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Potential paths for male-mediated gene flow to and from an isolated grizzly bear population

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Abstract. For several decades, grizzly bear populations in the Greater Yellowstone Ecosystem (GYE) and the Northern Continental Divide Ecosystem (NCDE) have increased in numbers and range extent. The GYE population remains isolated and although effective population size has increased since the early 1980s, genetic connectivity between these populations remains a long-term management goal. With only ~110 km distance separating current estimates of occupied range for these populations, the potential for gene flow is likely greater now than it has been for many decades. We sought to delineate potential paths that would provide the opportunity for male-mediated gene flow between the two populations. We first developed step-selection functions to generate conductance layers using ecological, physical, and anthropogenic landscape features associated with non-stationary GPS locations of 124 male grizzly bears (199 bear-years). We then used a randomized shortest path (RSP) algorithm to estimate the average number of net passages for all grid cells in the study region, when moving from an origin to a destination node. Given habitat characteristics that were the basis for the conductance layer, movements follow certain grid cell sequences more than others and the resulting RSP values thus provide a measure of movement potential. Repeating this process for 100 pairs of random origin and destination nodes, we identified paths for three levels of random deviation (θ) from the least-cost path. We observed broad-scale concordance between model predictions for paths originating in the NCDE and those originating in the GYE for all three levels of movement exploration. Model predictions indicated that male grizzly bear movement between the ecosystems could involve a variety of routes, and verified observations of grizzly bears outside occupied range supported this finding. Where landscape features concentrated paths into corridors (e.g., because of anthropogenic influence), they typically followed neighboring mountain ranges, of which several could serve as pivotal stepping stones. The RSP layers provide detailed, spatially explicit information for land managers and organizations working with land owners to identify and prioritize conservation measures that maintain or enhance the integrity of potential areas conducive to male grizzly bear dispersal.

Key words: connectivity; corridor; dispersal; gene flow; Greater Yellowstone Ecosystem; grizzly bear; movements; Northern Continental Divide Ecosystem; randomized shortest path; step-selection model; *Ursus arctos.*

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INTRODUCTION

Landscape connectivity has become a central tenet of biodiversity conservation and the number of published studies on this topic has increased substantially since 2008, largely because of new methodologies (Correa Ayram et al. 2016). Large mammalian carnivores have received particular attention because they have large home ranges and dispersal distances, occur at relatively low densities, have fragmented distributions, and often function as flagship species for conservation (Beier et al. 2008, Correa Ayram et al. 2016). Conserving movement corridors for mammalian carnivores is challenging because they frequently span large geographic areas comprised of complex landscape mosaics with varied land ownerships and uses. Limited funds and logistical constraints often necessitate prioritization of lands deemed vital for conservation, but identification of important habitat is often hampered by the lack of relevant movement data for focal species. Advances in analytical techniques combined with extensive, long-term Global Positioning System (GPS) data for grizzly bears (*Ursus arctos*) provided the opportunity to identify potential paths that may facilitate gene flow between populations in the Northern Continental Divide Ecosystem (NCDE) and the Greater Yellowstone Ecosystem (GYE). This important information need was identified by federal, state, and tribal managers (U.S. Fish and Wildlife Service 1993, 2017, Dood et al. 2006, Montana Department of Fish, Wildlife and Parks 2013).

Whereas the NCDE population is contiguous with grizzly bear populations in the Canadian Rocky Mountains (U.S. Fish and Wildlife Service 1993, Schwartz et al. 2003), current genetic data indicate the GYE population remains isolated (i.e., no evidence of recent immigrants; Haroldson et al. 2010, Proctor et al. 2012; Fig. 1; Appendix S1: Fig. S1). Concerns for the genetic health of the GYE population have lessened considerably with recent findings of a three- to fourfold increase in effective population size since the early 1980s (Kamath et al. 2015), exceeding the theoretical number for avoiding inbreeding depression (Frankham et al. 2014). Nonetheless, genetic connectivity between these populations remains a long-term management goal for the state of Montana as described in the Grizzly Bear Management Plan for Northwest Montana (Dood et al. 2006) and Southwest Montana (Montana Department of Fish, Wildlife and Parks 2013). Facilitation of natural movement, through habitat management, is favored over translocation of bears between ecosystems (Dood et al. 2006).

For several decades, grizzly bear populations in the GYE and NCDE have increased in numbers and range extent (Schwartz et al. 2006, Kendall et al. 2009, Mace et al. 2012, Bjornlie et al. 2014, Costello et al. 2016, Haroldson et al. 2016). Additionally, the presence of grizzly bears has been verified for 21 locations in the area between the occupied ranges of the NCDE and GYE. Unlike core habitats for these two populations, which are dominated by large expanses of public land with grizzly bear-specific habitat protections, areas of recent expansion are characterized by greater anthropogenic influence, and even more so are the landscapes between the two populations. The likelihood of future demographic linkage of these two populations is uncertain. However, dispersal in grizzly bears is male-biased (Blanchard and Knight 1991, McLellan and Hovey 2001, Proctor et al. 2004) and the potential for male-mediated genetic linkage between the NCDE and GYE is likely greater now than it has been for many decades. The estimate of closest proximity between current occupied ranges for these populations is ~110 km, which is within maximum dispersal distances (67–176 km) documented for males in the region (Blanchard and Knight 1991, McLellan and Hovey 2001, Proctor et al. 2004). Given that bear dispersals typically occur over time periods of one to multiple years, our goal was to identify paths between the NCDE and GYE populations with habitat conditions conducive to male dispersal.

Although potential habitat linkages and movement corridors for grizzly bears (Picton 1986, Walker and Craighead 1997, Dilkina et al. 2016) and black bears (*Ursus americanus*; Cushman et al. 2009) have been identified for this region, no such studies have been conducted using grizzly bear location data from either ecosystem. The randomized shortest path (RSP) algorithm, introduced to the field of movement ecology by Panzacchi et al. (2016), is a new methodological approach to predict the location of paths between functional areas based on step-selection functions (SSF) derived from individual-based movement data. By modulating the degree of randomness in simulated movements, the algorithm has the potential to

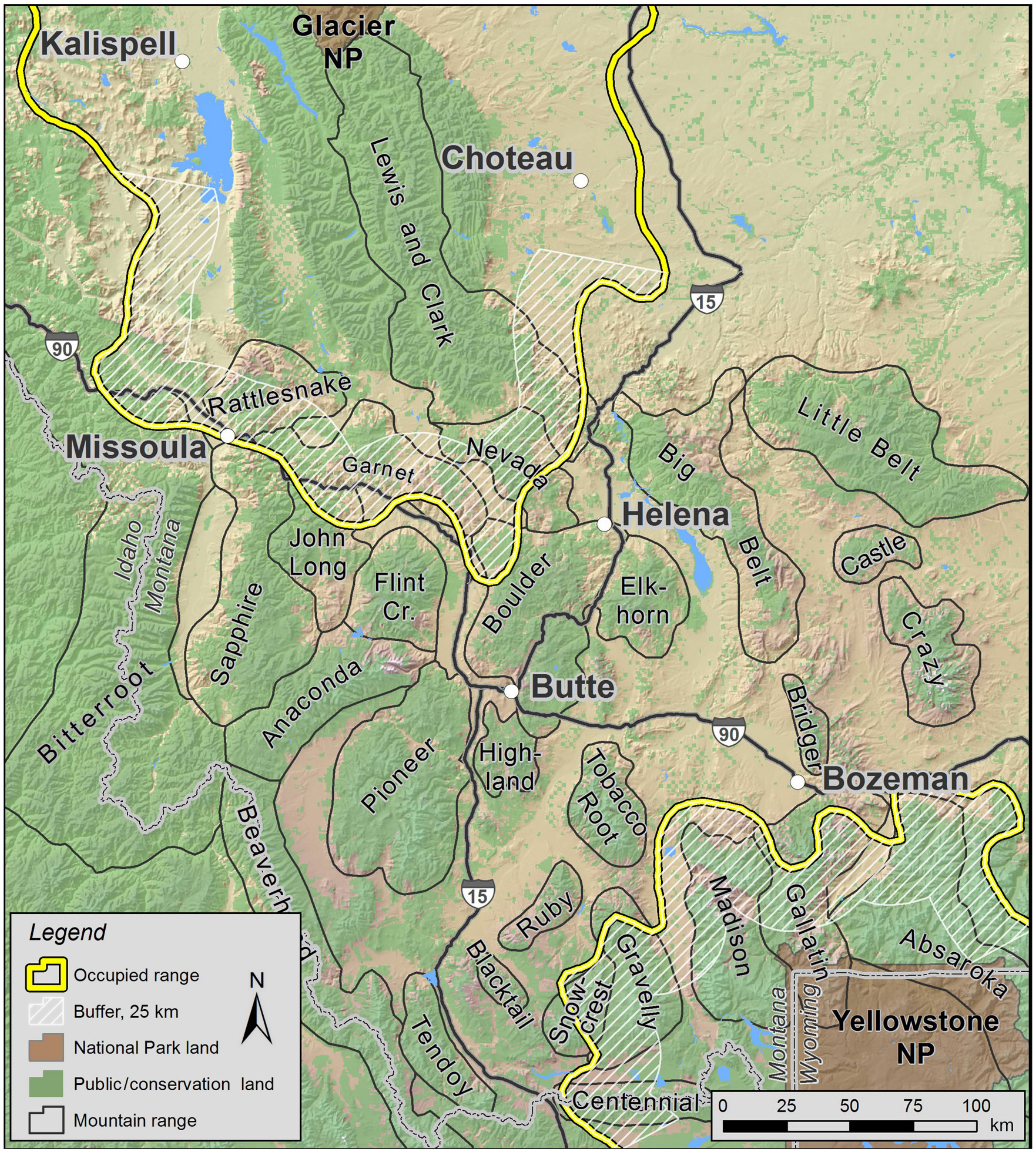

Fig. 1. Study area for delineating potential paths for male-mediated gene flow between the Northern Continental Divide Ecosystem (NCDE) and Greater Yellowstone Ecosystem (GYE) grizzly bear populations. Map (red rectangle in inset map) displays area between estimated occupied range in the NCDE to the north and the GYE to the south, where the randomized shortest path algorithm was applied. Green polygon in inset map shows the full extent of the study area where data informing the step-selection functions were collected from independent-age (≥2 yr old) male bears during 2000–2015 (also see Appendix S1: Fig. S1). Mountain ranges that appear in the text are named (Montana State Library 2014). Occupied range based on data through 2014 (Bjornlie et al. 2014, Costello et al. 2016).

better capture the movement ecology of species compared with optimal least-cost path (Walker and Craighead 1997, Cushman et al. 2009) or random-walk approaches (Clark et al. 2015). This approach was particularly appropriate for our objective to delineate potential paths for gene flow between the GYE and NCDE populations. It allowed us to explore the trade-off between optimal, short paths (likely important for successful immigration given the current distance between populations) vs. more exploratory paths (characteristic of a dispersing bear traversing unfamiliar landscapes).

STUDY AREA

The study area encompassed 357,773 km^2 and spanned 49 counties within western Montana, eastern Idaho, and northwestern Wyoming (Fig. 1). We used recent delineations of occupied grizzly bear range in the NCDE (Costello et al. 2016 [55,200 km^2; 2004–2014 data]) and GYE (IGBST, *unpublished data* [58,314 km^2; 2000–2014 data]), estimated based on Bjornlie et al. (2014), as the basis for our analyses. The NCDE consists of rugged mountain topography shaped by glaciation. West of the Continental Divide, vegetation at lower elevations is dominated by Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and spruce (*Picea* spp.). Non-forested, alpine habitats generally occur above 2000 m. Mountains abruptly transition to short-grass prairie and limber pine (*Pinus flexilis*) savannas along the eastern edge of the Rocky Mountains. The GYE consists of a high-elevation plateau surrounded by 14 mountain ranges with elevations >2130 m and contains the headwaters of three continental-scale rivers. Lower elevations (<1900 m) are characterized by grasslands or shrub steppes interspersed with open stands of juniper (*Juniperus scopulorum*), Douglas-fir, and limber pine. Douglas-fir forms the lowest-elevation forest community at around 1900–2200 m, whereas lodgepole pine dominates at mid-elevations. Engelmann spruce (*Picea engelmannii*), subalpine fir, and whitebark pine (*Pinus albicaulis*) form the upper tree line around 2900 m. Alpine tundra occurs at the highest reaches of all major mountain ranges.

The area of interest for potential paths between the NCDE and GYE consists of a complex of forested mountain ranges and open grassland and sagebrush valleys, interspersed with agricultural lands and human settlements at lower elevations (Fig. 1). Elevations range between 738 and 3883 m. The area contains about 43% forest cover, primarily distributed in the northern portion, whereas the southern portion contains more open grasslands with patches of shrub–scrub land and cultivated crops. Road densities are generally greater in this area than in the NCDE and GYE, and two interstate highways, I-90 and I-15, may act as potential barriers to grizzly bear movements. Private land ownership in this area (39%) is greater compared with the NCDE and GYE.

METHODS

GPS data

Grizzly bears were captured for research and management purposes using culvert traps or Aldrich leg-hold snares (Blanchard 1985), and a sample of independent-age (≥2 yr old) bears were fitted with radio transmitters (Telonics, Mesa, Arizona, USA). Grizzly bear capture and handling procedures used for this study were reviewed and approved by the respective Animal Care and Use Committees of the U.S. Geological Survey (ACUC no. 201201) and Montana Department of Fish, Wildlife and Parks (2004). Procedures conformed to the Animal Welfare Act and to U.S. Government principles for the use and care of vertebrate animals used in testing, research, and training. Captures were conducted under U.S. Fish and Wildlife Service Endangered Species Permit [Section (i) C and D of the grizzly bear 4(d) rule, 50 CFR17.40(b)], with additional state research permits for Wyoming, Montana, and Idaho, and National Park Service research permits for Yellowstone, Grand Teton, and Glacier national parks.

We restricted our analyses to male grizzly bears monitored with GPS transmitters during May 2000–October 2015. Because some remotely downloaded GPS data did not include activity data and may have lower precision than data stored in internal memory, we based all analyses on GPS data from the downloaded, on-board memory after collar retrieval, irrespective of transmitter type. We excluded three-dimensional and two-dimensional GPS fixes with PDOP >10 (D'Eon and Delparte 2005) or horizontal error >150 m to ensure fixes had minimal positional error relative to the spatial resolution of covariates (i.e., 300 m). Additionally, fixes collected during the typical denning months of December–April were excluded.

Step-selection function

We used SSF to quantify habitat selection for grizzly bears in the NCDE and GYE. As defined by Fortin et al. (2005), the SSF is exponential in form: $w(x) = \exp(x\beta)$, where x represents a vector of environmental covariates and β the associated coefficient vector estimated by conditional logistic regression. Grid cells with higher SSF scores ($w(x)$) have greater relative probabilities of being chosen by an animal. In circuit theory terminology, the spatial predictions of the SSF scores reflect a conductance surface (McRae et al. 2008).

All statistical analyses were carried out in the R computing environment (v3.3.1; R Core Team 2016). For each observed step (i.e., straight-line segment linking two successive GPS locations), we computed the step length and turning angle using the adehabitatLT package (v0.3.20; Calenge 2006). We excluded consecutive fixes <100 m apart from analysis because we were interested in characterizing habitat selection associated with active movements rather than passive movements or stationary states (Latham et al. 2011, Clark et al. 2015). Because our GPS data were from two different ecosystems and spanned two decades, GPS fix intervals varied. Most GPS transmitters were programmed to sample at intervals of ≤3.5 h so we included all steps that occurred within ≤4 h. We then applied an additional constraint of ≥100 valid steps for any bear within any year to ensure that data were representative of typical movements by individual bears for reliable estimation of individual-specific regression parameters (Fieberg et al. 2010).

Next, we paired each observed step with 10 steps that shared the same step origin, but with varying step lengths and turn angles, to compare the habitat chosen by the bear to those that were available (Thurfjell et al. 2014, Clark et al. 2015). We first computed a linear-circular correlation coefficient (Mardia 1976) between step length and turning angle to determine whether available steps could be generated by sampling step length independent of turning angle (Thurfjell et al. 2014). To fit a distribution to the range of observed step lengths (i.e., 100–15,000 m), we standardized all step lengths to a [0,1] interval. We then fit a beta distribution, chosen for its flexibility, to the transformed step lengths via maximum-likelihood estimation (MLE) using the fitdistrplus package (v1.0-7; Delignette-Muller and Dutang 2015). We fit a von Mises distribution, via MLE, to the observed turning angles using the circular package (v0.4-7; Agostinelli and Lund 2013).

We considered an extensive set of spatial covariates known or hypothesized to be associated with grizzly bear habitat selection and movements to construct a candidate model set for the step-selection analysis. Our focus was on identifying paths that show potential for male dispersal between the two populations. Zeller et al. (2012) suggested that estimation of resistance surfaces for pathways should take into account that animals may make movement decisions based on factors other than resource selection. However, grizzly bear dispersal often involves an extended period of several years, reflective of exploratory habitat selection behaviors of resident animals, rather than a rapid, long-distance movement (McLellan and Hovey 2001). Data on documented dispersal events are rare, so we used GPS data from a large sample of males from each population and assumed that habitat selection associated with non-stationary GPS locations (i.e., consecutive fixes ≥100 m apart) within their home ranges was generally reflective of how male grizzly bears explore the landscape. We classified covariates into the following themes (Singleton et al. 2004): land cover, road features, hydrological features, human presence, and topography (Appendix S1: Table S1). Using ArcGIS 10.2 (ESRI, Redlands, Washington, USA), we generated each covariate as a raster layer with 300-m resolution. We chose this resolution as a compromise between the need to accurately characterize habitats selected, the large extent of our study area, and computer processing capabilities. We measured several covariates using circular moving windows with a radius of 1500 m from the centroid of the center pixel based on typical daily movements of males (Schwartz et al. 2010).

For land cover, we reclassified the 2011 National Land Cover Database (NLCD; U.S. Geological Survey 2014) to construct a forest raster comprised of deciduous, evergreen, and mixed forests, as well as woody wetlands. Because grizzly bear movements and habitat use are often associated with the interface of forested and open habitats, we derived a covariate based on Euclidean distance to the nearest forest polygon (Nielsen et al. 2004, May et al. 2008, Stewart et al. 2013). Positive and negative distance values were associated with grid cells either outside or inside forest polygons, respectively. We used Fragstats (McGarigal et al. 2012) to generate a contagion index of natural land cover (i.e., all land-cover types from the reclassified 2011 NLCD data, but excluding cropland and urban areas) using a moving window with a 10-km radius representative of seasonal to annual male home ranges. We used this index to measure the extent to which patch types with natural land cover were aggregated or clumped. Higher values of contagion may result from landscapes with a few large, contiguous patches of natural land cover, whereas lower values generally characterize landscapes with many small and dispersed patches; contagion is inversely related to edge density (McGarigal et al. 2012). We generated a normalized difference vegetation index (NDVI), a relative measure of vegetative greenness (Mace et al. 1997), using the Google Earth Engine (GEE; Google Earth Engine Team 2015) as a median composite of Landsat 8 (U.S. Geological Survey 2016) imagery acquired between 2013 and 2015, during peak greenness (15 June–15 July); GEE processing corrected for geometric, radiometric, and atmospheric errors and individual pixels corresponding to clouds were excluded from the analysis. For road features, we used the National Transportation Dataset to derive distance and density covariates (U.S. Geological Survey 2015*b*). Grizzly bears generally avoid close proximity to roads, but this may vary depending on road type and, correspondingly, traffic volume (Mace et al. 1996, Chruszcz et al. 2003, Waller and Servheen 2005, Roever et al. 2010). Therefore, we computed the Euclidean distance to the nearest road separately for primary or secondary roads. Additionally, we derived linear density for primary or secondary roads per km^2, as measured within a 1500 m radius circular neighborhood. Primary roads were U.S., state, and county highways, whereas secondary roads encompassed all other roads, including unimproved roads. For hydrological features, we used the high-resolution National Hydrography Dataset (1:24,000 scale; U.S. Geological Survey 2015*a*) to derive distance and density covariates. Empirical evidence suggests that grizzly bear movements are often associated with riparian habitats, particularly on the open plains (Wilson et al. 2005). We computed the Euclidean distance to the nearest river or perennial stream, and the linear density of rivers or perennial streams per km^2 as measured within a 1500-m radius circular neighborhood. For human presence, we computed the density of housing units per census block, as defined by the U.S. Census Bureau (2010), using 2010 housing data (U.S. Department of Commerce 2010). We $\log_{10}$-transformed these data because the relative probability of bears moving through increasingly anthropogenic-influenced landscapes is not linear (Schwartz et al. 2010). For elevation, we resampled 30-m National Elevation Data (U.S. Geological Survey 2009) to a 300-m resolution and included a quadratic term to allow for a non-linear response. Because terrain features and topography may affect movement, we computed vector ruggedness measure using a 1500-m radius to provide a broad-scale measure of variation in aspect and slope (Sappington et al. 2007).

Using the covariates specified in Appendix S1: Table S1, we constructed a candidate set of 10 ecologically plausible models (Table 1). Our approach was to maximize predictive power of the model instead of estimating covariate effects. We addressed autocorrelation by fitting regression models to data from individual animals followed by averaging to determine population-level responses (Fieberg et al. 2010). All 10 candidate models contained six covariates that we considered essential for modeling grizzly bear habitat selection (Roever et al. 2010, Proctor et al. 2015, Ziółkowska et al. 2016): distance to forest edge, natural contagion, NDVI, home density, elevation (including its quadratic term), and ruggedness (Table 1). We then added landscape and habitat covariates in different combinations to reflect different hypotheses of how such features may influence grizzly bear exploration of the landscape. For water features, we included the distance to rivers and distance to perennial streams as an additive pair and as a combined covariate. Similarly, within the road feature theme, we included several combinations of road density and distance to roads covariates. We hypothesized that grizzly bear response to roads is a function of both traffic volume and road density, so we also included an additive covariate pair consisting of distance to highway and density of roads and highways combined.

Although we treated individual bears as the experimental unit, we performed model selection at the population level because our objective was to characterize typical habitat selection patterns

Table 1. Covariates included in candidate step-selection function models to predict habitat selection of independent-age (≥2 yr old) male grizzly bears monitored with GPS collars in the Northern Continental Divide Ecosystem and Greater Yellowstone Ecosystem, 2000–2015.

	Model									
Covariate	M_1	M_2	M_3	M_4	M_5	M_6	M_7	M_8	M_9	M_{10}
Distance to forest edge	×	×	×	×	×	×	×	×	×	×
Natural contagion	×	×	×	×	×	×	×	×	×	×
Normalized difference vegetation index	×	×	×	×	×	×	×	×	×	×
Distance to highway or secondary road			×	×						
Distance to highway + distance to secondary road	×	×								
Highway density + secondary road density					×	×				
Road and highway density							×	×		
Distance to highway + road and highway density									×	×
Distance to river or stream		×		×		×		×		×
Distance to river + distance to stream	×		×		×		×		×	
Home density ($\log_{10}$)	×	×	×	×	×	×	×	×	×	×
Elevation + elevation^2	×	×	×	×	×	×	×	×	×	×
Vector ruggedness measure	×	×	×	×	×	×	×	×	×	×

associated with bear movements (Fieberg et al. 2010). We estimated SSF parameters (β) separately for the two populations. We used conditional logistic regression via the survival package (v2.39-4; Therneau 2015) and evaluated candidate models using corrected Akaike's information criterion (AIC_c) scores (Hurvich and Tsai 1989, Burnham and Anderson 2002). To account for heterogeneity in bear habitat selection and to equally weight each individual bear, we implemented a two-stage modeling approach: After specifying the covariate structure of the SSF for each population, we fit the model to each individual bear (pooled over years) and then averaged the β values across individual bears to obtain population-level β values.

To evaluate the fit of each population's top model, we used the *k*-fold cross-validation procedure outlined in Boyce et al. (2002). We partitioned individual bears in each population into five subsamples. To ensure that sample sizes among partitions were comparable, we first stratified bears based on sample size (i.e., stratum one contained the top five bears with the largest sample sizes, stratum two included the next five bears, and so on) and then randomly assigned bears within each stratum to a partition. We then estimated the SSF using four of the five partitions as training data, and averaging β values across individual bears to obtain population-level models. For each population and test partition, we predicted SSF scores for each grid cell within the respective areas of grizzly bear occupied range and obtained scores for the locations within the withheld test partition. We divided all mapped (i.e., expected) scores into 10 bins based on quantiles and calculated the proportion of test locations (i.e., observed) that fell within each bin (Boyce et al. 2002, Thurfjell et al. 2014, Clark et al. 2015). For a model with good predictive capabilities, observed proportions are expected to increase with successively higher bins of SSF scores. We computed the Spearman rank correlation between the proportion and bin rank for each cross-validated model. We repeated the entire fivefold cross-validation procedure 100 times to examine whether model performance was consistent among alternative partitions of the data.

Randomized shortest path

We used the RSP algorithm in conjunction with the SSF models to identify potential paths for dispersal of grizzly bears between the NCDE and GYE (Panzacchi et al. 2016). The algorithm is analogous to a least-cost path analysis but subject to a given level of randomness that is controlled by the parameter θ. Lower values of θ result in greater exploration around the shortest path (θ = 0 equivalent to pure random walk), whereas larger values approach the equivalent of a least-cost path. By specifying a range of values for θ, paths can be identified for varying levels of trade-off between exploration and optimal exploitation of the landscape exhibited by individual bears. Animal movements occur through a sequence of linked nodes, as represented by grid cells. The RSP algorithm uses a conductance surface (i.e., the inverse of a friction surface) and θ to estimate the average number of net passages through each grid cell when moving from an origin to a destination node. Given the conductance layer derived from the spatial covariates in the SSF model, paths follow certain grid cell sequences more than others and the resulting RSP values thus provide a measure of movement potential. Collectively, the RSP values for all grid cells in the study region provide an assessment of potential paths for male dispersal.

Using the estimated SSF model for each population, we predicted a conductance surface for the entire study region based on 300-m grid cells. Conductance values for each cell i were based on the $\text{logit}^{-1}(x_i\beta)$, where x_i is the vector of covariate values associated with cell i and β the vector of estimated SSF model coefficients. To avoid conductance values compressing against the boundary of the [0,1] interval, we shifted each $x_i\beta$ value by subtracting the median $x_i\beta$ value for the entire study area (i.e., the median $x_i\beta$ value thus corresponds to a relative probability of 0.5; Panzacchi et al. 2016). We then computed a transition matrix using a Moore neighborhood (i.e., cells connected with their eight orthogonal and diagonal nearest neighbors) with the transition value between cells i and j within the neighborhood equal to $f(c_i, c_j) = \max(c_i, c_j) - c_i + c_j$, where c_i and c_j are the conductance values associated with each cell. Under this specification, the transition value is non-commutative and the transition matrix is asymmetric.

We used the 300-m grid cells to represent the collection of nodes through which animal movements occur. To define origin and destination nodes, we delineated a 25-km buffer zone spanning 500 km on the southern and northern boundaries within estimated grizzly bear occupied range in the NCDE and GYE, respectively (Fig. 1). We chose the eastern and western extents of each buffer to encompass locations where dispersal events were most likely to originate or terminate, based on our collective knowledge of grizzly bear movements in the two populations. For each population, we paired 100 random locations (origin nodes) within the 25-km buffer with a random location (destination node) in the opposing buffer. We computed RSP values for all grid cells in the study region for each pair of origin and destination nodes using the gdistance package (v1.1-9; van Etten 2015) with parameter values for θ of 0.01, 0.001, and 0.0001. Given the study area's spatial resolution and associated conductance values, we visually determined a θ value of 0.1 to be approaching the least-cost path. Bounded by θ values of 0 and 0.1 at the extremes, we chose three intermediate θ values by multiplicatively decreasing the defined maximum of 0.1 by consecutive powers of 10.

For each level of θ and node pair, we obtained a raster layer containing the average net number of passages through each grid cell. For each θ, we then summed the RSP raster layers for all 100 node pairs as an index of movement potential for simulated dispersal events from the NCDE to the GYE, and vice versa. Finally, for each value of θ, we multiplied the cumulative RSP layers for both populations together to delineate areas where predictions intersected, weighted by the respective number of net passages. Higher values identified areas where the NCDE and GYE models predicted a high number of passages, and lower values reflected fewer predicted paths for one or both models.

No data existed for a robust external validation of our predictions. However, 21 confirmed observations of grizzly bears $\geq$8 km outside of, and between, the two estimated grizzly bear occupied ranges (Montana Department of Fish, Wildlife and Parks, *unpublished data*; IGBST, *unpublished data*) provided an opportunity to corroborate model predictions. For each location, we computed its quantile value based on the distribution of all non-zero, cumulative RSP values from all grid cells within the rectangular area encompassing all primary paths and outlier observations (Figs. 2–4). Because we predicted movements in areas different from where these data were sampled, this analysis offered an ad-hoc, external validation of the paths.

RESULTS

We obtained GPS telemetry data from 173 male bears (NCDE = 33, GYE = 140) for a total of 309 bear-years (NCDE = 47, GYE = 262) over

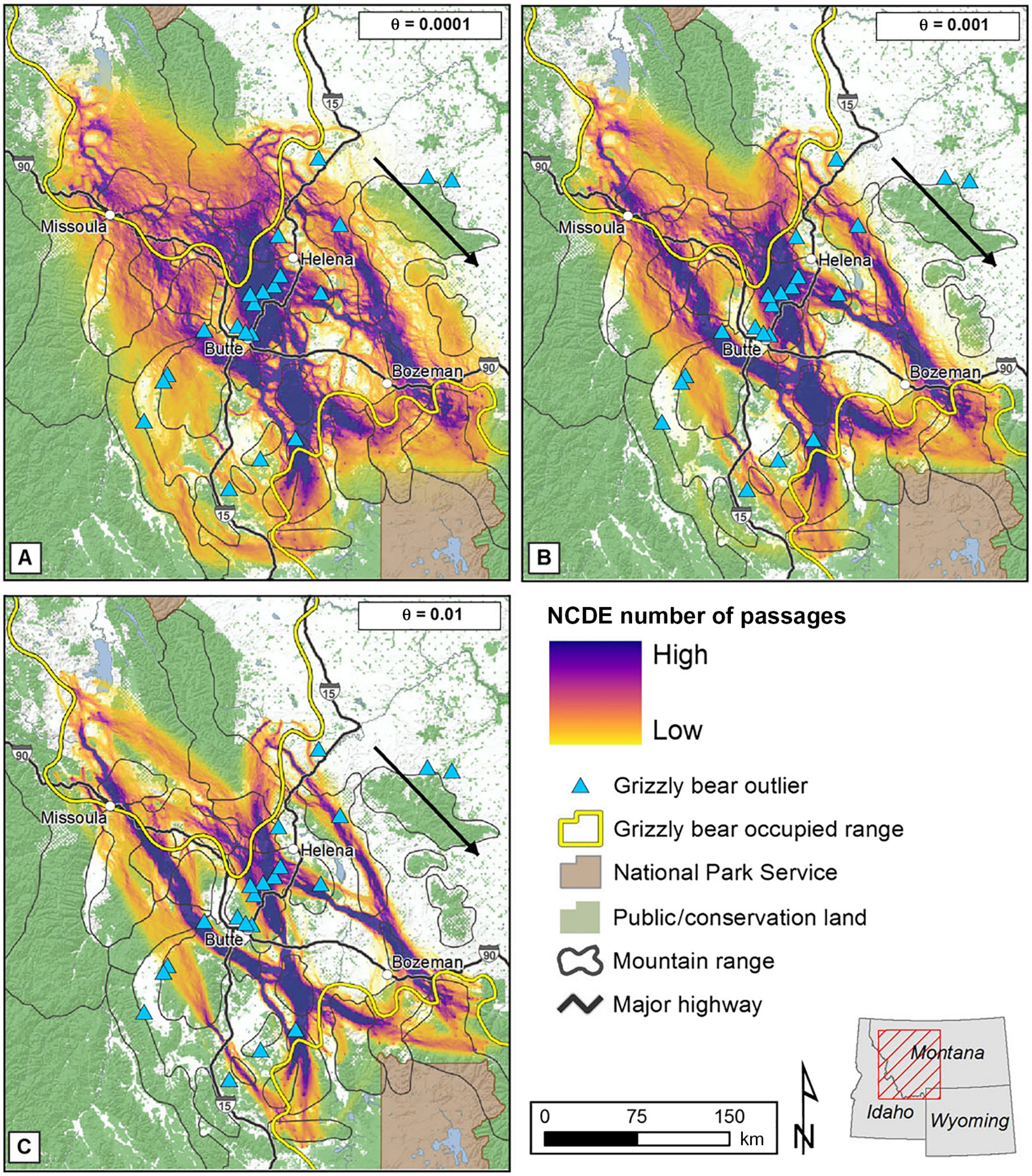

Fig. 2. Randomized shortest path (RSP) predictions of male grizzly bear movements from the Northern Continental Divide Ecosystem (NCDE) to the Greater Yellowstone Ecosystem (GYE) based on GPS movement data for males monitored in the NCDE, 2000–2015. Color gradient is based on cumulative values of RSPs for 100 pairs of origin–destination nodes, representing the average number of net passages for each grid cell. Three levels of θ are shown, representing different trade-offs between exploration and optimal exploitation of the landscape: (A) θ = 0.0001, (B) θ = 0.001, and (C) θ = 0.01. Locations of 21 confirmed records of grizzly bear presence are shown as blue triangles. Black arrow indicates direction of paths. Occupied range based on data through 2014 (Bjornlie et al. 2014, Costello et al. 2016).

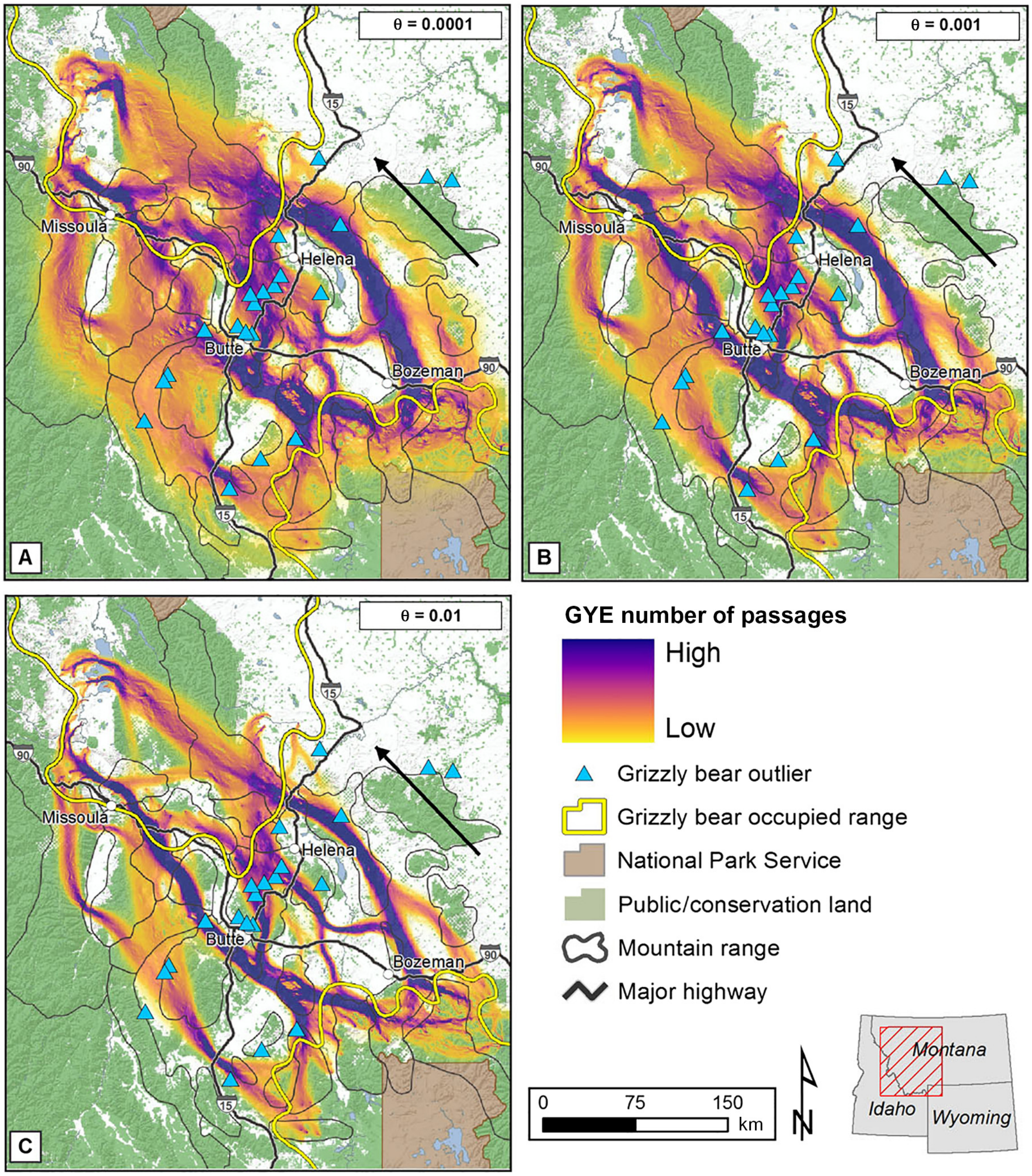

Fig. 3. Randomized shortest path (RSP) predictions of male grizzly bear movements from the Greater Yellowstone Ecosystem (GYE) to the Northern Continental Divide Ecosystem (NCDE) based on GPS movement data for males monitored in the GYE, 2000–2015. Color gradient is based on cumulative values of RSPs for 100 pairs of origin–destination nodes, representing the average number of net passages for each grid cell. Three levels of θ are shown, representing different trade-offs between exploration and optimal exploitation of the landscape: (A) θ = 0.0001, (B) θ = 0.001, and (C) θ = 0.01. Locations of 21 confirmed records of grizzly bear presence are shown as blue triangles. Black arrow indicates direction of paths. Occupied range based on data through 2014 (Bjornlie et al. 2014, Costello et al. 2016).

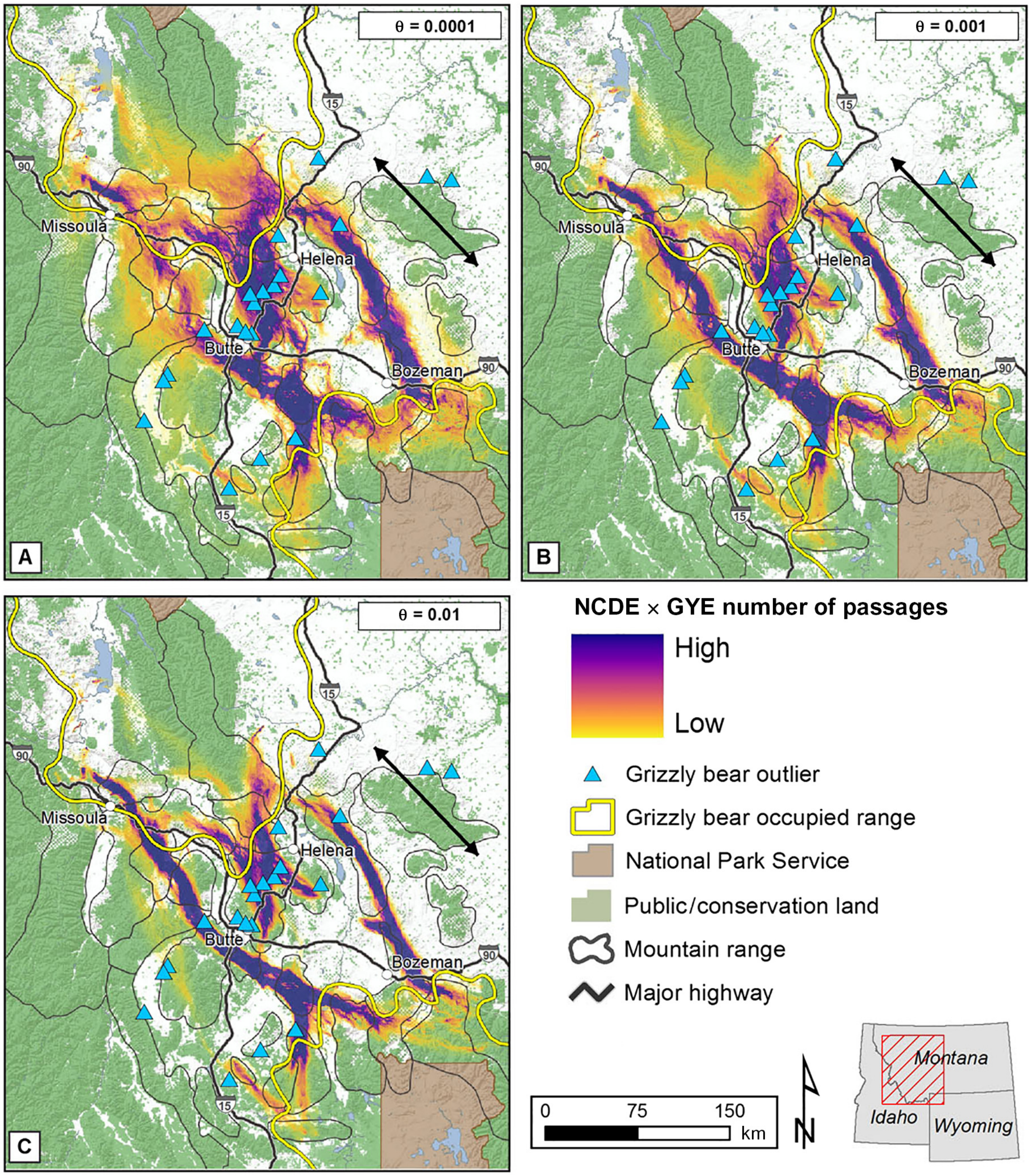

Fig. 4. Intersect of randomized shortest path (RSP) predictions of male grizzly bear movements between the Northern Continental Divide Ecosystem (NCDE) and Greater Yellowstone Ecosystem (GYE), 2000–2015. Color gradient is based on multiplication of cumulative values of RSPs for 100 pairs of origin–destination nodes for each population (Figs. 2, 3). Three levels of θ are shown, representing different trade-offs between exploration and optimal exploitation of the landscape: (A) θ = 0.0001, (B) θ = 0.001, and (C) θ = 0.01. Locations of 21 confirmed records of grizzly bear presence are shown as blue triangles. Black arrow indicates direction of paths. Occupied range based on data through 2014 (Bjornlie et al. 2014, Costello et al. 2016).

the period May 2000–October 2015. Telemetry monitoring resulted in 58,737 and 237,680 GPS fixes in the NCDE and GYE, respectively. After removing steps and individual bears that failed to meet our inclusion criteria, we retained 131 male bears (NCDE = 15, GYE = 116) spanning 212 bear-years (NCDE = 22, GYE = 190). Ages of bears ranged from two to 16 with a median of four years in the NCDE, and from two to 30 with a median of eight years in the GYE. The NCDE dataset contained 17,624 steps with step counts among individuals ranging from 112 to 4445. The GYE dataset contained 108,309 steps with step counts among individual bears ranging from 106 to 4491. Median step length was 520 m (range = 100–10,420) in the NCDE and 724 m (range = 100–14,520) in the GYE. Because longer step lengths occurred more frequently among GYE bears than NCDE bears, and because of landscape differences, we fit separate step-length distributions for each population (beta distribution parameter MLEs: $\alpha = 0.792$, $\beta = 16.532$ for NCDE; $\alpha = 0.708$, $\beta = 9.027$ for GYE). Mean step duration was 68.7 min (range = 26.6–240.0) for NCDE bears and 106.4 min (range = 26.7–240.0) for GYE bears. Turning angles exhibited directional persistence and were independent of step length ($R = 0.007$). Plots of turning angles indicated no practical difference between bears in the two populations. Because we had no ecological basis to assume directionality of movements would be different for the NCDE and GYE, we estimated a single, pooled turning angle distribution (von Mises parameter MLEs: $\mu = 0.020$, $\kappa = 0.607$). Median cumulative step length among individual bears was 484.4 km (range = 103.0–2013.0) for NCDE and 610.9 km (range = 57.2–2072.0) for GYE bears.

Table 2. Model selection results for step-selection models to predict movements of independent-age (≥2 yr old) male grizzly bears monitored with GPS collars in the Northern Continental Divide Ecosystem (NCDE) and Greater Yellowstone Ecosystem (GYE), 2000–2015.

Population	Model	k	AIC$_c$	ΔAIC$_c$	w_i	logL
NCDE	M_6	10	83,537.6	0.0	0.44	−41,758.8
	M_{10}	10	83,538.3	0.7	0.31	−41,759.1
	M_8	9	83,539.4	1.8	0.18	−41,760.7
	M_2	10	83,542.2	4.6	0.04	−41,761.1
	M_4	9	83,543.1	5.5	0.03	−41,762.5
	M_9	11	83,582.1	44.5	0.00	−41,780.0
	M_5	11	83,583.5	45.9	0.00	−41,780.8
	M_7	10	83,584.6	47.0	0.00	−41,782.3
	M_1	11	83,585.9	48.3	0.00	−41,781.9
	M_3	10	83,588.2	50.6	0.00	−41,784.1
GYE	M_9	11	515,059.2	0.0	1.00	−257,518.6
	M_7	10	515,110.2	51.0	0.00	−257,545.1
	M_{10}	10	515,110.5	51.3	0.00	−257,545.3
	M_5	11	515,111.8	52.6	0.00	−257,544.9
	M_1	11	515,158.1	98.9	0.00	−257,568.0
	M_8	9	515,161.1	101.9	0.00	−257,571.6
	M_6	10	515,163.1	103.9	0.00	−257,571.5
	M_3	10	515,194.4	135.2	0.00	−257,587.2
	M_2	10	515,206.1	146.9	0.00	−257,593.1
	M_4	9	515,240.3	181.1	0.00	−257,611.2

Note: Shown are differences in Akaike's information criteria for small sample sizes (AIC$_c$) between the model and lowest AIC$_c$ in the model set (ΔAIC$_c$), number of estimable parameters (k), model weight (w_i), and the log-likelihood (logL).

For the NCDE, several population-level models were parsimonious based on ΔAIC$_c$ values <2 (models M_6, M_{10}, and M_8; Table 2). We chose model M_{10} because it reflected biologically relevant covariates based on the hypothesis that bear response may be a function of both traffic volume associated with highways and overall density of roads and highways. Average Spearman rank correlations for the 100 iterations of fivefold cross-validation ranged from 0.743 to 0.990 (median = 0.939), indicating good predictive capacity within the NCDE. Individual-level models could not be fit for seven GYE bears because of zero variation in either the natural contagion or road–highway density covariate. Thus, population-level covariates were based on 109 male bears for a total of 177 bear-years and 98,655 steps. Model M_9 was most parsimonious among the candidate set by a large margin (ΔAIC$_c$ = 50.991; Table 2). Average Spearman rank correlations from fivefold cross-validation ranged from 0.678 to 0.969 (median = 0.862) for the 100 iterations, indicating good predictive capacity within the GYE.

The cumulative RSP layer based on the NCDE conductance map depicted numerous potential paths from the NCDE to the GYE. These included areas of dense paths that formed intersecting corridors linking mountain ranges in the center of the study area, and broader areas with more diffuse paths on the periphery (Fig. 2). Two corridors consisting of dense paths converged on the Tobacco Root Mountains. One originated in the Rattlesnake–Garnet ranges and traversed the John Long, Flint Creek, Anaconda, Pioneer, and Highland ranges, whereas the other originated in the Nevada–Garnet ranges and traversed the Boulder Mountains. After traversing the Tobacco Root Mountains, paths entered the GYE through the Madison or Gravelly ranges. Two other routes with dense paths originated in the southern Lewis and Clark Range and converged on the Bridger Range prior to entering the GYE. One followed the Nevada, Boulder, Elkhorn, and southern Big Belt Mountains, and the other traversed the Big Belt Mountains. Longer, more meandering paths were evident on the western and eastern peripheries, especially for models with $\theta = 0.0001$. Paths on the western periphery extended from the Bitterroot and Anaconda ranges and traversed the Pioneer and Blacktail ranges before reaching the Gravelly or Centennial ranges. Paths on the eastern periphery followed the Little Belt, Castle, and Crazy ranges.

For the GYE, the cumulative raster layers of the 100 RSP models also showed many potential paths leading from the GYE to the NCDE (Fig. 3). Areas with a high density of paths formed two corridors that originated in the Gravelly, Madison, or Gallatin ranges, converged on the Tobacco Root and Highland ranges, but then split to follow the Pioneer, Anaconda, Flint Creek, and John Long Mountains or the Boulder Mountains to enter the NCDE. Predicted paths originating in the Absaroka and Gallatin ranges were concentrated and formed a corridor along the Bridger and Big Belt Mountains or branched at the southern portion of the Big Belt Mountains to the Elkhorn and Boulder Mountains. Several alternative routes interconnecting these areas were evident as well. Predicted paths were moderately dense and formed a corridor that originated from the southern Madison Range and Centennial Mountains, and subsequently traversed the Snowcrest, Blacktail, Pioneer, Anaconda, and Sapphire Mountains. More diffuse paths on the western periphery also included the Tendoy, Beaverhead, and Bitterroot ranges. Diffuse paths on the eastern periphery included the Crazy Mountains and, to a lesser extent, the Castle and Little Belt ranges.

We observed broad-scale concordance between model predictions for paths originating in the NCDE and those originating in the GYE for all values of θ (Figs. 2, 3). Based on the weighted, spatial intersection of model predictions, there was low potential for movement within large portions of the area between the two ecosystems, generally reflecting wide, open, inter-mountain valleys encompassing human settlements and agriculture (Fig. 4). Models also agreed on a high density of paths forming several distinct routes in the central portion of the area, where path options were limited due to habitat fragmentation. Additionally, areas with high intersection of model predictions were associated with the Bridger and Big Belt Mountains in the east and the previously described routes between the Rattlesnake–Garnet ranges south of the NCDE and the Tobacco Root Mountains northwest of the GYE (Fig. 4).

Confirmed locations of grizzly bears beyond the occupied ranges generally were in grid cells predicted to have relatively high net passage rates (median quantile values = 0.75–0.87; Figs. 2–4), with generally higher values for the NCDE model compared with the GYE model (Table 3). Within each model, differences in quantiles across θ values were small, indicating little influence due to varying levels of movement exploration between nodes. Three locations (locations 8, 20, and 21) for the NCDE model and five locations (locations 4, 8, 16, 20, and 21) for the GYE model were in areas with lower predicted passage rates, whereas four locations (locations 8, 16, 20, and 21) had a low passage rate according to the intersection of model predictions (Table 3; Appendix S1: Fig. S2).

DISCUSSION

Although we observed fine-scale differences in our predicted paths, spatial concordance was high between models based on the NCDE vs. the GYE grizzly bear location data. Close agreement between the models is particularly germane when judging the validity of our results, given that we applied the models to areas beyond the origins of the training data (Boyce et al. 2002). Reliability of our model output was also supported by positive results of the fivefold cross-validation of the SSF component and our ad-hoc external validation of the RSP component using verified outlier observations of grizzly bears.

Model predictions, particularly those based on lower values of θ, indicated that grizzly bear paths between the populations might involve any number of routes. This result is not

Table 3. Information about confirmed grizzly bear locations observed between the occupied ranges of the Northern Continental Divide Ecosystem (NCDE) and Greater Yellowstone Ecosystem (GYE) populations, and individual and median quantile values of their location grid cells (as computed from the distributions of all non-zero, cumulative randomized shortest path [RSP] cell values within the rectangular area encompassing all predicted paths and outlier observations [Figs. 2–4]).

Loc. number (yr)	Type†	Cohort‡ (origin; if known)	Distance from 2014 occupied range (km)		Quantile of RSP distribution								
					NCDE model			GYE model			Intersect model		
			NCDE	GYE	θ = 0.0001	θ = 0.001	θ = 0.01	θ = 0.0001	θ = 0.001	θ = 0.01	θ = 0.0001	θ = 0.001	θ = 0.01
1 (1998)	M	SM (GYE)	141	19	0.54	0.59	0.65	0.64	0.62	0.59	0.60	0.63	0.62
2 (2005)	M	SM (NCDE)	43	113	0.87	0.92	0.92	0.92	0.98	1.00	0.91	0.97	0.98
3 (2010)	DNA	AM (NCDE)	8	137	0.91	0.86	0.86	0.67	0.67	0.67	0.85	0.80	0.78
4 (2010)	M	AM (NCDE)	40	80	0.88	0.83	0.77	0.42	0.52	0.53	0.56	0.66	0.65
5 (2014)	BP	S	163	34	0.66	0.76	0.72	0.93	0.92	0.89	0.84	0.86	0.79
6 (2015)	TO	AFC	22	100	0.99	0.98	0.97	0.93	0.93	0.93	0.97	0.96	0.96
7 (2016)	TO	S	32	93	0.76	0.68	0.63	0.57	0.57	0.52	0.68	0.64	0.57
8 (2016)	I	S	8	192	0.33	0.49	0.59	0.19	0.24	0.20	0.21	0.33	0.30
9 (2016)	BP, TP	S	89	120	0.73	0.79	0.84	0.75	0.80	0.84	0.78	0.83	0.87
10 (2016)	TP	S	96	119	0.67	0.75	0.77	0.74	0.82	0.86	0.75	0.81	0.82
11 (2016)	BP	S	60	83	0.93	0.93	0.89	0.67	0.64	0.59	0.86	0.81	0.74
12 (2016)	BP	S	25	106	0.94	0.94	0.93	0.92	0.91	0.94	0.94	0.93	0.94
13 (2016)	BP	S	18	96	0.97	0.96	0.95	0.90	0.91	0.92	0.95	0.94	0.95
14 (2016)	BP, C	SM (NCDE)	17	100	0.96	0.95	0.93	0.94	0.93	0.92	0.95	0.95	0.93
15 (2016)	BP, TO	S	10	104	0.98	0.95	0.95	0.94	0.93	0.94	0.97	0.95	0.95
16 (2016)	TP	S	37	85	0.57	0.60	0.61	0.38	0.44	0.41	0.45	0.50	0.48
17 (2016)	BP	S	131	115	0.60	0.56	0.53	0.80	0.73	0.66	0.73	0.68	0.60
18 (2017)	TP	S	132	9	0.99	0.99	0.97	0.93	0.94	0.95	0.97	0.98	0.97
19 (2017)	BP	S	49	137	0.91	0.90	0.91	0.94	0.91	0.82	0.93	0.92	0.90
20 (2017)	BP	SM§	90	167	0.37	0.32	0.30	0.28	0.25	0.14	0.31	0.28	0.16
21 (2017)	M	SM§	110	164	0.17	0.16	0.15	0.20	0.19	0.09	0.19	0.18	0.08
Median			43	104	0.87	0.83	0.84	0.75	0.80	0.82	0.84	0.81	0.79

Notes: Values of θ represent different trade-offs between exploration and optimal exploitation of the landscape, with greater exploration movements at lower values. Several within-year observations may be of the same individual bear.

† Type: BP, bear photographed; C, capture; M, mortality; DNA, hair DNA sample; I, investigated; TO, tracks observed; TP, tracks photographed.

‡ Cohort: AFC, adult female with cub-of-the-year; AM, adult male; S, solitary bear, unknown sex or age class; SM, subadult male.

§ Locations 20 and 21 are multiple records of two sibling males traveling together.

unexpected given that grizzly bears are generalists and occur in a wide variety of habitats, both across and within populations (Stirling and Derocher 1990). Therefore, with the exception of areas with low numbers of predicted passages (e.g., wide open valleys), we anticipate that sporadic bear sightings and possible interactions with humans may occur almost anywhere along the gradient of our model predictions. Still, the exploration vs. optimal exploitation trade-off component of the RSP procedure (i.e., modulation based on θ) enhanced our understanding of the range of potential paths available to grizzly bears. Whereas paths with the lowest level of exploration allowed us to identify the more direct routes that bears may use to move between the ecosystems, areas with greater predicted passage rates do not necessarily reflect superior habitat characteristics compared with areas with more diffuse paths. In fact, areas where paths are more scattered seem to reflect more contiguous habitats, as opposed to areas where anthropogenic influence is greater and path options are limited. For example, despite longer routes, the pattern of diffuse paths on the western periphery suggests ample movement options, likely as a function of large, contiguous areas of natural landscapes (forest and range land) with limited anthropogenic influence. As indicated by Panzacchi et al. (2016), RSP analyses are based on the assumption that animals have prior knowledge of the entire landscape but move neither optimally (i.e., following the shortest path) nor entirely at random, often exhibiting exploratory movements. This assumption is likely met for male grizzly bears moving within their home range, but may involve more exploration among dispersing bears. Therefore, we caution against a sole focus on the most heavily predicted corridors based on the larger θ value (i.e., Figs. 2C, 3C, 4C), and encourage consideration of alternative paths that reflect a greater level of exploration (panels A and B in Figs. 2–4).

We also emphasize that areas where we identified potential paths should not be interpreted as habitat linkages that provide conditions conducive to permanent grizzly bear occupancy as they may not represent the most likely areas for future range expansion. Identification of such areas will require a different approach, involving additional data (e.g., female locations, resting and denning locations) and likely different spatial covariates. The two types of connectivity were illustrated by Proctor et al. (2012). They reported that grizzly bear populations along the Canada–U.S. border area remained genetically connected through male immigration, but lacked demographic connectivity because habitat fragmentation (primarily transportation infrastructure and human settlements) severely inhibited movement of females.

Although our models provide information about possible routes for male-mediated gene flow, a key question is how high the likelihood of successful immigration is. Total distances of predicted paths in the central region range from approximately 135 to 210 km, whereas paths in the western periphery may exceed 350 km. These distances surpass average dispersal distances for male grizzly bears recorded in the northern Rocky Mountains (30–42 km), but overlap the range of maximum distances observed (67–176 km; Blanchard and Knight 1991, McLellan and Hovey 2001, Proctor et al. 2004). To date, the most remote verified observations of grizzly bears within the region between the populations were located ~110 km from the GYE and ~95 km from the NCDE (locations 9, 10, 11, and 17), confirming that movements within this distance range are possible (Table 3). Nonetheless, the probability of successful dispersal may still be low, despite recent population expansion. In fact, results of a first attempt to model movement between the populations support this notion: Based on the SSF we reported here, we initially used a correlated random-walk method similar to Clark et al. (2015). However, among 20,000 simulations consisting of 3000 steps (equivalent to one active season), very few simulated walks reached the vicinity of the destination population, and none were fully successful. It was only by constraining the starting and end nodes of paths using the RSP approach (Panzacchi et al. 2016) that we were able to predict potential paths linking the two populations. Thus, although our results delineate many possible paths for dispersal between the two ecosystems, successful immigration events will likely remain rare given the current distance between the populations. If the two populations continue to expand and this distance decreases, the likelihood of successful immigration will increase accordingly.

We identified several interconnected areas with concentrated paths along neighboring mountain ranges that may serve as stepping stones to male grizzly bear dispersal between the two ecosystems. Concentrated paths following the Big Belt and Bridger Mountains and the Boulder and Tobacco Root Mountains were similar to those identified by Picton (1986), Walker and Craighead (1997), and Cushman et al. (2009). However, our analyses placed much greater emphasis on potential paths following the Rattlesnake, Garnet, John Long, Flint Creek, Anaconda, Pioneer, and Highland Mountains. The Tobacco Root Mountains may be a particularly pivotal stepping stone, as many different paths converged on this mountain range. To date, no recent observations of grizzly bears have been confirmed within the Tobacco Root Mountains, despite DNA sampling efforts (Lukins et al. 2004) and surveillance based on observation reports (K. Frey, Montana Department of Fish, Wildlife and Parks, *personal communication*). Corridors delineated by Dilkina et al. (2016) for grizzly bears only partially aligned with those we identified in our study. One reason for this difference is likely related to different analytical approaches. Whereas our study relied on extensive GPS data to predict how bears may explore the landscape between the NCDE and

GYE, Dilkina et al. (2016) used optimization procedures based on landscape resistance to bear movement, defined based on qualitative weighting of habitat types and road density, combined with estimated costs of land acquisition given specific budget constraints.

In our analyses, we assumed the conductance surface values represent the willingness of a bear to traverse a given spatial unit, but we did not specifically evaluate the potential for transportation infrastructure to act as local barriers to movement. For example, our models were capable of accounting for grizzly bear avoidance of areas with high road density (Mace et al. 1996, Chruszcz et al. 2003, Waller and Servheen 2005, Roever et al. 2010), but were not equipped to identify specific multi-lane, high-volume highways that may impede movement (e.g., interstate highways I-90 and I-15). Nevertheless, our results can be used to identify sections of these highways where crossings might occur similar to Cushman et al. (2009), who identified 21 potential barriers to animal movement along predicted black bear corridors within our study region. Those barriers represented gaps in federal land ownership and major highways, areas in federal ownership but traversed by major highways, and areas where major highways paralleled corridors.

Interpretation of our analyses required a number of additional assumptions. First, we assumed that the sample used in our analyses adequately represented the population of male bears in each population. We also assumed that dispersing male bears explore new terrain in a manner similar to the observed movements of bears in our sample. Median ages for bears in our sample were four and eight for the NCDE and GYE, respectively, so observed movements were likely representative of bears within established home ranges, as well as more exploratory movements among young males. Given that dispersal is typically a gradual process, we believe this assumption was reasonable. Additionally, because of range expansion, landscape conditions on the periphery of occupied range are not substantially different from areas between the two ecosystems. We also assumed that selection of covariates was similar across seasons and across years for bears with multiple years of data and that any changes in covariate values during the period of 2000–2015 were negligible. Given that our sample size of individual bears was large, the concordance of results based on two independent datasets, the similarity of RSP quantiles associated with the 21 outlier locations across the three values of θ, and our careful selection of covariates associated with movement steps, we believe these assumptions were generally met. In drawing from the pooled distribution of step lengths and turning angles but estimating SSF parameters for each individual, we implicitly assumed that sampled bears exhibited similar movement behaviors but made individual choices depending on habitat availability within the reach of one step length. Finally, given the spatial resolution of the covariates, we assumed those choices were not affected by variation in our GPS fix rates (Thurfjell et al. 2014).

Our study provides detailed, spatially explicit information for land managers and organizations working with land owners to identify and prioritize conservation measures to maintain or enhance the integrity of areas supporting potential dispersal of male grizzly bears, such as conservation easements and land purchases; mitigation of highway and other infrastructure barriers across key paths; and proactive education and attractant management programs to prevent or reduce human–bear conflict. The predicted RSPs are available as GIS data layers (300 m pixel size) and can be used in landscape planning decisions (see https://doi.org/10.5066/f72v2f2w).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1969/full