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REVIEW

Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes?

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Summary

1. The need to conserve and create linkages among fragmented habitats has given rise to a range of techniques for maximizing connectivity. Methods to identify optimal habitat linkages face trade-offs between constraints on model inputs and biological relevance of model outputs. Given the popularity of these methods and their central role in landscape planning, it is critical that they be reliable and robust.

2. The most popular method used to inform habitat linkage design, least-cost path (LCP) analysis, designates a landscape resistance surface based on hypothetical 'costs' that landscape components impose on species movement, and identifies paths that minimize cumulative costs between locations.

3. While LCP analysis represents a valuable method for conservation planning, its current application has several weaknesses. Here, we review LCP analysis and identify shortcomings of its current application that decrease biological relevance and conservation utility. We examine trends in published LCP analyses, demonstrate the implications of methodological choices with our own LCP analysis for bighorn sheep *Ovis canadensis nelsoni*, and point to future directions in cost modelling.

4. Our review highlights three weaknesses common in recent LCP analyses. First, LCP models typically rely on remotely sensed habitat maps, but few studies assess whether such maps are suitable proxies for factors affecting animal movement or consider the effects of adjacent habitats. Secondly, many studies use expert opinion to assign costs associated with landscape features, yet few validate these costs with empirical data or assess model sensitivity to errors in cost assignment. Thirdly, studies that consider multiple, alternative movement paths often propose width or length requirements for linkages without justification.

5. *Synthesis and applications*. LCP modelling and similar approaches to linkage design guide connectivity planning, yet often lack a biological or empirical foundation. Ecologists must clarify the biological processes on which resistance values are based, explicitly justify cost schemes and scale (grain) of analysis, evaluate the effects of landscape context and sensitivity to cost schemes, and strive to optimize cost schemes with empirical data. Research relating species' fine-grain habitat use to movement across broad extents is desperately needed, as are methods to determine biologically relevant length and width restrictions for linkages.

Key-words: animal movement, connectivity, corridor, dispersal, fragmentation, linkage design, model validation

Introduction

Habitat fragmentation and isolation have long been considered among the greatest threats to the persistence of species (Karieva 1987; Quinn & Harrison 1988). Fragmentation increases a species' risk of extinction from inbreeding and genetic and demographic stochasticity (Wilcox & Murphy 1985; Mills & Smouse 1994), and limits the ability of populations to move in response to perturbations (e.g. harvest, habitat degradation or disturbance). The effects of fragmentation on dispersal and colonization, in particular, have received

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increasing attention as planners attempt to predict the response of species to climate change (e.g. Thomas *et al.* 2004; McLachlan, Hellmann & Schwartz 2007). Efforts to mitigate the impacts of habitat fragmentation by preventing or reversing population isolation are encompassed within the growing field of connectivity conservation (Crooks & Sanjayan 2006).

Promoting connectivity, the movement of species or genes between habitats, alleviates problems associated with habitat fragmentation (Crooks & Sanjayan 2006). Most efforts to conserve connectivity rely on the creation or protection of habitat linkages; i.e. land that promotes movement or dispersal of plants or animals between core habitats (Briers 2002; Beier, Majka & Spencer 2008; Fig. 1). However, while researchers generally agree that maintaining connectivity is essential to the persistence of fragmented subpopulations, they often disagree on the process by which linkages are designed for conservation (Rothley 2005). Although placement of linkages/corridors based on empirical observations of dispersal movement may be the most reliable method for designing connectivity networks (Hilty & Merenlender 2004; Graves *et al.* 2007) such data are sparse or non-existent for most species and most locations (Fagan & Calabrese 2006). As a result, conservation relies heavily on models of connectivity that may have little empirical basis. Conservation planners are faced with a critical question: will such models improve placement of linkages/corridors by explicitly incorporating habitat effects on movement, or will they result in misleading and potentially costly recommendations for conservation by concealing invalidated assumptions (Chetkiewicz, St. Clair & Boyce 2006)?

In this review, we evaluate the current use, strengths and weaknesses of least-cost path (LCP) analysis (Fig. 1; see Appendix S3 in Supporting information for a discussion of current LCP terminology), the most widely used modelling approach for design of habitat linkages (LaRue & Nielsen 2008; Phillips, Williams & Midgley 2008). We focus on applications of LCP analysis in which a single path or corridor is identified for placement between pairs of source patches. A detailed description of the steps involved in LCP analysis is provided in Figure 1. In short, LCP analysis evaluates potential animal movement routes across the landscape based on the cumulative 'cost' of movement (Chetkiewicz & Boyce 2009). Resistance of each landscape unit (usually a grid cell on a raster map) is intended to represent the sum of hypothetical energetic expenditures, mortality risks, or other facilitating or hindering effects of landscape elements on movement within the cell (Adriaensen *et al.* 2003; Fig. 1). In practice, resistance values in LCP models are usually assigned on an arbitrary scale meant to reflect 'high' or 'low' suitability (with respect to movement) of different landscape factors (e.g. land cover, human activity, etc.). Resistance values for each factor are weighted according to their perceived importance and combined (e.g. by geometric mean) to produce

Question	What areas need to be connected?	What landscape traits affect species' movement between these areas?	How will variation in these landscape traits affect animal movement?	How can these potential landscape effects be quantified?	To what degree does the landscape facilitate or impede movement between patches?	What is the easiest travel route between identified patches?	How can a least-cost path be translated into an optimal linkage?
Analysis	**Determine source pathces**	**Identify landscape variables to include in cost analysis**	**Rank variables according to resistance to movement**	**Develope cost scheme: assign resistance values and factor weights**	**Calculate cumulative cost surface from source patches**	**Identify least-cost path (LCP) between source patches**	**Design least-cost corridor (LCC)/ linkage (LCL)**
Definitions	**Source patches:** Areas that support or have potential to support the species of interest; sometimes restricted to breeding habitat	**Landscape variables:** Habitat traits *perceptible* by- and *likely to influence* – species' movement ➢ e.g. vegetation type, slope, elevation, water, human activities, food availability, escape cover	**Resistance**: a measure of reluctance to use habitat for movement (Adriaensen *et al.* 2003) or failure to move successfully	**Cost scheme:** Choice of resistance values and factor weights **Resistance value:** numerical score assigned to habitats or landscape traits to quantify resistance **Factor weight:** measure of importance of one habitat trait on movement decisions *relative* to other traits	**Effective distance:** Composite measure of connectivity between patches representing geographic (Euclidian) distance weighted by resistance of landscape elements traversed on a given path (Adriaensen *et al.* 2003)	**Least-cost path:** A swath of landscape that is one pixel wide and represents the lowest cumulative cost between two patches (Verbeylen *et al.* 2003)	**Corridor:** A slice of landscape encompassing the most permeable percentiles of the cost surface **Habitat linkage:** Connective land that promotes movement/dispersal for multiple species between core habitats (Beier *et al.* 2008; 2009)
Examples	Define source patches using: ▪ **Home ranges** ➢ e.g. minimum convex polygon, kernel density estimator ▪ **Point locations** ➢ e.g. direct observations, radio-telemetry, nest/den evidence ▪ **Habitat suitability analysis** ➢ e.g. Percentage of most suitable habitat ➢ Suitable habitat larger than a cut-off ▪ **Protected areas** ▪ **Expert opinion**	Decisions can be based on: ▪ **Expert opinion resource selection functions (RSF) or habitat suitability index (HSI)** ➢ Derived from regression of occurrence data on environmental variables ▪ **Analyses of animal movement behavior** ➢ e.g., radio or satellite telemetry, snow tracking ▪ **Landscape genetic analyses** ➢ e.g., correlation of habitat elements with genetic differences	Resistance may signify: ▪ **Mortality risks** ▪ **Reproductive costs** ▪ **Energetic costs** ▪ **Physical resistance** ▪ **Thermal stress** ▪ **Habitat suitability**	Cost schemes can be determined using: ▪ **Expert opinion** ➢ Analytical Hierarchical Process ➢ Mean response ➢ Qualitative ▪ **Species habitat preferences** ➢ Compositional analysis: time spent in each habitat type relative to availability ➢ RSF/HSI: Probabilistic map regressing presence on habitat variables ▪ **Analyses of animal movement behavior** ➢ Movement choice/speed in different habitat types and transitions ▪ **Gene flow:** ➢ Correlation of gene flow estimates with effective dist. of cost scheme	The cost value in each cell represents effective distance to the source patch, measured in the least effort (lowest cost) of moving over the cost surface	The model creates the most likely travel route by selecting a combination of cells that represent the shortest effective distance between two designated patches (LaRue and Nielsen 2008)	Corridors can be identified by: ▪ **Buffer/minimum width:** ➢ Buffer LCP to chosen width (e.g. home range size) ▪ **Least cost corridor/ Probable movement zone:** ➢ Combine multiple low-cost routes ➢ Lowest percentile (10%, 20%, etc) of cost paths ▪ **Circuit theory:** ➢ Delineate areas of landscape with highest "conductance" between patches ➢ Can incorporate patch characteristics ➢ Can be used to rank potential corridors, explore alternative corridors, and identify bottlenecks (McRae and Beier 2007)

Fig. 1. Introduction to important questions, steps and definitions for least-cost path modelling.

a single resistance value. We call this series of choices the 'cost scheme'. The 'effective distance', or cost of a path between habitat patches for a species, is the Euclidian distance weighted by the cumulative resistance values of all cells traversed (Adriaensen *et al.* 2003; Beier, Majka & Spencer 2008; Fig. 1). The LCP is the combination of cells that minimizes effective distance between two patches (Verbeylen *et al.* 2003) and is used to inform optimal placement of a linkage (Fig. 1).

Least-cost path analysis is an attractive technique for analysing and designing habitat corridors because it: (i) allows quantitative comparisons of potential movement routes over large study areas, (ii) can incorporate simple or complex models of habitat effects on movement and (iii) offers the potential to escape the limitations of analyses based solely on structural connectivity (i.e. designating areas simply as 'patch', 'matrix' or 'corridor') by modelling connectivity as it might be perceived by a species on a landscape ('functional connectivity'; Taylor, Fahrig & With 2006). However, as with any modelling approach, the effectiveness of LCP analysis is limited by the quality of input data. For instance, modellers often use expert opinion to assign resistance values to remotely sensed landscape traits (e.g. Adriaensen *et al.* 2003; see Fig. 1 & Table 1). Thus, the accuracy and value of these models depends on how strongly these coarse-grain habitat proxies and their assumed resistances correlate with actual habitat use/movement by focal species (Calabrese & Fagan 2004; Beier, Majka & Spencer 2008). Methods for defining habitat patches are often unclear or based largely on human rather than animal perception of habitats (Theobald 2006). In worst-case scenarios, LCP analyses are little more than subjective interpretations of coarse habitat maps, but the method has potential for much more. For example, ideal applications of LCP analysis would employ organism-centric approaches in which practitioners use species- and landscape-specific empirical data to quantify behavioural responses to finer-grain habitat elements (e.g. distribution of critical resources, escape cover and threats), to: (i) consider attributes of surrounding cells when assessing resistance of a cell and (ii) assess the likelihood of use for a path of known width and length (Adriaensen *et al.* 2003; Theobald 2006; Graves *et al.* 2007). While a challenging standard, such organism-centric approaches have the potential to reduce researcher bias and increase the replicability, defensibility and transparency of LCP and related analyses (Chetkiewicz & Boyce 2009).

In reviewing the use and application of LCP approaches we set out to address the following questions: (i) do recent studies employing LCP analysis shift emphasis from structural towards functional connectivity by considering species-specific behaviours and do they provide explicit, empirically derived justification for their choices? (ii) do researchers using LCP analysis attempt sensitivity analysis, model validation or compare multiple model outputs to assess the robustness of their projections? and (iii) how have researchers translated LCP model outputs into optimal linkage or corridor placement for their study areas?

Finally, to demonstrate the challenges of LCP analyses and highlight the sensitivity of LCP model outputs to input data, we present a case study in which we conduct an LCP analysis for desert bighorn sheep *Ovis canadensis nelsoni* (Merriam 1897) in southern California. We use our LCP analysis between two bighorn populations to examine congruence of outputs from two commonly used techniques for assigning cost schemes (expert opinion and gene flow optimization; see Figs. 1 and 2) and two scales of habitat suitability assessment (regionally-significant topographic/anthropogenic variables and locally-specific habitat traits).

Materials and methods

SELECTION OF PAPERS

We limited our analytical review to studies with the stated aim of designing optimal connectivity strategies for focal species. We performed a search in ISI Web of Knowledge (ISI 2010) using the following search terms: *least-cost* OR *cost-distance* OR *least-cost path* OR *least-cost-path* AND *connectivity* OR *corridor* OR *linkage* OR *conservation*. To reflect current trends in the peer reviewed literature, we restricted our search to 373 studies published between 2002 and 2010. We then refined the list to the subject areas Biodiversity and Conservation, Environmental Sciences and Ecology, and Genetics and Heredity, which reduced our pool to 135 results. We then further restricted our review to publications with the following keywords in the study abstract: *identify* OR *predict* OR *model* OR *delineate* OR *place* OR *validate* OR *draw* AND *linkage* OR *corridor* OR *optimal connection* OR *key connectivity area* OR *migration zone*. We excluded studies that used LCP analysis solely to predict occupancy, model species distributions (e.g. Verbeylen *et al.* 2003; Magle, Theobald & Crooks 2009), explain gene flow (e.g. Vignieri 2005) or predict how landscape changes might affect focal species (e.g. Graham 2001) if they did not explicitly aim to design or evaluate linkages. Finally, for each study that met our criteria for inclusion, we evaluated the following methodological choices: type of habitat data, choice of grain (cell size) and study extent, determination of cost schemes and source patches, consideration of effects of adjacent habitat, exploration of different resistance values, sensitivity analysis for other modelling choices and conversion of a 'path' to a 'corridor'.

BIGHORN SHEEP CASE STUDY

To test the sensitivity of LCP model outputs to input data, we compared two LCP models published for bighorn sheep populations in the Mojave Desert of California (Epps *et al.* 2007; Penrod *et al.* 2008), and two additional LCP models based on modifications of those published models. We chose two populations, San Gorgonio and Cushenbury, that exhibit clear evidence of connectivity in the recent past (Epps *et al.* 2010).

The 'Expert' model (Penrod *et al.* 2008) was based on a linkage design for nearby Joshua Tree National Park. The Expert model estimated resistance values using expert opinion and included dense woody vegetation as determined from the California Wildlife Habitat Relationship vegetation type (Mayer & Laudenslayer 1988). Areas of flat topography, urban areas and areas with high road density were all defined as highly resistant (up to 10 times more than the best habitat). The final combined model was calculated as:

$$\mathrm{Cost}_{\mathrm{EXPERT}} = \mathrm{topography} \times 0{\cdot}4 + \mathrm{habitat} \times 0{\cdot}4 + \mathrm{road\ density} \times 0{\cdot}2$$

where topography, habitat and road density were assigned resistances between 1 and 10, as specified by Penrod *et al.* (2008, pp. 7–10).

Table 1. Summary of recent studies that used least-cost path (LCP) modelling for habitat connectivity design (see Table S1 in Supporting Information for a more complete summary)

Study	Variables included[1]	Source of cost scheme[2]	Source patches[3]	Adjacent habitat[4]	Cost value ranges	Validation	Sensitivity analysis	Path to corridor[5]
Beazley *et al.* 2005	Forest cover (3); road density	EO; L; HSI; S	All 'suitable' habitat patches (HSI)	No	Unknown	Presence/absence of dung	No	Minimum width
Chetkiewicz & Boyce 2009	LCT (5); subregion; food resources; terrain; road density	RSF; RT	High RSF value polygons	No	Inverse of RSF coefficients	Telemetry locations;	No	Buffered: 350 m
Cushman, McKelvey & Schwartz 2008	LCT (26); elevation; slope; roads	EO; L; G	Individual locations;	No	1–10	Genetic distance	No	Smoothed: 2500 m radius parabolic kernel
Driezen *et al.* 2007	LCT (12); roads; water	L; PS	Unknown	No	1–1000	Experimental dispersal data	Compared 12 sets of costs	No
Epps *et al.* 2007	Slope (2); distance; barriers	G; RT	MCP; suitable habitat; EO	No	0·1–1·0	Radio- telemetry data	Compared multiple gene flow measures	No
Hepcan *et al.* 2009	VT (12); road density	EO; L	'Key Biodiversity Areas'	No	Unknown	No	No	Minimum width: 1 km
Joly, Morand & Cohas 2003	HT (7); roads; rivers	EO; L	Unknown	No	HT: 5–80; roads: 0–1	No	No	No
Kautz *et al.* 2006	LCT (16)	RT	HR and potential habitats (HSI)	No	LCT: 1–11; water: 15; road: 20	No	Partial: road and water	Post-analysis buffer
Kindall & Van Manen 2005	Forest cohesion, diversity, forest-agriculture edge density	Problem of occurrence model	50% fixed kernel HR	No	1–8	No	No	No
Kong *et al.* 2010	LUT (12)	EO	Urban green space > 12 ha connected to areas outside city	No	0·1–50 000	No	No	No
Larkin *et al.* 2004	HT (5) based on suitability model	EO; L	'Suitable' habitat (EO)	No	1; 10; 50; 100	No	Two cost schemes	No
LaRue & Nielsen 2008	LCT (8); distance to road and water; slope, human population density	EO	Areas where cougar may be living (EO)	Distance to road and water	0·19–1·92	No	No	Buffered LCP by 1 km
Li *et al.* 2010	LCT (9), slope; dist to water and human activities (3)	EO	Panda occurrence or suitable habitat	Distance to human activities	Reciprocal suitability: 0·002–0·098	No	No	Smoothed: 90 m cumulative kernel
Meegan & Maehr 2002	HT (2); roads	EO; L; RT	forest patches ≥500 ha	No	1,2 or 3	presence locations	No	No

Table 1. Continued

Study	Variables included[1]	Source of cost scheme[2]	Source patches[3]	Adjacent habitat[4]	Cost value ranges	Validation	Sensitivity analysis	Path to corridor[5]
Osborn & Parker 2003	HSI (2); distance to river, roads, and settlements	EO	Individual locations	Distance to settlement and road	Unknown	No	No	No
Rabinowitz & Zeller 2010	LCT; % tree/shrub cover; elevation; distance to road and settlement; human population density	EO	Jaguar conservation units	Distance to road and settlement	Integers 0–10	field interviews on-going	No	Selected lowest 0·1% of grid cell values
Rouget *et al.* 2006	'Suitability' (foraging model)	Unknown	Unknown	No	0; 300; 600; 900	No	No	Buffered to 1 km
Schadt *et al.* 2002	LCT (5); roads	EO; L	'Suitable' habitat: size, isolation, and forest cover	No	1–1000	No	Partial: 'matrix'	No
Shen *et al.* 2008	LC; bamboo cover; slope, elevation; aspect; distance to road and residential areas	EO	'Core' habitats based on LCT	Distance to residential area and road	1–50	No	Partial: land and bamboo cover	No
Singleton, Gaines & Lehmkuhl 2004	LCT (13); road density; human population density; slope	EO; L	Largest areas of low human influence with suitable LCT	No	0·1–1·0	No	No	Selected lowest 10% of cost surface
Stevens *et al.* 2006	LCT (6); water	Movement behaviour	Population MCP	No	3 Models: 1–10 000	Genetic dispersal rates	Compared multiple gene flow measures	No
Wang *et al.* 2008	NDVI; slope; aspect; distance to LCT	HSI on S	Individual locations	Distance to LUT	1–1 000	Presence; Gene flow	No	No
Wang, Savage & Shaffer 2009	VT (3)	EO; S	Breeding pair locations	No	1–10	Gene flow estimates	No	No
Wikramanayake *et al.* 2004	HT (3); elev.; LCT in buffer (5); patch size	EO; PS	Unknown	Distance to agriculture or population centre	1–25	No	No	Selected 10, 20 and 30% of lowest cost cells

[1]LCT, land cover type; LUT, land use type; HT, habitat type; VT, vegetation type; NDVI, Normalized Difference Vegetation Index. Number of cover/type categories is indicated in parentheses.
[2]L, literature; EO, expert opinion; RT, radiotelemetry; G, genetics; S, species presence locations; PS, previous studies HSI, habitat Suitability Index; RSF, resource selection function.
[3]HR, home range; MCP, minimum convex polygon.
[4]Did study consider adjacent habitat characteristics when determining resistance of cell?
[5]Did study go beyond least-cost path (LCP) to make a more biologically relevant recommendation, or least-cost corridor (LCC)?

The 'Optimized' model (Epps *et al.* 2007; Appendix S1 Supporting information) considered only topography and optimized resistance values using observed gene flow among populations over the entire study area, including those in our case study:

$$\text{Cost}_{\text{OPTIMIZED}} = \text{topography}$$

where areas with $>15\%$ slope and $<15\%$ slope were assigned resistances of 1 and 10 respectively.

Epps *et al.* (2007) recognized that their model was optimized for the southern California population as a whole, and would not account for locally specific habitat variables, such as the large amount of wooded habitat in the vicinity of the San Gorgonio and Cushenbury populations. Bighorn sheep typically avoid wooded habitat, presumably because of higher predation risk (e.g. DeCesare & Pletscher 2006). Therefore, we developed a third model ('Optimized Local') that added high resistance for any urban area (10 times higher) or wooded area (10 times higher) and calculated the final model as:

$$\text{Cost}_{\text{OPTIMIZED LOCAL}} = \text{topography} \times 0{\cdot}33 + \text{wooded habitat} \times 0{\cdot}33 + \text{urban area} \times 0{\cdot}33$$

where areas with $>15\%$ and $<15\%$ slopes were assigned resistances of 1 and 10, respectively, wooded habitat was assigned a cost of 10, and urban habitat was assigned a cost of 10. Non-wooded and non-urban areas were assigned a cost of 1.

Finally, to simulate the common situation where little is known about dispersal, we constructed a fourth model ('Incomplete') that was biologically relevant but omitted several important factors:

$$\text{Cost}_{\text{INCOMPLETE}} = \text{wooded habitat}$$

where areas with and without tree cover were assigned a cost of 10 and 1 respectively.

All input grids were re-sampled to 100 m resolution before combining into final cost grids. We calculated a single LCP for each model using Pathmatrix (Ray 2005). We used ArcMap and Corridor Designer (http://www.corridordesign.org/) to generate 'least-cost corridors' (Beier, Majka & Newell 2009; Fig. 1) representing the lowest 10% of possible least-cost paths for each model and estimated the area of overlap of those least-cost corridors.

Results

LITERATURE REVIEW

Twenty-four studies met our criteria for review. Each of the 24 used remotely-sensed land cover or habitat type as a proxy for habitat suitability and movement of focal species (Table 1). Study extent ranged from 10 to 4 000 000 km^2; and study grain (cell size) varied from 1 to 1 km^2 but most commonly corresponded with the grain of freely available Landsat imagery (900 m^2; see Table S1 in Supporting information for a complete summary of reviewed studies' methodological choices). Two studies distinguished only two types of habitat while all others included at least three habitat categories (Table 1). None of the 24 studies directly considered more organism-centric measures of microhabitat suitability, including those identified by authors as affecting animal habitat selection/movement, such as percentage habitat cover or distribution of food (Binzenhofer *et al.* 2005), presence of nutrient sources such as salt licks (Beazley *et al.* 2005), denning/nesting habitats (Singleton, Gaines & Lehmkuhl 2004), prey availability (Rabinowitz & Zeller 2010) or cover or escape terrain for predator avoidance (Wang *et al.* 2008). While some studies stated that habitat types serve as reliable proxies for predator presence and/or abundance of preferred foods (e.g. Driezen *et al.* 2007; Shen *et al.* 2008), no studies validated this assumption or included habitat distribution models of either predator or prey species.

Fourteen of the 24 studies evaluated in our review based their LCP analysis cost schemes (Fig. 1) on expert opinion, published literature, or both, although explanations of cost surface derivation were often lacking in sufficient detail to replicate analyses (Table 1). Of those, only three attempted to systematically and objectively translate expert opinion into cost schemes [e.g. using analytic hierarchy process or similar approaches (Banaikashani 1989; see Table S1 Supporting information)]. Six studies used telemetry or trapping (presence) data to designate costs. Three studies used relative gene flow, or combined gene flow and telemetry data, and two studies assigned resistance values using behavioural data from focal species. Across the surveyed studies, source habitat patches were variably defined as 'known population/individual locations' (10 studies), habitat deemed most 'suitable' by size, habitat type, or both (nine studies), or 'key conservation areas' (one study). Four studies did not define their source patches (Table 1). Eight studies included some effect of surrounding habitat in their cost designation (Table 1). Six studies partially based pixel cost on distance to particular habitat types or human activities. Kindall & Van Manen (2005) included forest/agriculture edge density in their cost measures while Wikramanayake *et al.* (2004) considered all areas within 1 km of agriculture or population centres to be 'poor habitat', regardless of habitat type.

Only four studies (17%) quantitatively assessed sensitivity of model-selected paths to *different* cost schemes for all variables, and these four consistently found their model outputs to be highly sensitive to input decisions (Table 1). Larkin *et al.* (2004) found overlap of only 0–51% among paths generated using different cost schemes. Stevens *et al.* (2006) and Epps *et al.* (2007) used multiple measures of gene flow to test LCP models and discovered that models were highly sensitive to different resistance values. Driezen *et al.* (2007) showed that the measurement of a species' ability to find low-cost sites depends heavily on the cost scheme used. Three other studies conducted partial sensitivity analysis: Schadt *et al.* (2002) found that changing resistance values of the matrix led to significantly different LCPs while Shen *et al.* (2008) discovered high model sensitivity to costs of bamboo and land cover. Kautz *et al.* (2006) did not detect model sensitivity to costs of roads and water. Only nine of the 24 studies attempted some form of model validation in the published results (Table 1). Four studies examined relative support for cost schemes based on gene flow. Four studies used presence data (telemetry or trapping) to validate their models, while one used presence and absence data (Beazley *et al.* 2005).

Only 10 of the 24 studies we evaluated attempted to move beyond a single-pixel wide path to consider more biologically relevant (Majka, Jenness & Beier 2007) least-cost corridors

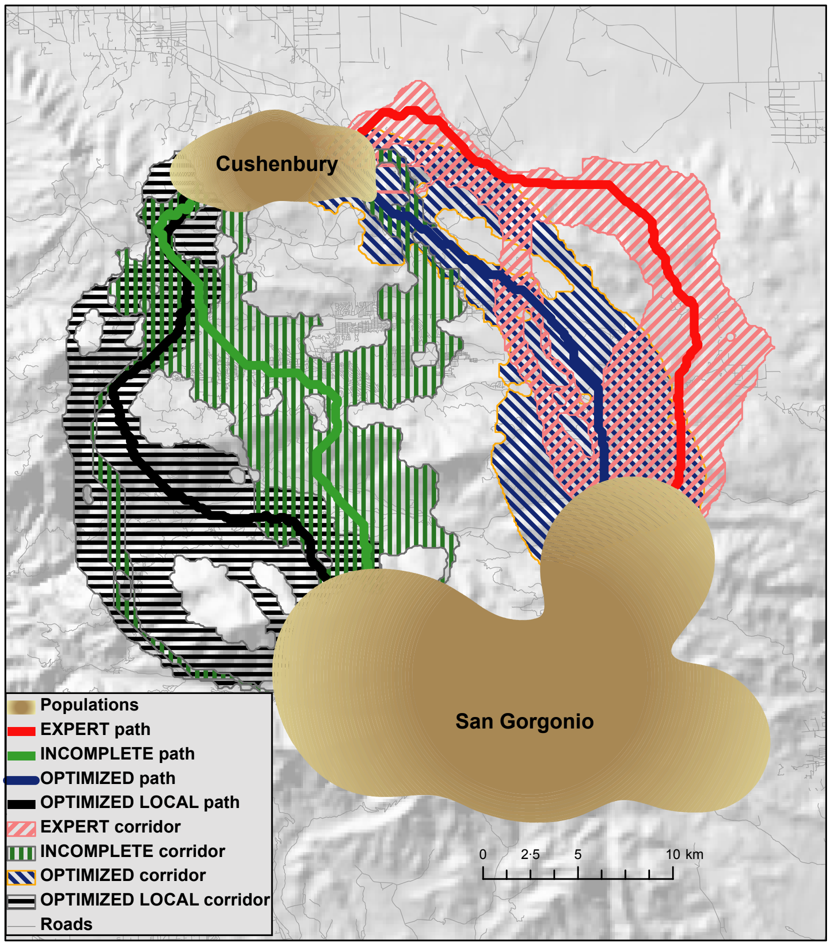

Fig. 2. A comparison of four least-cost path models between two bighorn sheep populations in southern California highlights the sensitivity of results to model inputs. Cost surfaces used to produce the four paths incorporate the following landscape characteristics: topography alone (Optimized model); wooded habitat alone (Incomplete model); topography, habitat and road density (Expert model); or topography, wooded habitat and urban areas (Optimized Local model). Total least-cost path length overlapped less than 2%; least-cost corridors based on the lowest 10% of the resistance surface overlapped from 0 to 44%.

(LCC; see Fig. 1) either by including minimum acceptable widths, buffering paths or selecting a percentage of least-cost cells (Table 1). Two studies included a minimum acceptable width cut-off. Kautz *et al.* (2006) found that one-pixel wide paths can go through extremely unsuitable habitat, and therefore buffered LCPs and rejected paths that passed through poor-quality habitat types. Four additional studies buffered their LCPs to make them wider. Three studies took a percentage of lowest grid cell values to make a least-cost corridor. However, empirical justifications for most of these analytical choices, such as buffer width, were not presented when defining LCCs.

CASE STUDY: LCP ANALYSIS OF BIGHORN SHEEP

The four LCP models compared in our analysis of two populations of desert bighorn sheep produced LCPs that varied widely in location and length (Fig. 2). Along-path distances for the four paths were 34·6 km (Expert), 21·6 km (Optimized), 31·7 km (Optimized Local) and 28·5 km (Incomplete); those paths overlapped < 2% of total length (Fig. 2). Least-cost corridors overlapped from 0 to 44% (average 13%; Table 2).

Discussion

LITERATURE REVIEW

Although LCP modelling has been touted as combining detailed geographical information with animal behaviour to move beyond structural towards functional connectivity

Table 2. Percentage overlap of least-cost corridors based on four connectivity models between two bighorn sheep populations

Model	Incomplete (%)	Expert (%)	Optimized (%)
Expert	0	–	–
Optimized	5	44	–
Optimized Local	30	0	0

analysis (Adriaensen *et al.* 2003; Theobald 2006), our review suggests current LCP model implementation often ignores factors that affect how animals utilize landscapes. Nearly, all recent LCP analysis-based studies employed coarse-grain environmental data layers to determine habitat connectivity, an approach that is often biased by researcher-perceived structural connectivity and runs the risk of missing important biological aspects of species' connectivity (Mortelliti & Boitani 2008). For instance, although scale of analysis has been shown to greatly impact strength of detected relationships, study grain was typically dictated by freely available remotely sensed data (see Table S1 Supporting information) rather than species perceptions of landscape features (Cushman & Lewis 2010; see Appendix S2 in Supporting information for recommendations on improving application of LCP analysis).

Overall, the strength of the correlation between remotely-sensed habitat layers and species' movement is relatively unknown and poorly validated (Chetkiewicz, St. Clair & Boyce 2006; Beier, Majka & Spencer 2008). Our analysis in no way rejects the utility of coarse proxy data, especially given the need to model movement over large landscapes, but illustrates the need to explore effects of scale, explicitly justify choice of scale, and conduct model sensitivity and validation (see Appendix S2 Supporting information). In many cases, remotely-sensed proxies may provide adequate coverage at limited cost, and may prove to be efficient for conservation planning in the face of limited time and funding [e.g. fishers (*Martes pennanti*): Caroll, Zielinski & Noss 1999; large carnivores: Schadt *et al.* 2002; bighorn sheep: Epps *et al.* 2007]. However, animals frequently select high-quality microhabitats in areas that appear unsuitable at a macro-level (Mortelliti & Boitani 2008). Animals often select against low quality habitat within largely suitable areas as well, and accounting for the presence of low quality habitat within otherwise high-quality habitat patches may significantly improve model predictions (e.g. Wang *et al.* 2008).

We suggest that those using LCP analysis should strive to evaluate the predictive power of coarse-grain proxies for focal species movement over a portion of the study range before constructing analytical models (see Appendix S2 Supporting information). For species and linkages above the scale of rapid dispersal movements, using resource selection function models (RSF) with LCP analysis appears to be a step forward from more arbitrary methods (e.g. Chetkiewicz & Boyce 2009). Hypothesis testing and model selection that compares critical scales of habitat use or movement for taxa will help to build a stronger foundation for linkage-design methodology. Better understanding of a species' perception of its environment will help modellers to identify appropriate scales of analysis and, thus, provide more reliable and accurate model outputs for practitioners (With, Gardner & Turner 1997; Uezu, Metzger & Vielliard 2005; Cushman & Lewis 2010).

LCP ANALYSIS OF BIGHORN SHEEP

Our LCP analysis of bighorn sheep in California demonstrated many of the challenges and uncertainties we highlight above. The four models used to identify LPCs for desert bighorn sheep were derived at different scales (e.g. metapopulation vs. population level) and yielded very different paths (Fig. 2). Use of 10% least-cost corridors for each scheme did little to reduce differences between the models (Fig. 2, Table 2). For instance, the corridor suggested by the Optimized model (developed over a much larger geographic area) did not overlap with the Optimized Local model, which included wooded and urban habitat (Fig. 2). The Optimized model only partly overlapped the Expert model corridor, which was based only on coarse habitat maps and expert opinion (Fig. 2). This case study makes clear that reasonable alternative models can lead to strikingly different conclusions regarding prioritization of land acquisition, easements or other management actions for linkage conservation.

HOW CAN WE IMPROVE LCP MODELLING?

Organisms respond differently to landscape elements depending on their perceptive range and characteristics of surrounding areas (Coulon *et al.* 2008; Richard & Armstrong 2010). Species' movements in one habitat type will often be affected by nearby disturbances such as man-made structures and light pollution (Beier 1995; Coulon *et al.* 2008), width of habitats (Laurance & Laurance 1999; Hilty & Merenlender 2004), traits of and distance to adjacent habitat (Binzenhofer *et al.* 2005; Anderson, Rowcliffe & Cowlishaw 2007; Richard & Armstrong 2010), and level of perceived cover and safety (Rizkalla & Swihart 2007; Beier, Majka & Spencer 2008). However, only 2 of 24 studies in this review were able to validate their model with behavioural data (Stevens *et al.* 2006; Driezen *et al.* 2007). Given the sensitivity of least-cost models to incorrect resistance specification, the best way to evaluate model performance would be comparison of predictions based on multiple methods and independent data sets (e.g. radiotelemetry movement data and landscape genetics: Cushman & Lewis 2010). Testing the role of individual behaviour, preference and perceptual range in habitat selection or movement decisions (e.g. radio or global positioning system tracking: Beier 1995; Cushman, Chase & Griffin 2010; Driezen *et al.* 2007; Richard & Armstrong 2010; experimental data: Stevens *et al.* 2006; Hadley & Betts 2010) and using model selection to better integrate these behavioural with ecological and landscape data will greatly improve connectivity design (see Appendix S2 Supporting information).

Determining the relationship between movement or gene flow and effective distance under a given cost scheme, and thus the maximum effective distance at which a corridor is useable by a given species, may be the most biologically important and widely ignored aspect of LCP and other connectivity analyses. Even the best-supported paths will not function as planned if their lengths exceed the movement capability of a focal species. For example, gene flow estimates (Epps *et al.* 2005, 2007) suggest that in our bighorn sheep example, only the corridors produced by the Optimized and Incomplete models would serve a connective function (21·6 and 28·5 km along-path lengths respectively) while the Expert and Optimized Local models would result in corridors too long to promote connectivity (35 and 31·7 km respectively). Yet, only two studies reviewed here (Schadt *et al.* 2002; Singleton, Gaines & Lehmkuhl 2004) considered cut-offs for maximum useable effective distance (the greatest effective distance a species can travel between patches) based on knowledge of species dispersal. One study used gene flow estimates to determine maximum effective distance (Epps *et al.* 2007; Appendix S1 Supporting information). We recommend that wherever possible, defensible estimates of maximum useable effective distance should be developed by analysing genetic or movement data as functions of effective distance (see Appendix S2 Supporting information). An alternative approach is to define resistance more explicitly in terms of biological parameters, such as mortality risk or energy expenditure based on demographic, diet or metabolic data, and use movement models based on those parameters to explore modelling choices (see Chetkiewicz, St. Clair & Boyce 2006). In general, a more explicit discussion of resistance in each study would improve linkage design and interpretation. For instance, does the resistance value used in an LCP analysis reflect the physical costs of moving through a cell, its mortality risk, or habitat value? Each definition may be defensible depending on the goals and scale of analysis, but each will have different implications, especially when considering maximum path lengths.

Individual animals rarely use a single optimum route, and single-pixel-wide LCPs are of limited biological value (Majka, Jenness & Beier 2007; McRae & Beier 2007; McRae *et al.* 2008; Pinto & Keitt 2009). Although alternative paths with comparable costs may exist on a landscape, studies regularly failed to consider larger swaths of low-cost grid cells (i.e. a least-cost corridor). Recently, circuit theory has been used to incorporate multiple pathways and patch characteristics when evaluating connectivity designs (McRae & Beier 2007; McRae *et al.* 2008). This method allows modelling alternative linkages, ranking potential corridors and reassigning values as pathways are removed (Fig. 1; see Appendix S2 Supporting information), but it is equally reliant on a biologically realistic resistance surface. Alternatively, researchers can select lowest percentiles of cost surfaces (Beier, Majka & Newell 2009; this study Fig. 2) or combine multiple low-cost routes in an LCP analysis to delineate 'probable movement zones' (Rayfield, Fortin & Fall 2010; see Appendix S2). While these alternatives may increase robustness to uncertainty in model parameters, selection of a percentile cut-off (e.g. lowest 10%) or combining a number of low-cost routes is still a subjective decision with unclear biological justification. Some of the techniques we describe above for optimizing or validating models of effective distance should also be applied to this problem.

Few studies examined in this review conducted sensitivity or uncertainty analyses, which are essential to the landscape planning process and should be a requirement of any LCP or related connectivity model (Beier, Majka & Newell 2009; Rayfield, Fortin & Fall 2010). Studies that conducted sensitivity analyses (Table 1) found that different cost schemes (both choice of factors incorporated in the resistance surface, as well as the weights and resistance values assigned) produced very different LCPs, although Beier, Majka & Newell (2009) found their models robust to uncertainty. Indeed, Beier, Majka & Newell (2009) methods for evaluating uncertainty should prove useful where data for optimizing cost schemes are sparse (see Appendix S2 Supporting information). Sensitivity to the choice of habitat factors, factor weights, resistance values, grain and definitions of least-cost corridors should all be considered (see Appendix S2 Supporting information). Our LCP analysis for desert bighorn sheep highlights the disparity of LCPs based on expert opinion, gene flow optimization models, and other reasonable combinations, as well as the point that models optimized over large areas may still need local modifications. Researchers should strive for replicability, objectivity and organism-centred methodology to improve efficacy of LCP and other models in connectivity conservation planning (see Appendix S2 Supporting information). To avoid accusations of 'black-box' modelling (e.g. Shrader-Frechette 2004), studies must clearly address details of model construction, assumptions and uncertainties. Through these improvements, connectivity science will more ably inform landscape planning.

Least-cost path analysis and other connectivity conservation approaches should be viewed as one piece of a larger landscape conservation puzzle. Least-cost modelling cannot fully incorporate quality, size or importance of individual source patches, thus, it is best applied as part of a wider conservation strategy for focal species. A current debate questions whether connectivity conservation strategies like LCP analysis bear consideration in conservation planning, or simply detract focus from more certain measures to protect high-quality breeding habitats (Doerr, Barrett & Doerr 2011; Hodgson *et al.* 2011). This debate promotes a dichotomy between high-quality breeding habitat and habitats designated for connectivity that may represent an overly simplistic view of connective habitats. Regardless, recent summaries (e.g. McLachlan, Hellmann & Schwartz 2007; Hodgson *et al.* 2011) emphasise that conservation of diverse and connected habitat mosaics is likely to be the safest approach for sustaining species on our rapidly changing planet.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Background information for the desert bighorn sheep case study on LCP methods.

Appendix S2. Recommendations for effective LCP analysis.

Appendix S3. A note on variation in least-cost terminology.

Table S1. Complete summary of recent studies that used least-cost path (LCP) modelling for habitat connectivity design.

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