to nearest habitat edge (Distance to Edge), landcover type where the forest category represented the intercept, and a random effect for individual. RSF results for the ungulate models are specific to their respective study areas (mule deer in the Okanogan, elk and white-tailed deer in the Northeast) whereas RSF results for the predator models (bobcat, cougar, coyote, and wolf) represent resource selection across both study areas.

Species	Season	Parameter	Estimate	SE	p-value
Bobcat	Summer	Intercept	-11.46	0.03	0
Bobcat	Summer	Elevation	0.07	0.02	0
Bobcat	Summer	Elevation ²	-0.02	0.01	0.11
Bobcat	Summer	Slope	-0.04	0.01	0
Bobcat	Summer	Road density	-0.07	0.01	0
Bobcat	Summer	Distance to water	0.04	0.01	0
Bobcat	Summer	Human modified	-0.19	0.02	0
Bobcat	Summer	Canopy cover	0.04	0.02	0.01

Bobcat	Summer	Distance to edge	-0.11	0.02	0
Bobcat	Summer	Landcover: Open grass	-0.31	0.04	0
Bobcat	Summer	Landcover: Other	-0.79	0.12	0
Bobcat	Summer	Landcover: Shrub mix	0.22	0.03	0
Bobcat	Summer	Landcover: Wetland	0.49	0.16	0
Bobcat	Winter	Intercept	-11.48	0.08	0
Bobcat	Winter	Elevation	-0.83	0.03	0
Bobcat	Winter	Elevation ²	0.12	0.01	0
Bobcat	Winter	Slope	0.19	0.02	0
Bobcat	Winter	Road density	-0.06	0.02	0
Bobcat	Winter	Distance to water	0	0.02	0.85
Bobcat	Winter	Human modified	-0.49	0.03	0
Bobcat	Winter	Canopy cover	0.05	0.02	0.02
Bobcat	Winter	Distance to edge	-0.01	0.02	0.65
Bobcat	Winter	Landcover: Open grass	-0.49	0.05	0
Bobcat	Winter	Landcover: Other	-1.47	0.2	0
Bobcat	Winter	Landcover: Shrub mix	-0.26	0.04	0
Bobcat	Winter	Landcover: Wetland	0.23	0.13	0.08
Cougar	Summer	Intercept	-11.81	0.02	0
Cougar	Summer	Elevation	-0.11	0.01	0
Cougar	Summer	Elevation ²	0.2	0.01	0
Cougar	Summer	Slope	-0.04	0.01	0
Cougar	Summer	Road density	-0.06	0.01	0
Cougar	Summer	Distance to water	-0.21	0.01	0
Cougar	Summer	Canopy cover	0.23	0.01	0
Cougar	Summer	Distance to edge	-0.21	0.01	0
Cougar	Summer	Landcover: Developed	-2.5	0.14	0
Cougar	Summer	Landcover: Open grass	-0.14	0.02	0
Cougar	Summer	Landcover: Other	-0.46	0.07	0
Cougar	Summer	Landcover: Shrub mix	0.22	0.02	0
Cougar	Summer	Landcover: Wetland	1.4	0.03	0
Cougar	Winter	Intercept	-11.44	0.03	0
Cougar	Winter	Elevation	-0.35	0.01	0
Cougar	Winter	Elevation ²	0	0.01	0.5
Cougar	Winter	Slope	0.34	0.01	0
Cougar	Winter	Road density	-0.02	0.01	0.02
Cougar	Winter	Distance to water	-0.06	0.01	0
Cougar	Winter	Human modified	0.05	0.01	0
Cougar	Winter	Canopy cover	0.15	0.01	0
Cougar	Winter	Distance to edge	-0.02	0.01	0.09

Cougar	Winter	Landcover: Open grass	-0.53	0.03	0
Cougar	Winter	Landcover: Other	-2.46	0.14	0
Cougar	Winter	Landcover: Shrub mix	-0.14	0.02	0
Cougar	Winter	Landcover: Wetland	0.91	0.06	0
Coyote	Summer	Intercept	-11.98	0.06	0
Coyote	Summer	Elevation	-0.01	0.02	0.51
Coyote	Summer	Elevation ²	0	0.01	0.77
Coyote	Summer	Slope	-0.4	0.01	0
Coyote	Summer	Road density	0.08	0.01	0
Coyote	Summer	Distance to water	0.05	0.01	0
Coyote	Summer	Distance to edge	-0.01	0.01	0.55
Coyote	Summer	Canopy cover	-0.19	0.01	0
Coyote	Summer	Landcover: Open grass	0.62	0.03	0
Coyote	Summer	Landcover: Other	0.32	0.06	0
Coyote	Summer	Landcover: Shrub mix	0.49	0.03	0
Coyote	Summer	Landcover: Wetland	0.87	0.08	0
Coyote	Winter	Intercept	-11.46	0.03	0
Coyote	Winter	Elevation	-0.05	0.02	0.01
Coyote	Winter	Elevation ²	-0.09	0.01	0
Coyote	Winter	Slope	-0.15	0.01	0
Coyote	Winter	Road density	0.07	0.01	0
Coyote	Winter	Distance to water	0.11	0.01	0
Coyote	Winter	Distance to edge	-0.04	0.01	0
Coyote	Winter	Canopy cover	-0.02	0.01	0.14
Coyote	Winter	Landcover: Open grass	0.06	0.03	0.04
Coyote	Winter	Landcover: Other	-0.41	0.06	0
Coyote	Winter	Landcover: Shrub mix	0.02	0.03	0.39
Coyote	Winter	Landcover: Wetland	0.47	0.08	0
Elk	Summer	Intercept	-11.61	0.02	0
Elk	Summer	Elevation	0.23	0.01	0
Elk	Summer	Elevation ²	-0.1	0	0
Elk	Summer	Slope	-0.03	0	0
Elk	Summer	Road density	-0.13	0	0
Elk	Summer	Distance to water	0.14	0	0
Elk	Summer	Canopy cover	-0.12	0.01	0
Elk	Summer	Distance to edge	-0.02	0	0
Elk	Summer	Landcover: Developed	0.44	0.02	0
Elk	Summer	Landcover: Open grass	0.14	0.02	0
Elk	Summer	Landcover: Other	-2.6	0.21	0
Elk	Summer	Landcover: Shrub mix	0.34	0.01	0

Elk	Summer	Landcover: Wetland	0.46	0.05	0
Elk	Winter	Intercept	-11.91	0.03	0
Elk	Winter	Elevation	0.37	0.01	0
Elk	Winter	Elevation ²	-0.2	0	0
Elk	Winter	Slope	-0.04	0	0
Elk	Winter	Road density	0.05	0	0
Elk	Winter	Distance to water	0.16	0	0
Elk	Winter	Human modified	0.02	0.01	0
Elk	Winter	Canopy cover	-0.29	0.01	0
Elk	Winter	Distance to edge	0.15	0	0
Elk	Winter	Landcover: Open grass	0.71	0.02	0
Elk	Winter	Landcover: Other	0.38	0.03	0
Elk	Winter	Landcover: Shrub mix	0.75	0.01	0
Elk	Winter	Landcover: Wetland	0.34	0.07	0
Mule Deer	Summer	Intercept	-11.34	0.02	0
Mule Deer	Summer	Elevation	0.02	0.01	0.01
Mule Deer	Summer	Elevation ²	-0.13	0.01	0
Mule Deer	Summer	Slope	0.02	0	0
Mule Deer	Summer	Road density	0.02	0	0
Mule Deer	Summer	Distance to water	-0.01	0	0
Mule Deer	Summer	Canopy cover	0	0	0.74
Mule Deer	Summer	Distance to edge	0.02	0	0
Mule Deer	Summer	Landcover: Developed	-0.36	0.04	0
Mule Deer	Summer	Landcover: Open grass	-0.15	0.01	0
Mule Deer	Summer	Landcover: Other	-0.66	0.02	0
Mule Deer	Summer	Landcover: Shrub mix	0.18	0.01	0
Mule Deer	Summer	Landcover: Wetland	0.4	0.03	0
Mule Deer	Winter	Intercept	-11.87	0.02	0
Mule Deer	Winter	Elevation	-0.09	0.01	0
Mule Deer	Winter	Elevation ²	0	0	0.12
Mule Deer	Winter	Slope	0.33	0	0
Mule Deer	Winter	Road density	-0.04	0	0
Mule Deer	Winter	Distance to water	0.05	0	0
Mule Deer	Winter	Canopy cover	-0.12	0	0
Mule Deer	Winter	Distance to edge	0.06	0	0
Mule Deer	Winter	Landcover: Developed	0.06	0.03	0.07
Mule Deer	Winter	Landcover: Open grass	0.32	0.02	0
Mule Deer	Winter	Landcover: Other	-1.48	0.09	0
Mule Deer	Winter	Landcover: Shrub mix	0.3	0.02	0
Mule Deer	Winter	Landcover: Wetland	-0.93	0.08	0

White-tailed Deer	Summer	Intercept	-11.52	0.02	0
White-tailed Deer	Summer	Elevation	0.03	0.01	0
White-tailed Deer	Summer	Elevation ²	-0.06	0.01	0
White-tailed Deer	Summer	Slope	-0.14	0.01	0
White-tailed Deer	Summer	Road density	0.09	0.01	0
White-tailed Deer	Summer	Distance to water	0.04	0.01	0
White-tailed Deer	Summer	Human modified	-0.13	0.02	0
White-tailed Deer	Summer	Canopy cover	0.02	0.01	0
White-tailed Deer	Summer	Distance to edge	-0.07	0.01	0
White-tailed Deer	Summer	Landcover: Developed	0	0.02	0.96
White-tailed Deer	Summer	Landcover: Open grass	0.14	0.01	0
White-tailed Deer	Summer	Landcover: Other	-0.86	0.11	0
White-tailed Deer	Summer	Landcover: Shrub mix	0.13	0.01	0
White-tailed Deer	Summer	Landcover: Wetland	0.51	0.04	0
White-tailed Deer	Winter	Intercept	-11.36	0.02	0
White-tailed Deer	Winter	Elevation	-0.05	0.01	0
White-tailed Deer	Winter	Elevation ²	-0.11	0	0
White-tailed Deer	Winter	Slope	-0.11	0.01	0
White-tailed Deer	Winter	Road density	0.05	0.01	0
White-tailed Deer	Winter	Distance to water	0.07	0.01	0
White-tailed Deer	Winter	Human modified	-0.12	0.01	0
White-tailed Deer	Winter	Canopy cover	-0.1	0.01	0
White-tailed Deer	Winter	Distance to edge	-0.1	0.01	0
White-tailed Deer	Winter	Landcover: Open grass	-0.25	0.02	0
White-tailed Deer	Winter	Landcover: Other	-0.63	0.03	0
White-tailed Deer	Winter	Landcover: Shrub mix	0.02	0.01	0.11
White-tailed Deer	Winter	Landcover: Wetland	-0.53	0.07	0
Wolf	Summer	Intercept	-11.68	0.08	0
Wolf	Summer	Elevation	0.05	0.03	0.03
Wolf	Summer	Elevation ²	-0.34	0.02	0
Wolf	Summer	Slope	-0.87	0.02	0
Wolf	Summer	Road density	0	0.01	0.93
Wolf	Summer	Distance to water	-0.38	0.02	0
Wolf	Summer	Human modified	-0.43	0.02	0
Wolf	Summer	Canopy cover	-0.02	0.02	0.13
Wolf	Summer	Distance to edge	-0.26	0.02	0
Wolf	Summer	Landcover: Open grass	0.1	0.04	0.02
Wolf	Summer	Landcover: Other	0.05	0.08	0.49
Wolf	Summer	Landcover: Shrub mix	0.06	0.04	0.09
Wolf	Winter	Intercept	-11.47	0.09	0

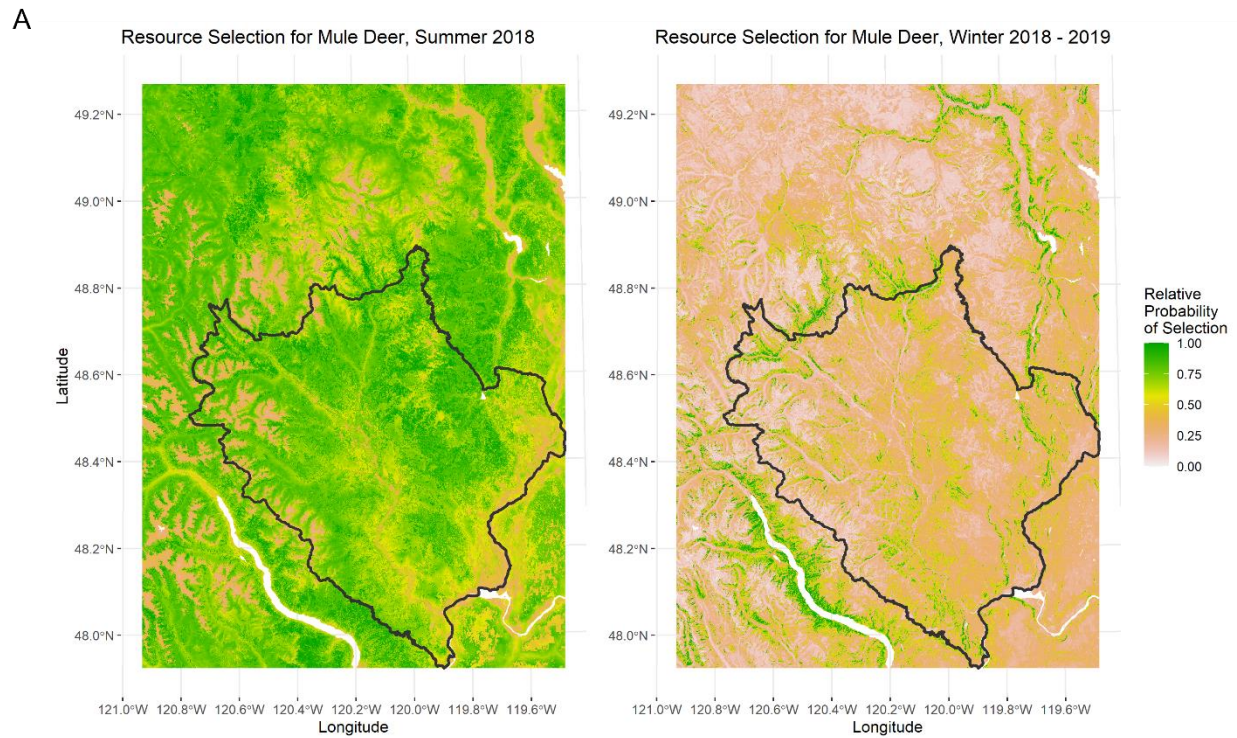
Wolf	Winter	Elevation	-0.14	0.03	0
Wolf	Winter	Elevation ²	-0.3	0.02	0
Wolf	Winter	Slope	-0.17	0.02	0
Wolf	Winter	Road density	-0.15	0.02	0
Wolf	Winter	Distance to water	-0.03	0.02	0.03
Wolf	Winter	Human modified	-0.33	0.02	0
Wolf	Winter	Canopy cover	-0.09	0.02	0
Wolf	Winter	Distance to edge	-0.35	0.02	0
Wolf	Winter	Landcover: Open grass	0.29	0.05	0
Wolf	Winter	Landcover: Other	-0.2	0.13	0.14
Wolf	Winter	Landcover: Shrub mix	0.23	0.04	0

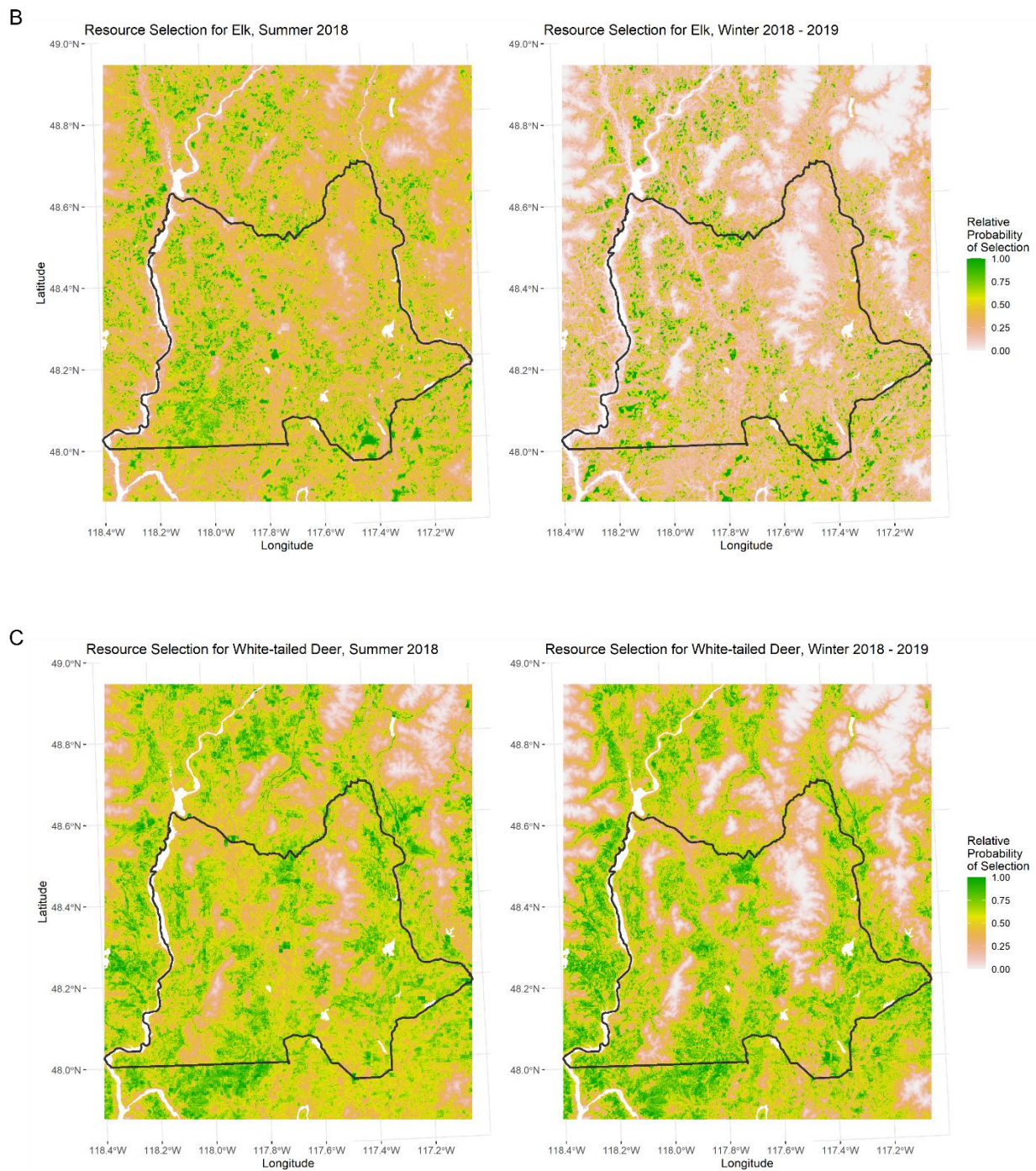
Table S1.3. Mean Spearman's rank-order correlation coefficients (ρ) and their standard errors for the 5-fold cross-validation of each season- and species-specific resource selection function (RSF). Each RSF was predicted annually for every species and season (summer 2018, 2019, 2020 and winter 2018-2109, 2019-2020, 2020-2021) using 5 training datasets and then cross-validated with testing data withheld from each training dataset.

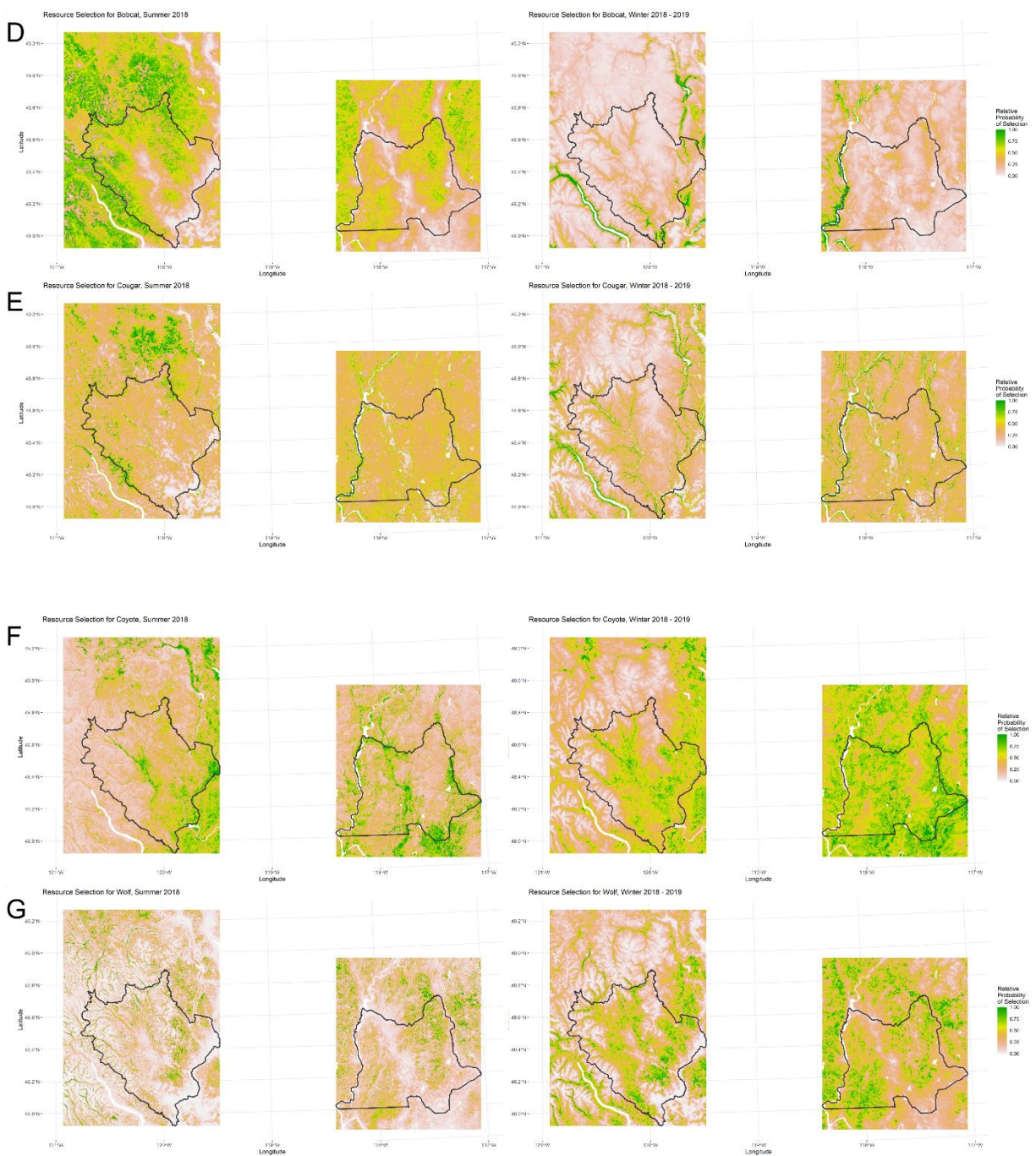
Species	Season	Year	Mean ρ	SE ρ
Bobcat	Summer	2018	0.86	0.02
Bobcat	Summer	2019	0.90	0.01
Bobcat	Summer	2020	0.89	0.01
Bobcat	Winter	2018-2019	0.96	0.00
Bobcat	Winter	2019-2020	0.96	0.00
Bobcat	Winter	2020-2021	0.97	0.01
Cougar	Summer	2018	0.99	0.00
Cougar	Summer	2019	0.97	0.01
Cougar	Summer	2020	0.99	0.00
Cougar	Winter	2018-2019	1.00	0.00
Cougar	Winter	2019-2020	1.00	0.00
Cougar	Winter	2020-2021	0.99	0.00
Coyote	Summer	2018	0.99	0.00
Coyote	Summer	2019	0.97	0.00
Coyote	Summer	2020	0.99	0.00
Coyote	Winter	2018-2019	0.98	0.00
Coyote	Winter	2019-2020	0.98	0.00
Coyote	Winter	2020-2021	0.98	0.01
Elk	Summer	2018	0.99	0.00
Elk	Summer	2019	0.99	0.00
Elk	Summer	2020	1.00	0.00
Elk	Winter	2018-2019	0.97	0.01

Elk	Winter	2019-2020	0.97	0.01
Elk	Winter	2020-2021	1.00	0.00
Mule Deer	Summer	2018	0.96	0.01
Mule Deer	Summer	2019	0.93	0.01
Mule Deer	Summer	2020	0.89	0.01
Mule Deer	Winter	2018-2019	0.99	0.00
Mule Deer	Winter	2019-2020	0.99	0.01
Mule Deer	Winter	2020-2021	0.97	0.01
White-tailed Deer	Summer	2018	0.96	0.01
White-tailed Deer	Summer	2019	0.96	0.01
White-tailed Deer	Summer	2020	0.97	0.01
White-tailed Deer	Winter	2018-2019	0.98	0.01
White-tailed Deer	Winter	2019-2020	0.99	0.01
White-tailed Deer	Winter	2020-2021	0.99	0.01
Wolf	Summer	2018	1.00	0.00
Wolf	Summer	2019	0.99	0.00
Wolf	Summer	2020	1.00	0.00
Wolf	Winter	2018-2019	1.00	0.00
Wolf	Winter	2019-2020	1.00	0.00
Wolf	Winter	2020-2021	1.00	0.00

Figure S1.1. Prediction maps of the relative probability of resource selection for mule deer (A), elk (B), white-tailed deer (C), bobcats (D), cougars (E), coyotes (F), and wolves (G) in summer 2018 and winter 2018 – 2019, in eastern Washington, USA. Mule deer were GPS-collared in only the Okanogan study area whereas elk and white-tailed deer were GPS-collared in only the Northeast study area. The RSF analyses and maps for these species were restricted to their respective study area. Resource selection was modeled across both study areas for bobcats, cougars, coyotes, and wolves because they were GPS-collared in both study areas. Resource selection maps for subsequent years (2019 – 2021) were very similar and not presented here.







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Appendix S2: Estimated state-dependent distribution parameters

The QQ-plots and autocorrelation function indicated relatively good fit for the turning angle parameters across all models. They suggested poorer fit for the step length parameters, owing to temporal autocorrelation in step length across all models. We adjusted the sine and cosine functions on step length to account for different time periods (e.g., 6, 12, or 24 hours) over which step length could be correlated due to diel activity patterns and adjusted GPS-collar relocation times to follow the same fix schedule. The autocorrelation was reduced across models, but the QQ-plots continued to indicate some unmodeled heterogeneity in step length. However, the 95% CIs for mean step length of the encamped and exploratory states did not overlap in any model (Appendix Table S2.2), indicating we were able to confidently differentiate the behavioral states despite temporal autocorrelation in the step lengths. Given we were not interested in predicting animal movement with these models but instead only interested in describing their movement behaviors and covariate relationships, we were less concerned with the influence of temporal autocorrelation on model fit.

Table S2.1. The estimated means and concentration parameters describing the state-dependent turning angles associated with an animal being in an encamped state or exploratory state based on species- and season-specific hidden Markov models (HMM).

Species	Study Area	Season	Parameter	Encamped	Exploratory
Cougar	Okanogan	Summer	Mean	0	0
Cougar	Okanogan	Summer	Concentration	0	0.56
Cougar	Okanogan	Winter	Mean	0	0
Cougar	Okanogan	Winter	Concentration	0	0.52
Cougar	Northeast	Summer	Mean	0	0
Cougar	Northeast	Summer	Concentration	0	0.65
Cougar	Northeast	Winter	Mean	0	0
Cougar	Northeast	Winter	Concentration	0	0.48
Coyote	Okanogan	Summer	Mean	0	0
Coyote	Okanogan	Summer	Concentration	0.12	0.25
Coyote	Okanogan	Winter	Mean	0	0
Coyote	Okanogan	Winter	Concentration	0	0.38
Coyote	Northeast	Summer	Mean	0	0
Coyote	Northeast	Summer	Concentration	0.23	0
Coyote	Northeast	Winter	Mean	0	0
Coyote	Northeast	Winter	Concentration	0	0.2
Elk	Northeast	Summer	Mean	0	0
Elk	Northeast	Summer	Concentration	0.16	0.29
Elk	Northeast	Winter	Mean	0	0
Elk	Northeast	Winter	Concentration	0.3	0.29
Mule Deer	Okanogan	Summer	Mean	0	0
Mule Deer	Okanogan	Summer	Concentration	0.09	0.05
Mule Deer	Okanogan	Winter	Mean	0	0

Mule Deer	Okanogan	Winter	Concentration	0.15	0.26
White-tailed Deer	Northeast	Summer	Mean	0	0
White-tailed Deer	Northeast	Summer	Concentration	0	0
White-tailed Deer	Northeast	Winter	Mean	0	0
White-tailed Deer	Northeast	Winter	Concentration	0.03	0.2
Wolf	Okanogan	Summer	Mean	0	0
Wolf	Okanogan	Summer	Concentration	0	0.32
Wolf	Okanogan	Winter	Mean	0	0
Wolf	Okanogan	Winter	Concentration	0	0.73
Wolf	Northeast	Summer	Mean	0	0
Wolf	Northeast	Summer	Concentration	0	0.38
Wolf	Northeast	Winter	Mean	0	0
Wolf	Northeast	Winter	Concentration	0	0.38

Table S2.2. The estimated mean and 95% confidence intervals (95% CI) describing the state-dependent step lengths (in meters) associated with animals being in an encamped state or exploratory state based on species- and season-specific hidden Markov models (HMM). We included sine and cosine transformations on hour and a categorical covariate for daylight (indicating whether it was day or night during each observation) to account for autocorrelation in step length associated with diel activity patterns. Step length was still mildly autocorrelated so 95% confidence intervals may be overly precise.

Species	Study Area	Season	Mean Encamped	95% CI Encamped	Mean Exploratory	95% CI Exploratory
Cougar	Okanogan	Summer	17.77	16.08 - 19.47	992.25	938.81 - 1045.7
Cougar	Okanogan	Winter	9.52	8.44 - 10.6	833.9	753.48 - 914.31
Cougar	Northeast	Summer	33.6	31 - 36.2	795.17	758.48 - 831.85
Cougar	Northeast	Winter	16.13	15.15 - 17.11	870.12	811.61 - 928.64
Coyote	Okanogan	Summer	26.21	20.37 - 32.04	911.4	861.43 - 961.36
Coyote	Okanogan	Winter	15.84	13.61 - 18.07	850.77	803.67 - 897.87
Coyote	Northeast	Summer	166.84	132.52 - 201.15	775.29	701.29 - 849.29
Coyote	Northeast	Winter	13.22	11.23 - 15.2	723.64	678.38 - 768.9

Elk	Northeast	Summer	139.81	132.26 - 147.37	419.51	408.44 - 430.58
Elk	Northeast	Winter	159.7	153.46 - 165.95	269.23	256.61 - 281.86
Mule Deer	Okanogan	Summer	122.07	119.76 - 124.39	293.47	287.49 - 299.45
Mule Deer	Okanogan	Winter	85.05	82.52 - 87.58	230.5	225.29 - 235.72
White-tailed Deer	Northeast	Summer	175.3	172.4 - 178.19	335.35	323.86 - 346.84
White-tailed Deer	Northeast	Winter	142.34	139.45 - 145.24	595.83	495.89 - 695.77
Wolf	Okanogan	Summer	53.95	41.44 - 66.47	2607.44	2343.46 - 2871.43
Wolf	Okanogan	Winter	23.27	17.85 - 28.7	1925.18	1698.69 - 2151.66
Wolf	Northeast	Summer	112.45	88 - 136.9	2127.28	1947.3 - 2307.27
Wolf	Northeast	Winter	14.14	10.17 - 18.12	2550.81	2140.38 - 2961.23

Appendix S3. Estimated transition probabilities

Table S3.1. Estimated transition probabilities for three carnivore species (cougars, coyotes, wolves) in response to covariates representing the relative probability of ungulate prey species site use [RSF(Elk), RSF(Mule Deer), and RSF(White-tailed Deer)], habitat features associated with predator hunting mode [terrain ruggedness index (TRI) and percentage of open habitat], habitat features associated with landscape permeability (distance to nearest road and presence of snow cover where No snow cover represents the intercept), and the 95% Confidence Intervals (95% CI) for each covariate effect. We interpreted covariates with 95% CIs that did not overlap 0 as significant.

Species	Season	Study Area	Transition	Parameter*	Estimate	95% CI
Cougar	Summer	Northeast	Trans.1->2	Intercept	-1.37	-1.44, -1.30
Cougar	Summer	Northeast	Trans.1->2	Terrain ruggedness	0.15	0.07, 0.24
Cougar	Summer	Northeast	Trans.1->2	Percent Open	-0.05	-0.11, 0.01
Cougar	Summer	Northeast	Trans.1->2	Nearest Road	-0.11	-0.17, -0.04
Cougar	Summer	Northeast	Trans.1->2	RSF(Elk)	0.03	-0.04, 0.10
Cougar	Summer	Northeast	Trans.1->2	RSF(White-tailed Deer)	0.12	0.04, 0.20
Cougar	Summer	Northeast	Trans.2->1	Intercept	-1.90	-1.97, -1.83
Cougar	Summer	Northeast	Trans.2->1	Terrain ruggedness	0.09	0.01, 0.17
Cougar	Summer	Northeast	Trans.2->1	Percent Open	0.13	0.07, 0.20
Cougar	Summer	Northeast	Trans.2->1	Nearest Road	-0.07	-0.14, 0.00
Cougar	Summer	Northeast	Trans.2->1	RSF(Elk)	-0.16	-0.23, -0.08
Cougar	Summer	Northeast	Trans.2->1	RSF(White-tailed Deer)	0.13	0.05, 0.21
Cougar	Summer	Okanogan	Trans.1->2	Intercept	-1.07	-1.16, -0.97
Cougar	Summer	Okanogan	Trans.1->2	Terrain ruggedness	0.17	0.07, 0.27
Cougar	Summer	Okanogan	Trans.1->2	Percent Open	-0.03	-0.13, 0.06
Cougar	Summer	Okanogan	Trans.1->2	Nearest Road	-0.20	-0.31, -0.10
Cougar	Summer	Okanogan	Trans.1->2	RSF (Mule Deer)	0.09	-0.01, 0.19
Cougar	Summer	Okanogan	Trans.2->1	Intercept	-1.75	-1.85, -1.64
Cougar	Summer	Okanogan	Trans.2->1	Terrain ruggedness	-0.09	-0.19, 0.02
Cougar	Summer	Okanogan	Trans.2->1	Percent Open	0.02	-0.08, 0.13
Cougar	Summer	Okanogan	Trans.2->1	Nearest Road	-0.19	-0.31, -0.08
Cougar	Summer	Okanogan	Trans.2->1	RSF(Mule Deer)	0.11	0.01, 0.22
Cougar	Winter	Northeast	Trans.1->2	Intercept	-1.40	-1.62, -1.17
Cougar	Winter	Northeast	Trans.1->2	Terrain ruggedness	0.13	0.05, 0.21
Cougar	Winter	Northeast	Trans.1->2	Percent Open	0.08	0.01, 0.15
Cougar	Winter	Northeast	Trans.1->2	Nearest Road	-0.11	-0.18, -0.04
Cougar	Winter	Northeast	Trans.1->2	Snow Cover (Y)	0.00	-0.23, 0.23
Cougar	Winter	Northeast	Trans.1->2	RSF(Elk)	0.11	0.03, 0.20
Cougar	Winter	Northeast	Trans.1->2	RSF(White-tailed Deer)	0.01	-0.08, 0.10

Cougar	Winter	Northeast	Trans.2->1	Intercept	-2.10	-2.33, -1.87
Cougar	Winter	Northeast	Trans.2->1	Terrain ruggedness	0.03	-0.05, 0.12
Cougar	Winter	Northeast	Trans.2->1	Percent Open	0.03	-0.05, 0.10
Cougar	Winter	Northeast	Trans.2->1	Nearest Road	-0.04	-0.12, 0.04
Cougar	Winter	Northeast	Trans.2->1	Snow Cover (Y)	0.49	0.25, 0.72
Cougar	Winter	Northeast	Trans.2->1	RSF(Elk)	-0.14	-0.23, -0.06
Cougar	Winter	Northeast	Trans.2->1	RSF(White-tailed Deer)	0.07	-0.03, 0.16
Cougar	Winter	Okanogan	Trans.1->2	Intercept	-1.94	-2.8, -1.08
Cougar	Winter	Okanogan	Trans.1->2	Terrain ruggedness	0.42	0.30, 0.53
Cougar	Winter	Okanogan	Trans.1->2	Percent Open	-0.23	-0.35, -0.11
Cougar	Winter	Okanogan	Trans.1->2	Nearest Road	-0.07	-0.21, 0.08
Cougar	Winter	Okanogan	Trans.1->2	Snow Cover (Y)	1.00	0.13, 1.87
Cougar	Winter	Okanogan	Trans.2->1	Intercept	-2.04	-2.95, -1.14
Cougar	Winter	Okanogan	Trans.2->1	Terrain ruggedness	0.33	0.22, 0.45
Cougar	Winter	Okanogan	Trans.2->1	Percent Open	-0.26	-0.37, -0.15
Cougar	Winter	Okanogan	Trans.2->1	Nearest Road	-0.12	-0.25, 0.00
Cougar	Winter	Okanogan	Trans.2->1	Snow Cover (Y)	0.44	-0.47, 1.35
Coyote	Summer	Northeast	Trans.1->2	Intercept	-1.03	-1.26, -0.81
Coyote	Summer	Northeast	Trans.1->2	Terrain ruggedness	0.05	-0.12, 0.22
Coyote	Summer	Northeast	Trans.1->2	Percent Open	-0.06	-0.19, 0.06
Coyote	Summer	Northeast	Trans.1->2	Nearest Road	0.14	0.00, 0.27
Coyote	Summer	Northeast	Trans.1->2	RSF(Elk)	0.03	-0.09, 0.16
Coyote	Summer	Northeast	Trans.1->2	RSF(White-tailed Deer)	0.04	-0.12, 0.19
Coyote	Summer	Northeast	Trans.2->1	Intercept	-0.83	-0.99, -0.66
Coyote	Summer	Northeast	Trans.2->1	Terrain ruggedness	-0.09	-0.27, 0.08
Coyote	Summer	Northeast	Trans.2->1	Percent Open	0.12	-0.01, 0.25
Coyote	Summer	Northeast	Trans.2->1	Nearest Road	0.10	-0.04, 0.23
Coyote	Summer	Northeast	Trans.2->1	RSF(Elk)	-0.08	-0.23, 0.06
Coyote	Summer	Northeast	Trans.2->1	RSF(White-tailed Deer)	0.09	-0.08, 0.26
Coyote	Summer	Okanogan	Trans.1->2	Intercept	0.84	0.64, 1.04
Coyote	Summer	Okanogan	Trans.1->2	Terrain ruggedness	-0.11	-0.31, 0.08
Coyote	Summer	Okanogan	Trans.1->2	Percent Open	0.15	-0.06, 0.36
Coyote	Summer	Okanogan	Trans.1->2	Nearest Road	0.14	-0.05, 0.34
Coyote	Summer	Okanogan	Trans.1->2	RSF(Mule Deer)	0.13	-0.07, 0.33
Coyote	Summer	Okanogan	Trans.2->1	Intercept	-2.43	-2.61, -2.25
Coyote	Summer	Okanogan	Trans.2->1	Terrain ruggedness	-0.23	-0.35, -0.12
Coyote	Summer	Okanogan	Trans.2->1	Percent Open	0.10	-0.02, 0.22
Coyote	Summer	Okanogan	Trans.2->1	Nearest Road	0.02	-0.09, 0.12
Coyote	Summer	Okanogan	Trans.2->1	RSF(Mule Deer)	0.19	0.07, 0.31
Coyote	Winter	Northeast	Trans.1->2	Intercept	1.06	-0.01, 2.14
Coyote	Winter	Northeast	Trans.1->2	Terrain ruggedness	0.34	0.08, 0.61
Coyote	Winter	Northeast	Trans.1->2	Percent Open	0.19	-0.11, 0.49

Coyote	Winter	Northeast	Trans.1->2	Nearest Road	0.20	-0.03, 0.43
Coyote	Winter	Northeast	Trans.1->2	Snow Cover (Y)	-1.17	-2.28, -0.05
Coyote	Winter	Northeast	Trans.1->2	RSF(Elk)	0.08	-0.14, 0.30
Coyote	Winter	Northeast	Trans.1->2	RSF(White-tailed Deer)	0.37	0.11, 0.64
Coyote	Winter	Northeast	Trans.2->1	Intercept	-3.50	-4.12, -2.88
Coyote	Winter	Northeast	Trans.2->1	Terrain ruggedness	-0.05	-0.25, 0.15
Coyote	Winter	Northeast	Trans.2->1	Percent Open	-0.29	-0.49, -0.10
Coyote	Winter	Northeast	Trans.2->1	Nearest Road	0.08	-0.08, 0.23
Coyote	Winter	Northeast	Trans.2->1	Snow Cover (Y)	0.52	-0.10, 1.15
Coyote	Winter	Northeast	Trans.2->1	RSF(Elk)	0.13	-0.02, 0.29
Coyote	Winter	Northeast	Trans.2->1	RSF(White-tailed Deer)	0.19	0.01, 0.37
Coyote	Winter	Okanogan	Trans.1->2	Intercept	0.12	-2.12, 2.37
Coyote	Winter	Okanogan	Trans.1->2	Terrain ruggedness	-0.06	-0.18, 0.05
Coyote	Winter	Okanogan	Trans.1->2	Percent Open	0.26	0.14, 0.39
Coyote	Winter	Okanogan	Trans.1->2	Nearest Road	0.04	-0.08, 0.17
Coyote	Winter	Okanogan	Trans.1->2	Snow Cover (Y)	0.32	-1.93, 2.57
Coyote	Winter	Okanogan	Trans.2->1	Intercept	-2.94	-4.71, -1.18
Coyote	Winter	Okanogan	Trans.2->1	Terrain ruggedness	0.11	0.03, 0.20
Coyote	Winter	Okanogan	Trans.2->1	Percent Open	-0.22	-0.3, -0.13
Coyote	Winter	Okanogan	Trans.2->1	Nearest Road	0.07	-0.01, 0.16
Coyote	Winter	Okanogan	Trans.2->1	Snow Cover (Y)	0.87	-0.90, 2.64
Wolf	Summer	Northeast	Trans.1->2	Intercept	-0.57	-0.71, -0.42
Wolf	Summer	Northeast	Trans.1->2	Terrain ruggedness	-0.07	-0.21, 0.08
Wolf	Summer	Northeast	Trans.1->2	Percent Open	0.05	-0.08, 0.17
Wolf	Summer	Northeast	Trans.1->2	Nearest Road	-0.18	-0.31, -0.05
Wolf	Summer	Northeast	Trans.1->2	RSF(Elk)	0.21	0.08, 0.34
Wolf	Summer	Northeast	Trans.1->2	RSF(White-tailed Deer)	-0.11	-0.27, 0.04
Wolf	Summer	Northeast	Trans.2->1	Intercept	-0.89	-1.05, -0.73
Wolf	Summer	Northeast	Trans.2->1	Terrain ruggedness	-0.15	-0.29, 0.00
Wolf	Summer	Northeast	Trans.2->1	Percent Open	-0.06	-0.18, 0.05
Wolf	Summer	Northeast	Trans.2->1	Nearest Road	0.15	0.04, 0.26
Wolf	Summer	Northeast	Trans.2->1	RSF(Elk)	-0.28	-0.4, -0.15
Wolf	Summer	Northeast	Trans.2->1	RSF(White-tailed Deer)	0.13	0.00, 0.26
Wolf	Summer	Okanogan	Trans.1->2	Intercept	-0.33	-0.48, -0.17
Wolf	Summer	Okanogan	Trans.1->2	Terrain ruggedness	-0.19	-0.36, -0.03
Wolf	Summer	Okanogan	Trans.1->2	Percent Open	0.01	-0.16, 0.18
Wolf	Summer	Okanogan	Trans.1->2	Nearest Road	0.05	-0.11, 0.21
Wolf	Summer	Okanogan	Trans.1->2	RSF(Mule Deer)	-0.16	-0.32, 0.00
Wolf	Summer	Okanogan	Trans.2->1	Intercept	-1.22	-1.43, -1.01
Wolf	Summer	Okanogan	Trans.2->1	Terrain ruggedness	-0.32	-0.46, -0.18
Wolf	Summer	Okanogan	Trans.2->1	Percent Open	-0.16	-0.3, -0.01

Wolf	Summer	Okanogan	Trans.2->1	Nearest Road	0.05	-0.09, 0.18
Wolf	Summer	Okanogan	Trans.2->1	RSF(Mule Deer)	0.30	0.16, 0.44
Wolf	Winter	Northeast	Trans.1->2	Intercept	0.11	-0.77, 0.99
Wolf	Winter	Northeast	Trans.1->2	Terrain ruggedness	0.01	-0.24, 0.25
Wolf	Winter	Northeast	Trans.1->2	Percent Open	0.22	-0.08, 0.51
Wolf	Winter	Northeast	Trans.1->2	Nearest Road	0.09	-0.14, 0.32
Wolf	Winter	Northeast	Trans.1->2	Snow Cover (Y)	0.38	-0.54, 1.30
Wolf	Winter	Northeast	Trans.1->2	RSF(Elk)	-0.05	-0.36, 0.25
Wolf	Winter	Northeast	Trans.1->2	RSF(White-tailed Deer)	0.39	0.11, 0.68
Wolf	Winter	Northeast	Trans.2->1	Intercept	-1.52	-2.2, -0.84
Wolf	Winter	Northeast	Trans.2->1	Terrain ruggedness	0.07	-0.11, 0.24
Wolf	Winter	Northeast	Trans.2->1	Percent Open	-0.06	-0.24, 0.11
Wolf	Winter	Northeast	Trans.2->1	Nearest Road	-0.03	-0.18, 0.13
Wolf	Winter	Northeast	Trans.2->1	Snow Cover (Y)	0.21	-0.47, 0.90
Wolf	Winter	Northeast	Trans.2->1	RSF(Elk)	-0.11	-0.30, 0.08
Wolf	Winter	Northeast	Trans.2->1	RSF(White-tailed Deer)	-0.05	-0.25, 0.15
Wolf	Winter	Okanogan	Trans.1->2	Intercept	0.61	-0.55, 1.78
Wolf	Winter	Okanogan	Trans.1->2	Terrain ruggedness	0.07	-0.15, 0.30
Wolf	Winter	Okanogan	Trans.1->2	Percent Open	0.17	-0.04, 0.38
Wolf	Winter	Okanogan	Trans.1->2	Nearest Road	0.04	-0.08, 0.17
Wolf	Winter	Okanogan	Trans.1->2	Snow Cover (Y)	-0.61	-1.79, 0.58
Wolf	Winter	Okanogan	Trans.1->2	RSF(Mule Deer)	-0.06	-0.32, 0.20
Wolf	Winter	Okanogan	Trans.2->1	Intercept	-1.78	-2.50, -1.06
Wolf	Winter	Okanogan	Trans.2->1	Terrain ruggedness	0.14	-0.02, 0.30
Wolf	Winter	Okanogan	Trans.2->1	Percent Open	-0.17	-0.32, -0.02
Wolf	Winter	Okanogan	Trans.2->1	Nearest Road	0.18	0.08, 0.27
Wolf	Winter	Okanogan	Trans.2->1	Snow Cover (Y)	0.08	-0.64, 0.81
Wolf	Winter	Okanogan	Trans.2->1	RSF(Mule Deer)	-0.12	-0.32, 0.07

*Inclusion of RSF(Elk), RSF(Mule Deer), and RSF(White-tailed Deer) depended on the study area. Relative probability of mule deer presence was included in predator models fitted to movement data from the Okanogan study area whereas relative probability of elk and white-tailed deer presence were included in predator models fitted with movement data from the Northeast study area.

Table S3.2. Estimated transition probabilities for three ungulate prey species (elk, mule deer, and white-tailed deer) in response to covariates representing the relative probability of stalking predator site use [RSF(Bobcat) and RSF(Cougar)], relative probability of cursorial predator site use [RSF(Coyote) and RSF(Wolf)], habitat features associated with predator hunting mode [terrain ruggedness index (TRI) and percentage of open habitat], habitat features associated with landscape permeability (distance to nearest road and presence of snow cover where no snow cover represents the intercept), and the 95% Confidence Intervals (95% CI) for each covariate effect. We interpreted covariates with 95% CIs that did not overlap 0 as significant.

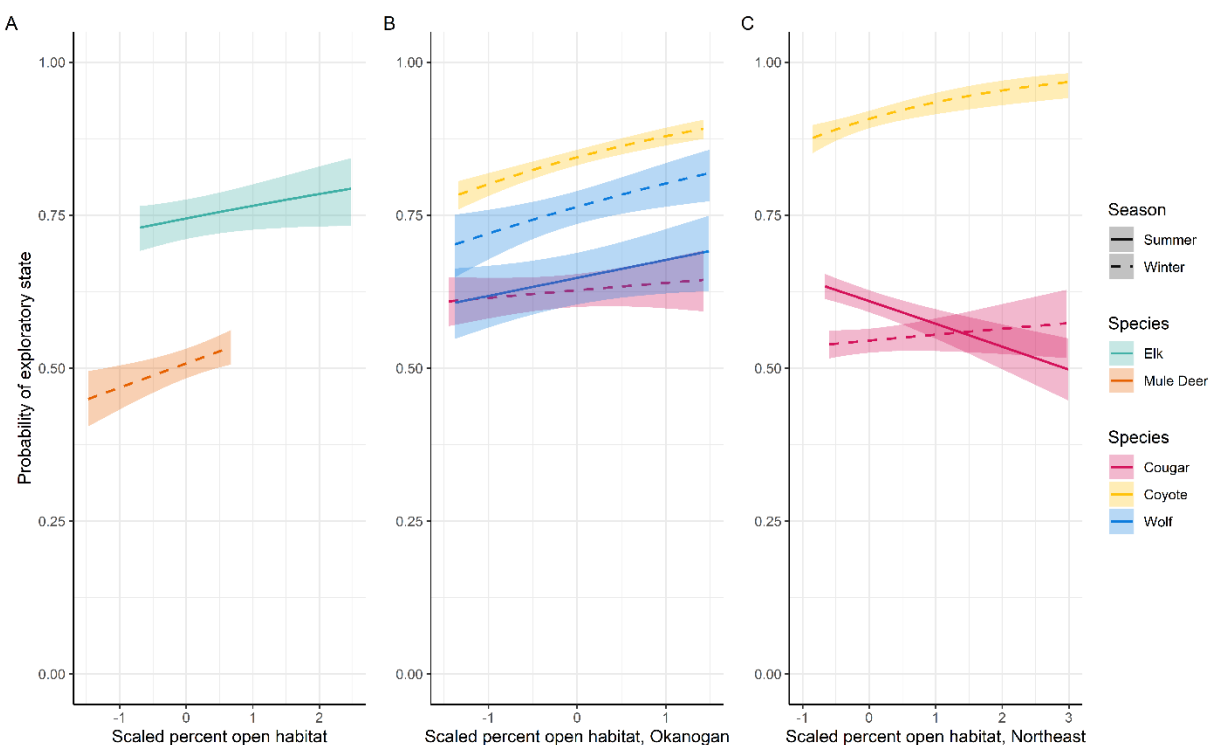
Species	Season	Study Area	Transition	Parameter	Estimate	95% CI
Elk	Summer	Northeast	Trans.1->2	Intercept	-1.79	-2.00, -1.58
Elk	Summer	Northeast	Trans.1->2	Terrain ruggedness	0.07	-0.10, 0.25
Elk	Summer	Northeast	Trans.1->2	Percent Open	-0.20	-0.34, -0.06
Elk	Summer	Northeast	Trans.1->2	Nearest Road	-0.23	-0.34, -0.12
Elk	Summer	Northeast	Trans.1->2	RSF(Cougar)	-0.35	-0.55, -0.15
Elk	Summer	Northeast	Trans.1->2	RSF(Wolf)	0.12	-0.03, 0.27
Elk	Summer	Northeast	Trans.1->2	RSF(Coyote)	0.13	-0.07, 0.33
Elk	Summer	Northeast	Trans.2->1	Intercept	-2.97	-3.25, -2.68
Elk	Summer	Northeast	Trans.2->1	Terrain ruggedness	1.15	0.96, 1.35
Elk	Summer	Northeast	Trans.2->1	Percent Open	-0.29	-0.46, -0.13
Elk	Summer	Northeast	Trans.2->1	Nearest Road	-0.22	-0.35, -0.08
Elk	Summer	Northeast	Trans.2->1	RSF(Cougar)	-0.29	-0.47, -0.11
Elk	Summer	Northeast	Trans.2->1	RSF(Wolf)	0.58	0.42, 0.73
Elk	Summer	Northeast	Trans.2->1	RSF(Coyote)	-0.04	-0.31, 0.23
Elk	Winter	Northeast	Trans.1->2	Intercept	-4.26	-4.81, -3.71
Elk	Winter	Northeast	Trans.1->2	Terrain ruggedness	-0.62	-1.00, -0.25
Elk	Winter	Northeast	Trans.1->2	Percent Open	0.19	-0.04, 0.43
Elk	Winter	Northeast	Trans.1->2	Nearest Road	0.16	-0.10, 0.42
Elk	Winter	Northeast	Trans.1->2	Snow Cover (Y)	-0.65	-1.20, -0.10
Elk	Winter	Northeast	Trans.1->2	RSF(Cougar)	-1.93	-2.41, -1.44
Elk	Winter	Northeast	Trans.1->2	RSF(Wolf)	0.37	0.12, 0.61
Elk	Winter	Northeast	Trans.1->2	RSF(Coyote)	0.02	-0.24, 0.28
Elk	Winter	Northeast	Trans.2->1	Intercept	-3.73	-4.28, -3.18
Elk	Winter	Northeast	Trans.2->1	Terrain ruggedness	0.77	0.45, 1.10
Elk	Winter	Northeast	Trans.2->1	Percent Open	-0.14	-0.41, 0.12
Elk	Winter	Northeast	Trans.2->1	Nearest Road	0.51	0.23, 0.78
Elk	Winter	Northeast	Trans.2->1	Snow Cover (Y)	0.45	-0.13, 1.03
Elk	Winter	Northeast	Trans.2->1	RSF(Cougar)	0.19	-0.10, 0.49
Elk	Winter	Northeast	Trans.2->1	RSF(Wolf)	0.98	0.69, 1.28
Elk	Winter	Northeast	Trans.2->1	RSF(Coyote)	1.02	0.65, 1.39
Mule Deer	Summer	Okanogan	Trans.1->2	Intercept	-4.02	-4.15, -3.90
Mule Deer	Summer	Okanogan	Trans.1->2	Terrain ruggedness	-0.58	-0.75, -0.42
Mule Deer	Summer	Okanogan	Trans.1->2	Percent Open	0.08	-0.06, 0.22
Mule Deer	Summer	Okanogan	Trans.1->2	Nearest Road	0.16	0.05, 0.27
Mule Deer	Summer	Okanogan	Trans.1->2	RSF(Cougar)	0.03	-0.09, 0.15
Mule Deer	Summer	Okanogan	Trans.1->2	RSF(Wolf)	-0.13	-0.25, 0.00
Mule Deer	Summer	Okanogan	Trans.1->2	RSF(Bobcat)	0.35	0.17, 0.52
Mule Deer	Summer	Okanogan	Trans.2->1	Intercept	-3.75	-3.88, -3.61
Mule Deer	Summer	Okanogan	Trans.2->1	Terrain ruggedness	0.45	0.30, 0.59
Mule Deer	Summer	Okanogan	Trans.2->1	Percent Open	0.02	-0.12, 0.16
Mule Deer	Summer	Okanogan	Trans.2->1	Nearest Road	0.03	-0.07, 0.14
Mule Deer	Summer	Okanogan	Trans.2->1	RSF(Cougar)	0.08	-0.06, 0.21
Mule Deer	Summer	Okanogan	Trans.2->1	RSF(Wolf)	0.11	-0.01, 0.23

Mule Deer	Summer	Okanogan	Trans.2->1	RSF(Bobcat)	0.55	0.35, 0.74
Mule Deer	Winter	Okanogan	Trans.1->2	Intercept	-2.40	-2.79, -2.01
Mule Deer	Winter	Okanogan	Trans.1->2	Terrain ruggedness	0.01	-0.14, 0.16
Mule Deer	Winter	Okanogan	Trans.1->2	Percent Open	0.13	0.01, 0.25
Mule Deer	Winter	Okanogan	Trans.1->2	Nearest Road	-0.04	-0.14, 0.07
Mule Deer	Winter	Okanogan	Trans.1->2	Snow Cover (Y)	-1.09	-1.49, -0.69
Mule Deer	Winter	Okanogan	Trans.1->2	RSF(Cougar)	-0.25	-0.40, -0.11
Mule Deer	Winter	Okanogan	Trans.1->2	RSF(Wolf)	0.01	-0.10, 0.12
Mule Deer	Winter	Okanogan	Trans.1->2	RSF(Bobcat)	0.23	0.12, 0.34
Mule Deer	Winter	Okanogan	Trans.1->2	RSF(Coyote)	0.14	0.01, 0.27
Mule Deer	Winter	Okanogan	Trans.2->1	Intercept	-3.16	-3.62, -2.70
Mule Deer	Winter	Okanogan	Trans.2->1	Terrain ruggedness	0.78	0.64, 0.92
Mule Deer	Winter	Okanogan	Trans.2->1	Percent Open	-0.04	-0.14, 0.07
Mule Deer	Winter	Okanogan	Trans.2->1	Nearest Road	-0.13	-0.23, -0.03
Mule Deer	Winter	Okanogan	Trans.2->1	Snow Cover (Y)	-0.36	-0.83, 0.11
Mule Deer	Winter	Okanogan	Trans.2->1	RSF(Cougar)	0.08	-0.05, 0.22
Mule Deer	Winter	Okanogan	Trans.2->1	RSF(Wolf)	0.15	0.04, 0.26
Mule Deer	Winter	Okanogan	Trans.2->1	RSF(Bobcat)	-0.15	-0.27, -0.03
Mule Deer	Winter	Okanogan	Trans.2->1	RSF(Coyote)	0.08	-0.09, 0.24
White-tailed Deer	Summer	Northeast	Trans.1->2	Intercept	-5.17	-5.38, -4.97
White-tailed Deer	Summer	Northeast	Trans.1->2	Terrain ruggedness	-0.11	-0.43, 0.20
White-tailed Deer	Summer	Northeast	Trans.1->2	Percent Open	0.17	-0.06, 0.39
White-tailed Deer	Summer	Northeast	Trans.1->2	Nearest Road	-0.09	-0.32, 0.13
White-tailed Deer	Summer	Northeast	Trans.1->2	RSF(Cougar)	-0.15	-0.51, 0.21
White-tailed Deer	Summer	Northeast	Trans.1->2	RSF(Wolf)	-0.67	-1.12, -0.22
White-tailed Deer	Summer	Northeast	Trans.1->2	RSF(Bobcat)	0.82	0.48, 1.15
White-tailed Deer	Summer	Northeast	Trans.1->2	RSF(Coyote)	0.17	-0.23, 0.58
White-tailed Deer	Summer	Northeast	Trans.2->1	Intercept	-4.25	-4.52, -3.98
White-tailed Deer	Summer	Northeast	Trans.2->1	Terrain ruggedness	0.21	-0.07, 0.50
White-tailed Deer	Summer	Northeast	Trans.2->1	Percent Open	0.12	-0.16, 0.40
White-tailed Deer	Summer	Northeast	Trans.2->1	Nearest Road	-0.24	-0.47, -0.01
White-tailed Deer	Summer	Northeast	Trans.2->1	RSF(Cougar)	0.62	0.38, 0.85

White-tailed Deer	Summer	Northeast	Trans.2->1	RSF(Wolf)	0.50	0.14, 0.86
White-tailed Deer	Summer	Northeast	Trans.2->1	RSF(Bobcat)	-0.02	-0.41, 0.37
White-tailed Deer	Summer	Northeast	Trans.2->1	RSF(Coyote)	-0.76	-1.19, -0.32
White-tailed Deer	Winter	Northeast	Trans.1->2	Intercept	-4.82	-5.2, -4.44
White-tailed Deer	Winter	Northeast	Trans.1->2	Terrain ruggedness	-0.01	-0.25, 0.22
White-tailed Deer	Winter	Northeast	Trans.1->2	Percent Open	-0.01	-0.19, 0.18
White-tailed Deer	Winter	Northeast	Trans.1->2	Nearest Road	0.00	-0.15, 0.14
White-tailed Deer	Winter	Northeast	Trans.1->2	Snow Cover (Y)	-0.01	-0.42, 0.40
White-tailed Deer	Winter	Northeast	Trans.1->2	RSF(Cougar)	-0.17	-0.50, 0.16
White-tailed Deer	Winter	Northeast	Trans.1->2	RSF(Wolf)	0.34	0.15, 0.53
White-tailed Deer	Winter	Northeast	Trans.1->2	RSF(Bobcat)	0.07	-0.13, 0.27
White-tailed Deer	Winter	Northeast	Trans.1->2	RSF(Coyote)	0.15	-0.06, 0.36
White-tailed Deer	Winter	Northeast	Trans.2->1	Intercept	-1.37	-1.81, -0.93
White-tailed Deer	Winter	Northeast	Trans.2->1	Terrain ruggedness	0.37	0.08, 0.67
White-tailed Deer	Winter	Northeast	Trans.2->1	Percent Open	-0.15	-0.33, 0.04
White-tailed Deer	Winter	Northeast	Trans.2->1	Nearest Road	-0.02	-0.22, 0.18
White-tailed Deer	Winter	Northeast	Trans.2->1	Snow Cover (Y)	-0.44	-0.93, 0.04
White-tailed Deer	Winter	Northeast	Trans.2->1	RSF(Cougar)	0.32	0.03, 0.62
White-tailed Deer	Winter	Northeast	Trans.2->1	RSF(Wolf)	0.60	0.34, 0.86
White-tailed Deer	Winter	Northeast	Trans.2->1	RSF(Bobcat)	-0.37	-0.65, -0.09
White-tailed Deer	Winter	Northeast	Trans.2->1	RSF(Coyote)	0.49	0.22, 0.76

Figure S3.1. Estimated probability cougars, coyotes, and wolves, and elk, mule deer, and white-tailed deer will be in an “exploratory” behavioral state in summer (solid line) and winter (dashed line). The probability of A) ungulates, B) predators in the Okanogan study area, or C) predators in the Northeast study area being in the exploratory state varied with increasing habitat openness (top figure), which we used to represent habitat complexity associated with predator hunting mode, and distance to nearest road (bottom figure), representing landscape permeability. Plotted relationships are based on covariate values that have been centered and scaled and all other covariates held at their mean value (0); the binary snow cover covariate was held at 1 in the winter results. The range of scaled RSF values on the x-axis varied in each species-specific analysis because the mean and standard deviation differed by species. The probability of these species being in an “encamped” behavioral state is the inverse of these plotted relationships and not included for simplicity.

Stationary state probabilities for ungulates and predators in response percentage of open habitat



Stationary state probabilities for ungulates and predators in response distance to nearest road

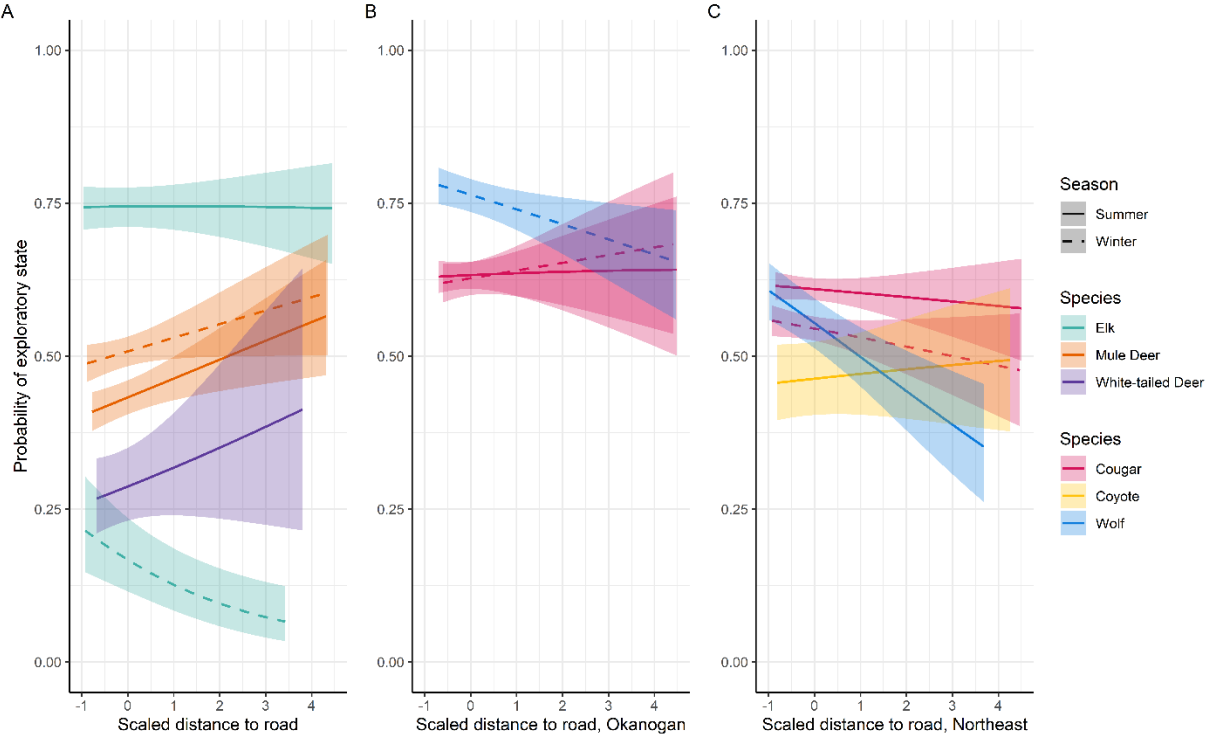
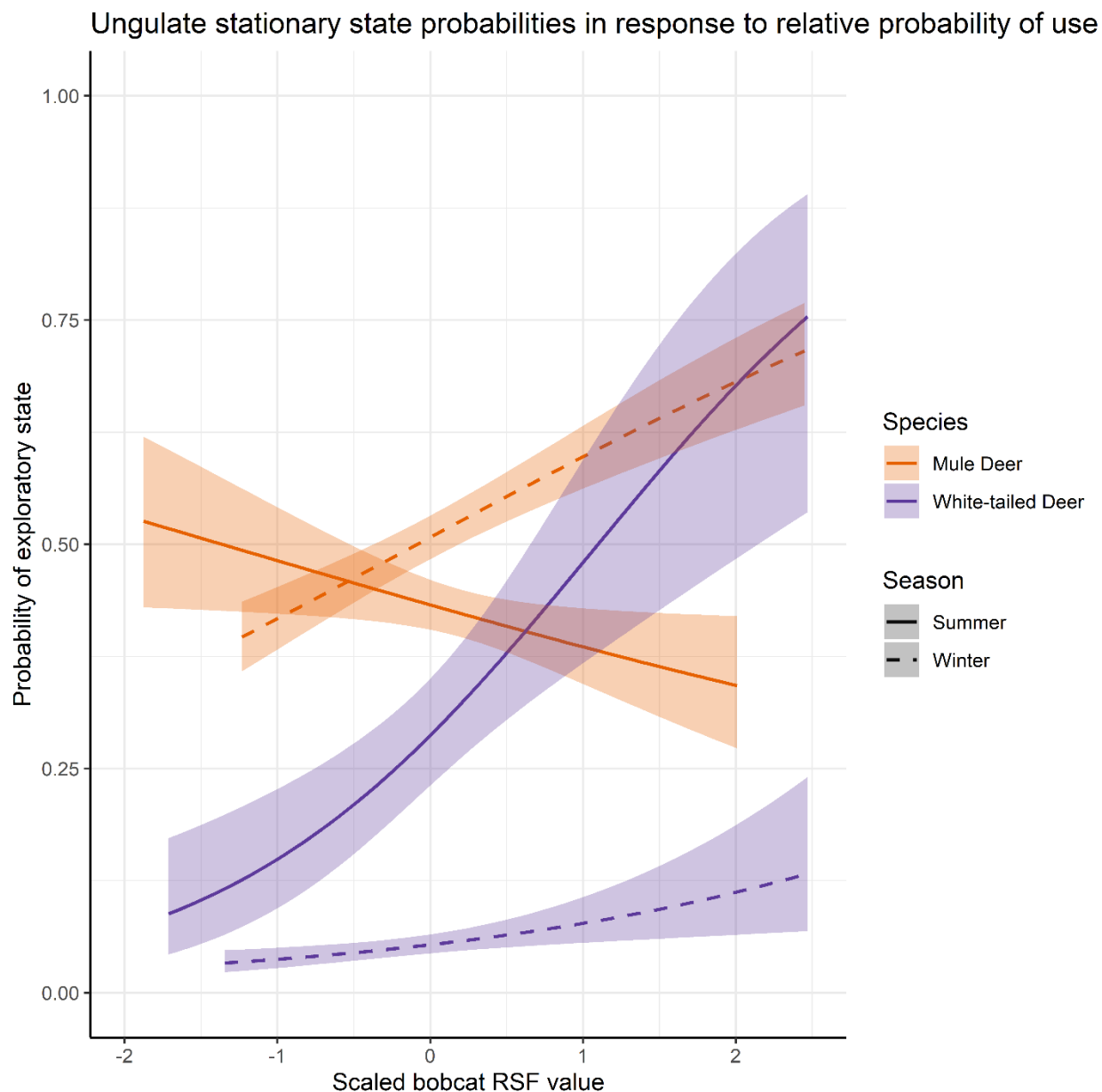


Figure S3.2. Estimated probability mule deer and white-tailed deer will be in an “exploratory” behavioral state in summer (solid line) and winter (dashed line) across the Okanogan and Northeast study areas in response to the relative probability of use by bobcats, represented by scaled bobcat RSF values. Plotted relationships are based on covariate values that have been centered and scaled and all other covariates held at their mean value (0); the binary snow cover covariate was held at 1 in the winter results. The range of scaled RSF values on the x-axis varied in each ungulate and season-specific analysis because the mean and standard deviation differed with each. The probability of these species being in an “encamped” behavioral state is the inverse of these plotted relationships and not included for simplicity.



APPENDIX C

Supplemental Materials for Chapter 4

Temporal responses to risky places and risky times in a multi-predator, multi-prey system

Appendix S1: Generalized linear mixed-effects models for latency analysis

Predator-prey GLMM

$$\text{TBD.pp}_i \sim \exp(\lambda.\text{pp}_i)$$

$$\lambda.\text{pp}_i = 1/\mu.\text{pp}_i$$

$$\log(\mu.\text{pp}_i) = \beta_0 + \beta_1 * \text{TRI}_i + \beta_2 * \text{Predator Species}_i + \beta_3 * \text{Season}_i + \beta_4 * (\text{TRI}_i \times \text{Predator Species}_i) + \alpha_{i, \text{cam}}$$

where TBD.pp is the i^{th} time-between-detections of a predator and prey species detected at a camera site (*cam*) and an exponentially distributed random variable with mean $\lambda.\text{pp}$, which is equal to the inverse of the mean time-between-detections ($\mu.\text{pp}$) and was regressed on the effects of an index for terrain ruggedness (TRI), the species of predator detected prior to the prey detection (Predator Species = bobcat, coyote, black bear, cougar, wolf), the season during which the observation occurred (Season = summer, fall, winter, spring), an interaction between TRI and Predator Species, and a random effect for camera site. Predator species and season were categorical variables.

Ungulate GLMM

$$\text{TBD.ung}_i \sim \exp(\lambda.\text{ung}_i)$$

$$\lambda.\text{ung}_i = 1/\mu.\text{ung}_i$$

$$\log(\mu.\text{ung}_{i, \text{cam}}) = \beta_0 + \beta_1 * \text{TRI}_i + \beta_2 * \text{Ungulate Species}_i + \beta_3 * \text{Season}_i + \beta_4 * (\text{TRI}_i \times \text{Ungulate Species}_i) + \alpha_{i, \text{cam}}$$

where TBD.ung is the i^{th} time-between-detections of two different ungulate species at a camera site (*cam*) and an exponentially distributed random variable with mean $\lambda.\text{ung}$, which is equal to the inverse of the mean time-between detections ($\mu.\text{ung}$) and was regressed on the effects of an index for terrain ruggedness (TRI), the species of ungulate detected prior to the focal ungulate detection (Ungulate Species = elk, moose, mule deer, white-tailed deer), the season during which the observation occurred (Season = summer, fall, winter, spring), an interaction between TRI and Ungulate Species, and a random effect for camera site. Ungulate species and season were categorical variables.

Appendix S2: Summary of photo-capture data

Table S2.1. Summary of independent detections of each species generated per season (Summer = 1 June – 30 Sept; Fall = 1 Oct – 30 Nov; Winter = 1 Dec – 31 Mar; Spring = 1 Apr – 31 May) by camera traps deployed in eastern Washington, June 2018 – 2021.

Season	Species	Independent detections (n)	Proportion of cameras
Summer	Black Bear	1208	0.73
Summer	Bobcat	431	0.35
Summer	Cougar	289	0.37
Summer	Coyote	2059	0.62
Summer	Elk	375	0.21
Summer	Moose	616	0.39
Summer	Mule Deer	3933	0.61
Summer	White-tailed Deer	7030	0.59
Summer	Wolf	84	0.11
Fall	Black Bear	149	0.26
Fall	Bobcat	158	0.25
Fall	Cougar	138	0.25
Fall	Coyote	1023	0.58
Fall	Elk	92	0.12
Fall	Moose	255	0.23
Fall	Mule Deer	2186	0.56
Fall	White-tailed Deer	3455	0.49
Fall	Wolf	41	0.07
Winter	Black Bear	6	0.02
Winter	Bobcat	167	0.20
Winter	Cougar	143	0.19
Winter	Coyote	1433	0.56
Winter	Elk	59	0.07
Winter	Moose	204	0.24
Winter	Mule Deer	1465	0.34
Winter	White-tailed Deer	4004	0.42
Winter	Wolf	36	0.08
Spring	Black Bear	244	0.37
Spring	Bobcat	156	0.25
Spring	Cougar	130	0.21
Spring	Coyote	898	0.54
Spring	Elk	138	0.14
Spring	Moose	142	0.23
Spring	Mule Deer	1856	0.55
Spring	White-tailed Deer	2493	0.48
Spring	Wolf	33	0.04

Table S2.2. Number of paired detections per season (n) used to estimate the time-between-detections of an ungulate immediately following the detection of a predator or different ungulate species at camera sites in eastern Washington, USA, 2018 – 2021. The Predator-Prey analyses paired observations based on the last image of a unique predator detection with the first image of the ungulate detected immediately after, where no other species were detected in between. The Ungulate analyses paired observations based on the last image of a unique ungulate detection with the first image of the next ungulate detection of a different species, where no other species were detected in between. The time between each pair of detections was then calculated in minutes. NA indicates the specific species pairing was not detected back-to-back during a given season.

Species pair	Analysis	Summer (n)	Fall (n)	Winter (n)	Spring (n)
Elk - Black Bear	Predator-Prey	23	3	NA	2
Elk - Bobcat	Predator-Prey	6	NA	2	5
Elk - Cougar	Predator-Prey	5	NA	1	4
Elk - Coyote	Predator-Prey	15	8	3	8
Elk - Moose	Ungulate	9	2	3	6
Elk - Mule Deer	Ungulate	8	1	2	5
Elk - White-tailed Deer	Ungulate	107	27	11	38
Elk - Wolf	Predator-Prey	1	NA	NA	NA
Moose - Black Bear	Predator-Prey	54	5	NA	6
Moose - Bobcat	Predator-Prey	17	6	5	2
Moose - Cougar	Predator-Prey	12	5	1	4
Moose - Coyote	Predator-Prey	37	13	14	11
Moose - Elk	Ungulate	8	2	1	4
Moose - Mule Deer	Ungulate	55	16	5	11
Moose - White-tailed Deer	Ungulate	103	43	30	20
Moose - Wolf	Predator-Prey	4	2	3	NA
Mule Deer - Black Bear	Predator-Prey	161	18	NA	53
Mule Deer - Bobcat	Predator-Prey	40	14	8	22
Mule Deer - Cougar	Predator-Prey	27	14	7	17
Mule Deer - Coyote	Predator-Prey	214	172	147	124
Mule Deer - Elk	Ungulate	5	4	1	8
Mule Deer - Moose	Ungulate	49	23	5	9
Mule Deer - White-tailed Deer	Ungulate	191	73	40	63
Mule Deer - Wolf	Predator-Prey	18	6	5	3
White-tailed Deer - Black Bear	Predator-Prey	187	19	NA	25
White-tailed Deer - Bobcat	Predator-Prey	72	21	20	13
White-tailed Deer - Cougar	Predator-Prey	45	31	26	19
White-tailed Deer - Coyote	Predator-Prey	311	149	226	135
White-tailed Deer - Elk	Ungulate	110	29	13	34
White-tailed Deer - Moose	Ungulate	117	45	22	19
White-tailed Deer - Mule Deer	Ungulate	188	72	48	62
White-tailed Deer - Wolf	Predator-Prey	13	3	4	1

Appendix S3: Temporal overlap analysis results

Table S3.1. Coefficient of overlapping estimates ($\bar{\Delta}$) and bootstrapped 95% confidence intervals (95% CI) measuring the amount of overlap in diel activity curves for each ungulate species at camera sites with low versus high levels of habitat complexity or risk of predator occurrence. Habitat complexity was represented by an index of terrain ruggedness (TRI) at each camera site. Cameras in areas below the mean TRI were considered low habitat complexity; cameras in areas above the mean TRI were considered high habitat complexity. Risk of predator occurrence was determined by whether a given predator species was detected at least once (high risk) or never detected (low risk) at a camera site. Temporal overlap was estimated seasonally for each ungulate species at each level and type of habitat complexity. Bobcat and coyote detections were not considered for elk or moose overlap analyses, and bears were excluded from all winter analyses. Estimates based on small sample sizes ($n < 20$ for at least one level of risk) were not considered for interpretation in text.

Species	Season	Risk type	$\bar{\Delta}$	95% CI	Low risk (n)	High risk (n)
Mule deer	Summer	TRI	0.88	0.85 - 0.91	1881	2052
Mule deer	Summer	Cougar detected	0.94	0.91 - 0.96	2661	1272
Mule deer	Summer	Wolf detected	0.93	0.9 - 0.95	3291	642
Mule deer	Summer	Black bear detected	0.88	0.85 - 0.9	1274	2659
Mule deer	Summer	Bobcat detected	0.96	0.94 - 0.97	2857	1076
Mule deer	Summer	Coyote detected	0.94	0.92 - 0.96	1357	2576
Mule deer	Fall	TRI	0.93	0.89 - 0.95	1147	1039
Mule deer	Fall	Cougar detected	0.93	0.89 - 0.96	1759	427
Mule deer	Fall	Wolf detected	0.88	0.8 - 0.93	2053	133
Mule deer	Fall	Black bear detected	0.96	0.93 - 0.98	1766	420
Mule deer	Fall	Bobcat detected	0.95	0.91 - 0.97	1764	422
Mule deer	Fall	Coyote detected	0.92	0.88 - 0.95	667	1519
Mule deer	Winter	TRI	0.86	0.81 - 0.9	586	879
Mule deer	Winter	Cougar detected	0.83	0.76 - 0.88	1130	335
Mule deer	Winter	Wolf detected	0.79	0.66 - 0.87	1419	46
Mule deer	Winter	Bobcat detected	0.87	0.8 - 0.92	1264	201
Mule deer	Winter	Coyote detected	0.86	0.79 - 0.91	216	1249
Mule deer	Spring	TRI	0.93	0.89 - 0.95	892	964
Mule deer	Spring	Cougar detected	0.93	0.88 - 0.95	1461	395
Mule deer	Spring	Wolf detected	0.87	0.79 - 0.92	1806	50
Mule deer	Spring	Black bear detected	0.91	0.87 - 0.94	984	872
Mule deer	Spring	Bobcat detected	0.93	0.9 - 0.96	1496	360
Mule deer	Spring	Coyote detected	0.9	0.86 - 0.93	626	1230
Elk	Summer	TRI	0.87	0.79 - 0.93	263	112
Elk	Summer	Cougar detected	0.91	0.85 - 0.95	231	144
Elk	Summer	Wolf detected	0.81	0.69 - 0.89	339	36
Elk	Summer	Black bear detected	0.86	0.78 - 0.92	88	287
Elk	Fall	TRI	0.81	0.66 - 0.9	66	26

Elk	Fall	Cougar detected	0.81	0.67 - 0.9	56	36
Elk	Fall	Black bear detected	0.79	0.65 - 0.88	45	47
Elk	Winter	TRI	0.78	0.6 - 0.89	40	19
Elk	Winter	Cougar detected	0.74	0.55 - 0.87	22	37
Elk	Spring	TRI	0.72	0.59 - 0.83	83	55
Elk	Spring	Cougar detected	0.76	0.63 - 0.85	63	75
Elk	Spring	Black bear detected	0.85	0.74 - 0.91	99	39
Moose	Summer	TRI	0.91	0.87 - 0.95	392	224
Moose	Summer	Cougar detected	0.9	0.84 - 0.94	199	417
Moose	Summer	Wolf detected	0.89	0.83 - 0.93	453	163
Moose	Summer	Black bear detected	0.88	0.81 - 0.93	85	531
Moose	Fall	TRI	0.92	0.85 - 0.96	189	66
Moose	Fall	Cougar detected	0.88	0.8 - 0.93	139	116
Moose	Fall	Wolf detected	0.9	0.81 - 0.95	191	64
Moose	Fall	Black bear detected	0.89	0.8 - 0.94	135	120
Moose	Winter	TRI	0.86	0.77 - 0.92	142	62
Moose	Winter	Cougar detected	0.82	0.69 - 0.91	148	56
Moose	Winter	Wolf detected	0.89	0.81 - 0.95	156	48
Moose	Spring	TRI	0.85	0.73 - 0.92	91	51
Moose	Spring	Cougar detected	0.88	0.78 - 0.94	82	60
Moose	Spring	Wolf detected	0.83	0.68 - 0.92	129	13
Moose	Spring	Black bear detected	0.9	0.8 - 0.95	82	60
White-tailed deer	Summer	TRI	0.94	0.92 - 0.96	6029	1001
White-tailed deer	Summer	Cougar detected	0.91	0.89 - 0.92	3948	3082
White-tailed deer	Summer	Wolf detected	0.93	0.91 - 0.95	6336	694
White-tailed deer	Summer	Black bear detected	0.88	0.86 - 0.91	1430	5600
White-tailed deer	Summer	Bobcat detected	0.91	0.89 - 0.93	4683	2347
White-tailed deer	Summer	Coyote detected	0.95	0.93 - 0.96	1476	5554
White-tailed deer	Fall	TRI	0.93	0.89 - 0.95	2903	552
White-tailed deer	Fall	Cougar detected	0.9	0.86 - 0.93	2444	1011
White-tailed deer	Fall	Wolf detected	0.88	0.81 - 0.92	3312	143
White-tailed deer	Fall	Black bear detected	0.94	0.91 - 0.96	2918	537
White-tailed deer	Fall	Bobcat detected	0.93	0.89 - 0.95	2670	785
White-tailed deer	Fall	Coyote detected	0.94	0.9 - 0.96	967	2488
White-tailed deer	Winter	TRI	0.87	0.84 - 0.9	3014	990
White-tailed deer	Winter	Cougar detected	0.93	0.91 - 0.95	2377	1627
White-tailed deer	Winter	Wolf detected	0.87	0.81 - 0.91	3785	219
White-tailed deer	Winter	Bobcat detected	0.94	0.91 - 0.96	3173	831
White-tailed deer	Winter	Coyote detected	0.91	0.87 - 0.94	555	3449
White-tailed deer	Spring	TRI	0.93	0.9 - 0.96	2178	315
White-tailed deer	Spring	Cougar detected	0.85	0.8 - 0.88	1811	682
White-tailed deer	Spring	Wolf detected	0.88	0.81 - 0.92	2455	38
White-tailed deer	Spring	Black bear detected	0.91	0.87 - 0.93	1749	744
White-tailed deer	Spring	Bobcat detected	0.92	0.88 - 0.95	2085	408

White-tailed deer	Spring	Coyote detected	0.95	0.93 - 0.97	600	1893
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Table S3.2. Coefficient of overlapping ($\bar{A}$) and bootstrapped 95% Confidence Intervals (95% CI) for each predator-prey pairing at camera sites with low terrain ruggedness index (TRI) values and camera sites with high TRI values. Sample sizes of the species-specific detections included in each analysis are also reported (n). The level of habitat complexity was based on the mean TRI where camera sites below the mean were considered to be in areas of low complexity and camera sites above the mean were considered to be in areas of high complexity. We considered the overlap of predator and prey diel activity curves to differ between areas with high or low TRI if the bootstrapped 95% CIs did not overlap the overlap coefficients and trending towards different if only one of the 95% CIs overlapped the opposite coefficient (bolded). Estimates based on small sample sizes ($n < 20$ for at least one species) were not considered for interpretation in text.

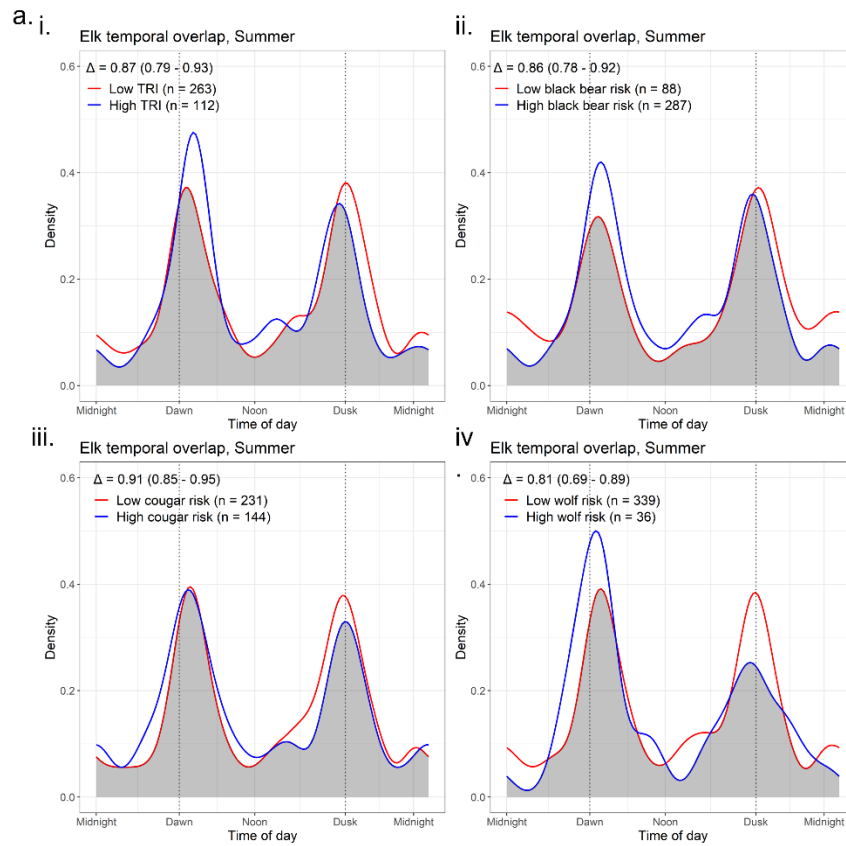
Prey species	Predator species	Season	Level of complexity	$\bar{A}$	95% CI	Prey (n)	Predator (n)
Elk	Bear	Fall	Low	0.63	0.46 - 0.78	41	28
Elk	Bear	Fall	High	0.69	0.27 - 0.9	6	5
Elk	Bear	Spring	Low	0.69	0.51 - 0.83	26	23
Elk	Bear	Spring	High	0.77	0.53 - 0.91	13	9
Elk	Bear	Summer	Low	0.75	0.67 - 0.82	199	261
Elk	Bear	Summer	High	0.69	0.58 - 0.79	88	122
Elk	Cougar	Fall	Low	0.77	0.6 - 0.89	28	21
Elk	Cougar	Fall	High	0.41	0.13 - 0.7	8	7
Elk	Cougar	Spring	Low	0.69	0.52 - 0.82	38	35
Elk	Cougar	Spring	High	0.45	0.24 - 0.67	37	12
Elk	Cougar	Summer	Low	0.83	0.72 - 0.91	97	79
Elk	Cougar	Summer	High	0.73	0.56 - 0.86	47	28
Elk	Cougar	Winter	Low	0.68	0.49 - 0.84	20	35
Elk	Cougar	Winter	High	0.74	0.48 - 0.89	17	8
Elk	Wolf	Summer	Low	0.71	0.51 - 0.86	24	13
Elk	Wolf	Summer	High	0.75	0.52 - 0.9	12	11
Moose	Bear	Fall	Low	0.78	0.62 - 0.89	81	27
Moose	Bear	Fall	High	0.72	0.53 - 0.87	39	14
Moose	Bear	Spring	Low	0.82	0.68 - 0.91	36	35
Moose	Bear	Spring	High	0.64	0.44 - 0.81	24	35
Moose	Bear	Summer	Low	0.66	0.6 - 0.71	325	475
Moose	Bear	Summer	High	0.68	0.6 - 0.76	206	235
Moose	Cougar	Fall	Low	0.78	0.66 - 0.88	91	49
Moose	Cougar	Fall	High	0.54	0.32 - 0.74	25	15
Moose	Cougar	Spring	Low	0.79	0.65 - 0.89	37	31
Moose	Cougar	Spring	High	0.63	0.44 - 0.8	23	22
Moose	Cougar	Summer	Low	0.86	0.79 - 0.92	235	126
Moose	Cougar	Summer	High	0.87	0.78 - 0.93	182	70
Moose	Cougar	Winter	Low	0.76	0.63 - 0.87	38	39

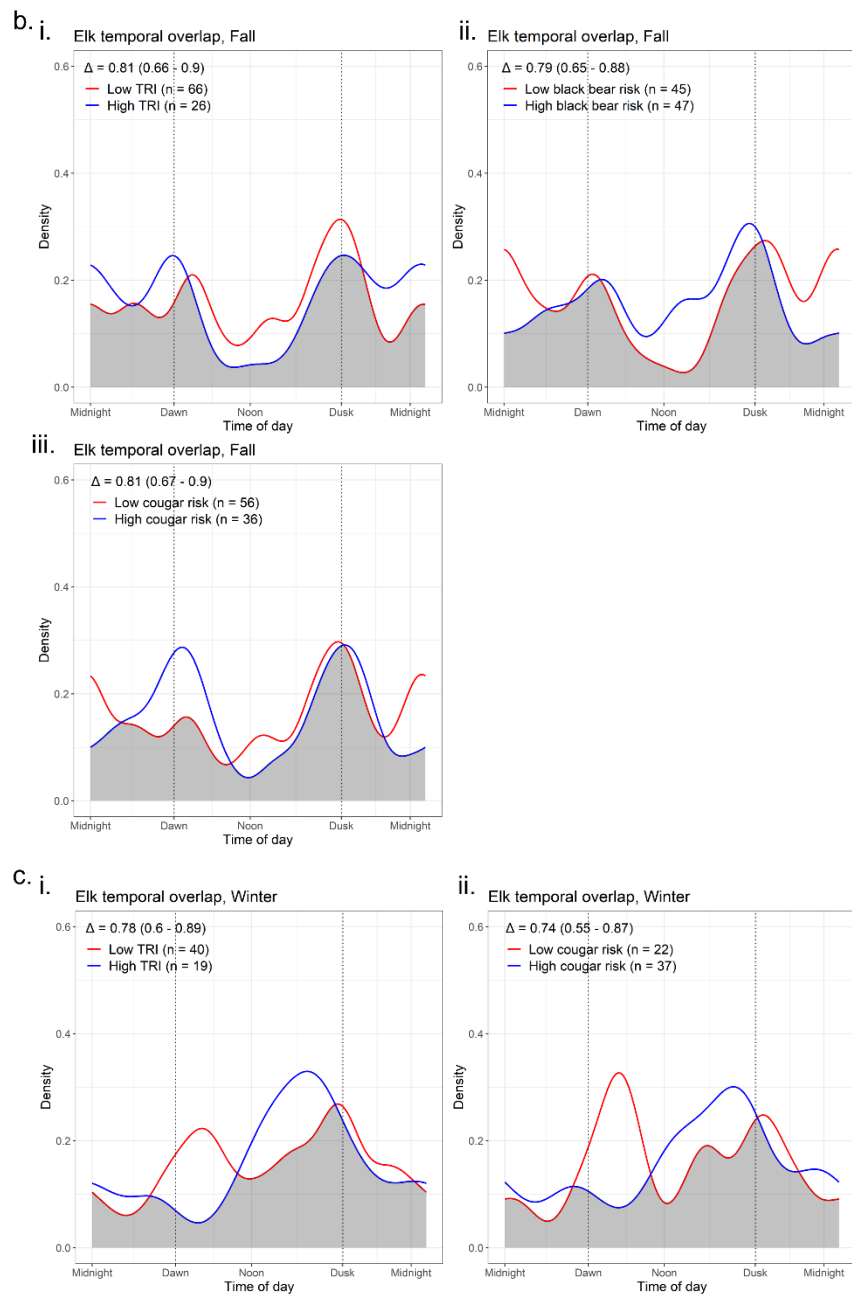
Moose	Cougar	Winter	High	0.65	0.42 - 0.82	18	15
Moose	Wolf	Fall	Low	0.77	0.6 - 0.88	41	21
Moose	Wolf	Fall	High	0.66	0.42 - 0.84	23	10
Moose	Wolf	Spring	Low	0.58	0.15 - 0.84	6	5
Moose	Wolf	Spring	High	0.54	0.24 - 0.78	7	14
Moose	Wolf	Summer	Low	0.85	0.75 - 0.92	100	37
Moose	Wolf	Summer	High	0.76	0.61 - 0.87	63	26
Moose	Wolf	Winter	Low	0.72	0.51 - 0.87	31	13
Moose	Wolf	Winter	High	0.84	0.66 - 0.94	17	8
Mule Deer	Bear	Fall	Low	0.81	0.7 - 0.89	152	50
Mule Deer	Bear	Fall	High	0.69	0.56 - 0.8	268	41
Mule Deer	Bear	Spring	Low	0.81	0.71 - 0.89	443	75
Mule Deer	Bear	Spring	High	0.8	0.71 - 0.87	429	92
Mule Deer	Bear	Summer	Low	0.72	0.68 - 0.76	1127	424
Mule Deer	Bear	Summer	High	0.72	0.68 - 0.77	1532	352
Mule Deer	Bobcat	Fall	Low	0.81	0.69 - 0.9	284	42
Mule Deer	Bobcat	Fall	High	0.77	0.63 - 0.89	138	32
Mule Deer	Bobcat	Spring	Low	0.62	0.47 - 0.76	99	39
Mule Deer	Bobcat	Spring	High	0.53	0.39 - 0.66	261	39
Mule Deer	Bobcat	Summer	Low	0.62	0.54 - 0.7	596	148
Mule Deer	Bobcat	Summer	High	0.6	0.52 - 0.67	480	153
Mule Deer	Bobcat	Winter	Low	0.72	0.53 - 0.86	102	16
Mule Deer	Bobcat	Winter	High	0.42	0.26 - 0.6	99	11
Mule Deer	Cougar	Fall	Low	0.84	0.71 - 0.92	221	35
Mule Deer	Cougar	Fall	High	0.59	0.44 - 0.73	206	18
Mule Deer	Cougar	Spring	Low	0.72	0.59 - 0.82	164	39
Mule Deer	Cougar	Spring	High	0.61	0.48 - 0.74	231	39
Mule Deer	Cougar	Summer	Low	0.77	0.69 - 0.85	616	77
Mule Deer	Cougar	Summer	High	0.73	0.64 - 0.82	656	80
Mule Deer	Cougar	Winter	Low	0.6	0.43 - 0.77	97	18
Mule Deer	Cougar	Winter	High	0.55	0.39 - 0.7	238	21
Mule Deer	Coyote	Fall	Low	0.9	0.85 - 0.94	930	333
Mule Deer	Coyote	Fall	High	0.87	0.82 - 0.92	589	285
Mule Deer	Coyote	Spring	Low	0.74	0.69 - 0.8	698	387
Mule Deer	Coyote	Spring	High	0.78	0.7 - 0.84	532	169
Mule Deer	Coyote	Summer	Low	0.79	0.75 - 0.83	1313	698
Mule Deer	Coyote	Summer	High	0.72	0.68 - 0.76	1263	589
Mule Deer	Coyote	Winter	Low	0.92	0.88 - 0.96	552	378
Mule Deer	Coyote	Winter	High	0.85	0.78 - 0.9	697	265
Mule Deer	Wolf	Fall	Low	0.77	0.58 - 0.9	103	12
Mule Deer	Wolf	Fall	High	0.74	0.54 - 0.87	30	12
Mule Deer	Wolf	Spring	Low	0.51	0.28 - 0.72	34	8
Mule Deer	Wolf	Spring	High	0.52	0.32 - 0.71	16	14
Mule Deer	Wolf	Summer	Low	0.79	0.64 - 0.89	281	20
Mule Deer	Wolf	Summer	High	0.73	0.58 - 0.84	361	20

Mule Deer	Wolf	Winter	Low	0.78	0.51 - 0.92	18	6
Mule Deer	Wolf	Winter	High	0.63	0.3 - 0.84	28	4
White-tailed Deer	Bear	Fall	Low	0.74	0.63 - 0.84	448	55
White-tailed Deer	Bear	Fall	High	0.7	0.51 - 0.85	89	14
White-tailed Deer	Bear	Spring	Low	0.79	0.72 - 0.86	666	87
White-tailed Deer	Bear	Spring	High	0.68	0.5 - 0.82	78	18
White-tailed Deer	Bear	Summer	Low	0.79	0.76 - 0.82	4867	558
White-tailed Deer	Bear	Summer	High	0.78	0.72 - 0.83	733	231
White-tailed Deer	Bobcat	Fall	Low	0.7	0.59 - 0.81	447	63
White-tailed Deer	Bobcat	Fall	High	0.63	0.5 - 0.75	338	33
White-tailed Deer	Bobcat	Spring	Low	0.35	0.24 - 0.46	315	46
White-tailed Deer	Bobcat	Spring	High	0.38	0.24 - 0.54	93	24
White-tailed Deer	Bobcat	Summer	Low	0.59	0.52 - 0.66	1677	169
White-tailed Deer	Bobcat	Summer	High	0.46	0.38 - 0.54	670	111
White-tailed Deer	Bobcat	Winter	Low	0.55	0.44 - 0.67	746	66
White-tailed Deer	Bobcat	Winter	High	0.66	0.5 - 0.8	85	31
White-tailed Deer	Cougar	Fall	Low	0.87	0.79 - 0.93	829	69
White-tailed Deer	Cougar	Fall	High	0.8	0.66 - 0.9	182	26
White-tailed Deer	Cougar	Spring	Low	0.55	0.44 - 0.66	588	63
White-tailed Deer	Cougar	Spring	High	0.74	0.56 - 0.87	94	15
White-tailed Deer	Cougar	Summer	Low	0.78	0.71 - 0.84	2709	149
White-tailed Deer	Cougar	Summer	High	0.53	0.43 - 0.63	373	73
White-tailed Deer	Cougar	Winter	Low	0.62	0.53 - 0.71	1056	86
White-tailed Deer	Cougar	Winter	High	0.77	0.64 - 0.87	571	34

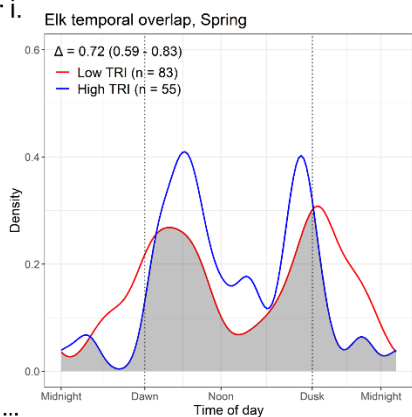
White-tailed Deer	Coyote	Fall	Low	0.78	0.73 - 0.83	2109	435
White-tailed Deer	Coyote	Fall	High	0.84	0.76 - 0.91	379	99
White-tailed Deer	Coyote	Spring	Low	0.6	0.56 - 0.64	1709	485
White-tailed Deer	Coyote	Spring	High	0.64	0.55 - 0.73	184	84
White-tailed Deer	Coyote	Summer	Low	0.72	0.69 - 0.75	4920	1006
White-tailed Deer	Coyote	Summer	High	0.63	0.57 - 0.68	634	368
White-tailed Deer	Coyote	Winter	Low	0.63	0.6 - 0.67	2569	680
White-tailed Deer	Coyote	Winter	High	0.87	0.8 - 0.92	880	180
White-tailed Deer	Wolf	Fall	Low	0.7	0.53 - 0.84	90	17
White-tailed Deer	Wolf	Fall	High	0.61	0.34 - 0.81	53	7
White-tailed Deer	Wolf	Spring	Low	0.28	0 - 0.79	16	3
White-tailed Deer	Wolf	Spring	High	0.48	0.21 - 0.72	22	5
White-tailed Deer	Wolf	Summer	Low	0.72	0.58 - 0.83	527	28
White-tailed Deer	Wolf	Summer	High	0.8	0.66 - 0.89	167	26
White-tailed Deer	Wolf	Winter	Low	0.64	0.47 - 0.78	196	13
White-tailed Deer	Wolf	Winter	High	0.74	0.5 - 0.88	23	9

Figure S3.1. Overlap plots of differences in diel activity curves for elk in summer (a), fall (b), winter (c), and spring (d), moose in summer (e), fall (f), winter (g), and spring (h), mule deer in summer (i), fall (j), winter (k), and spring (l), and white-tailed deer in summer (m), fall (n), winter (o), and spring (p) at camera sites with low versus high levels of habitat complexity and risk of predator occurrence (i – vi). Habitat complexity was represented by an index of terrain ruggedness (TRI) at each camera site where cameras in areas below the mean TRI were considered low habitat complexity. Risk of predator occurrence was determined by whether a given predator species was detected at least once (high risk) or never detected (low risk) at a camera site. The estimated coefficient of overlapping ($\bar{\Delta}$), bootstrapped 95% confidence intervals, and the number of detections (n) per level are reported in each overlap analysis.

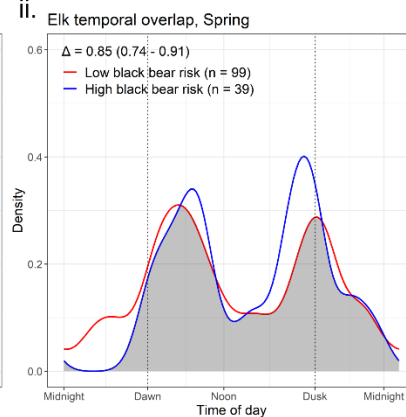




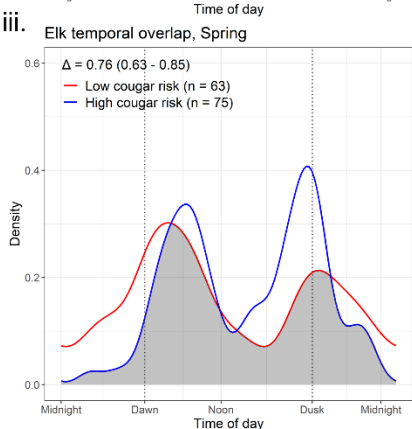
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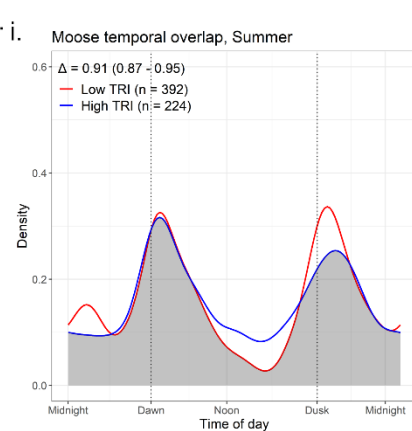
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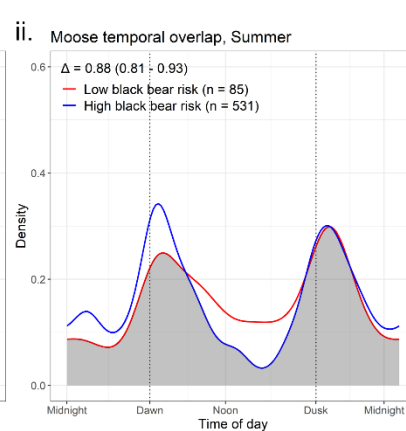
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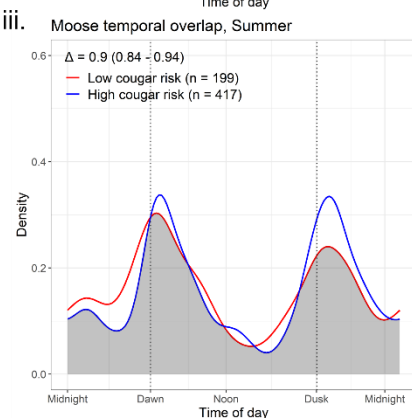
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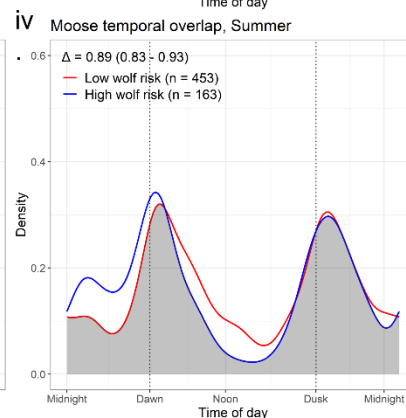
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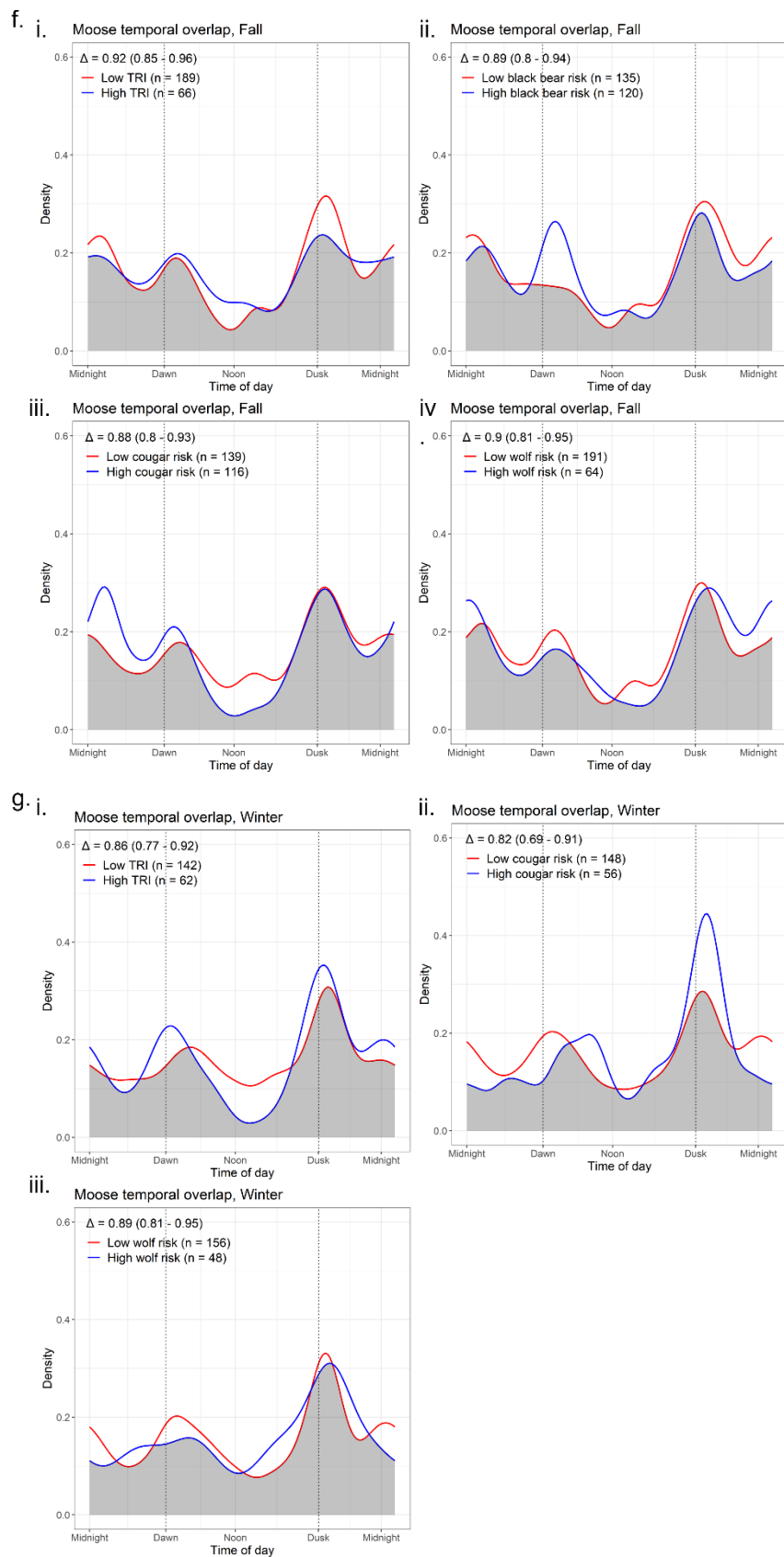


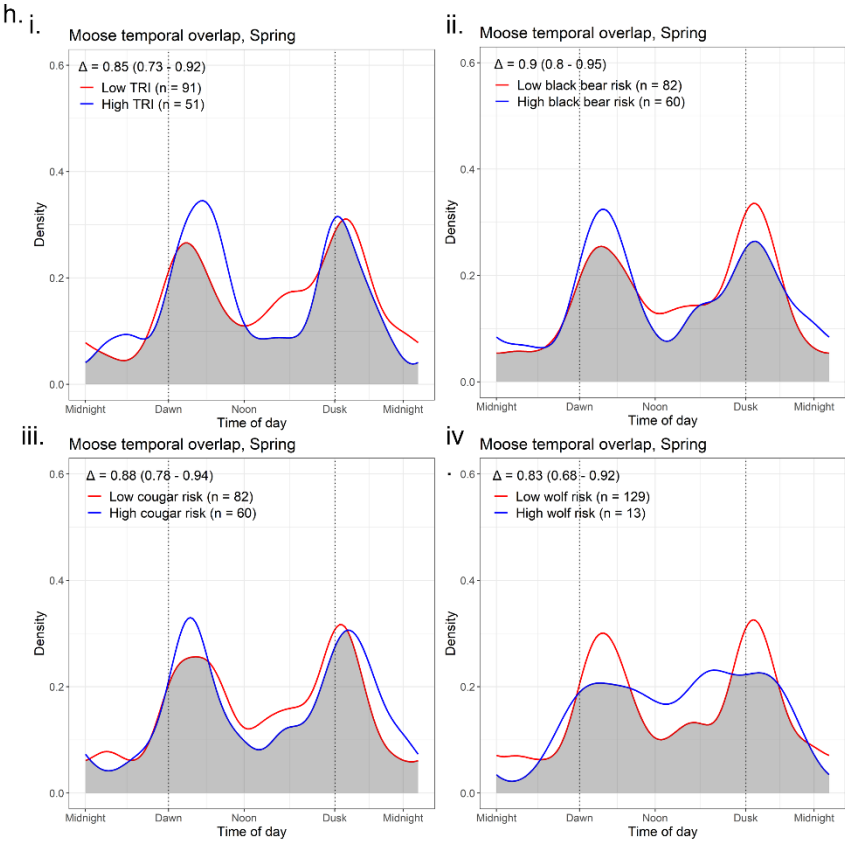
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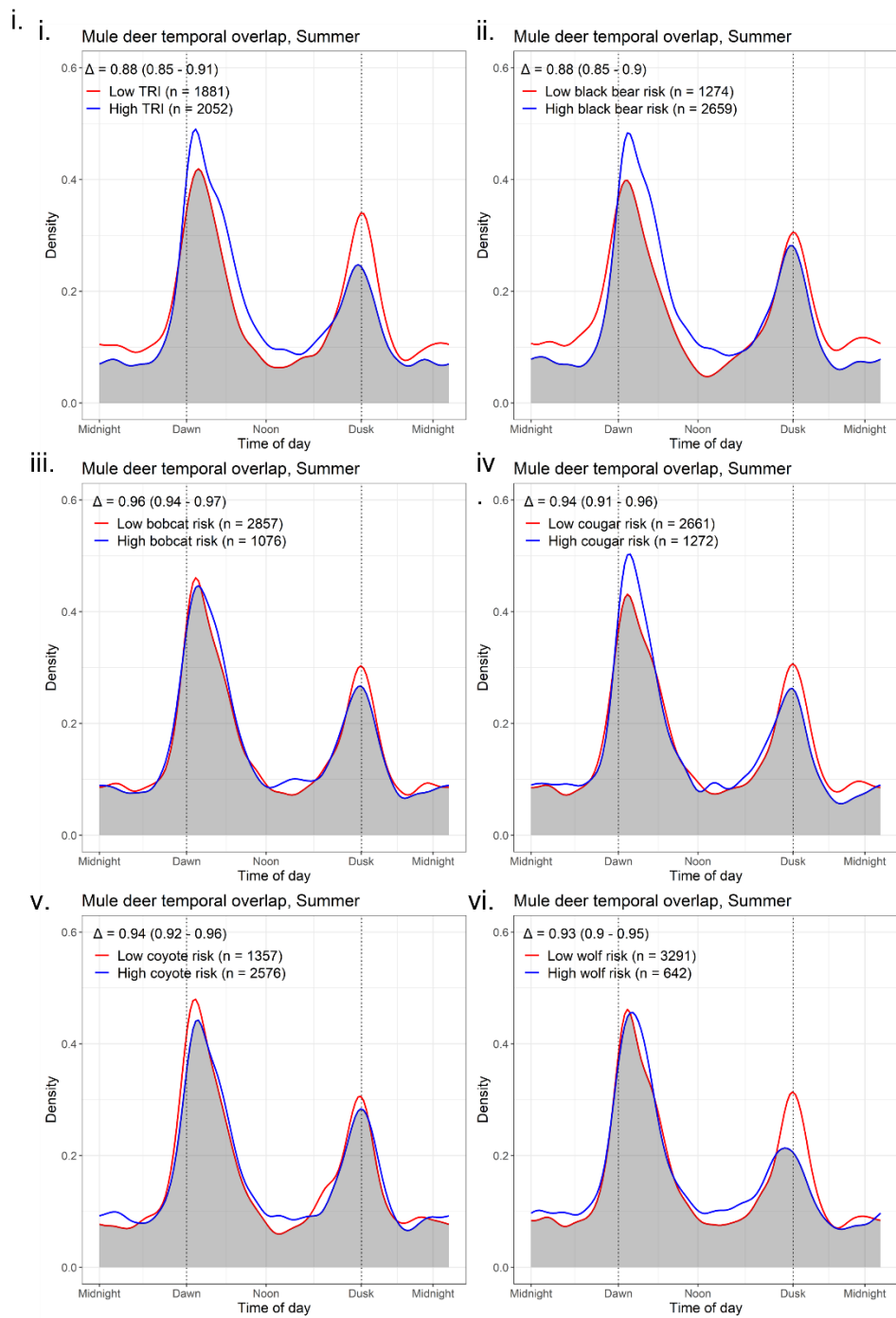


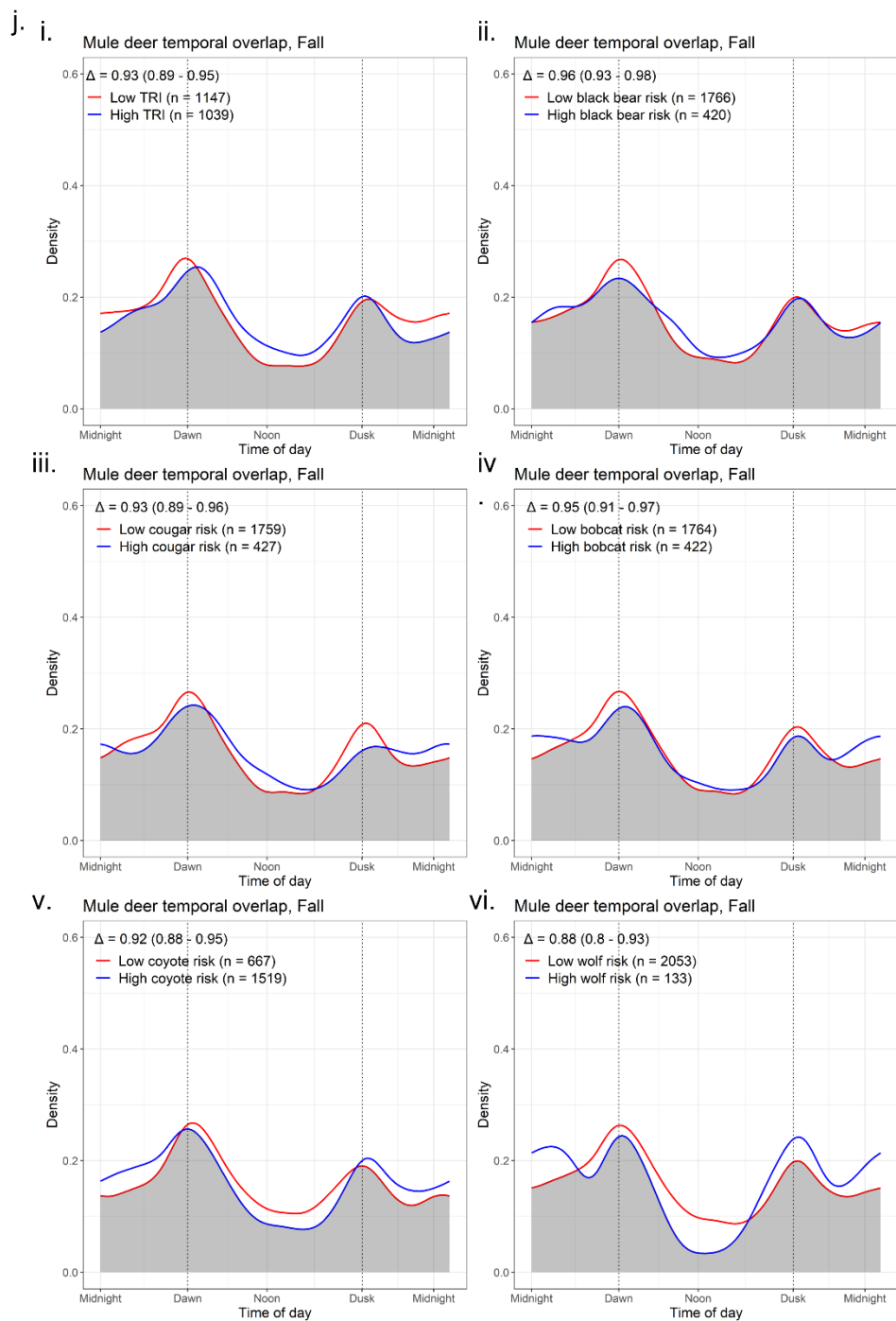
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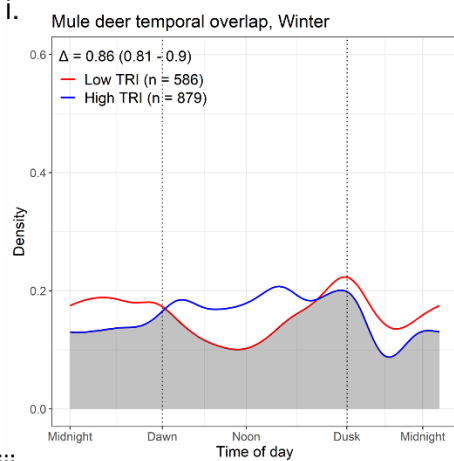




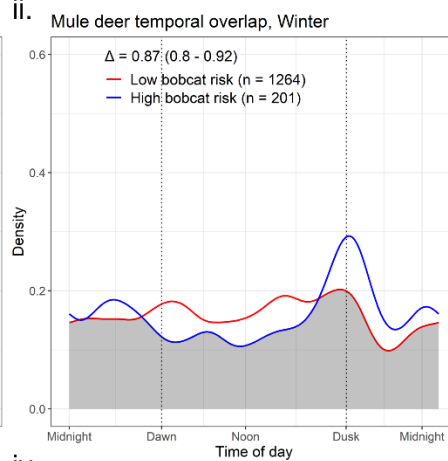




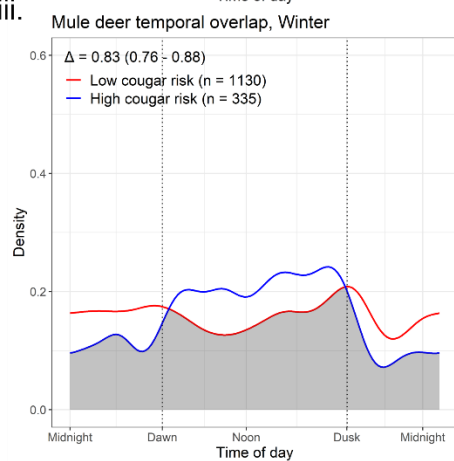
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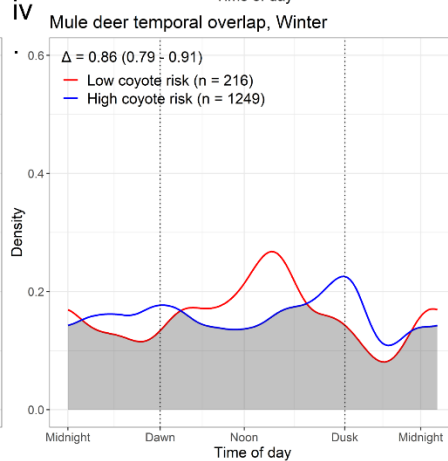
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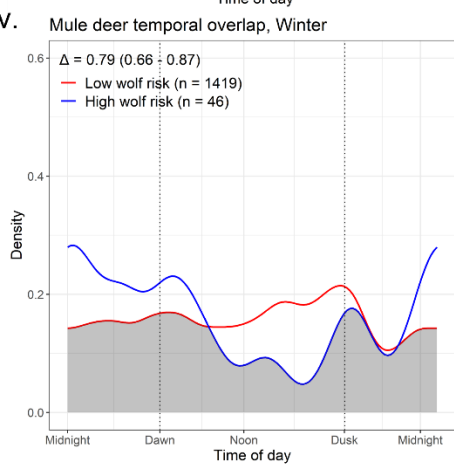
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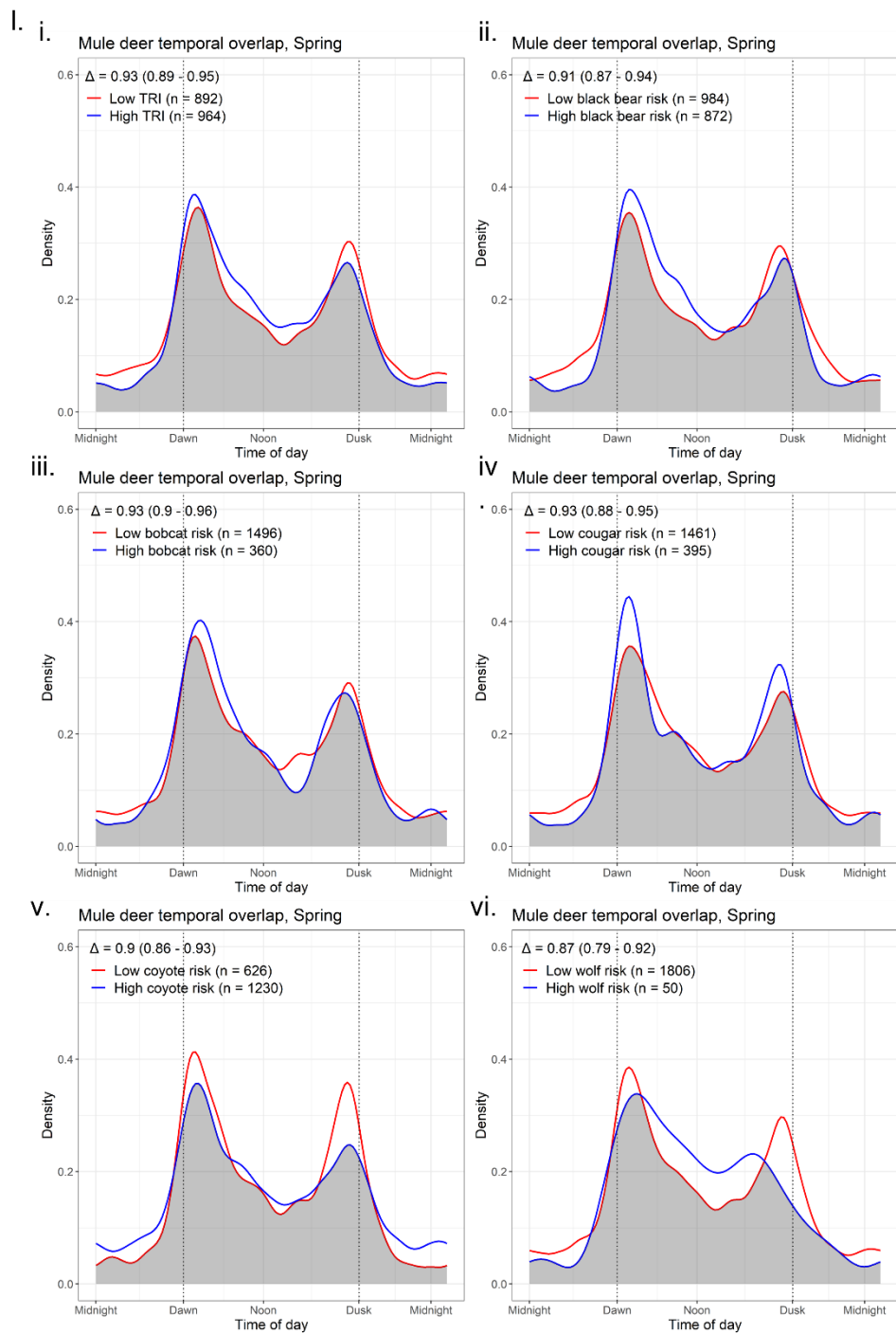


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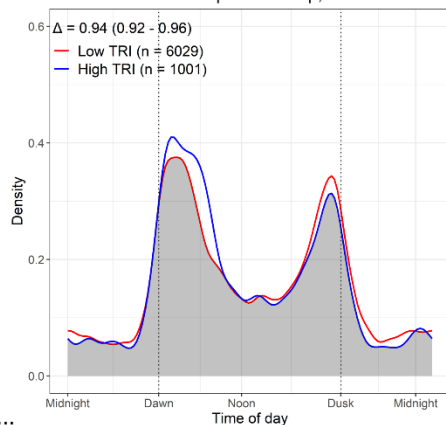
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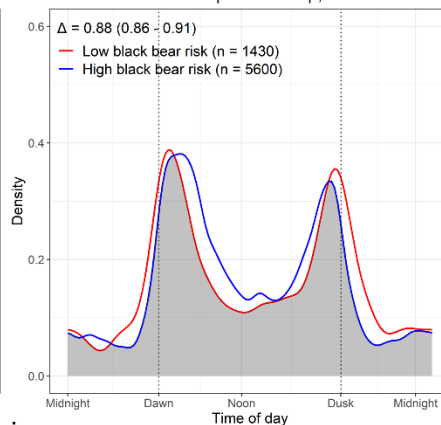
m. i.

White-tailed deer temporal overlap, Summer



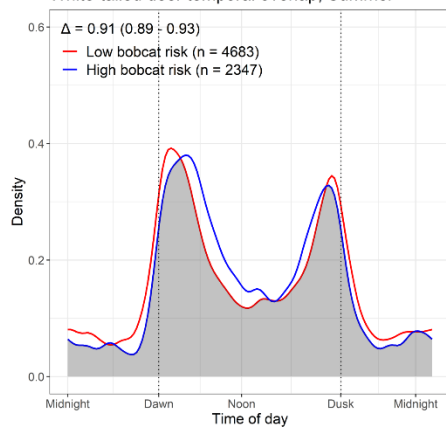
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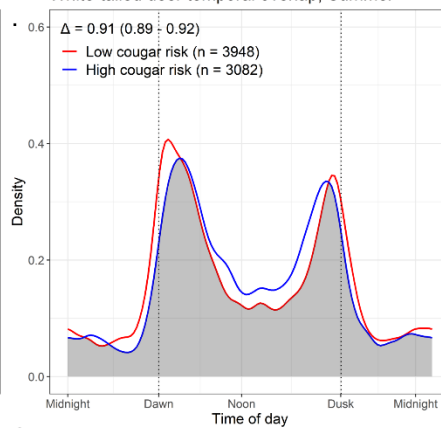
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White-tailed deer temporal overlap, Summer



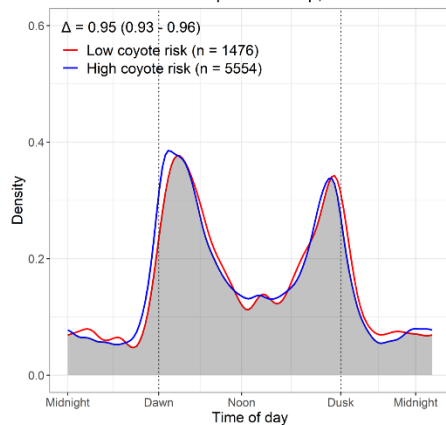
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White-tailed deer temporal overlap, Summer



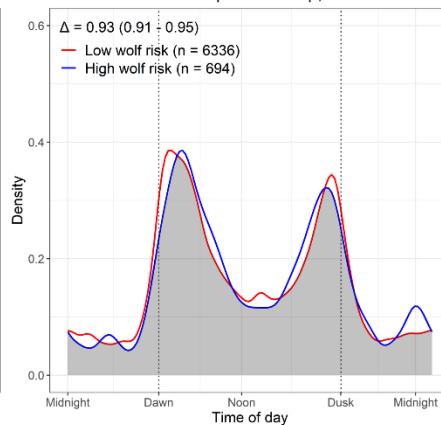
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White-tailed deer temporal overlap, Summer



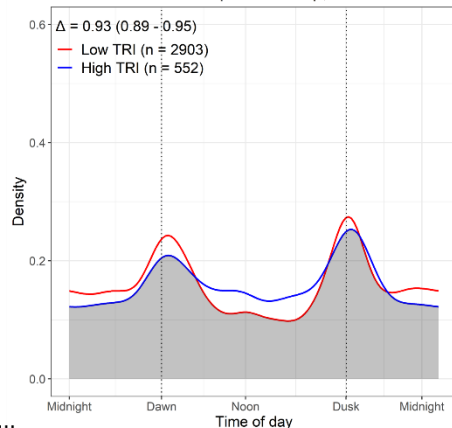
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White-tailed deer temporal overlap, Summer



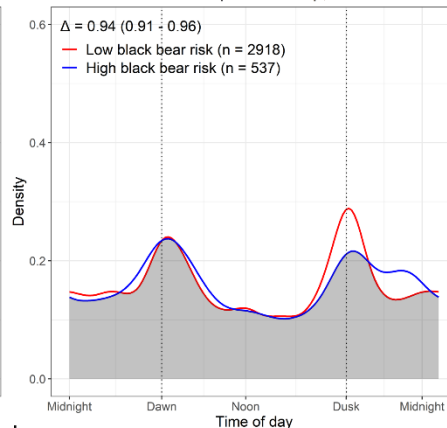
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White-tailed deer temporal overlap, Fall



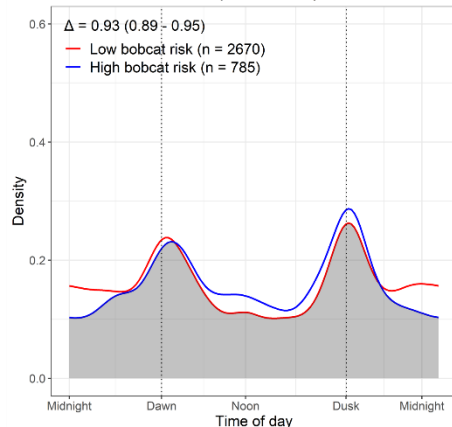
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White-tailed deer temporal overlap, Fall



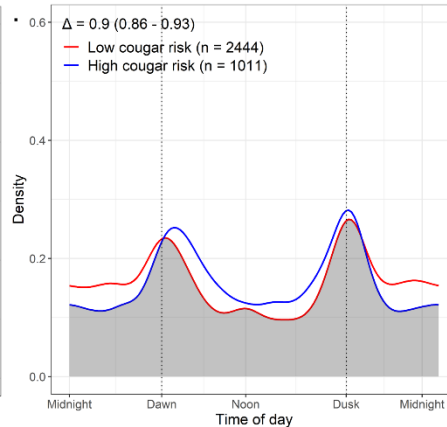
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White-tailed deer temporal overlap, Fall



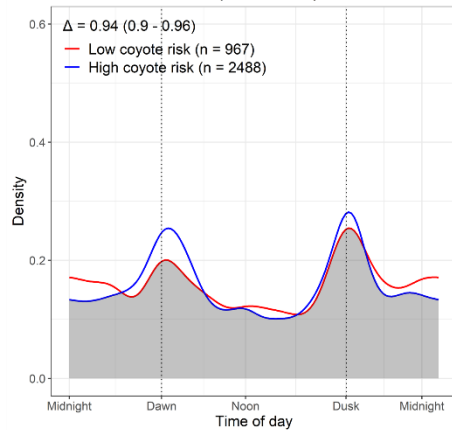
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White-tailed deer temporal overlap, Fall



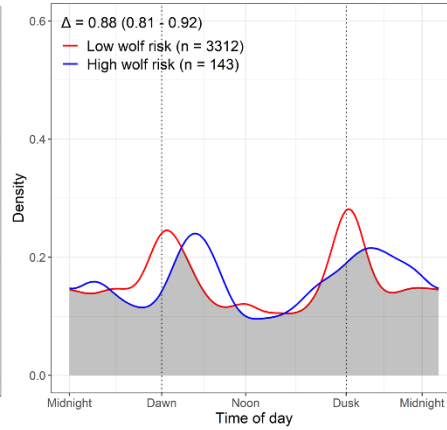
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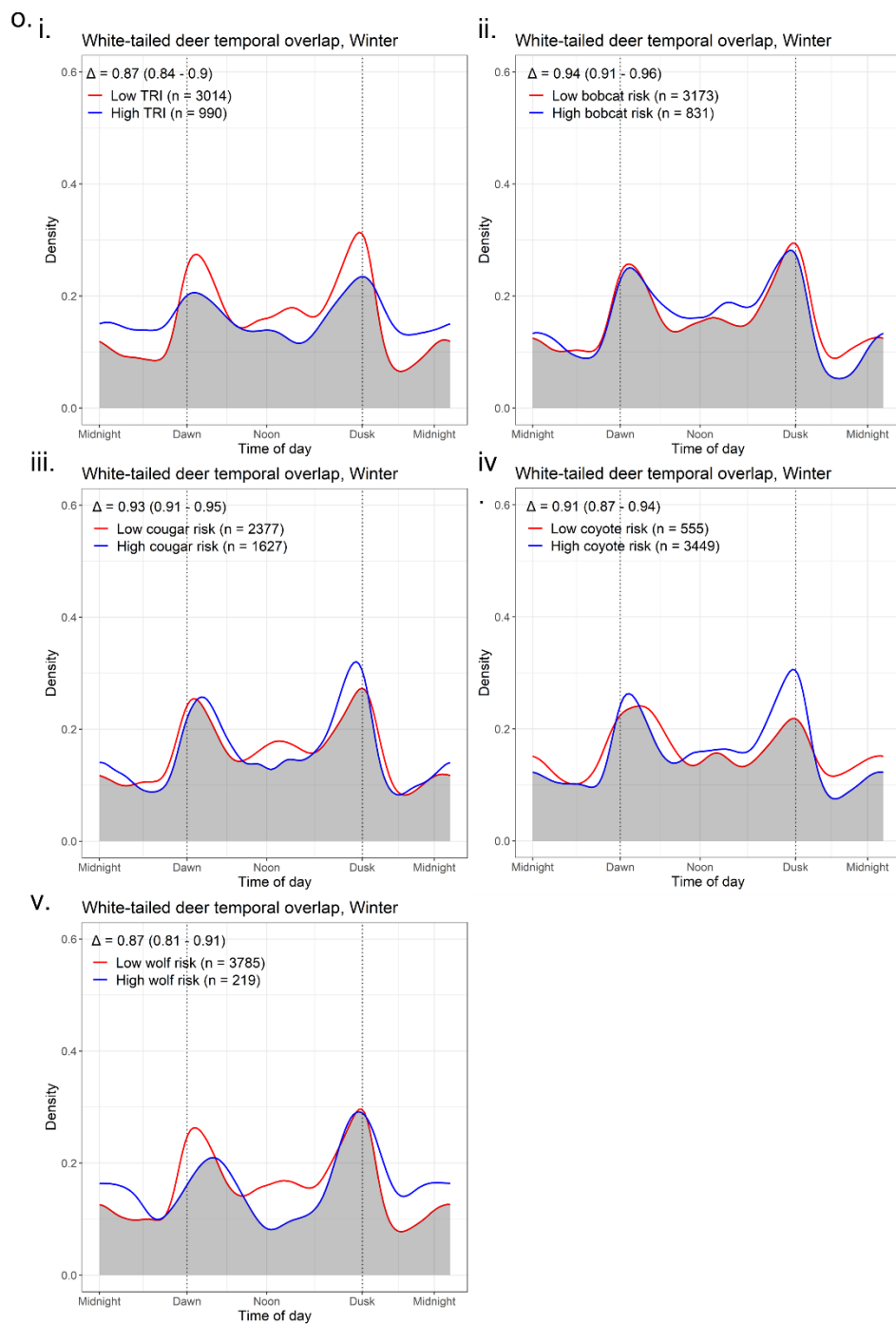
White-tailed deer temporal overlap, Fall



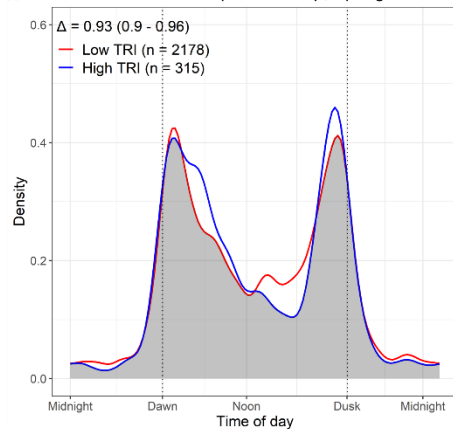
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White-tailed deer temporal overlap, Fall

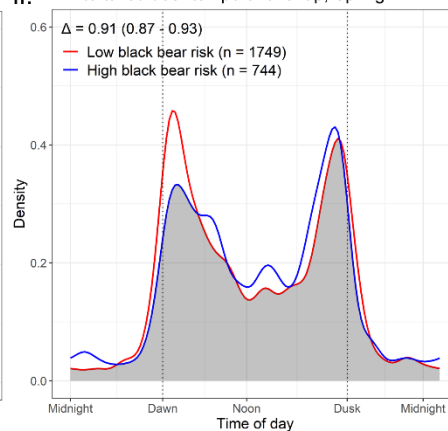




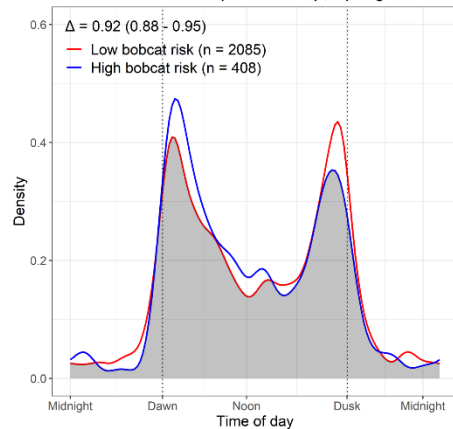
p. i. White-tailed deer temporal overlap, Spring



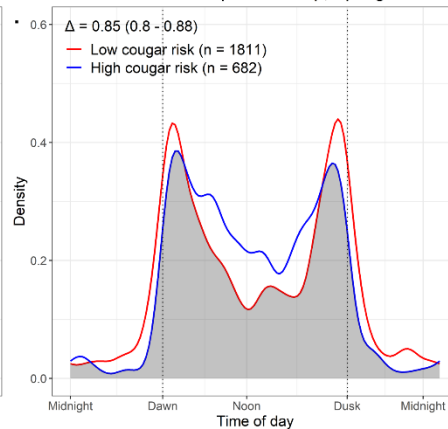
ii. White-tailed deer temporal overlap, Spring



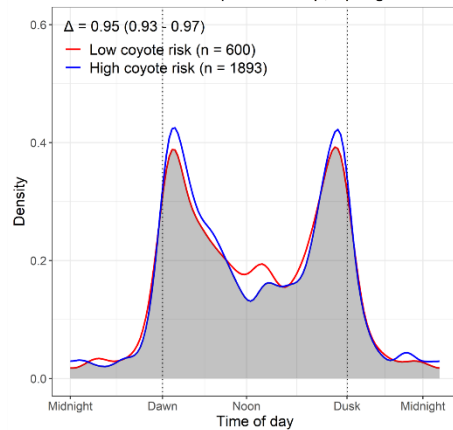
iii. White-tailed deer temporal overlap, Spring



iv. White-tailed deer temporal overlap, Spring



V. White-tailed deer temporal overlap, Spring



vi. White-tailed deer temporal overlap, Spring

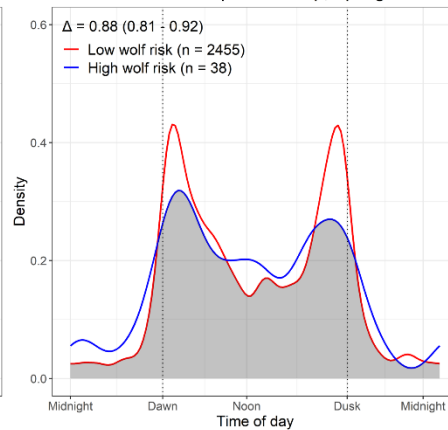
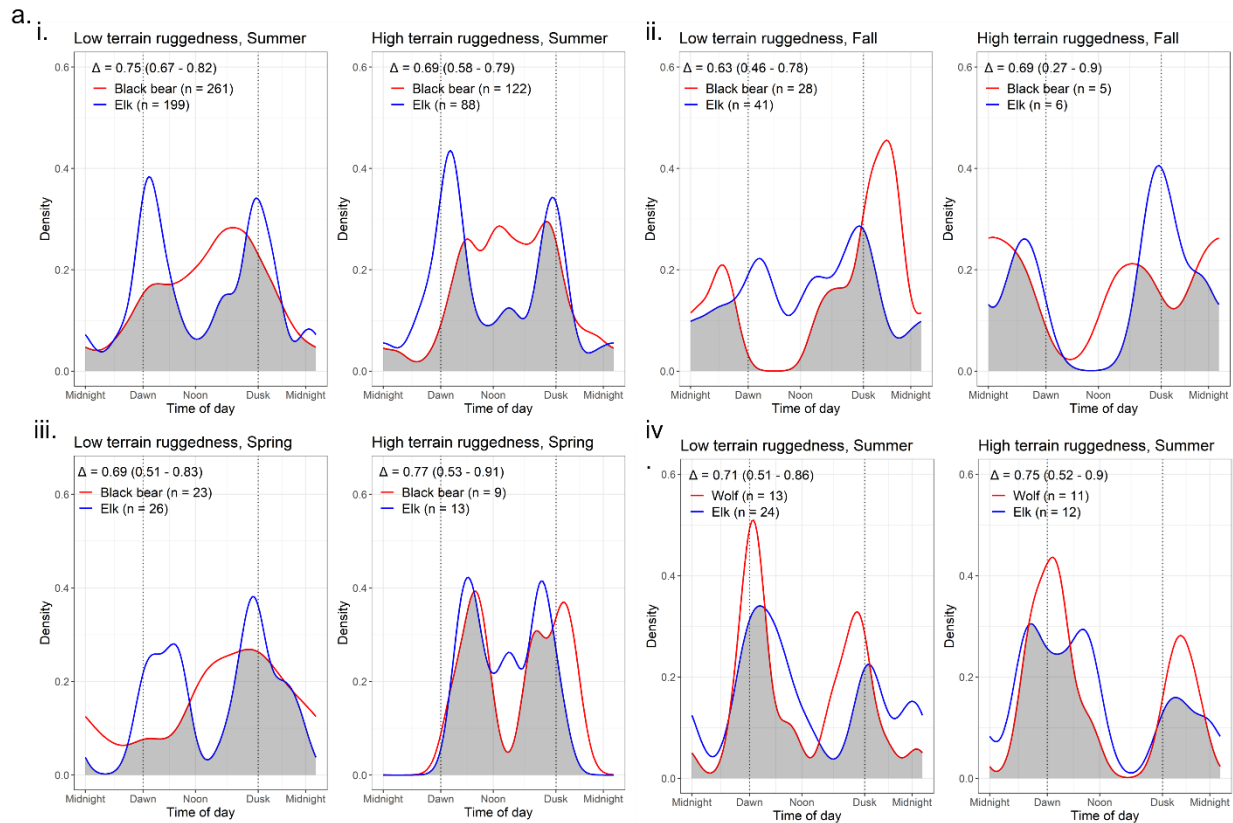
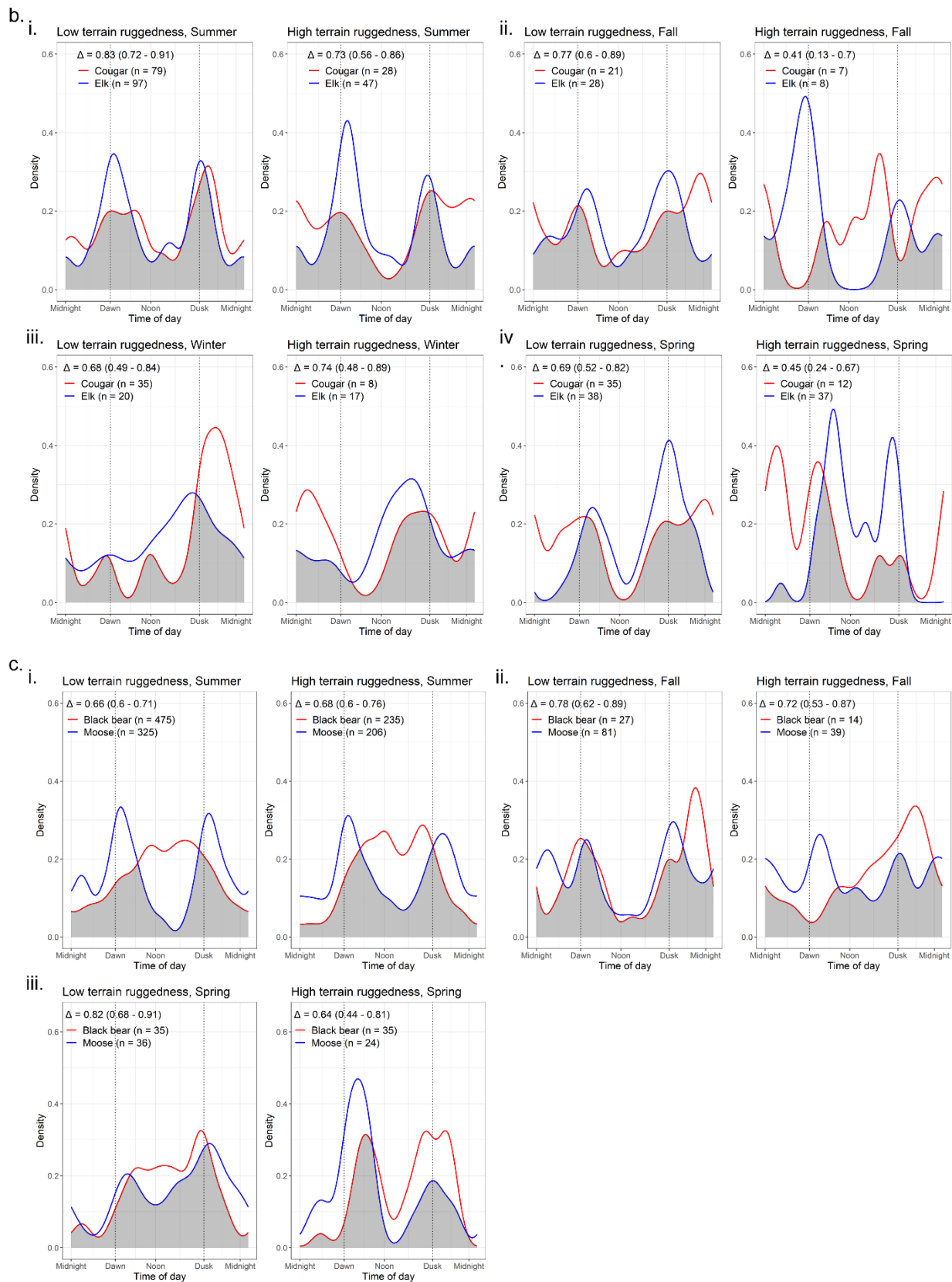
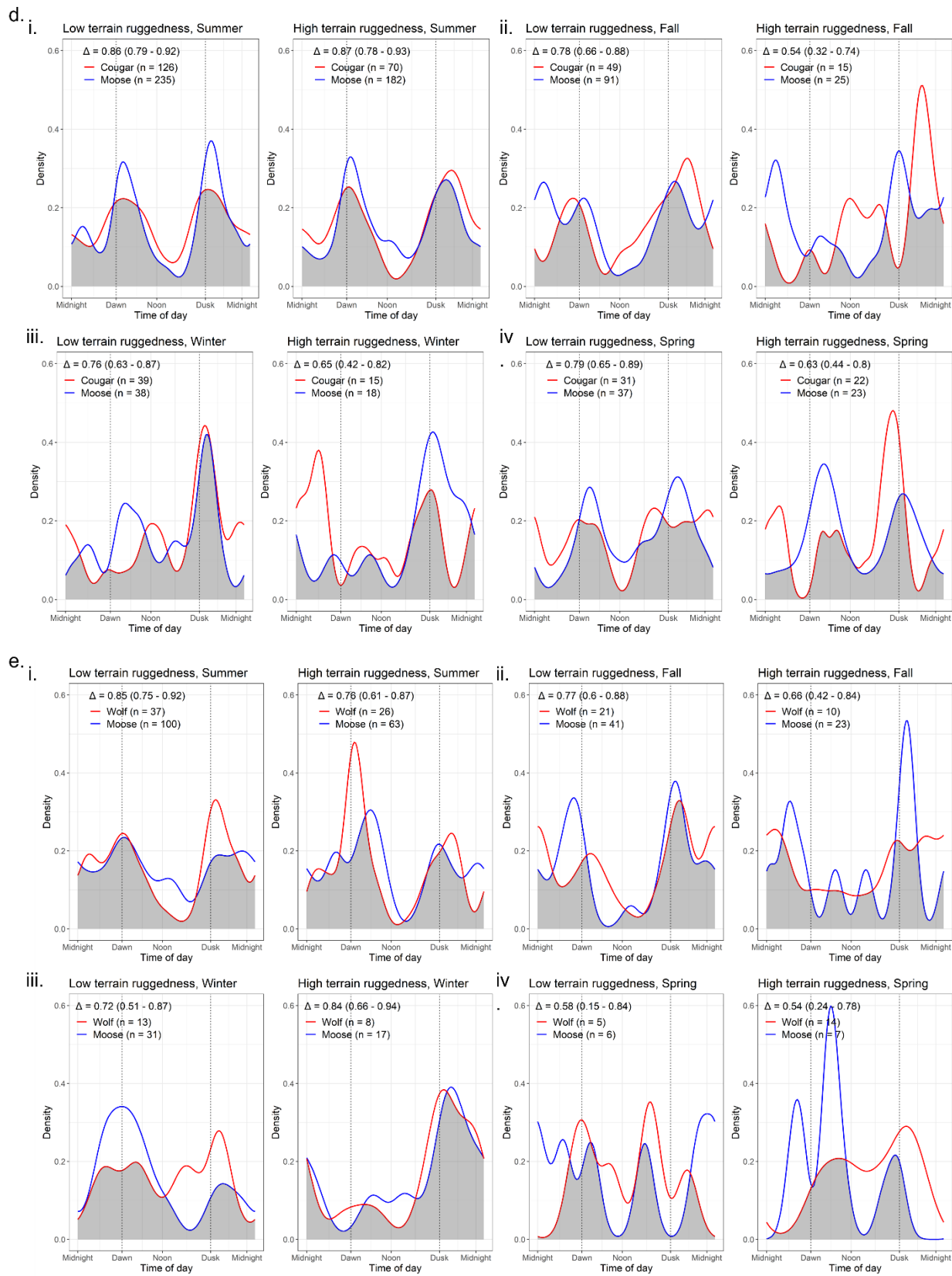
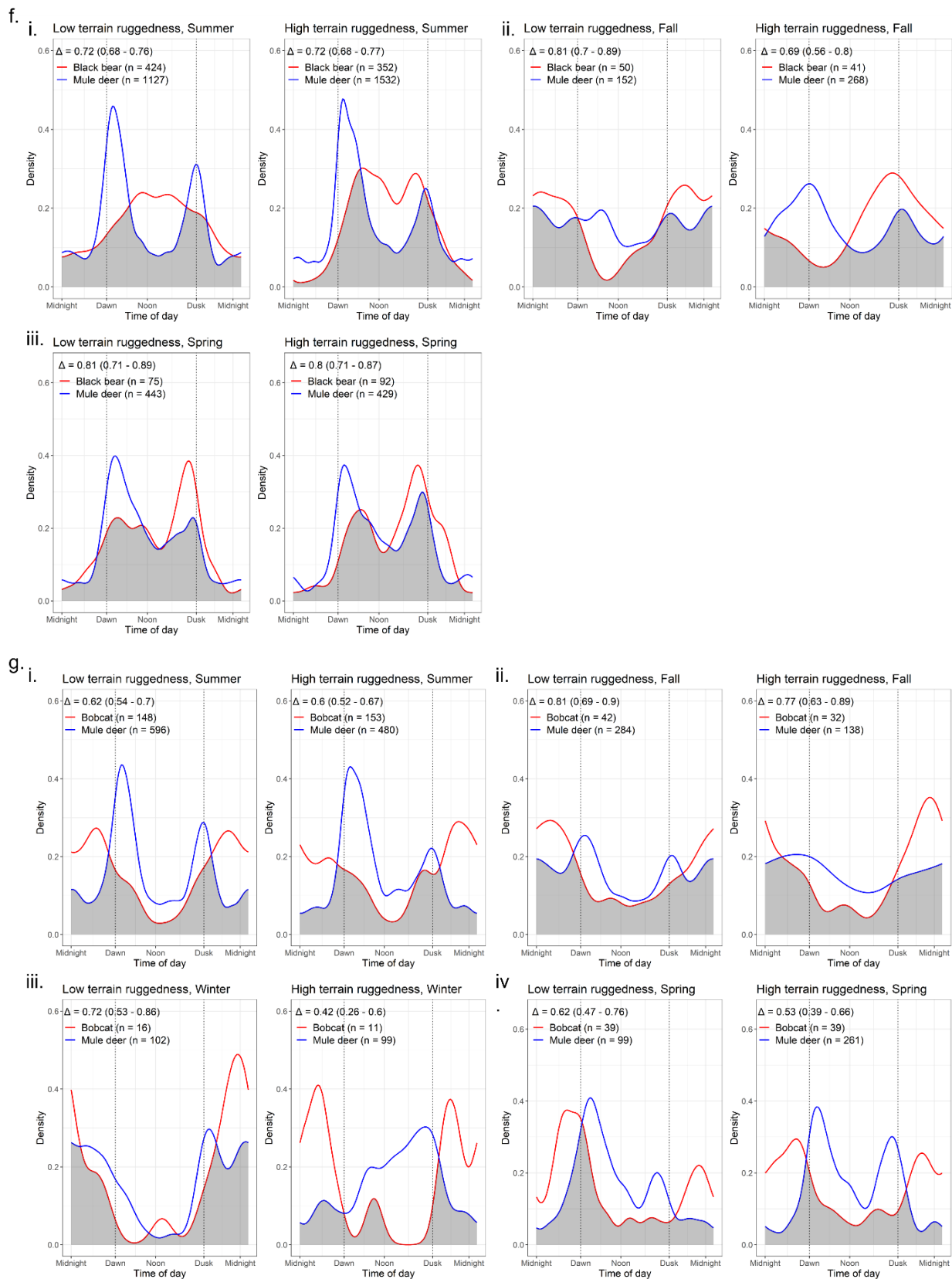


Figure S3.2. Temporal overlap plots of paired predator and prey diel activity curves at camera sites with low terrain ruggedness index values (TRI) compared to camera sites with high TRI values in eastern Washington, USA, 2018 – 2021. The estimated coefficient of overlapping ($\bar{\Delta}$), bootstrapped 95% confidence intervals, and sample sizes for number of detections of each species (n) are reported for elk – black bear (a), elk – wolf (a), elk – cougar (b), moose – black bear (c), moose – cougar (d), moose – wolf (e), mule deer – black bear (f), mule deer – bobcat (g), mule deer – cougar (h), mule deer – coyote (i), mule deer – wolf (j), white-tailed deer – black bear (k), white-tailed deer – bobcat (l), white-tailed deer – cougar (m), white-tailed deer – coyote (n), and white-tailed deer – wolf (o), in summer (i), fall (ii), winter (iii), and spring (iv). Black bears were excluded from winter analyses; temporal overlap with mesopredators (bobcats and coyotes) were not considered for elk and moose analyses.

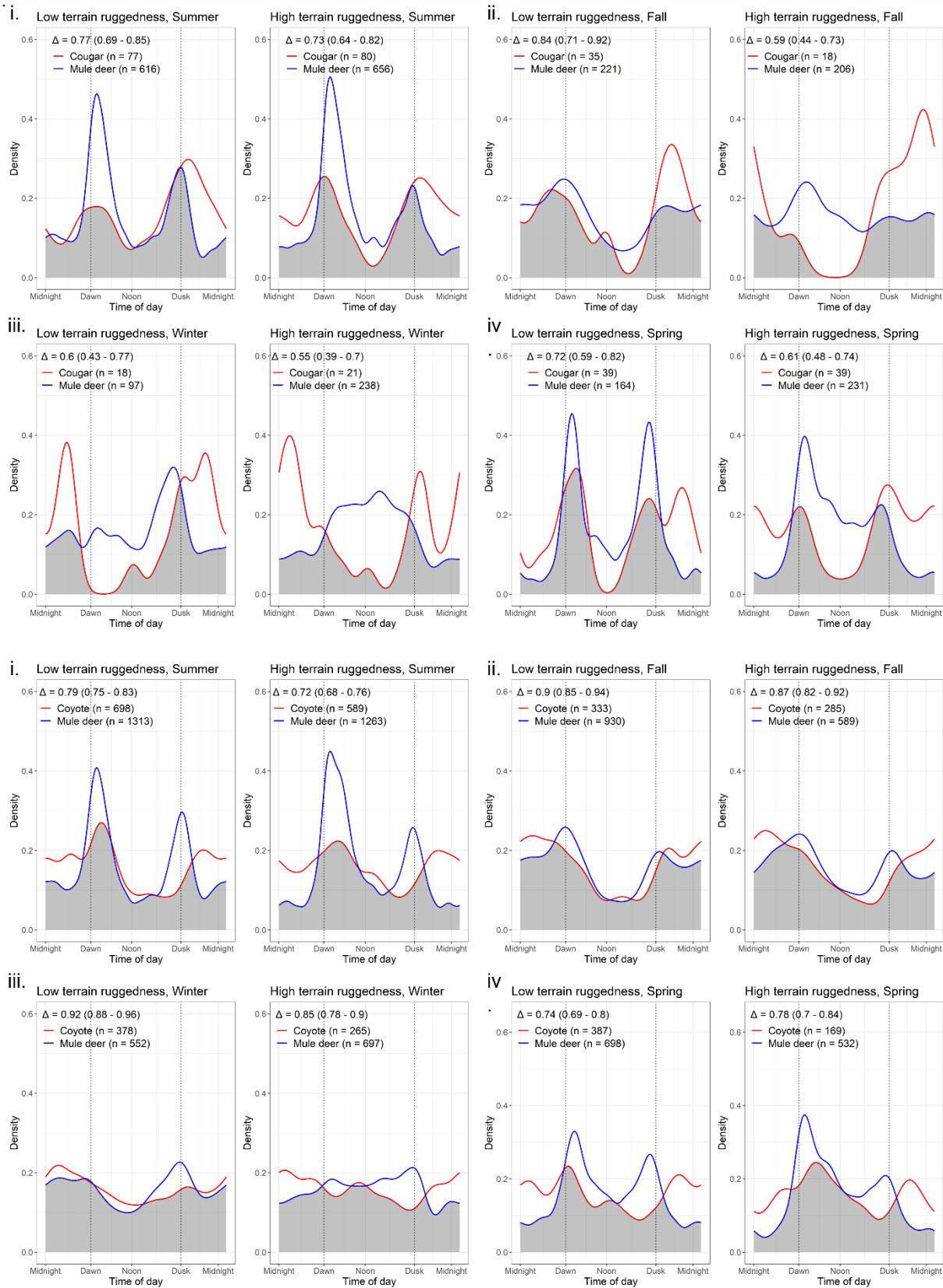


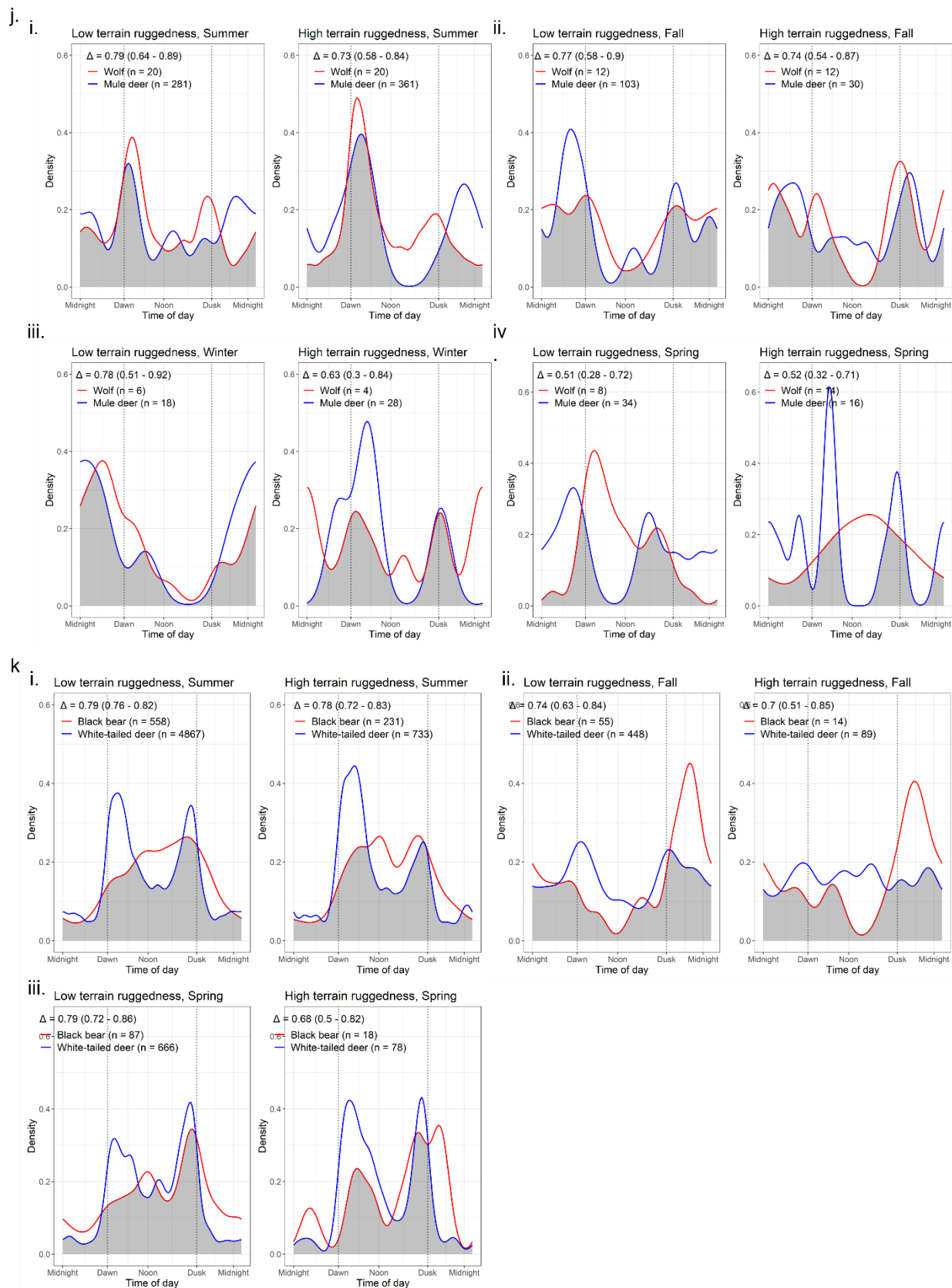


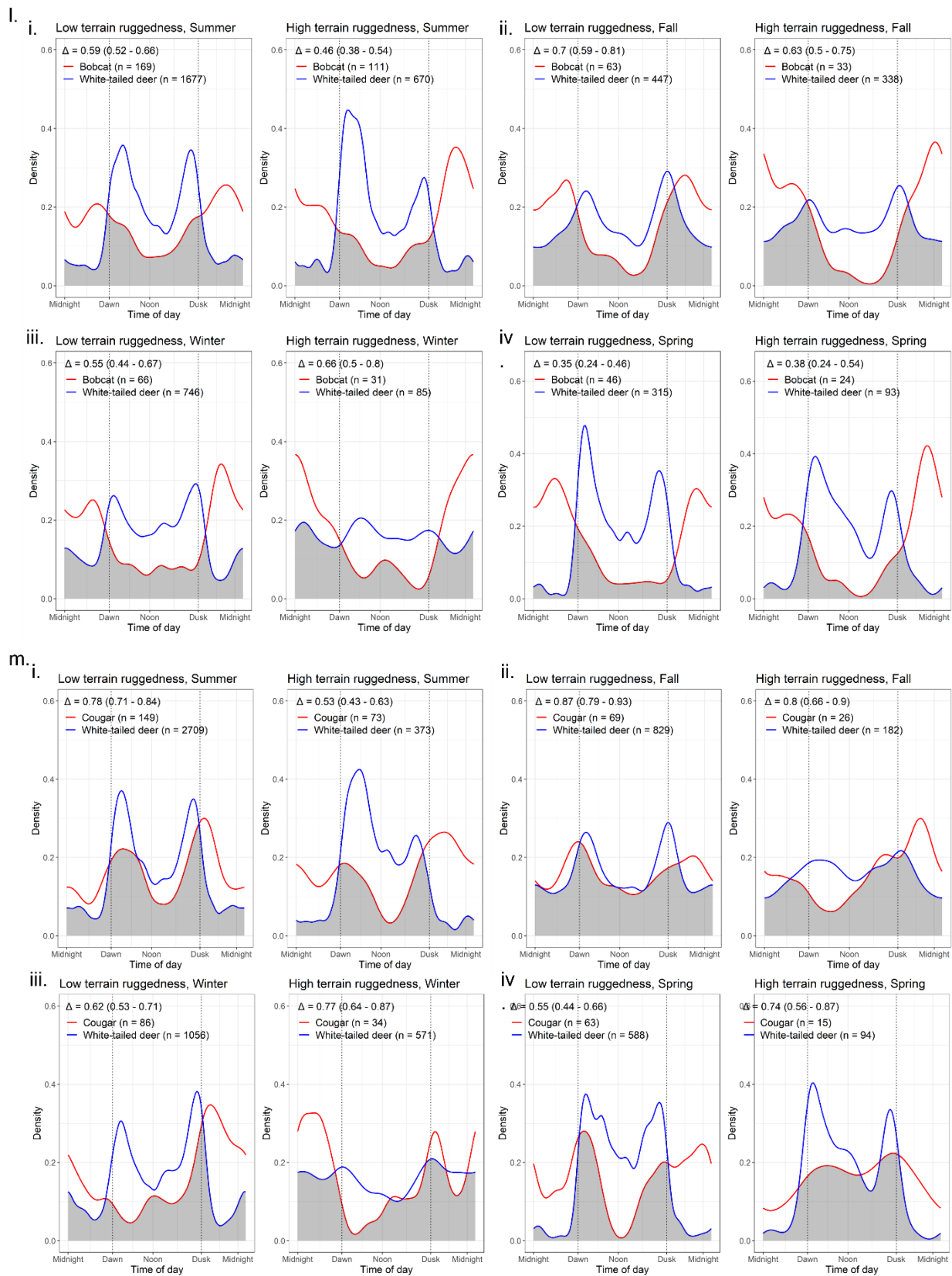


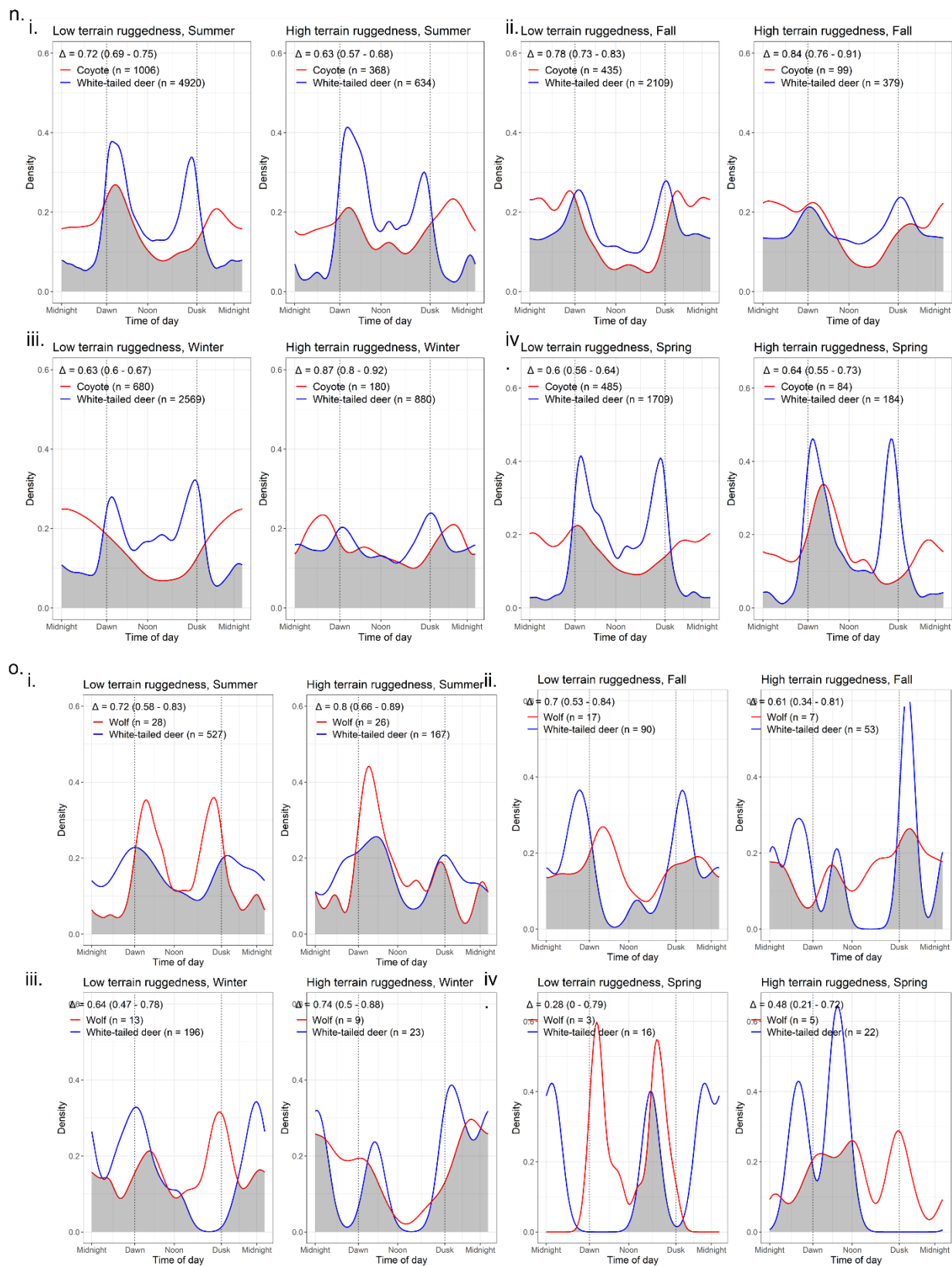


h.









Appendix S4: Latency analysis results

Table S4.1. Effect of terrain ruggedness (TRI), season (summer, fall, winter, and spring), predator species (bobcat, coyote, black bear, cougar, and wolf), and interactions between predator species and terrain ruggedness on the latency (time between detections) of an ungulate prey species detection following a predator detection. Bobcats in summer represents the intercept in all models. Coefficients whose 95% Credible Intervals (CRI) do not overlap 0 (bolded) were considered supported by the model.

Species	Parameter [†]	Estimate	95% CRI
Elk	Intercept	7.73	6.958 - 8.575
Elk	TRI	0.31	-0.005 - 0.647
Elk	Season: Fall	0.71	-0.143 - 1.633
Elk	Season: Winter	-0.11	-1.148 - 1.013
Elk	Season: Spring	0.23	-0.543 - 0.969
Elk	Predator: Coyote	-0.40	-1.284 - 0.454
Elk	Predator: Black bear	-0.06	-1.001 - 0.809
Elk	Predator: Cougar	-0.37	-1.397 - 0.653
Moose	Intercept	7.81	7.369 - 8.260
Moose	TRI	0.19	-0.163 - 0.576
Moose	Season: Fall	0.70	0.248 - 1.170
Moose	Season: Winter	0.94	0.377 - 1.528
Moose	Season: Spring	0.12	-0.389 - 0.663
Moose	Predator: Coyote	-0.25	-0.766 - 0.258
Moose	Predator: Black bear	-0.07	-0.597 - 0.441
Moose	Predator: Cougar	0.00	-0.651 - 0.670
Moose	Predator: Wolf	-0.19	-1.205 - 0.904
Moose	Predator: Coyote TRI	-0.20	-0.644 - 0.234
Moose	Predator: Black bear TRI	-0.05	-0.508 - 0.390
Moose	Predator: Cougar TRI	-0.57	-1.293 - 0.214
Moose	Predator: Wolf TRI	-0.44	-1.288 - 0.659
Mule deer	Intercept	7.57	7.309 - 7.840
Mule deer	TRI	0.21	-0.029 - 0.468
Mule deer	Season: Fall	0.10	-0.083 - 0.289
Mule deer	Season: Winter	0.41	0.190 - 0.622
Mule deer	Season: Spring	0.23	0.043 - 0.408
Mule deer	Predator: Coyote	0.26	-0.005 - 0.520
Mule deer	Predator: Black bear	0.33	0.036 - 0.608
Mule deer	Predator: Cougar	0.50	0.131 - 0.865
Mule deer	Predator: Wolf	0.40	-0.049 - 0.860
Mule deer	Predator: Coyote TRI	-0.11	-0.370 - 0.149
Mule deer	Predator: Black bear TRI	-0.06	-0.343 - 0.213
Mule deer	Predator: Cougar TRI	-0.05	-0.400 - 0.295
Mule deer	Predator: Wolf TRI	-0.26	-0.697 - 0.182
White-tailed deer	Intercept	7.46	7.240 - 7.680
White-tailed deer	TRI	0.01	-0.156 - 0.191

White-tailed deer	Season: Fall	0.27	0.101 - 0.445
White-tailed deer	Season: Winter	0.50	0.333 - 0.666
White-tailed deer	Season: Spring	0.07	-0.111 - 0.248
White-tailed deer	Predator: Coyote	-0.07	-0.291 - 0.152
White-tailed deer	Predator: Black bear	0.13	-0.122 - 0.387
White-tailed deer	Predator: Cougar	0.23	-0.054 - 0.521
White-tailed deer	Predator: Wolf	0.05	-0.611 - 0.776
White-tailed deer	Predator: Coyote TRI	-0.05	-0.241 - 0.142
White-tailed deer	Predator: Black bear TRI	0.26	0.023 - 0.492
White-tailed deer	Predator: Cougar TRI	-0.06	-0.279 - 0.164
White-tailed deer	Predator: Wolf TRI	0.01	-0.452 - 0.499

[†]Interactions between predator species and terrain ruggedness were excluded from the elk model owing to small sample sizes. Wolves were also excluded from the elk model owing to only one wolf-elk observation occurring in our data set.

Table S4.2. Effect of terrain ruggedness (TRI), season (summer, fall, winter, and spring), ungulate species (elk, moose, mule deer, and white-tailed deer), and an interaction between ungulate species and terrain ruggedness on the latency (time between detections) of different ungulate species at a camera. Coefficients whose 95% Credible Intervals (CRI) do not overlap 0 (bolded) were considered supported by the model.

Species	Parameter [†]	Estimate	95% CRI
Elk	Intercept [*]	7.33	6.548 - 8.151
Elk	TRI	0.26	0.022 - 0.527
Elk	Season: Fall	0.23	-0.261 - 0.744
Elk	Season: Winter	0.33	-0.321 - 1.003
Elk	Season: Spring	-0.18	-0.612 - 0.252
Elk	Ungulate: White-tailed Deer	0.03	-0.772 - 0.784
Elk	Ungulate: Moose	1.03	0.095 - 1.965
Moose	Intercept [*]	7.96	7.602 - 8.317
Moose	TRI	0.11	-0.172 - 0.394
Moose	Season: Fall	0.10	-0.253 - 0.465
Moose	Season: Winter	0.75	0.302 - 1.201
Moose	Season: Spring	0.31	-0.126 - 0.765
Moose	Ungulate: White-tailed Deer	-0.49	-0.887 - -0.101
Moose	Ungulate: Elk	-0.76	-1.467 - -0.022
Moose	Ungulate: White-tailed Deer TRI	0.07	-0.289 - 0.425
Moose	Ungulate: Elk TRI	0.09	-0.880 - 1.071
Mule deer	Intercept [*]	7.55	7.322 - 7.792
Mule deer	TRI	-0.01	-0.193 - 0.169
Mule deer	Season: Fall	-0.12	-0.390 - 0.162
Mule deer	Season: Winter	0.11	-0.308 - 0.533
Mule deer	Season: Spring	0.24	-0.051 - 0.546
Mule deer	Ungulate: Elk	-0.30	-0.978 - 0.415

Mule deer	Ungulate: Moose	0.41	0.005 - 0.813
Mule deer	Ungulate: Elk TRI	-0.07	-0.759 - 0.689
Mule deer	Ungulate: Moose TRI	0.01	-0.284 - 0.310
White-tailed deer	Intercept*	7.35	7.169 - 7.539
White-tailed deer	TRI	0.30	0.124 - 0.484
White-tailed deer	Season: Fall	0.18	-0.029 - 0.395
White-tailed deer	Season: Winter	0.25	-0.024 - 0.539
White-tailed deer	Season: Spring	0.22	-0.010 - 0.457
White-tailed deer	Ungulate: Elk	0.28	0.020 - 0.547
White-tailed deer	Ungulate: Moose	0.15	-0.089 - 0.397
White-tailed deer	Ungulate: Elk TRI	-0.17	-0.429 - 0.087
White-tailed deer	Ungulate: Moose TRI	-0.30	-0.555 - -0.043

†Interactions between ungulate species and TRI were excluded from the elk model owing to convergence issues.

*Intercept of the elk, moose, and white-tailed deer models represent the effect of mule deer in summer; the effect of white-tailed deer in summer represents the intercept of the mule deer model.

Table S4.3. Mean number of minutes (min) between the detection of an ungulate prey species following the detection of a predator species at camera sites in eastern Washington, USA, 2018 - 2021. The species-specific (Ungulate species) mean time-between-detections (Mean TBD) and 95% Credible Intervals (CRI) were predicted for each season (summer, fall, winter, spring) and predator species (bobcat, coyote, black bear, cougar, wolf) parameter while terrain ruggedness was held at its mean value. The overall mean number of minutes between a detection of an ungulate following that of a predator is bolded for comparison with the overall mean number of minutes between detections of different ungulates.

Ungulate species	Parameter†	Mean TBD (min)	95% CRI
Elk	Summer	2006.68	1258.10 - 3213.84
Elk	Fall	4425.48	1683.75 - 10239.82
Elk	Winter	1993.33	683.70 - 5049.80
Elk	Spring	2577.55	1305.65 - 4628.42
Elk	Bobcat	3364.96	1481.16 - 7167.53
Elk	Coyote	2158.71	1241.06 - 3652.87
Elk	Black bear	3093.71	1460.34 - 5954.48
Elk	Cougar	2385.66	893.77 - 5515.32
Elk	Overall mean	2750.76	1662.34 - 4628.62
Moose	Summer	2333.99	1708.06 - 3233.57
Moose	Fall	4788.25	2965.64 - 7513.94
Moose	Winter	6114.46	3480.21 - 10317.28
Moose	Spring	2699.81	1557.40 - 4556.22
Moose	Bobcat	4319.41	2619.01 - 6912.58
Moose	Coyote	3321.45	2386.60 - 4540.27

Moose	Black bear	3997.07	2590.76 - 5959.25
Moose	Cougar	4359.20	2477.80 - 7484.69
Moose	Wolf	3923.52	1402.04 - 9507.30
Moose	Overall mean	3984.13	2885.05 - 5589.89
Mule deer	Summer	2672.19	2273.82 - 3139.48
Mule deer	Fall	2962.56	2423.51 - 3609.49
Mule deer	Winter	4018.78	3215.56 - 4986.46
Mule deer	Spring	3354.10	2746.95 - 4081.89
Mule deer	Bobcat	2383.48	1832.94 - 3065.80
Mule deer	Coyote	3073.77	2707.22 - 3485.37
Mule deer	Black bear	3286.89	2701.28 - 3965.20
Mule deer	Cougar	3926.78	2921.56 - 5227.48
Mule deer	Wolf	3588.63	2401.00 - 5283.74
Mule deer	Overall mean	3251.91	2800.05 - 3786.39
White-tailed deer	Summer	1900.54	1606.40 - 2309.27
White-tailed deer	Fall	2500.35	2023.74 - 3128.06
White-tailed deer	Winter	3135.16	2534.09 - 3934.90
White-tailed deer	Spring	2036.29	1632.01 - 2570.90
White-tailed deer	Bobcat	2196.03	1758.85 - 2728.03
White-tailed deer	Coyote	2044.28	1812.58 - 2307.40
White-tailed deer	Black bear	2505.78	2070.69 - 3014.72
White-tailed deer	Cougar	2776.64	2216.89 - 3455.30
White-tailed deer	Wolf	2442.70	1213.79 - 4650.68
White-tailed deer	Overall mean	2393.08	2025.52 - 2907.10

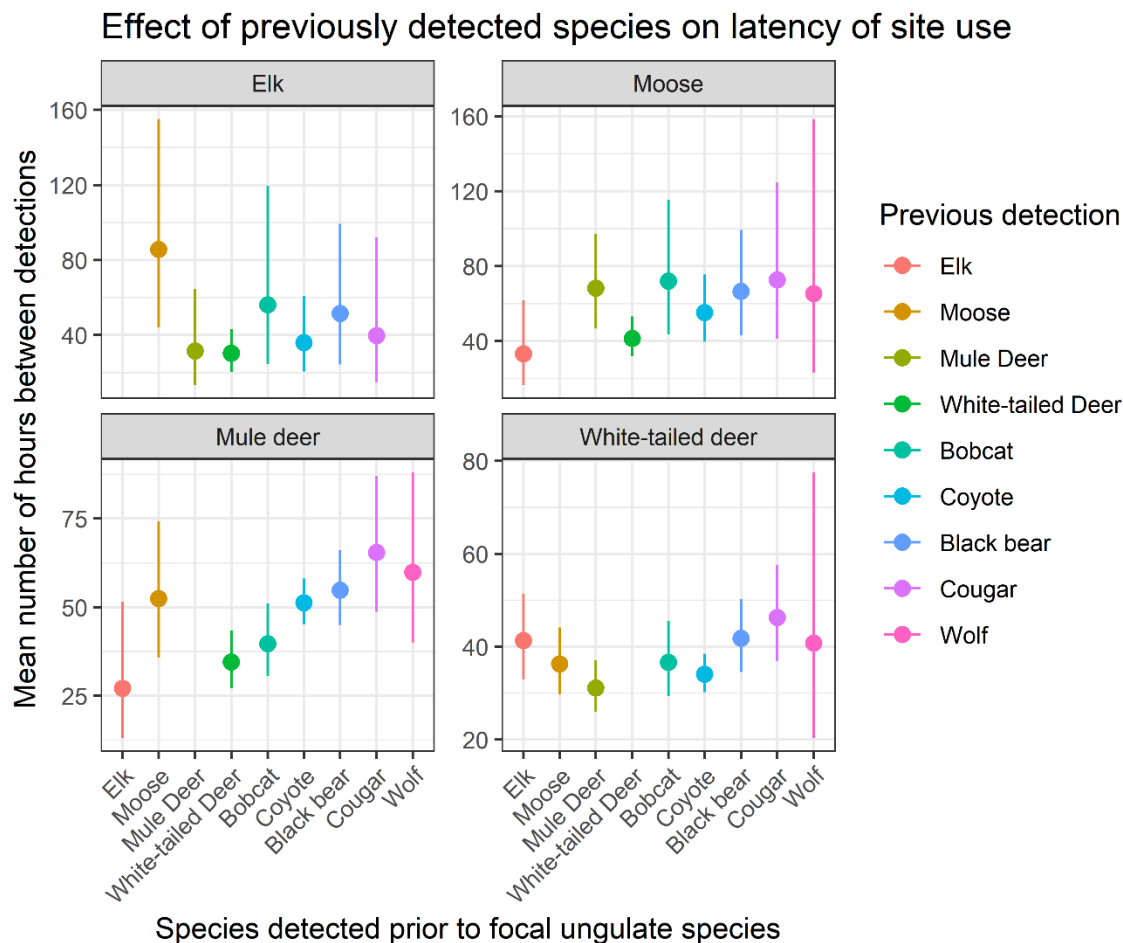
†Wolves were also excluded from the elk model owing to only one wolf-elk observation occurring in our data set.

Table S4.4. Mean number of minutes (min) between the detection of an ungulate prey species following the detection of another ungulate species at camera sites in eastern Washington, USA, 2018 - 2021. The species-specific (Ungulate species) mean time-between-detections (Mean TBD) and 95% Credible Intervals (CRI) were predicted for each season (summer, fall, winter, spring) and ungulate species (elk, moose, mule deer, and white-tailed deer) parameter while terrain ruggedness was held at its mean value. The overall mean number of minutes between a detection of an ungulate following that of a different ungulate is bolded for comparison with the overall mean number of minutes between detections between predators and ungulate prey.

Ungulate species	Parameter	Mean TBD (min)	95% CRI
Elk	Summer	2585.07	1597.43 - 4113.97
Elk	Fall	3349.80	1704.38 - 6127.88
Elk	Winter	3688.16	1822.42 - 6824.74
Elk	Spring	2175.20	1248.38 - 3570.18
Elk	Mule Deer	1887.71	797.26 - 3879.10
Elk	White-tailed Deer	1818.66	1218.79 - 2586.47
Elk	Moose	5142.30	2644.19 - 9301.19

Elk	Overall mean	2949.55	1837.36 - 4585.44
Moose	Summer	2028.54	1520.07 - 2673.98
Moose	Fall	2258.42	1546.52 - 3246.99
Moose	Winter	4347.30	2719.07 - 6666.91
Moose	Spring	2805.53	1797.60 - 4241.81
Moose	Mule Deer	4098.43	2807.10 - 5824.99
Moose	White-tailed Deer	2485.19	1916.15 - 3188.81
Moose	Elk	1996.22	988.73 - 3703.55
Moose	Overall mean	2859.95	2162.01 - 3763.53
Mule deer	Summer	2118.33	1606.84 - 2786.78
Mule deer	Fall	1895.50	1362.15 - 2607.19
Mule deer	Winter	2402.21	1495.73 - 3707.17
Mule deer	Spring	2713.22	1926.53 - 3750.53
Mule deer	White-tailed Deer	2071.90	1632.51 - 2607.44
Mule deer	Elk	1628.01	779.59 - 3093.32
Mule deer	Moose	3147.03	2146.70 - 4457.41
Mule deer	Overall mean	2282.31	1749.10 - 2970.84
White-tailed deer	Summer	1829.39	1580.24 - 2109.49
White-tailed deer	Fall	2197.81	1787.06 - 2684.11
White-tailed deer	Winter	2373.52	1797.67 - 3097.27
White-tailed deer	Spring	2290.69	1824.61 - 2853.68
White-tailed deer	Mule Deer	1865.38	1558.64 - 2219.92
White-tailed deer	Elk	2477.34	1973.43 - 3084.34
White-tailed deer	Moose	2175.83	1780.48 - 2645.84
White-tailed deer	Overall mean	2172.85	1893.13 - 2494.78

Figure S4.1. Effect of species and season on latency of ungulate detections at camera sites in eastern Washington, USA, 2018 – 2020. The estimated mean (and 95% Bayesian Credible Interval) number of hours between detections of the focal ungulate (elk, moose, mule deer, or white-tailed deer) following the detection of a different ungulate species or predator species, averaged across seasons, are plotted for each focal ungulate species.



APPENDIX D

Supplemental Materials for Chapter 5

Harry Potter and the anthropogenic impacts on spatial and temporal overlap of predators and prey in eastern Washington, USA

Appendix S1: Detection data summary

Table S1.1. Summary of wildlife species, cattle, and hunters detected by camera traps and percentage of cameras where each was detected during the summer grazing season (1 July – 29 Sept) and fall hunting season (1 Oct – 30 Nov) across two study areas in eastern Washington, USA 2018 – 2020. Detection events of wildlife species were considered independent when a ≥ 30 -minute interval elapsed between photographs of the same species at a given camera site; detection events for cattle and hunters were considered independent when a ≥ 5 -minute interval elapsed between photographs of cattle or hunters.

Species	Season	Independent detections (n)	Percent of cameras
Black Bear	Grazing	919	0.72
Black Bear	Hunting	148	0.26
Bobcat	Grazing	337	0.33
Bobcat	Hunting	151	0.25
Cattle	Grazing	2384	0.18
Cougar	Grazing	239	0.36
Cougar	Hunting	127	0.23
Coyote	Grazing	1722	0.64
Coyote	Hunting	970	0.58
Elk	Grazing	272	0.21
Elk	Hunting	89	0.12
Hunters	Hunting	823	0.31
Mule Deer	Grazing	3005	0.65
Mule Deer	Hunting	2058	0.55
White-tailed Deer	Grazing	5301	0.67
White-tailed Deer	Hunting	3161	0.49
Wolf	Grazing	72	0.10
Wolf	Hunting	41	0.07

Appendix S2: Multispecies occupancy model results

Effects of environmental predictors on co-occurrence, conditional occupancy, and detection probability

The effects of the environmental predictors on conditional occupancy varied by species but were relatively similar between the grazing season and hunting season analyses. In general, we found a positive or quadratic effect of elevation for many species in both seasons, indicating site use was highest at mid- to higher elevations for most species (Appendix S2: Tables S2.2 and S2.4). In the grazing season, conditional occupancy increased for black bears, bobcats, cougars, and moose as the percentage of forested habitat increased, whereas it decreased for mule deer (Appendix S2: Table S2.2). The percentage of forested habitat was less important for many species in the hunting season, where only bobcat site use increased with forested habitat whereas coyote and mule deer site use decreased with increasing forested habitat (Appendix S2: Table S2.4). In both seasons, elk, moose, and mule deer were more likely to use sites in the Northeast study area whereas mule deer were more likely to use sites in the Okanogan study area, consistent with known densities and distributions of these species in our study region (Appendix S2: Tables S2.2 and S2.4). Bobcats were also more likely to use sites in the Northeast whereas coyotes were more likely to use sites in the Okanogan in both seasons (Appendix S2: Tables S2.2 and S2.4). In addition, cougars were more likely to use sites in the Northeast during the grazing season whereas wolves were more likely to use sites in the Northeast during the hunting season (Appendix S2: Tables S2.2 and S2.4).

In addition to the effects of anthropogenic activity on detection probability (Tables 2 and 3), we also found that trail type strongly influenced detection probability in our models. During the grazing season, moose and all predator species were more likely to be detected on open roads compared to game trails whereas mule deer were less likely to be detected on open roads (Appendix S2: Table1 S2.1). The patterns were similar in the hunting season, where moose and all predator species except wolves were more likely to be detected on open roads compared to game trails (Appendix S2: Table1 S2.3).

Table S2.1. Estimated coefficients and standard errors (SE) for the effect of site- and survey-specific predictors on the probability of detecting a predator [1] and prey [2] species at a camera site during a one-week sampling occasion in the grazing season (1 July – 29 Sept) in eastern Washington, 2018 – 2020. Trail type indicated whether a camera was monitoring a trail or road; grazing allotment indicated whether a camera was deployed on public land where grazing was permitted; weekly cattle activity was represented by the sum of independent detections of cattle at a camera site per sampling occasion; cameras on trails in areas where public grazing was not permitted represented the intercept. Bolded estimates and SE indicate the predictor was significant (p -value ≤ 0.05) or trending towards significant (p -value ≤ 0.1)*.

[1:2] Predator: prey pairing	[1] Intercept (SE)	[1]	[1]	[1]	[2] Intercept (SE)	[2]	[2]	[2]
		Trail type (SE)	Grazing allotment (SE)	Weekly cattle activity (SE)		Trail type (SE)	Grazing allotment (SE)	Weekly cattle activity (SE)
Black Bear:	-1.55	0.36	0.08	-0.05	-1.42	0.20	-0.38	0.13
Elk	(0.09)	(0.1)	(0.11)	(0.05)	(0.18)	(0.21)	(0.32)	(0.12)

Black Bear:	-1.55	0.37	0.07	-0.05	-2.13	1.11	0.02	-0.32
Moose	(0.09)	(0.1)	(0.11)	(0.05)	(0.16)	(0.16)	(0.15)	(0.13)
Black Bear:	-1.54	0.36	0.08	-0.05	0.11	-0.31	-0.19	0.03
Mule Deer	(0.09)	(0.1)	(0.11)	(0.05)	(0.06)	(0.09)	(0.09)	(0.04)
Black Bear:								
White-tailed	-1.55	0.37	0.07	-0.05	0.57	-0.04	-0.89	0.00
Deer	(0.09)	(0.1)	(0.11)	(0.05)	(0.07)	(0.09)	(0.11)	(0.04)
Bobcat:	-2.51	0.99	0.51	0.03	0.11	-0.31	-0.19	0.03
Mule Deer	(0.23)	(0.22)	(0.17)	(0.04)	(0.06)	(0.09)	(0.09)	(0.04)
Bobcat:								
White-tailed	-2.45	0.94	0.51	0.04	0.57	-0.04	-0.88	
Deer	(0.24)	(0.22)	(0.17)	(0.05)	(0.07)	(0.09)	(0.11)	0 (0.04)
	-2.99	1.08	-0.14	-0.14	-1.43	0.21	-0.35	0.13
Cougar: Elk	(0.2)	(0.18)	(0.23)	(0.13)	(0.18)	(0.21)	(0.31)	(0.11)
Cougar:	-2.94	1.08	-0.15	-0.14	-2.12	1.12	0.04	-0.25
Moose	(0.19)	(0.19)	(0.22)	(0.13)	(0.16)	(0.16)	(0.15)	(0.13)*
Cougar:	-2.94	1.11	-0.14	-0.11	0.11	-0.31	-0.19	0.03
Mule Deer	(0.19)	(0.19)	(0.22)	(0.13)	(0.06)	(0.09)	(0.09)	(0.04)
Cougar:								
White-tailed	-2.96	1.14	-0.12	-0.12	0.57	-0.04	-0.88	0.00
Deer	(0.19)	(0.19)	(0.22)	(0.12)	(0.07)	(0.09)	(0.11)	(0.04)
Coyote:	-0.83	0.37	0.02	0.10	0.11	-0.31	-0.19	0.03
Mule Deer	(0.07)	(0.09)	(0.09)	(0.04)	(0.06)	(0.09)	(0.09)	(0.04)
Coyote:								
White-tailed	-0.83	0.37	0.02	0.10	0.57	-0.04	-0.88	0.00
Deer	(0.07)	(0.09)	(0.09)	(0.04)	(0.07)	(0.09)	(0.11)	(0.04)
	-3.26	1.27	0.53	0.31	-1.42	0.20	-0.38	0.13
Wolf: Elk	(0.45)	(0.43)	(0.44)	(0.31)	(0.18)	(0.21)	(0.32)	(0.12)
Wolf:	-3.25	1.26	0.52	0.31	-2.13	1.11	0.02	-0.32
Moose	(0.45)	(0.43)	(0.44)	(0.31)	(0.16)	(0.16)	(0.15)	(0.13)
Wolf: Mule	-3.46	1.48	0.55	0.30	0.11	-0.31	-0.19	0.03
Deer	(0.46)	(0.44)	(0.43)	(0.3)	(0.06)	(0.09)	(0.09)	(0.04)
Wolf:								
White-tailed	-3.26	1.27	0.51	0.31	0.57	-0.04	-0.89	0.00
Deer	(0.46)	(0.43)	(0.45)	(0.31)	(0.07)	(0.09)	(0.11)	(0.04)

*Weekly cattle activity trended toward having a significant effect (p-value = 0.06) on moose detection probability in the cougar-moose co-occurrence model.

Table S2.2. Estimated coefficients and standard errors (SE) for the effects of habitat and grazing predictors on the log odds of the probability that a predator (1st-order interactions: *f*1) or prey (1st-order interactions: *f*2) species used a camera site in the absence of the other and the effect of grazing predictors on the log odds of the probability that both species used a camera site together (2nd-order interactions: *f*12) during the grazing season in eastern Washington, (1 July – 29 Sept, 2018 – 2020). Habitat variables (elevation, elevation², percent forest, and study area) were only included in the 1st-order interactions; the mean number of weekly cattle detections (cattle activity) and whether cameras were deployed on public grazing allotments were included in all interactions to evaluate how cattle grazing influenced occurrence and co-occurrence of predators and prey. Lands where public grazing was not permitted in the Okanogan study area represented the intercept. NAs indicate the predictor was excluded owing to poor convergence; “—” indicates the predictor was not considered. Bolded estimates and SE indicate the predictor was significant (p-value ≤0.05) or trending towards significant (p-value ≤0.1)[†].

Predator: prey pairing	Order of interaction	Intercept (SE)	Study area (SE)	Elevation (SE)	Elevation ² (SE)	Percent forest (SE)	Cattle activity (SE)	Grazing allotment (SE)
Black Bear: Elk	<i>f</i> 1	1.08 (0.35)	0.29 (0.44)	0.18 (0.18)	-0.45 (0.14)	0.84 (0.23)	0.58 (0.51)	0.91 (0.46)
Black Bear: Moose	<i>f</i> 1	1.38 (0.41)	0.00 (0.43)	0.15 (0.19)	-0.46 (0.14)	0.80 (0.23)	0.64 (0.53)	0.86 (0.46)[†]
Black Bear: Mule Deer	<i>f</i> 1	1.27 (0.36)	-0.30 (0.49)	0.10 (0.18)	-0.43 (0.14)	0.82 (0.22)	0.64 (0.81)	-0.31 (0.82)
Black Bear: White-tailed Deer	<i>f</i> 1	0.88 (0.53)	0.28 (0.50)	0.23 (0.19)	-0.45 (0.14)	0.84 (0.23)	0.26 (0.72)	0.93 (0.49)[†]
Bobcat: Mule Deer	<i>f</i> 1	0.15 (0.36)	-1.20 (0.56)	0.61 (0.23)	-0.07 (0.17)	0.47 (0.20)	-0.16 (0.34)	-0.13 (0.81)
Bobcat: White-tailed Deer	<i>f</i> 1	-0.60 (0.60)	-0.51 (0.53)	0.71 (0.23)	-0.07 (0.17)	0.48 (0.20)	0.99 (0.57)[†]	0.26 (0.53)
Cougar: Elk	<i>f</i> 1	0.63 (0.49)	-1.22 (0.62)	0.60 (0.34)	0.31 (0.26)	0.86 (0.41)	0.25 (0.31)	0.49 (0.72)
Cougar: Moose	<i>f</i> 1	0.46 (0.53)	-1.30 (0.60)	0.44 (0.31)	0.32 (0.24)	0.65 (0.32)	0.43 (0.40)	0.51 (0.73)
Cougar: Mule Deer	<i>f</i> 1	0.88 (0.49)	-1.41 (0.70)	0.49 (0.29)	0.22 (0.23)	0.63 (0.29)	0.51 (0.80)	0.60 (1.24)
Cougar: White-tailed Deer	<i>f</i> 1	0.05 (0.78)	-1.16 (0.71)	0.53 (0.29)	0.24 (0.23)	0.68 (0.28)	-1.37 (0.72)[†]	0.78 (0.73)
Coyote: Mule Deer	<i>f</i> 1	-0.40 (0.27)	-0.07 (0.40)	-1.02 (0.19)	0.31 (0.13)	-0.25 (0.15)	-0.05 (0.25)	0.18 (0.57)
Coyote: White-tailed Deer	<i>f</i> 1	-0.75 (0.52)	1.03 (0.45)	-0.81 (0.18)	0.28 (0.13)	-0.29 (0.15)	1.80 (0.83)	0.22 (0.38)
Wolf: Elk	<i>f</i> 1	-1.07 (0.52)	-0.74 (0.74)	1.37 (0.43)	-0.42 (0.28)	0.02 (0.27)	-0.65 (0.61)	-0.58 (0.66)
Wolf: Moose	<i>f</i> 1	-1.33 (0.63)	-0.54 (0.77)	1.30 (0.45)	-0.39 (0.28)	0.02 (0.27)	-0.66 (0.61)	-0.61 (0.66)

Wolf: Mule Deer	<i>f</i> 1	-0.78 (0.51)	0.73 (1.28)	1.50 (0.44)	-0.48 (0.30)	0.02 (0.27)	-0.33 (0.80)	-0.99 (1.10)
Wolf: White-tailed Deer	<i>f</i> 1	-1.09 (0.96)	-0.80 (0.88)	1.35 (0.43)	-0.42 (0.28)	0.04 (0.27)	-0.82 (0.96)	-0.35 (0.81)
Black Bear: Elk	<i>f</i> 2	-1.81 (2.00)	-2.92 (0.63)	-0.42 (0.31)	-0.54 (0.34)	-0.26 (0.22)	-3.17 (7.94)	1.62 (1.55)
Black Bear: Moose	<i>f</i> 2	0.75 (0.50)	-3.26 (0.65)	1.48 (0.31)	-0.27 (0.19)	0.52 (0.20)	0.44 (0.33)	1.41 (0.57)
Black Bear: Mule Deer	<i>f</i> 2	-0.98 (0.50)	3.07 (0.43)	0.87 (0.20)	-0.49 (0.17)	-0.61 (0.20)	-0.05 (1.01)	-0.79 (0.69)
Black Bear: White-tailed Deer	<i>f</i> 2	2.15 (0.55)	-3.40 (0.50)	-1.18 (0.26)	-0.63 (0.24)	-0.40 (0.23)	0.50 (1.06)	-0.08 (0.89)
Bobcat: Mule Deer	<i>f</i> 2	-0.65 (0.38)	3.11 (0.44)	0.89 (0.20)	-0.58 (0.17)	-0.50 (0.19)	-0.55 (0.4)	-0.07 (0.55)
Bobcat: White-tailed Deer	<i>f</i> 2	2.36 (0.44)	-3.29 (0.50)	-1.27 (0.27)	-0.69 (0.24)	-0.43 (0.23)	1.60 (0.56)	-0.07 (0.47)
Cougar: Elk	<i>f</i> 2	-1.04 (0.79)	-3.01 (0.73)	-0.44 (0.31)	-0.58 (0.35)	-0.24 (0.23)	0.12 (0.34)	2.02 (1.05)
Cougar: Moose	<i>f</i> 2	0.29 (0.54)	-2.87 (0.64)	1.42 (0.31)	-0.35 (0.18)	0.46 (0.20)	0.24 (0.40)	1.78 (0.80)
Cougar: Mule Deer	<i>f</i> 2	-0.44 (0.51)	3.01 (0.45)	0.87 (0.20)	-0.55 (0.17)	-0.48 (0.20)	0.56 (0.79)	0.25 (0.84)
Cougar: White-tailed Deer	<i>f</i> 2	2.37 (0.55)	-3.40 (0.53)	-1.20 (0.27)	-0.74 (0.24)	-0.41 (0.24)	0.48 (0.38)	0.27 (0.57)
Coyote: Mule Deer	<i>f</i> 2	-1.05 (0.34)	3.11 (0.43)	1.01 (0.21)	-0.60 (0.17)	-0.44 (0.19)	-0.59 (0.4)	-0.01 (0.55)
Coyote: White-tailed Deer	<i>f</i> 2	2.63 (0.44)	-3.70 (0.53)	-1.00 (0.26)	-0.73 (0.24)	-0.29 (0.22)	2.50 (0.86)	-0.31 (0.58)
Wolf: Elk	<i>f</i> 2	-0.22 (0.32)	-2.86 (0.61)	-0.34 (0.33)	-0.61 (0.34)	-0.15 (0.20)	-0.18 (0.20)	0.56 (0.60)
Wolf: Moose	<i>f</i> 2	0.81 (0.37)	-3.25 (0.65)	1.45 (0.32)	-0.27 (0.18)	0.53 (0.19)	0.45 (0.33)	1.44 (0.57)
Wolf: Mule Deer	<i>f</i> 2	-0.27 (0.34)	3.21 (0.53)	1.11 (0.32)	-0.59 (0.18)	-0.48 (0.19)	0.07 (0.18)	-0.07 (0.56)
Wolf: White-tailed Deer	<i>f</i> 2	2.70 (0.43)	-3.43 (0.51)	-1.12 (0.28)	-0.68 (0.24)	-0.34 (0.22)	1.00 (0.32)	0.00 (0.42)
Black Bear: Elk	<i>f</i> 12	1.75 (2.00)	—	—	—	—	2.99 (7.95)	-1.22 (1.62)
Black Bear: Moose	<i>f</i> 12	0.12 (0.46)	—	—	—	—	NA	NA
Black Bear: Mule Deer	<i>f</i> 12	0.48 (0.52)	—	—	—	—	0.06 (1.01)	1.30 (0.86)
Black Bear: White-tailed Deer	<i>f</i> 12	0.67 (0.53)	—	—	—	—	0.55 (1.08)	-0.06 (0.98)
Bobcat: Mule Deer	<i>f</i> 12	0.06 (0.53)	—	—	—	—	0.85 (0.50)[†]	0.54 (0.83)

Bobcat: White-tailed								
Deer	<i>f</i> ₁₂	0.81 (0.59)	—	—	—	—	-0.89 (0.59)	-0.12 (0.70)
Cougar: Elk	<i>f</i> ₁₂	0.77 (0.95)	—	—	—	—	-1.56 (1.41)	-2.05 (1.26)
Cougar: Moose	<i>f</i> ₁₂	0.66 (0.64)	—	—	—	—	-0.34 (0.46)	-0.60 (0.94)
Cougar: Mule Deer	<i>f</i> ₁₂	-0.16 (0.65)	—	—	—	—	-0.54 (0.82)	-0.16 (1.10)
Cougar: White-tailed								
Deer	<i>f</i> ₁₂	0.82 (0.71)	—	—	—	—	1.77 (0.78)	-0.82 (0.95)
Coyote: Mule Deer	<i>f</i> ₁₂	0.82 (0.40)	—	—	—	—	0.76 (0.44)[†]	0.26 (0.64)
Coyote: White-tailed								
Deer	<i>f</i> ₁₂	0.70 (0.50)	—	—	—	—	-1.75 (0.84)	0.24 (0.61)
Wolf: Elk	<i>f</i> ₁₂	-0.25 (0.63)	—	—	—	—	NA	NA
Wolf: Moose	<i>f</i> ₁₂	0.18 (0.60)	—	—	—	—	NA	NA
Wolf: Mule Deer	<i>f</i> ₁₂	-1.62 (1.21)	—	—	—	—	-0.67 (1.17)	0.28 (1.13)
Wolf: White-tailed								
Deer	<i>f</i> ₁₂	-0.03 (0.89)	—	—	—	—	0.36 (1.19)	-0.59 (1.11)

[†]Grazing activity trended towards having a significant effect on bobcat conditional occupancy (p-value = 0.09) in the bobcat – white-tailed deer model, on cougar conditional occupancy (p-value = 0.06) in the cougar – white-tailed deer model, and on bobcat – mule deer (p-value = 0.09) and coyote – mule deer (p-value = 0.08) co-occurrence. Grazing allotments trended towards having a significant effect on black bear conditional occupancy (p-value = 0.06) in the black bear – moose and black bear – white-tailed deer co-occurrence models.

Table S2.3. Estimated coefficients and standard errors (SE) for the effect of site- and survey-specific predictors on the probability of detecting a predator [1] and prey [2] species at a camera site during a one-week sampling occasion in the hunting season (1 Oct – 30 Nov) in eastern Washington, 2018 – 2020. Trail type indicated whether a camera was monitoring a trail or road; grazing allotment indicated whether a camera was deployed on public land where grazing was permitted; weekly cattle activity was represented by the sum of independent detections of cattle at a camera site per sampling occasion; cameras on trails in areas where public grazing was not permitted represented the intercept. Bolded estimates and SE indicate the predictor was significant (p-value ≤ 0.05) or trending towards significant (p-value ≤ 0.1)*.

[1:2] Predator: prey pairing	[1] Intercept (SE)	[1] Trail type (SE)	[1] Public Land (SE)	[1] Weekly Hunter Activity (SE)	[2] Intercept (SE)	[2] Trail type (SE)	[2] Public Land (SE)	[2] Weekly Hunter Activity (SE)
Black Bear:	-2.95	0.73	0.27	0.00	-2.29	0.24	0.37	0.02
Elk	(0.37)	(0.24)	(0.32)	(0.07)	(0.47)	(0.35)	(0.44)	(0.25)
Black Bear:	-2.84	0.70	0.14	0.01	-2.37	0.61	0.82	-0.13
Moose	(0.49)	(0.24)	(0.47)	(0.06)	(0.59)	(0.25)	(0.58)	(0.16)
Black Bear:	-2.88	0.71	0.21	0.01	0.41	0.12	-0.59	0.02
Mule Deer	(0.61)	(0.25)	(0.55)	(0.06)	(0.15)	(0.12)	(0.15)	(0.04)
Black Bear:								
White-tailed	-2.75	0.67	0.08	0.01	1.07	0.10	-0.71	0.00
Deer	(0.51)	(0.25)	(0.47)	(0.07)	(0.12)	(0.12)	(0.13)	(0.1)
Bobcat:	-1.86	1.51	-1.34	-0.06	0.42	0.12	-0.59	0.02
Mule Deer	(0.32)	(0.26)	(0.33)	(0.08)	(0.15)	(0.11)	(0.15)	(0.04)
Bobcat:								
White-tailed	-2.01	1.71	-1.32	-0.01	1.07	0.11	-0.71	-0.01
Deer	(0.33)	(0.24)	(0.32)	(0.07)	(0.12)	(0.12)	(0.13)	(0.1)
	-2.75	0.69	-0.26	0.20	-2.39	0.31	0.41	0.00
Cougar: Elk	(0.42)	(0.24)	(0.36)	(0.15)	(0.47)	(0.34)	(0.44)	(0.24)
Cougar:	-2.75	0.69	-0.26	0.20	-2.73	0.56	1.23	-0.15
Moose	(0.42)	(0.24)	(0.36)	(0.15)	(0.49)	(0.25)	(0.48)	(0.16)
Cougar:	-2.69	0.71	-0.41	0.21	0.41	0.12	-0.59	0.02
Mule Deer	(0.41)	(0.24)	(0.38)	(0.14)	(0.15)	(0.12)	(0.15)	(0.04)
Cougar:								
White-tailed	-2.01	0.59	-0.91	0.20	1.07	0.10	-0.71	0.00
Deer	(0.42)	(0.25)	(0.39)	(0.15)	(0.12)	(0.12)	(0.13)	(0.1)
Coyote:	-0.54	0.58	-0.52	0.03	0.42	0.12	-0.59	0.02
Mule Deer	(0.11)	(0.12)	(0.12)	(0.04)	(0.15)	(0.12)	(0.15)	(0.04)
Coyote:								
White-tailed	-0.55	0.58	-0.5	0.03	1.07	0.10	-0.71	0.00
Deer	(0.11)	(0.12)	(0.12)	(0.04)	(0.12)	(0.12)	(0.13)	(0.1)
	-2.39	0.46		-0.14	-2.39	0.31	0.42	0.01
Wolf: Elk	(0.65)	(0.65)	NA	(0.21)	(0.48)	(0.35)	(0.44)	(0.24)
Wolf:	-2.44	0.34		-0.21	-2.54	0.45	1.15	-0.17
Moose	(0.6)	(0.6)	NA	(0.22)	(0.49)	(0.24)*	(0.48)	(0.16)

Wolf: Mule	-2.64	0.63		-0.11	0.41	0.12	-0.59	0.02
Deer	(0.57)	(0.57)	NA	(0.19)	(0.15)	(0.11)	(0.15)	(0.04)
Wolf:								
White-tailed	-2.42	0.49		-0.13	1.07	0.11	-0.71	0.00
Deer	(0.66)	(0.65)	NA	(0.2)	(0.12)	(0.12)	(0.13)	(0.1)

*Trail type trended towards having a significant effect (p-value = 0.06) on moose detection probability in the wolf-moose co-occurrence model.

Table S2.4. Estimated coefficients and standard errors (SE) for the effects of habitat and hunting predictors on the log odds of the probability that a predator (1st-order interactions: f_1) or prey (1st-order interactions: f_2) species used a camera site in the absence of the other and the effect of hunting predictors on the log odds of the probability that both species used a camera site together (2nd-order interactions: f_{12}) during the hunting season in eastern Washington, (1 Oct – 30 Nov, 2018 – 2020). Habitat variables (elevation, elevation², percent forest, and study area) were only included in the 1st-order interactions; the mean number of weekly hunter detections (hunter activity) and whether a camera was deployed on public land were included in all interactions to evaluate how hunting influenced occurrence and co-occurrence of predators and prey. Private land in the Okanogan study area represented the intercept. NAs indicate the predictor was excluded from the linear model owing to poor convergence; “—” indicates the predictor was not considered. Bolded estimates and SEs indicate the predictor was significant (p-value ≤ 0.05) or trending towards significant (p-value ≤ 0.1)[†].

Predator: prey pairing	Order of interaction	Intercept (SE)	Study area (SE)	Elevation (SE)	Elevation ² (SE)	Percent forest (SE)	Hunter activity (SE)	Public land (SE)
Black Bear: Elk	f_1	-0.38 (0.51)	0.72 (0.63)	0.29 (0.27)	-0.21 (0.23)	0.61 (0.32)	0.16 (0.18)	NA
Black Bear: Moose	f_1	-0.19 (0.88)	0.32 (0.59)	0.11 (0.30)	-0.24 (0.23)	0.52 (0.31)	NA	0.37 (0.86)
Black Bear: Mule Deer	f_1	0.00 (1.24)	-0.67 (0.84)	0.12 (0.30)	-0.17 (0.24)	0.56 (0.30)	-0.29 (0.43)	0.13 (1.27)
Black Bear: White-tailed Deer	f_1	0.52 (1.05)	-0.16 (0.67)	0.19 (0.30)	-0.25 (0.24)	0.49 (0.30)	0.23 (0.26)	0.11 (1.05)
Bobcat: Mule Deer	f_1	-0.85 (0.64)	1.02 (0.79)	0.47 (0.35)	0.05 (0.26)	0.75 (0.32)	1.88 (0.94)	1.19 (0.68)[†]
Bobcat: White-tailed Deer	f_1	-1.15 (0.69)	1.28 (0.74)	0.52 (0.29)	0.11 (0.27)	0.89 (0.31)	NA	NA
Cougar: Elk	f_1	1.28 (0.74)	-1.13 (0.70)	0.71 (0.39)	-0.34 (0.24)	0.55 (0.42)	-0.08 (0.19)	NA
Cougar: Moose	f_1	1.28 (0.74)	-1.13 (0.70)	0.71 (0.39)	-0.34 (0.24)	0.55 (0.42)	-0.08 (0.19)	NA
Cougar: Mule Deer	f_1	1.3 (0.72)	-2.12 (1.03)	0.53 (0.42)	-0.35 (0.28)	0.58 (0.44)	NA	NA
Cougar: White-tailed Deer	f_1	0.76 (1.21)	-1.09 (0.98)	0.54 (0.36)	-0.16 (0.25)	0.4 (0.33)	NA	NA
Coyote: Mule Deer	f_1	0.32 (0.29)	0.28 (0.48)	-0.79 (0.20)	0.15 (0.15)	-0.53 (0.17)	1.22 (0.45)	NA
Coyote: White-tailed Deer	f_1	-0.56 (0.45)	1.1 (0.46)	-0.47 (0.20)	-0.01 (0.14)	-0.46 (0.16)	NA	NA
Wolf: Elk	f_1	-0.71 (0.56)	-2.94 (0.85)	2.94 (0.82)	-1.24 (0.50)	-0.56 (0.34)	1.13 (0.46)	NA
Wolf: Moose	f_1	-1.76 (0.78)	-1.95 (0.98)	2.66 (0.84)	-1.15 (0.50)	-0.60 (0.36)	3.04 (0.85)	NA
Wolf: Mule Deer	f_1	-1.06 (0.55)	-4.46 (1.07)	3.15 (0.82)	-1.26 (0.54)	-0.35 (0.36)	1.02 (0.42)	NA

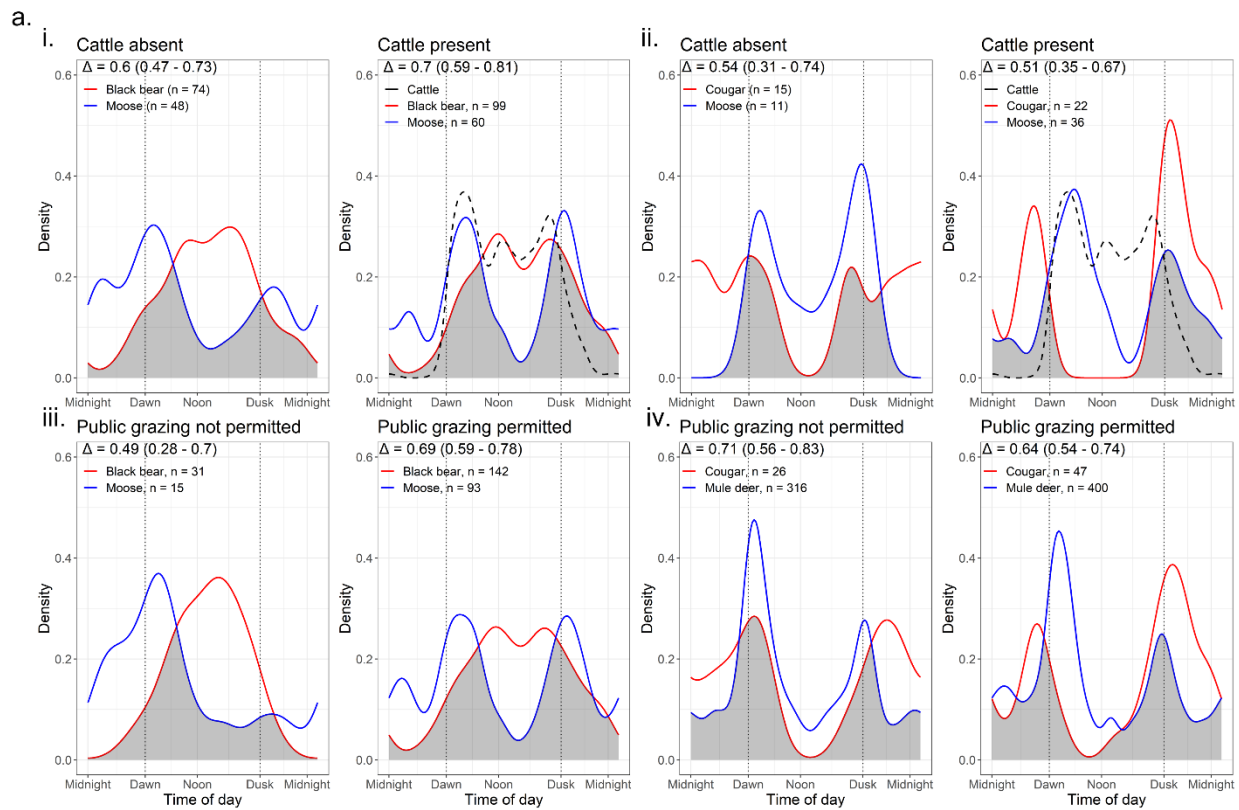
Wolf: White-tailed Deer	<i>f</i> 1	-0.52 (0.98)	-3.08 (1.00)	2.88 (0.80)	-1.22 (0.5)	-0.56 (0.34)	1.16 (0.45)	NA
Black Bear: Elk	<i>f</i> 2	-1.65 (0.90)	-2.73 (0.76)	-1.37 (0.60)	-1.11 (0.65)	-0.37 (0.32)	0.14 (0.45)	NA
Black Bear: Moose	<i>f</i> 2	-0.34 (0.82)	-3.28 (0.56)	1.34 (0.36)	-0.22 (0.20)	-0.17 (0.22)	NA	0.85 (0.73)
Black Bear: Mule Deer	<i>f</i> 2	-1.25 (0.78)	4.37 (0.56)	0.87 (0.27)	-0.91 (0.20)	-0.98 (0.25)	-0.35 (0.3)	-0.31 (0.76)
Black Bear: White-tailed Deer	<i>f</i> 2	3.19 (0.73)	-3.05 (0.43)	-1.63 (0.36)	-1.14 (0.33)	0.26 (0.23)	0.13 (0.28)	-1.13 (0.66)[†]
Bobcat: Mule Deer	<i>f</i> 2	-0.78 (0.66)	4.43 (0.54)	0.95 (0.28)	-0.93 (0.20)	-0.74 (0.25)	0.04 (1.30)	0.30 (0.63)
Bobcat: White-tailed Deer	<i>f</i> 2	2.88 (0.61)	-3.4 (0.53)	-1.8 (0.38)	-1.16 (0.33)	-0.05 (0.27)	0.01 (0.20)	-1.68 (0.65)
Cougar: Elk	<i>f</i> 2	-0.46 (0.39)	-2.46 (0.67)	-1.33 (0.61)	-1.21 (0.64)	-0.13 (0.27)	0.06 (0.22)	NA
Cougar: Moose	<i>f</i> 2	0.67 (0.35)	-3.43 (0.59)	1.56 (0.36)	-0.27 (0.20)	-0.12 (0.21)	0.32 (0.16)	NA
Cougar: Mule Deer	<i>f</i> 2	-0.61 (0.87)	4.54 (0.73)	0.93 (0.28)	-0.91 (0.21)	-1.00 (0.27)	-0.01 (0.20)	-1.47 (0.87)[†]
Cougar: White-tailed Deer	<i>f</i> 2	2.94 (0.73)	-2.94 (0.46)	-1.77 (0.38)	-1.2 (0.33)	0.17 (0.24)	-0.02 (0.19)	-1.6 (0.62)
Coyote: Mule Deer	<i>f</i> 2	-1.02 (0.40)	4.24 (0.48)	0.88 (0.23)	-0.93 (0.19)	-0.85 (0.23)	-0.12 (0.18)	NA
Coyote: White-tailed Deer	<i>f</i> 2	1.73 (0.70)	-3.26 (0.46)	-1.58 (0.36)	-1.11 (0.33)	0.31 (0.22)	-0.69 (0.4)[†]	-0.23 (0.64)
Wolf: Elk	<i>f</i> 2	-0.45 (0.48)	-2.47 (0.70)	-1.32 (0.67)	-1.21 (0.65)	-0.13 (0.28)	0.06 (0.44)	NA
Wolf: Moose	<i>f</i> 2	0.45 (0.42)	-3.34 (0.63)	1.42 (0.38)	-0.16 (0.20)	-0.13 (0.23)	1.62 (0.63)	NA
Wolf: Mule Deer	<i>f</i> 2	-1.69 (0.54)	4.81 (0.60)	0.65 (0.24)	-0.84 (0.20)	-0.81 (0.23)	-0.37 (0.33)	NA
Wolf: White-tailed Deer	<i>f</i> 2	2.09 (0.43)	-3.19 (0.48)	-1.76 (0.40)	-0.92 (0.32)	0.16 (0.22)	0.07 (0.28)	NA
Black Bear: Elk	<i>f</i> 12	1.9 (1.07)	--	--	--	--	-0.14 (0.52)	NA
Black Bear: Moose	<i>f</i> 12	0.35 (0.63)	--	--	--	--	NA	NA
Black Bear: Mule Deer	<i>f</i> 12	0.50 (1.14)	--	--	--	--	0.55 (0.5)	0.52 (1.15)
Black Bear: White-tailed Deer	<i>f</i> 12	-0.71 (1.03)	--	--	--	--	-0.25 (0.38)	0.46 (1.1)
Bobcat: Mule Deer	<i>f</i> 12	-0.26 (1.02)	--	--	--	--	-0.06 (1.33)	-0.73 (1.00)
Bobcat: White-tailed Deer	<i>f</i> 12	-0.16 (0.70)	--	--	--	--	-0.09 (0.28)	1.75 (0.70)

Cougar: Elk	<i>f</i> ₁₂	NA	--	--	--	--	NA	NA
Cougar: Moose	<i>f</i> ₁₂	NA	--	--	--	--	NA	NA
Cougar: Mule Deer	<i>f</i> ₁₂	-1.63 (1.33)	--	--	--	--	-0.20 (0.22)	3.16 (1.30)
Cougar: White-tailed Deer	<i>f</i> ₁₂	-1.16 (1.06)	--	--	--	--	-0.03 (0.29)	2.06 (0.81)
Coyote: Mule Deer	<i>f</i> ₁₂	0.16 (0.45)	--	--	--	--	NA	NA
Coyote: White-tailed Deer	<i>f</i> ₁₂	1.7 (0.59)	--	--	--	--	0.69 (0.39)[†]	-0.85 (0.46)[†]
Wolf: Elk	<i>f</i> ₁₂	-0.03 (0.90)	--	--	--	--	0 (0.5)	NA
Wolf: Moose	<i>f</i> ₁₂	1.42 (0.78)	--	--	--	--	-1.76 (0.72)	NA
Wolf: Mule Deer	<i>f</i> ₁₂	1.94 (0.83)	--	--	--	--	0.13 (0.38)	NA
Wolf: White-tailed Deer	<i>f</i> ₁₂	-0.22 (0.91)	--	--	--	--	-0.19 (0.37)	NA

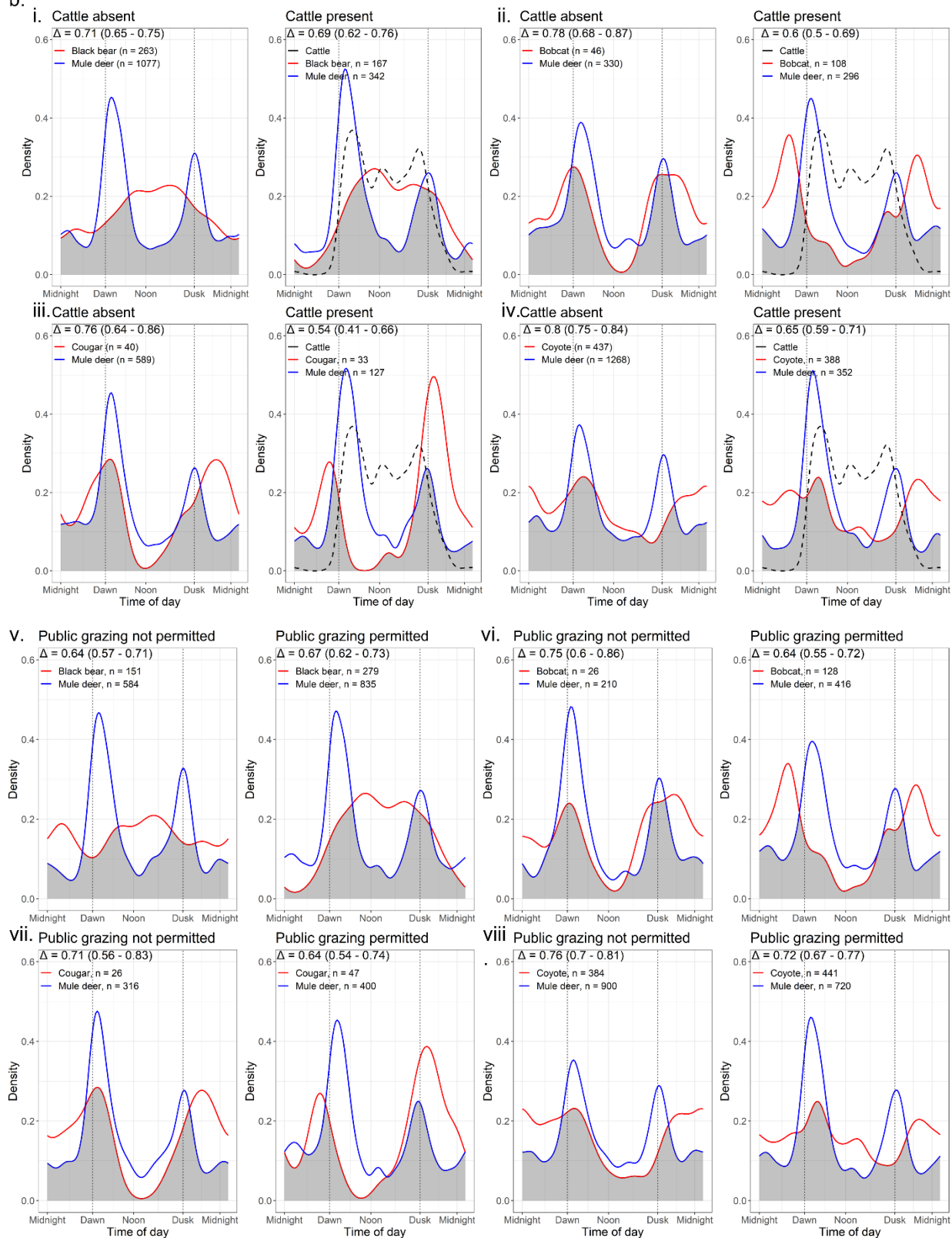
[†]Hunter activity trended towards having a significant effect on white-tailed deer conditional occupancy (p-value = 0.09) and on co-occurrence (p-value = 0.08) in the coyote – white-tailed deer model. Public land trended towards having a significant effect on white-tailed deer conditional occupancy (p-value = 0.09) in the black bear – white-tailed deer model, on bobcat conditional occupancy (p-value = 0.08) in the bobcat – mule deer model, on mule deer conditional occupancy (p-value = 0.09) in the cougar – mule deer model, and on coyote – white-tailed deer co-occurrence (p-value = 0.06).

Appendix S3: Temporal overlap results

Figure S3.1. Temporal overlap plots of paired predator (blue) and prey (red) diel activity curves at camera sites where cattle were detected compared to camera sites where cattle were not detected, and at cameras that were deployed in grazing allotments compared to cameras deployed in areas where public grazing was not permitted in the Okanogan study area in eastern Washington, USA, 2018 – 2020. The estimated coefficient of overlapping ($\bar{\Delta}$), bootstrapped 95% confidence intervals, and sample sizes for number of detections (n) of each species are reported for moose – predator activity curves (a) with cattle activity (i – iii) and grazing allotments (iv), mule deer – predator activity curves (b) with cattle activity (i – iv) and grazing allotments (v – viii), and white-tailed deer – predator activity curves (c) with cattle activity (i – iii) and grazing allotments (iv – vi) in the grazing season (1 July – 29 Sept). Cattle activity curve (black dashed line) plotted for reference.



b.



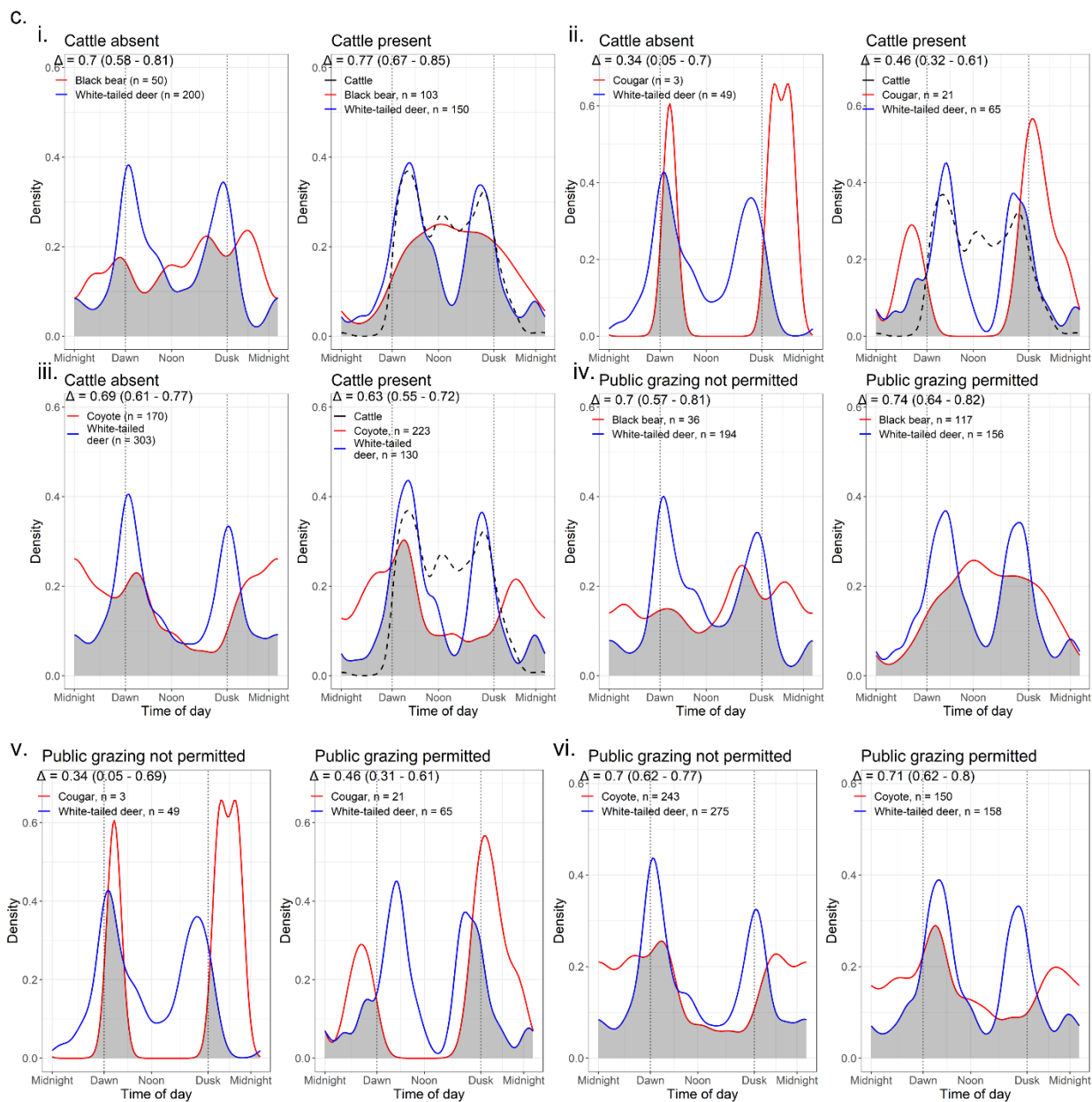


Figure S3.2. Coefficient of overlapping estimates ($\bar{\Delta}$) and bootstrapped 95% confidence intervals (CI) measuring the amount of temporal overlap between activity curves of each species when they were detected at camera sites where cattle were or were not detected (cattle activity) and cameras on grazing allotments compared to cameras in areas where public grazing was not permitted (grazing allotment) in the grazing season (1 July – 29 Sept), as well as at cameras where hunters were and were not detected (hunter activity) and where cameras were on public versus private land during the hunting season (1 Oct – 30 Nov) in eastern Washington, USA, 2018 – 2021.

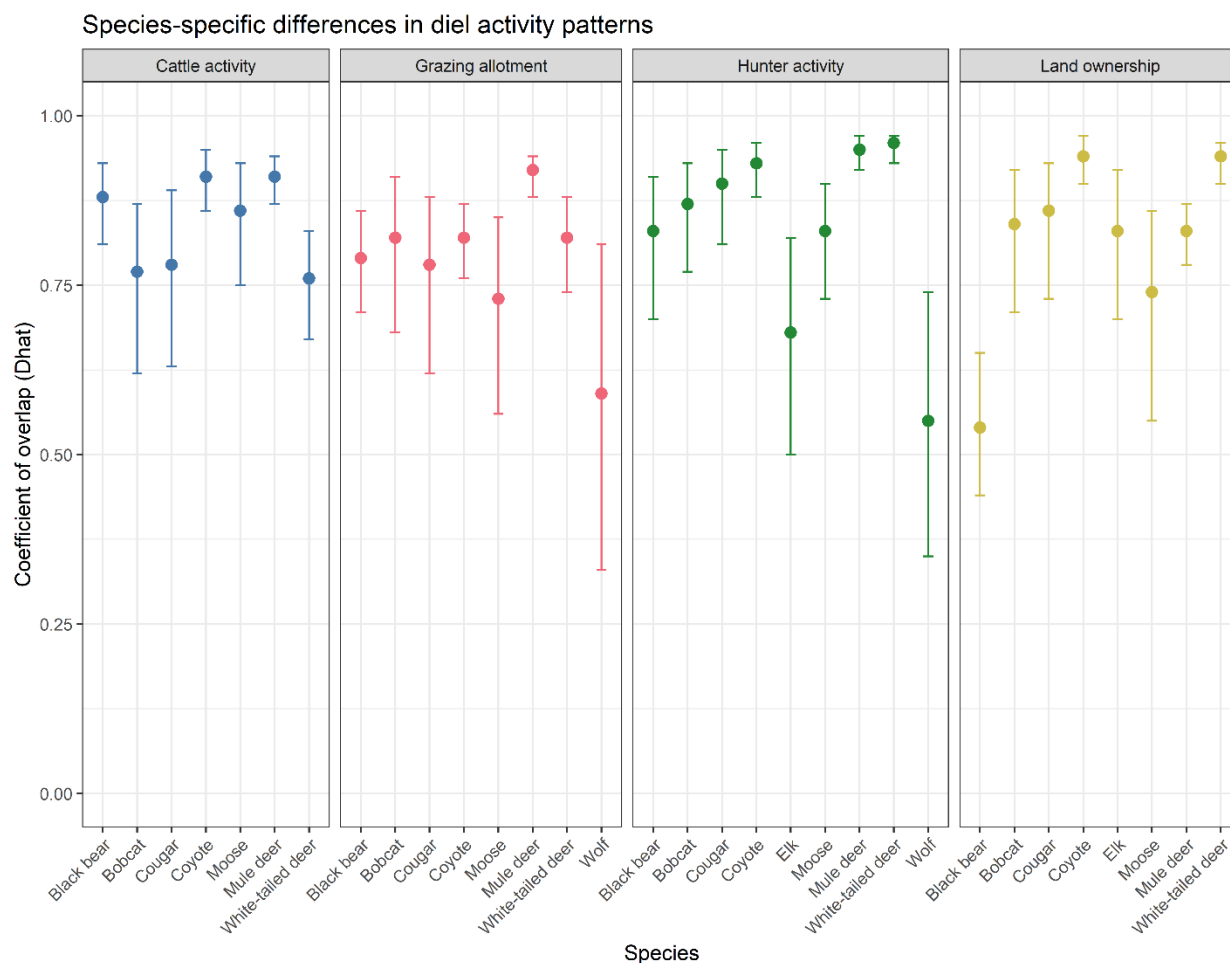
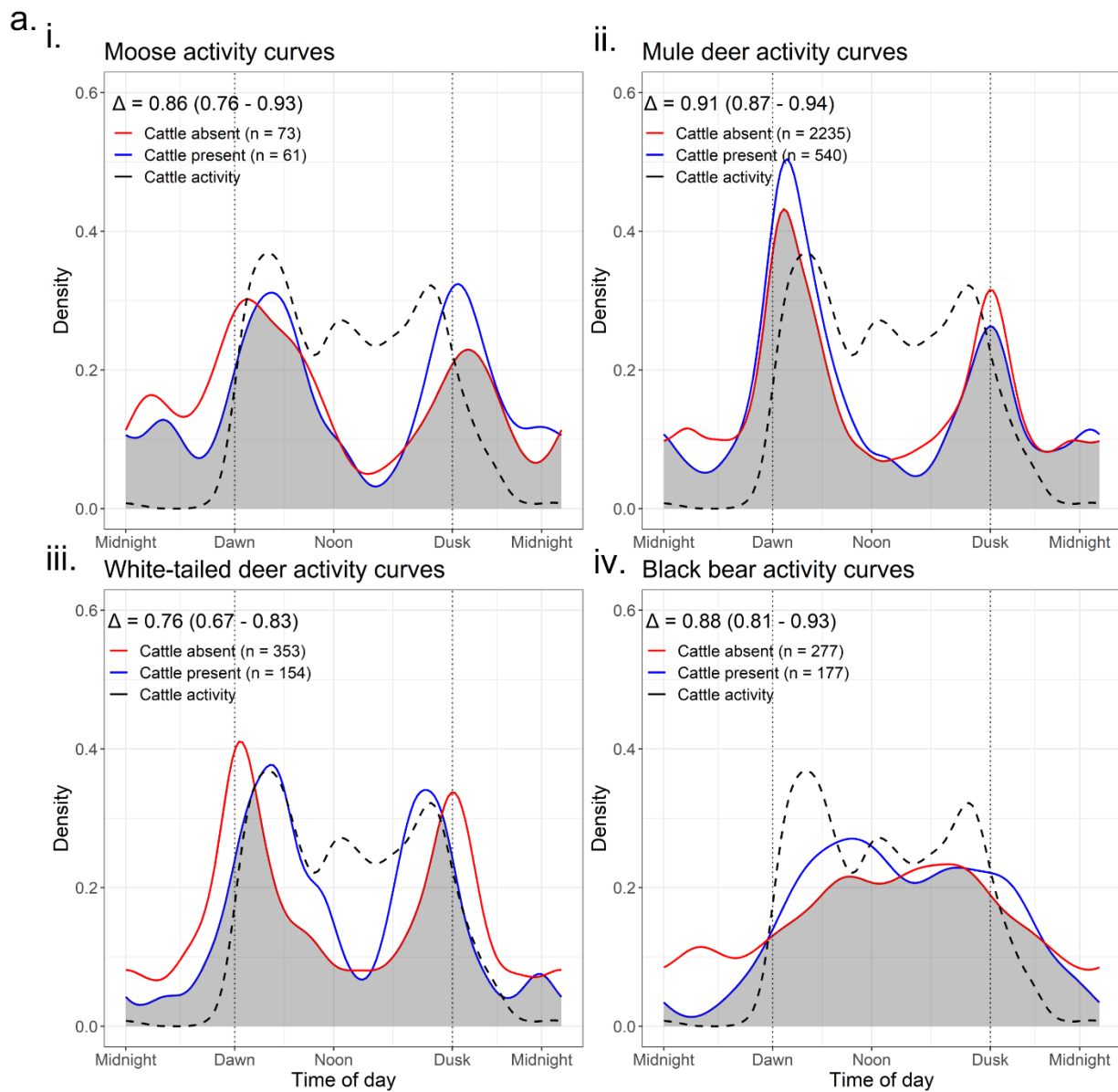
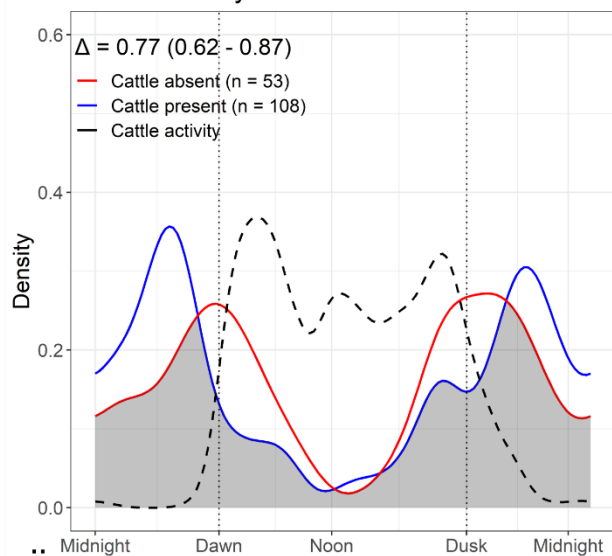


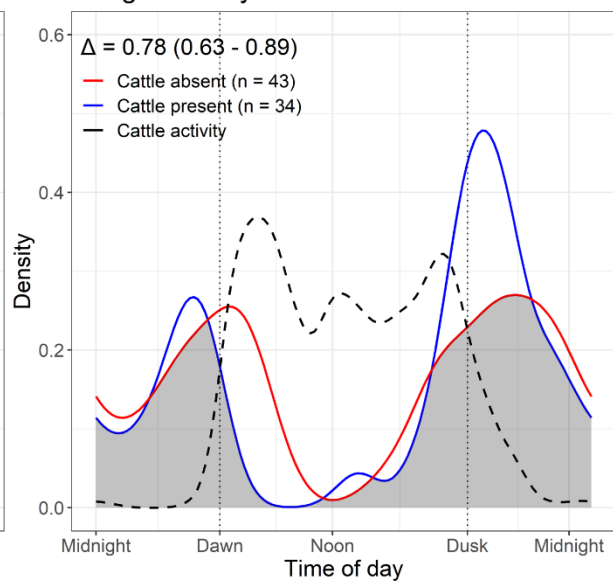
Figure S3.3. Temporal overlap plots of the diel activity curves for each species at camera sites with varying levels of anthropogenic activity in eastern Washington, 2018 – 2020. Activity curves, their coefficient of overlapping ($\bar{\Delta}$), bootstrapped 95% confidence intervals, and number of detections (n) of each species are plotted for prey (i – iii) and predators (iv – vii) at cameras where cattle were and were not detected (a) and for prey (i – iii) and predators (iv – viii) at cameras deployed on grazing allotments versus areas where public grazing was not permitted (b) during the grazing season (1 July – 29 Sept; Okanogan study area only), as well as for prey (i – iv) and predators (v – ix) at cameras where hunters were and were not detected (c), and for prey (i – iv) and predators (v – viii) at cameras deployed on public versus private land (d) during the hunting season (1 Oct – 30 Nov; Northeast and Okanogan study areas).



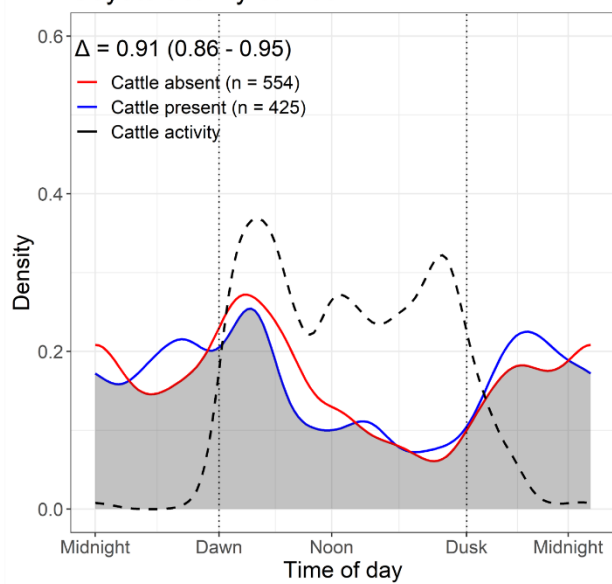
V. Bobcat activity curves



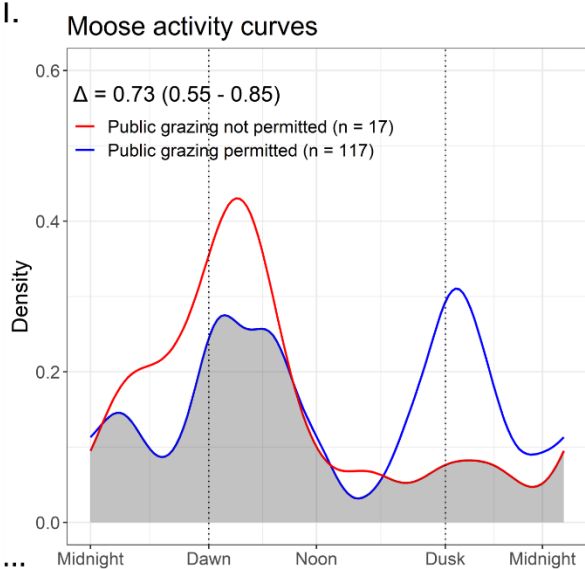
vi. Cougar activity curves



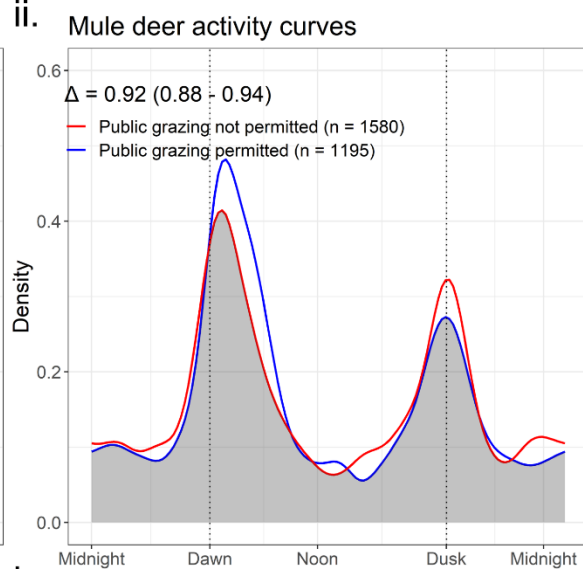
vii. Coyote activity curves



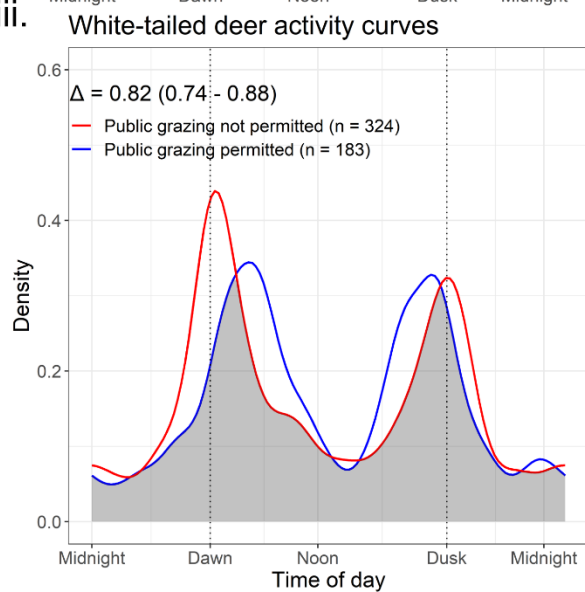
b. i.



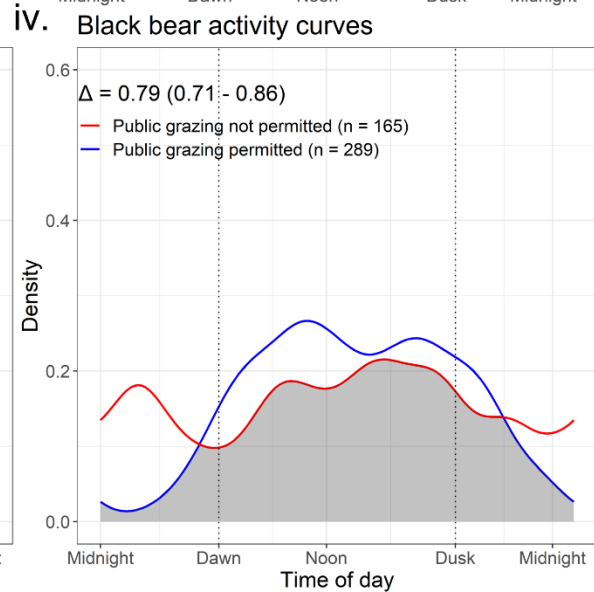
ii.



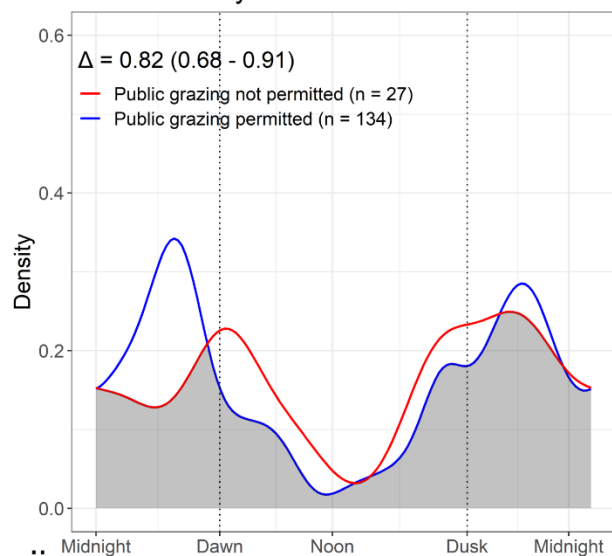
iii.



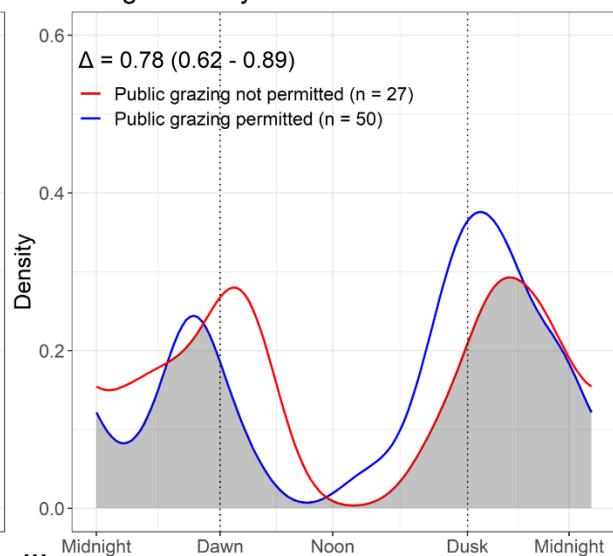
iv.



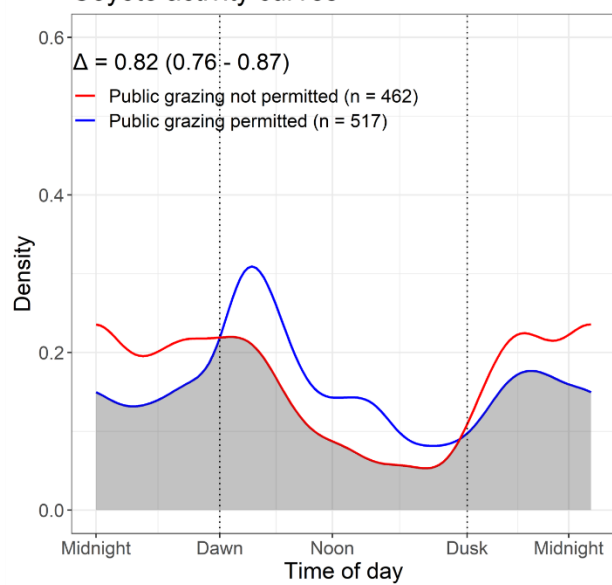
V. Bobcat activity curves



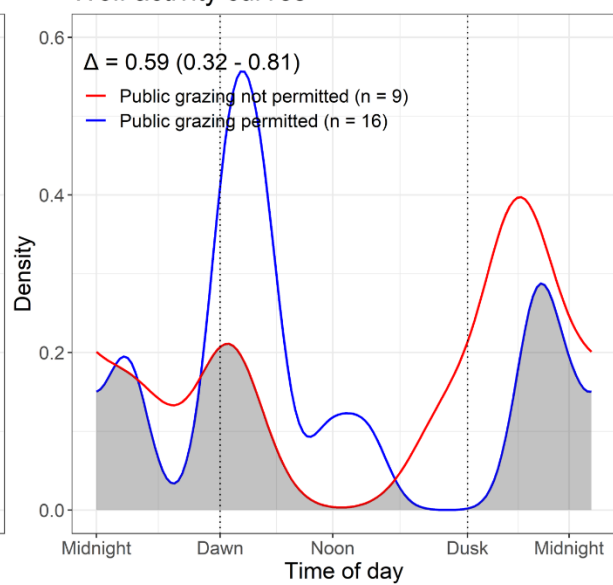
vi. Cougar activity curves



vii. Coyote activity curves

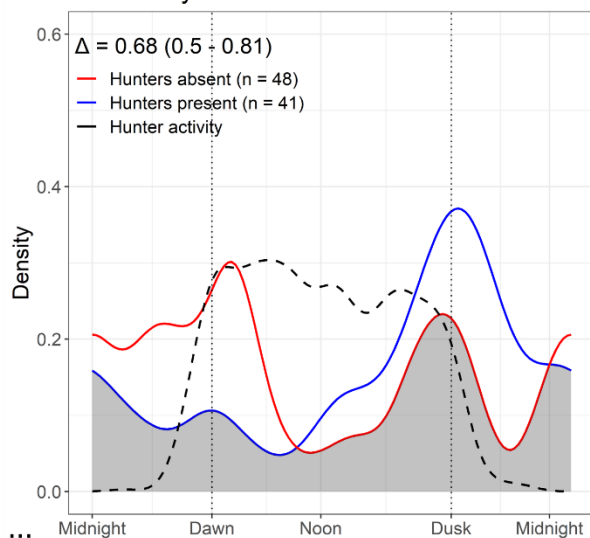


viii. Wolf activity curves

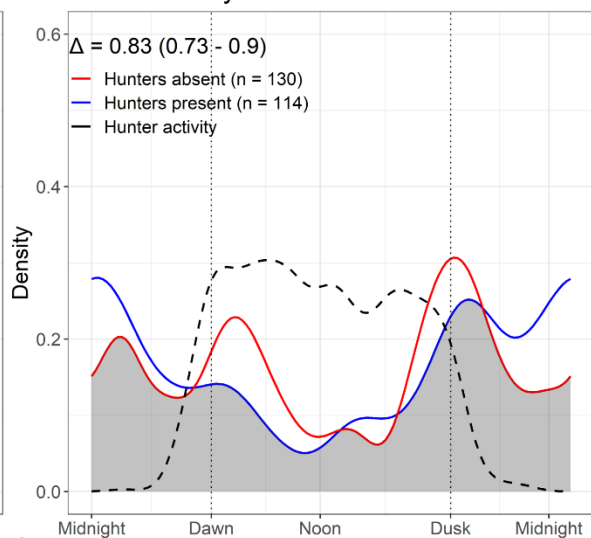


C. i.

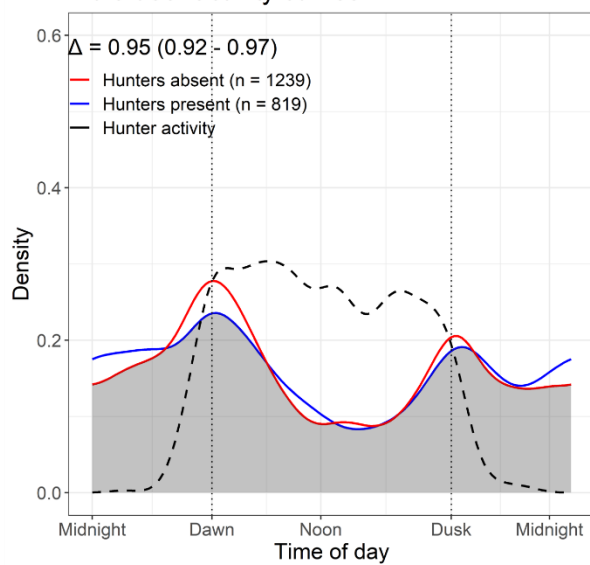
Elk activity curves



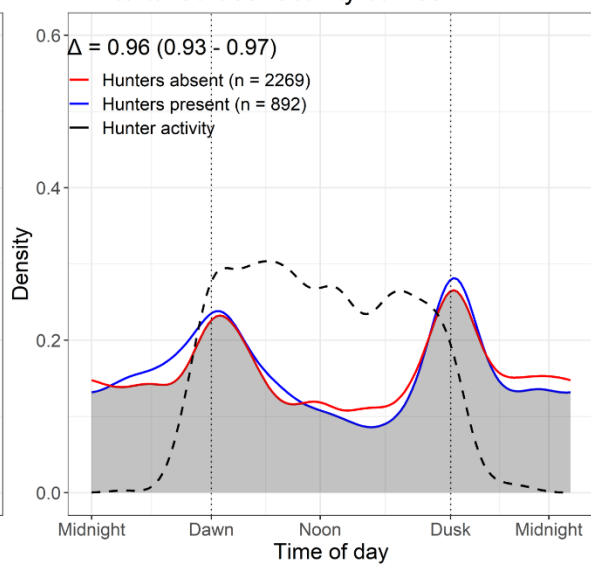
ii. Moose activity curves



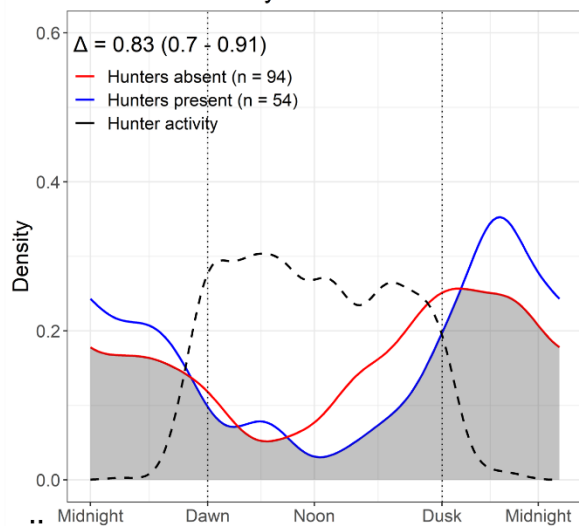
iii. Mule deer activity curves



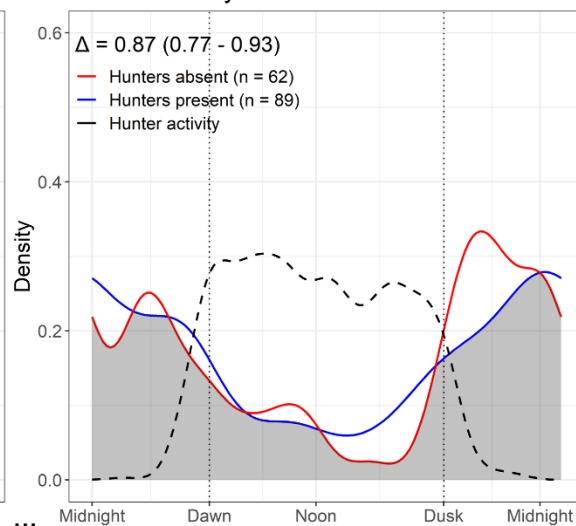
iv. White-tailed deer activity curves



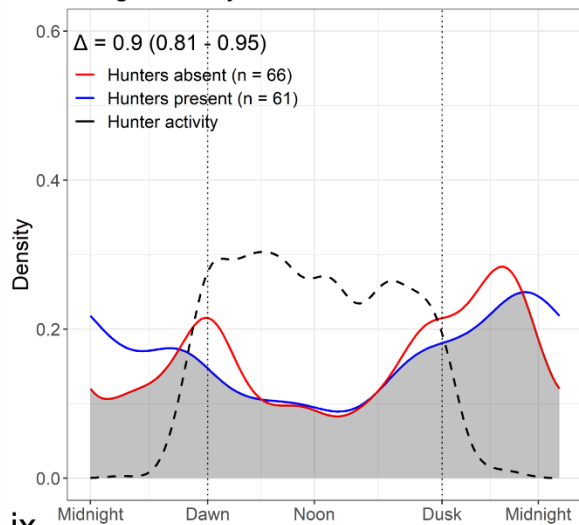
V. Black bear activity curves



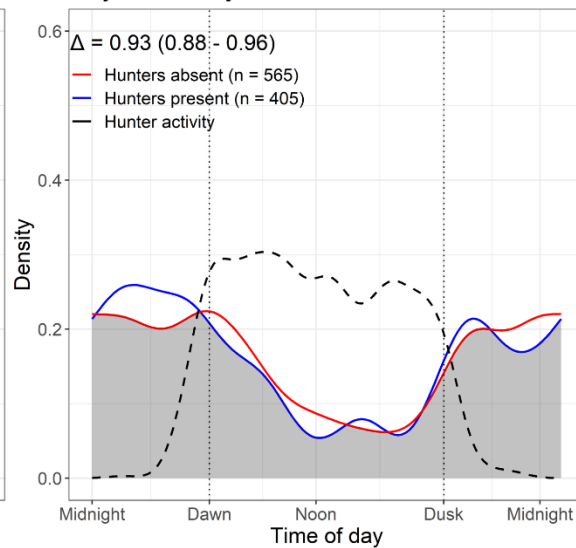
vi. Bobcat activity curves



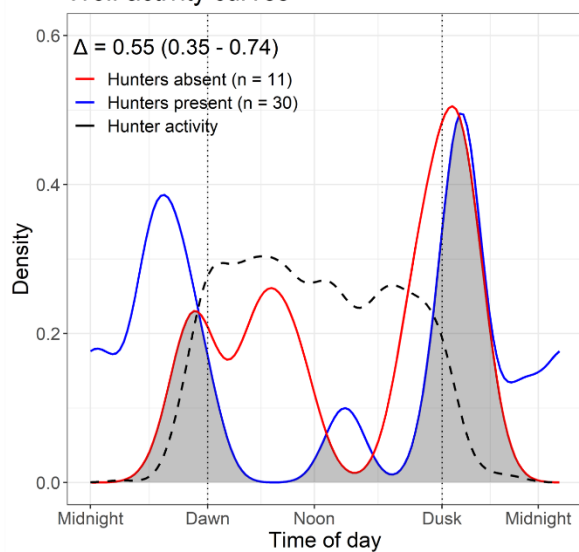
vii. Cougar activity curves



viii. Coyote activity curves

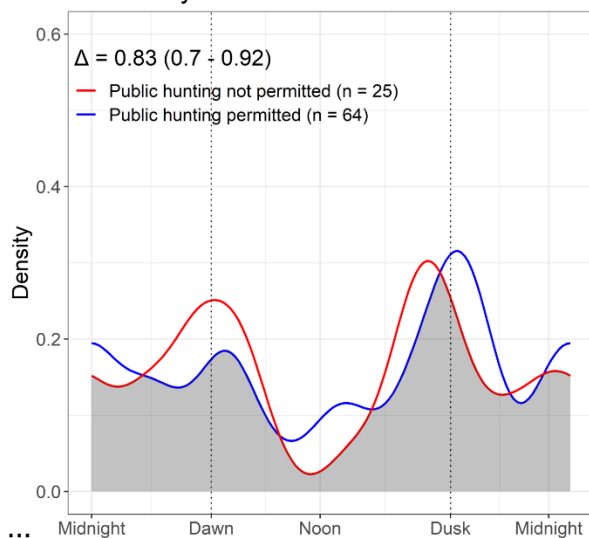


ix. Wolf activity curves

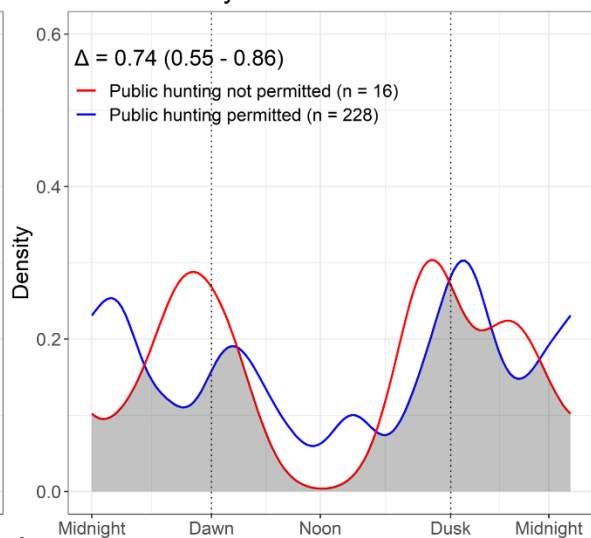


d. i.

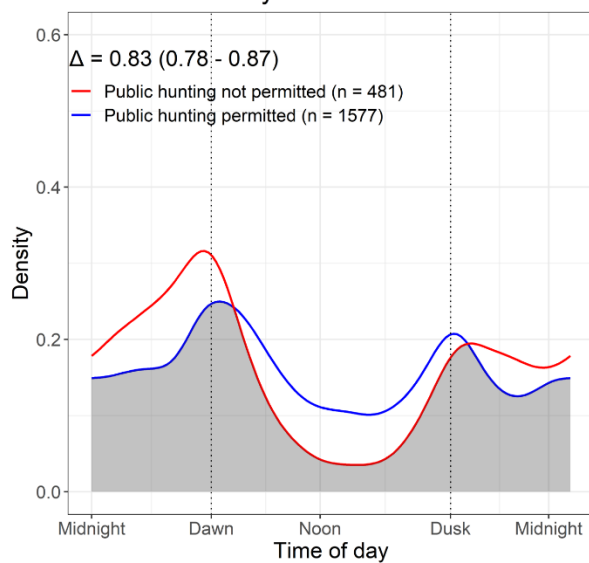
Elk activity curves



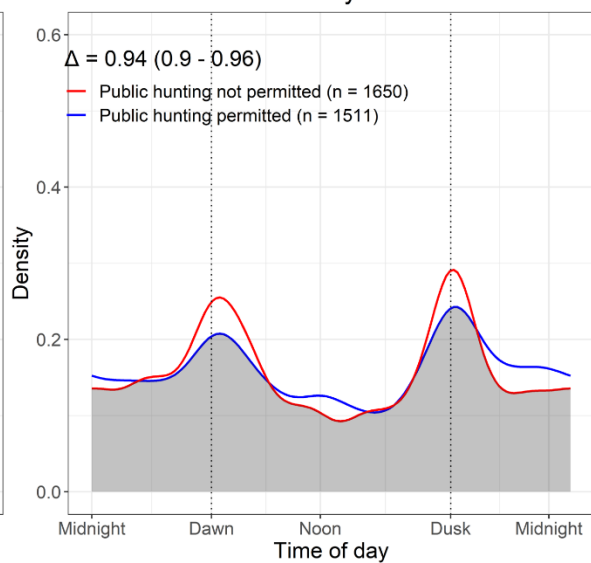
ii. Moose activity curves



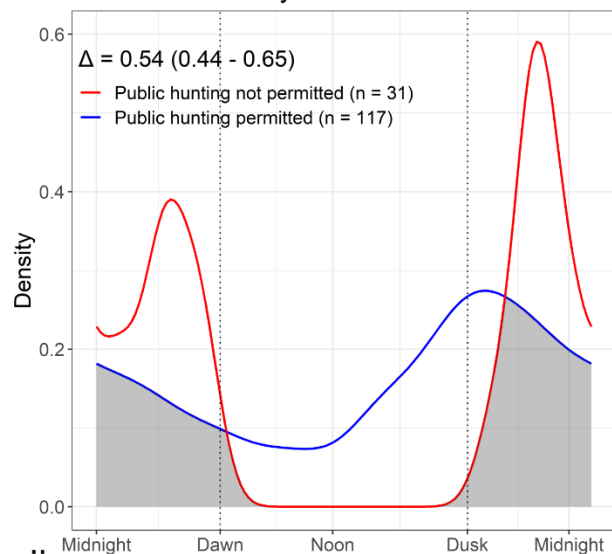
iii. Mule deer activity curves



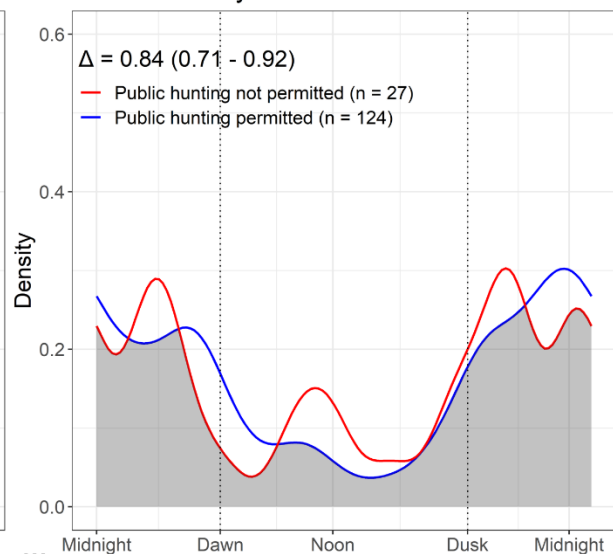
iv. White-tailed deer activity curves



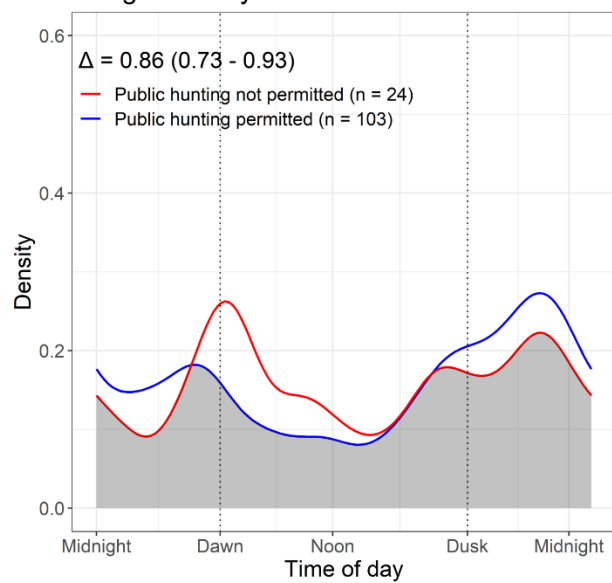
V. Black bear activity curves



vi. Bobcat activity curves



vii. Cougar activity curves



viii. Coyote activity curves

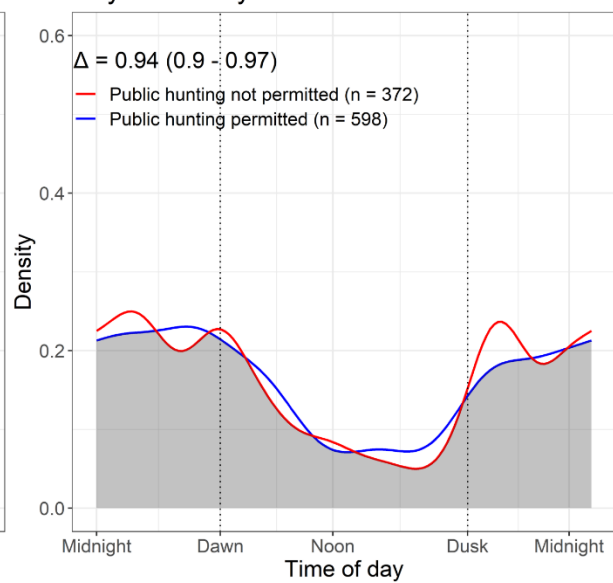
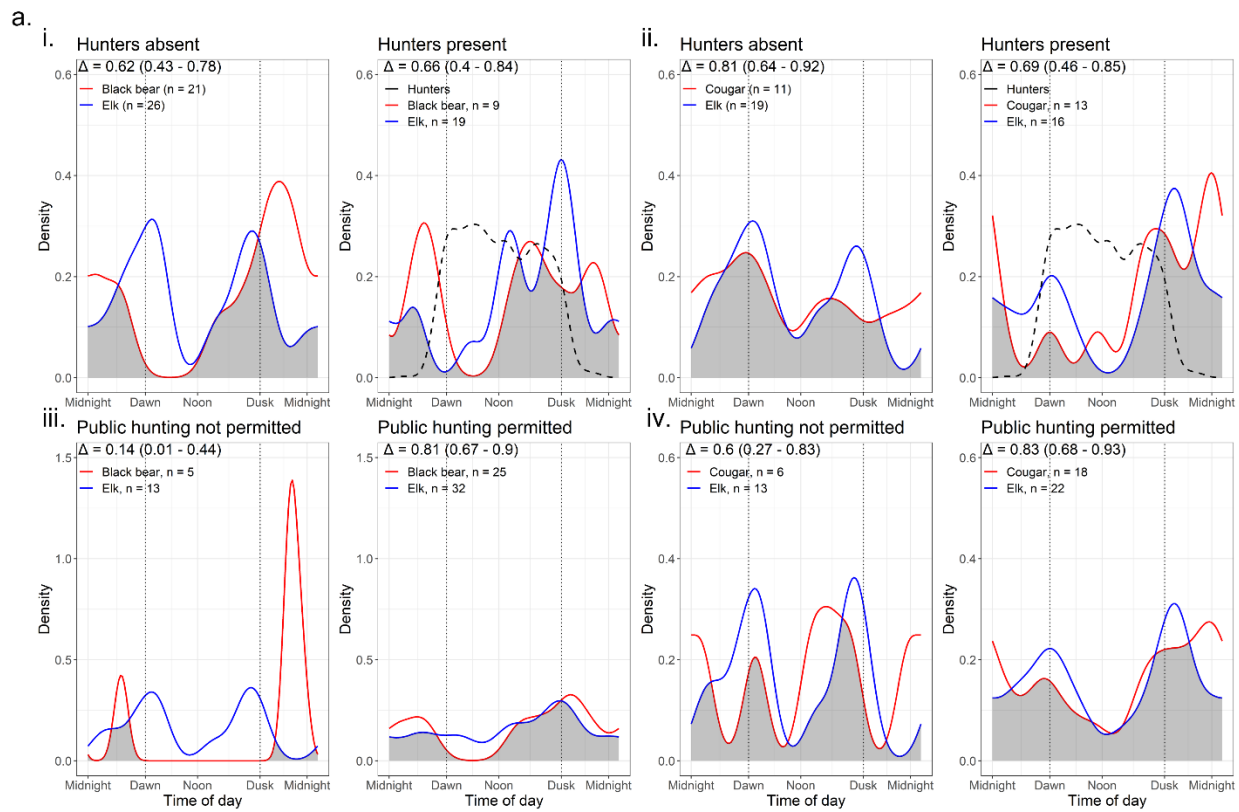
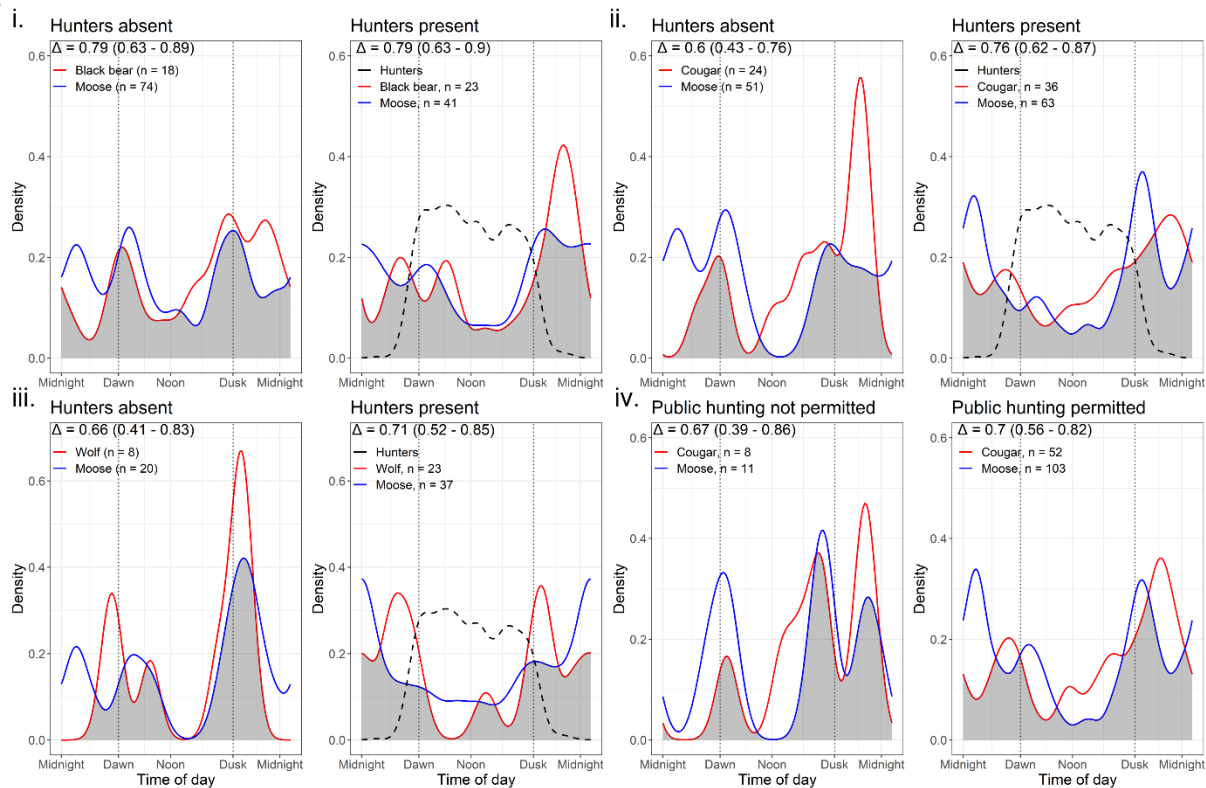


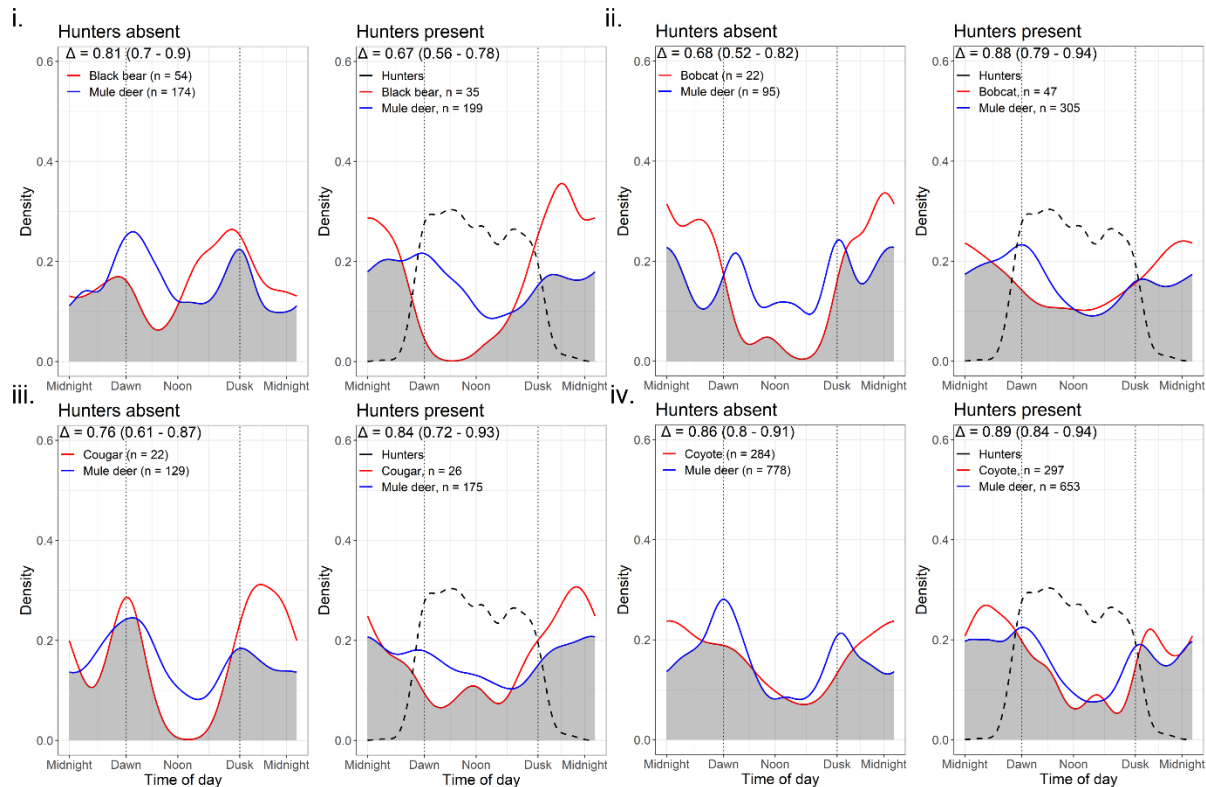
Figure S3.4. Temporal overlap plots of paired predator (blue) and prey (red) diel activity curves at camera sites where hunters were detected compared to camera sites where hunters were not detected, and at cameras deployed on public land compared to cameras deployed on private land in two study areas in eastern Washington, USA, 2018 – 2020. The estimated coefficient of overlapping ($\bar{\Delta}$), bootstrapped 95% confidence intervals, and sample sizes for number of detections (n) of each species are reported for elk – predator activity curves (a) with hunter activity (i – iii) and land ownership (iv), moose – predator activity curves (b) with hunter activity (i – iii) and land ownership (iv), mule deer – predator activity curves (c) with hunter activity (i – v) and land ownership (vi – viii), and white-tailed deer – predator activity curves (d) with hunter activity (i – v) and land ownership (vi – ix) in the hunting season (1 Oct – 30 Nov). Hunter activity curve (black dashed line) plotted for reference.

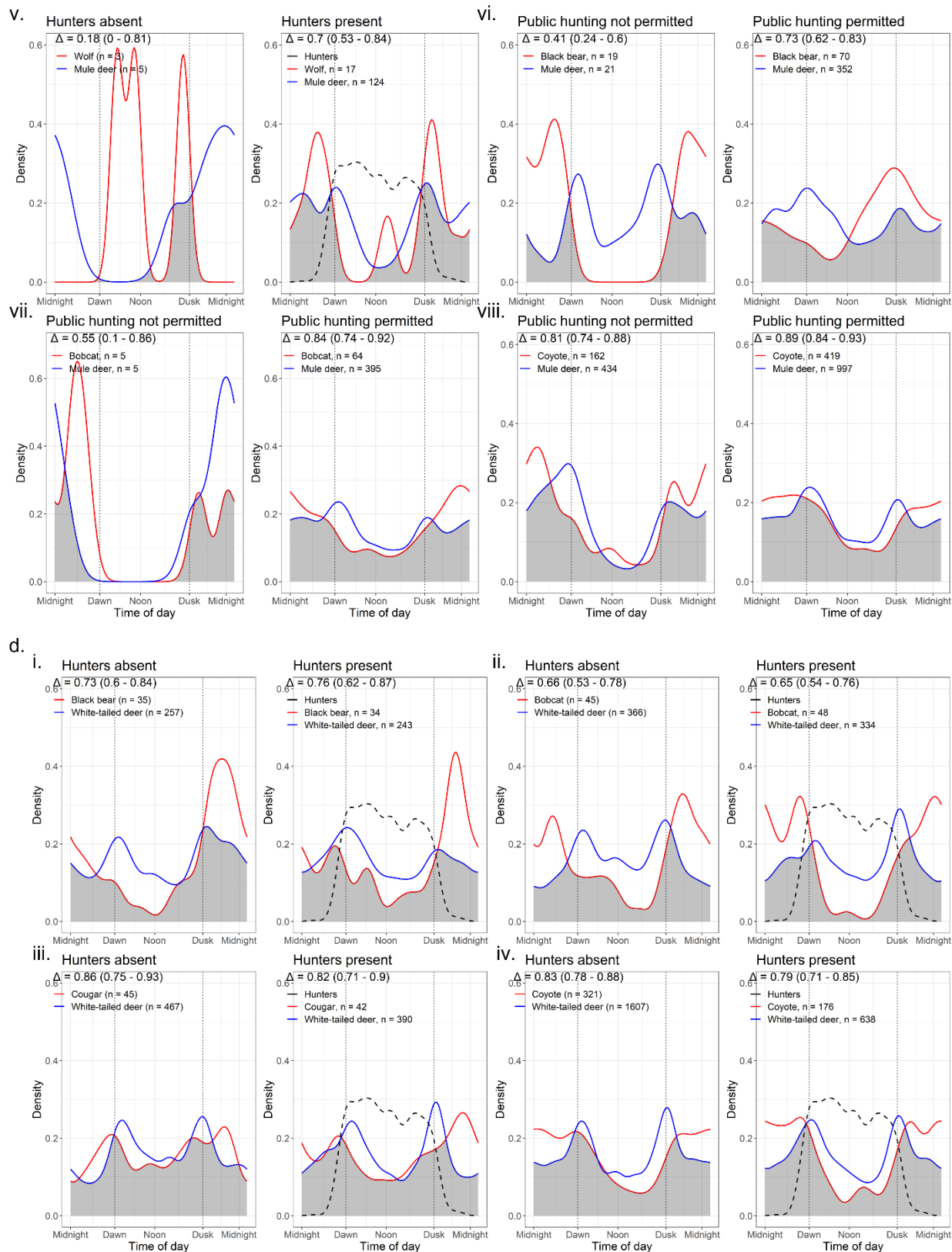


b.

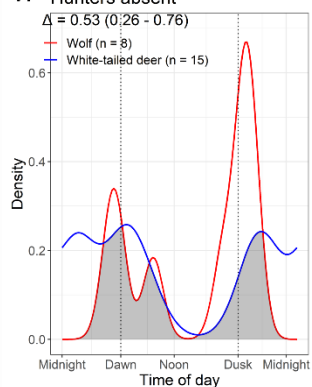


c.

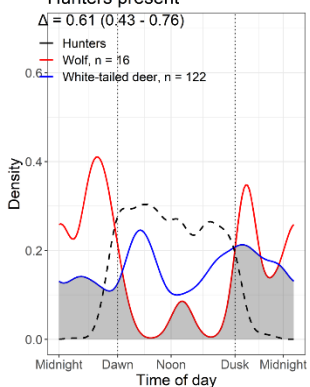




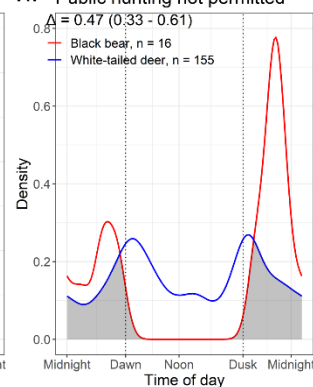
V. Hunters absent



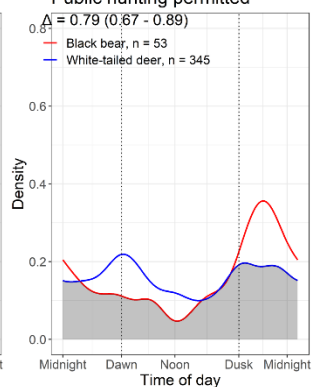
Hunters present



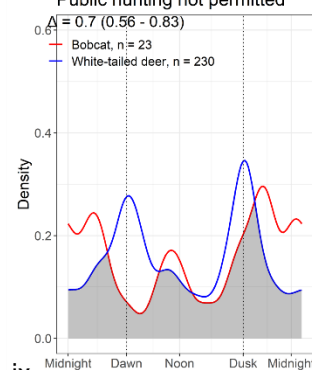
VI. Public hunting not permitted



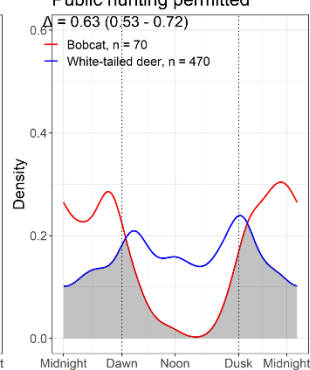
Public hunting permitted



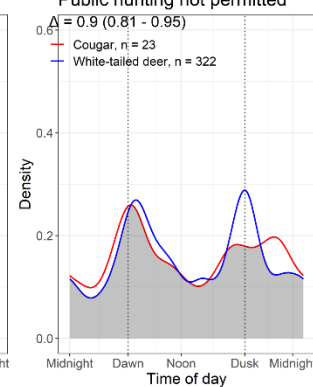
vii. Public hunting not permitted



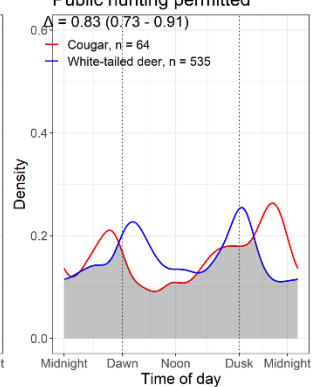
Public hunting permitted



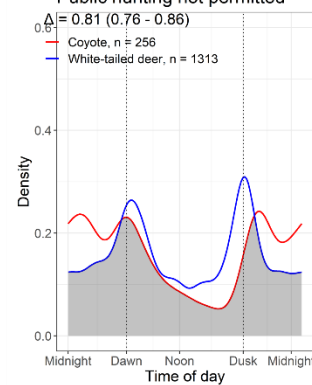
viii. Public hunting not permitted



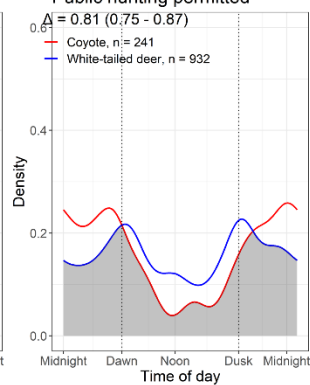
Public hunting permitted



ix. Public hunting not permitted



Public hunting permitted



VITA

Ms. Sarah B. Bassing is a graduate researcher in the Quantitative Ecology Lab at the University of Washington School of Environmental and Forest Sciences. In her research, Ms. Bassing uses a variety of non-invasively sampled data, telemetry data, and statistical analyses to study how wildlife interact with their environment, each other, and humans. In addition to her doctoral studies, Ms. Bassing holds two degrees from the University of Montana, including a Bachelor of Science and Master of Science in Wildlife Biology.

