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Research Article

Grizzly Bear Connectivity Mapping in the Canada–United States Trans-Border Region

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ABSTRACT Fragmentation is a growing threat to wildlife worldwide and managers need solutions to reverse its impacts on species' populations. Populations of grizzly bears (*Ursus arctos*), often considered an umbrella and focal species for large mammal conservation, are fragmented by human settlement and major highways in the trans-border region of southern British Columbia, northern Montana, Idaho, and northeastern Washington. To improve prospects for bear movement among 5 small fragmented grizzly bear subpopulations, we asked 2 inter-related questions: Are there preferred linkage habitats for grizzly bears across settled valleys with major highways in the fragmented trans-border region, and if so, could we predict them using a combination of resource selection functions and human settlement patterns? We estimated a resource selection function (RSF) to identify high quality backcountry core habitat and to predict front-country linkage areas using global positioning system (GPS) telemetry locations representing an average of 12 relocations per day from 27 grizzly bears (13F, 14M). We used RSF models and data on human presence (building density) to inform cost surfaces for connectivity network analyses identifying linkage areas based on least-cost path, corridor, and circuit theory methods. We identified 60 trans-border (Canada–USA) linkage areas across all major highways and settlement zones in the Purcell, Selkirk, and Cabinet Mountains encompassing 24% of total highway length. We tested the correspondence of the core and linkage areas predicted from models with grizzly bear use based on bear GPS telemetry locations and movement data. Highway crossings were relatively rare; however, 88% of 122 crossings from 13 of our bears were within predicted linkage areas (mean = 8.3 crossings/bear, SE = 2.8, range 1–31, 3 bears with 1 crossing) indicating bears use linkage habitat that could be predicted with an RSF. Long-term persistence of small fragmented grizzly bear populations will require management of connectivity with larger populations. Linkage areas identified here could inform such efforts.

KEY WORDS circuit theory, GPS telemetry, grizzly bear, population fragmentation, resource selection function, RSF, trans-border, *Ursus arctos*.

Fragmentation of populations threatens species' persistence and thus biodiversity (Wilcove et al. 1998, Fahrig 2003) by interrupting ecological processes including gene flow (Frankham 2006), inter-population dynamics (Moilanen and Hanski 2006), and demographic rescue (Martin et al. 2000, Peery et al. 2010). Several large mammals, including American black bear (*Ursus americanus*; Dixon et al. 2007, van Manen et al. 2012), wolverine (*Gulo gulo*; Cegelski et al. 2006), mountain caribou (*Rangifer tarandus*; van Oort et al. 2011), pronghorn antelope (*Antilocapra americana*; Poor et al. 2012), bighorn sheep (*Ovis canadensis*; Epps et al. 2007), and grizzly bear (*Ursus arctos*; Proctor et al. 2005, 2012) are affected by population fragmentation at the southern extent of their North American distributions. Consequently, increasing attention is being given to the issue of connectivity of populations (Calabrese and Fagan 2004) in North America (Apps et al. 2007, Chetkiewicz and Boyce 2009, Ford et al. 2009), and worldwide (Crooks and Sanjayan 2006, Hilty et al. 2006).

There is growing interest in identifying wildlife corridors or linkage areas to reverse habitat and population fragmentation (Beier et al. 2006, 2011; Chetkiewicz et al. 2006; Li et al. 2010), with numerous methods being used (see reviews by Urban et al. 2009, Rayfield et al. 2011). There has been an evolution of least-cost modeling (Adriaensen et al. 2003, Sawyer et al. 2011) to include network analyses such as graph theory (Urban and Keitt 2001, Chetkiewicz et al. 2006) and

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more recently circuit theory (McRae et al. 2008, Walpole et al. 2012). These newer methods predict multiple alternative pathways that can become swaths of connectivity routes or broader corridors (Rayfield et al. 2011), providing a more detailed exploration of potential movement routes and corridor variability (Walpole et al. 2012).

Extensive population-level fragmentation of grizzly bears exists throughout the Canada–USA trans-border region of southern British Columbia (BC) and Alberta in Canada, and northern Montana, Idaho and Washington in the United States (Proctor et al. 2012; Fig. 1a). Five small fragmented subpopulations (<100 bears) have minimal or no female interchange with neighboring subpopulations and are separated by human settlement, highway traffic, and human-caused mortalities (Wakkinen and Kasworm 2004; Proctor et al. 2007, 2012). Long-term survival of these small, threatened subpopulations will depend on successful management that reconnects them with a larger adjacent regional subpopulation in the Central Purcell-Selkirk mountain area that numbers more than 500 bears (Proctor et al. 2012, Fig. 1b). Part of this management challenge is that regionally, female grizzly bear dispersal occurs gradually over several years (McLellan and Hovey 2001*a*) and over short distances (McLellan and Hovey 2001*a*, Proctor et al. 2004*a*). This dispersal pattern results in prolonged exposure of grizzly bears to mortality risk when in proximity to human settlements and highway traffic. In contrast to female bears, males move longer distances (McLellan and Hovey 2001*a*, Proctor et al. 2004*a*) with the ability to mediate nDNA gene flow (Proctor et al. 2012), although they too experience mortality in human-settled valleys (McLellan 1998, McLellan et al. 1999), contributing to fragmentation of populations (Proctor et al. 2012). Immigration of both sexes is necessary for range expansion and in some cases demographic and genetic rescue (Piessens et al. 2004; e.g., Cabinet Mountains of northwest Montana, Kasworm et al. 2007, 2011). Proctor et al. (2012) recommended management actions to increase linkage areas between regional subpopulations in an effort to enhance survival and demographic interchange. We define linkage areas as the best available habitat connecting patches of backcountry habitat through human-settled valleys and across major highways.

Linkage areas for bears have been identified elsewhere based on analyses of multiple highway crossings by grizzly bears in Alaska (Graves et al. 2007) and black bears in Idaho (Lewis et al. 2011). This direct approach is useful where bears are still crossing highways. However, in our region, grizzly bears infrequently cross highways, especially in areas associated with human settlement (Proctor et al. 2012). Therefore, we need a predictive method for identifying linkage areas and of equal importance is a mechanism to test the efficacy of these predictions, a challenge when real highway crossing data are limited.

We addressed this challenge by incorporating resource selection function (RSF; Manly et al. 2002) models built

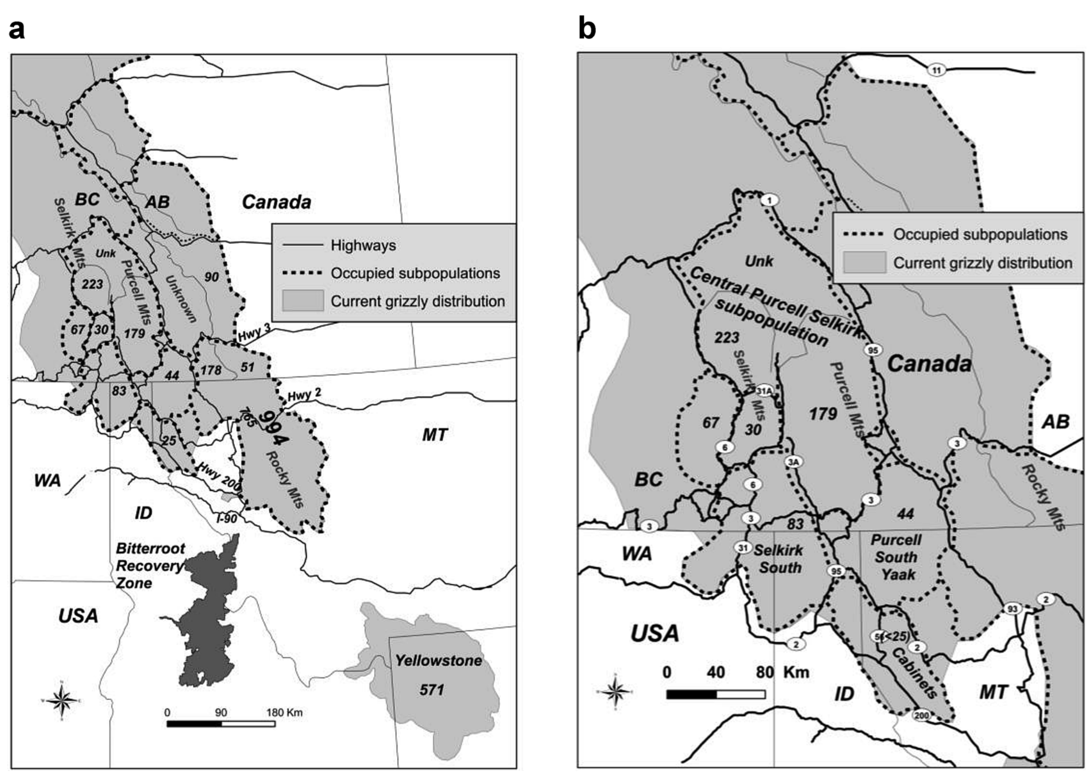

Figure 1. (a) Trans-border regional grizzly bear distribution, including the unoccupied Bitterroot Recovery Zone, with occupied subpopulations as adapted from Proctor et al. (2012). (b) Focal study area of the South Selkirk and Purcell Mountains of southeastern British Columbia, northwestern Montana, northern Idaho, and northeastern Washington, including major highways. Numbers represent empirically derived population estimates for each subpopulation (see references within Proctor et al. 2012).

from grizzly bear global positioning system (GPS) telemetry data to predict backcountry areas of higher quality habitat, and then linkage areas through human-settled valleys. We combined RSF modeling with least-cost modeling (Larkin et al. 2004, Kindall and van Manen 2007, Chetkiewicz and Boyce 2009), and circuit theory (McRae et al. 2008), to identify and map linkage areas across population fractures within our study area.

Our goal was to answer 2 interrelated questions: Are there preferred linkage habitats for grizzly bears across major highways and settled valleys in the fragmented trans-border region, and if so, could we predict them using a combination of resource selection functions and human settlement patterns? Identifying linkage habitat would allow us to potentially manage human development and activity to enable bears to move between subpopulations with a reduced mortality risk. This should improve the potential to re-establish the processes of inter-area dispersal, connectivity, gene flow, demographic rescue of small isolated subpopulations, and provide adaptive options for climate change should they be necessary.

STUDY AREA

Our study area was within the Canada–USA trans-border region of the South Selkirk, Purcell, and Cabinet Mountains of southeastern BC, northwestern Montana, northern Idaho, and northeastern Washington (Fig. 2). It was selected to span several human-settled valleys with major highways that were previously identified as fractures to grizzly bear populations (Proctor et al. 2012). This area is mountainous throughout and is primarily conifer forest, with occasional wetlands, avalanche paths, alpine areas above tree line, and other non-treed habitats. The region supports a timber industry and sporadic mining on both sides of the border that have left a network of backcountry roads. Mountain ranges are separated by valleys containing major highways and railways that connect urban centers and often support a linear assemblage of rural landowners or communities along portions of their length. Average summer traffic volumes range between approximately 2,000 vehicles per day (vpd) along US Highways 2, 200, and 95, approximately 3,600 vpd along BC Highway 3A, and approximately 4,300 vpd along BC Highway 3. Human settlement along highways varies from stretches with continuous rural settlement to stretches with very little development (Proctor et al. 2012). Occasional villages of up to 1,000 people, to towns of over 20,000 people, occur throughout the region. Valley widths vary from less than 500 m to 7 km. Wide, flat valleys tend to be extensively settled or dominated by agriculture, whereas narrow valleys are typically characterized by sporadic rural development.

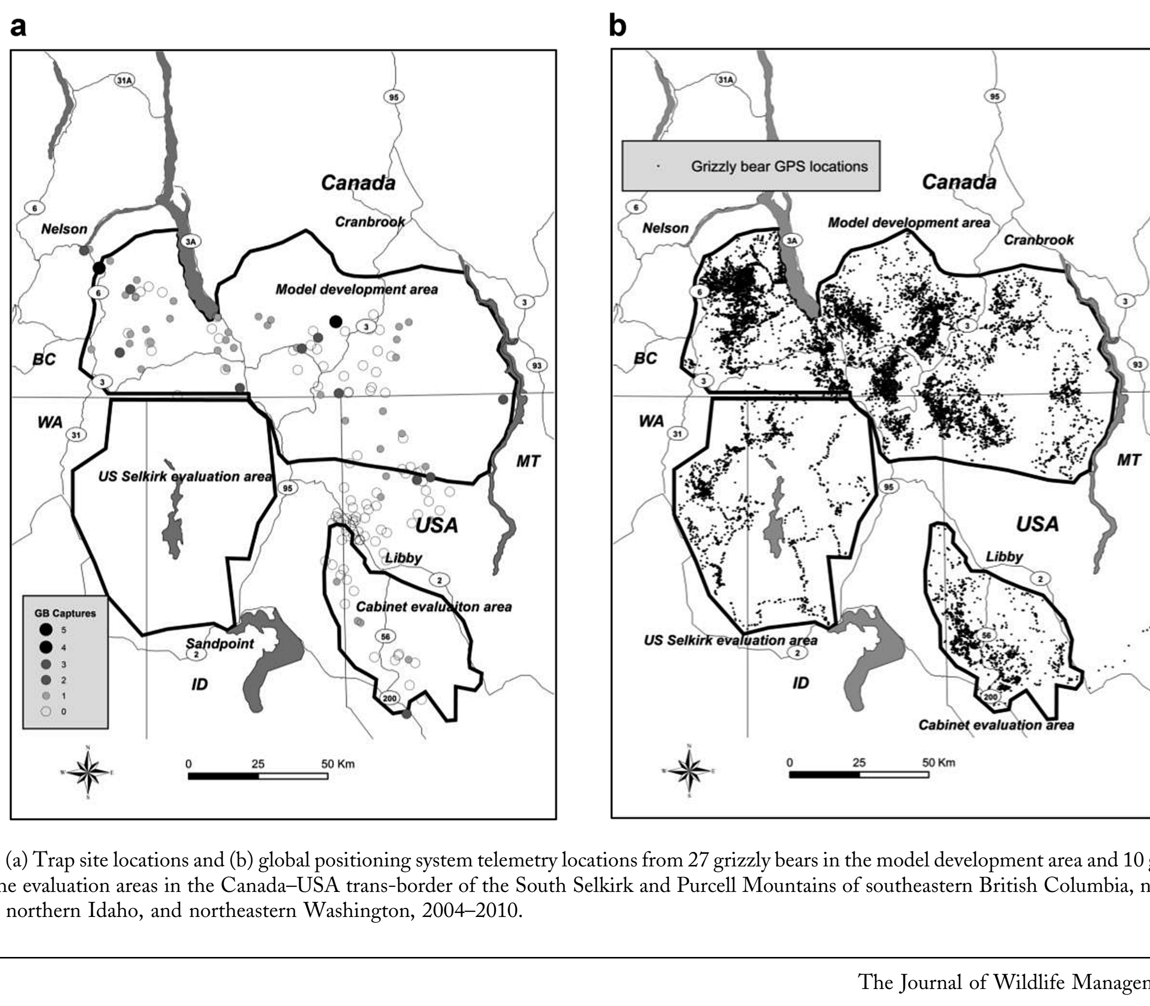

Figure 2. (a) Trap site locations and (b) global positioning system telemetry locations from 27 grizzly bears in the model development area and 10 grizzly bears (GB) in the evaluation areas in the Canada–USA trans-border of the South Selkirk and Purcell Mountains of southeastern British Columbia, northwestern Montana, northern Idaho, and northeastern Washington, 2004–2010.

METHODS

We assessed habitat selection at the scales of our entire multi-mountain range study area and across the active period of grizzly bears from spring to fall and for both female and male bears because we were most interested in a general model for the region. Our choice of analysis scales was based on our goal of identifying linkage areas connecting areas of high quality habitat across our Canada–USA trans-border region. We derived a single, multi-season model to identify general linkages because bears cross highways throughout their active period and linkage areas would not likely be managed seasonally. We also were interested in identifying linkage habitat that potentially would be used by both male and female bears because both are experiencing fragmentation (Proctor et al. 2005, 2012). Further, although female movement and home-range size is less than for than males (Proctor et al. 2004*a*), food resources (McLellan and Hovey 1995) and general habitat use (McLellan and Hovey 2001*b*, Wielgus et al. 2002) are similar between the sexes and therefore we expected linkage areas to be similar.

We used the RSF to identify areas of higher quality habitat, which we term, core habitat or simply core areas. We then used core areas as inputs for least cost modeling, serving as both the start and end points for linkage analyses. By using areas of higher quality habitat as termini for our linkage analyses, predicted linkage habitat was connecting areas with potentially higher densities of bears, maximizing the potential for inter-area connectivity.

Grizzly Bear GPS Location Data

We deployed GPS-telemetry collars on 27 grizzly bears in 2004–2010. We captured bears with Aldrich foot snares and occasionally with culvert traps. In Canada, our bear handling procedures were in accordance with the Canada Council on Animal Care Standards. In the United States, methods were similar to those described by Jonkel (1993) and were in accordance with the University of Montana Institutional Animal Care and Use Committee (protocol identification number is 007-06CSFWB-040106). We used Telonics Inc. (Mesa, AZ) Spread Spectrum radio-collars (and occasionally store-on-board collars) and remotely downloaded bear locations on a periodic basis.

To maximize our spatial coverage with our sparse density of bears (Proctor et al. 2007, 2012), we balanced collaring effort between trapping in areas with high bear use and thus high likelihood of captures, areas where low densities constrained trap success, and areas accessible by road. Fortunately, many bears used all or most of their ecosystems, particularly males, which helped us attain broader spatial coverage.

We collared most bears in May or June and monitored them for 1–3 years with monitoring usually spanning at least 2 non-denning periods (i.e., spring summer, fall). The collars were programmed to collect bear locations every 1–4 hr depending on collar size (smaller bears carried smaller collars with less battery life) and age of bears (subadult bears carried collars designed to drop off earlier so as to not interfere with neck growth). Because we used only 2D and 3D fixes, overall fix success (the proportion of 2D and 3D fixes relative to fix attempts) was 84%. Mean positional dilution of precision (PDOP), an imperfect index to positional accuracy, was 4.58 (SD = 0.30) for all 2D and 3D locations. Our final dataset had an average of 12.4 (SD = 7.2) locations per day per bear across the non-denning (active) period. We also assessed potential location bias for canopy closure, which was the variable with the most potential for low fix success rate (Frair et al. 2004). We placed 13 GPS radio collars at ground level in conifer forest with canopy cover from 0% to 75% canopy and found no relationship between fix rate and canopy closure ($R^2 = 0.07$; regression significance, $P = 0.64$).

Because unequal observations among animals can lead to biased population-level estimates (Gillies et al. 2006) and most bears had 1,500–2,500 locations, we used a maximum of 2,500 locations from most bears by removing every nth location from any 1 bear with >2,500 locations. We also used data from 4 bears with <1,000 locations to maximize our spatial coverage and the number of different animals in the dataset. To test the effect of including these bears, we compared RSF models for the bears with <1,000 locations to bears with >1,000 locations and found the resulting RSFs differed by only 1 variable, supporting our decision to pool the locations from bears with unequal sample sizes (Table S1, available online at www.onlinelibrary.wiley.com).

Grizzly Bear Habitat Modeling

We tested the appropriateness of combining male and female locations for RSF analysis by comparing individual sex RSF models using the same techniques that we used to develop our combined-sex RSF model (described below). The top 2 variables (greenness and canopy openness) accounted for the majority of the pseudo R^2 in both the individual sex models as well as our both-sex model providing support for pooling the sexes (Table S2, available online at www.onlinelibrary.wiley.com).

We divided grizzly bear GPS telemetry data into 2 groups. We used an 80% random sample for model training, and withheld the remaining 20% of bear locations for model evaluation (Boyce et al. 2002, Nielsen et al. 2002). We used a k-fold cross evaluation method where $k = 5$ (Boyce et al. 2002). We used the GPS telemetry locations and an equal number of available (random) locations from within the composite home ranges of all grizzly bears to develop a resource selection function (Boyce and McDonald 1999, Manly et al. 2002, Nielsen et al. 2002). We estimated the parameters of the exponential RSF using logistic regression (Manly et al. 2002) and transformed predictions from the RSF using the logistic function to normalize the right skewing of exponential RSF values, and then mapped predictions at a 100-m scale in ArcGIS 10.1 (ESRI, Redlands, CA). We performed logistic regression using the statistical software package STATA (Intercooled 9.2, College Station, TX).

Model building was based on the principles of Hosmer and Lemeshow (1989) and more recently referred to as purposeful selection of variables (Bursac et al. 2008). We tested all predictor variables for pairwise correlations (Chatterjee et al. 2000) and only terrain ruggedness and compound topographic index were correlated and therefore not used in the same model during the stepwise process. We fit all variables and their quadratic relationships individually (uni-variable analyses) and ranked them for their explanatory power (pseudo R^2) and significance. We then built multi-variable models by adding non-correlated variables in a forward stepwise fashion starting from higher to lower pseudo R^2. We compared models sequentially by explanatory power (pseudo R^2) after each variable addition to decide if a variable improved model predictability. When a variable increased the pseudo R^2 by at least 5%, we retained that variable in the model; when a variable increased the pseudo R^2 <5% we did not retain it to favor a parsimonious model. To ensure that final variable selection was not unduly influenced by the order of variables added to the model, we also applied a reverse stepwise model procedure.

We used the Huber–White sandwich estimator in the robust cluster option in STATA to calculate standard errors because non-independent locations can lead to biased standard errors and overestimated significance of model parameters (White 1980, Nielsen et al. 2002, 2004*a*). Because the bears were the unit of replication, we used individuals to denote the cluster, thus avoiding autocorrelation and/or pseudo-replication of locations within individual bears.

We assessed the performance of the final selection model to predict bear use using both independent GPS telemetry data from the same area and telemetry data from an area adjacent area to where our model was developed. Therefore, our study had 2 evaluation areas that we refer to as the model development area and the model evaluation area. The model development area encompassed 9,269 km^2 north and south of BC Highway 3 as it crosses the Purcell Mountains and Highway 3A between the Selkirk and Purcell ranges of southeast BC and northwest Montana (Fig. 2). The model evaluation area extended across US Highways 2, 95, and 200 (Fig. 2) and included 4,721 km^2 in the Selkirk Mountains and 2,093 km^2 in the US Cabinet Mountains (Fig. 2). Our GPS telemetry data spatially covered most of our model development area given some practical sampling constraints (Fig. 2, also described above). We used the correlation of the selection ratios (use/availability) between our model development dataset and our evaluation datasets to assess whether the RSF model predicted use in the 2 areas using independent GPS telemetry locations. Use was the proportion of transformed grizzly bear RSF scores within each of 10 binned RSF score intervals relative to the total number of grizzly bear locations. Availability was area-adjusted, or the proportion of RSF scores within an RSF interval bin relative to the total area. In the United States we used 2,398 GPS telemetry locations from 5 bears (4 female and 1 male) in the Cabinet Mountains (Fig. 2), and 5,617 locations from 5 bears (1 female and 4 male) in the Selkirk South area. We omitted the locations from the Cabinet Mountains in model development because several of the bears were part of an augmentation program (Kasworm et al. 2011), so they may have been less familiar with the habitat while wearing their radio collars. We did not include the locations from the United States Selkirks in model development because data were sparse for the amount of area encompassed. Instead, these bears provided independent datasets to evaluate model predictions after our model was predicted (spatially extrapolated) to their respective areas.

Environment Variables

We used variables that were most consistently measured across the study area and between Canada and the United States including human-use, terrain, forest cover, and other ecological variables (Table 1). Ecosystem characteristics and human uses in the adjacent south Selkirk and south Purcell Mountains are similar (Meidinger and Pojar 1991) allowing development and prediction of models to these areas. Lowlands are dominated by cedar–hemlock (*Thuja plicata–Tsuga heterophylla*) forests and upland forests are dominated by Engelmann spruce–subalpine fir (*Picea engelmannii–Abies lasiocarpa*). Douglas fir (*Psuedotsuga mensiezii*) forests are somewhat more common in the southern portions of the Purcell range (Meidinger and Pojar 1991). Human uses are relatively similar across the region and include timber harvest, some mining, ungulate hunting, and other forms of recreation.

We obtained baseline thematic mapping land-cover variables (recently logged, alpine, avalanche, and riparian), vegetation resource inventory variables (dominant tree species forest cover types, canopy cover), and backcountry resource roads (i.e., associated with timber harvest, mining) from the BC Ministry of Forests, Lands, and Natural Resource Operations in Canada. Land-cover information for the United States was from the United States Forest Service. Alpine, avalanche, burned, and riparian habitats contain a variety of grizzly bear food resources (McLellan and Hovey 1995, Mace et al. 1996, McLellan and Hovey 2001*b*). We used forest cover variables (Table 1) because they often have been found to influence grizzly bear habitat selection (Zager et al. 1983, Waller and Mace 1997, Apps et al. 2004, Nielsen et al. 2004*c*). Greenness, an index of leafy green productivity, correlates with a diverse set of bear food resources and is often found to be a good predictor of grizzly bear habitat use (Mace et al. 1996, Nielsen et al. 2002). We derived greenness from 2005 Landsat imagery using a tassled cap transformation (Crist and Ciccone 1984, Manley et al. 1992). We derived terrain variables of elevation, compound topographic index (CTI), solar radiation, and terrain ruggedness from a digital elevation model (DEM) in ArcGIS. The CTI is an index of soil wetness estimated from a DEM in a geographic information system (GIS) using the script from Rho (2002). We estimated solar radiation for the summer solstice (day 172), using a DEM, and the ARC macro language (AML) from Kumar et al. (1997) that was modified by Zimmerman (2000) called shortwavc.aml. Finally, we estimated terrain ruggedness from the DEM based on methods from Riley et al. (1999) and scripted as an ArcInfo AML called TRI.aml (terrain ruggedness index) by Evans (2004). These terrain variables have been shown to influence the distribution of grizzly bear foods (Apps et al. 2004; Nielsen et al. 2004*c*, 2010) and also affect local human use. We included elevation

Table 1. Description and data ranges of predictive variables used to develop a multi-variable resource selection function model of grizzly bear habitat selection in 2004–2010 in the South Selkirk and Purcell Mountains of southeastern British Columbia, northwestern Montana, northern Idaho, and northeastern Washington. Selection is signified by a + symbol and avoidance by a − symbol. Double symbols (+ + or − −) indicate the variable was included in our best multi-variable model. We used all variables and their quadratic relationships in uni-variable analyses.

Variable category	Variable	Units	Data range	Selection or avoidance
Forest cover				
	Canopy openness	Percent	0–100	++
	Recently logged	Categorical	0 or 1	+
	Lodgepole pine	Categorical	0 or 1	−
	Douglas fir	Categorical	0 or 1	−
	Spruce-fir	Categorical	0 or 1	+
	Deciduous	Categorical	0 or 1	Neutral
Land cover				
	Alpine	Categorical	0 or 1	+ +
	Avalanche	Categorical	0 or 1	+
	Riparian	Categorical	0 or 1	+ +
Ecological				
	Greenness	Continuous	0.002–0.997	+ +
	Elevation	m	271–3,732	+ +
	Terrain ruggedness	Unitless	0–1,008	+
	Wetness (CTI[a])	Unitless	3.4–27.2	+
	Solar radiation	kj/m^2	218–29,494	Neutral
Human				
	Highway	Categorical	0 or 1	−
	Human development	Categorical	0 or 1	−
	Forest roads	Categorical	0 or 1	−

[a] Compound topographic index.

as a variable because grizzly bears in our region use high country extensively, which may be for a variety of reasons (e.g., high elevation habitat types, thinner forest cover with more edible ground-based vegetation, human avoidance). We digitized highway and human developments from 1:50,000 topographic maps and ortho-photos. We buffered highway, human developments, and backcountry roads by 500 m on either side to reflect their influence on grizzly bear habitat use (Mace et al. 1996). Human-use variables have been demonstrated repeatedly to correlate with habitat selection by grizzly bears (Mace et al. 1996, 1999; Nielsen et al. 2002; Apps et al. 2004). Although none of the predictors were direct measures of food resources or human activities, each factor has been proposed to correlate with resources and behaviors used by bears or activity of humans (Mace et al. 1996; Nielsen et al. 2002, 2006, 2009; Apps et al. 2004). We did not partition our analysis by season or sex because our goal was to predict multi-seasonal linkage habitat through human-settled valleys for both male and female grizzlies.

Identification of Core Areas

We used the final RSF to classify core habitat as the areas where predicted values of use exceeded availability in the logistic transformation of RSF values. This threshold of habitat selection was identified as areas where the selection ratio (proportion of use/proportion of availability) was >1. We applied our model to the entire regional study area to map grizzly bear core habitat to be used for least cost modeling of linkage areas. Where applicable, generally in more northern areas of our study region, we excluded mountain peaks that are rock and ice, typically above 2,300 m elevation. We delineated core habitat polygons as a cluster of cells above our selection threshold and $>9.0\ km^2$ because this approximated the average daily foraging requirement of an adult female (Gibeau et al. 2001).

Identification of Linkage Areas

To identify linkage areas, we used a combination of least cost modeling that included circuit theory (McRae et al. 2008) using the software Linkage Mapper (McRae and Kavanagh 2011) in ArcGIS 10.1. Inputs for linkage analysis were the suite of higher quality core grizzly bear habitats used as start and end points and a resistance layer.

We developed a cost (resistance) surface in a GIS by combining the reciprocal of our RSF values (Manly et al. 2002, Chetkiewicz and Boyce 2009) with a layer that consisted of the density of buildings. We derived the building density layer in a GIS with a moving window over a 500-m circular radius. We developed the building layer by digitizing buildings from 1:20,000 topographic maps that contained building data and ortho-photos (to update older topographic map information). The building density layer represented mortality risk and was added because our final RSF model did not contain anthropogenic factors often avoided by grizzly bears (highways and human settlement). Human-caused mortality is a well-known influence on grizzly bears in our region (up to 85% of mortalities; McLellan et al. 1999) and settlement and human-caused mortality contribute to the fragmentation of bear populations in this system (Kendall et al. 2009, Proctor et al. 2012). Use of a building density value of area surrounding a pixel allowed clusters of homes or farms to have a higher resistance value than 1 isolated home. We standardized the building density layer and the inverse of the RSF layer, and weighted them equally, because in our experience bear mortality near human development provides as much resistance to successful bear movement as unsuitable landscape traits.

Within Linkage Mapper we ran the "Build Network and Map Linkages" tool that used our total cost layer to calculate cumulative landscape resistance to movement between core area termini. This process yielded corridors and least-cost paths from which we calculated the cost-weighted-distance/Euclidean distance (CWD/ED) ratio as a relative index of how difficult movement through a linkage area may be for bears. We measured the CWD over the least-cost path and the Euclidean distance was the geographic distance between termini. We then ran the Pinchpoint Mapper tool (McRae 2012) within Linkage Mapper that uses Circuitscape (McRae and Shah 2009) within the corridors identified in the previous step using a 20-km truncated corridor width. We chose 20 km for a maximum corridor width because we did not want to constrain outputs to distances less than this threshold. Circuitscape calculates current flow, or potential bear movement routes (herein called pathways), over multiple pathways between core areas based on cumulative resistances derived from the habitat (RSF scores) and mortality risk (building density) total cost layer. Output displays depict the variation in alternative pathways (open circuits) and can identify pinch points where movement is concentrated in narrow pathways, or broadens out with less concentrated paths. We took areas along highways where pathways were concentrated (>0.006 flow density in Pinchpoint Mapper output map) into clusters and considered them linkage areas. The decision to identify linkage areas rather than more narrow corridors reflects our observation of how grizzly bears use the landscape and simultaneously provides managers with alternative options when applying specific actions to establish and manage linkage areas.

To evaluate our linkage area predictions, we calculated the percentage of highway crossings by grizzly bears that were within the predicted linkage areas. Because of the time interval between GPS locations, the precise location of a crossing was rarely known. Therefore, we considered a crossing to be within the predicted linkage area if there were successive points on both sides of a highway within our linkage area, and 1 point was within 1 km of the highway. We also counted crossings that were within 3 km of the highway if the angle between the line connecting successive points on each side of the highway was $>60^{\circ}$ to the highway and the entire line was within a linkage and/or core area. We also compared our predicted linkages to both Jones (2012), who used similar methods (RSF, least-cost modeling and circuit theory), but used fewer very high frequency (VHF) telemetry locations, and to Apps et al. (2007), who did not use corridor analysis but produced an RSF derived from DNA survey data without the addition of circuit theory. We overlaid the 3 linkage predictions and visually compared them because of the different formats of the results.

RESULTS

Grizzly Bear GPS Locations

Our resulting telemetry dataset had 34,143 GPS telemetry locations from 27 grizzly bears (13 males and 14 females) and a reasonable spatial coverage across the study area (Fig. 2b). Mean number of GPS locations per bear was 1,630 (SD = 702) with 14 of 27 bears having between 2,000 and 2,500 locations (5 bears with 1,500–2,000 locations, 4 bears with 1,000–1,500 locations, 1 bear with 500–1,000 locations, and 3 bears with <500 locations). Temporal representation was skewed towards summer with April having 3% of locations, May 8%, June 14%, July 25%, August 25%, September 21%, and October 5%. April and October are months when bears typically enter and exit dens and their on-air dates would therefore be affected by den emergence and entrance. We obtained a lower percentage of observations in May and June than July–September because we did most of our trapping in May and June, and dates prior to capture would not be collecting locations in that year.

Grizzly Bear Habitat Modeling

Our final RSF habitat model contained greenness, canopy openness, alpine, riparian, and elevation variables (Tables 1 and 2, Fig. 3). A backward stepwise model was identical to our final model, suggesting that the forward process did not bias the final set of variables based on their order of addition to the model during the development process. All 5 *k*-fold models were similar, with only minor variations in variable coefficients (Table S3, available online at www.onlinelibrary.wiley.com). All variables in the final model were positively related to grizzly bear habitat selection (Table 2). Selection ratios from our model development and evaluation datasets indicated that the threshold for habitat selection occurred when transformed RSF scores were >0.5 (Fig. 4). Seventy percent of all grizzly bear GPS locations had RSF values

Table 2. The final resource selection function (RSF) model for predicting grizzly bear habitat selection across the South Selkirk and Purcell Mountains of southeastern British Columbia, northwestern Montana, northern Idaho, and northeastern Washington, 2004–2010.

				95% CI	
Variable	Coefficient	Robust SE	Robust probability	Lower	Upper
Greenness	14.597	1.517	<0.001	11.625	17.57
Canopy openness	0.014	0.002	<0.001	0.009	0.018
Alpine	0.801	0.312	0.010	0.190	1.412
Elevation 100 m[a]	0.108	0.049	0.025	0.013	0.204
Riparian	1.091	0.407	0.007	0.292	1.890
Constant	−11.524	1.330	<0.001	−14.122	−8.927

[a] We multiplied the elevation coefficient and CIs that were in meters, by 100 for display purposes.

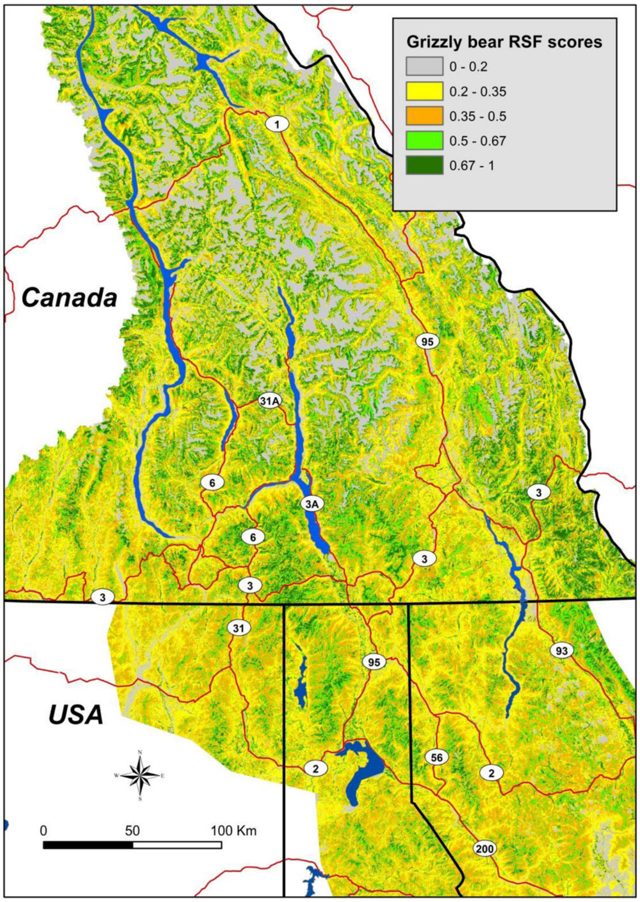

Figure 3. Resource selection function (RSF) predicting grizzly bear habitat selection applied in the Canada–USA trans-border region from data collected in 2004–2010. Areas of green and darker green represent the best available higher-quality habitat patches.

>0.5, our threshold for defining core areas (see Fig. 4), whereas 52% of the model development area and the model evaluation area were identified as core habitat. The Spearman correlation between the area-adjusted binned RSF scores from the model development area dataset (80%) and the model evaluation dataset (20%) was $r_s = 0.99$ (Fig. 4). When the model was applied to our adjacent evaluation areas, the rank correlation between the predicted and observed area-adjusted bins for RSF scores $r_s = 0.95$ for the Cabinet Mountain area and $r_s = 0.81$ for the United States Selkirk South area (Fig. 4).

Identification of Linkage Areas

We identified 60 linkage areas across 13 highways (Fig. 5) encompassing 24% of 2,418 km of highway. Mean linkage area width (along highways) was 9.8 km (SE = 0.55, range 1–20 km, 31 were <10 km and 22 were 10–15 km). The amount of landscape resistance varied among our predicted linkage areas. The CWD/ED ratios ranged from 1.24 to 11.93 (Fig. 6, Appendix I). For example, along BC Highway 3 in the Purcell Mountains, we identified 6 linkage areas with varying CWD/ED ratios ranging from 2.4 to 3.1 (Fig. 6a). Along US highways separating the Cabinet Mountains from the Yaak area (Highway 2) and the South Selkirk Mountains (Highway 95), these ratios had minimal variation (Fig. 6b).

Highway crossings were relatively rare, although 88% of 122 eligible highway crossings from 13 bears were within predicted linkage areas (mean = 8.3 crossing/bear, SE = 2.8, range: 1–31, 3 bears only 1 crossing, see example in Fig. 6c), indicating bears use preferred linkage habitat and that we could predict them using linkage modeling based on RSFs. Along Canada Highway 1, our model predicted 6 linkage areas identified by Jones (2012) and 2 linkage sites that were not predicted by Jones (2012, Fig. 7a). Along Highway 3 in the Canadian Rocky Mountains, our predictions of linkage areas aligned reasonably well with those of Apps et al. (2007; Fig. 7b), especially south of Fernie and immediately east and west of Sparwood. North of Fernie, Apps et al. (2007) predicted 1 linkage area that we did not.

DISCUSSION

Our RSF-based predictions of core habitats and linkage areas were consistent with the majority of inter-area movements of grizzly bears across major highways, suggesting bears used preferred habitat that could be predicted with an RSF as linkages between core areas. In highly fragmented environments, inter-area movements between subpopulations may be more important than the internal demographics of each subpopulation (Lande 1987). Proctor et al. (2005, 2012) found sex-biased fragmentation of grizzly bear populations, with females being more fractured than males. Female immigration increases the probability of recovery and long-term persistence for small, threatened populations by acting as a hedge against stochastic demographic variation (mortality and/or low reproduction). The short and gradual female natal dispersal (McLellan and Hovey 2001*a*, Proctor et al. 2004*a*) points to the importance of selecting wide linkage areas that female bears can live within while reducing mortality risk along settled highways to promote successful inter-subpopulation movement and dispersal.

Other efforts to provide connectivity options for wildlife subpopulations have focused on various types of crossing structures to facilitate movement across busy highways, including Highway 1 in Banff National Park (Ford et al. 2009), Montana Highway 93 (McCoy 2005), and Idaho Highway 95 (Lewis et al. 2011). Although crossing structures can be important tools to reduce highway mortalities and enhance wildlife connectivity, Proctor et al. (2012) found human settlements to be the most important fracturing force for grizzly bears regionally. This pattern suggests that management strategies that reduce grizzly bear mortality from human conflict and minimize human densities in linkage areas may help increase successful inter-area movements.

Corridor width along highways is challenging to estimate because no clear methods exist for determining it (Sawyer et al. 2011). Broad linkage areas with low human densities may be most appropriate for grizzly bears because in our region they have relatively large home ranges and can be readily killed when attracted to human food sources in human

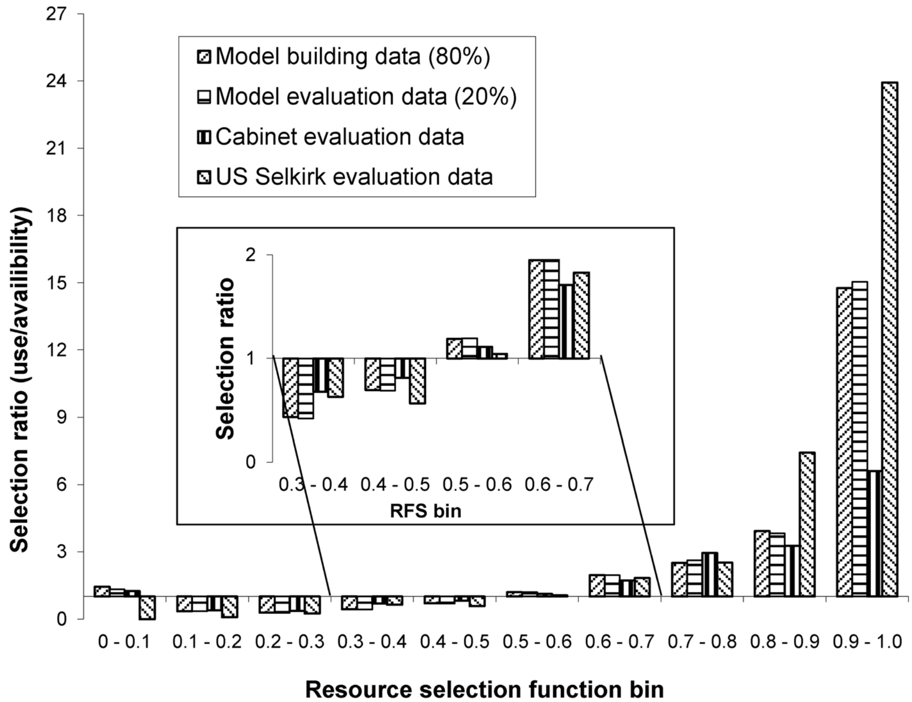

Figure 4. Grizzly bear habitat selection ratio (use/availability) for 10 ordinal-ranked resource selection function (RSF) bins describing model performance for model training (80%) and testing (20%) data in the South Selkirk and Purcell Mountains of southeastern British Columbia, Canada, 2004–2010. Additional model evaluation data described for the Selkirk and Cabinet Mountains in the United States based on model extrapolations. Bin 1 represents the lowest transformed RSF score ranging from 0 to 0.10, bin 2 from 0.1 to 0.2, etc. The inset shows that the transition between habitat avoidance and selection occurred when the transformed RSF score was >0.5 and the selection ratio was >1.0.

environments. Human-caused mortality associated with settlement along highways is a primary mechanism of population fragmentation in our region (Proctor et al. 2012). These realities underpinned our decision not to constrain our linkage area analysis below a 20-km corridor width. This was a reasonable decision because we had only 1 linkage area that approached 20 km in highway length whereas 88% of linkage areas along highways were <15 km wide. Selecting linkage habitat with pathway densities >0.006 was an arbitrary decision, but represented densities 20% above the overall mean (0.005). Although this threshold identified habitat with the highest movement potential, it also identified linkage areas that varied between 1 and 20 km in width. This variability, although based on an arbitrary cutoff in pathway density, provided us with a reasonably objective method to differentiate corridor widths across our study area. The variability in corridor width also has the potential to provide managers and land use planners considering inter-area connectivity, flexibility in management options within and between linkage areas (see Management Implications below).

Identification of grizzly bear linkage areas was the primary objective of Apps et al. (2007) and Jones (2012). The fact that our linkage predictions lined up reasonably well with both efforts, yet were developed from a different study area (and different mountain range in the case of Apps et al. 2004), suggests our resource selection model and linkage predictions may represent characteristics that apply to bears regionally. In regard to Apps et al. (2007) efforts, our similar results suggest that analyses derived from DNA surveys (Apps et al. 2007), and GPS telemetry (this effort), can both yield results useful for management.

Our RSF model contained only variables that were positively related to grizzly bear habitat selection, even though we also tested in model development variables that bears often avoid. Grizzly bear RSF habitat models often show avoidance of backcountry forest roads (Mace et al. 1996, Wielgus and Vernier 2003, Ciarniello et al. 2007, Proctor et al. 2008). Our initial uni-variable analyses of potential predictors of grizzly bear selection identified backcountry road avoidance as a significant variable (Table 1), but not after considering other environmental factors in the final multi-variable model. Some bears in our sample appeared to use habitats near forestry roads that were closed to motorized vehicle use, and thus they were not avoided. This is consistent with Wielgus and Vernier (2003) and Wielgus et al. (2002), who found no selection or avoidance of restricted roads in the South Selkirk Mountains. In the South Selkirk Mountains of southern BC, a large proportion of our GPS telemetry data came from this same area; the area contains approximately 550 km^2 that has had 30 years of private-land access management on restricted roads that excluded recreational traffic (Wielgus et al. 2002, Wielgus and Vernier 2003). Also, a number of forestry roads in the Purcell South Yaak area in the United States were closed to motorized vehicle use for wildlife conservation during our study (Wakkinen and Kasworm 1997, Kasworm et al. 2011), and thus not likely avoided by grizzly bears.

Habitat-selection models built from variables that do not contain anthropogenic factors allow for prediction of higher-

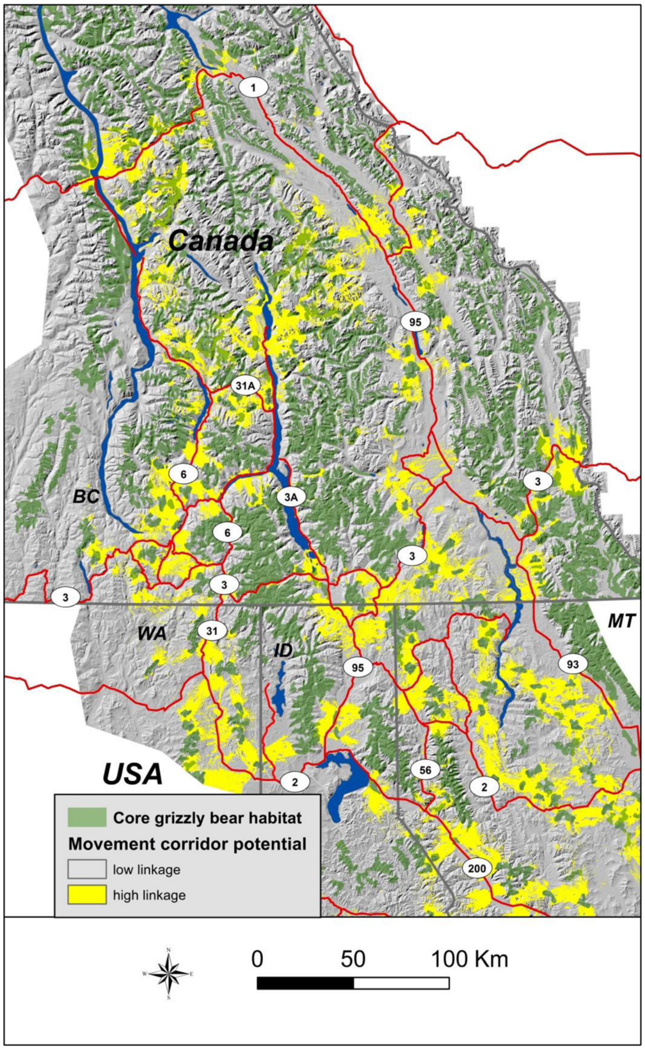

Figure 5. Core grizzly bear habitats (green polygons) linked across major highways in the Canada–USA trans-border region by identified linkage areas (yellow), based on least cost modeling and circuit theory corridor analysis of data from 2004–2010. Yellow areas were linkage prediction results from circuit theory analyses within Circuitscape software (McRae et al. 2008) where current density was >0.006 in Pinchpoint Mapper outputs. Numbers indicate names of major highways. Results are simplified to 1 color because of the broad scale of the map (see details of predictions in Figs. 8 and 9 and Appendix I.

quality habitat without the influence of human use such as backcountry roads or settlements. Human environments and habitats with roads carry a mortality risk to grizzly bears (Mace et al. 1996; McLellan et al. 1999; Nielsen et al. 2004*b*, 2006; Proctor et al. 2012). Understanding where bears might be attracted to high-quality habitat associated with human features can be important in identifying attractive sinks (Nielsen et al. 2006), which is valuable for focusing management action. For example, if high-quality linkage habitats also contained excessive open forestry roads, a potential management strategy would be to limit motorized access on a portion of those roads to reduce the mortality risk to bears (Schwartz et al. 2010, Boulanger and Stenhouse 2014). If a high-quality linkage area is near human settlement, a strategy might be to increase human-bear conflict management to reduce mortality risk.

Because many valley bottoms have been usurped for human use (McLellan 1998), there is a perception that grizzly bears in our region are a high-elevation species. However, even though elevation had a positive relationship with selection in our model, our results demonstrate that they used habitats across the full gradient of elevations from valley bottoms (riparian) through mid-elevations (open canopy forests) to higher elevations (alpine). This result is similar to those found by McLellan and Hovey (2001*b*) where bears were shown to prefer lower valley bottom habitats seasonally where such areas contain good grizzly bear habitat and did not have extensive human settlement. Furthermore, the pattern of displacement from many human-settled valley bottoms, and a measure of avoidance of backcountry forest roads in our uni-variable analysis, indicates that the habitat selection by our sample of bears already includes some measure of human influence (e.g., a portion of bears selection of higher elevation habitats may be human avoidance).

Our RSF indirectly reflects available food resources but does not model them directly (Nielsen et al. 2010). As with other studies, we found greenness to be one of the best predictors of bear occurrence (Mace et al. 1999, Nielsen et al. 2002, Boyce and Waller 2003, Ciarniello et al. 2007), and it may be associated with plant-based bear foods (Stevens 2002). Greenness can be associated with a suite of habitat types that display high annual leafy-green (deciduous) productivity (White et al. 1997, Stevens 2002), making it useful for extrapolation across different land cover types. Habitats associated with high greenness in our study area included avalanche chutes, riparian, alpine, and regenerating cut blocks (logged areas). Many avalanche paths, for instance, have high greenness values because of the presence of lush herbs, forbs, and berries and, as a result, are often well-used bear habitat (McLellan and Hovey 1995, Mace et al. 1996). Cut blocks also frequently contain bear foods (Waller and Mace 1997, Nielsen et al. 2004*a*). Riparian habitat, typically found in valley bottoms, was ubiquitous across our study area, and has been shown to be an important habitat for grizzly bears (McLellan and Hovey 1995, 2001*b*).

Our average GPS collar fix rate was 84%. Low GPS collar fix rates have been associated with dense canopy cover and rugged terrain (Moen et al. 1996, D'Eon et al. 2002, D'Eon 2003, Frair et al. 2004), behavior (bedding) and morphology (Bowman et al. 2000, D'Eon and Delparte 2005, Moe et al. 2007, Schwartz et al. 2009), traveling (Graves and Waller 2006, Heard et al. 2008), satellite configuration and sky visibility, position of the collar on the animal (Moen et al. 1997, Frair et al. 2004, Graves and Waller 2006, Graves et al. 2013), time of day and season (Belant and Follmann 2002, Heard et al. 2008), frequency of sampling (Mills et al. 2006), and battery fatigue (Gau et al. 2004).

Although several of these factors may have affected our collar fix rates, missed fixes in our study followed a pattern that was most consistent with bedding behavior. Specifically, fix rate was inversely related to mean activity level (measured with in-collar activity sensors) with mean activity values for unsuccessful fixes being significantly lower than those for successful fixes ($t = -6.0$, $P < 0.001$). Similarly, Schwartz

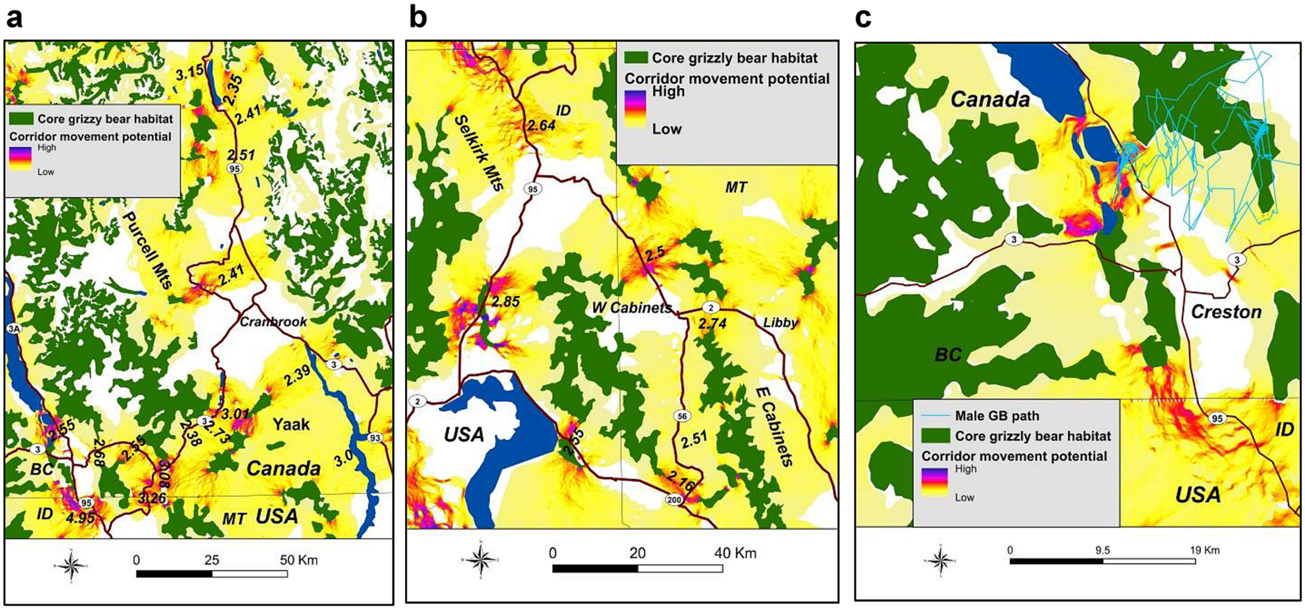

Figure 6. Linkage area predictions for grizzly bears, 2004–2010, (a) along British Columbia (BC) Highway 3 in the Purcell Mountains and Highway 95 between the Purcell and Rocky Mountains, (b) in the Montana-Idaho border region with linkage areas between the Selkirk, Cabinet, and Purcell-Yaak areas, and (c) in the Creston Valley, BC, which separates the Selkirk and Purcell Mountains. Additionally, we overlaid a male grizzly bear's locations displayed as a path (light blue) within the Creston Valley predicted linkage area. Linkage areas are generally yellow with concentrated current flow, and thus corridor potential, grading to red and purple. Numbers are the cost weighted distance/Euclidean distance ratios for linkage areas. Lower numbers have less landscape resistance. Numbers in white ovals indicate names of major highways.

et al. (2009) found that low activity associated with bedding was strongly associated with missed fixes by the same collars and activity sensors we used (Telonics, Generation III Spread Spectrum radio-collars). Therefore, our results may underestimate habitat selection of bedding sites and emphasize instead foraging and movement behaviors.

We do not think our 16% missing fixes indicate bias against detecting animals in dense canopy cover. First, our study area

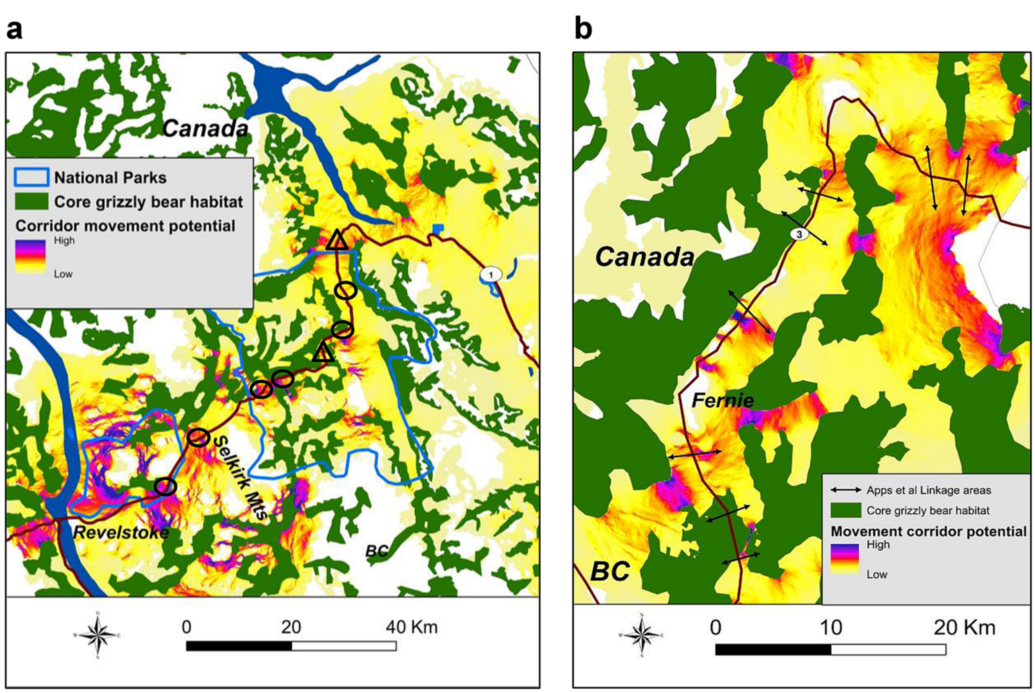

Figure 7. (a) Comparisons with linkage predictions for grizzly bears between this project (2004–2010) and those of Jones (2012) along Canada Highway 1 in the Selkirk Mountains of British Columbia (BC). Circles are predicted linkage areas by both Jones (2012) and this project and triangles are where this project predicted a linkage area but Jones (2012) did not. (b) Comparisons of linkage predictions between this project and those of Apps et al. (2007; arrows) along BC Highway 3 in the Rocky Mountains. Note 1 Apps linkage area arrow that was not predicted by this project just to the northeast of Fernie. Depictions of linkage predictions of Jones (2012) and Apps et al. (2007) are displayed in a similar format as their original publications to avoid inaccuracies related to the adaptation process.

contained only 2% of the total area with heavy canopy cover (<30% openness). Second, we found no correlation between canopy cover and fix success with 13 stationary collars in locations that varied from 0% to 75% canopy cover in our study area ($R^2 = 0.07$, $P = 0.68$). Thirdly, Frair et al. (2004) found no type I or II errors or bias in RSF coefficients related to conifer canopy cover in RSF models with GPS data loss <30%.

MANAGEMENT IMPLICATIONS

The value of identifying core and linkage areas is to inform targeted management. We note that our identification of core habitats does not mean backcountry management should be limited to these areas, they merely represent the current areas of better quality habitat. To conserve grizzly bears across this landscape, management also needs to occur beyond these core areas. However, by focusing connectivity efforts within our identified linkage areas, rather than entire highway and settlement corridors, there is a greater return on management effort and likelihood of success. For example, within linkage areas, management actions could minimize human-generated bear attractants (a well-known association with bear mortalities), reduce human access and use of secondary roads, and reduce, or at minimum, not increase, human development (e.g., subdivisions) and densities (Proctor et al. 2008, 2012). There are several scales with which to use our results to inform connectivity management. At the regional scale among linkage areas (Fig. 5), we recommend that a prioritization plan be developed for connectivity management based on factors such as relative conservation importance, threats, and opportunities for management. Within highway segments, these factors may reveal the linkage area with the most advantageous cost/benefit ratio. Within any highway segment or specific linkage area, the length along a highway and the model predictions from our linkage maps can be used to prioritize management relative to available alternatives (e.g., concentrated pathways or pinch-points vs. diffuse pathways). For example, several linkage areas are the focus of re-establishing connectivity between the small Purcell South Yaak and South Selkirk grizzly bear subpopulations and the large (>500 grizzly bears) Central Purcell-Selkirk bear subpopulation to the north of BC Highways 3 and 3A, respectively (Fig. 1b, and see Proctor et al. 2012). Efforts include private land purchases by land conservation non-government organizations (ENGOs) accompanied by attractant reduction programs as well as other connectivity-oriented management strategies (Proctor et al. 2008). We recommend that other species be analyzed similarly to our methods to develop a multi-species connectivity management strategy where feasible.

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Appendix I

Linkage area predictions identified through least cost modeling and circuit theory corridor analysis using Linkage Mapper GIS software.

Linkage areas a) along BC Highways 3, 6 & 31A in the Selkirk Mountains of southern BC, b) along Highways 2, 57, & 31 in northern Idaho and northeast Washington, and c) along Highways 2 & 200 in western Montana. Concentrated current flow is depicted by areas grading to red and purple and represent potential linkage areas between patches of higher quality habitat (green polygons). Numbers are the Cost Weighted Distance / Euclidiean Distance ratios for linkage areas. Lower numbers have less landscape resistance.