Bassing Sarah (Orcid ID: 0000-0001-6295-6372)
Gardner Beth (Orcid ID: 0000-0002-9624-2981)

Are we telling the same story? Comparing inferences made from camera trap and

telemetry data for wildlife monitoring

Sarah B. Bassing[1], Melia Devivo[2], Taylor R. Ganz[1], Brian N. Kertson[3], Laura R. Prugh[1], Trent Roussin[4, 1], Lauren Satterfield[1], Rebecca M. Windell[1], Aaron J. Wirsing[1], and Beth Gardner[1]

[1] *School of Environmental and Forest Sciences, University of Washington, Seattle, Washington*

[2] *Washington Department of Fish and Wildlife, Spokane Valley, Washington*

[3] *Washington Department of Fish and Wildlife, Snoqualmie, Washington*

[4] *Washington Department of Fish and Wildlife, Colville, Washington*

Corresponding author: Sarah B. Bassing, email: sarah.bassing@gmail.com

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.

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 murres (*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.

Methods

Study areas — Photo-capture and telemetry data were collected across two study areas in eastern

Washington, USA, from June 2018 – March 2020 (Fig. 1). The Northeast study area (4,535 km^2;

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 km^2; 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 tridentate*) and antelope bitterbrush (*Purshia tridentat*).

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 km^2 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 Supplemental Materials).

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.

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). 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 Mammalogists (Sikes 2016).

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 km^2) 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).

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).

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.

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 makes 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.

Results

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 1).

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 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 1).

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, 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-value ≤ 0.1) affected the probability of occurrence varied by species and season (Table 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). 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). We found no significant relationships between any habitat predictors and bobcat, elk, or wolf occupancy in winter or elk occupancy in summer (Table 2).

Covariate effects on detection probability also varied by species and season in the occupancy models (Appendix S1: Table S1). Trail type significantly influencing detection probability (p-value ≤ 0.1) for most species, but with notable differences between predators and prey (Appendix 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 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 S1: Table S1). Finally, coyotes and white-tailed deer were more likely to be detected in winter as temperature increased (Appendix S1: Table S1).

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-value ≤ 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). 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). 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). The percentage of forested habitat had a significant positive effect on resource selection for most species in both seasons (Table 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). 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). 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).

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, Fig. 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), 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 3, Fig. 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 3, Fig. 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 3, Fig. 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 3, Fig. 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). 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).

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 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 3).

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. 4 and Appendix 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 3). For example, the distribution maps yielded similar patterns of predicted use and relative selection across the study

areas for bobcats in summer, mule deer in winter, and cougars in both seasons (Fig. 4 and Appendix 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 3, Fig. 5 and Appendix 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 S1: Figure S2).

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 in 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.

Conflict of Interest

The authors declare no conflict of interest.

Author contributions

S. B. Bassing designed and performed camera-based field work, conducted data analyses, and wrote the initial manuscript draft; T. R. Ganz, L. Satterfield, and R. M. Windell designed and performed collar-based field work; T. Roussin performed collar- and camera-based field work; M. Devivo, B. N. Kertson, L. R. Prugh, and A. J. Wirsing assisted with study design and collar-based field work; B. Gardner assisted with study design, data analysis, and manuscript revisions; All authors reviewed and edited the manuscript.

Citations

Aarts, G., M. MacKenzie, B. McConnell, M. Fedak, and J. Matthiopoulos. 2008. Estimating space-use and habitat preference from wildlife telemetry data. Ecography 31:140–160.

Atwood, T. C., E. M. Gese, and K. E. Kunkel. 2007. Comparative patterns of predation by cougars and recolonizing wolves in Montana's Madison Range. Journal of Wildlife Management 71:1098–1106.

Bailey, L. L., J. E. Hines, J. D. Nichols, and D. I. Mackenzie. 2007. Sampling design trade-offs in occupancy studies with imperfect detection: Examples and software. Ecological Applications 17:281–290.

Baratchi, M., N. Meratnia, P. J. M. Havinga, A. K. Skidmore, and B. A. G. Toxopeus. 2013. Sensing solutions for collecting spatio-temporal data for wildlife monitoring applications: A review. Sensors 13:6054–6088.

Bassing, S. B. 2022. v1.0.1 SarahBassing/Bassing_et_al_Cameras_and_Collars: Manuscript accepted. Zenodo. <https://doi.org/10.5281/zenodo.6886515>.

Bassing, S. B., M. Devivo, T. Ganz, B. Kertson, L. Prugh, T. Roussin, L. Satterfield, R. Windell, A. Wirsing, and B. Gardner. 2022. Dataset from "Are we telling the same story? Comparing inferences made from camera trap and telemetry data for wildlife monitoring." Dryad, Dataset. <https://doi.org/10.5061/dryad.g4f4qrfsv>.

Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beery, S., D. Morris, and S. Yang. 2019. Efficient pipeline for camera trap image review. <http://arxiv.org/abs/1907.06772>.

Van Beest, F. M., B. Van Moorter, and J. M. Milner. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. Animal Behaviour 84:723–735.

Del Bosco, T. 2021. An Eulerian perspective on spring migration in mule deer. Utah State University. <https://digitalcommons.usu.edu/etd/8104>.

Boyce, M. S., J. Pitt, J. M. Northrup, A. T. Morehouse, K. H. Knopff, B. Cristescu, and G. B. Stenhouse. 2010. Temporal autocorrelation functions for movement rates from global positioning system radiotelemetry data. Philosophical Transactions of the Royal Society B:

Biological Sciences 365:2213–2219.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Broadley, K., A. C. Burton, T. Avgar, and S. Boutin. 2019. Density-dependent space use affects interpretation of camera trap detection rates. Ecology and Evolution 9:14031–14041.

Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. Bayne, and S. Boutin. 2015. Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology 52:675–685.

Calenge, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Caulkett, N., and T. Shury. 2014. Human safety during wildlife capture. Pages 181–187 *in* G. West, D. Heard, and N. Caulkett, editors. Zoo Animal and Wildlife Immobilization and Anesthesia. Second edition. John Wiley & Sons, Incorporated, Oxford, UK.

Clover, M. R. 1954. A portable deer trap and catch-net. California Fish and Game 40:367–373.

Cusack, J. J., A. J. Dickman, J. M. Rowcliffe, C. Carbone, D. W. Macdonald, and T. Coulson. 2015. Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. PLoS ONE 10:e0126373.

Dickie, M., S. R. McNay, G. D. Sutherland, M. Cody, and T. Avgar. 2020. Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. Journal of Animal Ecology 89:623–634.

Efford, M. G., and D. K. Dawson. 2012. Occupancy in continuous habitat. Ecosphere 3:32.

Farr, T. G., P. A. Rosen, E. Caro, R. Crippen, R. Duren, S. Hensley, M. Kobrick, M. Paller, E. Rodriguez, L. Roth, D. Seal, S. Shaffer, J. Shimada, J. Umland, M. Werner, M. Oskin, D.

Burbank, and D. Alsdorf. 2007. The Shuttle Radar Topography Mission. Reviews of Geophysics 45:1–33.

Fieberg, J., J. Matthiopoulos, M. Hebblewhite, M. S. Boyce, and J. L. Frair. 2010. Correlation and studies of habitat selection: Problem, red herring or opportunity? Philosophical Transactions of the Royal Society B: Biological Sciences 365:2233–2244.

Fieberg, J., J. Signer, B. Smith, and T. Avgar. 2021. A 'How to' guide for interpreting parameters in habitat-selection analyses. Journal of Animal Ecology 90:1027–1043.

Fiske, I. J., and R. B. Chandler. 2011. Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43.

Fletcher, R. J., T. J. Hefley, E. P. Robertson, B. Zuckerberg, R. A. McCleery, and R. M. Dorazio. 2019. A practical guide for combining data to model species distributions. Ecology 100:1–15.

Forrester, T. D., and H. U. Wittmer. 2013. A review of the population dynamics of mule deer and black-tailed deer Odocoileus hemionus in North America. Mammal Review 43:292–308.

Frame, P. F., and T. J. Meier. 2007. Field-assessed injury to wolves captured in rubber-padded traps. Journal of Wildlife Management 71:2074–2076.

Gaillard, J., M. Festa-bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:249–251.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

Gould, M. J., W. R. Gould, J. W. Cain, and G. W. Roemer. 2019. Validating the performance of occupancy models for estimating habitat use and predicting the distribution of highly-mobile species: A case study using the American black bear. Biological Conservation 234:28–36.

Greenberg, S. 2019. Timelapse user guide version 2.2.2.9. <http://saul.cpsc.ucalgary.ca/timelapse/pmwiki.php?n=Main.Download2>. Accessed 1 Apr 2020.

Haulton, S. M., W. F. Porter, and B. A. Rudolph. 2001. Evaluating 4 methods to capture white-tailed deer. Wildlife Society Bulletin 29:255–264.

Hawkins, R. E., L. D. Martoglio, and G. G. Montgomery. 1968. Cannon-netting deer. Journal of Wildlife Management 32:191–195.

Hebblewhite, M., and D. T. Haydon. 2010. Distinguishing technology from biology: A critical review of the use of GPS telemetry data in ecology. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2303–2312.

Hofmann, G. S., I. P. Coelho, V. A. G. Bastazini, J. L. P. Cordeiro, and L. F. B. de Oliveira. 2016. Implications of climatic seasonality on activity patterns and resource use by sympatric peccaries in northern Pantanal. International Journal of Biometeorology 60:421–433.

Hofmeester, T. R., J. P. G. M. Cromsigt, J. Odden, H. Andrén, J. Kindberg, and J. D. C. Linnell. 2019. Framing pictures: A conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. Ecology and Evolution 9:2320–2336.

Hofmeester, T. R., N. H. Thorsen, J. P. G. Cromsigt, J. Kindberg, H. Andren, J. D. C. Linnell,

and J. Odden. 2021. Effects of camera-trap placement and number on detection of members of a mammalian assemblage. Ecosphere 12:e03662.

Iannarilli, F., J. Erb, T. W. Arnold, and J. R. Fieberg. 2021. Evaluating species-specific responses to camera-trap survey designs. Wildlife Biology 1:wlb.00726.

Jacobs, C. E., and D. E. Ausband. 2018. An evaluation of camera trap performance - What are we missing and does deployment height matter? Remote Sensing in Ecology and Conservation 4:352–360.

Jessup, D. A. 1982. The use of the helicopter in the capture of free-roaming wildlife. Pages 289–303 *in* L. Nielsen, J. C. Haight, and M. E. Fouler, editors. Chemical Immobilization of North American Wildlife. he Wisconsin Humane Society Inc., Milwaukee, Wisconsin.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use–availability data: Theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347–357.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Kertson, B. N., R. D. Spencer, J. M. Marzluff, J. Hepinstall-Cymerman, and C. E. Grue. 2011. Cougar space use and movements in the wildland-urban landscape of western Washington. Ecological Applications 21:2866–2881.

Kock, M. D., D. A. Jessup, R. K. Clark, C. E. Franti, and R. A. Weaver. 1987. Capture methods in five subspecies of free-ranging bighorn sheep: an evaluation of drop-net, drive-net, chemical immobilization and the net-gun. Journal of wildlife diseases 23:634–640.

Koehler, G. M., and M. G. Hornocker. 1991. Seasonal resource use among mountain lions, bobcats, and coyotes. Journal of Mammalogy 72:391–396.

Kolowski, J. M., and T. D. Forrester. 2017. Camera trap placement and the potential for bias due to trails and other features. PLoS ONE 12:e0186679.

Koshkina, V., Y. Wang, A. Gordon, R. M. Dorazio, M. White, and L. Stone. 2017. Integrated species distribution models: combining presence-background data and site-occupany data with imperfect detection. Methods in Ecology and Evolution 8:420–430.

Lahoz-Monfort, J. J., G. Guillera-Arroita, and B. A. Wintle. 2014. Imperfect detection impacts the performance of species distribution models. Global Ecology and Biogeography 23:504–515.

Latham, A. D. M., M. C. Latham, D. P. Anderson, J. Cruz, and M. Hebblewhite. 2015. The GPS craze: six questions to address before deciding to deploy GPS technology on wildlife. New Zealand Journal of Ecology 39:142–152.

Lele, S. R., E. H. Merrill, J. Keim, and M. S. Boyce. 2013. Selection, use, choice and occupancy: Clarifying concepts in resource selection studies. Journal of Animal Ecology 82:1183–1191.

Lenoir, J., and J. C. Svenning. 2015. Climate-related range shifts - a global multidimensional synthesis and new research directions. Ecography 38:15–28.

Linhart, S. B. 1983. Managing coyote damage problems with nonlethal techniques: Recent advances in research. Proceedings of the Eastern Wildlife Damage Conference 105–118.

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

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2017. Modeling Heterogeneous Detection Probabilities. Pages 313–338 *in*. Occupancy Estimationg and Modeling: Infering Patterns and Dynamics of Species Occurrence. 2nd

edition. Academic Press, London, United Kingdom.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical analysis and design for field studies. 2nd edition. Kluwer Academic Press, Boston, Massachusetts.

Mann, G. K. H., M. J. O'Riain, and D. M. Parker. 2015. The road less travelled: assessing variation in mammal detection probabilities with camera traps in a semi-arid biodiversity hotspot. Biodiversity and Conservation 24:531–545.

Martin, K. 1998. The role of animal behavior studies in wildlife science and management. Wildlife Society Bulletin 26:911–920.

Matthiopoulos, J., J. Fieberg, G. Aarts, H. L. Beyer, J. M. Morales, and D. T. Haydon. 2015. Establishing the link between habitat selection and animal population dynamics. Ecological Monographs 85:413–436.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. Écoscience 16:238–247.

McClintock, B. T., R. Langrock, O. Gimenez, E. Cam, D. L. Borchers, R. Glennie, and T. A. Patterson. 2020. Uncovering ecological state dynamics with hidden Markov models. Ecology Letters 23:1878–1903.

Meek, P. D., G. Ballard, A. Claridge, R. Kays, K. Moseby, T. O'Brien, A. O'Connell, J. Sanderson, D. E. Swann, M. Tobler, and S. Townsend. 2014. Recommended guiding principles for reporting on camera trapping research. Biodiversity and Conservation 23:2321–2343.

Merrick, M. J., and J. L. Koprowski. 2017. Should we consider individual behavior differences in applied wildlife conservation studies? Biological Conservation 209:34–44.

Mesinger, F., G. DiMego, E. Kalnay, K. Mitchell, P. C. Shafran, W. Ebisuzaki, D. Jović, J. Woollen, E. Rogers, E. H. Berbery, M. B. Ek, Y. Fan, R. Grumbine, W. Higgins, H. Li, Y. Lin, G. Manikin, D. Parrish, and W. Shi. 2006. North American regional reanalysis. Bulletin of the American Meteorological Society 87:343–360.

Miller, D. A. W., K. Pacifici, J. S. Sanderlin, and B. J. Reich. 2019. The recent past and promising future for data integration methods to estimate species' distributions. Methods in Ecology and Evolution 10:22–37.

Mueller, T., and W. F. Fagan. 2008. Search and navigation in dynamic environments - From individual behaviors to population distributions. Oikos 117:654–664.

National Oceanic and Atmospheric Administration. 2021. Monthly Summaries. National Centers for Environmental Information. <https://www.ncei.noaa.gov/maps/monthly-summaries/>. Accessed 10 Nov 2021.

O'Brien, T. G., M. F. Kinnaird, and H. T. Wibisono. 2003. Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Animal Conservation 6:131–139.

O'Connell, A. F., and L. L. Bailey. 2011. Inference for occupancy and occupancy dynamics. Pages 191–205 *in* A. F. O'Connell, J. D. Nichols, and K. U. Karanth, editors. Camera traps in animal ecology: methods and analyses. Springer, New York, New York.

O'Connell, A. F., J. D. Nichols, and K. U. Karanth. 2011. Camera traps in animal ecology: methods and analyses. A. F. O'Connell, J. D. Nichols, and K. U. Karanth, editors. Springer, New York, New York.

Phillips, E. M., J. K. Horne, J. E. Zamon, J. J. Felis, and J. Adams. 2019. Does perspective matter? A case study comparing Eulerian and Lagrangian estimates of common murre (Uria

aalge) distributions. Ecology and Evolution 9:4805–4819.

Popescu, V. D., P. de Valpine, and R. A. Sweitzer. 2014. Testing the consistency of wildlife data types before combining them: The case of camera traps and telemetry. Ecology and Evolution 4:933–943.

Priddel, D., N. Carlile, D. Portelli, Y. Kim, L. O'Neill, V. Bretagnolle, L. T. Ballance, R. A. Phillips, R. L. Pitman, and M. J. Rayner. 2014. Pelagic distribution of Gould's Petrel (Pterodroma leucoptera): Linking shipboard and onshore observations with remote-tracking data. Emu 114:360–370.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing , Vienna, Austria. <https://www.r-project.org/>. Accessed 29 Apr 2021.

Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence–absence data or point counts. Ecology 84:777–790.

Shimada, T., M. Thums, M. Hamann, C. J. Limpus, G. C. Hays, N. N. FitzSimmons, N. E. Wildermann, C. M. Duarte, and M. G. Meekan. 2021. Optimising sample sizes for animal distribution analysis using tracking data. Methods in Ecology and Evolution 12:288–297.

Sikes, R. S. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Sollmann, R. 2018. A gentle introduction to camera-trap data analysis. African Journal of Ecology 56:740–749.

Soulsbury, C. D., H. E. Gray, L. M. Smith, V. Braithwaite, S. C. Cotter, R. W. Elwood, A. Wilkinson, and L. M. Collins. 2020. The welfare and ethics of research involving wild animals: A primer. Methods in Ecology and Evolution 11:1164–1181.

Specht, H. M., H. T. Reich, F. Iannarilli, M. R. Edwards, S. P. Stapleton, M. D. Weegman, M. K. Johnson, B. J. Yohannes, and T. W. Arnold. 2017. Occupancy surveys with conditional replicates: An alternative sampling design for rare species. Methods in Ecology and Evolution 8:1725–1734.

Street, G. M., J. R. Potts, L. Börger, J. C. Beasley, S. Demarais, J. M. Fryxell, P. D. McLoughlin, K. L. Monteith, C. M. Prokopenko, M. C. Ribeiro, A. R. Rodgers, B. K. Strickland, F. M. van Beest, D. A. Bernasconi, L. T. Beumer, G. Dharmarajan, S. P. Dwinnell, D. A. Keiter, A. Keuroghlian, L. J. Newediuk, J. E. F. Oshima, O. Rhodes, P. E. Schlichting, N. M. Schmidt, and E. Vander Wal. 2021. Solving the sample size problem for resource selection functions. Methods in Ecology and Evolution 12:2421–2431.

Strickland, M. D., and L. L. McDonald. 2006. Introduction to the special section on resource selection. Journal of Wildlife Management 70:321–323.

Tanwar, K. S., A. Sadhu, and Y. V Jhala. 2021. Camera trap placement for evaluating species richness, abundance, and activity. Scientific Reports 11:23050.

Tremblay, Y., S. Bertrand, R. W. Henry, M. A. Kappes, D. P. Costa, and S. A. Shaffer. 2009. Analytical approaches to investigating seabird-environment interactions: A review. Marine Ecology Progress Series 391:153–163.

VerCauteren, K. C., J. Beringer, and S. E. Hygnstrom. 1997. Use of netted-cage traps in population management and research of urban white-tailed deer. Proceedings of the Great Plains Wildlife Damage Control 13:138–142.

Wakefield, E. D., R. A. Phillips, P. N. Trathan, J. Arata, R. Gales, N. Huin, R. Graham, S. M. Waugh, H. Weimerskirch, and J. Matthiopoulos. 2011. Habitat preference, accessibility, and competition limit the global distribution of breeding Black-browed Albatrosses. Ecological

Monographs 81:141–167.

Washington Department of Fish and Wildlife. 2003. Observations of mule deer habitat use, movements, and survival in Chelan County, Washington. Olympia, WA. <https://www.chelanpud.org/rr_relicense/study/reports/4768_3.pdf>.

Washington Department of Fish and Wildlife. 2016. Washington State mule deer management plan. Washington Department of Fish and Wildlife. Olympia, WA. <https://wdfw.wa.gov/publications/01755/>.

Washington Department of Fish and Wildlife, Confederated Colville Tribes, Spokane Tribe of Indians, USDA-APHIS Wildlife Services, and U.S. Fish and Wildlife Service. 2019. Washington gray wolf conservation and management 2018 annual report. Ellensburg, WA, USA. <https://wdfw.wa.gov/publications/02062>.

Watanuki, Y., R. M. Suryan, H. Sasaki, T. Yamamoto, E. L. Hazen, M. Renner, J. A. Santora, P. D. O'Hara, and W. J. Sydeman. 2016. Spatial ecology of marine top predators in the North Pacific: Tools for integrating across datasets and identifying high use areas. PICES Scientific Report No. 50:1–55.

Western Regional Climate Center. 2016. Washington. SOD USA Climate Archive. <https://wrcc.dri.edu/summary/Climsmwa.html>. Accessed 10 Nov 2021.

Williams, C., B. F. Kelley, B. G. Smith, and T. R. Lillybridge. 1995. Forested plant associations of the Colville National Forest. Portland, OR. <http://adsabs.harvard.edu/abs/2003AGUFMGC52A..06G>.

Williams, C., and T. R. Lillybridge. 1983. Forested plant associations of the Okanogan National Forest. <https://ir.library.oregonstate.edu/concern/defaults/9g54xk129>.

Williams, J. J., and T. Newbold. 2021. Vertebrate responses to human land use are influenced by

their proximity to climatic tolerance limits. Diversity and Distributions 27:1308–1323.

Tables

Table 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.

Table 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 km^2), 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 $\leq$ 0.1 for occupancy models, p-value $\leq$ 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)**

Model	Species	Season							
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)
	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.

Table 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.

Species	Season	Mean Detection	Mean Occupancy	Road Effect	Collared Sex	Elev.	Percent Forest	Percent Grass†	Percent Shrub†	Road Density	Slope	Correlation (r)*
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/ -	NA
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
	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/ +	NA
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/ -	NA
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/ - | NA |

[†]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 could not be calculated for these analyses.

Figure captions

Figure 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.

Figure 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 these were too numerous to show. Instead, 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.

Figure 3. Correlations between estimated coefficients and confidence intervals for the effects of elevation, percent forest, percent grass, percent shrub, and road density on (a) bobcat, (b) cougar, (c) coyote, (d) elk, (e) mule deer, (f) white-tailed deer, and (g) wolf occurrence and resource selection in 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.

Figure 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.

Figure 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.
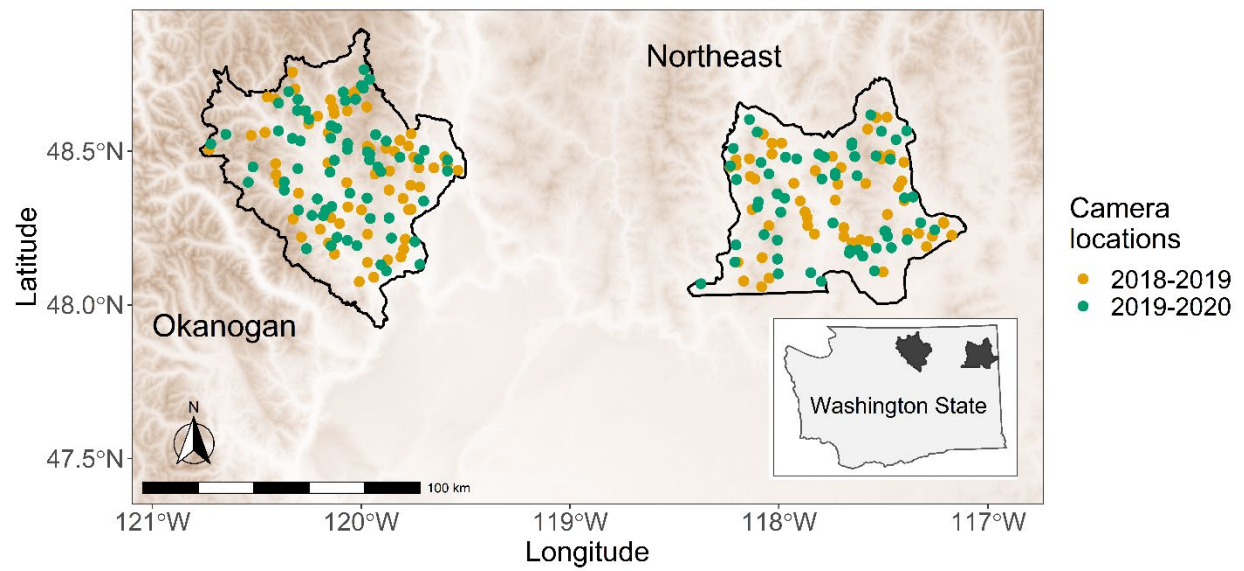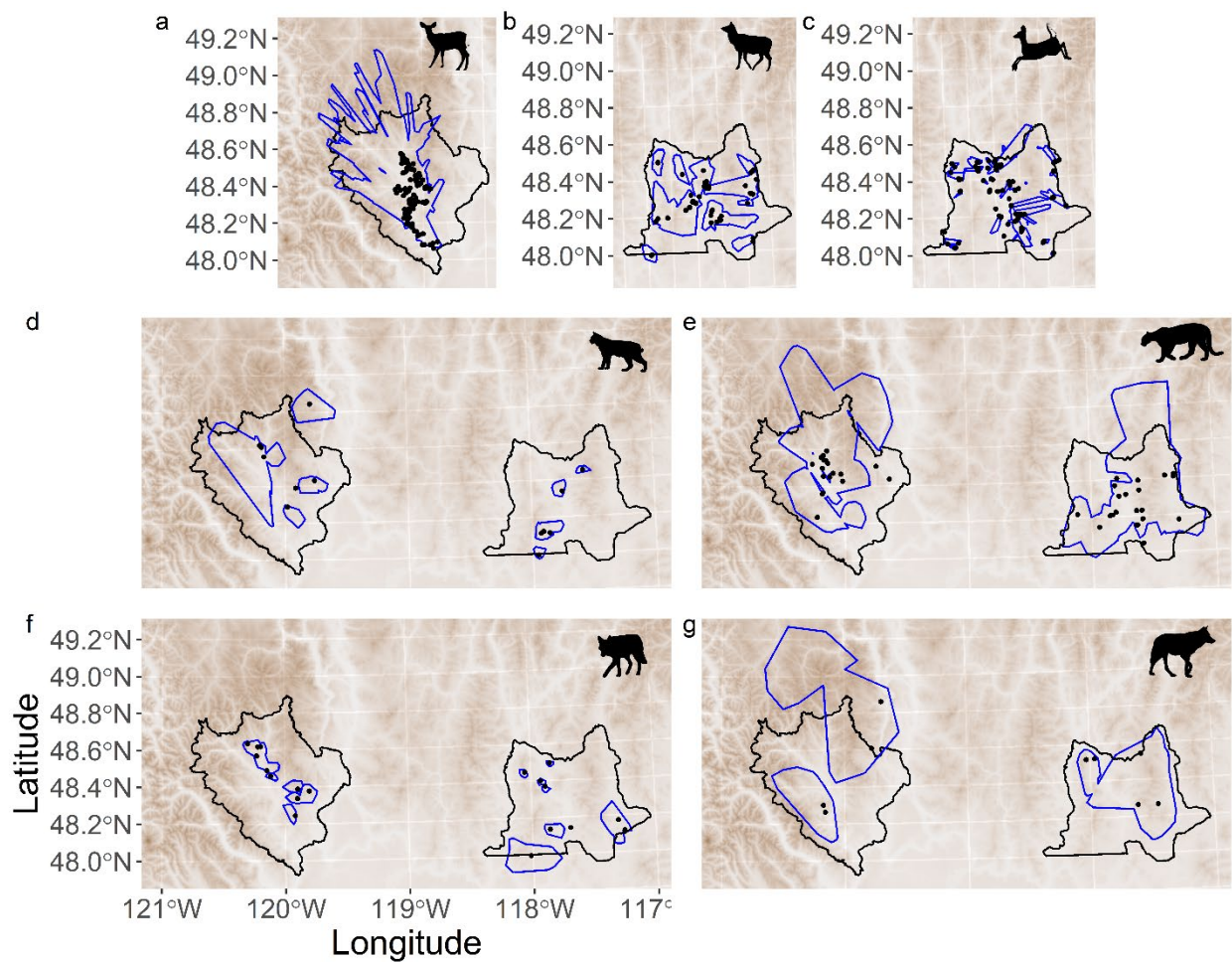
Figure 1

Figure 2

Figure 3

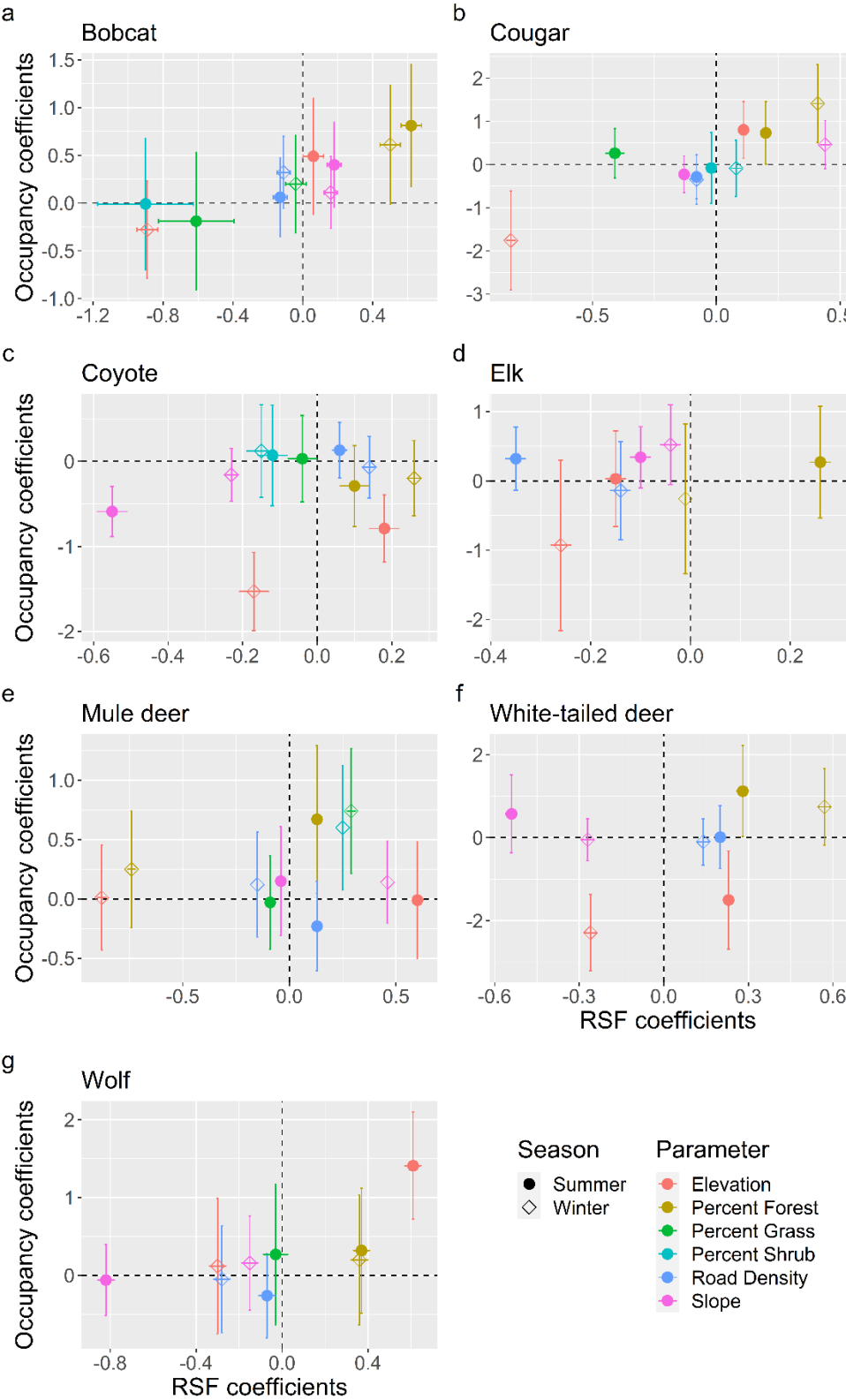Correlation between estimated occupancy and RSF coefficients

Figure 4

Consistent predicted space use

a Bobcat summer occupancy model

Bobcat summer RSF

Probability of site use
- (0,0.2]
- (0.2,0.4]
- (0.4,0.6]
- (0.6,0.8]
- (0.8,1]

Re-scaled relative probability of selection
- (0,0.2]
- (0.2,0.4]
- (0.4,0.6]
- (0.6,0.8]
- (0.8,1]

b Mule deer winter occupancy model

Mule deer winter RSF

Probability of site use
- (0,0.2]
- (0.2,0.4]
- (0.4,0.6]
- (0.6,0.8]
- (0.8,1]

Re-scaled relative probability of selection
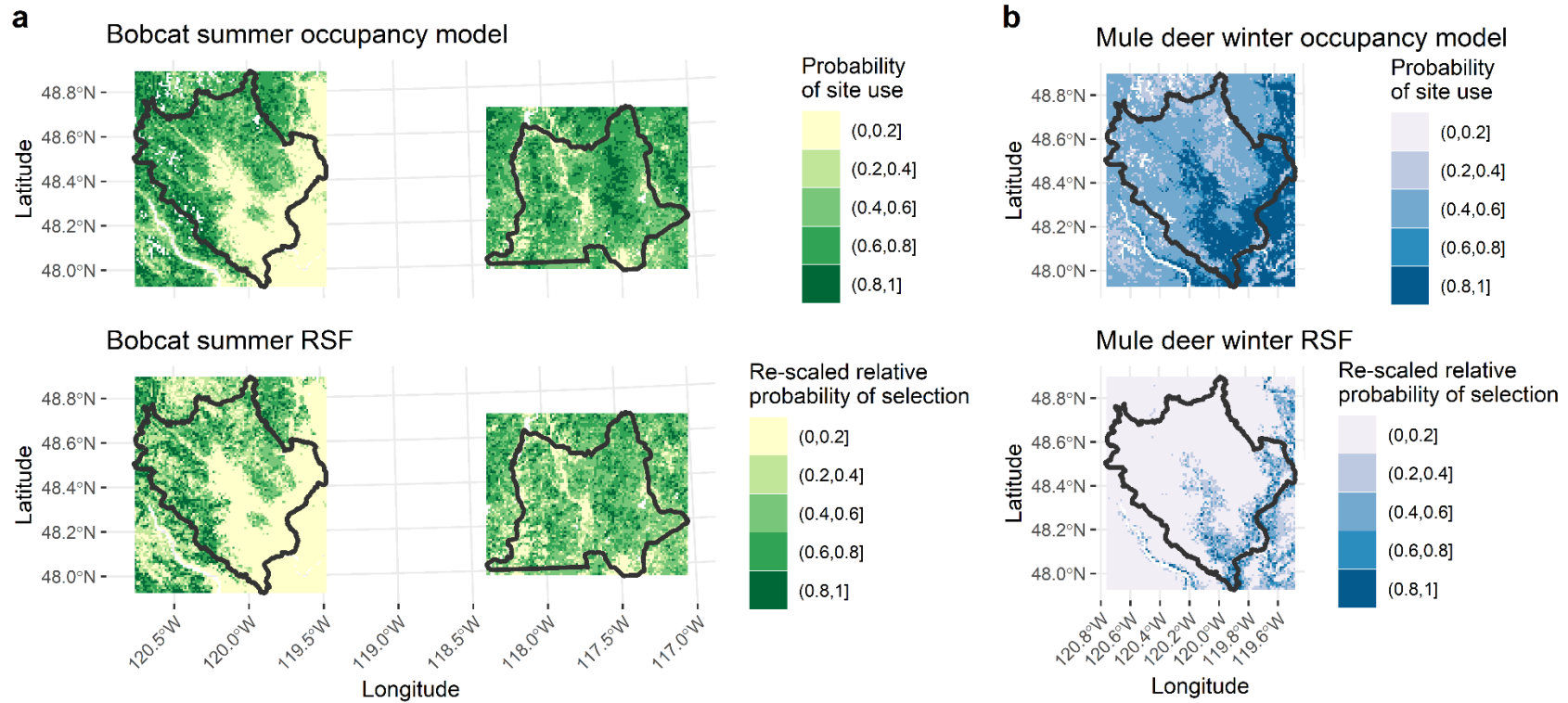- (0,0.2]
- (0.2,0.4]
- (0.4,0.6]
- (0.6,0.8]
- (0.8,1]

Figure 5

Inconsistent predicted space use

a Coyote summer occupancy model

b White-tailed deer summer occupancy model

Coyote summer RSF

White-tailed deer summer RSF

Probability
of site use

(0,0.2]
(0.2,0.4]
(0.4,0.6]
(0.6,0.8]
(0.8,1]

Re-scaled relative
probability of selection

(0,0.2]
(0.2,0.4]
(0.4,0.6]
(0.6,0.8]
(0.8,1]