Grizzly bear habitat selection across the Northern Continental Divide Ecosystem

Sarah N. Sells [a,*], Cecily M. Costello [b], Paul M. Lukacs [c], Lori L. Roberts [b], Milan A. Vinks [b]

[a] *Montana Cooperative Wildlife Research Unit, Wildlife Biology Program, University of Montana, Missoula, MT 59812, USA*
[b] *Montana Fish, Wildlife and Parks, 490 N Meridian Rd, Kalispell, MT 59901, USA*
[c] *Wildlife Biology Program, W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA*

ARTICLE INFO

ABSTRACT

Understanding habitat selection is challenging but key for species of conservation concern, including grizzly bears (*Ursus arctos*). Here we demonstrate an approach for understanding and predicting habitat use over multiple stages that test hypotheses of animal behavior, use newly gained knowledge to mechanistically simulate individual movements, translate results to predictive habitat maps, and test their predictive power across a large spatiotemporal scale. Grizzly bears in the Northern Continental Divide Ecosystem of northwest Montana served as our study system. Mechanistically modeling grizzly bear movements demonstrated that grizzly bears have highly individualistic spatial behaviors. Some individuals avoided whereas others preferred areas of vegetation green-up, terrain ruggedness, forest edge, riparian areas, building densities, and secure habitat. Such individualism supported the need for an individual-based modeling approach to understand and predict grizzly bear behavior. External validation using >375,000 GPS locations for 261 individuals over nearly 2 decades demonstrated mean Spearman rank scores of >0.90 across seasons and years, and overall scores of 1.0. The top 5 classes of our predictive habitat maps contained 73.5 % of female fixes and 83.6 % of male fixes, and the top class (comprising 10 % of mapped area) contained 25.6 % and 41.7 % of female and male fixes, respectively. Results of this research provide tools for conservation planning and serve as the basis for future grizzly bear research within our study system and beyond. Our multi-stage approach for understanding and predicting habitat use has high utility for conservation of myriad threatened species around the globe.

1. Introduction

Habitat loss and degradation are major drivers of threatened species declines globally (Ripple et al., 2014; Schipper et al., 2008). Understanding habitat selection is crucial for maintaining viable populations, assessing recovery potentials, informing population reintroductions, and mitigating human-wildlife conflicts (e.g., Johnson et al., 2004; Mladenoff et al., 1999). Conservation decisions informed by habitat selection are particularly relevant for large carnivores whose populations often span landscapes with varied uses and ownerships.

Grizzly bears (*Ursus arctos*) provide a prime example of the need for understanding habitat selection. With the arrival of Europeans, persecution and habitat loss caused grizzly bears to decline from a population of approximately 50,000 individuals to only 4 fragmented populations within the continental United States by 1975 (fws.gov). These populations have increased and expanded due to collaborative conservation efforts and protections under the Endangered Species Act. Eventual connectivity between populations is a conservation goal, as is establishment of populations in currently unoccupied recovery areas (USFWS 1993). An understanding of habitat selection by grizzly bears within existing populations is crucial for predicting potential linkage zones and suitable habitat. Today, one of the largest populations in the continental US occurs in the Northern Continental Divide Ecosystem (NCDE; Fig. 1), where population estimates exceed 1000 animals (Costello and Roberts, 2021). As this large and expanding population is likely to be a primary source for establishing connectivity to other existing or potential populations, understanding habitat selection by bears in this population is especially key.

Our objective was to identify and demonstrate a powerful method for understanding and predicting habitat use, using grizzly bears in the NCDE as a study system. Grizzly bear habitat selection has been widely studied (e.g., Mace et al., 1999; McLellan and Hovey, 2001; Milakovic

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et al., 2012; Waller and Mace, 1997). Our work built on Hooker et al. (2021) and Peck et al. (2017) who employed step selection functions to simulate bear movements. Recently, Whittington et al. (2022) used step selection and hidden Markov models to simulate grizzly bear movements and validate habitat models around the town of Canmore in Alberta, Canada. Here, we developed a multi-stage approach employing individual-based step selection functions to test hypotheses of grizzly bear behavior, mechanistically simulate individual bear movements, translate results to predictive habitat maps, and externally test their predictive power across a broad spatial and temporal scale (Fig. 2).

Habitat selection by grizzly bears is driven primarily by efforts to obtain and store energy for growth, reproduction, and hibernation, but is also modified by intraspecific social factors and human influences (Schwartz et al., 2003). We focused our analyses on landscape variables associated with these drivers and for which data were widely available (Appendix). We hypothesized that grizzly bear habitat selection involved maximizing access to foods while minimizing energy expenditure, risks from conspecifics, and exposure to humans (Table 1). We further hypothesized that trade-offs among these drivers would result in variable strengths of predictors among cohorts. We expected females would show strong selection for food-related variables to acquire energy for reproduction. Given that adult males often possess ample fat reserves and are capable of foregoing constant feeding, we expected their habitat selection would show strong relationships with variables associated with minimizing energy expenditure and exposure to humans. Finally, we expected the strength of selection for some variables would be lessened

for subordinate bears (females and subadult males), due to their need to avoid adult males.

2. Methods

2.1. Study area

Our study area comprised the NCDE Recovery Zone (RZ), the Demographic Monitoring Area (demarcating the extent of population monitoring; DMA), and a 100 km buffer zone around the RZ boundary within the US (due to lack of data for Canada), comprising an area of 133,496 km² (Fig. 1). The NCDE's historically glaciated, rugged topography consisted of forested habitats interspersed with meadows and shrublands at mid to lower elevations and alpine habitats above ~2000 m. Mountains transitioned to short grass prairie at low elevations. To the north and west, the maritime-influenced climate produced dense forest and broad-leaved shrublands. To the south and east, drier conditions produced more diffuse forests, evergreen shrublands, and prairie grasslands with distinct riparian corridors. Public lands dominated the RZ (93 %) and rest of the DMA (63 %). Towns and corporate timberlands dominated private lands to the west, while ranchlands and agriculture dominated private lands to the east and south.

2.2. GPS data

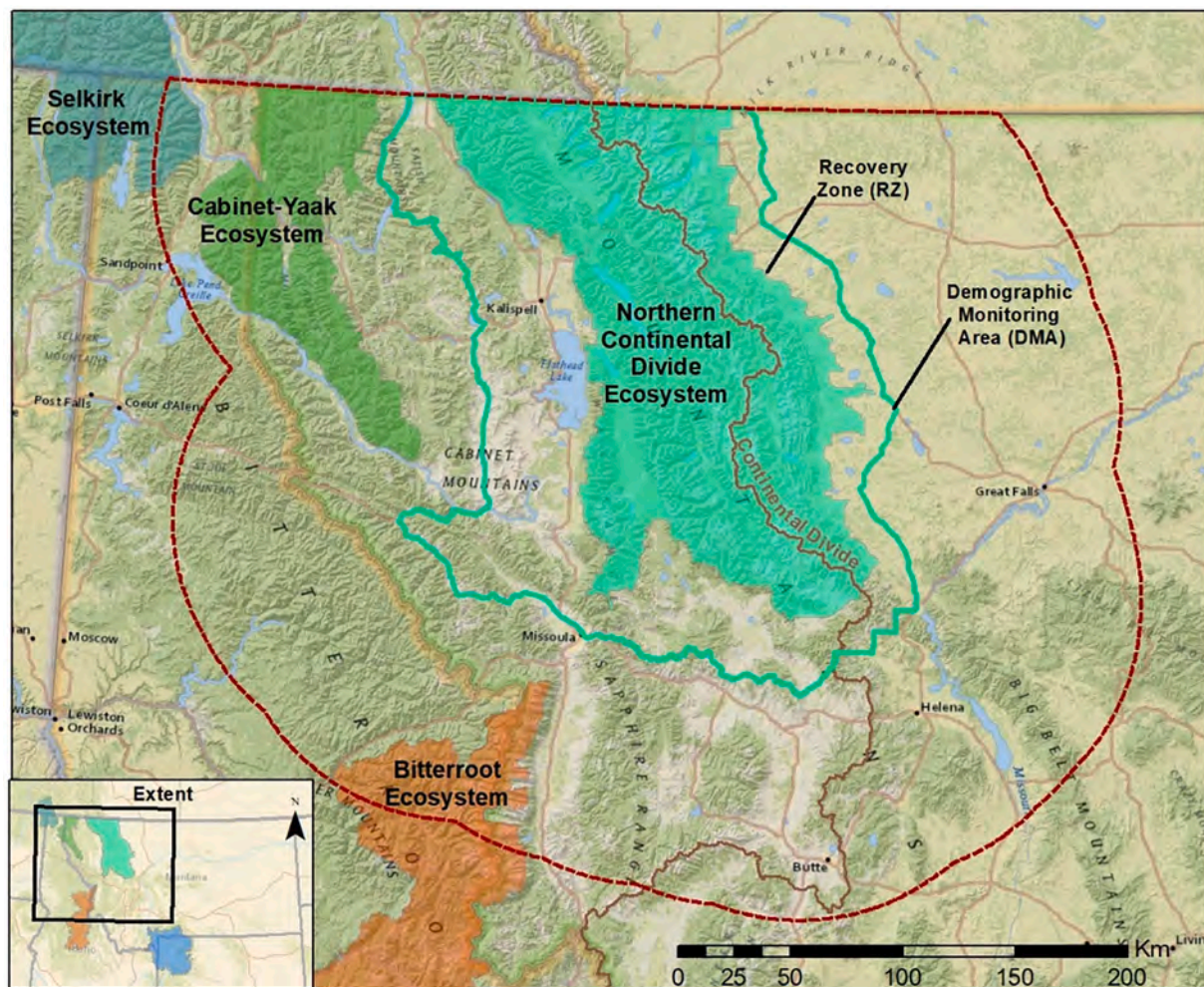To model and understand grizzly bear movements, we employed

Fig. 1. The study area comprised the NCDE RZ and DMA, and a 100 km buffer zone around the RZ boundary (red dashed line) within the US. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
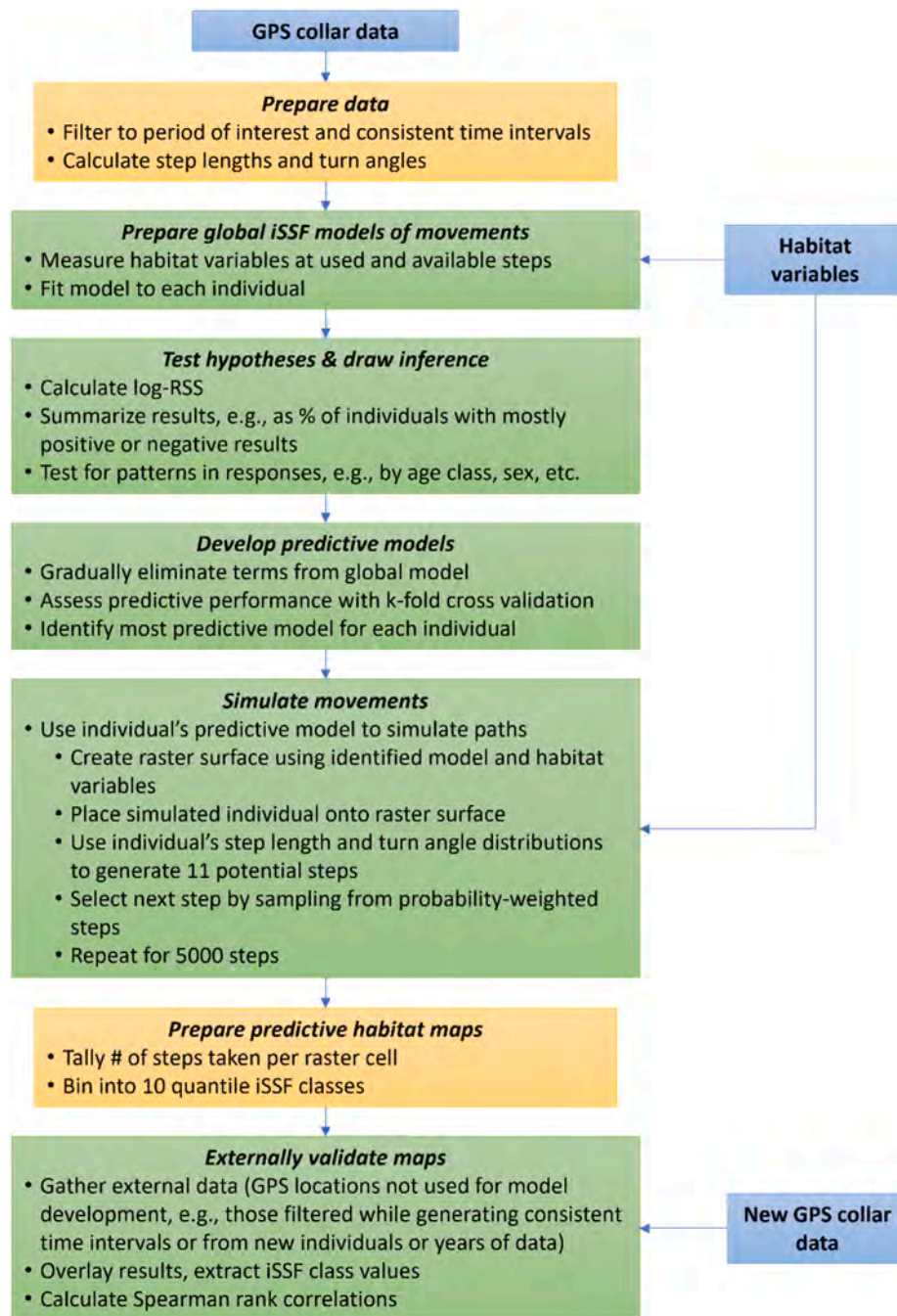
GPS collar data

Prepare data
- Filter to period of interest and consistent time intervals
- Calculate step lengths and turn angles

Prepare global iSSF models of movements
- Measure habitat variables at used and available steps
- Fit model to each individual

Habitat variables

Test hypotheses & draw inference
- Calculate log-RSS
- Summarize results, e.g., as % of individuals with mostly positive or negative results
- Test for patterns in responses, e.g., by age class, sex, etc.

Develop predictive models
- Gradually eliminate terms from global model
- Assess predictive performance with k-fold cross validation
- Identify most predictive model for each individual

Simulate movements
- Use individual's predictive model to simulate paths
  - Create raster surface using identified model and habitat variables
  - Place simulated individual onto raster surface
  - Use individual's step length and turn angle distributions to generate 11 potential steps
  - Select next step by sampling from probability-weighted steps
  - Repeat for 5000 steps

Prepare predictive habitat maps
- Tally # of steps taken per raster cell
- Bin into 10 quantile iSSF classes

Externally validate maps
- Gather external data (GPS locations not used for model development, e.g., those filtered while generating consistent time intervals or from new individuals or years of data)
- Overlay results, extract iSSF class values
- Calculate Spearman rank correlations

New GPS collar data

Fig. 2. Conceptual framework of a multi-stage method to test hypotheses of animal behavior, mechanistically simulate movements, translate results into predictive maps, and externally validate the maps across space and time. Blue boxes indicate data inputs, yellow boxes indicate data preparation steps, and green boxes indicate analysis steps. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

integrated step selection functions (iSSFs; Avgar et al., 2016, Signer et al., 2019) and data from grizzly bears monitored via GPS transmitters from 2003 to 2021 (Fig. 2). Grizzly bears were captured using culvert traps or foot-hold snares for population trend research or management purposes (i.e., after conflicts with humans). Bears were aged from a premolar tooth (Stoneberg and Jonkel, 1966) or based on tooth eruption, wear and coloring. Telonics GPS transmitters (Argos or Iridium) were placed primarily on independent-aged bears ($\geq$2 years old) including most research-captured females, a sample of research-captured males, and most management-captured bears. All grizzly bears were handled following protocols approved by the Montana Animal Care and Use Committee (Montana Fish Wildlife and Parks, 2004).

2.3. Data preparation

We used package amt (Signer et al., 2019) in Program R (R Core Team, 2022) to process grizzly bear GPS data (Fig. 2). We excluded data from denning months (Dec – Apr) and dates when bears were trapped, released, or killed. We filtered fixes to 3-hour intervals ($+/-$ 45 min) to generate movement tracks for each bear of approximately equal sampling intervals (Avgar et al., 2016). We then filtered out steps of <100 m (to omit stationary steps, as we aimed to model movements) and >15,000 m (to omit suspect steps; Appendix). We paired each used step with 10 control steps from the same starting point but with step lengths and turn angles drawn randomly from each individual's gamma and von

Table 1

Variables for grizzly bear habitat selection and associated hypotheses and predictions.

Variable	Predicted relationship & biological reasoning	Alternative prediction
Normalized difference vegetation index (NDVI)	Positive relationship (to increase access to foods)	Uncertain or negative relationship (if avoiding conspecifics, or functional response due to access to high local food availability)
Terrain ruggedness	Negative to intermediate (to balance energy expenditures versus security from humans and dominant bears)	Positive (to obtain seasonal resources or maximize security)
Distance to forest edge	Negative to intermediate (to balance security versus access to food)	Strongly negative (for security from humans or dominant bears)
Density of forest edge	Positive (to increase access to foods)	Negative (for security from humans or dominant bears)
Density of riparian	Positive (to increase access to food, thermal cover, and water)	Uncertain or negative relationship (to avoid dominant bears or if access to high local riparian densities)
Density of buildings	Negative (to decrease exposure to human risk)	Positive (to access anthropogenic food resources)
Distance to secure (unroaded) habitat	Negative (to increase security from human risk)	Uncertain or positive relationship (if functional response due to access to high local levels of secure habitat, or conditioned to human presence)

Mises distributions, respectively, as summarized from their movement data (Signer et al., 2019).

At each used and control step, we measured the normalized difference vegetation index (NDVI), terrain ruggedness, distance to forest edge, density of forest edge, density of riparian, density of buildings, and distance to secure habitat (Table 1; Appendix). We prepared each dataset in programs R (R Core Team, 2022) and ArcGIS as rasters with 300 m resolutions, chosen to balance accuracy in habitat variable representations across the large study area with computer processing needs.

We assumed that food availability is suitably indexed by NDVI measured during peak green-up (Jun 15 – Jul 15 in the NCDE; Peck et al., 2017), and used package MODIStsp (Busetto and Ranghetti, 2016) to obtain data during peak green-up each year from 2005 to 2020, which we then averaged at each raster cell (Appendix). For ruggedness, we used package Elevatr (Hollister, 2020; Z = 12) to obtain elevation data, aggregated data to 300 m cell size, and used package spatialEco (Evans, 2018) to calculate ruggedness as the vector ruggedness measure (Sappington et al., 2007). For distance to forest edge, we obtained the 2016 National Land Cover Dataset (mrlc.gov), reclassified data to forest (deciduous, evergreen, mixed forests, and woody wetlands) and non-forest (remaining classes), identified forest boundaries with the boundaries function in package raster (Hijmans, 2022), measured Euclidean distance, and converted cells within forest to negative values. Negative and positive distances thus represented areas inside and outside forest polygons, respectively. For density of forest edge, we measured forest edge km per km^2. For density of riparian, we obtained National Hydrography Datasets (usgs.gov), selected waterbody boundaries, rivers, streams, and artificial paths outside waterbody boundaries, and measured line density per km^2. We measured ruggedness, density of forest edge, and density of riparian as line density (km per km^2) with search radii of 1100 m and 1500 m from the cell centroid to represent typical daily movements for females and males, respectively (Schwartz et al., 2010). For density of buildings, we obtained the Microsoft Buildings Footprint dataset (github.com/Microsoft/USBuildingFootprints), calculated centroids of each building footprint, and measured point density per km^2. For distance to secure habitat, we obtained the

USFWS Grizzly Bear Secure Core dataset (usfws.gov), selected polygons identified as grizzly bear secure core (areas >500 m from roads on federal, state, and tribal lands), and measured Euclidean distance to these polygons (0 distance represented cells within secure cores).

2.4. Hypothesis tests

We developed models and tested our hypotheses of habitat selection for grizzly bears in the NCDE (Table 1) via iSSFs, which provide a mechanistic means for predicting space use (Fig. 2; Avgar et al., 2016). The approach compares covariates associated with animal locations and random locations accessible from each animal location. Models use a likelihood equivalent of a Cox proportional hazards model to estimate conditional selection coefficients. The iSSF has exponential form, whereby $w(x) = \exp.(x\beta)$; $w(x)$ is the iSSF score, x is a vector of habitat covariates, and β is the coefficient vector estimated via conditional logistic regression (Avgar et al., 2016; Signer et al., 2019). Higher iSSF scores indicate greater relative probabilities of selection.

We used Program R (R Core Team, 2022) and package amt (Signer et al., 2019) to fit a global iSSF model with all habitat covariates to each grizzly bear. Each habitat covariate included a quadratic term to allow for nonlinear effects (e.g., because there may be points of satiation or maximum optimality; Table 1). Grizzly bear habitat selection and movements can be influenced by numerous traits, including sex, age, reproductive status, prior experience with humans, and local habitat (Schwartz et al., 2003). Fitting the model to each bear enabled each individual's behavior to be investigated separately.

To investigate support for hypotheses, we evaluated each bear's log relative selection strength (log-RSS) across the range of values encountered for each habitat covariate (Avgar et al., 2017; Fieberg et al., 2021). To prepare log-RSS values, following Signer et al. (2019) we sequenced the covariate of interest from lowest to highest observed values (sequence length = 200) using the range of conditions encountered near the bear's track (i.e., as measured at selected and random steps). We used the bear's iSSF model and the log_rss function in package amt (Signer et al., 2019) to predict the log-RSS and its corresponding 95 % confidence interval (CI) at each value (Fieberg et al., 2021). We then plotted results as the sequence of log-RSS values, interpreted as the log-RSS between each value of location 1 relative to location 2, where both locations are assumed to be equally accessible and only differ in their values of the covariate of interest. All results were on original scales (distance in meters, density in km^2, or indices of NDVI or ruggedness) and each bear's results extended across the range of conditions encountered. We summarized each individual's response as "mostly positive" (≥50 % of the individual's 200 log-RSS values were > 0, and < 50 % of the 200 associated CI values encompassed 0), "mostly negative" (≥50 % of the individual's 200 log-RSS values were < 0 and < 50 % of the 200 CI values encompassed 0), or "mostly uncertain" (≥50 % of the 200 CI values encompassed 0).

After summarizing results, we tested for patterns in responses using chi-squared tests to determine if propensity for a positive versus negative response to each habitat variable was associated with age, management status, relocation history, and location relative to the Continental Divide. We classified bears as adults if their average age during years of collar deployment was ≥6 years, and remaining bears as subadults. We classified individuals as management bears if ever captured in response to conflicts with humans, and research bears otherwise. Bears with relocation history were relocated ≥ once. Bears were classified as "east" or "west" of the Continental Divide, and as "RZ" or "DMA," depending on where most (≥50 %) of their steps fell.

2.5. Predictive model development

We next prepared a predictive iSSF for each bear for use in simulating habitat selection (Fig. 2). We internally evaluated predictive capacity of the global candidate model for each bear (all habitat covariates

as quadratic terms) using 100 iterations of 25 % testing data and 75 % training data via k-fold cross-validation (Boyce et al., 2002). For each iteration, we used the training data subset to fit the global model, calculated resulting iSSF scores for the landscape, and used the cut function in package raster (Hijmans, 2022) to determine cut point values to bin results into 10 equal-area classes. We next used the fitted model to predict iSSF scores for the testing data subset and partitioned resulting scores into the iSSF classes using the cut point values identified in the previous step. We then calculated Spearman rank correlations to assess rank correlation between iSSF class and frequency of testing data iSSF scores within each class, where a good model fit should have monotonically increasing scores in the higher classes. We repeated these series of calculations 4 times to rotate which 25 % of the data were used for testing, and the entire process 100 times before calculating the overall mean Spearman rank correlation score for the global model's predictive capacity. We then gradually eliminated or re-added terms from the global model and determined which model formulation maximized cross-validation scores for each bear. We considered any model with a Spearman rank correlation of ≥ 0.65 to be suitable for simulations.

2.6. Simulations and predicted habitat

We used each identified iSSF to simulate movements and predict habitat selection (Fig. 2). For each bear, we created a raster surface of iSSF values using the identified model. We calculated values as $\exp.(\beta x_i)$ (Northrup et al., 2022); β is the coefficient vector of the estimated iSSF model and x_i the vector of habitat covariates of cell i. We then trimmed extremes using the 0.025 and 0.975 quantile values and normalized remaining values to a 0–1 scale (Squires et al., 2013). We next initiated each simulation from a random point within the DMA. We used the bear's observed step length and turn angle distributions to randomly select the first step length and bearing, and thereafter to generate 11 steps within the study area (Peck et al., 2017). Each step received a probability weight equal to its iSSF value divided by the sum of the 11 step values. A step was selected by sampling from the probability-weighted steps. This cycle occurred for 5000 steps, reflecting the approximate steps over three annual active seasons (May through Nov) when sampled at 3-hour intervals. We completed 100 iterations of this sequence per bear. Simulation results were the sum of times each grid cell was selected during simulations.

We prepared predictive habitat maps for males and females from simulation results. To do so, we binned results within the DMA into 10 equal area quantile classes of relative probability of use, such that lowest use was class 1 and highest use was class 10 (Morris et al., 2016). To further understand predicted habitat, we measured habitat variables for each of the class values and created boxplots of results.

2.7. External validation

Lastly, we externally validated predictive capacity of the habitat maps for each sex using GPS fixes omitted from model development (May 1 – Nov 30, 2003–2021; no filtering for step lengths or intervals applied; Fig. 2). We overlaid female and male GPS locations onto the respective habitat maps and extracted habitat values. We area-adjusted frequencies of steps (as the quantile breakpoints led to slight differences in area per class) and calculated Spearman rank correlations (Boyce et al., 2002). To determine if predictive capacity varied for results west versus east of the Continental Divide or within the RZ versus DMA, we subset location data to each area and again validated results. We next evaluated predictive capacity for 15-day intervals of the primary active season (May – Nov), for individual year, and for individuals by subsetting locations accordingly and validating results for subsets with ≥ 500 fixes. Finally, we evaluated predictive capacity for early spring (Mar 1 – Apr 30, prior to the primary active season for which models were developed) to evaluate how well these models predicted habitat related

to denning and spring habitat post den emergence.

3. Results

Data for 166 GPS-collared female grizzly bears were available (Appendix). Filtering data for iSSF analyses yielded data for 47 individuals ($n = 59,756$ fixes, mean 1271 per individual) collected over 120 bear-years (mean = 2.6 years of data/bear, range 1–6 years) from May 2004 to Sept 2020. Mean age was 8.4 years (range 1–26 years). Of the 47 females, 18 were subadults, 20 were classified as management bears, 30 were west of the Continental Divide, and 33 were primarily in the RZ. Median step length was 1167 m, and step length and turn angle distributions varied by individual (Appendix).

Data for 99 GPS-collared male grizzly bears were available, of which 20 individuals had sufficient data for analysis ($n = 16,331$ fixes, mean = 817 per individual) collected over 40 bear-years (mean = 2.0 years of data/bear, range 1–4 years) from May 2003 to June 2020. Mean age was 4.7 years (range 2–16 years). Of the 20 individuals, 16 were subadults, 11 were management bears, 18 were west of the Continental Divide, and 14 were primarily in the RZ. Median step length was 1291 m, and step length and turn angle distributions varied by individual (Appendix).

Female and male responses varied widely for every habitat variable measured (Fig. 3, Table 2, Appendix). Based on chi-squared tests, there was generally no evidence that propensity for positive versus negative responses was associated with age class, management status, relocation history, or location relative to the Continental Divide or RZ. However, females classified as management bears (p-value = 0.083) or who had a relocation history (p-value = 0.060) were more likely to react positively toward density of riparian.

Upon identifying an iSSF for each bear that maximized predictive power (Appendix), mean internal cross validation score was 0.92 for females (min 0.65, max 0.99) and 0.93 for males (min 0.83, max 0.99) after omitting one bear per sex whose score was too low to reliably predict movement (0.31 and 0.56, respectively).

Simulated steps were distributed throughout the DMA and extended into surrounding areas (Fig. 4). Areas of highest step densities were generally located within or near the RZ. Outside the RZ, movements were generally diffuse to the west and south. On the east, however, movements were concentrated within specific pathways associated with forested river corridors.

Within the DMA, greatest relative use by simulated bears often occurred in valleys and along the Rocky Mountain Front (Fig. 4; Appendix). Predicted use increased with NDVI (Fig. 5). The top ranked habitat use bin had low terrain ruggedness. Predicted use concentrated in areas closer to forest edges and of higher forest edge densities. Predicted use correlated positively with higher riparian densities, particularly for males. Density of buildings was consistently low across ranks of predicted use, as was distance to secure habitat, particularly for females.

External model validation revealed high predictive capacity (Fig. 6). Spearman rank correlation scores were 1.0 for both females and males (based on 248,731 female and 128,449 male GPS locations not used for model development, 2003–2021, representing 164 females and 97 males). Predictive capacity east ($n = 85,847$) versus west ($n = 291,333$) of the Continental Divide was 0.99 and 1.0 for females, and 0.98 and 1.0 for males, respectively. Predictive capacity in the RZ ($n = 257,927$) versus DMA ($n = 119,253$) was 1.0 and 1.0 for females, and 0.99 and 1.0 for males, respectively. Scores remained high across the primary active season (May – Nov; female mean = 0.98, male mean = 0.95). Predictive maps were less accurate but still reasonable for early spring (Mar 1 – Apr 30, $n = 30,569$ female fixes and 15,024 male locations; female mean = 0.70, male mean = 0.76). Scores were high across years of our study (female mean = 0.93, male mean = 0.90). In total, the top 5 classes of our predictive habitat maps (comprising 50 % of the DMA) contained 73.5 % of female fixes and 83.6 % of male fixes, and the top class (comprising 10 % of the DMA) contained 25.6 % and 41.7 % of female and male fixes, respectively.
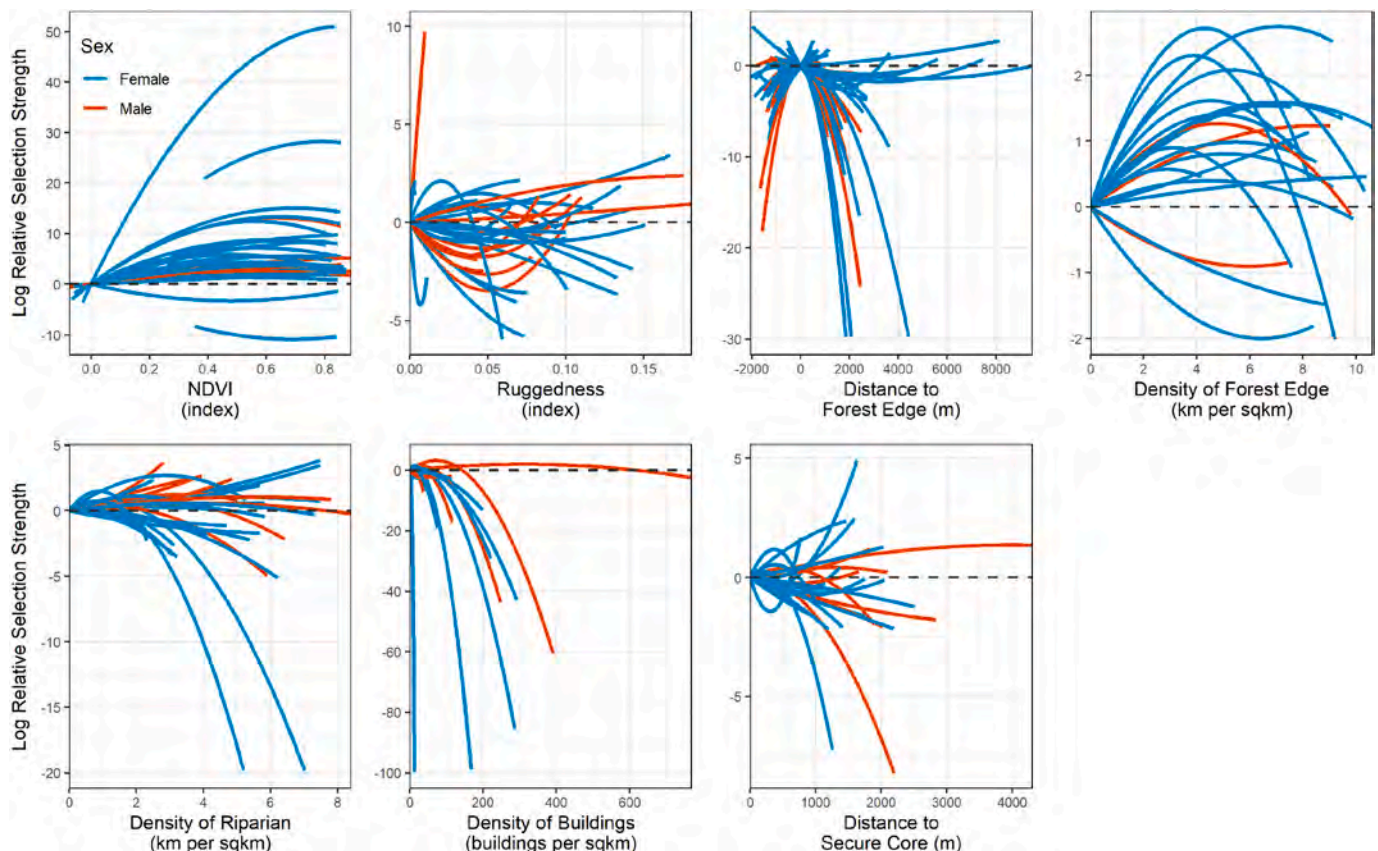
Fig. 3. Female (blue) and male (red) responses to habitat variables. Each line represents an individual's log relative selection strength (log-RSS) between each value of location 1 relative to location 2, where both locations were assumed to be equally accessible and only differed in their values of the covariate of interest. Responses were "mostly positive" (≥50 % of log-RSS values were > 0), "mostly negative" (≥50 % of log-RSS values were < 0), or "mostly uncertain" (≥50 % of CI values encompassed 0; not shown). Each line extends the range of conditions the bear encountered except where extreme values are trimmed (full plots with uncertain responses and all CIs shown in Appendix).

4. Discussion

Our method for understanding and predicting habitat use for species of conservation concern provided greater understanding of spatial behavior of our study species and a strong predictive capacity. Our multi-stage approach first tested hypotheses of animal behavior and then used the new knowledge to mechanistically simulate individual movements, translate results to predictive habitat maps, and test their predictive power across a large spatiotemporal scale (Fig. 2). In addition to serving as a case study for a means to understand and predict habitat use for species of conservation concern, this work improves understanding of how grizzly bears interact with their environments and are influenced by natural and human-related features. Simulations yielded predictive habitat maps that highlight areas likely to be repeatedly selected, and external validation demonstrated high predictive capacity across space and time.

Grizzly bears in the Northern Continental Divide Ecosystem demonstrated highly individualistic spatial behavior. Unsurprisingly for a generalist species (Schwartz et al., 2003), variation in attraction and avoidance was evident in response to every habitat measure in our analysis (Fig. 3, Table 2, Appendix). Accordingly, across individuals there was support for each of our primary or alternative hypotheses. Because our models did not include interaction terms, responses to each habitat variable should not be strictly interpreted alone. Given the vast study area, some of the individual variation in behavior is likely related to variable habitats encountered. For example, while most bears generally selected for areas with higher NDVI, they varied more widely in their response to terrain ruggedness and density of riparian. These differences may also represent functional responses to available

resources. Primary productivity and food availability may be more heavily influenced by topography and presence of streams in areas with drier versus moister conditions, and bears may respond accordingly. Our tests comparing bears east (drier) versus west (moister) of the Continental Divide did not detect this difference, but perhaps this dichotomy was too coarse. In the future, more localized studies may reveal informative differences in selection for variables as they relate to regional food economies (Mealey, 1980). The varied response to covariates also may be related to conspecific competition for space or learned behavior passed from mother to offspring. For example, as expected under an ideal free distribution (Fretwell and Lucas, 1969), some individuals may opt to maintain home ranges in seemingly sub-optimal areas (e.g., with lower NDVI values) if there are many conspecifics in otherwise more desirable areas.

Results also demonstrated likely differences in behavior between sexes. Although these differences were potentially confounded by the proportion of subadult versus adult bears represented in each group (38 % of females were subadults, versus 80 % of males), results supported our hypotheses about how habitat use may vary by sex. Female habitat selection more positively correlated with NDVI, supporting our hypothesis about the importance of food resources in female spatial behavior (Table 2). We expected this relationship would occur given the importance of body mass to sustain dependent young and hibernation (Schwartz et al., 2003). Males appeared more averse to ruggedness overall (Table 2, Fig. 5), which we hypothesized may be an outcome of attempts to reduce energy expenditure given their larger body masses. Indeed, Carnahan et al. (2021) found that grizzly bears use less steep slopes and reduce speed on steep terrain to conserve energy.

As hypothesized, grizzly bears in the NCDE, and females in

Table 2

Percentage of individuals ($n = 47$ females and 20 males) responding to habitat variables as "mostly positive" (≥ 50 % of log-RSS values were > 0 and < 50 % of the associated CI values encompassed 0), "mostly negative" (≥ 50 % of log-RSS values were < 0 and < 50 % of CI values encompassed 0), or "mostly uncertain" (≥ 50 % of CI values encompassed 0).

Variable	Trend for females (%)			Trend for males (%)		
	Negative	Positive	Uncertain	Negative	Positive	Uncertain
NDVI	4.3	59.6	36.2	0.0	30.0	70.0
Ruggedness	29.8	19.1	51.1	40.0	20.0	40.0
Distance to forest edge	72.3	6.4	21.3	45.0	5.0	50.0
Density of forest edge	4.3	36.2	59.6	5.0	10.0	85.0
Density of riparian	23.4	27.7	48.9	5.0	50.0	45.0
Density of buildings	23.4	8.5	68.1	30.0	20.0	50.0
Distance to secure habitat	27.7	12.8	59.6	20.0	20.0	60.0

particular, were generally attracted to the interface of forested and non-forested areas (Fig. 5, Table 2). Females may prefer these areas to meet energetic needs and protect cubs if, as hypothesized, forest edges contain more diverse foods than interior forest and offer security relative to open areas. Similarly, grizzly bears elsewhere have been observed to select for forest edge (Blanchard, 1983; Frąckowiak et al., 2014), areas transitional from shrub to conifer (Stewart et al., 2013), and clearcuts edges (Nielsen et al., 2004). We do not expect all forest edge to be of equal use to bears, however; given that much of the NCDE is publicly owned, many forest edges interface with other natural areas. Where humans predominate, particularly beyond the DMA, we expect forest edge to be of less utility when interfacing with anthropogenic developments.

Male grizzly bears were often attracted to riparian areas (Fig. 5; Table 2). This supports the hypothesis that males may select these areas for their productivity, cover from humans, and thermal regulation. In contrast, nearly a quarter of females had mostly negative responses to density of riparian (Table 2). This aligns with existing evidence that to protect cubs, females segregate from males (Ciarniello et al., 2007), use different areas of the landscape (Elfström et al., 2014), and avoid concentrations of other bears (Suring et al., 2006). Interestingly, females classified as management bears and with relocation histories positively selected for riparian areas, suggesting riparian habitat may provide security for bears aversely conditioned to humans. Alternatively, most human settlement, and thus management captures, occurred in lower elevations, where riparian areas may encompass the most abundant cover and food resources.

Males and females showed mostly similar overall responses to human-related habitat variables (Fig. 3, Table 2). Most bears avoided areas of greater building densities and bears exposed to higher densities had highly negative responses. The handful of individuals with mostly positive responses showed weak selection and experienced only low building densities. Positive selection for human developments may occur during years or seasons of low food quality or availability, as found for black bears (Johnson et al., 2015).

At least some individuals were averse to areas farther from secure habitat (Fig. 3, Table 2). For females in particular, habitat predicted to be of higher use was closer to or within secure habitat (Fig. 5). Because secure habitat accounts for absence of roads, these results likely demonstrate some individuals' avoidance of roads and human activity (Mace et al., 1996). In contrast, the overall weak response to secure habitat by males likely reflects the generally larger movements and larger home ranges used by males (Schwartz et al., 2010), which may inhibit the ability by at least some individuals to consistently remain close to secure habitat. Given that much of the RZ is secure habitat protected as wilderness or specifically to enhance grizzly bear use, we suspect the importance of such areas may be further enhanced beyond the RZ where bears encounter less secure habitat.

Our individual models and habitat maps had high predictive capacity based on external validation using >375,000 grizzly bear locations for 164 females and 97 males (Fig. 6), despite inevitable modeling assumptions. For example, we assumed that habitat variables were static

temporally; however, predictive capacity was high across our nearly 20-year study. Pooling data for each bear assumed that an individual's movement behaviors were consistent across years. We expect individuals alter spatial behaviors to some extent as they age and learn about their surroundings, or when accompanied by dependent young, and this likely underlies the more variable individual validation performances. The predictive habitat maps also assume that our sample of modeled females and males was representative of the population and that the included habitat variables suitably explained movement decisions. Our sample of research-captured bears was designed to be representative of the population. Although bears captured in conflict situations represented a biased sample, inclusion of these bears enabled us to estimate habitat selection across a wider range of human influences. Additionally, our use of steps ≥ 100 m apart to develop models focused on movements rather than stationary states; however, resulting habitat maps remained predictive of all external grizzly bear locations available, including those < 100 m apart.

The predictive habitat map indicated that highly selected habitat was distributed throughout the RZ and was present across large areas outside of the RZ. This supports previous analyses indicating full occupancy by reproductive females within DMA management units (Costello and Roberts, 2021). In most of the ecosystem, habitats predicted to be selected and avoided by grizzly bears were heavily interspersed, substantiating the value of the RZ as core grizzly habitat and providing evidence of efficacy of habitat protections, like access management. More contiguous areas of highly selected habitat occurred in large valleys, often coincident with human settlement, indicating grizzly bears and humans likely selected for similar landscape characteristics, i.e., less rugged, more productive sites. Areas of low-density, rural human development often provide both natural and anthropogenic foods for grizzly bears. Some bears make use of these resources, often by shifting to a nocturnal activity pattern when human activity is high (Lamb et al., 2020). Nonetheless, our analyses suggested a limit to this overlap between grizzly bears and humans. Some of the more contiguous areas predicted to be highly avoided by bears were associated with the highest human densities, such as Kalispell, a city of >25,000 people (census. gov). Other more contiguous areas of predicted avoidance were characterized by a lack of forest cover, like open prairie habitat to the east of the NCDE. Even in these human-developed and prairie areas, however, some networks of selected habitat occurred, primarily near riparian corridors.

Large landscape mapping based on movement decisions by actual bears may prove valuable for informing conservation decisions. For example, site-specific predictions of habitat use could help identify areas for conservation easements on private lands or placement of crossing structures across high-volume roads. Habitat maps could also help identify how to mitigate negative impacts on grizzly bear habitat use from development, recreation, or vegetation management. With the availability of these predictions over a vast landscape, like the NCDE, maps like these could also be used to help evaluate the cumulative impacts of individual actions. Finally, maps can be re-evaluated in future years as new data become available and updated via new simulations as
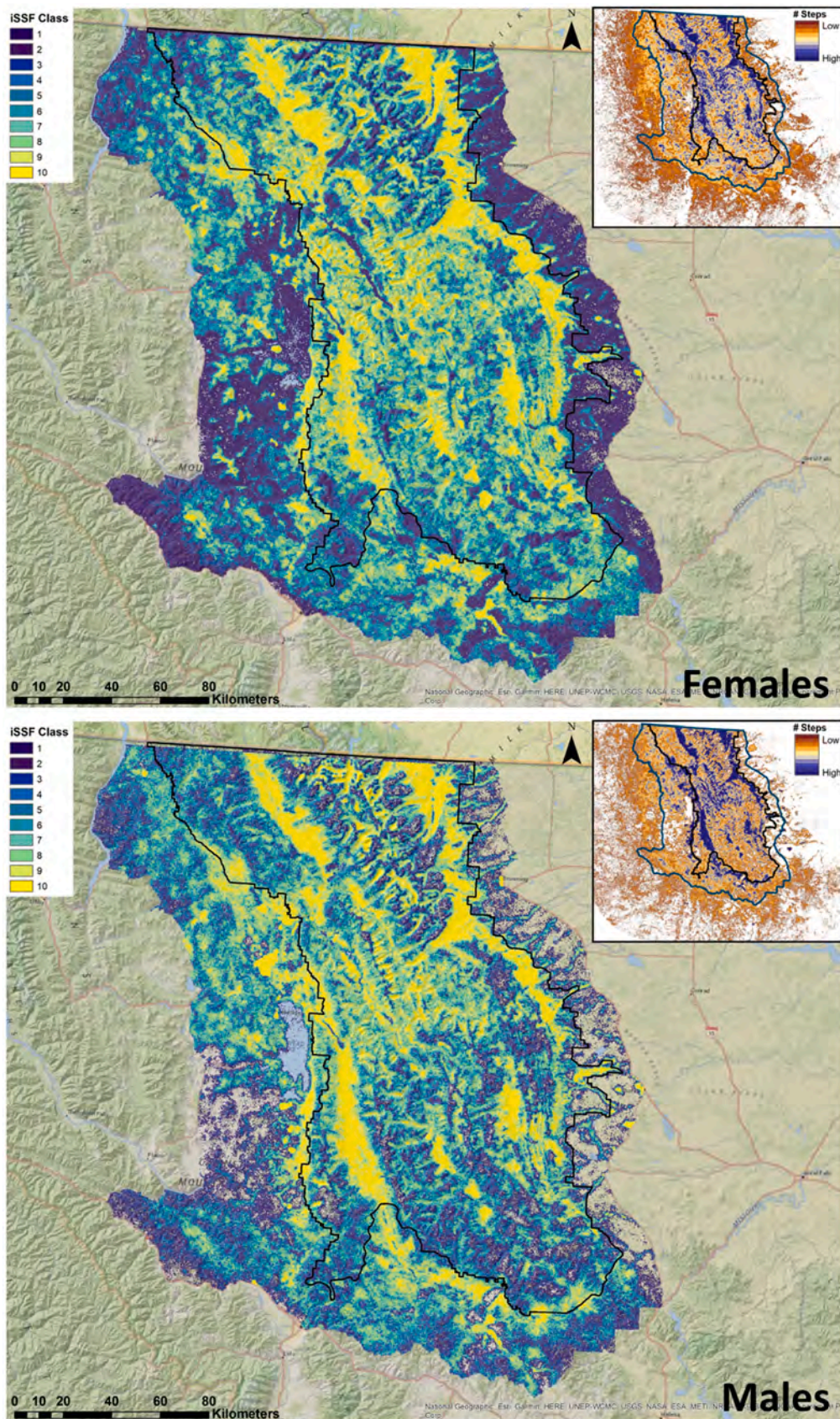
Fig. 4. Predictive habitat map for females (upper panel) and males (lower panel). The upper right inset maps reveal the number of times each cell was chosen during simulated movements (see Appendix for larger versions). Values in each main panel represent the quantile-binned relative habitat use values, as summarized within the DMA where simulated movements originated.
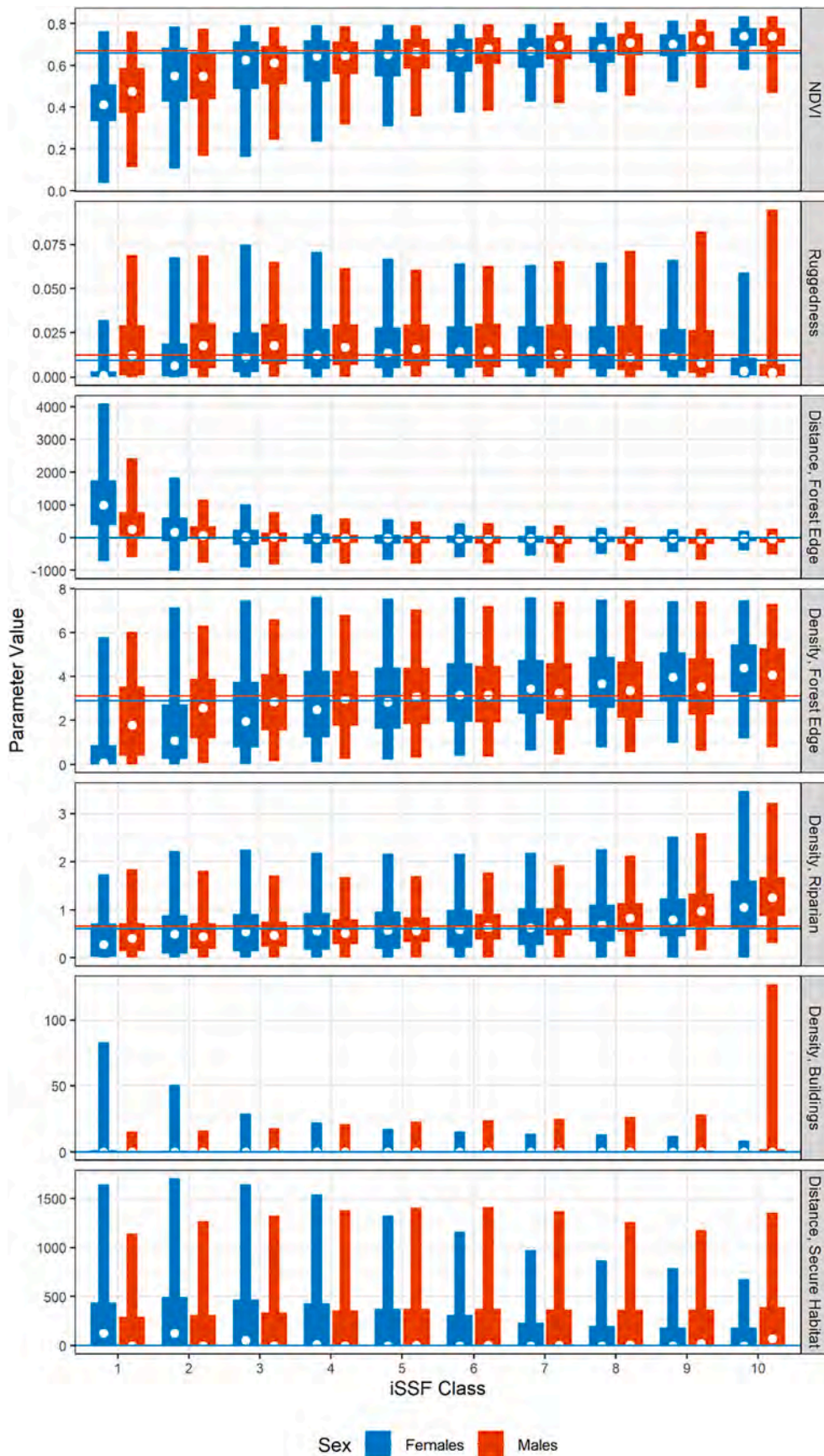
Fig. 5. Summarized cell values for habitat variables as measured within each of the 10 quantiles of predicted habitat use within the NCDE DMA (Fig. 4). White dots are median values, boxes are 50 % interquartile ranges, and thin lines extend to the 95 % values. Horizontal lines indicate median values available on the landscape (these slightly differ by sex for variables calculated within mean daily movement distances).
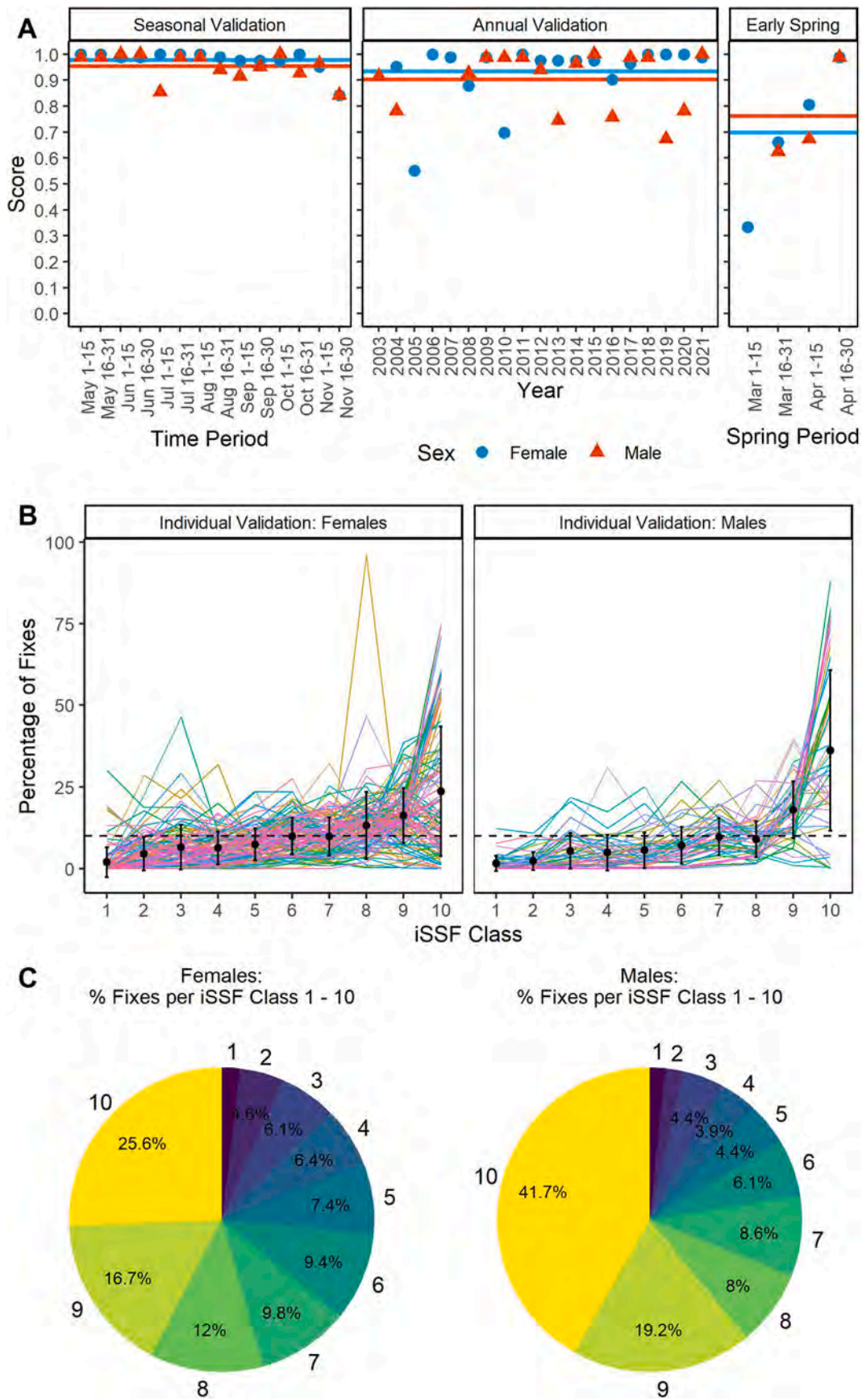
Fig. 6. External validation of predictive habitat maps based on >375,000 grizzly bear fixes for 261 individuals: Spearman rank correlation scores for 15-day intervals of the active season, individual years, and early spring (Panel A; horizontal lines indicate means); percentages of fixes in each iSSF class (1−10) for individuals (Panel B; each line represents one bear); and combined percentages of fixes in each iSSF class (Panel C).

future conditions change.

Our approach provides a powerful way to understand and predict habitat use for species of conservation concern, following a multi-stage method to test hypotheses of animal behavior, mechanistically simulate movements, translate results into predictive maps, and externally validate the maps across space and time. Applying this approach to our study system contributed knowledge about grizzly bear space use and predictive habitat maps. Our approach has high utility for conservation of myriad threatened species around the globe, and simultaneously provides a strong foundation for future research. For example, predictive models developed from this approach can be used to further simulate potential corridors among populations, and to test external predictive capacity for other populations. Such efforts would be particularly useful for conservation planning, such as for highway or railway crossing structures and areas to target for further habitat protections.

Glossary

DMA	demographic monitoring area for grizzly bears
iSSF	Integrated Step Selection Function
iSSF score	the score derived from the iSSF based on conditional selection coefficients for each habitat variable and the habitat variables encountered at the site
iSSF class	a factor between 1 and 10, representing relative probability of use, such that lowest use is class 1 and highest use class 10
Log-RSS	Log relative selection strength, i.e., the relative selection strength between each value of location 1 relative to location 2, where both locations are assumed to be equally accessible and only differ in their values of the covariate of interest
NCDE	Northern Continental Divide Ecosystem for grizzly bears
NDVI	normalized difference vegetation index
RZ	recovery zone for grizzly bears
Secure core	areas >500 m from roads on federal, state, and tribal lands

Impact statement

Mechanistically modeling grizzly bear movements provided tools for conservation planning and a basis for future research.

Statements

- The work is all original research carried out by the authors.
- All authors agree with the contents of the manuscript and its submission to the journal.
- No part of the research has been published in any form elsewhere.
- The manuscript is not being considered for publication elsewhere.
- Any research in the paper not carried out by the authors is fully acknowledged in the manuscript.
- All sources of funding are acknowledged in the manuscript, and authors have declared any direct financial benefits that could result from publication.
- All appropriate ethics and other approvals were obtained for the research. Specifically, all grizzly bears were handled following protocols approved by the Montana Animal Care and Use Committee (Montana Fish Wildlife and Parks, 2004. *Biomedical protocol for free-ranging Ursidae in Montana: black bears (Ursus americanus) and grizzly bears (Ursus arctos horribilis): capture, anesthesia, surgery, tagging, sampling, and necropsy procedures.*)

CRediT authorship contribution statement

Sarah Sells, Cecily Costello, and Paul Lukacs conceived the ideas and designed methodology; Cecily Costello, Lori Roberts, and Milan Vinks collected the data; Sarah Sells analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109813.

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