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Use of resource selection functions to identify conservation corridors

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Summary

1. Corridors are commonly used to connect fragments of wildlife habitat, yet the identification of conservation corridors typically neglects processes of habitat selection and movement for target organisms. New technologies and analytical tools make it possible to better integrate landscape patterns with behavioural processes. We illustrate the integration of resource selection functions (RSFs) and least-cost path (LCP) analyses for the purpose of corridor planning for two large carnivores.

2. We used RSFs developed from Global Positioning System telemetry data to predict the seasonal distribution of two large carnivores: grizzly bears *Ursus arctos* and cougars *Puma concolor*. We then applied LCP analyses to identify potential corridors in two fragmented montane landscapes – Canmore and Crowsnest Pass – in Alberta, Canada.

3. Grizzly bear habitat selection in both areas positively correlated with greenness in all seasons and soil wetness and proximity to water in the summer when both variables were associated with bear forage. During spring, grizzly bear occurrence in Canmore inversely correlated with road density.

4. For cougars, habitat selection varied by region: it negatively correlated with road density in Canmore during non-winter and positively correlated with terrain ruggedness in Crowsnest Pass. Cougar occurrence during the non-winter season in Canmore positively correlated with greenness.

5. For each species, seasonal RSFs were used to develop a cost surface for LCP analyses to identify potential corridor locations in each study area. Overlaying the paths for the two species highlighted where the landscape could support corridors for both species and potential highway crossing zones. The telemetry data supported some of these modelled crossings.

6. *Synthesis and applications*. We show how to integrate RSFs and least-cost modelling to identify corridors for conservation. We focus on two large carnivores in the Canadian Rocky Mountains to identify potential corridors in Canmore and provide a framework for corridor planning in Crowsnest. We suggest that our approach is applicable to many other target species in addition to large carnivores in human-dominated landscapes.

Key-words: connectivity, corridor, cougar, grizzly bear, habitat selection, least-cost path, resource selection functions

Introduction

Corridors connect fragments of wildlife habitat and are a fundamental component of conservation management, particularly in regional- and continental-scale corridor initiatives in North America (Nelson, Day, & Sportza 2003; Beier *et al.* 2006). Scientists, planners and managers have applied a variety of methods to identify and design conservation corridors, yet these methods typically ignore processes of habitat selection by animals and their movement (Chetkiewicz St Clair & Boyce 2006; Beier, Majka & Spencer 2008). These processes are usually incorporated into various expert-based and statistical modelling approaches (Noss & Daly 2006).

Three types of statistical models have been used to identify corridors: (i) individual-based models, (ii) spatially explicit population models, and (iii) models based on estimates of ecological or effective distance such as least-cost modelling. Individual-based models permit evaluation of an individual's responses to a landscape through measures of landscape resistance, but they often require large amounts of data (Tracey

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2006). Spatially explicit population models are used to evaluate the demographic consequences of having linkages between habitat patches. However, these models are poorly suited for evaluating fine-scale, within-home-range, animal movements or impacts of local barriers such as roads (Carroll 2006). Least-cost modelling represents an intermediate approach to corridor planning, in terms of data requirements and model complexity (Adriaensen *et al.* 2003). These models evaluate potential animal routes across the landscape based on the 'cost' of animal movement between locations, or termini (Beier *et al.* 2008), and have been applied to a number of species (Theobald 2006). Understanding how animals use landscapes requires that the landscape be described as a gradient along a continuum of selection (Fischer, Lindenmayer & Fazey 2004). While most least-cost modelling relies on expert opinion to parameterize the model and develop the cost surface (Beier *et al.* 2008), resource selection functions (RSFs) provide a data-based method for achieving this (Manly *et al.* 2002).

Resource selection functions developed for focal species in a particular landscape advance least-cost modelling in several ways. First, they rely on species and landscape-specific empirical data making the approach to corridor design more rigorous, defensible and transparent (Noss & Daly 2006). Second, RSFs can be generated at multiple scales depending on the extent of the landscape and the scale of management application (Boyce 2006). Finally, RSF models can be developed to reflect species- and landscape-specific variations in seasonal resource selection. Combining RSF models with least-cost modelling for corridor planning can integrate the functional connectivity of landscapes (*sensu* Taylor, Fahrig & With 2006) while maintaining the visual advantage of structural connectivity-based approaches (Chetkiewicz *et al.* 2006).

We explored the application of RSF models with least-cost modelling for corridor planning in two areas in the Canadian Rocky Mountains of Alberta – the Canmore region of the Bow Valley (hereafter, Canmore) and the Crowsnest Pass area (hereafter, Crowsnest) (Chadwick 2000). Both areas have been identified as critical areas for movement, particularly of grizzly bears *Ursus arctos* L. within the regional Yellowstone-to-Yukon Conservation Initiative (Nelson *et al.* 2003). We selected grizzly bears and cougars *Puma concolor* L. as target species based on their ecological and behavioural resiliency in fragmented habitats (Weaver, Paquet & Ruggiero 1996) and provincial management and regional conservation priorities (e.g. Carroll, Noss & Paquet 2001). We were also interested in understanding whether corridor designs would be complementary or redundant between these two species during the seasons of overlap with both species (spring, summer and autumn) and during the winter when only cougars were active on the landscape. We collected location data from grizzly bears and cougars with Global Positioning System (GPS) radiocollars during 2000–2004 to develop seasonal RSFs that predict animal distribution in each landscape. We used these models in a least-cost path (LCP) analysis to identify corridors in both areas by connecting paths to two polygons or termini in each season across the study areas. While our objective was to provide information for local wildlife managers and conservation organizations to improve corridor planning for large carnivores in Canmore and Crowsnest, the approach can be applied to other target species (e.g. Beier *et al.* 2006, 2008).

Materials and methods

STUDY AREAS

Canmore region of the Bow River Valley

The Canmore region of the Bow River Valley (51°05′N, 155°22′W) is *c.* 110 km west of Calgary, east of Banff National Park and north of Kananaskis Country in Alberta, Canada (Fig. 1). Canmore, part of the Rocky Mountain Natural Region of Alberta (Natural Regions Committee 2006) is characterized by some of the best-protected montane habitat for large carnivores in Alberta, including Banff National Park and a number of provincial parks (Donelon 2004). However, the quality of this habitat is undermined by a rapidly growing human population in the town of Canmore (*c.* 11 600 permanent residents; Herrero & Jevons 2000), bisection by the Trans-Canada Highway, one of the busiest transportation routes in Canada (summer traffic = 21 000 vehicles per day; Alexander, Waters & Paquet 2005), and its proximity to Calgary, projected to exceed 1·5 million people by 2030 (Stelfox, Herrero & Ryerson 2005). In addition, a two-lane paved highway and a two-track transcontinental railway, further challenge wildlife movements through the Bow River Valley (Clevenger & Wierzchowski 2006). To address these challenges to wildlife movement, the Bow Corridor Ecosystem Advisory Group (BCEAG) designated a number of wildlife corridors through Canmore that connect Banff National Park and other protected areas in the region (BCEAG 1999). Corridor location and designs were based on guidelines in Beier & Loe (1992) and extrapolated from corridor research conducted in Banff National Park. The study extent represents the composite minimum convex polygon (MCP) of locations of grizzly bears and cougars captured and collared within Wildlife Management Unit 410 (425 km^2), that includes the town of Canmore and the currently designated corridor network (BCEAG 1999).

Crowsnest Pass in the Crowsnest River Valley

The Crowsnest Pass (49°37′N, 114°4′W) is a 32-km-long valley of montane and grassland vegetation located along the Crowsnest River in south-western Alberta, adjacent to the Alberta–British Columbia border, 269 km south-west of Calgary (Fig. 1). The Crowsnest also lies within the Rocky Mountain Natural Region (Natural Regions Committee 2006). In contrast to Canmore, Crowsnest is managed for multiple uses including forestry, oil and gas, and livestock grazing. The municipality of Crowsnest is comprised of five communities and two hamlets (population *c.* 6000) along a two-lane highway (Highway 3) that bisects the valley (daily traffic volume = 7000 vehicles per day) with a railroad supporting eight to 16 freight trains per day (Apps *et al.* 2007). Recent discussions of twinning Highway 3 through Crowsnest and ongoing residential developments have prompted concerns about carnivore conservation in the region (Proctor *et al.* 2005). The study extent represents the composite MCP of locations of grizzly bears and cougars captured within the boundaries of Wildlife Management Unit 303 (1657 km^2), that includes three broad movement corridors identified within the municipality based on grizzly bear sightings.

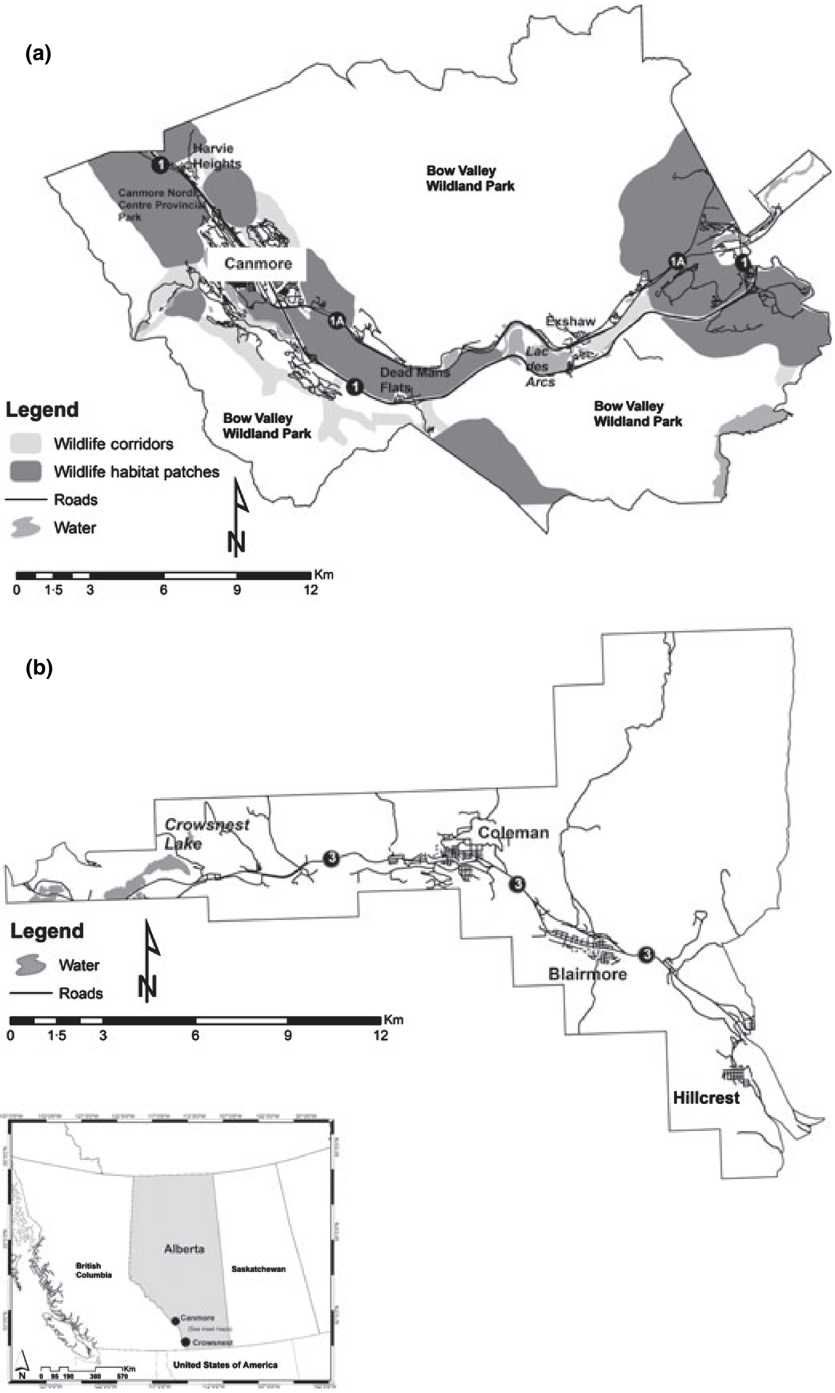

Fig. 1. (a) Canmore study area in Alberta based on Wildlife Management Boundary (WMU) 410 as well as currently designated wildlife corridors and habitat patches. (b) Crowsnest study area in Alberta illustrating WMU 303. Inset map shows study area locations in Alberta, Canada.

DATA SOURCES

Grizzly bear and cougar telemetry data

During the springs of 2000–2004, four grizzly bears (two females and two males) were captured and collared in Canmore and four grizzly bears (two females and two males) in Crowsnest, using culvert traps, leg and pail snares, and aerial darting (Cattet, Caulkett & Stenhouse 2003). During the winters of 2000–2004, five cougars (four females and one male) were captured and collared in Canmore and 13 cougars (seven females and six males) in Crowsnest by tracking cougars in snow with trained hounds (Hornocker 1970). Grizzly bears were fitted with Televilt-Simplex™ GPS radiocollars (Lindesberg, Sweden) programmed to acquire a fix every 1 or 2 h. Cougars were fitted with smaller Televilt collars programmed to acquire a fix every 1 or 4 h. Sampling rates were based on battery life calculations and constraints associated with recapture operations to replace failing batteries. Capture protocols were approved by Animal Care Committees for the University of Alberta and Alberta Sustainable Resource Development (AB SRD), following the Canadian Council on Animal Care guidelines.

Digital data

Potential explanatory variables for grizzly bear and cougar distributions were derived from 13 geographic information system (GIS) layers with a 30-m-pixel resolution (Table 1). Landcover was reclassified to five classes, estimated from a combination of MODIS, Landsat TM imagery and a digital elevation model with an overall accuracy of 88% (κ = 0·70) (McDermid, Franklin & LeDrew 2005). We also used natural subregions (Natural Regions Committee 2006), distance to water, distance to forest and percentage crown closure, derived from TM imagery, and a digital elevation model (McDermid *et al.* 2005). Terrain variables included slope, elevation and topographic ruggedness index (TRI) (Evans 2004). TRI was calculated at 30-m resolution using the difference between the elevation in one pixel with the surrounding eight neighbouring cells (but for an alternative, see Sappington, Longshore & Thompson 2007). Food resources for grizzly bears and cougars included a green vegetation index (GVI) and compound topographic index (CTI) (Evans 2004). CTI is the steady-state wetness index derived from slope and the upstream contributing area per unit width. We also developed an elk *Cervus elaphus* L. RSF using annual provincial government winter surveys, elevation, road density and distance to water. Each pixel in this layer had a RSF score associated with the relative probability of elk occurrence. Human use was modelled using road density based on a 2-km window (Mace *et al.* 1996).

DATA ANALYSES

Resource selection functions

Following retrieval of the GPS collars, location data were imported into ArcGIS 9.0 (Environmental Systems Research Institute, Inc., Redlands, CA, USA). To address GPS fix biases due to habitat and terrain characteristics associated with early models of Televilt collars (e.g. Frair *et al.* 2004), we developed a GIS layer quantifying the probability of obtaining a fix (P_{FIX}) (Hebblewhite, Percy, & Merrill 2007) that ranged from 49% to 96% in Canmore and from 25% to 95% in Crowsnest. The P_{FIX} values were used to weight location data during RSF model development (see below).

Home ranges for each grizzly bear and cougar were created using Hawth's Analysis Tools for ArcGIS (hereafter, Hawth's Tools) (Beyer 2004). A random point generator was used to identify 'available' habitat locations within each individual's home range at a sampling intensity of five points per km^2 (Nielsen, Boyce & Stenhouse 2004a). To create RSFs, we compared seasonal grizzly bear and cougar GPS locations with available locations within individual home ranges. To reflect resource selection variability by season, we partitioned the grizzly data into spring (*c.* 30 April–15 June), summer (16 June–10 August) and autumn (11 August–*c.* 7 November) seasons (Munro *et al.* 2006). Cougar data were partitioned into two seasons: winter (15 November–15 April) and non-winter (16 April–14 November) (Jalkotzy, Ross & Wierzchowski 1999). Resource selection for both species was evaluated at the third-order scale (within home ranges; Johnson 1980) and followed a Design III protocol where availability was sampled for each individual (Manly *et al.* 2002).

Species-specific seasonal models were created following model-fitting procedures in Hosmer & Lemeshow (2000). All continuous variables were tested for collinearity using Pearson correlation coefficients. Correlations between slope, TRI, crown closure and elevation with $|r| \geq 0{\cdot}7$ were not included in the same model. Nonlinear relationships were tested among all continuous covariates by including a quadratic term and we selected the form that resulted in the largest increase in the χ^2-statistic for the robust Wald test. We used robust standard errors clustered on individual animals (Nielsen *et al.* 2004a) and applied probability weights generated from the P_{FIX} layer described above to create a main effects model. The main effects model was refit using mixed effects linear regression with individual animal as a random intercept to address unbalanced sample sizes (Gillies *et al.* 2006). These models were compared with five candidate models using an information theoretic approach (Burnham & Anderson 1998). In all cases,

Table 1. Description and characteristics of environmental variables used to model the probability of occurrence of grizzly bears and cougars in the Rocky Mountains, Alberta, Canada

Variable group	Variable name	Abbrev.	Resolution (m)	Units	Data range
Landcover	Upland forest	UFOR	30	Category	0 or 1
	Upland herb	UHERB	30	Category	0 or 1
	Shrub	SHRB	30	Category	0 or 1
	Water	WATER	30	Category	0 or 1
	Barren	BARRN	30	Category	0 or 1
Subregions	Montane	MONT	30	Category	0 or 1
	Subalpine	SUB	30	Category	0 or 1
	Alpine	ALP	30	Category	0 or 1
	Distance to water	DWAT	30	km	0–2·3
	Distance to forest	DFOR	30	km	0–11
	Per cent crown closure	PCC	30	%	0–99
Food resources	Greenness	GVI	30	Unitless	0–85
	Elk RSF	ELK	30	Unitless	1·7–8·1
	Compound topographic index	CTI	30	Unitless	2·3–26
Terrain	Topographic ruggedness index	TRI	30	Unitless	0–249
	Slope	SLP	30	degrees	0–74
	Elevation	ELEV	30	m	1213–3069
Humans	Road density	RDENS	30	km km^{-2}	0–12

the seasonal models were selected, and we report only these models in our results.

Model fit was assessed using a *k*-fold cross-validation (Boyce *et al.* 2002). We also evaluated the predictive performance of RSF models by randomly dividing the GPS locations into two groups before model development: 80% of the data comprised a 'model-training' group and the remaining 20% comprised a 'model-testing' group for validation (Johnson *et al.* 2006). We compared the observed (withheld model-testing sample) and expected numbers of GPS locations with chi-squared, Spearman rank and linear regression (Johnson *et al.* 2006). All statistical analyses were conducted in Stata 9.2 (Stata Corporation 2005).

Least-cost path analyses

We used the RSFs to create source patches (high RSF value polygons) within each study area. We reclassified each landscape based on the two top-ranked RSF bins generated from validated seasonal models (range 4-9 bins). We converted the re-binned raster surface into polygons using ArcGIS and calculated the area, perimeter, surface area-to-perimeter ratios, and centre of each polygon using Hawth's Tools. Where possible, we selected polygons that met existing corridor guidelines for habitat patches in the Bow Valley, 4·5 km^2 and 1·2 km wide, based on minimum security areas for female grizzly bears in the Bow Valley (BCEAG 1999).

We used the inverse of the species-specific seasonal RSF models to generate a cost surface for LCP analyses. Through this subjective translation (*sensu* Beier *et al.* 2008), we assumed that pixels with higher RSF values afforded lower costs to movement than those with low RSF values. The centre of each high RSF value polygon became source and end termini for the LCP algorithm to generate pathways on either side of the highways within each WMU. We used the largest one or two polygons as possible pairs (i.e. not all possible pairs of polygons) in the analysis. As the path created is a single pixel width wide (30 m), we buffered each path at 350 m following guidelines recommended for carnivores (BCEAG 1999).

We merged seasonal LCPs by species to explore the overall location and extent of species-specific corridors throughout the year. While this union of all the species-specific corridors offered one possible conservation corridor plan, we also intersected species-specific LCPs to show managers where potential corridors for both species overlapped at any time of the year. Finally, we compared the highway crossing locations predicted by the LCPs with actual crossings of cougars and grizzly bears. We examined each species separately because cougars and grizzly bears showed differences in the use of highway crossing structures in adjacent Banff National Park (Clevenger & Waltho 2005).

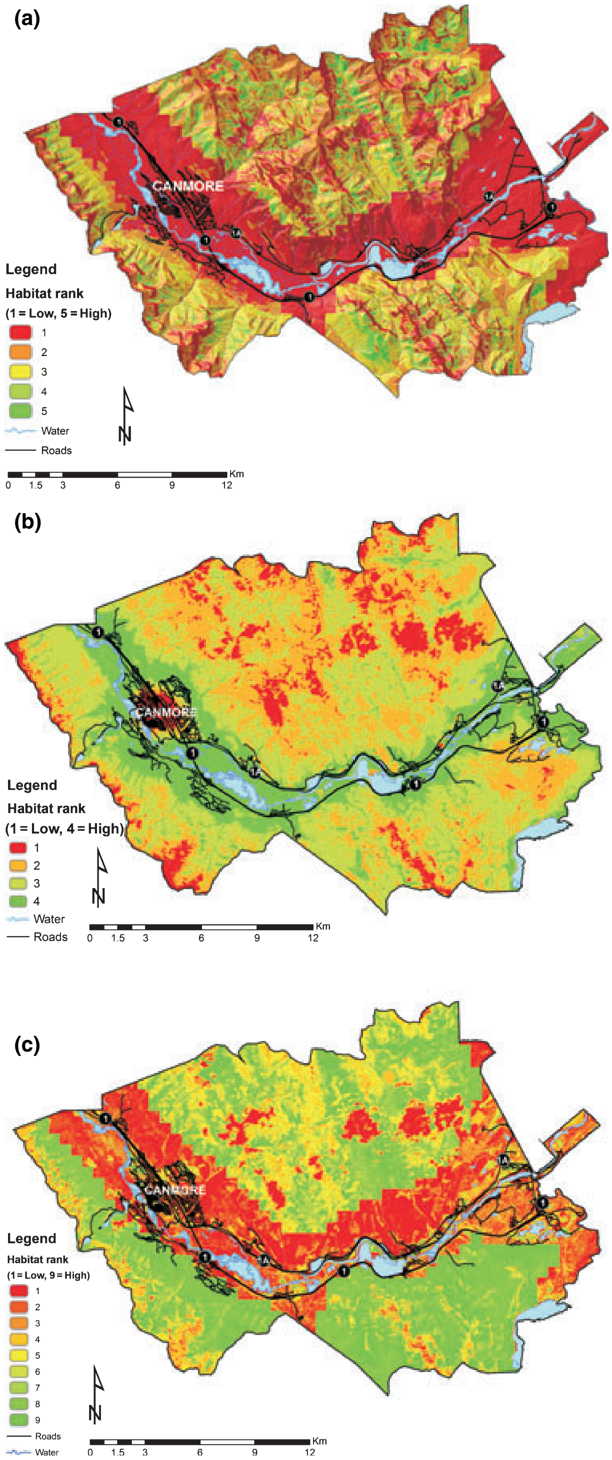

Fig. 2. Predicted probability of grizzly bear occurrence in the Canmore during: (a) spring; (b) summer and (c) autumn.

Results

RESOURCE SELECTION FUNCTIONS

Canmore

A total of 10 643 GPS locations (189–2906 per bear) were used to develop seasonal models for grizzly bears in Canmore (Fig. 2). Grizzly bears selected sites with higher greenness and low and intermediate road densities in spring and summer respectively (Fig. 3). Selection for landcover varied seasonally, but generally grizzly bears selected herb and shrub landcovers over upland forest. They also selected alpine and subalpine subregions over montane subregions (Fig. 3). During spring, slope also had a significant nonlinear effect on grizzly bear locations, whereas,

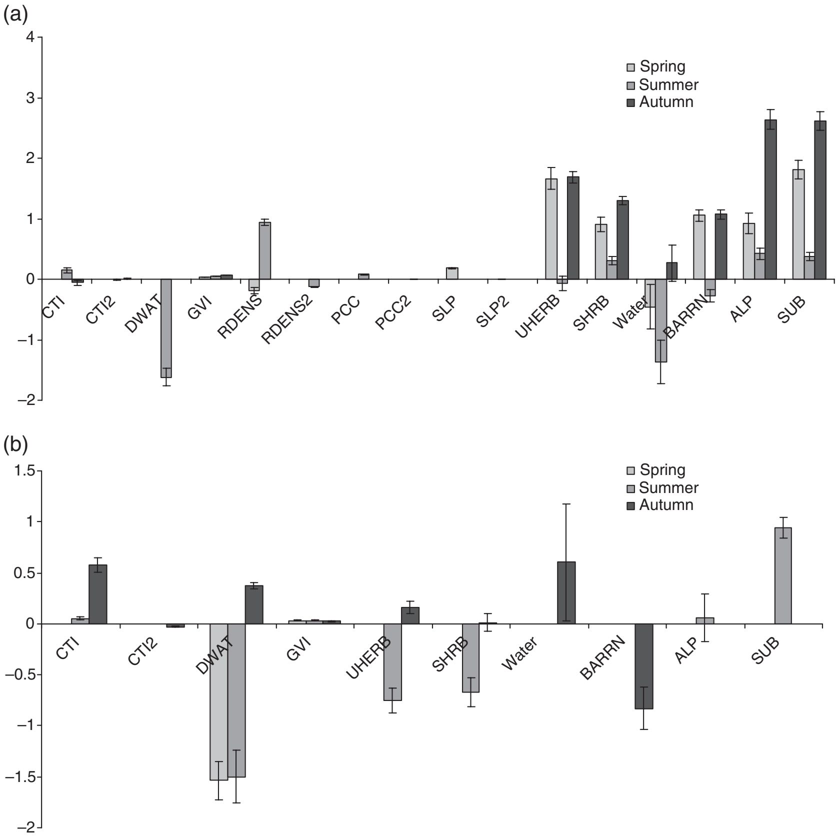

Fig. 3. Seasonal resource selection by grizzly bears in (a) Canmore and (b) Crowsnest. See Table 1 for descriptions of variables.

during summer, grizzly bears were closer to water, selected sites with intermediate soil wetness, and areas ≤ 40% crown closure (Fig. 3). Predictive accuracy for seasonal models using withheld model-testing data was excellent (spring; $r^2 = 0{\cdot}971$, $r_s = 0{\cdot}900$, $P < 0{\cdot}05$, summer; $r^2 = 0{\cdot}985$, $r_s = 1{\cdot}000$, $P < 0{\cdot}001$, autumn; $r^2 = 0{\cdot}899$, $r_s = 0{\cdot}937$, $P < 0{\cdot}001$).

A total of 4845 GPS locations (296–1173 per cougar) were used to develop seasonal models for cougars in Canmore (Fig. 4). Models consistently included variables for crown closure and road density and cougars selected montane over alpine or subalpine subregions (Fig. 5). During winter, cougars selected intermediate crown closures (~50%), sites with road densities ≤ 3·5 km km^{-2} and were more likely to be found at intermediate elevations around 1600 m in all landcover types except upland forest (Fig. 5). During the rest of the year, cougars were closer to water features, selected intermediate greenness values (~40), higher percentage crown closures (i.e. more cover) and lower road densities (Fig. 5). Predictive accuracy for seasonal models using withheld model-testing data was excellent in the non-winter season ($r^2 = 0{\cdot}979$, $r_s = 1{\cdot}000$, $P < 0{\cdot}001$) and good in the winter season ($r^2 = 0{\cdot}798$, $r_s = 0{\cdot}77$, $P < 0{\cdot}07$).

Crowsnest Pass

A total of 6643 GPS locations (53–1192 per bear) were used to develop seasonal models for grizzly bears in Crowsnest (Fig. 6). Similar to Canmore, grizzly bears in Crowsnest selected sites with higher greenness. Unlike Canmore, grizzly bears in Crowsnest were closer to water features, although this relationship was weak during autumn (Fig. 3). During spring, grizzly bears also were more likely to be found at intermediate elevations (~1500 m) in alpine regions compared with during summer when they were found at sites with drier soils in upland forest in subalpine regions. During autumn, grizzly bears selected locations with intermediate soil wetness and relatively higher elevations in upland herb landcover rather than upland forest sites. Predictive accuracy for seasonal models using withheld model-testing data was excellent (spring; $r^2 = 0{\cdot}975$, $r_s = 0{\cdot}943$, $P < 0{\cdot}005$, summer; $r^2 = 0{\cdot}948$, $r_s = 0{\cdot}90$, $P < 0{\cdot}05$, autumn; $r^2 = 0{\cdot}924$, $r_s = 1{\cdot}000$, $P < 0{\cdot}001$).

A total of 5741 GPS locations (97–801 per cougar) were used to develop seasonal models for cougars in the Crowsnest Pass (Fig. 7). Unlike Canmore, cougars in Crowsnest consistently selected sites with intermediate terrain ruggedness scores and selected upland forest over other landcover types, except during winter when they selected shrub sites compared with upland forest and montane subregions (Fig. 5). During winter, cougars were associated with drier soil sites, whereas during non-winter, cougars were closer to forest cover (Fig. 5). Predictive accuracy for seasonal models using withheld model-testing data was excellent (non-winter season; $r^2 = 0{\cdot}965$, $r_s = 0{\cdot}943$, $P < 0{\cdot}005$, winter; $r^2 = 0{\cdot}958$, $r_s = 0{\cdot}900$, $P < 0{\cdot}05$).

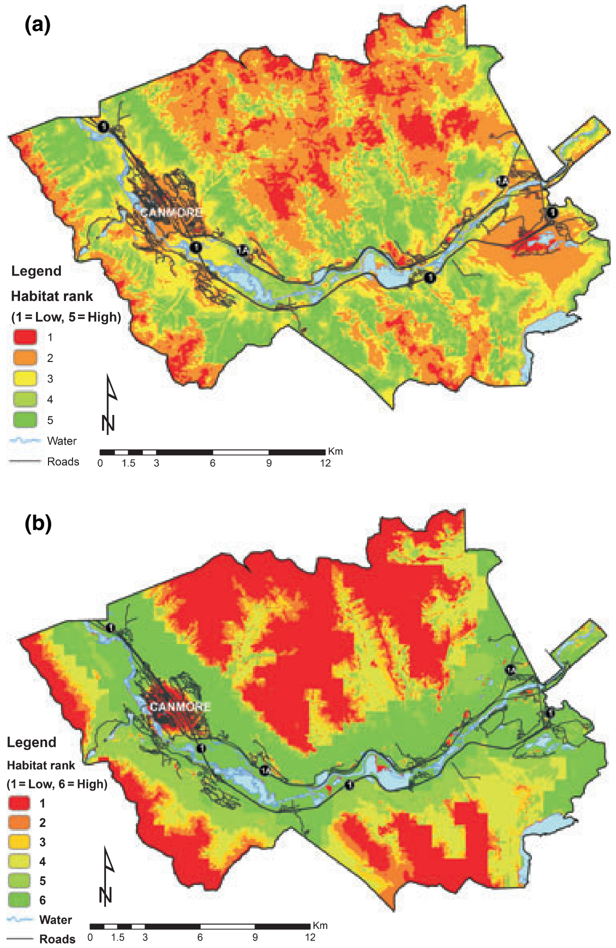

Fig. 4. Predicted probability of cougar occurrence in the Canmore during: (a) the non-winter season and (b) the winter season.

LEAST-COST PATH ANALYSES

Canmore

Fifteen polygons were generated from the highest seasonal grizzly bear RSF models. Eighteen LCPs between polygons were then merged and identified as potential grizzly bear corridors, some of which paralleled existing corridor designations. Three bears from this study each crossed the TransCanada Highway once during spring and at least six times during summer. Two crossings fell within 30 m of crossing locations predicted by seasonal LCPs. None of the four telemetered bears crossed during autumn.

Ten polygons were generated from the highest seasonal Canmore cougar RSF models. Eight LCPs between these polygons were then merged and identified as potential corridor locations for cougars. The LCPs generated from cougar RSFs crossed the highway and other linear features in three places. Study cougars crossed the TransCanada Highway at least 19 times and crossed Highway 1A at least twice outside winter and the TransCanada Highway at least seven times during winter. Three cougars crossed Highway 1A at least 20 times. These cougar crossing locations closely aligned with the LCP-predicted crossing site in the central region of the study area.

Intersecting all seasonal LCPs for cougars and grizzly bears in Canmore produced a number of areas of overlap. The resultant overlapped LCPs in the central portion of the valley, north of the highways, represented observed highway crossings by both species for all seasons (Fig. 8).

Crowsnest Pass

Thirteen polygons were generated from the highest seasonal grizzly bear RSFs in Crowsnest. Nineteen LCPs between polygons were merged and identified as potential corridor locations for grizzly bears in Crowsnest. The LCPs crossed Highway 3 in three different sites. None of the four study grizzly bears crossed Highway 3 during any season.

Thirteen polygons were generated from the highest seasonal Crowsnest cougar RSF values. Eight LCPs between polygons were identified and merged to illustrate potential corridor locations for cougars. LCPs crossed Highway 3 in two areas that were common for both seasons. During the non-winter season, three study cougars crossed Highway 3 at least 25 times and, during the winter, three study cougars crossed Highway 3 at least 11 times. Some of these crossings aligned with those predicted by the LCPs.

Six intersected LCPs for cougars and grizzly bears in Crowsnest crossed the highway, including an LCP in the eastern portion of the study area that represented multi-seasonal corridors for both cougars and grizzly bears (Fig. 8).

Discussion

Resource selection by grizzly bears varied by season and study area, similar to other RSF studies for grizzly bears in mountainous regions (Nielsen *et al.* 2004a,b; Ciarniello *et al.* 2007). Food resources, measured as greenness and soil wetness, were important predictors for grizzly bear distribution throughout the year in our study. The importance of greenness in grizzly bear models is consistent with their omnivorous diets and the need for quality forage and herbaceous resources to maximize weight gain and fat deposition for hibernation (Rode, Robbins & Shipley 2001; Robbins, Schwartz & Felicetti 2004). Measures of proximity to water sources and soil wetness indices (CTI) were important components of summer models in both areas. Soil wetness indices were useful in describing local patterns of certain bear food items such as bearberry *Arctostaphylos uva-ursi* and *Equisetum* spp. (Nielsen *et al.* 2004a) and grizzly bears feeding on ungulates during spring and autumn often were located closer to water within forest sites (Munro *et al.* 2006).

Our results suggest that road density might not be a reliable proxy for human influence on grizzly bears in these landscapes. In Canmore, grizzly bears selected areas of low road density during spring and low-to-intermediate road densities during summer, whereas in Crowsnest road density was not a reliable predictor of grizzly bear occurrence patterns. How grizzly bears and other large mammals respond to roads depends on

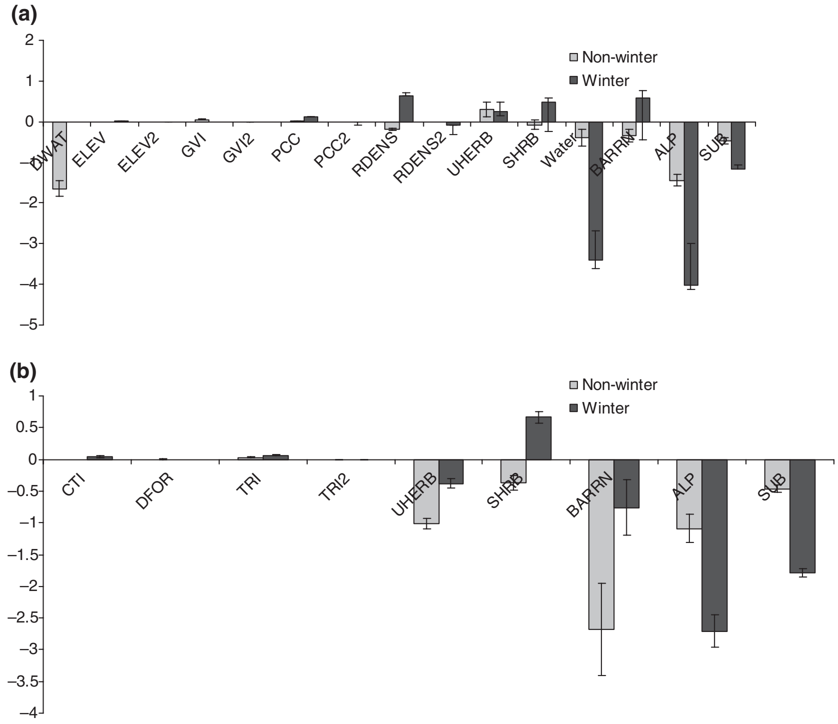

Fig. 5. Seasonal resource selection by cougars in (a) Canmore and (b) Crowsnest. See Table 1 for descriptions of variables.

the overall amount of favourable habitat around the roads, the configuration of the roads and the road types within the landscape (Frair *et al.* 2008). Grizzly bears in Alberta may be attracted to roads and their habitats because of the availability of preferred food resources as has been shown in managed forests (Munro *et al.* 2006; Roever, Boyce & Stenhouse 2008). Within the Banff-Bow Valley, grizzly bears consistently used areas closer to low-volume, two-lane paved roads, but they were also more likely to die near roads (Gibeau *et al.* 2002; Chruszcz *et al.* 2003). Consequently, roadside habitats may actually represent attractive sinks (Nielsen, Boyce & Stenhouse 2006). Beier *et al.* (2008) suggested that a distance-to-road metric rather than road density was a more relevant proxy for human disturbance. However, determining the relationship between bears, roads and corridor placement in human-dominated landscapes might require finer scale temporal and spatial measures of human use (e.g. Donelon 2004) or species- and landscape-specific modelling in response to road networks (e.g. Frair *et al.* 2008).

Cougars in both landscapes were consistently associated with montane subregions throughout the year and shrub landcover types during winter. The montane subregion, represented by river valley bottoms in both landscapes, presents optimal climate and cover relative to subalpine and alpine areas. The use of shrub landcover in winter is likely to be associated with prey availability, especially deer *Odocoileus* spp. We suspect that the avoidance of subalpine and alpine subregions in winter also is tied to snow accumulation and prey availability (Murphy, Ross & Hornocker 1999). In Canmore, greenness was an important predictor of cougar occurrence during the non-winter season, a finding supported by other cougar studies where greenness was considered a surrogate for ungulate prey (Jalkotzy *et al.* 1999). Improved data on local prey abundance and distribution during winter would be likely to improve cougar winter selection models in both study areas. Measures of terrain ruggedness were more useful in describing cougar occurrence, as has been shown for cougars in other regions of Alberta (Jalkotzy *et al.* 1999). Cougars require abundant horizontal and vertical cover provided by vegetation and topography to facilitate their ambush style of hunting (Murphy *et al.* 1999). We suspect that terrain ruggedness might be important for providing escape habitats for cougars during the hunting season (winter) in Crowsnest Pass. Understanding the spatial distribution of human-caused cougar mortalities (*sensu* Riley & Malecki 2001) would be valuable for refining local models of occurrence and distribution, particularly winter habitats.

Cougar and grizzly bear models were more similar between species within study areas than they were for the same species between study areas. Canmore cougar models showed a pattern of avoidance of roads in the non-winter season similar to that of grizzly bear seasonal models. During winter, when grizzly bears were denning, cougars still selected areas with low-to-intermediate road densities. We found fewer similarities between cougar and grizzly bear models for Crowsnest. Our results highlight the challenge of identifying multi-species corridors given seasonal variations in resource selection and individual variation in behaviour. Managers may decide to select one species over the other or select specific seasons when both species may be more likely to overlap in terms of movement and habitat selection to guide corridor planning. Taken together, combining RSFs and LCPs could provide options for ranking corridors based on conservation objectives and offer opportunities to identify restoration and other

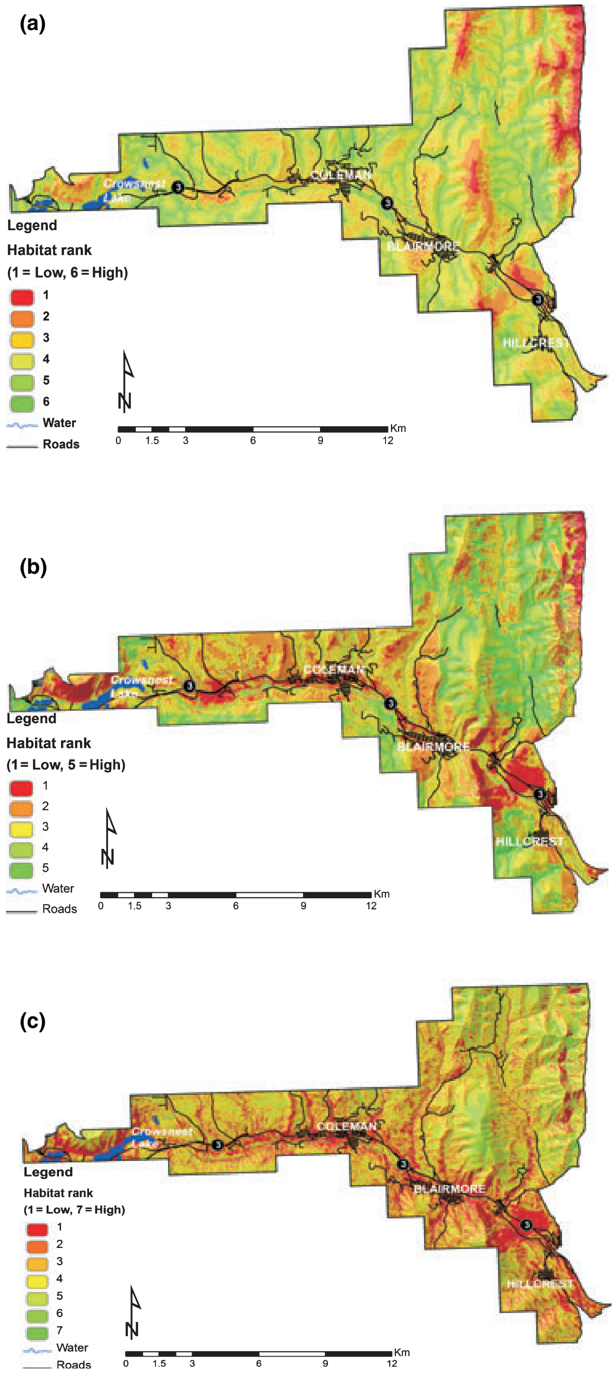

Fig. 6. Predicted probability of grizzly bear occurrence in Crowsnest during (a) spring, (b) summer, and (c) autumn.

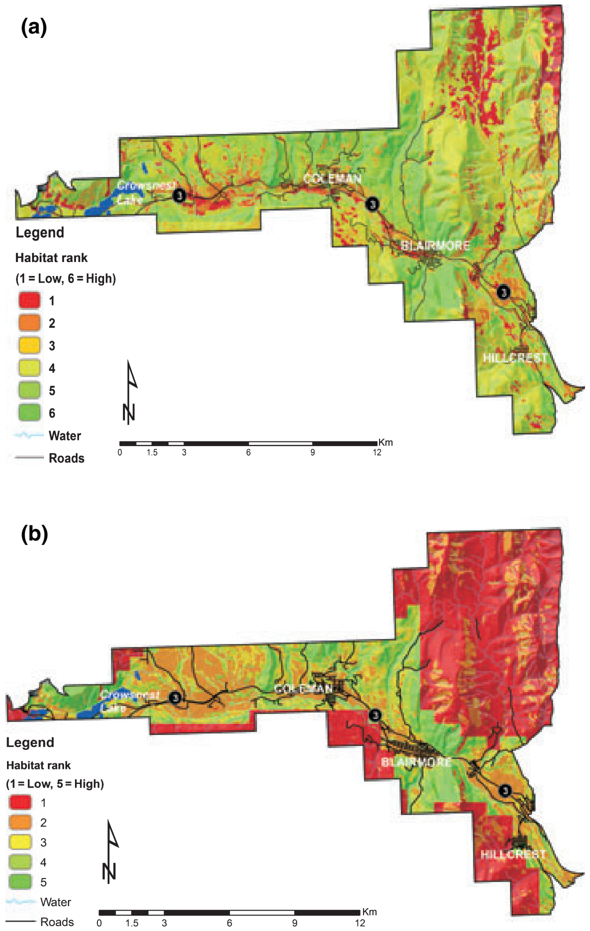

Fig. 7. Predicted probability of cougar occurrence in Crowsnest during (a) the non-winter season, and (b) the winter season.

management needs within corridors, e.g. trail closures. Our analyses suggest that there are some options for planning in both landscapes that could include multiple corridors and some areas that warrant further investigation for inclusion within corridor planning. Using the RSF models in a LCP analysis for both study areas helped identify species-specific corridors as well as translating species-specific and seasonal details from RSF models into more general corridor guidelines.

The RSF-informed LCP analyses provided a quantitative, functionally based and repeatable way of identifying potential corridors for conservation. LCP results depend on the location of source and end termini and assumptions of the cost surface (Beier *et al.* 2008). Using the RSFs to identify the largest polygons of high-quality habitat as the LCP sources, our approach is an improvement over more qualitative methods that presume measures of habitat quality (e.g. Singleton, Gaines & Lehmkuhl 2004). Managers could develop specific criteria for termini as well as define their locations for LCP analyses based on other land-use considerations such as proximity to housing developments and human activities.

We used the inverse of the RSF and assumed that high-quality habitat presents lower costs or friction for movement and lowest risk of mortality – a common assumption in many carnivore LCP modelling studies (e.g. Carroll & Miquelle 2006; Theobald 2006). Yet, some data suggest that individuals travel faster through habitats of low suitability, and have slower movements (assumed to have higher costs) in preferred habitats (Palomares 2001; Dickson, Jenness & Beier 2005). In human-dominated landscapes, both conditions may apply. For example, Whittington, St Clair & Mercer (2005) found that movements of wolves *Canis lupus* L. were more tortuous

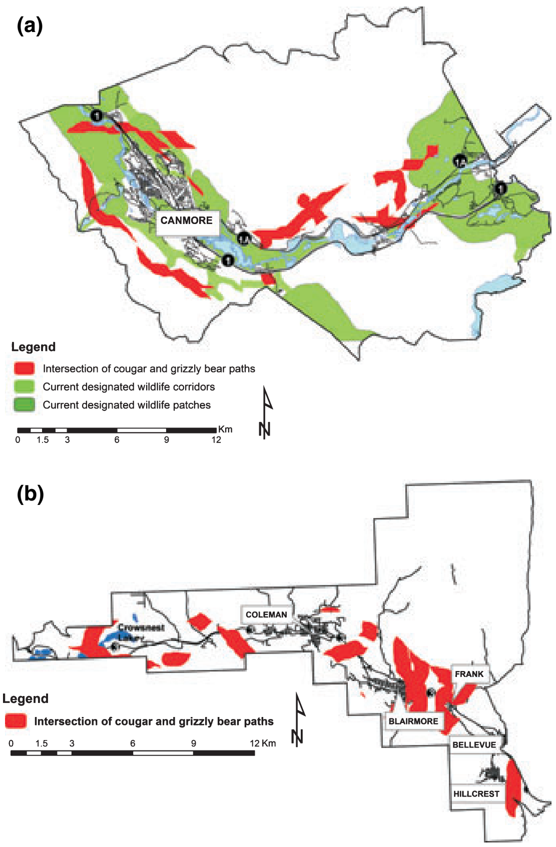

Fig. 8. Intersected least-cost paths highlight areas of overlap for cougars and grizzly bears during various seasons in (a) Canmore, and (b) Crowsnest.

(e.g. higher cost) near both predation sites (e.g. high-quality habitats) and high-use trails (e.g. low-quality habitats). They suggested that the highly tortuous movements in low-quality habitats were used to avoid contact with humans. Field validation through the increasing use and availability of GPS data for various species in different landscapes will be invaluable in addressing the relationship between cost surfaces and resultant paths and corridor designations (Gonzales & Gergel 2007).

Finally, we used buffered LCPs as our least-cost modelling approach. Buffering LCPs creates a uniform, albeit subjective, corridor width that avoids the problem of a pixel-wide path, but it does not guarantee that high RSF values occur along its length. A least-cost corridor (LCC) approach always includes pixels with the highest RSF values (lowest cost) but may not result in a uniform width (Beier *et al.* 2008). However, managers may not want corridors based on the highest RSF values, particularly if large carnivores and people are sharing the same landscape. Our approach offers managers the opportunity to explore these kinds of questions and to define assumptions about 'movement' with respect to resource selection for corridor planning.

Our results, therefore, suggest that integrating RSF and LCP models can guide corridor designs for multiple species. RSFs enhance our understanding of the factors affecting species distribution and habitat selection, while the RSF-informed LCP results suggest possible corridor locations. When these paths were intersected for both species, the results were rarely a linear 'corridor'. In Canmore, two potential 'crossing' areas were outside of currently designated corridors or patches. In Crowsnest, areas of intersection occurred within areas broadly outlined in draft corridor maps. Despite the stated desire of managers to have corridors that function for multiple species, our results show that even for two large carnivores that share the same landscapes at certain times of the year, corridor identification can vary between species and with season. While RSF-informed LCPs offer an important advance in addressing functional connectivity, there is no guarantee that the identified corridors will ensure population persistence (Taylor *et al.* 2006). RSFs and LCPs, though spatially explicit, are still static models, providing a snapshot of current (or recent) relationships between individuals and their habitats, rather than long-term functionality. The fundamental challenge will be linking corridor planning with regional landscape management to identify the contribution of corridors to population persistence (Carroll 2006).

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