



Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery

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ARTICLE INFO

Article history:

Received 24 January 2012

Received in revised form 13 July 2012

Accepted 17 July 2012

Keywords:

Canada lynx

Connectivity

Corridors

Least-cost paths

Montana

Resource selection

ABSTRACT

Maintaining connectivity with source populations is especially important for populations of boreal species at the southern edge of their distributions, where anthropogenic disturbance and climate change can be a threat. In the conterminous United States, Canada lynx *Lynx canadensis* is a federally threatened boreal species that may require connectivity with northern populations to persist. Connectivity is a function of movement between patches and the likelihood that patches are suitable for resident populations. Therefore, we combined resource selection, step selection, and least-cost path models to define empirically movement corridors for lynx in the Northern Rocky Mountains. We used telemetry data for 64 lynx monitored during 1998–2007 to create a broad-scale resource selection model that predicted probable lynx habitat across the species' distribution in the Northern Rocky Mountains. Our model indicated that lynx selected home ranges at mid-elevations with low surface roughness and high canopy cover. Based on a subset of 37 (16 females, 21 males) adult lynx fitted with GPS collars from 2005 to 2007, we then tested the extent to which remotely-sensed indices of environmental heterogeneity, including greenness, normalized difference vegetation index, surface roughness, and a principal component that indexed stand age, could characterize landscape connectivity for lynx. We found that connectivity between lynx habitat in Canada and that in the conterminous US is facilitated by only a few putative corridors that extend south from the international border. Maintaining the integrity of these connectivity corridors is of primary importance to lynx conservation in the Northern Rockies.

Published by Elsevier Ltd.

1. Introduction

Populations at the periphery of species' ranges are important for long-term conservation due to a greater potential for speciation and potentially greater survivorship than core populations when species experience sharp range contractions (Lesica and Allendorf, 1995; Channell and Lomolino, 2000; Carroll, 2007). Peripheral populations often occupy suboptimal habitats (Brown, 1984), making them vulnerable to a loss of connectivity with larger source populations (Root, 1998; Thomas et al., 2001). Moreover, peripheral populations may be particularly at risk where they face high levels of anthropogenic disturbance (Channell and Lomolino, 2000; Schaefer, 2003). Canada lynx (*Lynx canadensis*), listed as threatened

under the Endangered Species Act in the contiguous US, exhibits population dynamics that lag those in their range core in Canada (McKelvey et al., 2000). Thus, lynx conservation in the contiguous US hinges in part on maintaining population connectivity between Canada and the US. However, maintaining connectivity for lynx may become increasingly difficult due to climate and anthropogenic change, as evidenced by reduced connectivity of other boreal species (van Oort et al., 2011). Preserving connectivity throughout the northern Rocky Mountains (hereafter Northern Rockies) is central to the conservation of many boreal species that are listed or proposed as threatened or endangered under the Endangered Species Act including Canada lynx, wolverine (*Gulo gulo*), grizzly bear (*Ursus arctos*), and woodland caribou (*Rangifer tarandus caribou*). Long-term population recovery of these species requires maintenance of short and long-distance connectivity (Clark et al., 2002). Thus, managers need approaches and tools that identify and maintain connectivity for such species across differing spatial scales (Carroll et al., 2010).

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Important conservation efforts focus on identifying and maintaining corridors that connect local carnivore populations (Chetkiewicz and Boyce, 2009) and their habitats (Rabinowitz and Zeller, 2010). However, identifying conservation corridors requires several stages of analyses that link species distributions to suitable habitat across scales (Beier et al., 2009). For example, patches of habitat that likely contain resident populations can be generated from a broad-scale spatial gradient in habitat suitability. Next, a probabilistic surface that predicts fine-scale movement decisions can depict the functional connectivity between these populations, as defined by resource-movement relationships (Beier et al., 2009; Richard and Armstrong, 2010; Dancose et al., 2011). Reviews of movement ecology (Fahrig, 2007) and corridor conservation (Chetkiewicz et al., 2006) recommend the integration of both disciplines using least-cost path techniques. Thus, incorporating these broad- and fine-scale species-habitat relationships is useful to identify areas most important for species connectivity (i.e. corridors) (Fahrig, 2007; Dancose et al., 2011).

In this study, we integrate three commonly used spatial modeling approaches that combine patterns of broad-scale habitat residency and fine-scale movement behavior into a single depiction of connectivity for Canada lynx in the Northern Rockies. First, we use resource selection functions (RSFs) to identify patches of suitable habitat for population residency (Mladenoff et al., 1995). Second, we complement this broad-scale RSF with fine-scale analyses of step selection functions (SSF; Fortin et al., 2005); the SSF relates animal movement to fine-scale habitat heterogeneity. Last, we use least-cost path analysis to translate our multi-scaled habitat models into a spatial depiction of lynx habitat connectivity across the Northern Rockies.

To facilitate practical application of our results for conservation planning, we characterized habitat resources of lynx using spatial data layers that are widely available and represent climatic, topographic, and vegetative heterogeneity. We included data layers that index important characteristics of lynx resource use, such as horizontal vegetative cover (Squires et al., 2010). Because horizontal cover decreases during winter (after deciduous leaf-fall), we expected to observe seasonal differences in lynx movement relative to vegetative indices (Squires et al., 2010). Finally, in an effort to prioritize conservation efforts, we quantified the relative likelihood of lynx crossing major highways, as roads are one of the major hypothesized anthropogenic threats to lynx connectivity (Carroll et al., 2001) in their southern distribution. Evaluating highway crossings is an important conservation application given the potential impacts of increased vehicle traffic on road networks in the Northern Rockies (Carroll et al., 2001).

2. Methods

2.1. Study area

Our study area encompassed the occupied range of lynx within the Northern Rockies as estimated from a compilation of lynx distribution data collected from 1998 to 2007. The study area border followed natural topographic and vegetative boundaries to generally encompass all forested regions with recent evidence of lynx presence, including all telemetry locations we documented for resident lynx from 1998 to 2007 ($N = 81,523$ locations, Fig. 1); this study area represented our best estimate of the current distribution of lynx in western Montana. The study area spanned a total of 36,096 km² and included private lands, federal- and state-managed multiple-use public lands, the Bob Marshall Wilderness Complex, and Glacier National Park. The Northern Rockies is home to a diverse boreal carnivore community, many of whom are also of special concern, including gray wolves (*Canis lupus*), grizzly bear,

wolverine, and fisher (*Martes pennanti*). Elevation on the study area ranged from 530–3190 m and forests varied from dry ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) stands at lower elevations to lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) at high-elevation sites.

2.2. Lynx capture and monitoring

To identify lynx habitat at a broad spatial scale, we used location data from 64 lynx that were monitored as adults and had been located at least 20 times within a consistent home range (median $N_{\text{locations}} = 561$). Lynx were captured from 1998 to 2007 using a combination of box traps, foothold traps and foot snares following Kolbe et al. (2003). Animals were fitted with very high frequency (VHF) radio-collars (Advanced Telemetry Systems, Isanti, Minnesota, USA), some of which also included Argos platform transmitter terminals (PTTs; Sirtrack Ltd., Havelock North, New Zealand) or store-on-board global positioning system (GPS) units (Lotek Wireless, Newmarket, Ontario, Canada). We used VHF ($N = 23$), Argos ($N = 6$), and GPS ($N = 35$) data to estimate home ranges; location accuracy varied among these 3 types of telemetry, but all were sufficient for identifying home ranges at a broad scale (Appendix A). To study movement at a fine scale, we used a subset of 37 (16 females, 21 males) adult lynx fitted with GPS collars that were captured from 2005 to 2007. We programmed GPS collars to obtain locations every 30 min throughout discrete 24-h periods, every other day during both winter (December–April) and summer (May–September).

2.3. Predicting resident habitat patches using RSF

To define lynx habitat, we calculated a resource selection function based on logistic regression (Manly et al., 2002) that quantified the environmental characteristics of resident lynx home ranges relative to those available across their range in the Northern Rockies (second-order habitat selection; Johnson, 1980). We used 80% fixed kernel lynx home ranges ($N = 64$; Rodgers et al., 2007) to characterize lynx use for comparison with random circular home ranges ($N = 1000$) equal in area to the median lynx home range (39.6 km²; Katnik and Wielgus, 2005) that characterized home range availability across the study area. Random home ranges were sampled within the species' range as defined in the Northern Rockies (see Study Area description; Fig. 1).

We used a combination of categorical maps and continuous indices based on satellite imagery to capture vegetative heterogeneity across the study area, hypothesizing that each may serve as an index to factors important to lynx ecology. We considered environmental variables that characterized vegetative, topographic, and climatic spatial heterogeneity (Table 1). Specifically, we were interested in remotely sensed vegetation indices that may serve as surrogates for field-based measures of vegetative heterogeneity found to be important in previous studies, such as horizontal cover or stand age (Squires et al., 2010). For continuous variables we calculated the average value in each used and random home range, and for categorical values we calculated the proportion of each used and random home range within each category (Table 1).

We used logistic regression in SYSTAT 11.0 (Systat Software, Inc., Richmond, California, USA) to compare used to random home ranges. We weighted random-used cases as 0.0064:1 to provide a balanced comparison of 64 used to 64 available home ranges and avoid inflating statistical precision while still allowing a large and representative random sample of habitat availability. We constructed multivariate logistic models of resource selection from important ($P < 0.25$) variables that we identified using univariate logistic regression according to Hosmer and Lemeshow (2000).

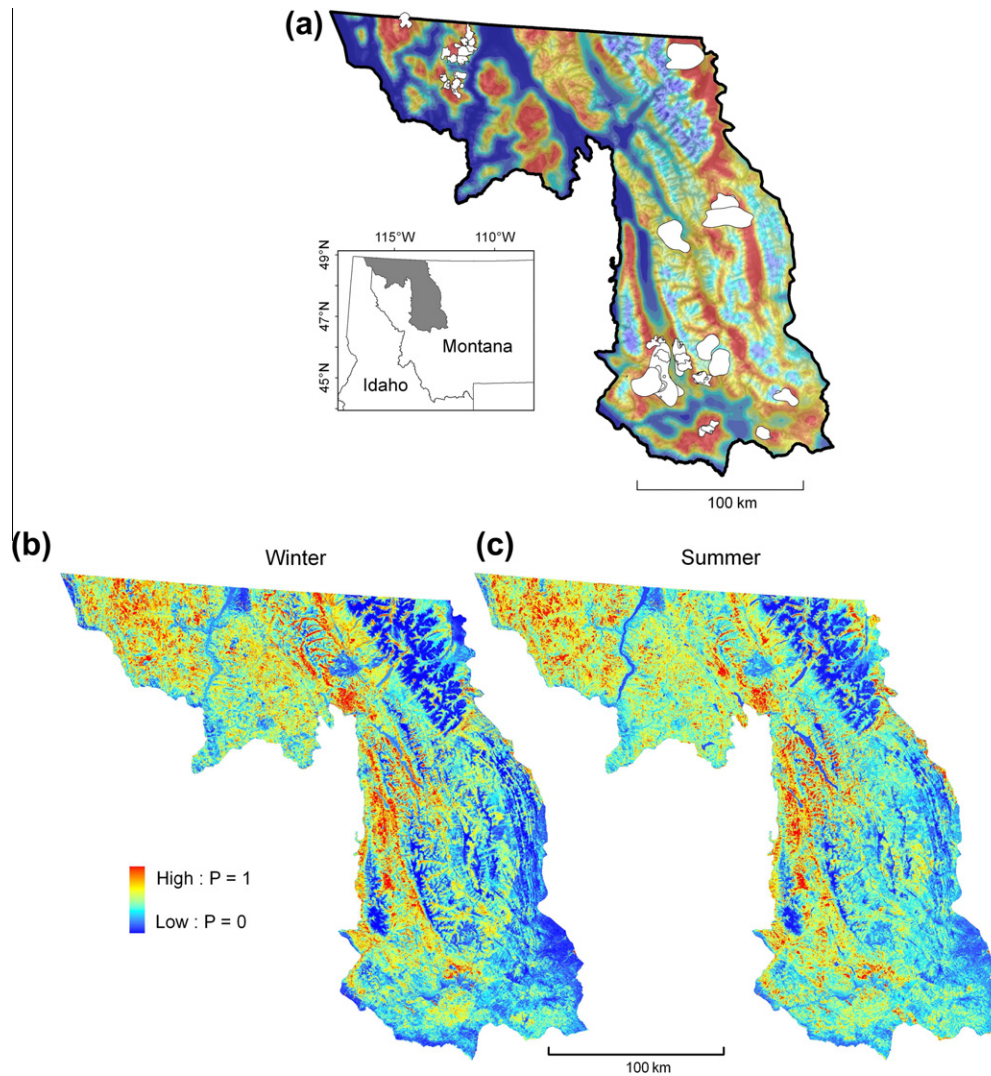


Fig. 1. Selection probability surfaces for: (a) home-range level resource selection function of Canada lynx (white polygons indicate lynx home ranges) within the northern Rocky Mountains; winter (b) and summer (c) population-level models of step selection functions for Canada lynx movement in the Northern Rocky Mountains, 2005–2007.

Before inclusion in a final model, we further evaluated variables in terms of their stability, collinearity, biological meaningfulness, interpretability, and their contribution to the model log-likelihood (Squires et al., 2010). We added variables to multivariate models using a manual forward-stepping procedure based on the strength of univariate relationships as measured by Wald statistics. We then evaluated whether to retain added variables to multivariate models according to biological reasoning and statistical likelihood ratio tests (Hosmer and Lemeshow, 2000). We selectively added and removed variables from multivariate models to see if this changed the sign or standard errors of variable coefficients to ensure that our final model was stable and with low collinearity among predictor variables (Hosmer and Lemeshow, 2000).

For model evaluation, we used 2-fold cross-validation to assess model predictions by randomly dividing our sample of lynx ($N = 64$) into two subsets and re-estimating the coefficients of our best model for each subset. We then assessed predictive capacity of each subset model with Spearman-rank correlation statistics that essentially tested if withheld lynx home ranges were indeed concentrated in areas of high predicted probabilities of use (Boyce et al., 2002). We then spatially applied the multivariable RSF across the study area using:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i), \quad (1)$$

where β_i is the RSF coefficient for each predictor variable (i), x_i is the value of each predictor variable (i), and $w(x)$ is a predicted value relative to the probability of use as lynx resident habitat (Boyce et al., 2002). To estimate a binary surface of low- versus high-probability habitat for resident lynx, we used a conservative cut-off value equal to the lowest predicted value of the observed sample of lynx home ranges.

2.4. Lynx movement modeling using step-selection functions

Similar to RSFs (Manly et al., 2002), step selection functions are based on case-control logistic regression of used and available steps and provide a powerful method for quantifying how organisms respond to their environment using biologically meaningful scales of availability (Fortin et al., 2005). To study the behavior of lynx specifically when moving, we used a hierarchical set of rules to remove GPS locations collected when lynx were likely stationary according to Olson et al. (2011). This involved using step length and turn angle data from movement paths to distinguish 'active' from 'resting' GPS locations (Morales et al., 2004). To distinguish true movement from that induced by GPS error, we compared the step length and turn angles leading to each GPS location to the distribution of step lengths and turn angles from test collars

Table 1

Variables used to quantify resource selection and movement behavior of Canada lynx in response to environmental heterogeneity.

Type	Variable name	Description	Source
Vegetation variables	CC.open	Canopy closure < 10%	VMAP (Brewer et al., 2004)
	CC.low	Canopy closure ≥ 10% & < 25%	
	CC.mod	Canopy closure ≥ 25% & < 60%	
	CC.high	Canopy closure ≥ 60%	
	VEG.alpine	Rock, ice and grasslands above 2000 m	
	VEG.grass	Grasslands and open clear cuts	
	VEG.shrub	Shrub	
	VEG.xeric	Ponderosa pine, Douglas-fir, and western larch forests	
	VEG.mesic	Engelmann spruce, subalpine fire and lodgepole pine forests	
	VEG.other	Water and developed	
Vegetation indices	NDVI	Normalized differenced vegetation index	Pettorelli et al. (2005)
	Bright	Tasseled-cap brightness	Crist et al. (1986)
	Green	Tasseled-cap greenness	
	Wet	Tasseled-cap wetness	Schriever and Congalton (1995)
	PCA	Single band principle component analysis	
Topography	Elev	Elevation (kilometers)	USGS
	Elev ²	Elevation (kilometers) squared	
	Slope	Slope (degrees)	Jenness, 2004
	Roughness	A ratio of 3-dimensional to 2-dimensional terrain surface area	
	Aspect	Cosine transformed into a linear variable between southwest (215°) and northeast (35°)	
	TPI	Topographic position index (500 m scale)	
	Dist_H2O	Distance to water	
Climate	T.avg	Average daily temperature	PRISM Climate Group (2006)
	Precip	Average annual precipitation	NOHRSC 2004
	Snow	Average winter snow depth	

known to be in a stationary position. Segments that had a length or turn-angle within the 70th percentile of the stationary test collar's segment distribution were classified initially as 'resting'; the remaining segments were classified as 'active'. Among the remaining 'active' segments, we removed GPS points which spiked abruptly away from clusters of consecutive 'resting' points. We used a non-linear curve fitting procedure (Johnson et al., 2002) to determine that a 2-state model (distinguishing stationary and moving states) provided the best fit to observed lynx movements (Appendix B). We used matched case-control logistic regression to compare environmental features associated with observed steps between sequential lynx GPS locations to those associated with 5 control steps, with each case identified using a stratifying variable (Fig. 2; Hosmer and Lemeshow, 2000). Case-control logistic regression minimizes variance associated with the stratified variable and the associated autocorrelation inherent in spatial data collected along a track over short time intervals (Craiu et al., 2008). We generated control steps by randomly sampling step lengths and turn

angles from their respective distributions in lynx GPS data (Fortin et al., 2005).

We treated marked animals as the experimental unit, thus addressing the most common problems associated with resource selection analyses including the pooling of data across individuals (Thomas and Taylor, 2006). We constructed individual SSF models for each animal and season (winter [December–April] and summer [May–August]) using SAS (SAS Institute, Cary, NC). We then averaged logistic coefficients across individual lynx as an estimate of the population-level effect of predictor variables on the relative probability of use (Sawyer et al., 2009). We used a t-statistic to test if coefficients averaged across individuals were significantly different from zero ($\alpha \leq 0.1$), and included only significant variables in the population-level model for each season (Hosmer and Lemeshow, 2000). We considered the same suite of vegetative, topographic, and climatic variables as when estimating the lynx habitat RSF. Prior to modeling, we identified and removed predictor variables with high ($|r| > 0.50$) multicollinearity based on Pearson's pairwise correlation analyses. We did not use an information theoretic approach such as Akaike's Information Criterion (Burnham and Anderson, 2002) for model selection because these methods lack standardized approaches to retain the animal as the experimental unit and build a population-level model from common predictor variables (Sawyer et al. 2009).

We mapped seasonal (winter and summer) projections of spatially referenced use surfaces of lynx movement using the coefficients from the population-level SSF model in Eq. (1). We then re-scaled SSF predicted values to probability of use values between 0 and 1 by dividing each raster cell value by the maximum predicted value. To remove the effect of a few extreme outliers, we included only the range of predicted values contained within the 5th – 95th percentiles for the final SSF probability surface.

2.5. Mapping lynx connectivity

We integrated our multi-scale analyses of lynx habitat and movement behavior with a least-cost path analysis to assess connectivity across the species' distribution in the Northern Rockies

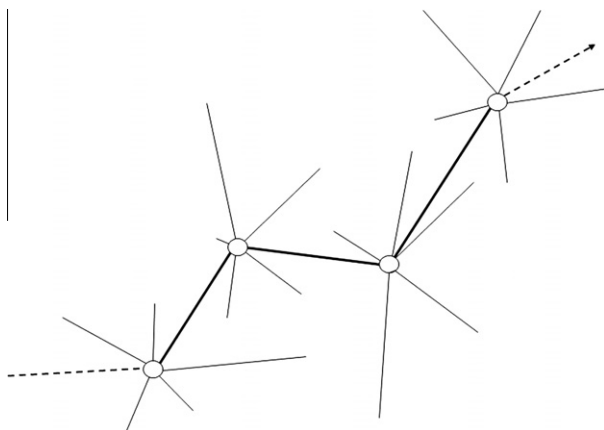


Fig. 2. Depiction of step-selection function that compared used (—) lynx movement steps to 5 controls (---) at each GPS location.

(Chetkiewicz et al., 2006; McKelvey et al., 2011). We used the “Cost Distance” and “Cost Path” functions in ArcGIS® Desktop 9.2 (ESRI, Redlands, CA, USA) to determine least cost paths from source points in the north to destination points in the south (Cushman et al., 2009). We spaced potential source points uniformly at 7 km intervals along the Canadian border in high probability lynx habitat and we randomly located destination points within all patches of high-probability lynx habitat in the Northern Rockies. The western section of the study area was divided from the rest of the study area by a large reservoir (Lake Koocanusa), which creates a geographical barrier to movement between east and west sections. Therefore, we restricted western source points ($N = 9$) to western destination points ($N = 25$) and eastern source points ($N = 12$) to eastern destination points ($N = 200$). To create least-cost paths that reflect connectivity of ecologically meaningful areas for lynx, we used the binary RSF model of lynx habitat to identify habitat likely to be occupied by lynx and limited source and destination points to those areas. We converted the SSF probability surface to a resistance surface for least-cost path analysis using the reciprocal of the probability values, so that areas with high probabilities of use had low resistance values, and areas with low probabilities of use had high resistance values.

Once least cost paths were generated, we determined the routes most likely used by lynx by summing the total number of paths and calculating the percent of this total for routes in which multiple paths overlapped. To evaluate where highways potentially impacted connectivity, we counted the number of putative path crossings per km for 10-km segments of highway throughout the species' distribution in the Northern Rockies.

3. Results

3.1. Lynx habitat in the northern rockies

In the northern Rocky Mountains, Canada lynx selected home ranges at mid-elevations ($X = 1681$ m, $SD = 116$ m, range = 1425–1998 m) with low surface roughness, high canopy cover, and little open grassland vegetation ($X^2_5 = 94.482$, $P < 0.001$; Table 2). The spatial predictive surface resulting from the RSF model indicated lynx habitat in the Northern Rockies is distributed in patches at a landscape scale (Fig. 1). Spearman-rank correlation statistics from 2-fold cross-validation of ranked model prediction bins and the frequency of values for withheld home ranges were 0.845 and 0.941 for each fold of data, suggesting good predictive fit.

3.2. Lynx movements from step-selection functions

From 2005 to 2007, we modeled how lynx responded to landscape heterogeneity based on 33 lynx (22,401 GPS locations) during winter and 28 lynx (20,615 GPS locations) during summer. During winter, SSF coefficients averaged across individuals were

Table 2

Resource selection function coefficients (β), standard errors (SE), Wald statistics (Z) and probability values comparing Canada lynx ($N = 64$) home ranges in the northern Rocky Mountains to randomly available home ranges ($N = 1000$) with multivariate logistic regression, 1998–2007.

Variable	β	SE	Z	P
Elevation	128.898	34.047	3.786	<0.001 ^a
Elevation2	−36.277	9.852	−3.682	<0.001
Surface roughness	−50.051	12.105	−4.135	<0.001
High canopy cover ($\geq 60\%$)	3.102	2.154	1.440	0.150
Grass Cover (%)	−11.147	7.152	−1.559	0.119
Intercept	−59.641	28.002	−2.130	0.033

^a Global Likelihood Ratio Test relative to null model: $X^2_5 = 94.482$, $P < 0.001$.

significantly different from zero ($\alpha \leq 0.1$) for all significant predictor variables except for aspect and TPI (Table 3). Lynx during winter preferentially traversed habitats characterized by high greenness and NDVI compared to available movement segments, but they generally avoided habitats characterized by high PCA (Table 3, Fig. 1). During summer, coefficients averaged across individuals were significantly different from zero ($\alpha \leq 0.1$) for all significant predictor variables except for aspect (Table 3). Lynx preferred habitat for movement in summer was generally characterized by a greater distance from water (drainages) and with high greenness, NDVI, PCA, and TPI (Fig. 1). Overall lynx were consistently selective of high values of greenness and NDVI and low values of surface roughness regardless of season. Lynx did not exhibit selection ($P = 0.127$) for PCA during summer, but did prefer low PCA values during winter (Table 4). The spatial application of SSF predictive models revealed patterned responses of lynx movement behavior to habitat fragmentation, as indexed by continuous, remotely-sensed vegetation metrics greenness, NDVI, and PCA (Fig. 3). Additionally, population SSF models resulted in spatial movement surfaces that were generally similar seasonally with the exception of some contraction in preferred movement habitats at the southeastern extent of the species' range in the Northern Rockies (Fig. 1).

3.3. Lynx connectivity

We generated 2625 least cost paths between all habitat patches identified with the RSF model across a resistance surface defined by the SSF model. We found a primary putative corridor for connectivity of lynx from Canada to the Northern Rockies that extended from the Whitefish Range in the north, along the western front of the Swan Range and ended near Seeley Lake, MT (Fig. 4). The majority of paths (up to 64%, $N = 1673$) followed all or a portion of this route, before branching off to destination points in high-probability lynx habitat identified in our RSF model. A second putative corridor extended along the east side of Glacier National Park to the Bob Marshall Wilderness Complex. In general, connectivity paths did not vary seasonally, but there were some seasonal differences in paths in mountainous areas near Glacier National Park (Fig. 4). Paths that were located in the western portion of the study area ($N = 225$) were less concentrated, which may be partially explained by our treatment of the Lake Koocanusa reservoir as a barrier, the relatively smaller total area of resident patches within this isolated portion of the study area, and the close proximity to lynx habitat across the Canadian border.

The majority of least cost paths crossed the US Highway 2 transportation corridor to the north of the Hungry Horse reservoir near the town of Hungry Horse, MT (Fig. 5). In both summer and winter, the 10 km stretch of US Highway 2 near the town of Hungry Horse

Table 3

Numbers of Canada lynx with negative and positive relationships to predictor variables in the Northern Rocky Mountains based on step-selection coefficients from case-control logistic regression, 2005–2007.

	Aspect	Dist_H20 ^a	Green ^a	NDVI ^a	PCA ^a	Rough ^a	TPI ^b
Winter ($N = 33$)							
Negative	15	23	1	8	25	21	14
Positive	18	10	32	25	8	12	19
Summer ($N = 28$ lynx)							
Negative	17	6	2	3	9	22	8
Positive	11	22	26	25	19	6	20

^a Predictor variables with averaged coefficients across individuals significantly ($\alpha \leq 0.1$) different than zero for inclusion in population-level models.

^b TPI predictor variable was significant only for inclusion in summer population model.

Table 4

Coefficients for population-level, step-selection function models of Canada lynx in the Northern Rocky Mountains by season, 2005–2007.

Variable	Summer			Winter		
	β	SE	P	β	SE	P
Dist_H20	0.301	0.099	0.005	−0.269	0.120	0.033
Green	0.020	0.003	<0.001	0.033	0.003	<0.001
NDVI	2.243	0.368	<0.001	1.343	0.348	0.001
PCA	0.005	0.003	0.127	−0.014	0.003	<0.001
Rough	−2.296	0.731	0.004	−3.059	0.808	0.001
TPI	0.004	0.002	0.025			

had the largest number of simulated lynx paths (154.4 and 126.8 paths per km, respectively) connecting northern populations to destination points in the study area. Relatively fewer predicted

paths crossed other 2-lane highways, though minor crossing areas were identified along Montana Highways 83, 89, 93, 141, and 200 across the study area (Fig. 5).

4. Discussion

4.1. Lynx movement corridors

We used empirical models of both broad-scale resident habitat and fine-scale movement behavior to collectively identify functional corridors for lynx conservation. We proposed that connectivity of lynx in the Northern Rockies is maintained by a primary north–south corridor that extends from the Canadian border and proceeds south along the west side of the Bob Marshall Wilderness Complex. We also identified a putative corridor that traverses the

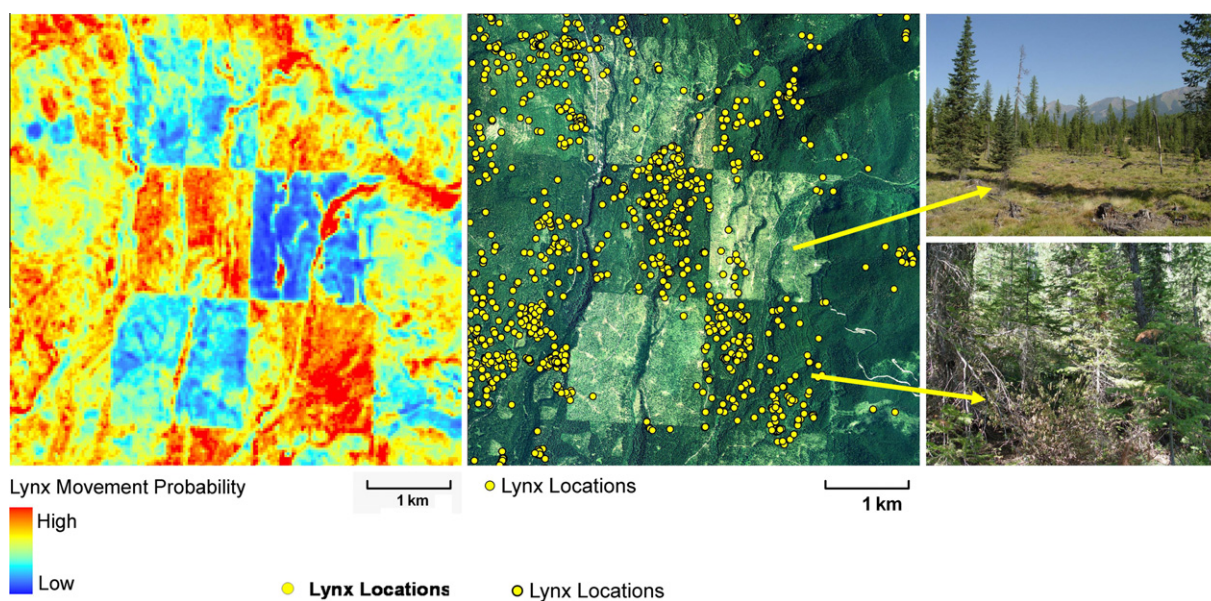


Fig. 3. Fragmentation from forest thinning decreased the probability of Canada lynx movements based on a population-level, step-selection function; 2005–2007.

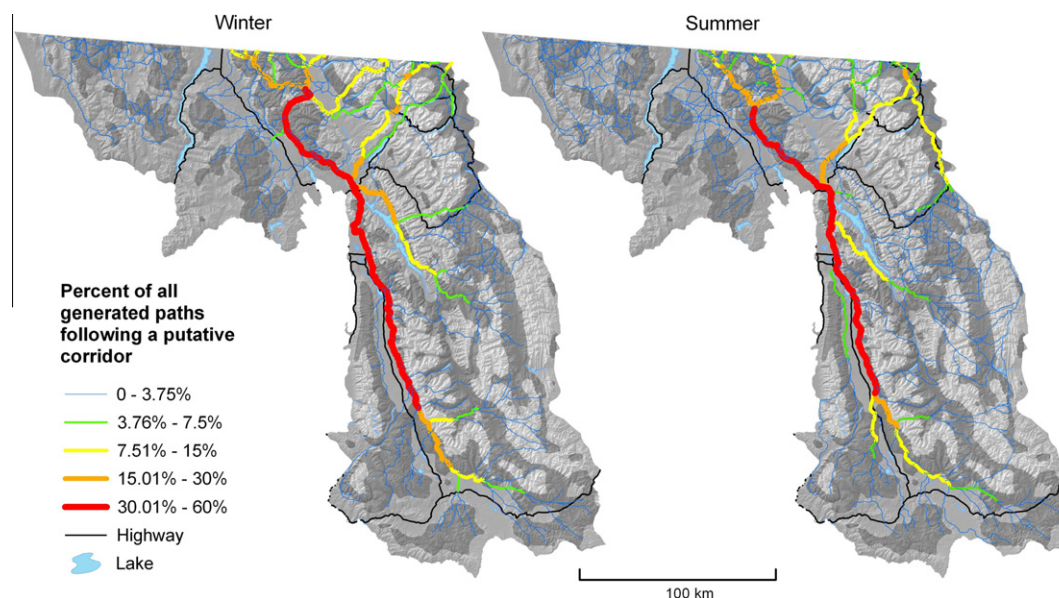


Fig. 4. Putative corridors facilitating dispersal from northern populations to patches capable of supporting Canada lynx (shaded areas) in the Northern Rocky Mountains based on least-cost path analysis of movement surfaces empirically defined using population-level, step-selection models, 2005–2007.

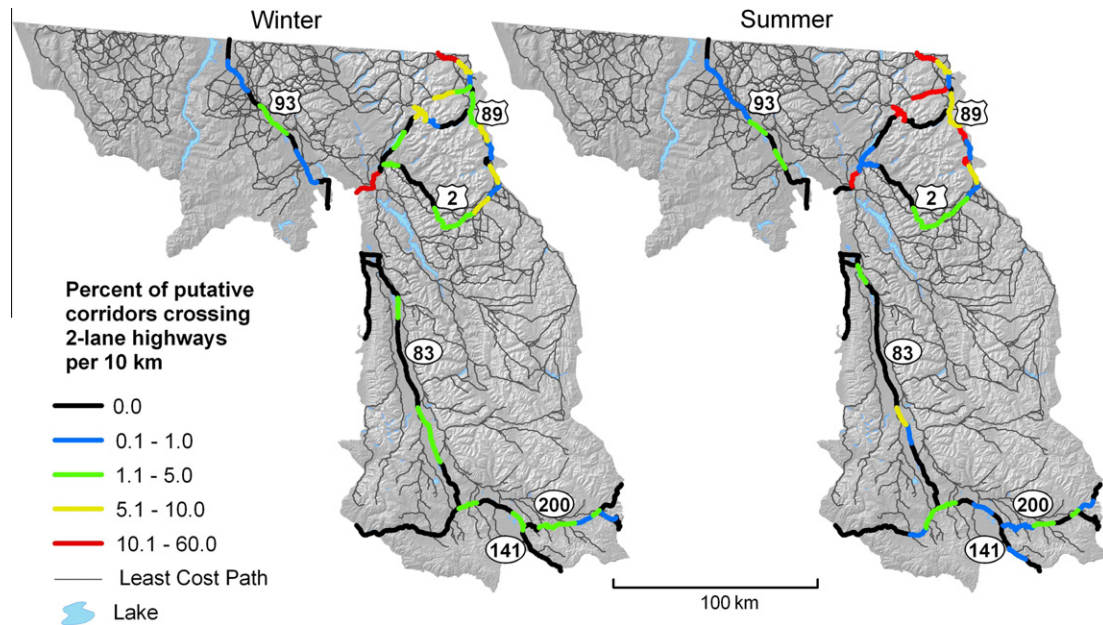


Fig. 5. Percent of all putative corridors out of all possible paths that crossed given 10 km stretches of 2-lane highway based on least-cost path analysis within the distribution of Canada lynx in the Northern Rocky Mountains by season, 2005–2007.

east side of Glacier National Park that connects Canada to northern portions of the Bob Marshall Wilderness. The putative movement corridors we identified for lynx also show reasonable correspondence with previously published models for wolverine (Schwartz et al., 2009), wolves (Oakleaf et al., 2006) and grizzly bears (Mace et al., 1999). Thus, considerable conservation value may be gained by combining habitat selection and movement analyses to identify corridors in the Northern Rockies for other focal species, such as wolves, grizzly bears, fisher and wolverine (i.e., Carroll et al., 2001).

Some species follow unique patterns of habitat selection during dispersal movements (Soulsbury et al., 2011), whereas others do not (Newby, 2011). We assumed when we defined putative corridors that lynx during dispersal would respond similarly to a resistance surface derived from within home-range movements. We initially hoped to test formally whether dispersing and resident lynx responded similarly to landscape heterogeneity, but this was impossible due to a small sample of dispersal movements. We assumed that broad-scale data layers adequately quantified environmental heterogeneity for SSF and RSF modeling (Brambilla et al., 2009). The models we developed were based on data layers that are widely available to landscape managers, but these model covariates only coarsely quantify the underlying environmental heterogeneity. For these reasons, the putative corridors that we present may be treated as testable hypotheses for further study using both spatial and genetic methods.

Rates of movement have direct biological importance in how organisms respond to their environment (Johnson et al., 2002). Many factors affect an organism's movement rates, including physiological constraints, environmental factors, and behavior. Overall, lynx movement rates in our study area averaged 6.9 km/day (Appendix C), which is considerably higher than those reported at northern latitudes during periods of high hare density but similar to those during cyclic lows (Ward and Krebs, 1985). It seems likely that southern lynx, with lower hare densities and higher movement rates in general, would be more vulnerable to factors negatively affecting connectivity. We found no statistical evidence for an "inter-patch" or dispersal movement state (Appendix B).

4.2. Response to environmental heterogeneity

Our prediction that lynx would exhibit seasonal differences in their response to environmental heterogeneity was only partially supported. In addition to consistent selection for high NDVI and greenness regardless of season, lynx appeared to conserve energy by preferentially selecting travel routes with low topographic heterogeneity, as observed for other mammals (Bruggeman et al., 2007), including carnivores (Dickson et al., 2005). We found no selection ($P = 0.127$) for areas with increased PCA values during summer; however, lynx avoided these areas during winter (Table 4). Principal components analysis of visible and near-infrared light is correlated with leaf-area index, and used to discriminate between vegetation types such as coniferous forests, shrubs, and grasslands (Wang et al., 2001). In our study area, PCA values tended to decrease in mature forests and increase in young, regenerating forest stands. Patterns of PCA selection support previous evidence of the reliance on older forests during winter and younger forests during summer by both lynx (Koehler et al., 2008; Squires et al., 2010) and snowshoe hares (Griffin and Mills, 2009). Although lynx corridors were generally similar seasonally, their respective role for conservation may depend on seasonal patterns of lynx dispersal. During the breeding season in late winter, males may exhibit extra-home range movement when they seek females. However, lynx in southern populations often make significantly longer exploratory or dispersal movements when prey availability is highest during summer (Apps, 2000; Aubry et al., 2000; Squires and Oakleaf, 2005). Thus, the winter corridors we identify may best provide for local connectivity of neighboring breeding populations, whereas summer corridors may facilitate long-distance dispersal such as those from range core to periphery.

Ideally, movement studies elucidate the behavioral response of organisms to environmental heterogeneity (Schick et al., 2008). We predicted that remotely-sensed vegetation indices would serve as broad-scale surrogates adequate for distinguishing lynx movement behaviors likely associated with an important fine-scale component of Canada lynx habitat, horizontal cover. Implicit in our approach is that animals are able to select "best" least-cost paths

rather than turning around after starting down a poor quality path or starting down a poor quality path knowing that conditions improve down the track. Previous research has emphasized the importance of horizontal cover for both lynx (Moen et al., 2008; Fuller and Harrison, 2010; Squires et al., 2010) and their primary prey, snowshoe hares (*Lepus americanus*; Griffin and Mills, 2009). When building SSF models from strictly satellite-derived indices, we found that lynx were most consistently sensitive to positive values of NDVI and greenness when traversing landscapes (Table 4). High values of NDVI correlate with dense vegetation cover, such as evergreen trees in winter or dense shrubs and regenerating forests in summer, while low values correlate with barren areas (Gamon et al., 1995). Greenness also provides an index of the density of green vegetation and correlates with plant biomass and net primary productivity; like NDVI, greenness values often increase and then decrease as forests age (Crist et al., 1986; Carroll et al., 2001). The relationship between remotely-sensed indices and horizontal cover has not been explicitly tested, but the consistent predictive capacity of these indices in lynx movement models suggest them as candidate surrogates for this typically field-measured variable.

4.3. Fragmentation and highway crossings

Habitat fragmentation is clearly detrimental to some taxa (Crooks, 2002; Laurance, 2008), but the impact of fragmentation on meso-carnivores is not well understood. Results from our population-level model indicate that changes to vegetation structure can increase landscape resistance to lynx movements (Fig. 3), however, there is no evidence that this currently is causing genetic isolation (Schwartz et al., 2002). Although lynx are capable of crossing hundreds of kilometers of unsuitable habitat, as evidenced by verified locations in prairie ecosystems (McKelvey et al., 2000), lynx in the Northern Rockies are sensitive to changes in forest structure and tend to avoid forest openings (Koehler, 1990; Squires et al., 2010). The extent to which fragmentation from roads and urbanization can impact connectivity of meso-carnivore populations likely depends on the physical design of highway improvements, the surrounding environmental features, the density of increased urbanization, and the increased traffic volume (Clevenger and Waltho, 2005; Grilo et al., 2009). Carnivores are especially vulnerable to highway-caused mortality in areas with dense and high-traffic volume roadways (Clevenger et al., 2001). For example, 20% of mortalities (13 out of 65) of reintroduced lynx in Colorado were due to vehicle collisions (Devineau et al., 2010), as well as 19% (16 out of 83) of reintroduced lynx in the Adirondack Mountains of New York (Aubry et al., 2000). In Germany, 45% of the mortalities of subadult Eurasian lynx (*Lynx lynx*) are caused by traffic accidents (Kramer-Schadt et al., 2004). In adjacent south-eastern British Columbia, lynx avoided crossing highways within their home ranges (Apps, 2000).

We documented 44 radiocollared lynx with home ranges within an 8 km buffer of 2-lane highways; only 12 of these individuals crossed the highway (Squires, unpublished data). Although the exact crossing locations were unknown, straight lines between subsequent telemetry locations all bisected the highway within a 10 km stretch predicted by our model as a likely crossing area. These observations increase our confidence in our predicted crossing zones of highways that bisect lynx putative corridors in the Northern Rockies. Given that increased traffic and urbanization are projected for the Northern Rockies (Hansen et al., 2002), mitigation such as land purchases and conservation easements may be necessary to preserve connectivity among lynx populations. If traffic volume greatly increases across corridors, the construction of wildlife crossing structures may be an appropriate conservation strategy; however the degree to which these structures effectively

connect lynx populations is currently unknown (Clevenger and Waltho, 2005).

Acknowledgments

We thank the Tri-agency Group for the Montana Forest Highway Program, Western Federal Lands Highway Division of the Federal Highway Administration, the Montana Department of Transportation, the University of Montana, and US Forest Service, Region 1 for providing funding. We also thank the many technicians that worked under difficult field conditions to make this study possible. We acknowledge the Lolo and Kootenai National Forests for providing housing and other logistical support. We especially thank J. Claar, recently retired as USFS National Carnivore Leader, for his continued support of meso-carnivore research throughout the Northern Rockies.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.07.018>.

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