Grizzly bear movement models predict habitat use for nearby populations

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ABSTRACT

Conservation planning and decision-making can be enhanced by ecological models that reliably transfer to times and places beyond those where models were developed. Transferrable models can be especially helpful for species of conservation concern, such as grizzly bears (*Ursus arctos*). Currently, only four grizzly bear populations remain in the contiguous United States. We evaluated transferability of previously derived individual-based, integrated step selection functions (iSSFs) developed from GPS-collared grizzly bears in the Northern Continental Divide Ecosystem by applying them within the nearby Selkirk (SE), Cabinet-Yaak (CYE), and Greater Yellowstone Ecosystems (GYE). We simulated 100 replicates of 5000 steps for each iSSF in each ecosystem, summarized relative use into 10 equal-area classes for each sex, and overlaid GPS locations from bears in the SE, CYE, and GYE on resulting maps. Spearman rank correlations between numbers of locations and class rank were ≥ 0.96 within each study area, indicating models were highly predictive of grizzly bear space use in these nearby populations. Assessment of models using smaller subsets of data in space and time demonstrated generally high predictive accuracy for females. Although generally high across space and time, predictive accuracy for males was low within some watersheds and in summer within the SE and CYE, potentially due to seasonal effects, vegetation, and food assemblage differences. Altogether, these results demonstrated high transferability of our models to landscapes in the Northern Rocky Mountains, suggesting they may be used to evaluate habitat suitability and connectivity throughout the region to benefit conservation planning.

1. Introduction

Predictive models are most useful for conservation when developed through rigorous scientific methodology and when their accuracy and robustness has been validated (Chivers et al., 2014; Roberts et al., 2017; Tredennick et al., 2021). Commonly, model performance is evaluated through *k*-fold cross-validation (i.e., by repeatedly splitting data into *k* testing versus training sets) or external validation (i.e., holding back a test dataset from model development; Boyce et al., 2002; Tredennick et al., 2021). However, empirical models are generally most reliable for the time and location of data used to fit the model. It is less common that model transferability (i.e., accuracy in predictions beyond the spatio-temporal scale of the underlying data; Yates et al., 2018) is tested against

different times or places, commonly in part because of a lack of data to do so (Roberts et al., 2017; Wenger and Olden, 2012; Yates et al., 2018). Evaluation of model transferability can entail data that were not used for model development, including data from alternate timeframes and entirely different geographic areas. A model that is informative for conservation decisions and that can be accurately transferred to such broader contexts has potential utility for conservation.

Conservation of at-risk species, such as grizzly bears (*Ursus arctos*), demands reliable and accurate ecological models because inaccurate predictions and knowledge may contribute to the loss of populations or species. Over the past century, persecution and habitat loss led to near extirpation of grizzly bears throughout most of their range in the continental United States (fws.gov/species/grizzly-bear-ursus-arctos-horri

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bilis; Schwartz et al., 2003; USFWS, 2022). By the 1970s, only a few fragmented populations remained, from a previous population numbering approximately 50,000 individuals. Given threats facing the remnant populations, grizzly bears in the continental U.S. were listed as Threatened under the Endangered Species Act in 1975. Six recovery zones, located in different ecosystems, were established in the 1990s (Fig. 1), and populations slowly increased in four of these areas. Recent numbers included >1000 individuals each in the Northern Continental Divide Ecosystem (NCDE; Costello and Roberts, 2021) and Greater Yellowstone Ecosystem (GYE; Haroldson et al., 2022), >44 individuals on the U.S. side of the Selkirk Ecosystem (SE; Kasworm et al., 2021b), and >50 individuals in the Cabinet-Yaak Ecosystem (CYE; Kasworm et al., 2021a; Kendall et al., 2016). However, no resident grizzly bears are known to occupy the North Cascade (NCE) or Bitterroot Ecosystems (BE).

To better understand habitat selection by grizzly bears, Sells et al. (2022) developed and validated individual-based integrated step-selection functions (iSSFs) for 65 grizzly bears monitored in the NCDE (including 19 males and 46 females). Step-selection functions, developed from global positioning system (GPS) location data, are highly versatile models that can be used to study and predict habitat selection, movement corridors, dispersal, and human-wildlife interactions (Fortin et al., 2005; Thurfjell et al., 2014). Sells et al. (2022)'s models involved

variables that could be measured across a large landscape and were previously identified as important to habitat selection by this generalist omnivore (Peck et al., 2017; Schwartz et al., 2003). External validation with data omitted from model development demonstrated that the models were highly predictive of habitat use within the NCDE (Sells et al., 2022), but transferability was unknown.

Our objective was to build on Sells et al. (2022) to evaluate the transferability of their models to a larger landscape spanning multiple ecoregions. If the NCDE models could be accurately transferred to nearby populations, this would demonstrate reliability of applying the models to predict habitat use for nearby areas with few or no data, including potential connectivity corridors between populations or in uninhabited areas like the BE or NCE. We therefore simulated movements within the SE, CYE, and GYE using the 65 models Sells et al. (2022) developed from NCDE bears, summarized results to estimate relative habitat selection, and assessed model transferability over space and time using location data for bears in the SE, CYE, and GYE.

2. Methods

2.1. Study area

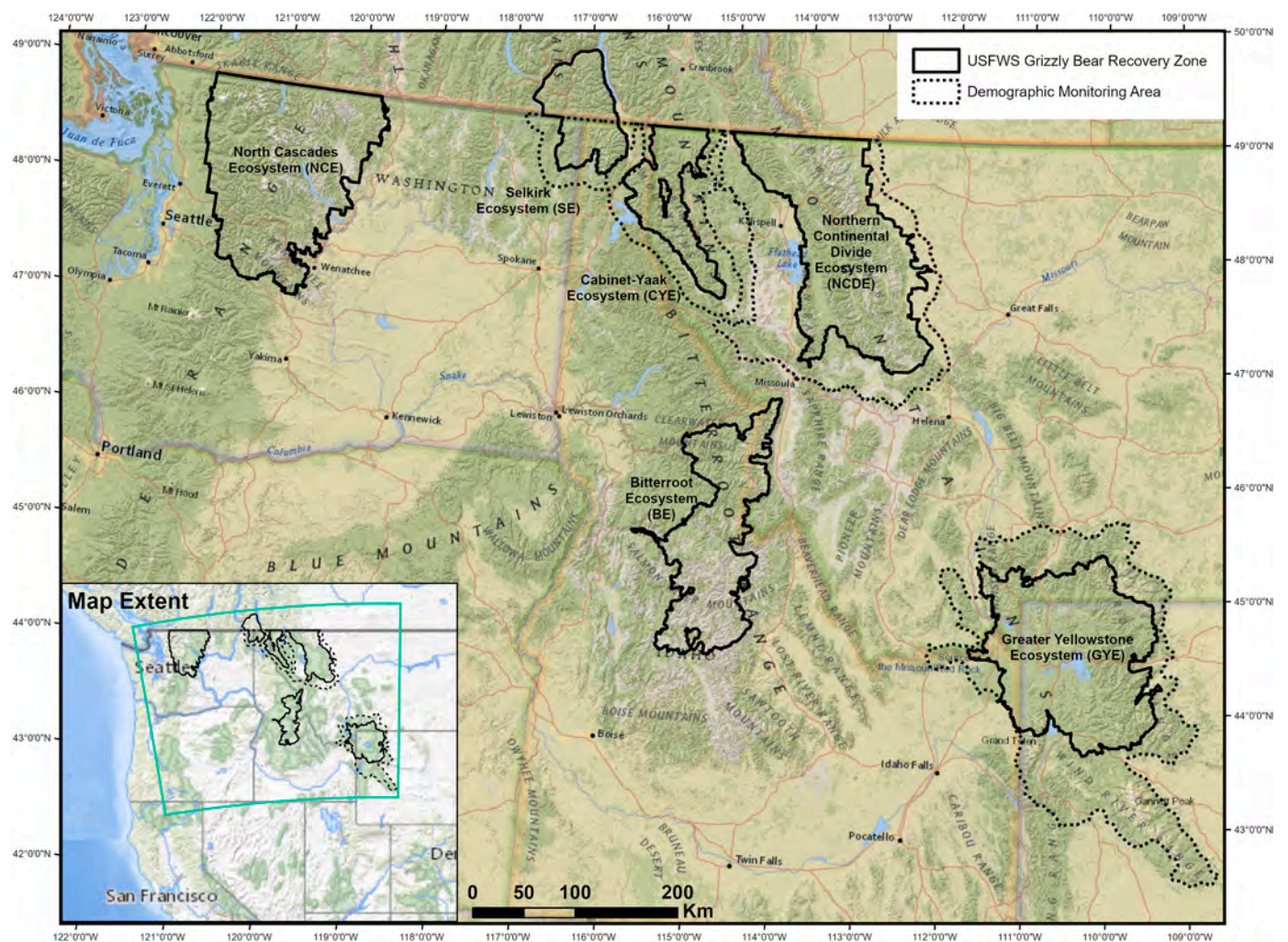Our study area included the NCDE, SE, CYE, and GYE, located in

Fig. 1. Study areas were the four Recovery Zones currently occupied by grizzly bears in the U.S. Northern Rocky Mountains and their surrounding Demographic Monitoring Areas (DMA) or 10-mile buffers, including the Northern Continental Divide Ecosystem (NCDE), Selkirk Ecosystem (SE), Cabinet-Yaak Ecosystem (CYE), and Greater Yellowstone Ecosystem (GYE). Two additional ecosystems (the North Cascades and Bitterroot) had no known populations. Basemap credit: National Geographic World Map; Sources: Esri, HERE, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS User Community.

Washington, Idaho, Montana, and Wyoming, USA (Fig. 1). Location data used to create the 65 grizzly bear iSSFs (Sells et al., 2022) were collected from bears outfitted with GPS collars in and around the NCDE Recovery Zone (RZ), primarily within the 42,600-km^2 Demographic Monitoring Area (DMA; Costello et al., 2016). GPS location data for grizzly bears for the present study were collected within the 49,900-km^2 DMA for the GYE (IGBST, 2012), within the 6325 km^2 area encompassed by the SE RZ and a 10-mile buffer (Kasworm et al., 2021b), and within the 14,800 km^2 area encompassed by the CYE RZ and a 10-mile buffer (Kasworm et al., 2021a).

Our study area was within the Rocky Mountains but spanned multiple ecoregions characterized by variations in climatic, physiographic, and ecological features (Omernik and Griffith, 2014). The moist, maritime-influenced Northern Rockies ecoregion encompassed 100 % of the SE and CYE and 26 % of the NCDE. The higher-elevation Canadian Rockies ecoregion encompassed 45 % of the NCDE. The drier Middle Rockies ecoregion, lacking a strong maritime influence, made up 16 % of the NCDE and 98 % of the GYE.

Forests of Douglas-fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) were common to all these montane regions, as were treeless alpine communities at the highest elevations. Representation of other tree species varied. Forests in the Northern Rockies often included ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*). The more open canopy forests of the Canadian and Middle Rockies often included lodgepole pine (*P. contorta*), limber pine (*P. flexilis*), and whitebark pine (*P. albicaulis*). Understory shrub and herbaceous communities also varied, notably with more soft mast (e.g., *Vaccinium* spp.) present in moister regions. Shrub- or grass-covered intermontane valleys were especially frequent in the Middle Rockies, where mountain-fed perennial streams were associated with distinct riparian communities. Shortgrass prairie and sagebrush (*Artemisia* spp.) shrublands were the primary natural communities on the eastern edges of the NCDE (where the Northwestern Glaciated Plains represented 13 % of the area) and GYE (where the Wyoming Basin ecoregion represented 2 % of the area). All RZs were dominated by public lands (>90 %), administered by the U.S. Forest Service or National Park Service. Private lands were more frequent on the periphery of DMAs, with forestry, ranching, and recreation the predominate land uses.

2.2. NCDE models

Previously, Sells et al. (2022) developed iSSFs for 65 NCDE bears (46 females and 19 males) during the primary active season (May–Nov; Appendix). Sells et al. (2022) used each model to compare covariates associated with a bear's locations and random locations accessible from each used location (Avgar et al., 2016). Location data were sampled at 3-h intervals (+/− 45 min) for ≥1 year during 2003–2020 (Appendix: Table A1). Of the 65 NCDE bears, 39 % of females and 79 % of males were classified as subadults (≤5 years in age) with average ages of 8.4 years for females (range 1–26) and 4.7 years for males (range 2–16). Most bears lived west of the Continental Divide (65 % of females and 95 % of males), and 43 % of females and 53 % of males were collared in response to human conflicts whereas the remaining individuals were collared for population trend monitoring.

Sells et al. (2022) selected model covariates that had strong biological reasoning and that were broadly available within the U.S. (Table A2). Covariates were the normalized difference vegetation index (NDVI, as an index to food abundance) during peak green-up (Jun 15–Jul 15), terrain ruggedness, distance to and density of forest edge, density of riparian areas, density of buildings, and distance to secure habitat (i.e., as defined by the U.S. Fish and Wildlife Service, areas on public, state, and tribal lands >500 m from roads). Sells et al. (2022) represented all covariates as rasters with 300-m grid cells. 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. Higher iSSF scores indicate greater relative probabilities of selection. To develop the iSSFs for NCDE bears, Sells et al. (2022) iteratively eliminated terms from the global model to determine the model formulation that maximized the cross-validation score for each bear. As a result, some bears retained the global model whereas others were assigned reduced models with fewer variables (Table A3).

2.3. Simulations

We repeated the simulation methods developed in Sells et al. (2022) (Fig. 2). Starting with the SE DMA, we first buffered the DMA by 100 km and clipped this polygon to the United States boundary (due to lack of covariate data for Canada). Within this buffered DMA and starting with the first of the 65 NCDE bear models, we used that individual's iSSF to create a raster surface, calculated as $\exp(\beta x_i)$ where β is the coefficient vector of the estimated iSSF and x_i the vector of habitat covariates of cell *i* (Northrup et al., 2022). After trimming extremes using the 0.025 and 0.975 quantile values, we normalized remaining values to a 0–1 scale (Squires et al., 2013). We then initiated 100 simulations from random locations within the SE DMA using that bear's iSSF. 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 DMA. 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 procedure was repeated for 5000 steps, reflecting the number of steps over three annual active seasons (May–Nov) when sampled at 3-h intervals. After completing the 100 simulations for the first NCDE bear, we repeated the above steps for the remaining 64 individuals. Simulation results for the SE were the sum of times each grid cell in the DMA was selected across the set of simulations for all individuals of each sex. We then repeated this entire process for the CYE and GYE DMAs.

2.4. Location data from nearby populations

To assess model performance, we used available GPS location data for bears monitored within the SE, CYE, and GYE during 2010–2021. We retained all data for bears ≥ two years of age. We used data for the primary active season (May–Nov) for our analyses as these dates matched the dates from which the NCDE models were developed. However, we also retained winter locations (Dec–Apr) to assess model performance during this period, as some bears remain active for portions of this season. To avoid including multiple locations of denning bears, we omitted duplicate locations per individual during winter months if latitude and longitude locations were identical in the first 3 decimal places. Remaining location data for grizzly bears included locations for 15 females and 10 males in the SE, 17 females and 30 males in the CYE, and 42 females and 124 males in the GYE (Table 1).

2.5. Assessment of transferability

After completing simulations, we prepared sex-specific predicted habitat use maps for the SE, CYE, and GYE DMAs by binning summed results into 10 quantile iSSF classes of relative probability of use; lowest use was given rank 1 and highest use rank 10 (Morris et al., 2016). Due to low sample sizes of GPS locations in the SE and CYE (Table 1) and overlap of the two study areas (Fig. 1), we prepared an SE/CYE combined map by calculating the mean iSSF class values in cells where the study areas overlapped (rounded to the nearest integer). After preparing maps for the SE/CYE and GYE, we created boxplots comparing values of habitat variables among iSSF classes in each ecosystem, including the NCDE results from Sells et al. (2022).

To assess predictive capacity of our maps, we overlaid the primary active season (May–Nov) location data for SE/CYE and GYE bears on the
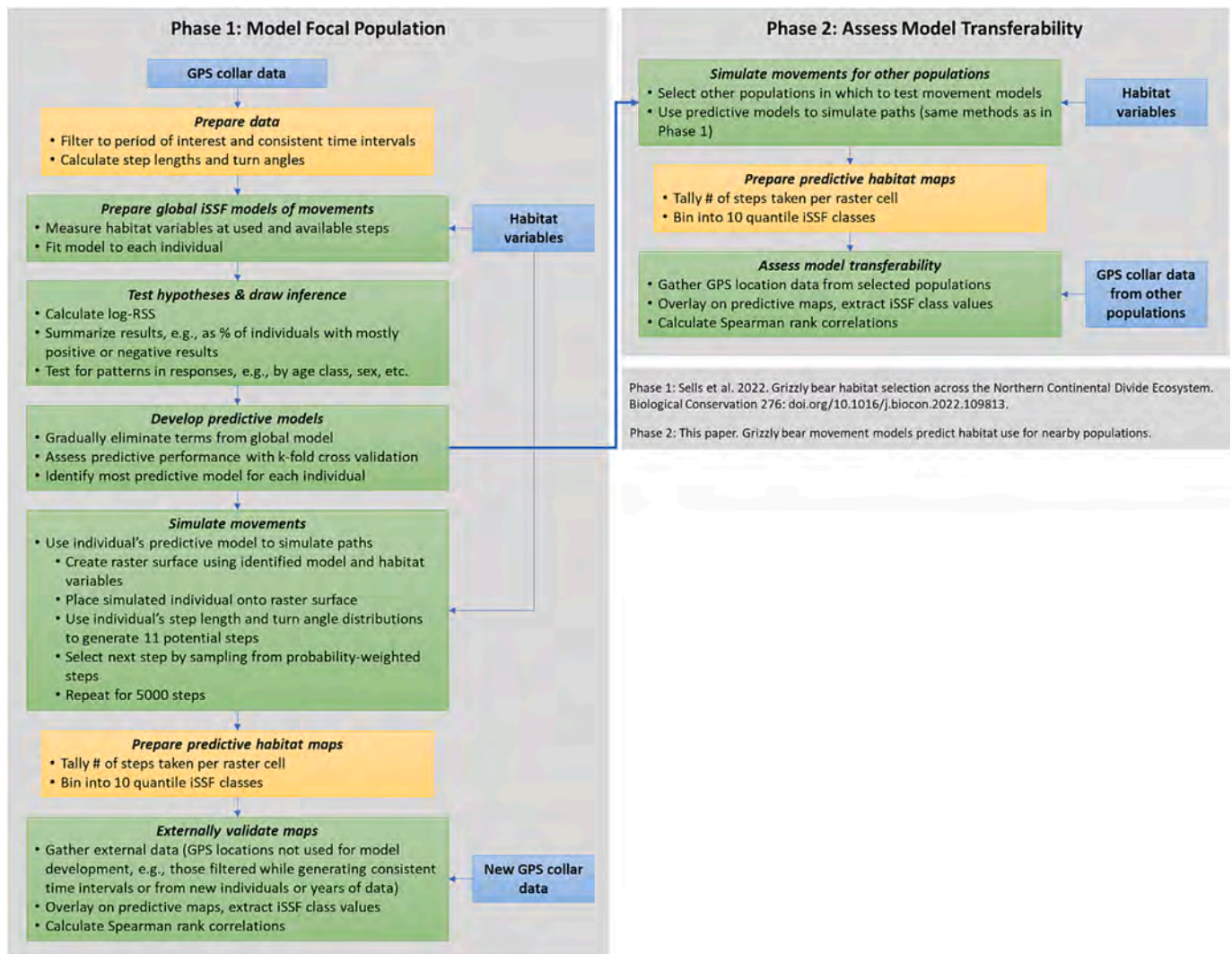
Fig. 2. Our study represented the second phase of a multi-phase study. In the first phase, Sells et al. (2022) focused on developing models for a focal population, the NCDE. In the second phase, we assessed model transferability by applying our models to nearby populations in the GYE, CYE, and SE.

Table 1
Sample sizes for grizzly bear GPS location data collected during 2010–2021 and used for testing transferability of models built using data from the NCDE to three other study areas.

Study area	Sex	n individuals	total n locations	n/individual (mean)	n/individual (SD)	n/individual (min)	n/individual (max)
SE	Female	15	16,760	1117	1265	1	3674
SE	Male	10	16,529	1653	1343	21	3647
CYE	Female	17	39,642	2332	2856	15	10,821
CYE	Male	30	33,548	1118	1085	33	3928
GYE	Female	42	209,104	4979	3290	192	14,009
GYE	Male	124	317,615	2561	2162	53	11,591
	Totals	240	651,827				

respective maps and extracted iSSF class values. We area-adjusted counts of locations (i.e., number of locations per class divided by the number of cells per class, because the quantile breakpoints led to slight differences in area per class) and calculated Spearman rank correlations between class values and counts of locations (Boyce et al., 2002).

To further assess predictive capacity, we also calculated Spearman rank correlations for temporal and spatial subsets of the grizzly bear GPS locations representing seasons, 3-year intervals, individual bears with ≥250 locations, and watersheds (classified to the subbasin level, usgs. gov/national-hydrography) containing ≥250 locations. Based on the authors' knowledge of grizzly bear behavior, we defined seasons as

spring (May 1–Jun 30; primary mating season), summer (Jul 1–Aug 31; primary berry season), fall (Sep 1–Nov 30; hyperphagia season), and winter (Dec 1–Apr 30; primary denning season).

3. Results

Simulations enabled producing predicted habitat maps for the SE/ CYE and GYE (Fig. 3). In each ecosystem, predicted use increased with NDVI, though the effect was much less pronounced in the SE/CYE (Fig. 4). The top-ranked iSSF classes (i.e., those with greatest relative predicted use) had low terrain ruggedness, closer proximity to forest
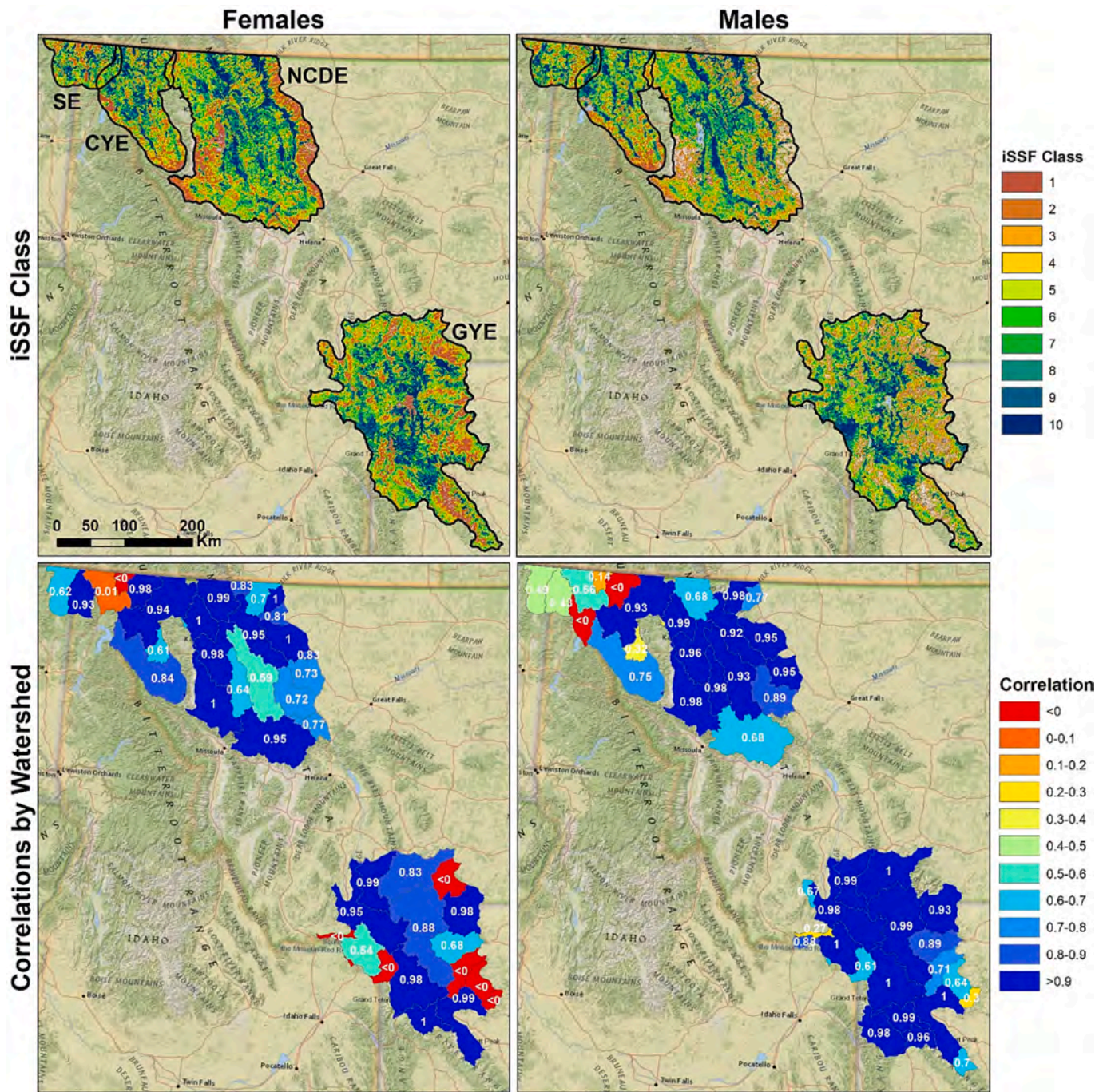
Fig. 3. Predicted habitat maps for male and female grizzly bears in the U.S. Northern Rockies and assessment of predictive accuracy by watershed. Top panel: predicted habitat maps for females and males. These were derived from simulations using integrated Step Selection Functions (iSSFs) developed for 65 bears in the NCDE (Sells et al., 2022). After completing simulations for the SE, CYE, and GYE, we tallied the numbers of steps by simulated bears in each raster cell and binned results into 10 equal-area iSSF classes of relative habitat use (1 = lowest relative predicted use, 10 = highest relative predicted use). Bottom panel: Spearman rank correlations within each watershed show relative accuracy of mapped predictions, based on GPS locations of bears in the SE, CYE, and GYE (values closer to 1 are more accurate). NCDE results are included in each panel for comparison.

edges, and higher forest edge densities. Particularly for males, predicted use correlated positively with higher riparian densities. Predicted use in relation to density of buildings was consistently low, as it was in relation to distance to secure habitat, except in the SE/CYE.

In the SE/CYE, Spearman rank correlations were 1.0 each for males and females, as calculated using the predicted habitat map (Fig. 3) and the GPS locations from SE/CYE bears (Table 1). The top five iSSF classes (6–10, representing 50 % of the landscape) for males contained 58.2 % of their locations, and the top five classes for females contained 75.0 %

of locations (Fig. 5). The top class for males (class 10, 10 % of the landscape) contained 14.1 % of all male locations, whereas the top class for females contained 24.6 % of female locations. For temporal subsets of the GPS locations, we found that correlations were consistently high for females across seasons and years (>0.79). Correlations for males were high across seasons (>0.89), with exception of summer (Jul 1–Aug 31; correlation = −0.41). Correlations for males across years also varied. Correlations by watershed varied for both sexes, with mostly good performance for females and mixed performance for males (Fig. 3).

Fig. 4. Summarized cell values for habitat variables as measured within each of the 10 iSSF classes of predicted habitat use within the SE/CYE, GYE, and NCDE study areas. White dots are median values, boxes are 50 % interquartile ranges, and thin lines extend to the 95 % values measured within cells for each quantile. Horizontal lines represent the median value measured within each study area.
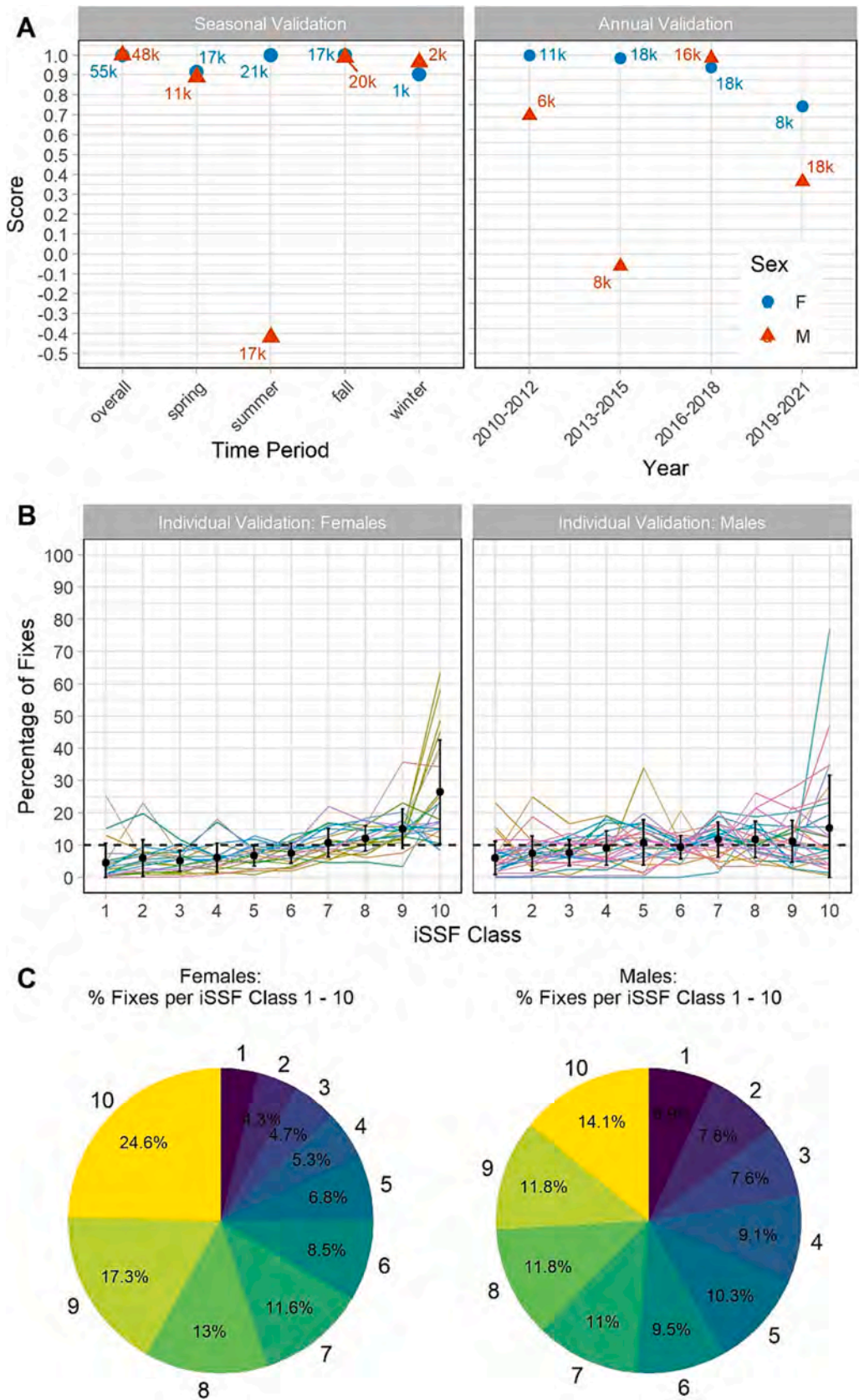
Fig. 5. Results of external validation comparing GPS locations of SE and CYE grizzly bears to habitat maps produced through simulations using individual-based models of 65 bears in the NCDE (Sells et al., 2022): Spearman rank correlation scores for seasons and years (Panel A; annotation represents sample sizes); percentages of locations in each iSSF class (1 = lowest relative predicted use, 10 = highest relative predicted use) for individuals (Panel B; each line represents one bear; bars depict means +/− SD); and overall percentages of locations in each iSSF class (Panel C).

In the GYE, Spearman rank correlation was 1.0 for males and 0.96 for females, as calculated using the predicted habitat map (Fig. 3) and the GPS locations from GYE bears (Table 1). In total, 76.3 % of male locations and 72.4 % of female locations occurred in the top five classes for each sex (Fig. 6). The top class contained 28.8 % of all male locations and 25.3 % of all female locations. For temporal subsets of GPS locations, we found that correlations were consistently high across seasons (>0.78) and years (>0.99) with exception of females in 2019–2021 (0.38). Correlations by watershed were generally high for males; the same was true for females with exception of several small watersheds (Fig. 3).
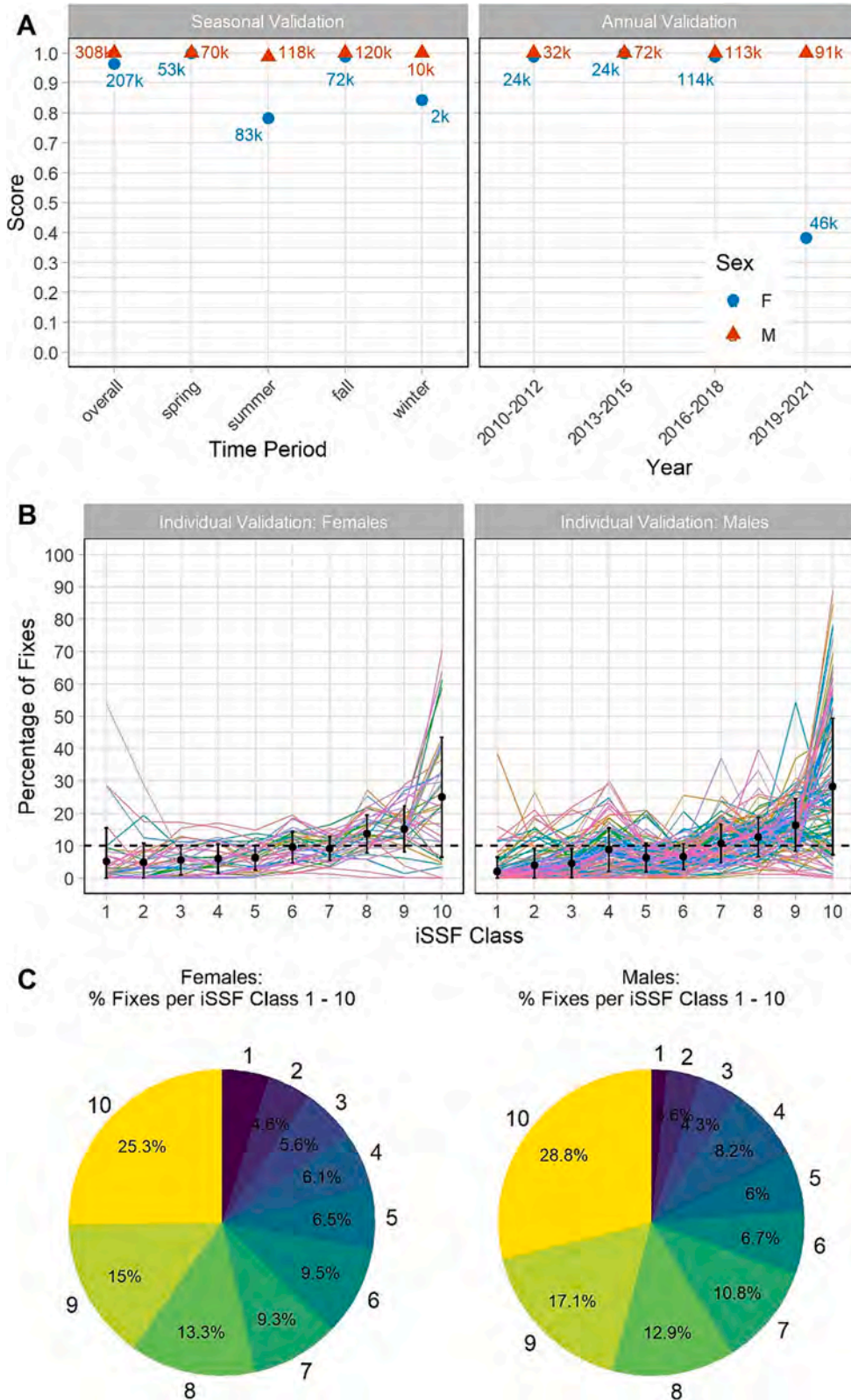

Fig. 6. Results of external evaluation comparing GPS locations of GYE grizzly bears to habitat maps produced through simulations using individual-based models of 65 bears in the NCDE (Sells et al., 2022): Spearman rank correlation scores for seasons and years (Panel A; annotation represents sample sizes); percentages of locations in each iSSF class (1 = lowest relative predicted use, 10 = highest relative predicted use) for individuals (Panel B; each line represents one bear; bars depict means +/− SD); and overall percentages of locations in each iSSF class (Panel C).

4. Discussion

Ecological models are generally most applicable to the time and place from which their underlying data arose. Ideally, conservation decisions are made using inferences from models specific to the area of conservation concern. However, conservation practitioners do not often have models available for every time and place of conservation concern, and therefore must rely on models developed in other times or systems to make decisions. For example, grizzly bears have been recolonizing their former range in the U.S. Northern Rocky Mountains. Predictions for potential connectivity corridors are of great interest to inform decisions, such as how to proactively protect key connectivity habitats. Conservation groups are likewise interested in predicting future habitat use in currently unoccupied ecosystems (the BE and NCE). Given that data are lacking to develop models specific to these areas, data from an existing population like the NCDE can be leveraged to make predictions for these areas if model transferability can be demonstrated.

Our study demonstrates that reliable predictions were obtained by applying models developed for NCDE grizzly bears to the three other grizzly bear populations in the U.S. Northern Rocky Mountains. In the SE, CYE, and GYE, predictive accuracy was high when comparing all GPS locations for bears in these areas with iSSF classes derived from simulations using the NCDE models. The NCDE, and the data informing model development, spanned multiple ecoregions (Omernik and Griffith, 2014), including those dominating the SE, CYE, and GYE. The good performance of the models in these large, mostly single-ecoregion study areas provides evidence that model predictions are robust to various landscapes in the region. Sells et al. (2022) intended for NCDE model covariates to be broadly applicable to grizzly bear space use over space and time. Our findings provide evidence that this was indeed the case.

Predictive accuracy involving smaller subsets of location data was more variable than overall tests. Because the NCDE models were developed to be general (Sells et al., 2022), we correctly anticipated that accuracy would sometimes be lower at finer spatial and temporal scales. For example, accuracy was low in some watersheds, particularly on the periphery of study areas. Those watersheds with poor accuracy were generally smaller and had lower sample sizes of individual bears and GPS locations (Appendix: Figs. A4–A6). Other examples of poorer accuracy perhaps hint at mismatches between models and observed habitat use for certain times or individuals (Figs. 4–6). Comparisons of covariate values within study areas and within iSSF classes provided potential explanations for reduced accuracy in some areas and times. Of the seven variables measured, the most notable differences between study areas were associated with NDVI, distance to secure habitat, and density of forest edge (Fig. 4).

We intended NDVI to serve as an index of food availability, based on research showing that NDVI is associated with grizzly bear habitat selection (Mace et al., 1999; Nielsen et al., 2002; Ziółkowska et al., 2016). Supporting this expectation, a narrowing range of higher NDVI values was observed with increasing iSSF class in the NCDE and GYE, and the top four or five classes had median values above the median values available in the study areas. However, almost all classes in SE and CYE had median NDVI values roughly equal to the study area-wide median value. The range of NDVI values available within each study area may be reflective of relative moisture gradients, with potentially wettest conditions (high NDVI values) in the SE and CYE and driest (low NDVI values) in the GYE (Appendix: Fig. A1; Omernik and Griffith, 2014). We suspect the overall high NDVI values occurring in the SE and CYE (and some watersheds in particular; Fig. 3 and Appendix: Fig. A1) may reduce the relationship between NDVI and habitat selection for at least some SE and CYE bears. Because most NCDE models included NDVI (89 % of females and 100 % of males Appendix Table A3; Sells et al., 2022), the transferability of those models may be reduced when applied to areas with particularly high NDVI values, especially during summer months. Furthermore, NDVI may not be a strong predictor for some important seasonal foods that occur at finer spatial scales and which are used

heavily within some watersheds, such as huckleberries (*Vaccinium* spp.) or army cutworm moths (*Euxoa auxiliaris*; Kasworm et al., 2021b; Kasworm et al., 2021a). Periods of low accuracy for SE and CYE males (2013–2015 and 2019–2021; Fig. 5) coincided with years of generally greater huckleberry production (Kasworm et al., 2021b; Kasworm et al., 2021a). Highly variable seasonal food resources like berries may lead to different foraging strategies and resulting space use. If NDVI poorly correlates to these resources, models with this variable would likely have lower accuracy during periods when bears focus on such seasonal foods.

Grizzly bears avoid roads (Mace et al., 1999; Martin et al., 2010; Northrup et al., 2012; Proctor et al., 2019; Waller and Servheen, 2005) and greater road densities increase risk of mortality (Schwartz et al., 2010). In our analyses, roads were represented as distance to secure habitat (i.e., areas with no motorized access) on public, state, and tribal lands, and many NCDE models contained this covariate (67 % of female models and 63 % of male models; Appendix Table A3; Sells et al., 2022). Simulations revealed a narrowing range of shorter distances to secure habitat with increasing iSSF class in all study areas among females. In contrast, there was a widening range of longer distances among males, particularly in the SE and CYE, where values in the top class were mostly above the median available. The relative scarcity of areas closer to secure habitat (Appendix: Fig. A3) may have reduced the transferability of the models to the SE and CYE, particularly for males that occupy large home ranges. Additionally, the overall tendency of males to make longer movements (Sells et al., 2022) and use larger areas (Schwartz et al., 2010) likely makes staying near secure habitat more challenging for this sex.

Both sexes appeared to be attracted to the interface of forested and non-forested areas and sites of higher forest edge density (Fig. 4). Areas far from forest edge were only present in the lowest classes, and the highest classes centered on 0 distance with very low variation. We also observed increasing levels of forest edge density with increasing iSSF classes for all study areas; however, differences from the median available were generally greatest within the NCDE and SE/CYE. The GYE generally had the highest median level of forest edge density, reflecting the higher frequency of open habitats in the Middle Rockies ecoregions (Appendix: Fig. A2; Omernik and Griffith, 2014) and potentially reducing its influence as a component of habitat selection. Sells et al. (2022) hypothesized that forest edges provide food resources, security from humans and other bears, and opportunity for thermal regulation (Blanchard, 1983; Frąckowiak et al., 2014; Nielsen et al., 2004; Stewart et al., 2013), and found that distance to and density of forest edge were included in 59 % and 83 % of female models and 79 % and 79 % of male NCDE models, respectively (Appendix: Table A3).

Remaining variables by iSSF class were generally represented similarly across study areas (Fig. 4). As in the NCDE, males seemed more averse to ruggedness overall, which Sells et al. (2022) expected would be an outcome of attempts to reduce energy expenditure given their larger body mass (Carnahan et al., 2021). Density of riparian habitat was similar across study areas, with males especially attracted to riparian areas. Sells et al. (2022) expected bears would be attracted to riparian areas to access food, security, and thermal regulation (Blanchard, 1983; Frąckowiak et al., 2014; Nielsen et al., 2004; Rogers et al., 2021; Stewart et al., 2013). Both sexes generally avoided areas with higher densities of buildings, presumably because of associated human activities (Frąckowiak et al., 2014). The higher range of building densities in iSSF class 10 for males within the SE/CYE and NCDE likely reflects some males habituated to humans (these individuals were often outfitted with GPS collars in response to conflicts, e.g., after obtaining food rewards near homes).

We expect the general selection patterns by grizzly bears for these habitat variables (Fig. 4) to persist at larger spatial extents, but anticipate that accuracy of model predictions may decline with distance from the NCDE as overall conditions change. Therefore, further analyses may be needed before applying models to more distant areas, such as the NCE

in Washington State (Fig. 1). For example, if the lower predictive performance for SE and CYE males during summer months (Fig. 5) was found to be related to behavioral differences, rather than to low sample size or limitations of applying NDVI in dense forested habitats (Huang et al., 2021; Phillips et al., 2008), then supplementing or replacing NCDE-derived models with models derived from SE and CYE males (or other locally derived data, where available) might be appropriate for application to the NCE.

We expect the overall approach as described in Sells et al. (2022) and here would be useful for numerous other species of conservation concern. Conservation decisions can be informed by results of landscape mapping based on movement decisions of individuals (Thurfjell et al., 2014; Sells et al., 2022). Compared with developing models for each new area of conservation concern, models with demonstrated transferability can be more cost-effective and timely and can thus enhance conservation decisions. Our study demonstrates that individual-based movement models developed for one population may be transferable for reliable application to other nearby populations with careful external validation of predictive accuracy. This validation, in turn, provides the groundwork for application of these models to identify movement corridors and predict future population expansions. Predicted high-use habitat could help identify areas for conservation easements on private lands; placement of crossing structures to mitigate barrier effects of transportation infrastructure; and how to mitigate negative effects of development, recreation, or vegetation management.

Glossary

BE	Bitterroot Ecosystem for grizzly bears
CYE	Cabinet-Yaak Ecosystem for grizzly bears
DMA	demographic monitoring area for grizzly bears
GYE	Greater Yellowstone Ecosystem 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
NCDE	Northern Continental Divide Ecosystem for grizzly bears
NCE	North Cascades Ecosystem for grizzly bears
NDVI	normalized difference vegetation index
SE	Selkirk Ecosystem for grizzly bears
Secure core	areas >500 m from roads on federal, state, and tribal lands

Impact statement

Mechanistically modeling grizzly bear movements for one population yielded models transferable to nearby populations, thus providing tools for conservation planning.

CRediT authorship contribution statement

Sarah Sells, Cecily Costello, and Paul Lukacs conceived the ideas and designed methodology; Cecily Costello, Frank van Manen, Mark Haroldson, Wayne Kasworm, Justin Teisberg, Milan Vinks, and Dan Bjornlie 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.2023.109940.

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