Mechanistic movement models for bighorn sheep and rocky mountain elk in the northern Crown of the Continent

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Introduction

In the realm of conservation biology, the study of wildlife movement and connectivity has emerged as a pivotal area of research, particularly within ecologically significant regions such as the Rocky Mountains and the Yellowstone to Yukon (Y2Y) corridor (Hebblewhite et al. 2022). These landscapes are not only iconic for their natural beauty but also for their critical role in sustaining biodiversity and facilitating ecological processes across North America. The movement patterns of species like bighorn sheep and elk within these areas are of particular interest due to their ecological and cultural significance, serving as indicators of habitat health and connectivity. These ungulates rely on vast, interconnected landscapes to access seasonal resources, maintain genetic diversity through breeding, and navigate the challenges posed by natural and anthropogenic barriers.

The importance of connectivity in these regions cannot be overstated, with the Rockies and Y2Y acting as vital conduits for wildlife migration and movement across diverse ecosystems (Bolliger et al. 2020, Newmark et al. 2023, Pither et al. 2023). These corridors support the flow of genes, individuals, and species, thereby enhancing ecosystem resilience and adaptability in the face of changing environmental conditions. However, the increasing fragmentation of these landscapes due to human activities—such as urban development, road construction, and resource extraction—can present challenges to maintaining ecological connectivity (Fryxell and Sinclair 1988, Kauffman et al. 2021). This fragmentation can disrupt traditional wildlife movement patterns, potentially leading to reduced genetic diversity, population declines, and the loss of critical ecosystem functions.

Given these challenges, there is a pressing need for rigorous, predictive models of wildlife habitat use and movement. Such models can offer invaluable insights into the complex interplay between wildlife and their habitats, enabling conservationists to identify and mitigate barriers to movement. By focusing on the movements of bighorn sheep and elk, this work aims to contribute to the development of these models, leveraging advanced statistical techniques and extensive field data to enhance our understanding of how these species interact with their environment. Through this research, we seek not only to advance scientific knowledge but also to inform practical conservation strategies that can help preserve the ecological integrity of the Rockies and Y2Y corridor for future generations.

Methods

We predicted space use for bighorn sheep and elk across ~85,000 sq. km of southeast British and southwest Alberta (Figure 1). For both species, we considered two seasons, winter and summer, defined for each individual animal based on seasonal migratory behavior classified in Migration Mapper. For animal-years without migratory information, we defined season start and end dates using the median dates for that herd calculated from animals with data. We further broke the winter season for elk into migratory and resident winter models to ensure these different behaviours were captured individually. Our raw telemetry datasets included 187 bighorn sheep and 295 elk which had ~370,000 and ~991,000 GPS relocations, respectively.

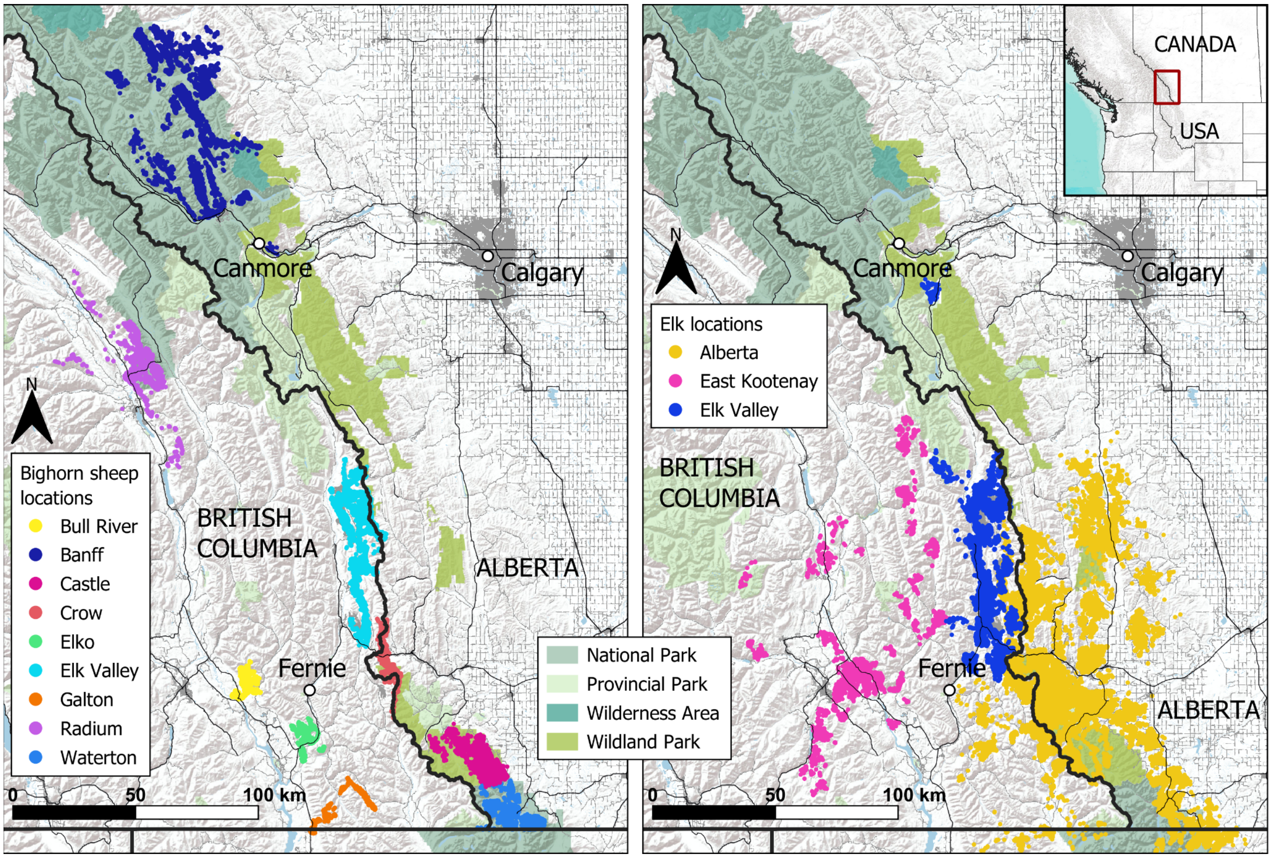

Figure 1. Map of summer and winter GPS locations, shown by study, of bighorn sheep (left) and elk (right) included in integrated step selection functions.

Second-order resource selection functions to guide simulation starting point placements

For each season, we fit a resource selection function (RSF) to the data to estimate where animals placed their home ranges within the overall study area (2nd order selection). We used the 'ctmm' package in Program R to calculate 95% autocorrelated kernel density estimate (AKDE) home ranges for each animal-season-year that had >20 GPS locations across >30 days. Home ranges are a probabilistic estimate of where animals occur if they exhibit home ranging behavior (restricted space use), and are tracked for a long period. For animal-season-years that did not exhibit home-ranging behavior, which we defined as AKDE home ranges >100 km^2 for sheep and >250 km^2 for elk, we instead calculated occurrence distributions. In contrast to home ranges, occurrence distributions are probabilistic estimates of where animals occur during the sampling period itself (in our case, a single season). The 2nd order RSF compared environmental covariates at random locations within the geographic union of home ranges and occurrence distributions to those at random locations distributed throughout the study area. We made spatial predictions from this second-order RSF, and classified map pixels into 10 equal-area bins, from lowest to highest relative probability of use. We used these seasonal binned maps to inform starting locations for simulated utilization distributions, described below.

Mixed-effects integrated step-selection functions

We then ran mixed-effects integrated step-selection functions (iSSF) for each season to predict finer-scale habitat selection within the home range/occurrence distributions, allowing for variation in habitat selection responses across individual sheep and elk. We resample GPS location data to one location every ~10 hours to ensure an equal relocation interval across all sheep. After resampling, our full datasets (across all seasons) included 128,000 locations from 167 sheep and 244,000 locations from 276 elk. Throughout an animal's movement path, an iSSF compares environmental conditions at each observed (GPS) location to randomly sampled locations that are available to the animal at that specific time step based on its movement behavior. We sampled available (random) steps from parametric distributions fit to step lengths and turn angles between successive observed locations. Because we predicted space use over an expansive study area with large environmental gradients, we attempted to account for regional variation in habitat selection in elk by incorporating generalized functional responses (GFR), which are interactions between local-scale habitat selection and broad-scale habitat availability. For example, elk with higher canopy cover in their home range may end up selecting for greenness more strongly than elk that occur in open agricultural areas. We did not use GFRs in sheep iSSFs.

Simulating utilization distributions from fitted iSSFs

To create maps of the relative probability of use for each season, we used the distributions for step length and turning angle, along with selection coefficients from each seasonal iSSF to simulate individuals moving around and selecting habitat on the landscape. We randomly selected locations within the top three map bins (top 30% of pixels) of the second-order seasonal RSFs (described above) as starting points. Restricting start points to this spatial extent prevented simulated animals from starting in locations where they were unlikely to exist, such as glaciers, reservoirs, areas with too much snow load or too far from escape terrain (sheep), or areas too far from cover (elk). For wintering sheep, we used a different process to guide starting points, due to their very restricted spatial distribution. Instead of sampling starting points within the top three bins of the 2nd order RSF, we sampled them from within the geographic union of winter home ranges/occurrence distributions and separate winter range polygons provided by British Columbia and Alberta provincial government biologists.

At each time step, simulated animals probabilistically selected a location from a suite of 100 available locations, where each step's relative probability of selection was calculated using coefficients from the fitted iSSF model. We used the ‘rvnorm’ function in Program R to simulate a separate set of habitat coefficients for each simulated animal using the full variance-covariance matrices of our top models (Kerman and Gelman 2007). This accounted for individual variability in habitat selection responses and propagated model uncertainty to our simulated movement paths. We used the number of times each 180-m map pixel was visited by animals as an index of the relative probability of use. For sheep, we simulated 500,000 animals that were active for 186 days in winter and 156 days in summer, with one location every 10 hours, resulting in ~223 million total steps for winter and ~187 million total steps per summer. For elk, simulation periods were 162 days in winter and 134 days in summer (for both migrant and residents), for ~194 million and 161 million total steps, respectively.

Within-sample model validation
After binning a seasonal UD into 10 (roughly) equal-area bins, we overlaid all real GPS locations that were included in that season's model, extracted the UD map bin for each location, and calculated the area-adjusted frequency for each bin. We then calculated the Spearman's rank correlation between bin (1 to 10) and area-adjusted frequency for each animal, as a metric of within-sample validation. A well calibrated model should have more locations in higher bins across all animals.

Results

We were able to fit predictive models for each species and gain insights into movement and habitat selection across the broad ecological gradients within our focal region. iSSF models for elk revealed selection for a variety of forage, as evidenced by selection for EVI, reduced distance to grass/shrub, and selection for reclaimed mine areas (Figure 2). Elk showed context-dependent relationships with canopy cover, which they generally avoided, more so in winter, but also in summer in productive landscapes. There was selection for less rugged terrain, and a general avoidance of human footprint features across seasons (active mines, highways, towns, and reservoirs). Elk were observed to have longer step lengths (moving faster and farther) in landscapes with higher productivity (EVI), less canopy cover, less rugged terrain, and in valley bottoms and ridge tops.

In both winter and summer, bighorn sheep selected for lower canopy cover, steep slopes, barren mountainsides, and escape terrain (barren/rock edge) (Figure 3). Sheep showed avoidance of active mines, selection for reclaimed mine areas, and avoided water crossings. Herbaceous cover was selected in winter, while shrub cover was selected in summer. Sheep avoided crossing highways in the winter and generally were not near highways in summer due to being at high elevations. Sheep took longer steps in lower canopy cover and mellower slopes.

Simulated utilization distributions revealed critical corridors for each species. During the winter, elk were primarily restricted to the Rocky Mountain Trench and Elk Valley in BC, although some potential winter habitats were predicted near the upper Flathead and Kootenay Rivers (Figure 4). In AB, the eastern front and foothills of the Rocky Mountains, as well as small portions of the Bow Valley, provided wintering habitat. Summer habitat for resident animals was primarily focused on similar habitats to winter, as evidenced by their non-migratory behaviour. The distribution of migrant animals in the summer included most of the mountainous and productive valley bottoms throughout the region.

Sheep winter ranges are typically very restricted in the region (Figure 5). Our application of 2nd order RSF's for starting locations produced simulated distributions that were much broader than observed by experts. As a result, we used expert-defined winter ranges to initialize simulation locations. The result was a more specific winter range UD that still benefited from inference from the iSSF and allowed simulated animals to move within and between ranges. The summer range for sheep was much broader.

Models typically validated well (r>0.8) suggesting good fit of the observed data to the modelled UD. The elk model showed high concordance with observed data across seasons and regions (Figure 6). The sheep model fit well for both seasons and most regions, but some poor model fit for some individuals and regions was apparent (Figure 7). The Galton range data were a notable exception, which may be explained by either these sheep's use of a human shield (border crossing and housing) that decouples traditional association with anti-predator habitat or that most of their used winter range was in Montana and we were not able to capture their selection for this area. The Canadian side of their winter range is heavily treed and they only use it occasionally in the winter. We observed individuals in Radium with a poor fit that may also relate to the use of human shields, which we did not capture here. Except for these few instances, we conclude that the models produced here for sheep and elk are reasonably well fit to the observed data and provide predictive estimates for utilization across the region.

We paired the sheep and elk UD's created here with previously developed models for grizzly bear using the same methods to compare utilization between species (Figure 8). This multi-species perspective produced community-level insights on key areas. Elk and bears overlapped in a lot of the region, with hotspots for both species in the Flathead, Elk Valley, Front range and Foothills of the Rockies in AB, Bow Valley, and upper Rocky Mountain Trench. There was less overlap between sheep and elk or bear, but some overlap occurred in the Elk Valley, especially the upper Elk Valley and Fording River area, portions of Waterton National Park, and the upper Flathead.

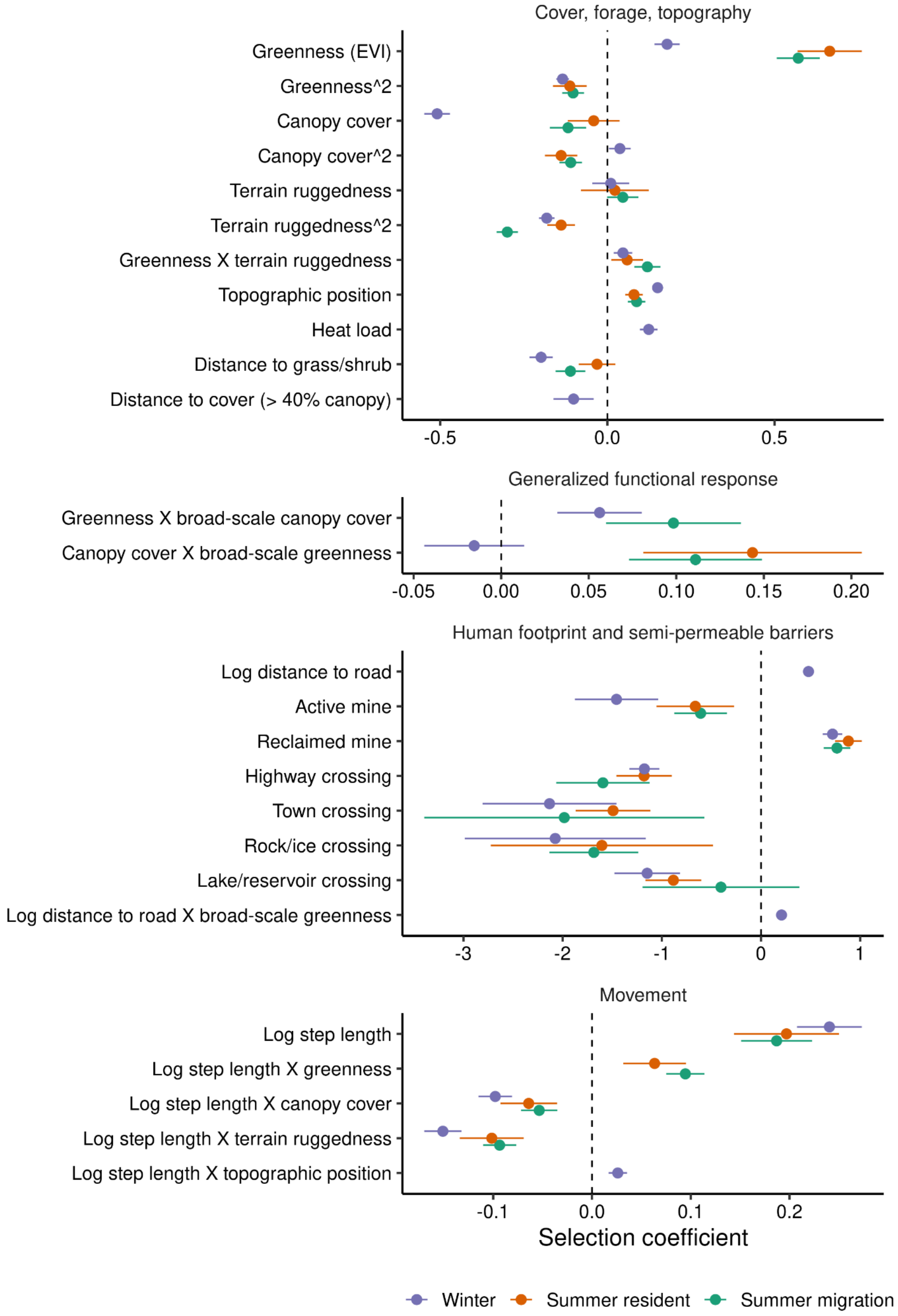

Figure 2. Selection coefficients for all model terms included in integrated step-selection functions fit to GPS collar data from 276 elk from 2002–2021 in the southern Canadian Rocky Mountains. Transparent points show individual-level responses (random slopes; if applicable), while points with black outlines and error bars intervals depict fixed-effects coefficients and associated 95% confidence intervals.

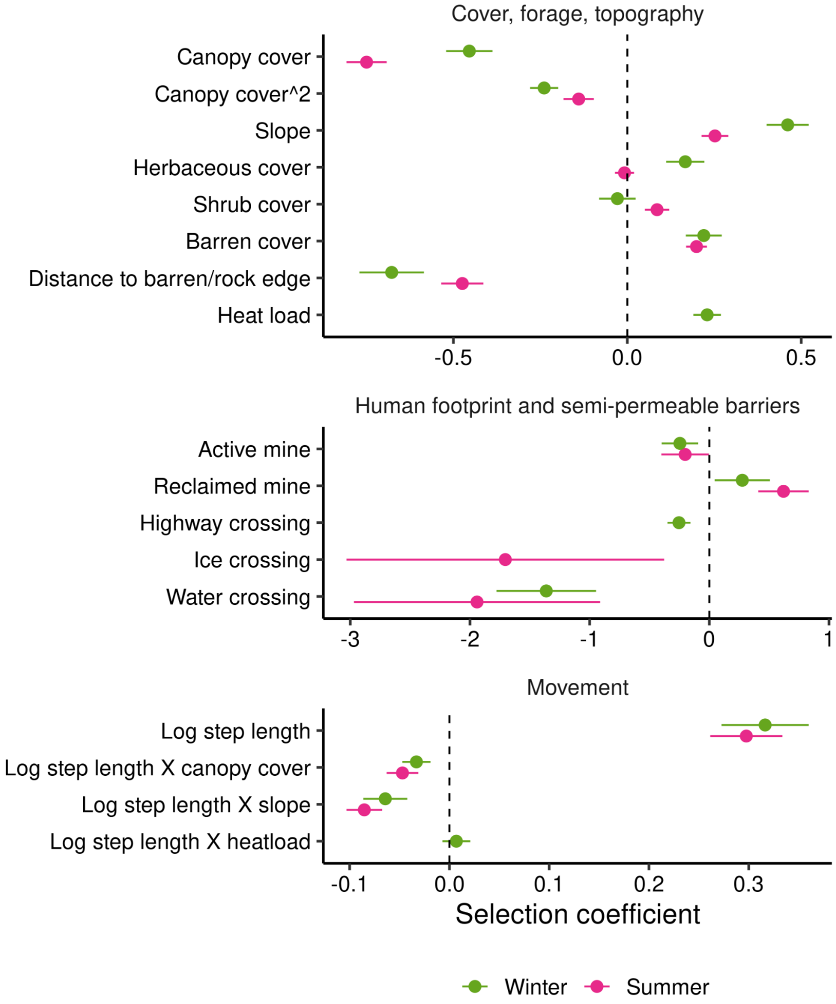

Figure 3. Selection coefficients for all model terms included in integrated step-selection functions fit to GPS collar data from 167 sheep from 2007–2021 in the southern Canadian Rocky Mountains. Transparent points show individual-level responses (random slopes; if applicable), while points with black outlines and error bars intervals depict fixed-effects coefficients and associated 95% confidence intervals.

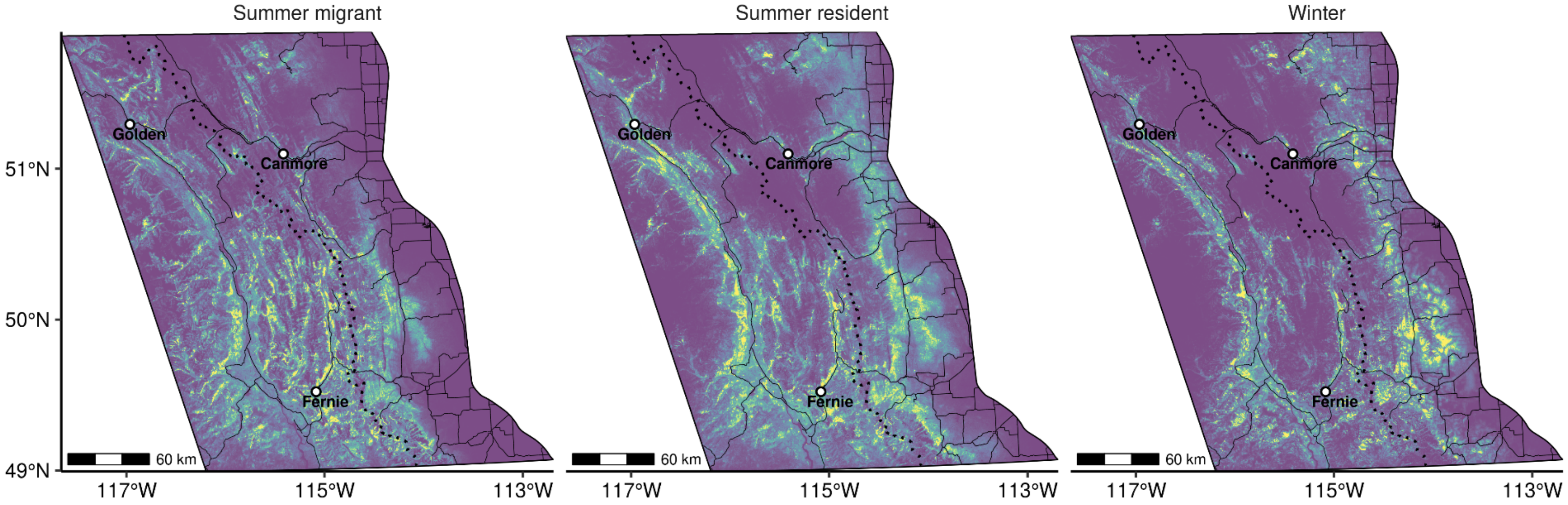

Figure 4. Predicted seasonal utilization distributions created using individual-based simulations from integrated step-selection functions fit to GPS collar data from 276 elk from 2007–2021 in the southern Canadian Rocky Mountains. We calculated the 99% quantile of mapped predictions in the utilization distributions and set all higher pixel values to this value to ease visual interpretation.

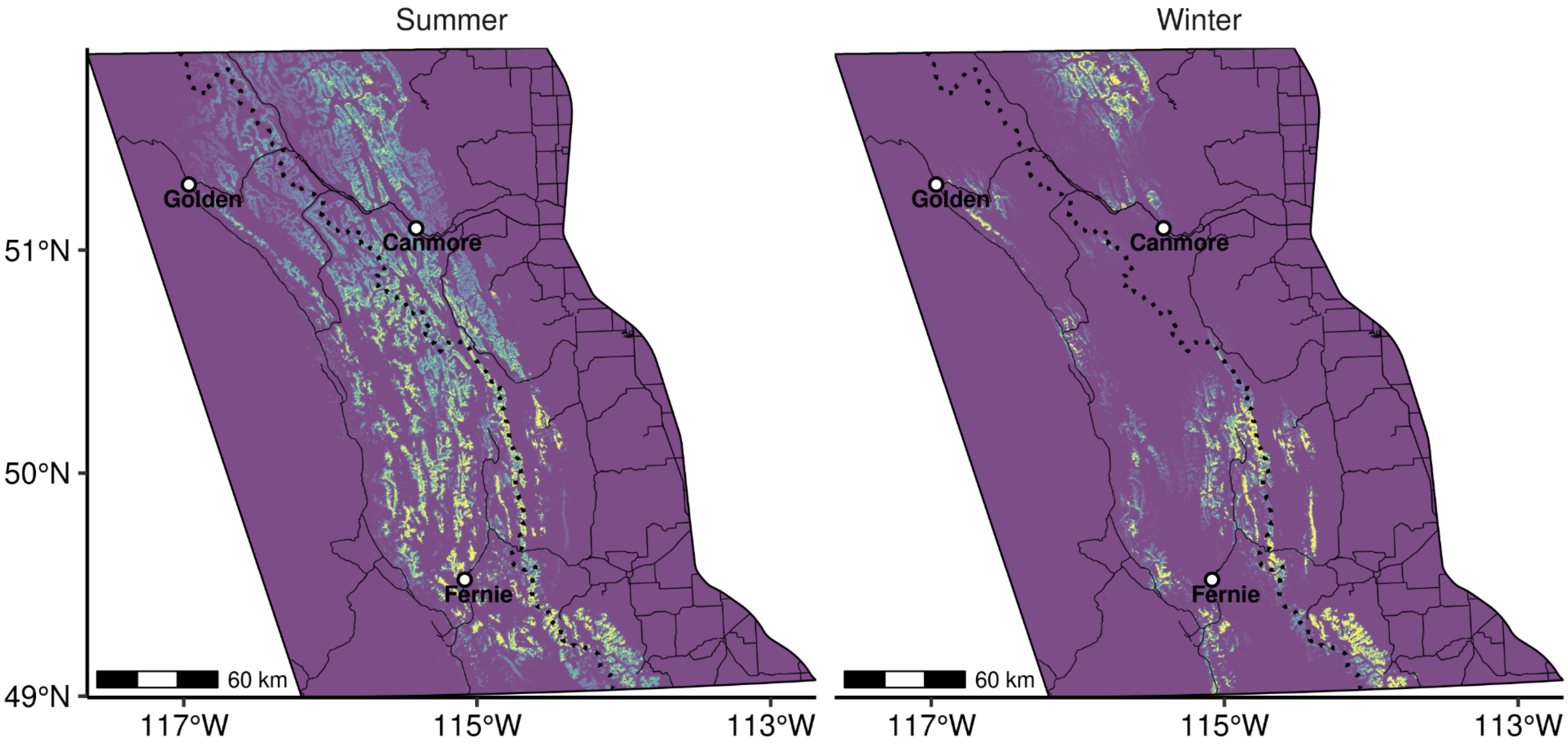

Figure 5. Predicted seasonal utilization distributions created using individual-based simulations from integrated step-selection functions fit to GPS collar data from 167 sheep from 2002–2021 in the southern Canadian Rocky Mountains. We calculated the 99% quantile of mapped predictions in the utilization distributions and set all higher pixel values to this value to ease visual interpretation.

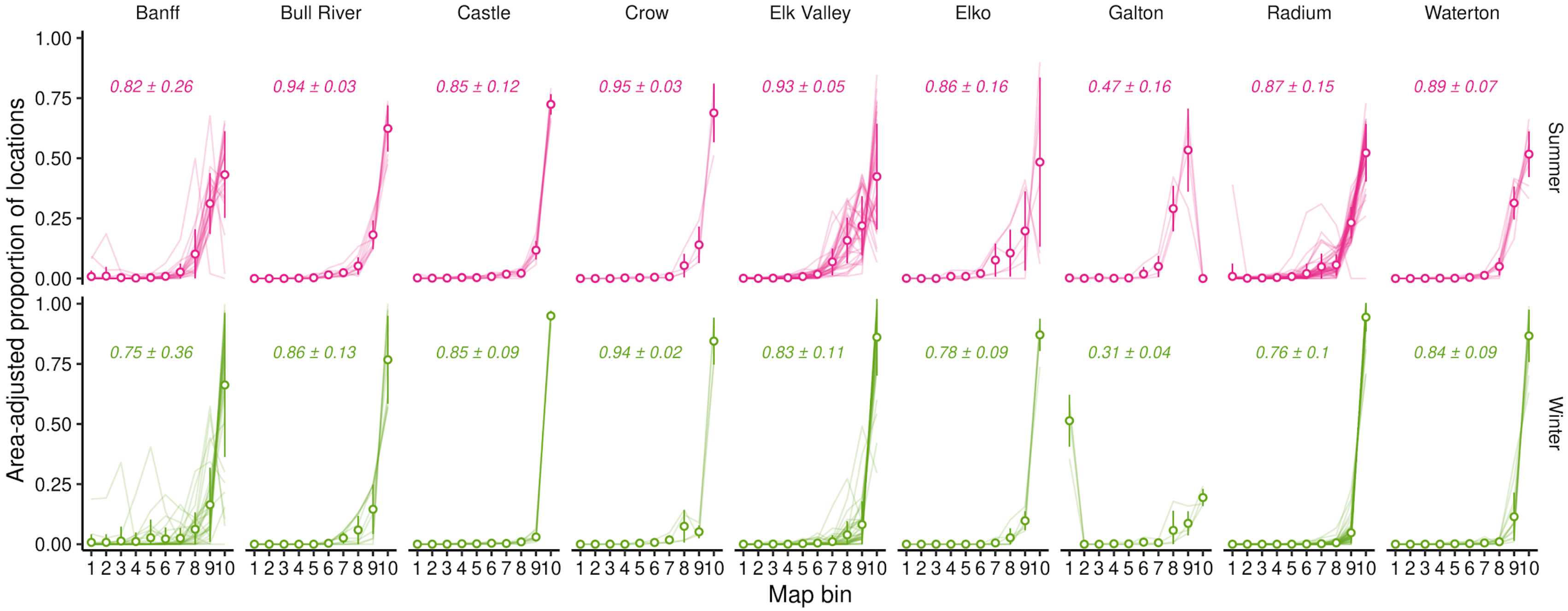

Figure 6. Within-sample validation for three studies showing the area-adjusted average proportions of used locations that fell into each of the 10 (nearly equal-area) bins of utilization distributions, where each individual line is a separate sheep and validation results are depicted by season and study. Utilization distributions were created from individual-based simulations of integrated step-selection functions fit to GPS collar data from 167 bighorn sheep from 2007–2021 in the southern Canadian Rocky Mountains. Text annotation displays the mean ± 1 standard deviation of Spearman's rank correlations across all individuals in that season-study.

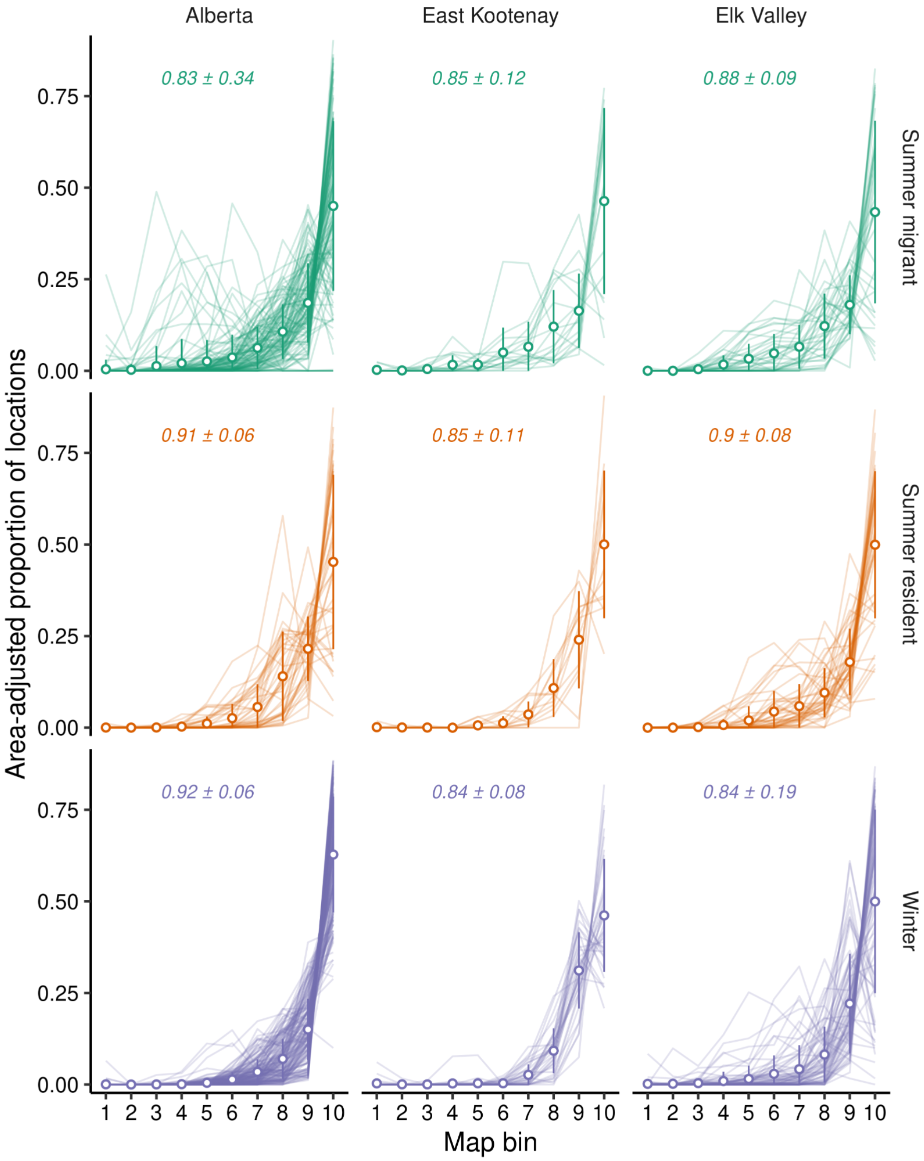

Figure 7. Within-sample validation for three studies showing the area-adjusted average proportions of used locations that fell into each of the 10 (nearly equal-area) bins of utilization distributions, where each individual line is a separate elk and validation results are depicted by season and study. Utilization distributions were created from individual-based simulations of integrated step-selection functions fit to GPS collar data from 276 elk from 2002–2021 in the southern Canadian Rocky Mountains. Text annotation displays the mean ± 1 standard deviation of Spearman’s rank correlations across all individuals in that season-study.

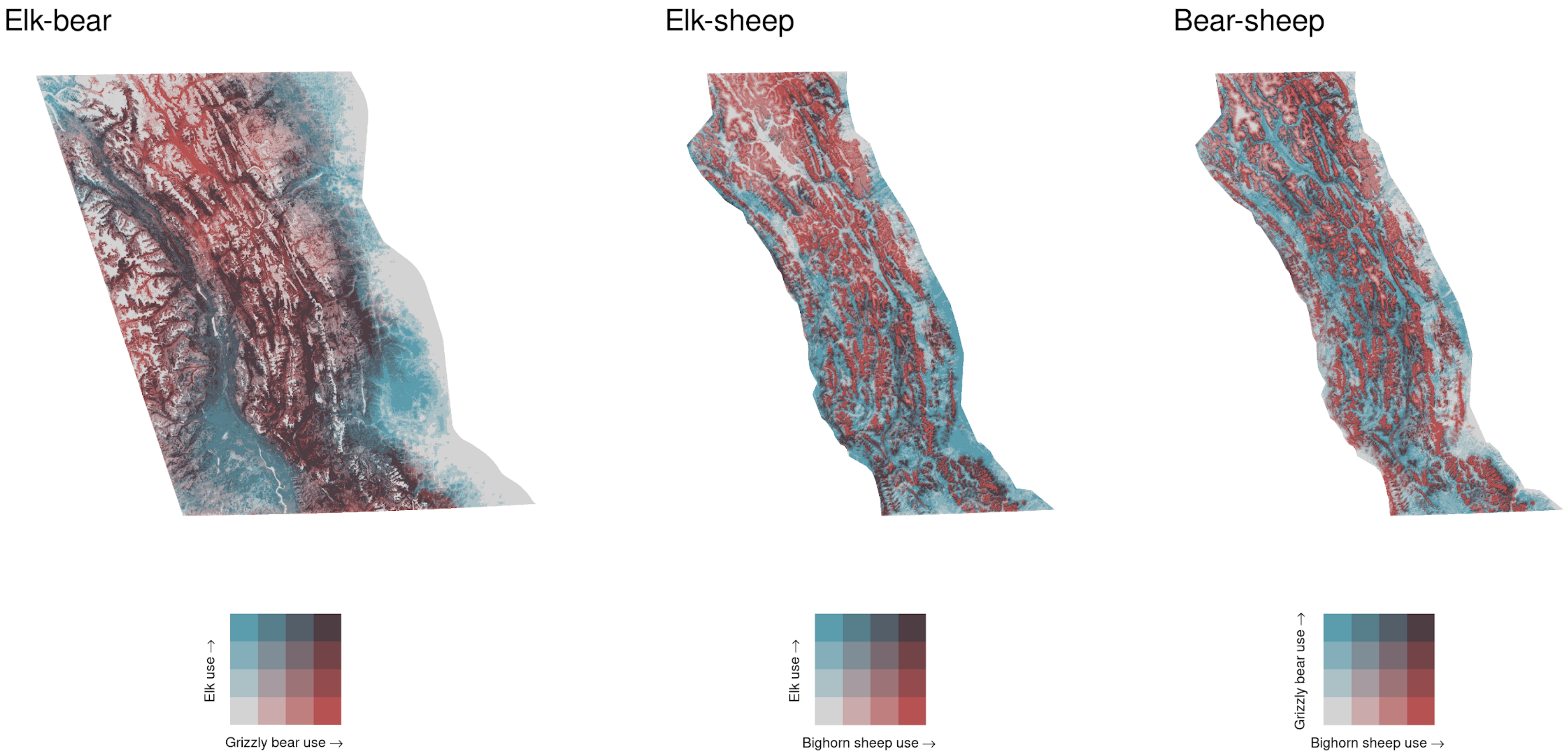

Figure 8. Bivariate correlation maps of annual predicted relative probabilities of use between pairs of species. Annual utilization distributions (UDs) for each species were created by summing raster values across seasons, weighting by season duration. Seasons included were as follows: spring, summer and fall for grizzly bear, summer migrant and winter for elk, and summer and winter for bighorn sheep.

Discussion

The development of GPS tracking technology for wildlife over the past 20 years has provided unprecedented insights into the movement and behaviour of many species. Here we leverage an abundance of previously collected data and newly developed analytical approaches to assess the space use, movement, and connectivity of bighorn sheep and rocky mountain elk in the southern Canadian Rocky Mountains. Our analysis advances the ecological understanding and conservation of these species in three key ways: 1) we fit sophisticated mechanistic movement models to hundreds of thousands of GPS relocations for each species, providing key insights into how vegetation, topography, and human features change their habitat use and movement, 2) we provide wall-to-wall utilization distributions for each species that can be used to inform land use decisions, 3) in combination with the grizzly bear utilizations previously developed, we assess hotspots that support multi-species habitat use and movement.

The approach used here is a significant advance over traditional approaches to modelling wildlife movement and connectivity. Historically connectivity modelling would involve running some form of a least-cost path algorithm over a map of habitat suitability. Although this is a good starting point and this approach has helped spark the field of movement ecology and connectivity, at no point is the movement of animals included in the analysis itself. Suitability maps are usually based on expert opinion or the occurrence of animals, but not movement per se. Similarly, the least cost paths provide appealing visuals, with wispy trails of corridors or pinch points that are satisfying to the eye, but these maps are rarely validated to confirm whether animals use these areas as corridors. Given that these maps are not made from movement data, one can not assume they represent movement or connectivity without such validation. Conversely, the approach we apply here is directly linked to animal movement through the iSSF which simultaneously models animals' selection for habitats and movement behaviour. The simulation approach allows for ecologically informed distributions of simulated animals that move based on rules directly inferred from movement data. We believe this approach allows for evidence-based and defensible parameterization of movement models and allows for transparent validation.

The abundance of telemetry data in the region was certainly an asset for this analysis but challenges were still encountered. There were instances where groups of animals would exhibit context-dependent behaviour, which was challenging to capture in a global model of movement.

For example, during the winter, bighorn sheep selected for high-elevation habitats along the continental divide but selected for low-elevation habitats on the west slope and foothills of the Rockies. We believe this is related to unique high-elevation grassland habitats and high wind speeds that clear these grasslands of snow along the continental divide, a situation not found elsewhere in our study area. Presumably with good spatial layers of snow depth and wind speeds, we could capture this effect with a functional response, however, we repeatedly struggled to find snow depth and wind speed layers that were accurate across our study area and available at a fine grain. Similarly, non-migratory behaviour is increasingly common in elk, leading to very different habitat selection during the summer between migrants and residents. We solved this problem by creating separate summer models for each migrant type, but important questions arise, such as whether we should weight these equally in conservation planning when the migratory behaviour is usually considered the “preferred” behaviour due to resident elk causing issues with crop damage and vehicle collisions year round. Finally, it appeared that in some cases animals used human presence to avoid predation via a human shield. Such behaviour likely explained why bighorn sheep live primarily within the town of Radium, however, food resources on the golf course are also likely a contributing factor. In such cases where animals are using a human shield, their selection for certain habitats can be much different than in areas where no such shield exists, again complicating the creation of a global model to explain wildlife movement and habitat use across diverse areas.

For both bighorn sheep and elk, the relatively coarse ~10-hour relocation interval posed several modelling challenges, which ultimately affected our inference and ability to predict connectivity. First, iSSFs typically require fitting parametric distributions to turning angles between successive locations. These distributions can then be modified through interactions with step length, which indicates whether faster movements are associated with more directional persistence, or through interactions with habitat covariates, which indicate if movements are straighter or more circuitous in certain habitats. However, the empirical turning angles in our dataset included many instances of “turning around”, likely due to the relocation interval, and we were unable to fit von Mises distributions that captured this behavior. Therefore, when simulating movements from fitted iSSFs, we were forced to draw turning angles from uniform distributions, which did not accurately reflect their movement behavior. More frequent relocations might have allowed us to better capture these turn angles and simulate more realistic movement.

Second, the coarse relocation interval dissuaded us from using a path-based iSSF approach, where instead of extracting covariates at the start and endpoints of steps, we would extract them along the steps themselves. We chose a point-based approach because there was too much uncertainty around the actual paths of the animal in a ~10-hour period. A path-based approach, as in Hofmann et al. 2023, would allow us to simulate utilization distributions by counting the number of simulated paths (rather than simulated points) that intersect each raster cell. Compared to the point-based approach, which highlights areas where animals spend the most time, the path-based approach would also highlight corridors through which animals move quickly and therefore spend relatively little time. These corridors are important for connectivity as they facilitate movement between habitat patches.

There are some key inferences from our multi-species utilization distributions. At a high level, some key areas emerge for elk and grizzly bears, such as the Flathead and Elk Valleys, the upper Rocky Mountain trench north of Invermere, Kananaskis country, Livingstone-Porcupine hills, and the Bow Valley. Habitat for sheep was more restricted, especially in the winter. Key areas for sheep occurred along the low elevation west slope of the Rocky Mountains, Elk Valley and along the continental divide, and north of Banff. The habitat for all three species declined rapidly east of the Foothills in Alberta due to the conversion of these lands to agriculture. Vast tracts of the mountainous areas were unsuitable to grizzly bears or elk due to being steep rock, while these same areas were highly used by sheep. Human features such as roads, active mine areas, and cities consistently reduced animal use of areas and in many cases restricted movement.

Our approach made efficient use of an abundance of telemetry data that had not been compiled for integrated insights such as this. Analyzing data across regions provided ecological parameter space to fit general models and assess how models were validated across these regions and seasons. Our approach explicitly linked the behaviour and movement patterns of animals as inferred from the telemetry data to the predicted maps of use, providing a mechanistically informed prediction of space use.

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