Received: 13 February 2024 | Revised: 4 May 2025 | Accepted: 30 May 2025

DOI: 10.1111/csp2.70088

CONTRIBUTED PAPER

Conservation Science and Practice
A journal of the Society for Conservation Biology
Open Access

WILEY

Changing grizzly bear space use and functional connectivity in response to human disturbance in the southern Canadian Rocky Mountains

Eric C. Palm[1,2] | **Clayton D. Apps**[3] | **Tal Avgar**[4,5] | **Melanie Dickie**[5] | **Bruce N. McLellan**[6] | **Joseph M. Northrup**[7] | **Michael A. Sawaya**[8] | **Julie W. Turner**[5] | **Jesse Whittington**[9] | **Erin L. Landguth**[10] | **Katherine A. Zeller**[2] | **Clayton T. Lamb**[5]

[1]Computational Ecology Lab, School of Public and Community Health Sciences, University of Montana, Missoula, Montana, USA

[2]Rocky Mountain Research Station, Aldo Leopold Wilderness Research Institute, US Forest Service, Missoula, Montana, USA

[3]Aspen Wildlife Research Inc., Powell River, British Columbia, Canada

[4]Department of Biology, Irving K. Barber Faculty of Science, University of British Columbia, Vancouver, British Columbia, Canada

[5]Wildlife Science Center, Biodiversity Pathways Ltd., Kelowna, British Columbia, Canada

[6]International Union for the Conservation of Nature, Bear Specialist Group, D'Arcy, British Columbia, Canada

[7]Wildlife Research and Monitoring Section, Ontario Ministry of Natural Resources and Forestry and Environmental and Life Sciences Graduate Program, Trent University, Peterborough, Ontario, Canada

[8]Sinopah Wildlife Research Associates, Missoula, Montana, USA

[9]Parks Canada, Banff National Park Resource Conservation, Banff, Alberta, Canada

[10]Computational Ecology Lab and Center for Population Health Research, School of Public and Community Health Sciences, University of Montana, Missoula, Montana, USA

Correspondence
Eric C. Palm, Computational Ecology Lab, School of Public and Community Health Sciences, University of Montana, Missoula, MT, USA.
Email: e2palm@gmail.com; epalm@mso.umt.edu

Funding information
Wilburforce Foundation; Rocky Mountain Research Station; Habitat Conservation Trust Foundation; Elk Valley Regional Land Trust; Yellowstone to Yukon Conservation Initiative; University of Montana; Nature Conservancy of Canada; National Program for Ecological Corridors

Abstract

Understanding wildlife responses to human disturbance is essential for developing effective conservation and management strategies. Grizzly bears in the southern Canadian Rocky Mountains face increasing habitat alteration from roads, forest harvest, human settlements, and mining, which can alter the way animals move through the landscape. Deleterious effects on genetic exchange, demographic connectivity, and access to key resources can occur if movements are dramatically altered. We used integrated step-selection functions (iSSF) to model movement and habitat selection for 109 GPS-collared grizzly bears across an 85,000 km^2 multi-use landscape in southeastern British Columbia and southwestern Alberta. We then simulated individual grizzly bear movements from fitted iSSFs to predict changes in population-level space use and functional connectivity under the following scenarios: (1) without current levels of human disturbance, (2) under current conditions, and (3) with a defined increase in human disturbance. Bears avoided crossing highways but

were attracted to areas alongside highways in areas with relatively low forage availability at a broad spatial scale, such as in Banff National Park and the Kananaskis region. Females generally avoided moving through towns in spring and summer, while males were more likely to do so. Additional footprints of proposed mines and expanded human settlements in a potential future scenario were predicted to further decrease functional connectivity for grizzly bears on top of prior connectivity losses from existing human disturbance. Our study builds upon existing work simulating animal space use from fitted iSSFs by incorporating individual-level variation into population-level simulations and by fitting functional responses that help capture broad-scale variation in behavior and improve model transferability to new areas. Our results provide insights into grizzly bear movement and connectivity in an area of high conservation importance, and our predictive maps can be used to directly inform transboundary management actions and conservation planning.

KEYWORDS

conservation, functional connectivity, habitat selection, human development, integrated step selection, movement ecology, utilization distribution

1 | INTRODUCTION

Wildlife movement is a fundamental ecological process that facilitates the acquisition of food, search for mates, and security from threats (Turchin, 1998). Habitat change through loss, fragmentation, and degradation can impede animal movement, thereby reducing access to resources and increasing their vulnerability to mortality while moving within and between habitat patches (Lindenmayer & Fischer, 2013). Reductions in movements in response to human influence have been documented across many species of mammals around the world, with far-reaching effects on multiple ecosystem processes (Tucker et al., 2018). Further, declining functional connectivity via reduced movement success among and between habitat patches can decrease the spatial distribution, abundance, and population persistence of animals (Bowne & Bowers, 2004; Fahrig, 2007).

Understanding how increasing human disturbance affects wildlife movement is necessary for developing effective wildlife conservation and management strategies (Doherty & Driscoll, 2018). Here, we focus on the movement, habitat selection, and connectivity of grizzly bears (*Ursus arctos*) in the southern Canadian Rocky Mountains (Figure 1), where a growing footprint of roads, mines, human settlement, and other infrastructure has negatively affected their movements, behavior, and survival (Ciarniello et al., 2007; McLellan & Shackleton, 1988; Nielsen et al., 2004; Northrup, Pitt, et al., 2012). As a result of this development, some subpopulations in this region have become increasingly isolated with minimal demographic interchange, and bears living in close proximity to humans rely on connectivity to nearby wilderness areas to offset human-caused mortality and to sustain viable populations (Lamb et al., 2020; Proctor et al., 2012). Identifying factors affecting grizzly bear habitat selection and mapping predicted space use in this region is key to proactive conservation and land planning. Safeguarding the movement of grizzly bears in this region (and movements between this region and populations south of the Canada–USA border) is important, given the near complete loss of connectivity that has occurred farther south between the Greater Yellowstone population and neighboring USA populations, and given the challenges in establishing connectivity corridors once lost (Sells et al., 2023).

Integrated step-selection analyses are an attractive approach for assessing movement, habitat selection, and connectivity from telemetry data because they relax the assumption that movement and habitat selection are independent, simultaneously estimate parameters for both processes, and model interactions between the two (Avgar et al., 2016). Practitioners can simulate individual animal paths parameterized by these models to estimate population-level utilization distributions, which are more accurate than maps from traditional resource selection models that assume constant resource availability across space and time (Signer et al., 2017, 2024). For example, Sells et al. (2022, 2023) simulated movements from iSSFs fitted to individual bears to predict connectivity between

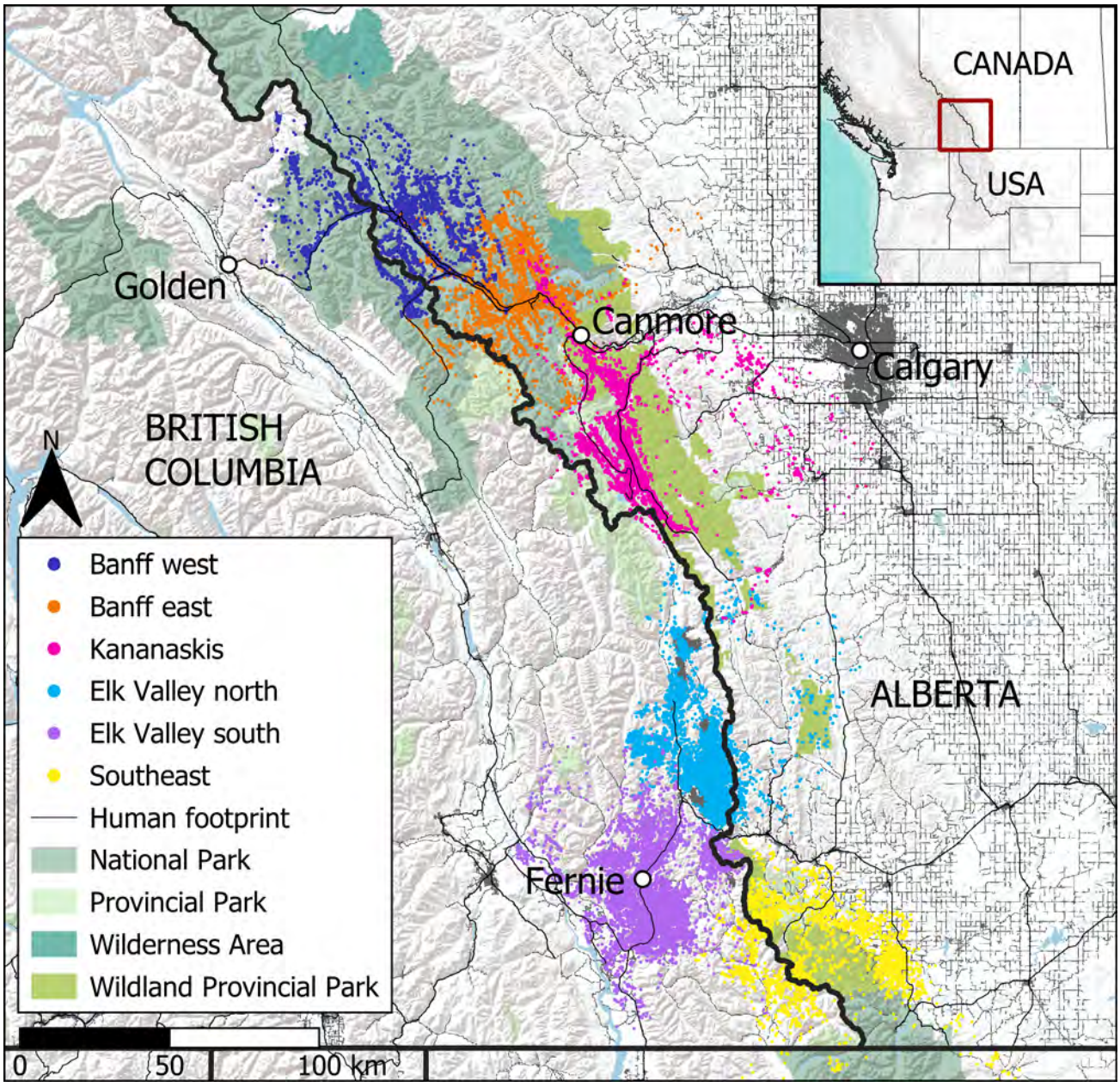

FIGURE 1 Study area for grizzly bear space use and functional connectivity analyses in the southern Canadian Rocky Mountains showing locations of grizzly bear GPS locations, collected from 2000 to 2020, used to fit integrated step-selection functions. Colors of GPS locations indicate different regions within the study area that were used in spatial cross-validation of the models. Assignment of individuals to regions was based on location centroid.

grizzly bear recovery areas in the United States, while Whittington et al. (2022) used behavioral state-based SSFs to predict connectivity losses for grizzly bears and wolves under a proposed human development expansion in Alberta's Bow Valley. Others have used simulations to predict dispersal corridors and interpatch connectivity (Hofmann et al., 2023), and to quantify barrier effects of highways on connectivity (Aiello et al., 2023).

Simulations from fitted integrated step-selection functions (iSSFs) also provide a means to estimate Merriam connectivity, a type of functional connectivity defined as per-individual movement success between and within habitat patches (Fahrig et al., 2021). Merriam connectivity explicitly incorporates species-specific movement capability and structural landscape effects on connectivity. Quantifying connectivity directly from simulated trajectories obviates the need to separately predict landscape resistance (e.g., via transformed spatial predictions from a habitat selection model) for use in connectivity analyses such as cost-distance or circuit theory (Zeller et al., 2012),

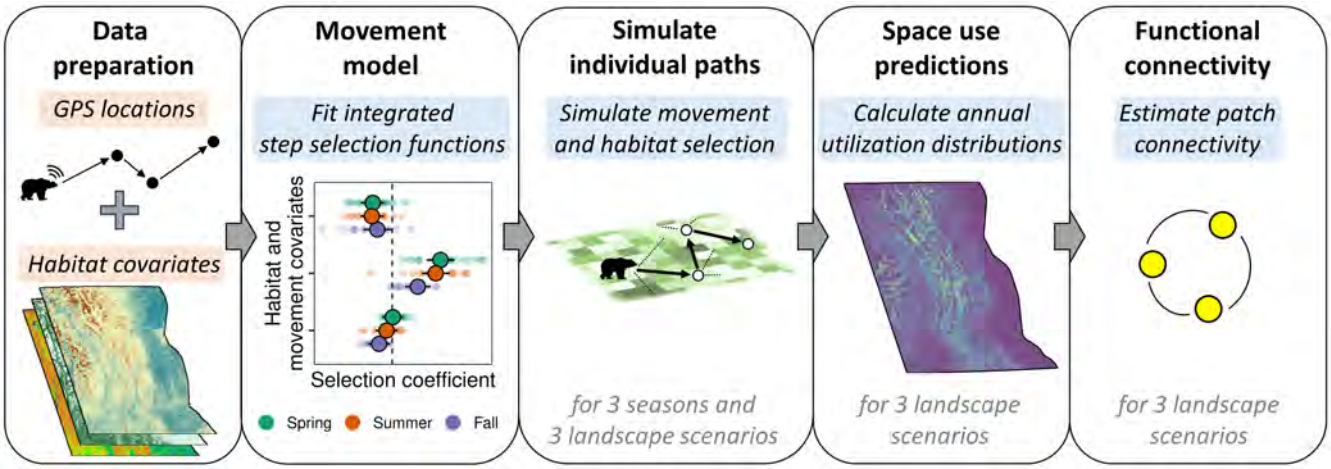

FIGURE 2 Steps for predicting annual space use and functional connectivity using simulations parameterized from integrated step-selection functions fitted to GPS location data from 109 grizzly bears from 2000 to 2020 in the southern Canadian Rocky Mountains.

which require predefined path destinations and assume animals have perfect knowledge of landscape resistance and exhibit consistent movement behavior.

We used a multi-step approach (Figure 2) to predict grizzly bear movements, habitat selection, and functional connectivity under a scenario without current human disturbance, under current conditions, and under a potential future scenario with additional human disturbance. We build upon existing studies that simulate trajectories from fitted movement models by incorporating uncertainty and individual-level variation into population-level simulations, explicitly accounting for seasonal variation in movement and habitat selection, and fitting generalized functional response terms (Matthiopoulos et al., 2011) to help capture broad-scale variation in behavioral responses and improve model transferability to new areas (Paton & Matthiopoulos, 2016).

First, we fitted iSSFs to estimate the degree to which a suite of habitat attributes affected grizzly bear movements, with a particular focus on how human infrastructure and broad-scale variation in habitat availability influenced habitat selection. These iSSFs explicitly modeled sex-specific variation in movement and habitat selection. We hypothesized that grizzly bear movement behavior would generally reflect a tradeoff between access to high-quality forage and exposure to humans, and that these behavioral responses would differ between sexes and across seasons (Nielsen et al., 2010; Roever et al., 2008; Table S1). We then simulated individual movements from fitted iSSFs to predict population-level utilization distributions (UD) at a spatial extent large enough to help guide conservation planning at regional, national, and international levels (Hilty et al., 2020; Pither et al., 2023). Finally, we predicted changes to grizzly bear functional connectivity by calculating movement success of simulated animals within and between habitat patches in a subset of our study area with high amounts of existing and proposed human disturbance, high bear densities, and frequent human-bear conflicts.

2 | METHODS

2.1 | Study area

Our study area consisted of 85,000 km^2 of southeastern British Columbia (BC) and southwestern Alberta (AB), including a large portion of the southern Canadian Rocky Mountains (Figure 1). At a broad spatial scale, this region provides important connectivity along the continental divide between highly fragmented animal populations in the south and larger ones to the north and west (Apps et al., 2007). The Rocky Mountains form a narrow (50–100 km) corridor between the developed prairies to the east and the settled valley of the Rocky Mountain Trench to the west, and encompass large swaths of protected areas, including several national parks, provincial parks, and provincial wildland areas. Several major highways cross the region, primarily along valley bottoms but also across several high mountain passes. Human settlement is largely confined to valley bottoms, low-elevation foothills, and prairies, and most mining activity occurs in the Elk Valley and nearby areas in the south. Recent increases in tourism and associated traffic, ongoing development of coal mines in the south, and human population growth have increased habitat alteration in the region. Agricultural development is widespread in the eastern prairie and foothills portion of our study area and localized in valley bottoms in the mountains. In AB, grizzly bear hunting was banned in 2006, and the species is

listed as Threatened under the Wildlife Act (Government of Alberta, 2022). Hunting of grizzly bears was legal outside of national parks in BC until it was banned in late 2017.

2.2 | Telemetry data

We used GPS collar data from grizzly bears captured throughout the southern Canadian Rocky Mountains. Bears were captured using multiple methods, including darting from a helicopter, leg restraints, and culvert traps. Full details on bear capture methods and animal care protocols can be found in Northrup, Pitt, et al., 2012, McLellan, 2015, Lamb et al., 2020, and Whittington et al., 2022. Our initial dataset included 305,619 GPS locations from 159 GPS-collared grizzly bears whose collars collected data between 2000 and 2020. We resampled GPS location data to a relocation interval of ~6 hours to maintain a consistent sampling rate across individuals for our iSSFs and to maximize sample sizes throughout the study extent and across different collaring efforts. This relocation interval limited the spatial domain available to an animal at a given time step to be within a distance reachable within 6 h. We captured seasonal differences in movement and habitat selection behavior by assigning location data into one of three time periods, which were modified slightly from the seasons used by McLellan and Hovey (1995) that were based on changes in grizzly bear diet. Our seasons were: spring (den emergence–July 15), summer (July 16–Sept 15), and fall (Sept 15–den entrance). We fitted separate iSSFs for each season.

2.3 | Habitat covariates

A major focus of our analyses was to understand grizzly bear behavioral responses to different types of human disturbance, including roads (separated into highways and non-highways), mines, and towns. Highways and non-highway roads were represented as static distance decay variables, which were negative exponential transformations of distances to the nearest feature (e.g., Nielsen et al., 2009). We expected these two road types would have different effects on bears behavior due to differences in vehicle speed and traffic volumes (Gibeau et al., 2002; Northrup, Pitt, et al., 2012; Waller & Servheen, 2005). We also represented highways as static semi-permeable movement barriers, binary variables indicating whether each step (i.e., the straight line connecting consecutive locations) intersected a highway. We acknowledge that the straight-line "steps" are modeling heuristics rather than actual movement paths, and, in some scenarios, bears might have traveled parallel to a winding highway rather than crossing it. Nevertheless, our approach provides a parsimonious way to estimate semi-permeable barrier effects in an iSSF. We represented mines (annual variable) and towns (static variable) in our models as either semi-permeable movement barriers or binary footprint variables, which indicated whether the location at the end of a step intersected the mine footprint, and we used log-likelihood to determine which variable type was best for each. We used static semi-permeable movement barrier variables for alpine areas that were either glaciated or predominantly rock and for large (>2.5 km^2) lakes and reservoirs. See Appendix 1 in Data S1 for details on creation of human footprint, distance decay, and semi-permeable barrier variables.

We also sought to quantify selection behavior in response to forage, terrain ruggedness index (TRI; calculated using a 3 × 3 pixel window with an elevation raster; Wilson et al., 2007), and canopy cover. We hypothesized that grizzly bears would select areas with high vegetation greenness, measured using raw annual values of either enhanced vegetation index (EVI) or delta EVI (growing season EVI—winter EVI), which would strongly correlate with high-quality forage such as deciduous shrubs and forbs. We compared log likelihoods of full models using either EVI or delta EVI to determine which to use in final models.

We hypothesized that bears would avoid the most rugged terrain and generally select low to intermediate canopy cover. To help distinguish between deciduous shrubs and forbs versus deciduous trees, we interacted greenness with canopy cover. In spring and summer models, we also included an interaction between greenness and elevation to help capture intermediate-to-high-elevation areas of high greenness such as avalanche paths and alpine meadows. We predicted bears would more strongly select these areas relative to low-elevation agricultural areas because they often contain an abundance of high-quality bear forage (Serrouya et al., 2011). We assumed the first spring location for each bear-year was near its den, and we included a "distance to spring start" variable in all three seasonal models. We hypothesized that most bears in our dataset exhibited range-resident behavior and that the coefficient for "distance to spring start" would be negative. We resampled all raster data to 180-m resolution for iSSFs and subsequent simulations to balance spatial resolution with computation time. See Table S2 for additional details on all habitat covariates used in iSSFs.

2.4 | Integrated step-selection functions

We fitted point-based iSSFs in a generalized linear mixed modeling (GLMM) framework using the R package

"glmmTMB", version 1.0.2.1 (Brooks et al., 2017; Muff et al., 2020). iSSFs discretize animal movement paths into individual steps and restrict the availability domain for each step based on the animal's current location and their typical movement behaviors. We extracted habitat covariate values at the end of each step to characterize habitat selection and at the start of each step for movement-habitat interactions (Fieberg et al., 2021). We estimated stratum-specific intercepts as random effects with a fixed large variance in a conditional Poisson regression, following Muff et al. (2020). We fitted a random slope at the individual level for every covariate, except on generalized functional response interaction terms (see below) and on terms where their inclusion prevented model convergence. Model coefficients for a main variable (e.g., greenness) represented female selection and the corresponding interaction term including sex (e.g., greenness × sex) represented the difference in selection for a variable for males compared to females. See Appendix 1 in Data S1 for more details on iSSFs.

We visualized behavioral responses to habitat conditions by plotting relative selection strength (Avgar et al., 2017) predictions across the full range of values for a covariate in the input dataset relative to its average value in that season (i.e., 0 for centered and scaled continuous covariates). We held all other continuous covariates constant at their average values (i.e., 0) and binary variables at 0, so the relative selection strength for each value of a covariate x_1 with a selection coefficient of β_1 was $\exp(\beta_1 x_1)$.

2.5 | Generalized functional responses in iSSFs

Exploratory plots of selection ratios calculated within bins of several continuous variables (e.g., distances to roads and highways) showed pronounced variation in selection behavior across different portions of the study area in both sexes (Figures S1 and S2). We attempted to account for this broad-scale variation in grizzly bear behavior in our models by fitting generalized functional response terms, which are interactions between habitat variables at the ends of steps and broader-scale habitat availability (Matthiopoulos et al., 2011). Fitting generalized functional response terms can improve a model's ability to accurately predict responses across heterogeneous or novel environments while still capturing local extremes in resource availability (Matthiopoulos et al., 2011; Paton & Matthiopoulos, 2016). We estimated the broad-scale availability of greenness, terrain ruggedness, and canopy cover by calculating the average pixel value within a circular moving window of 315 km^2, which roughly corresponded to the average seasonal home range size of a female grizzly bear from past studies in the area (Graham & Stenhouse, 2014; see Appendix 1 in Data S1 for details on generalized functional response terms).

2.6 | iSSF model selection

For each season, we started with a full model structure that included quadratic terms for canopy cover, TRI, and elevation, predicting that bears would select for intermediate values of each of these variables. We also included greenness, all types of human disturbance, and semi-permeable barrier variables for rock/ice and water bodies. However, we prioritized accurate spatial predictions over consistency in model structure across seasons, and we removed or retained model terms depending on model performance (i.e., individual Spearman's rank correlations) in the spatial cross-validation processes described below.

2.7 | Mapping utilization distributions using simulations from fitted iSSFs

We simulated movement paths from fitted iSSFs to predict seasonal population-level UDs across the entire study area (Signer et al., 2017). We randomly sampled starting locations for the spring UD simulation from the top 40% of mapped predicted relative probabilities of use from a second-order RSF. This process captured grizzly bears' primary distribution within the mountains, foothills and mountain valleys, and their broad-scale avoidance of eastern prairies (see Appendix 1 in Data S1 for details on determining starting locations for simulated trajectories).

We simulated a separate set of habitat coefficients for each simulated bear with the "mvrnorm" function in Program R using the full variance–covariance matrices of our top models (Kerman & Gelman, 2007). This accounted for individual variability (i.e., variation from individual-level random slopes) in population-level habitat selection responses and propagated model uncertainty to our simulated movement paths (see Appendix 1 in Data S1 for more details on simulations from fitted iSSFs).

We simulated 1,500,000 paths with 4 locations per day within our study area for 68 days in the spring, 61 days in the summer, and 47 days in the fall (median season durations across all bear-years), equal to 1 year of movement. Each seasonal simulation included an equal number of paths (i.e., 750,000) for females and males. We created seasonal UDs by tallying the total number of locations that fell in each 180-m raster pixel. We then calculated annual UDs by summing the three seasonal

rasters and dividing each pixel's value by the total number of steps across all seasons. Finally, we created sex-specific seasonal and annual UDs using the same process but with simulated paths subsetted by sex.

2.8 | Validation of iSSFs

We evaluated the seasonal iSSFs using two different spatial cross-validation procedures with individual blocking (Roberts et al., 2017) that tested the ability of our models to predict grizzly bear relative use in areas where we withheld from model training (see Appendix 1 in Data S1 for details on spatial cross validation). Both procedures split the study area into six validation regions, which contained between 9% and 19% of the total locations within a season: Banff National Park west, Banff National Park east, Kananaskis, Elk Valley north, Elk Valley south, and Southeast (Figures 1 and S3). We also assessed the capacity of our UDs to predict relative use for external data by overlaying GPS location data from 30 grizzly bears in the southern portion of the study area (Elk Valley north: $n = 5$; Elk Valley south: $n = 5$; Southeast: $n = 20$) on our final sex-specific binned seasonal UDs, extracting UD bins for each location by sex, and calculating Spearman's rank correlations of area-adjusted proportions across bins for each bear.

2.9 | Assessing scenarios of human disturbance

We fit separate iSSFs to predict how current habitat selection and space use differed from a disturbance-free land-use scenario and may change under a potential future scenario with additional human disturbance. For the disturbance-free scenario, we eliminated distance to road and highway variables, mine footprints, and semi-permeable barriers for towns and highways from our simulations (see Appendix 1 in Data S1 for more details on creating disturbance scenarios). For the additional disturbance scenario, we assumed all currently proposed coal mines were constructed and towns (>100 buildings/km^2) extended their footprint outward by 500 m. This scenario is plausible in the next 25–50 years given the expansion of mining and housing developments in the study area over the last century, but it does not include potential restoration of disturbed areas.

2.10 | Predicting changes in functional connectivity

Under the additional disturbance scenario, the area in and around southeast BC's Elk Valley would experience the largest increase in human disturbance footprint in the study area, including 228 km^2 of proposed coal mines and 50 km^2 of expanded human settlement. We calculated a metric of movement success by counting the number of simulated paths that moved between locations (nodes) within high-use habitat patches in this area under each disturbance scenario (see Appendix 1 in Data S1 for details on creating nodes within high-use habitat patches across scenarios for calculating Merriam connectivity). For each scenario, we counted the number of simulated paths that traveled between any two nodes (i.e., a successful movement) for all possible pairs of nodes. Our predictions included both between- and within-patch connectivity, both of which are important for functional connectivity (Cavanaugh et al., 2014). Distances between nodes (range = 12–109 km) represented grizzly bear movements within a home range up to movements spanning roughly three (males) to six (females) annual home ranges, based on average home range sizes in the region (Graham & Stenhouse, 2014). Finally, we calculated the percent change in movement success between nodes from the disturbance-free scenario to current conditions, and from current conditions to the additional disturbance scenario.

3 | RESULTS

3.1 | iSSFs

After resampling tracks to one location every ~6 h and removing bear-seasons with <21 days of locations, our final iSSF dataset included 69,414 GPS locations from 109 bears (Table 1). We did not include distance to roads or highways in the fall model, when there was no clear pattern in selection ratios across a range of distances from these features in either sex (Figures S1 and S2). Log likelihood supported using a footprint variable over a crossing variable for mines and a crossing variable over a footprint variable for towns in all top models. Use of mine footprints in summer, lake crossings in all seasons, and town crossings in spring and summer were too rare on the landscape to fit random slopes. We only retained generalized functional response terms with broad-scale greenness, as they explained far more variation than interactions with broad-scale canopy cover and TRI. See Table S3 for the covariate structure of final seasonal iSSFs. We report fixed-effect model coefficients and 95% confidence intervals or their ranges for selected variables (see Table S4a–c and Figure S4a,b for additional coefficients, confidence intervals, and random slope standard deviations from all three seasonal models).

TABLE 1 Summary of GPS locations used in the integrated step-selection functions for 109 grizzly bears from 2000 to 2020 in the southern Canadian Rocky Mountains.

	# of locations		# of bears		Mean ± SD locations per bear		Mean ± SD days with location	
Season	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**	**Female**	**Male**
Spring	17,177	9137	52	43	330 ± 238	212 ± 153	93 ± 63	62 ± 42
Summer	15,066	6474	48	31	314 ± 209	209 ± 134	89 ± 55	59 ± 34
Fall	11,374	5552	50	27	227 ± 155	206 ± 96	66 ± 43	57 ± 27

3.1.1 | Cover, forage, and topography

Male grizzly bears selected for lower elevations than females in spring and fall (elevation × sex: β_{spring} [95% CI] = −0.40 [−0.65–−0.15], β_{fall} = 0.50 [−0.87–−0.13]) and selected for flatter terrain than females in spring (TRI_end × sex: β = −0.17 [−0.30–−0.04]; Figure S5). Both sexes selected areas with high greenness (β range, all seasons = 0.40–0.72) and low-to-intermediate terrain ruggedness in all seasons, although relative selection for greenness in both sexes was higher in spring and summer than in fall (Figure S5). Selection for high greenness in both sexes increased at higher elevations in spring and summer (greenness_end × elevation_end β range = 0.22–0.31) and increased in open areas in the summer and fall (greenness × canopy_cover_end β range: −0.25–−0.04), although this selection was not statistically significant for males in summer. Male and female bears selected low to intermediate canopy cover in all seasons (Figure S5).

3.1.2 | Movement

Nearly 89% (female = 96%, male = 74%) of all GPS locations in the final dataset used to fit iSSFs were < 20 km from the first location in that bear-year, suggesting strong range resident behavior, especially for females. We did observe obvious exploratory forays (defined as >40 km displacement) in 28 of 188 (15%) of bear-years (female = 5%, male = 31%). Accordingly, the distance to spring start variable was strongly negative for both sexes in all three seasonal models (β range = −1.11–−0.58), although male bears traveled farther from their spring starting location in spring and summer than females. Faster movements were more directional across all seasons and both sexes, as indicated by positive coefficients for the interaction between cosine turn angle and log step length (β range = 0.08–0.17), and this relationship was stronger in males than in females in summer and fall (cosine turn × angle log step length × sex: β_{summer} = 0.06 [0.02–0.09], β_{fall} = 0.06 [0.03–0.09]). Both sexes tended to move slower in areas with more rugged terrain and higher canopy cover during all seasons (Figure S6). Females moved faster at higher elevations during summer, but slower at higher elevations during fall, while elevation had little effect on male movement speed. During fall, male movement was more directional than that of females (cosine turn angle × sex: β = 0.11 [0.04–0.19]).

3.1.3 | Semi-permeable barriers and human footprint

Females avoided crossing all types of semi-permeable movement barriers more than males in all three seasons, although the difference was only statistically significant for town crossings during summer. Both sexes avoided crossing highways (β range, all seasons = −1.11–−0.58) and high elevation rocky or glaciated areas (β range, all seasons = −1.31–−0.51) during all three seasons, although male avoidance of high elevation rocky or glaciated areas was not significant in spring (Figure 3). An exponential decay with α = 0.01 (avoidance attenuation at ∼300 m from the feature) provided the best fit for "distance to highway" and "distance to road" variables. The main effects of these variables were not statistically significant on their own in any combination of season and sex. However, the degree of selection or avoidance of highways and roads in both spring and summer depended on broad-scale variation in greenness (see *Generalized Functional Responses* below; Figure 4). Both sexes avoided mine footprints in all seasons except males in the fall (β range = −1.54–0.19), but this avoidance was only statistically significant for females in summer. This lack of statistical significance was likely because mines were relatively rare on the landscape and relatively few bears encountered these features. In two cases (one female in spring and one male in fall), bears were habituated to mining activity (Figure 3).

3.1.4 | Generalized functional responses

Responses to canopy cover, greenness, roads, highways, and rock/ice barriers varied as a function of the broad-

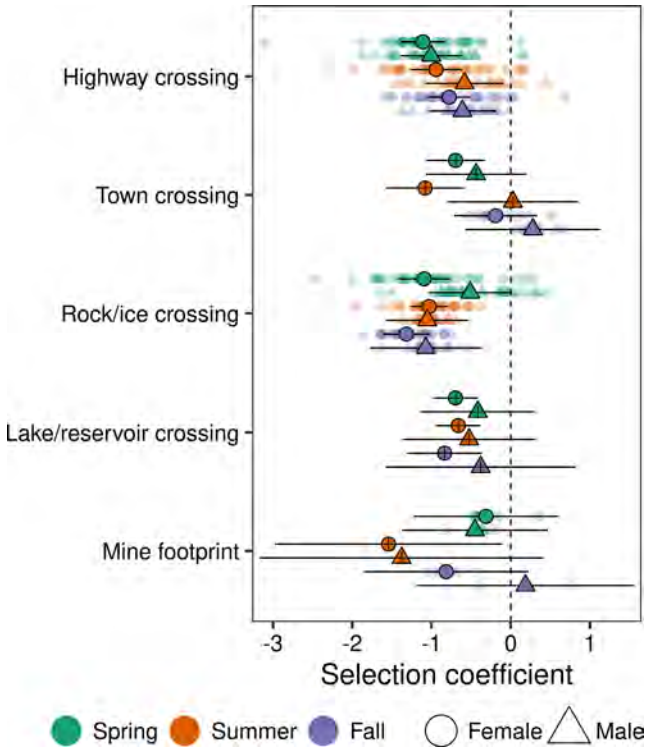

FIGURE 3 Selection coefficients, shown by season and sex, for binary semi-permeable movement barriers ("crossing") and human footprint variables for grizzly bears from integrated step-selection functions fitted to GPS location data from 109 bears from 2000 to 2020 in the southern Canadian Rocky Mountains. Transparent points show individual-level coefficients (random slopes), while points with black outlines and error bars intervals depict fixed-effects coefficients and associated 95% confidence intervals (based on fixed effects only). To calculate selection strength for males (sex = 1), we summed variable coefficients from females (sex = 0) with those from corresponding variable × sex interaction terms. Points denoted with + indicate variables without random slopes.

scale greenness in an area (Figure 4). In spring and summer, lower broad-scale greenness consistently increased the relative selection for areas near roads in both sexes (d_road_end × greenness_broad_end β range = 0.09–0.15) and increased selection for areas near highways for females (d_hwy_end × greenness_broad_end: $\beta_{spring} = 0.09$ [0.03–0.15], $\beta_{summer} = 0.09$ [0.03–0.16]). Lower broad-scale greenness was also associated with selection of lower canopy cover during summer and fall in both sexes (canopy_cover_end × greenness_broad_end: β range = 0.10–0.44) and with a selection of higher greenness in fall, although the male response in fall was not significant (greenness_end × greenness_broad_end: $\beta_{female} = -0.13$ [−0.22–−0.04], $\beta_{male} = -0.12$ [−0.25–0.01]; Figure 4). In spring and summer, bears were more likely to move across high elevation rock and ice in areas with lower broad-scale greenness (Figure S4a).

3.2 | Simulated utilization distributions from iSSFs

The annual UD under current conditions showed areas of high predicted use mostly occurred in mountain valleys in the northern portion of the study area, which included large expanses of high-elevation rock and ice (Figure 5). Predicted use was more evenly distributed across elevations in southern areas. However, males were predicted to use lower elevations than females in all seasons throughout the study area (Figures S7, S8). We calculated the areas within 50% and 95% volume contours of simulated UDs by sex as we increased the number of paths simulated and found that these areas remained relatively stable above ~500,000 paths for both sexes (Figure S9). We also found that the relative percent change in pixel values of a seasonal UD (pooled sexes) approached zero as the simulation duration increased (e.g., 10 days to 68 days for spring; Figure S10). Across seasons, an average of 0.9% (range = 0.3%–1.6%) of steps for females and 2.1% (range = 0.5%–3.7%) for males in each seasonal simulation were not realized because simulated movement paths reached the study area boundary.

Simulated and real step lengths were similar across seasons and sexes (Figure S11), but simulated movements showed fewer instances of "turning around" (turn angles in radians near π and − π) across all seasons and both sexes (Figure S12). Simulated movements also showed less directional persistence than real movements for females in all seasons, but more slightly more directional persistence than real movements for males in spring and summer. Mapping a random subset of simulated paths showed that they captured similar general patterns of use and avoidance as real GPS paths (e.g., avoidance of high-elevation rock and glaciers), but also that their movements were much less linear in valley bottoms (Figure S13). Simulating movements on a potential future landscape surrounding BC's Elk Valley with human disturbance footprints resulted in correspondingly larger areas that were avoided by bears, while the percent change in relative probability of use from a human disturbance-free landscape to current conditions highlighted the degree to which roads and highways impeded movements throughout the area (Figure 5).

3.3 | Predicted changes in functional connectivity

Predicted connectivity within and between habitat patches declined throughout much of the Elk Valley, BC area from a scenario free of human disturbance to

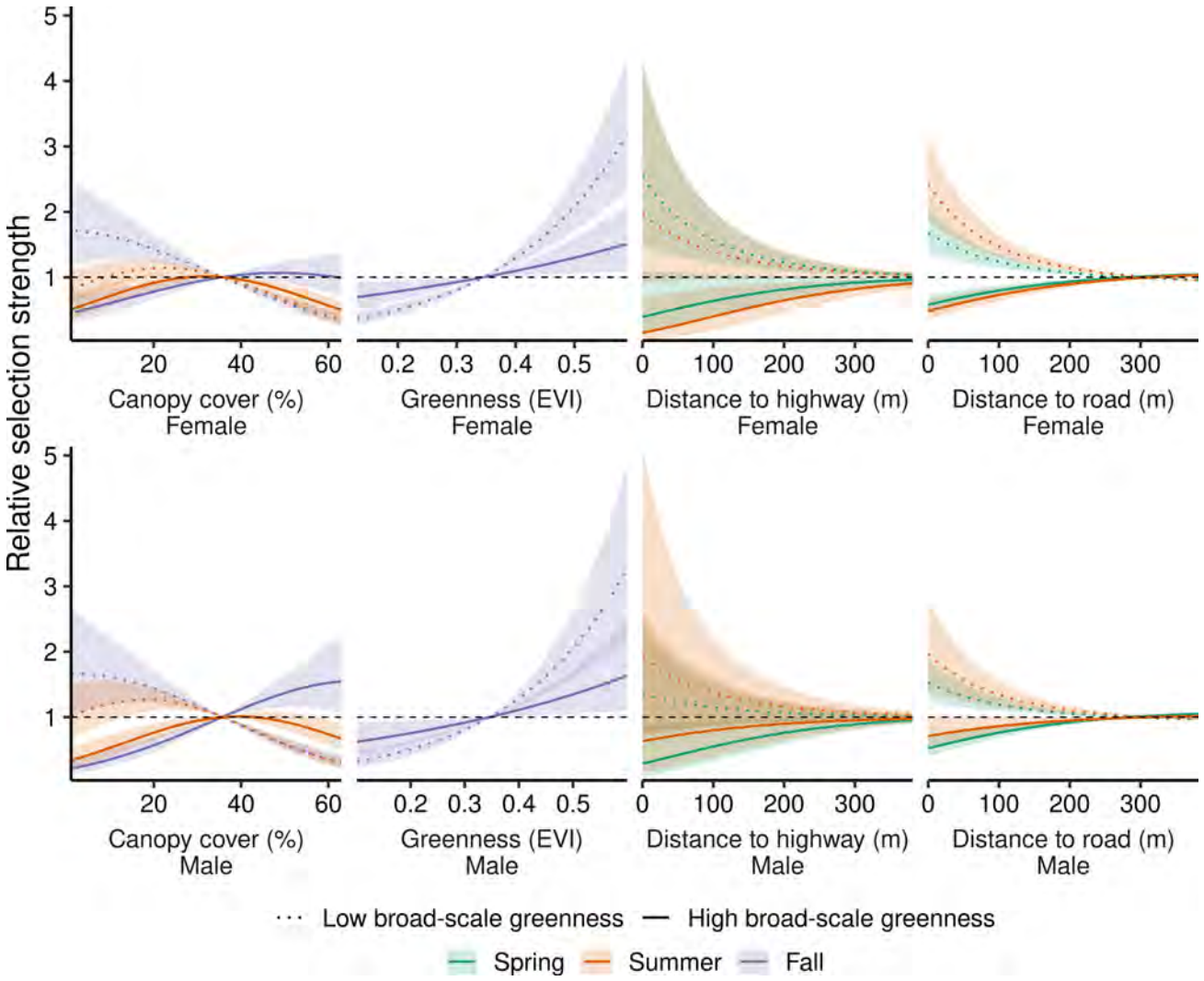

FIGURE 4 Predicted relative selection strength of grizzly bears, shown by season, across a range of habitat covariates as a function of broad-scale greenness. Broad-scale greenness is the average greenness (enhanced vegetation index) value in a circular 315-km^2 moving window and was used as a proxy for broad-scale forage availability. Predictions are from integrated step-selection functions fitted to GPS location data from 109 bears from 2000 to 2020 in the southern Canadian Rocky Mountains. Variable ranges on the x-axis include the middle 95% of values available to bears (excluding values below and above the 2.5% and 97.5% quantiles, respectively). Low and high values of broad-scale greenness used in the plot were 0.20 and 0.45, respectively. Selection strength for a covariate is relative to its average value (from the model input data) during that season, represented by the dotted line at y = 1. Shaded regions indicate 95% confidence intervals based on fixed effects only. Certain covariates do not appear in all top seasonal models. Remaining covariates in the models were held constant at their average values for making predictions.

current conditions (Figure 6). Eighty percent of edges connecting nodes showed declines in predicted connectivity across both sexes (females = 82%, males = 76%), with a mean (± SD) difference of −10.5% ± 12.8% across sexes (females = −10.9% ± 13.3%, males = −9.4% ± 12.7%) including declines for all connections that spanned highways. Predicted connectivity declined for 73% of edges (females = 73%, males = 66%) from current conditions to an additional disturbance scenario with larger town footprints and proposed coal mines, although the magnitude of losses (mean difference = −4.4% ± 8.6%; females = −5.1% ± 8.87%, males = −4.2% ± 9.3%) was generally lower than the changes from a disturbance-free landscape to current conditions. The largest predicted declines from current conditions to the additional disturbance scenario occurred in the northern end of the valley near the town of Elkford (Figure 6). We predicted slight increases in functional connectivity to some habitat patches to the east and southeast under the additional disturbance scenario, possibly reflecting simulated bears that circumvented the entire area containing additional disturbance footprints.

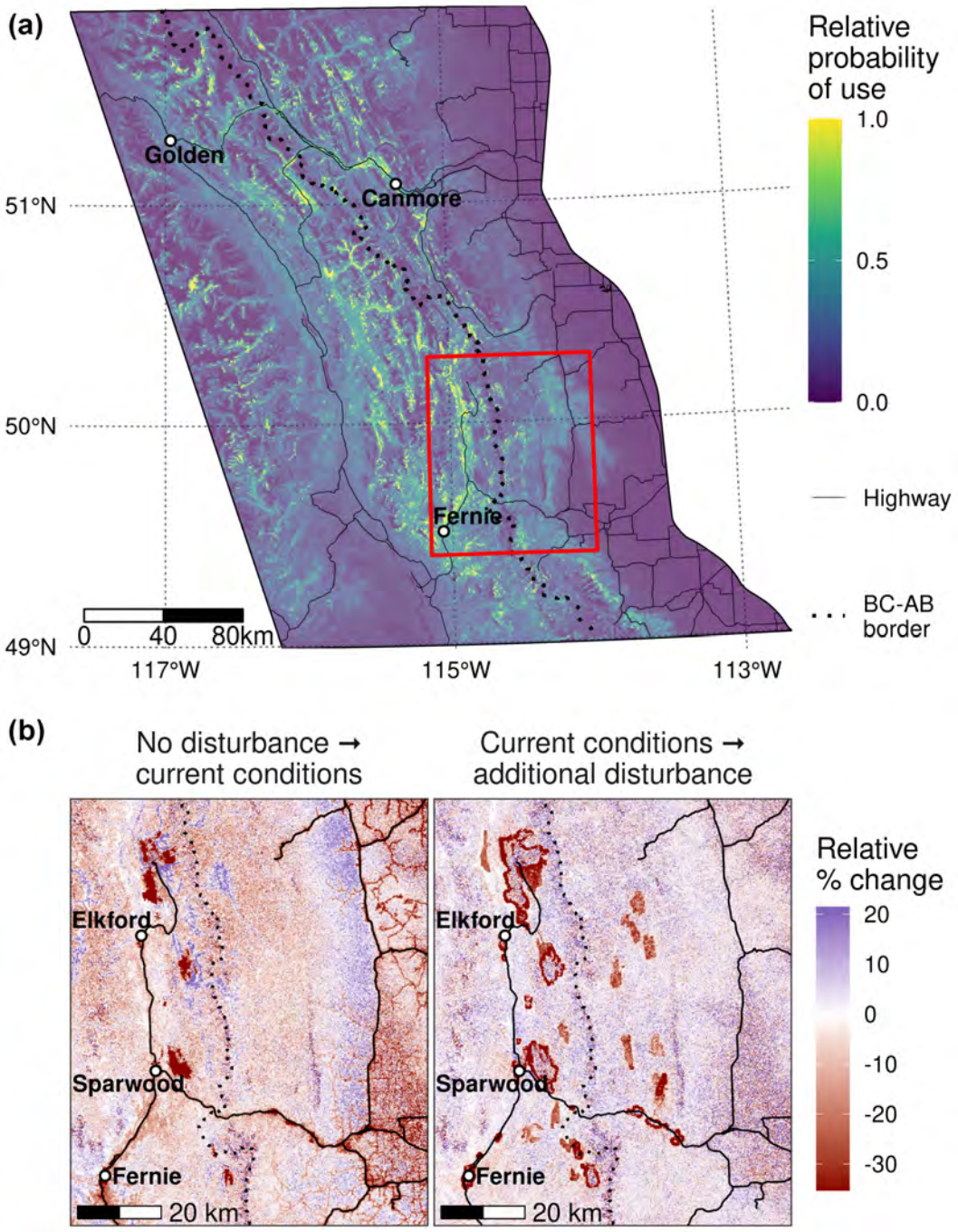

FIGURE 5 Predicted annual utilization distribution for grizzly bears under current conditions (both sexes pooled) for the entire study extent (a), estimated as the sum of three seasonal utilization distributions (spring, summer, and fall), and the relative percent change in predicted probabilities of use between a disturbance-free scenario and current conditions, and between current conditions and a scenario with additional human disturbance (b), in a subset of the study area outlined in red in (a). Annual utilization distributions were simulated from integrated step-selection functions fitted to GPS location data from 109 grizzly bears from 2000 to 2020 in the southern Canadian Rocky Mountains. We calculated the 99% quantile of raw mapped predictions in the utilization distributions and set all higher pixel values to this value to ease visual interpretation in (a). Similarly, we calculated the 1% and 99% quantiles of relative percent change and set all pixel values lower, and higher, respectively, to these values in (b). Depicted relative probabilities of use in (a) are raw pixel values rescaled to be between 0 and 1.

3.4 | Validation of iSSFs

Ranges of mean Spearman's rank correlation values (S_r) across individuals using pixel values extracted from the binned seasonal UDs at used locations for each of the six validation regions were 0.85–0.97 in spring females, 0.70–0.94 in spring males, 0.89–0.98 in summer females, 0.33–0.95 in summer males, 0.50–0.94 in fall females, and 0.66–0.92 in fall males (Figure S14; see Figure S15 for

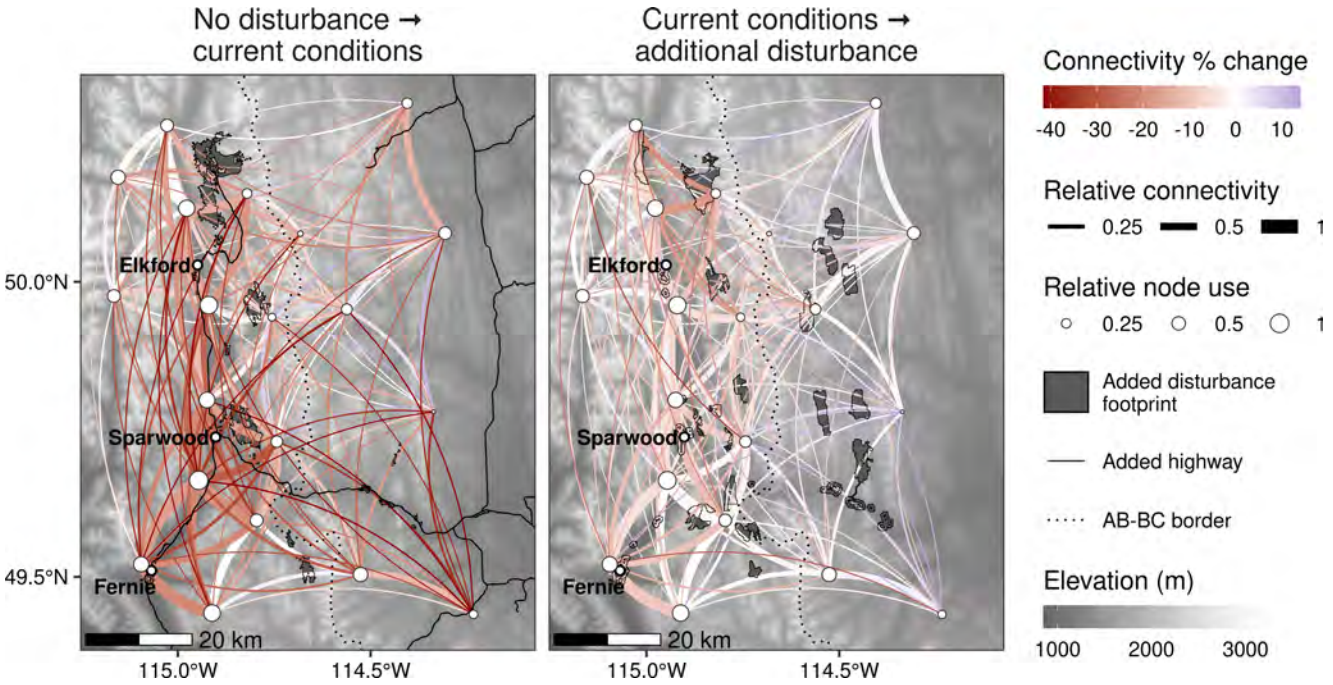

FIGURE 6 Predicted percent change in connectivity for grizzly bears (both sexes pooled) from a disturbance-free scenario to current conditions (left panel), and current conditions to a scenario with additional coal mines and expanded town footprints (right panel) in the Elk Valley, British Columbia. Nodes were sampled from the top 30% of pixel values in all three of the disturbance-free scenario, current conditions, and additional disturbance scenario annual utilization distributions, which were simulated from integrated step-selection functions fitted to GPS location data from 109 grizzly bears from 2000 to 2020 in the southern Canadian Rocky Mountains. Relative connectivity was defined as the relative number of simulated trajectories that successfully traveled between a pair of nodes in the start period for each panel. Relative node use was defined as the relative number of successful simulated trajectories whose locations fell within the intersection of a 1 km radius around the node and the habitat patch containing that node at the start period for each panel. Percent change was estimated by counting the number of simulated trajectories that successfully traveled between a pair of nodes in the start (n_{start}) and end (n_{end}) periods and calculating $(1 - n_{end}/n_{start}) \times 100$. We calculated the 1% and 99% quantiles of percent change and set all pixel values lower and higher, respectively, to these values to ease visual interpretation.

binned annual UDs). Mean S_r values were >0.70 in 14 of 18 season-region-sex combinations, with exceptions for both sexes in the Southeast region during fall, and for males in the Kananaskis and Southeast regions during summer. For each region, UHC plots depicted the degree to which models fitted using training data from all other regions predicted used habitats accurately (Figures S16a–c, S17). The models generally predicted used distributions of covariates well, with some exceptions. The spring model struggled to predict used distributions of terrain ruggedness in Elk Valley north and south, overestimated use of low elevation areas in Elk Valley north, and did not accurately predict the used distribution of greenness in the Southeast. In both summer and fall, there were mismatches in the predicted versus observed distributions for used locations for canopy cover in Banff National Park east, Elk Valley south, and Kananaskis. The fall model failed to accurately predict the used distribution for lower elevations in Banff National Park west and in higher elevations in both Elk Valley regions and Kananaskis (Figure S16c). The spring and summer models underestimated highway crossings in Banff National Park east and Kananaskis, and underestimated rock/ice crossings in Banff National Park west (Figure S17). The external validation of seasonal UDs using GPS locations from the southern portion of the study area showed better predictive performance in the spring ($S_{r\ female} = 0.82 \pm 0.20$ [SD]; $S_{r\ male} = 0.90 \pm 0.09$) and summer ($S_{r\ female} = 0.84 \pm 0.25$; $S_{r\ male} = 0.79 \pm 0.28$) than in the fall ($S_{r\ female} = 0.72 \pm 0.23$; Figure S18).

4 | DISCUSSION

We simulated individual movements from fitted iSSFs to predict habitat selection and functional connectivity for grizzly bears across a large swath of the southern Canadian Rocky Mountains and adjacent areas under three scenarios of human disturbance. Comparing movement success between and within habitat patches from simulations across these scenarios highlighted declining functional connectivity in an important movement corridor

with high bear densities and frequent human-bear conflicts. Our mixed-effects iSSFs allowed us to simultaneously estimate animal movement across a large, regional population and habitat selection responses while explicitly accounting for individual-level variation in these responses (Avgar et al., 2016; Muff et al., 2020). By simulating individual movements directly from fitted iSSFs, we predicted grizzly bear space use and connectivity that resulted from a realistic movement process.

We observed considerable variation in grizzly bear behavioral responses to varying conditions throughout our study area. For example, generalized functional responses showed that bears avoided areas near highways and roads when they had an abundance of productive vegetation within their home range, but bears whose home ranges had lower vegetation productivity strongly selected areas closer to highways and roads. The increased selection for roadsides in low productivity areas was typified by the highly protected Alberta park bears (those in the BNPW, BNPE, and KAN validation regions), where the open forest canopy along roadsides provided attractive foods such as grasses and forbs during the spring and summer and berries such as buffaloberry (*Shepherdia canadensis*) along forest edges during the summer and fall. Roadsides and nearby riparian areas were especially attractive relative to the dry pine stands and expanses of rock and ice that largely composed these landscapes. Outside of protected areas, increased use of roadsides by bears struggling to meet nutritional demands could represent an ecological trap where attractive roadside forage exposes bears to higher rates of collisions and conflicts with people (Lamb et al., 2017; Nielsen et al., 2004). These results suggest that effective conservation actions for grizzly bears in lower productivity areas may be different from those elsewhere. For example, in low-productivity areas where bears frequently use roadsides, early detection systems or personnel in vehicles with flashing lights—a practice that is common in some protected areas—could alert motorists and potentially reduce collision risk. Alternatively, habitat restoration in areas away from human infrastructure should attract bears while decreasing their exposure to risk. If grizzly bear movements and behaviors within home ranges reflect those during longer-distance movements, these targeted actions could also increase broader scale connectivity across the region.

Grizzly bears avoided crossing most human-associated features across the study area. Both male and female grizzly bears consistently avoided crossing highways in all seasons and regions, including regions such as Banff National Park West and Kananaskis, where they selected areas near roads. Comparisons of predicted space use and movement success from a disturbance-free landscape to current conditions highlighted the degree to which highways have impeded grizzly bear movements. Bears also strongly avoided moving across high-elevation rocky terrain, glaciers, and towns in all seasons. A portion of semi-permeable barrier crossings in our dataset were likely false positives due to our relocation interval of 6 h that may not have captured animals traversing around the feature despite the straight-line path between successive points intersecting these features. Therefore, we may have underestimated their avoidance of crossing some of these features. Semi-permeable barriers collectively constrained grizzly bear movements to relatively narrow corridors in some areas, such as the Elk and Bow River valleys. For example, Koocanusa Reservoir bisects 50 km of the Canadian Rocky Mountain Trench and presented a barrier that no collared grizzly bears crossed. Other large reservoirs are found throughout the grizzly bear range of British Columbia, and although bears may occasionally swim across, our analysis suggests these features create a barrier to movement. Avoidance of towns and mines was partially captured by the positive greenness coefficients, which likely contributed to the lack of statistical significance for the mine coefficients in spring and fall. Some bears used lower elevation areas in the spring (e.g., Bow River Valley) and fall (e.g., Elk Valley) compared to the summer months (Figure S8), likely in response to a combination of snowpack and forage availability (McLellan & Hovey, 2001a). Some valley bottoms are particularly attractive to bears in the fall during their fall hyperphagia period due to hunter-killed ungulate carcasses, native fruiting shrubs, residential fruit trees, and small-scale livestock producers (Lamb et al., 2017, 2023). The presence of residential attractants in towns may help explain the weak avoidance of town crossings by both sexes in the fall, increasing the risk of conflicts with humans during this period.

Any predictions of animal space use across a large area, and those in areas beyond the spatial extent of model input data, should always be interpreted with caution (Beyer et al., 2010), perhaps especially for a highly-mobile omnivore. Grizzly bears in this region are known to exhibit considerable dietary plasticity to help meet their high energetic requirements (McLellan & Hovey, 1995; Roberts et al., 2014) sometimes relying on locally abundant foods, such as fish (Mowat et al., 2013) or whitebark pine (*Pinus albicaulis*) seeds (Hamer, 2021), that are not captured by remotely-sensed GIS layers such as those used in our models. Therefore, our predictions may underestimate the relative use of certain areas that are important for grizzly bears. Despite many potential pitfalls of simulating space use for a wide-ranging generalist species, our UDs generally performed well in rigorous spatial cross-validation and external validation

(Figures S14, S16a–c, S17, S18), and they should be valuable for informing large-scale conservation planning. These validation procedures helped identify strengths and weaknesses in our iSSFs. For example, UHC plots supported the use of a quadratic term for canopy cover, as canopy cover distributions for both used locations and model predictions showed higher densities at intermediate values than the distribution for available locations (Figure S16a–c). On the other hand, UHC plots showed our models did not accurately predict the relatively high highway crossing rates in portions of Banff National Park and the Kananaskis region (Figure S17). Explicitly modeling the effects of highway crossing structures and the lack of hunting in parks might have better captured this behavior. The UD-based validation underestimated the predictive capacity of our models in some areas because we simulated UDs using annual layers from a single year (i.e., 2020) rather than simulating separate UDs for all 21 years in our study period and matching location years to simulation years in the validation. However, most combinations of season, region, and sex with poor UD-based validation (i.e., Kananaskis males) had very low sample sizes and a high proportion of bears exhibiting exploratory forays into the eastern prairies.

Our models did not account for all factors that contribute to movement and habitat selection for grizzly bears, and some variables were likely indirect proxies for habitat attributes to which bears were functionally responding. We did not explicitly incorporate mortality risk from humans, so some instances where we predicted high relative use near human disturbances may be examples of maladaptive habitat selection (Lamb et al., 2023; Northrup, Stenhouse, & Boyce, 2012). Further, we did not explicitly account for factors such as competition, mortality risk from conspecifics (Mattson et al., 1987), human attractants (Wilson et al., 2005), human recreation (Ladle et al., 2019), and habituation to humans (Herrero et al., 2005), all of which may lead to increased use of suboptimal areas (e.g., those with low greenness and in close proximity to humans). By fitting random slopes in our iSSFs and propagating uncertainty into simulations, we may have implicitly modeled some habituation to humans, such as a strong selection for mines in a small subset of bears (Figure 3). Similarly, accounting for sex in our models led to differences in predicted space use by sex, potentially capturing some behaviors associated with conspecific mortality risk (e.g., females with cubs avoiding areas frequently used by adult males).

Our simulated UDs largely represented within-home-range movements necessary to carry out daily requirements (Riordan-Short et al., 2023) rather than long-distance dispersal, which is rarely captured in animal movement data. However, given that grizzly bear dispersal in our study area primarily occurs in gradual range shifts or expansions over a period of months to years (McLellan & Hovey, 2001b; Proctor et al., 2004), some areas of high predicted use in our UDs may overlap with dispersal corridors. We suggest that future efforts explore differences in space use and functional connectivity by age class, as younger animals often inhabit riskier areas. Further, linking connectivity to demography could highlight areas with additional connectivity losses due to high mortality risk that are not fully captured by movement data alone (Vasudev et al., 2023).

Expansion of human settlements and resource extraction projects into grizzly bear movement corridors and foraging areas creates challenges for people, wildlife managers, and conservation efforts. We focused our assessment of changing space use and functional connectivity for grizzly bears on BC's Elk Valley and the adjacent eastern slopes of the Rocky Mountains in Alberta. This area has existing and proposed mining of rich metallurgical coal deposits, along with dispersed human settlements that also rely on agriculture, forestry, and recreation tourism. The area is situated where the Rocky Mountains narrow to less than 70 km, and may serve as an important north–south corridor facilitating broad-scale genetic connectivity in grizzly bears (Palm et al., 2023). Our simulations suggest that the combined effects of new coal mines and expanded human settlements would lead to further declines in local functional connectivity of grizzly bears along the length of the Elk Valley, moving some bears toward the east side of the continental divide in Alberta to an area with less productive habitat. Given the magnitude of existing connectivity declines predicted by our simulations, land managers need to consider that connectivity losses in this area could eventually limit the movements of bears from adjacent undisturbed areas that currently help avert local extirpations (Lamb et al., 2020).

Existing grizzly bear connectivity in the southern Canadian Rocky Mountains demographically supports populations, including some in the USA, that would rapidly decline without it (Lamb et al., 2023, Northrup, Stenhouse, & Boyce, 2012). Areas where bears and extensive human development (towns, transportation corridors, and agriculture) overlap can act as sink habitats where bears are not able to reproduce fast enough to offset high mortality (Nielsen et al., 2006). Consistent with past studies, our results suggest that bears are at higher risk of conflict with humans during fall, when they are more likely to visit residential areas to access high-calorie human foods prior to denning (Lamb et al., 2017). Connectivity in this region currently allows for grizzly bear population persistence in these areas through both within-home-range movement and immigration from adjacent areas (Lamb et al., 2023). This source-sink dynamic and demographic rescue has been observed

widely across our study area (Braid & Nielsen, 2015; Lamb et al., 2020; Nielsen et al., 2004; Northrup, Stenhouse, & Boyce, 2012). If future human-caused habitat alteration impedes functional connectivity to the point that dispersing animals can no longer offset in situ demographic losses, grizzly bear populations in these sink areas will decline. Grizzly bears are a wide-ranging iconic species (Steenweg et al., 2023; Tardiff & Stanford, 1998), and mitigating human disturbances that impede their movements should also improve connectivity for other wildlife species such as black bears (*Ursus americanus*), elk (*Cervus canadensis*), and wolverines (*Gulo gulo*). Conservation groups, resource companies, and municipalities can use our spatial predictions to optimize land parcel selection, inform strategic planning, protect existing movement corridors, and avoid degradation of areas where future connectivity is predicted to increase. Restoring degraded land or increasing landscape permeability using a combination of highway crossing structures and wildlife exclusion fencing could help reduce potential negative effects of future development on regional wildlife connectivity (Clevenger & Ford, 2010; Sawaya et al., 2014). Reducing grizzly bear mortality in valley bottoms through management of human attractants and coexistence programs would benefit bears and people by decreasing conflict and increasing safety (Proctor et al., 2018). Ensuring sufficient, connected valley-bottom habitat and enabling safe movement across highways, around towns, and around future developments is essential to alleviating the long-standing demographic and genetic fragmentation challenges facing grizzly bears in the southern portion of their range (Proctor et al., 2012).

AUTHOR CONTRIBUTIONS

Clayton T. Lamb, Katherine A. Zeller, and Eric C. Palm conceived the study. Eric C. Palm wrote the manuscript with help from Clayton T. Lamb. Eric C. Palm led the data analysis with help from Clayton T. Lamb and Katherine A. Zeller. Clayton D. Apps, Clayton T. Lamb, Bruce N. McLellan, Joseph M. Northrup, Michael A. Sawaya, and Jesse Whittington collected GPS location data. All authors provided valuable feedback and contributed to the final manuscript.

ACKNOWLEDGMENTS

We thank Cheryl Chetkiewicz, Tony Clevenger, Stephen Herrero, John Paczkowski and Gordon Stenhouse for sharing their grizzly bear GPS location data.

FUNDING INFORMATION

This research was supported in part by the USDA Forest Service, Rocky Mountain Research Station, Aldo Leopold Wilderness Research Institute. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or US Government determination or policy. Computational resources from the University of Montana's Computational Ecology Lab contributed to this research (NSF award numbers 2018112 and 1925267). We acknowledge support from Yellowstone to Yukon Conservation Initiative, Canadian National Program for Ecological Corridors, Nature Conservancy of Canada, Elk Valley Regional Land Trust, Habitat Conservation Trust Foundation, and Wilburforce Foundation.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data and code to run integrated step selection functions and simulate utilization distributions, along with final versions of utilization distributions by season, sex, and disturbance scenario are available for download at https://doi.org/10.5281/zenodo.15685561.

ORCID

Eric C. Palm https://orcid.org/0000-0002-5330-4804
Tal Avgar https://orcid.org/0000-0002-8764-6976
Joseph M. Northrup https://orcid.org/0000-0001-6319-4138
Julie W. Turner https://orcid.org/0000-0001-5449-5449
Jesse Whittington https://orcid.org/0000-0002-4129-7491
Erin L. Landguth https://orcid.org/0000-0002-7044-346X
Clayton T. Lamb https://orcid.org/0000-0002-1961-0509

REFERENCES

Aiello, C. M., Galloway, N. L., Prentice, P. R., Darby, N. W., Hughson, D., & Epps, C. W. (2023). Movement models and simulation reveal highway impacts and mitigation opportunities for a metapopulation-distributed species. *Landscape Ecology*, *38*, 1085–1103.

Apps, C. D., Weaver, J. L., Paquet, P. C., Bateman, B., & McLellan, B. N. (2007). Carnivores in the Southern Canadian Rockies: Core Areas and Connectivity Across the Crowsnest Highway. WCS Canada Conservation Report No. 3. Wildlife Conservation Society Canada, Toronto, Ontario.

Avgar, T., Lele, S. R., Keim, J. L., & Boyce, M. S. (2017). Relative selection strength: Quantifying effect size in habitat- and step-selection inference. *Ecology and Evolution*, *7*, 5322–5330.

Avgar, T., Potts, J. R., Lewis, M. A., & Boyce, M. S. (2016). Integrated step selection analysis: Bridging the gap between resource selection and animal movement. *Methods in Ecology and Evolution*, *7*, 619–630.

Beyer, H. L., Haydon, D. T., Morales, J. M., Frair, J. L., Hebblewhite, M., Mitchell, M., & Matthiopoulos, J. (2010). The

interpretation of habitat preference metrics under use–availability designs. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *365*, 2245–2254.

Bowne, D. R., & Bowers, M. A. (2004). Interpatch movements in spatially structured populations: A literature review. *Landscape Ecology*, *19*, 1–20.

Braid, A. C. R., & Nielsen, S. E. (2015). Prioritizing sites for protection and restoration for grizzly bears (Ursus arctos) in southwestern Alberta, Canada. *PLoS One*, *10*, e0132501.

Brooks, M. E., Kristensen, K., Koen, A. M., van Benthem, J., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*, 378–400.

Cavanaugh, K. C., Siegel, D. A., Raimondi, P. T., & Alberto, F. (2014). Patch definition in metapopulation analysis: A graph theory approach to solve the mega-patch problem. *Ecology*, *95*, 316–328.

Ciarniello, L. M., Boyce, M. S., Seip, D. R., & Heard, D. C. (2007). Grizzly bear habitat selection is scale dependent. *Ecological Applications*, *17*, 1424–1440.

Clevenger, A. P., & Ford, A. T. (2010). Wildlife crossing structures, fencing, and other highway design considerations. In J. P. Beckmann, A. P. Clevenger, M. P. Huijser, & J. A. Hilty (Eds.), *Safe passages: Highways, wildlife, and habitat connectivity*. Island Press.

Doherty, T. S., & Driscoll, D. A. (2018). Coupling movement and landscape ecology for animal conservation in production landscapes. *Proceedings of the Royal Society B: Biological Sciences*, *285*, 20172272.

Fahrig, L. (2007). Non-optimal animal movement in human-altered landscapes. *Functional Ecology*, *21*, 1003–1015.

Fahrig, L., Arroyo-Rodríguez, V., Cazetta, E., Ford, A., Lancaster, J., & Ranius, T. (2021). Landscape connectivity. In *The Routledge handbook of landscape ecology*. (pp. 67–88). Routledge.

Fieberg, J., Signer, J., Smith, B., & Avgar, T. (2021). A 'how to' guide for interpreting parameters in habitat-selection analyses. *Journal of Animal Ecology*, *90*, 1027–1043.

Gibeau, M. L., Clevenger, A. P., Herrero, S., & Wierzchowski, J. (2002). Grizzly bear response to human development and activities in the Bow River watershed, Alberta, Canada. *Biological Conservation*, *103*, 227–236.

Government of Alberta. (2022). *Alberta wildlife act. Page revised statutes of Alberta 2000 chapter W-10*. Edmonton, AB.

Graham, K., & Stenhouse, G. B. (2014). Home range, movements, and denning chronology of the grizzly bear (*Ursus arctos*) in west-central Alberta. *The Canadian Field-Naturalist*, *128*, 223–234.

Hamer, D. (2021). Use of Whitebark pine (*Pinus albicaulis*) seeds by GPS-collared grizzly bears (*Ursus arctos*) in Banff National Park, Alberta. *The Canadian Field-Naturalist*, *135*, 61–67.

Herrero, S., Smith, T., DeBruyn, T. D., Gunther, K., & Matt, C. A. (2005). From the field: Brown bear habituation to people—Safety, risks, and benefits. *Wildlife Society Bulletin*, *33*, 362–373.

Hilty, J., Worboys, G., Keeley, A., Woodley, S., Lausche, B., Locke, H., Carr, M., Pulsford, I., Pittock, J., White, J. W., Theobald, D., Levine, J., Reuling, M., Watson, J., Ament, R., & Tabor, G. (2020). Guidelines for conserving connectivity through ecological networks and corridors. Best practice protected area Guidelines Series 30:122.

Hofmann, D. D., Cozzi, G., McNutt, J. W., Ozgul, A., & Behr, D. M. (2023). A three-step approach for assessing landscape connectivity via simulated dispersal: African wild dog case study. *Landscape Ecology*, *38*, 981–998.

Kerman, J., & Gelman, A. (2007). Manipulating and summarizing posterior simulations using random variable objects. *Statistics and Computing*, *17*, 235–244.

Ladle, A., Avgar, T., Wheatley, M., Stenhouse, G. B., Nielsen, S. E., & Boyce, M. S. (2019). Grizzly bear response to spatio-temporal variability in human recreational activity. *Journal of Applied Ecology*, *56*, 375–386.

Lamb, C. T., Ford, A. T., McLellan, B. N., Proctor, M. F., Mowat, G., Ciarniello, L., Nielsen, S. E., & Boutin, S. (2020). The ecology of human–carnivore coexistence. *Proceedings of the National Academy of Sciences*, *117*, 17876–17883.

Lamb, C. T., Mowat, G., McLellan, B. N., Nielsen, S. E., & Boutin, S. (2017). Forbidden fruit: Human settlement and abundant fruit create an ecological trap for an apex omnivore. *Journal of Animal Ecology*, *86*, 55–65.

Lamb, C. T., Smit, L., Mowat, G., McLellan, B., & Proctor, M. (2023). Unsecured attractants, collisions, and high mortality strain coexistence between grizzly bears and people in the Elk Valley, southeast British Columbia. *Conservation Science and Practice*, *5*, e13012.

Lindenmayer, D. B., & Fischer, J. (2013). *Habitat fragmentation and landscape change: An ecological and conservation synthesis*. Island Press.

Matthiopoulos, J., Hebblewhite, M., Aarts, G., & Fieberg, J. (2011). Generalized functional responses for species distributions. *Ecology*, *92*, 583–589.

Mattson, D. J., Knight, R. R., & Blanchard, B. M. (1987). The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *Bears: Their Biology and Management*, *7*, 259–273.

McLellan, B. N. (2015). Some mechanisms underlying variation in vital rates of grizzly bears on a multiple use landscape. *The Journal of Wildlife Management*, *79*, 749–765.

McLellan, B. N., & Hovey, F. W. (1995). The diet of grizzly bears in the Flathead River drainage of southeastern British Columbia. *Canadian Journal of Zoology*, *73*, 704–712.

McLellan, B. N., & Hovey, F. W. (2001a). Habitats selected by grizzly bears in a multiple use landscape. *The Journal of Wildlife Management*, *65*, 92–99.

McLellan, B. N., & Hovey, F. W. (2001b). Natal dispersal of grizzly bears. *Canadian Journal of Zoology*, *79*, 838–844.

McLellan, B. N., & Shackleton, D. M. (1988). Grizzly bears and resource-extraction industries: Effects of roads on behaviour, habitat use and demography. *Journal of Applied Ecology*, *25*, 451–460.

Mowat, G., Heard, D. C., & Schwarz, C. J. (2013). Predicting grizzly bear density in Western North America. *PLoS One*, *8*, e82757.

Muff, S., Signer, J., & Fieberg, J. (2020). Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. *Journal of Animal Ecology*, *89*, 80–92.

Nielsen, S. E., Cranston, J., & Stenhouse, G. B. (2009). Identification of priority areas for grizzly bear conservation and recovery in Alberta, Canada. *Journal of Conservation Planning*, *5*, 38–60.

Nielsen, S. E., Herrero, S., Boyce, M. S., Mace, R. D., Benn, B., Gibeau, M. L., & Jevons, S. (2004). Modelling the spatial distribution of human-caused grizzly bear mortalities in the central

Rockies ecosystem of Canada. *Biological Conservation*, *120*, 101–113.

Nielsen, S. E., McDermid, G., Stenhouse, G. B., & Boyce, M. S. (2010). Dynamic wildlife habitat models: Seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. *Biological Conservation*, *143*, 1623–1634.

Nielsen, S. E., Stenhouse, G. B., & Boyce, M. S. (2006). A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation*, *130*, 217–229.

Northrup, J. M., Pitt, J., Muhly, T. B., Stenhouse, G. B., Musiani, M., & Boyce, M. S. (2012). Vehicle traffic shapes grizzly bear behaviour on a multiple-use landscape. *Journal of Applied Ecology*, *49*, 1159–1167.

Northrup, J. M., Stenhouse, G. B., & Boyce, M. S. (2012). Agricultural lands as ecological traps for grizzly bears: Agricultural lands as ecological traps. *Animal Conservation*, *15*, 369–377.

Palm, E. C., Landguth, E. L., Holden, Z. A., Day, C. C., Lamb, C. T., Frame, P. F., Morehouse, A. T., Mowat, G., Proctor, M. F., Sawaya, M. A., Stenhouse, G., Whittington, J., & Zeller, K. A. (2023). Corridor-based approach with spatial cross-validation reveals scale-dependent effects of geographic distance, human footprint and canopy cover on grizzly bear genetic connectivity. *Molecular Ecology*, *32*, 5211–5227.

Paton, R. S., & Matthiopoulos, J. (2016). Defining the scale of habitat availability for models of habitat selection. *Ecology*, *97*, 14–2241.1.

Pither, R., O'Brien, P., Brennan, A., Hirsh-Pearson, K., & Bowman, J. (2023). Predicting areas important for ecological connectivity throughout Canada. *PLoS One*, *18*, e0281980.

Proctor, M. F., Kasworm, W. F., Annis, K. M., MacHutchon, A. G., Radandt, T. G., & Servheen, C. (2018). Conservation of threatened Canada-USA trans-border grizzly bears linked to comprehensive conflict reduction. *Human-Wildlife Interactions*, *12*, 348–372.

Proctor, M. F., McLellan, B. N., Strobeck, C., & Barclay, R. M. R. (2004). Gender-specific dispersal distances of grizzly bears estimated by genetic analysis. *Canadian Journal of Zoology*, *82*, 1108–1118.

Proctor, M. F., Paetkau, D., Mclellan, B. N., Stenhouse, G. B., Kendall, K. C., Mace, R. D., Kasworm, W. F., Servheen, C., Lausen, C. L., Gibeau, M. L., Wakkinen, W. L., Haroldson, M. A., Mowat, G., Apps, C. D., Ciarniello, L. M., Barclay, R. M. R., Boyce, M. S., Schwartz, C. C., & Strobeck, C. (2012). Population fragmentation and inter-ecosystem movements of grizzly bears in western Canada and the northern United States. *Wildlife Monographs*, *180*, 1–46.

Riordan-Short, E., Pither, R., & Pither, J. (2023). Four steps to strengthen connectivity modeling. *Ecography*, *1-13*, e06766.

Roberts, D. R., Bahn, V., Ciuti, S., Boyce, M. S., Elith, J., Guillera-Arroita, G., Hauenstein, S., Lahoz-Monfort, J. J., Schröder, B., Thuiller, W., Warton, D. I., Wintle, B. A., Hartig, F., & Dormann, C. F. (2017). Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography*, *40*, 913–929.

Roberts, D. R., Nielsen, S. E., & Stenhouse, G. B. (2014). Idiosyncratic responses of grizzly bear habitat to climate change based on projected food resource changes. *Ecological Applications*, *24*, 1144–1154.

Roever, C. L., Boyce, M. S., & Stenhouse, G. B. (2008). Grizzly bears and forestry: II: Grizzly bear habitat selection and conflicts with road placement. *Forest Ecology and Management*, *256*, 1262–1269.

Sawaya, M. A., Kalinowski, S. T., & Clevenger, A. P. (2014). Genetic connectivity for two bear species at wildlife crossing structures in Banff National Park. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20131705.

Sells, S. N., Costello, C. M., Lukacs, P. M., Roberts, L. L., & Vinks, M. A. (2022). Grizzly bear habitat selection across the northern continental divide ecosystem. *Biological Conservation*, *276*, 109813.

Sells, S. N., Costello, C. M., Lukacs, P. M., Roberts, L. L., & Vinks, M. A. (2023). Predicted connectivity pathways between grizzly bear ecosystems in Western Montana. *Biological Conservation*, *284*, 110199.

Serrouya, R., Mclellan, B. N., Pavan, G. D., & Apps, C. D. (2011). Grizzly bear selection of avalanche chutes: Testing the effectiveness of forest buffer retention. *The Journal of Wildlife Management*, *75*, 1597–1608.

Signer, J., Fieberg, J., & Avgar, T. (2017). Estimating utilization distributions from fitted step-selection functions. *Ecosphere*, *8*, 1–11.

Signer, J., Fieberg, J., Reineking, B., Schlägel, U., Smith, B., Balkenhol, N., & Avgar, T. (2024). Simulating animal space use from fitted integrated step-selection functions (iSSF). *Methods in Ecology and Evolution*, *15*, 43–50.

Steenweg, R., Hebblewhite, M., Burton, C., Whittington, J., Heim, N., Fisher, J. T., Ladle, A., Lowe, W., Muhly, T., Paczkowski, J., & Musiani, M. (2023). Testing umbrella species and food-web properties of large carnivores in the Rocky Mountains. *Biological Conservation*, *278*, 109888.

Tardiff, S. E., & Stanford, J. A. (1998). Grizzly bear digging: Effects on subalpine meadow plants in relation to mineral nitrogen availability. *Ecology*, *79*, 2219–2228.

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F. M., Blake, S., Blaum, N., ... Mueller, T. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, *359*, 466–469.

Turchin, P. (1998). *Quantitative analysis of movement: Measuring and modeling population redistribution in animals and plants*. Oxford University Press.

Vasudev, D., Fletcher, R. J., Srinivas, N., Marx, A. J., & Goswami, V. R. (2023). Mapping the connectivity–conflict interface to inform conservation. *Proceedings of the National Academy of Sciences of the United States of America*, *120*, e2211482119.

Waller, J. S., & Servheen, C. (2005). Effects of transportation infrastructure on grizzly bears in northwestern Montana. *Journal of Wildlife Management*, *69*, 985–1000.

Whittington, J., Hebblewhite, M., Baron, R. W., Ford, A. T., & Paczkowski, J. (2022). Towns and trails drive carnivore movement behaviour, resource selection, and connectivity. *Movement Ecology*, *10*, 17.

Wilson, M. F. J., O'Connell, B., Brown, C., Guinan, J. C., & Grehan, A. J. (2007). Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. *Marine Geodesy*, *30*, 3–35.

Wilson, S. M., Madel, M. J., Mattson, D. J., Graham, J. M., Burchfield, J. A., & Belsky, J. M. (2005). Natural landscape features, human-related attractants, and conflict hotspots: A

spatial analysis of human–grizzly bear conflicts. *Ursus*, *16*, 117–129.

Zeller, K. A., McGarigal, K., & Whiteley, A. R. (2012). Estimating landscape resistance to movement: A review. *Landscape Ecology*, *27*, 777–797.

SUPPORTING INFORMATION

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

How to cite this article: Palm, E. C., Apps, C. D., Avgar, T., Dickie, M., McLellan, B. N., Northrup, J. M., Sawaya, M. A., Turner, J. W., Whittington, J., Landguth, E. L., Zeller, K. A., & Lamb, C. T. (2025). Changing grizzly bear space use and functional connectivity in response to human disturbance in the southern Canadian Rocky Mountains. *Conservation Science and Practice*, *7*(8), e70088. https://doi.org/10.1111/csp2.70088