Estimating effective landscape distances and movement corridors: comparison of habitat and genetic data

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Abstract. Resistance models provide a key foundation for landscape connectivity analyses and are widely used to delineate wildlife corridors. Currently, there is no general consensus regarding the most effective empirical methods to parameterize resistance models, but habitat data (species' presence data and related habitat suitability models) and genetic data are the most widely used and advocated approaches. However, the practical consequences of applying one or the other approach have not been well studied. To address this knowledge gap, we performed a comparative study on the implications of using habitat suitability versus genetic data for determining effective landscape distances (a proxy inversely related to isolation among patches) based on least-cost and circuit-theoretic approaches, and for identifying potential movement corridors. For our comparison, we used data for the Cantabrian brown bear in Spain, an endangered population for which connectivity has been identified as a major conservation concern. Our results show that for brown bears, habitat models tend to overestimate resistance to movement through non-optimal areas, whereas genetic data yield higher estimates of effective distances within habitat areas. Therefore, our results suggest that (1) dispersal might be generally less constrained by landscape conditions than habitat utilization in home ranges, and that (2) dispersing animals might be more flexible in their movement behavior than residents are in their habitat resource utilization behavior, with records for residents dominating species occurrence data and subsequent habitat models. The assessed approaches provided dissimilar connectivity models with notable differences in patterns of predicted corridors across the study area, mainly due to differences in predicted connections between subpopulations. Our results highlight that the functional differences in habitat vs. genetic data, as well as the assumptions and potential limitations of different analytical approaches that use these data, need to be considered more carefully in connectivity modeling and subsequent corridor delineation.

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INTRODUCTION

The establishment and conservation of corridors has been widely suggested as a key means to facilitate movement between wildlife habitat patches and to preserve and enhance landscape and population connectivity (Simberloff et al. 1992). The classical concept of corridors as narrow strips of habitat that facilitate movements of organisms between habitat patches (Rosenberg et al. 1997) has been recently broadened. Rather than experiencing landscapes as categorical mosaics (habitat vs. non habitat), it is more likely that organisms experience the landscape matrix as a gradient of differential permeability (Cushman et al. 2010). This generalization mainstreams the concept of resistance to movement and suggests reconceptualization of connectivity problems to address how species movement is affected by landscape features across a range of spatial scales. Formally, landscape resistance represents an integration of multiple behavioral and physiological factors such as aversion, energy expenditure, or mortality risk when moving through a particular environment (Zeller et al. 2012). In a practical sense, landscape resistance is a spatial layer that reflects step-wise costs of moving through each cell in a raster map for least cost path analyses (Singleton et al. 2002) or the relative probability of moving across the cell for circuit theory-based analyses (McRae et al. 2008).

Since modeling landscape resistance is increasingly used as the basis to predict population connectivity and therefore is a crucial step in identifying movement corridors, resistance modeling has received much attention from corridor designers (Beier et al. 2008, Spear et al. 2010, Zeller et al. 2012). However, despite the existence of multiple and varied approaches, there is no consensus on how to best parameterize resistance surfaces (Zeller et al. 2012). Parameterizing resistances involves identifying and combining the important resistant factors (e.g., land cover, transport infrastructure, etc.) that affect the species' movement in an optimal way to realistically estimate the cost of movement through any location in the landscape. Resistance values have usually been determined by assigning resistance scored on an arbitrary scale (Beier et al. 2008, Pereira et al. 2011) on the basis of expert opinion itself or in combination with literature review (Larkin et al. 2004, Kautz et al. 2006). However, such approaches have frequently been shown to perform poorly (Beier et al. 2008, Shirk et al. 2010). To address these limitations, some authors have suggested that habitat suitability models predicting species occurrence on the basis of empirical data may provide a better estimation of resistance (Ferreras 2001, Chetkiewicz et al. 2006, O'Brien et al. 2006, Beier et al. 2008). This approach essentially implies that animal movements are influenced by the same environmental factors as habitat selection (e.g., Chetkiewicz et al. 2006, Wasserman et al. 2010, Zeller et al. 2012). More recently, the field of landscape genetics has shown great potential to provide more rigorous methods to parameterize resistance models by inferring the influences of landscape on realized population connectivity (Spear et al. 2005, Cushman et al. 2006, Storfer et al. 2007, Balkenhol et al. 2009). Individual-based analysis comparing pairwise genetic distances to pairwise effective distances under multiple landscape resistance hypothesis are a powerful tool for supporting conservation efforts (Cushman et al. 2006, 2013a, Epps et al. 2007, Segelbacher et al. 2010).

Understanding how different approaches can affect the analyses that aim to identify conservation corridors is a critical issue given the large conservation implications and investments that are potentially derived from such analyses. In this paper we addressed this issue by comparing predicted movement corridors and effective distances (derived from least cost analysis and circuit theory) across alternative resistance surface scenarios based on different parameterization methodologies: habitat modeling and landscape genetics. We also assessed how two different variable integration approaches (additive and multiplicative) affected the predictions and implications of landscape genetic models of resistance.

Our aim was to gain insights into the differences and similarities between the results obtained using the different approaches, their potential limitations, and consequent management implications. We considered brown bear (*Ursus arctos*) in the Cantrabrian Range (NW Spain) as the focal species. Brown bear is a long-lived omnivorous mammal with a solitary social structure and promiscuous mating system

(Nores and Naves 1993, Schwartz et al. 2003). Males and females have intra and inter-sexually overlapping home ranges (Dahle and Swenson 2003) and dispersal primarily occurs by males, while females typically are philopatric (Swenson et al. 1998). Brown bear is highly dependent on large landscapes with low human-footprint and large extents of forest cover (Clevenger et al. 1997, Apps et al. 2004, Mateo-Sánchez et al. 2014a). The brown bear population in the Cantabrian Range suffered a dramatic decline in the last several centuries as a result of human persecution and progressive loss and fragmentation of its habitat (Naves et al. 2003). We considered this population highly suited for this analysis for the following reasons. (1) In the Cantabrian Range, brown bears occur in two small, apparently isolated and endangered subpopulations, with about 220 individuals in total (Pérez et al. 2014). Connectivity has been identified as a major conservation concern for this species, with potentially large implications for actual planning and conservation measures in the study area (Ballesteros and Palomero 2012). (2) Brown bears and other large mammals are of particular interest for connectivity networks because these species operate at broad scales and occur at low densities, which imply that their populations are more likely to be affected by the loss of connectivity (Beier et al. 2008). (3) Large amounts of habitat and genetic data are available for the species and recent research has focused on landscape resistance and connectivity for this species (Pérez et al. 2009, 2010, Mateo-Sánchez et al. 2014a, b) which provides a unique opportunity for the comparative analyses needed to effectively tackle the aforementioned objectives.

MATERIALS AND METHODS

Study area

The study was carried out in the Cantabrian Range (northwestern Spain). This area is within a larger transnational initiative covering protected areas from the Cantabrian Range to the Western Alps (SW Europe), in which previous studies on connectivity and the barrier effect of roads for forest mammals have focused (Gurrutxaga et al. 2011, Jongman et al. 2011). The region is 49,472 km^2 in extent and contains the whole known range of the native populations of the brown bear

in Spain, its peripheral areas and the belt area between the two subpopulations. As shown in Fig. 1, both subpopulations occupy a similar area of about 2,500 km^2 each and are separated by about 50 km of unoccupied range.

Landscape resistance parameterization

Landscape resistance was parameterized under three different scenarios based on different methodological approaches (habitat scenario, genetic-multiplicative scenario, and genetic-additive scenario), as described next. All resistance maps were produced with a spatial resolution of 100 m.

Habitat suitability as a proxy for resistance to movement.—A plausible way to empirically estimate relationships between connectivity and environmental conditions is to assume that habitat quality has a direct (inverse) relationship with resistance to movement (e.g., Pullinger and Johnson 2010, Kuemmerle et al. 2011, Mateo-Sánchez et al. 2014b). We used this approach in our first parameterization scenario (habitat scenario), in which we created a resistance surface where resistance to movement was obtained through an inverse function of habitat suitability. We used a multiscale suitability habitat model developed by Mateo-Sánchez et al. (2014a) to predict brown bear occurrence in the study area. After transformation every pixel represented the unit cost of crossing each location, so that the lowest resistance value represented the cost of moving through the highest quality habitat. Landscape variables included in the model were landscape composition (percentage of landscape covered by forest), forest canopy cover and density of buildings (Mateo-Sánchez et al. 2014a, b).

Landscape genetics to infer resistance to movement.—We used individual-based landscape genetics approaches to produce resistance models under two different scenarios (Mateo-Sánchez et al., in press). Specifically, we used genetic samples of brown bears genotyped at 17 polymorphic microsatellite loci to quantify genetic structure and measured the genetic distance among samples as the proportion of shared alleles (Bowcock et al. 1994). The relationship between the genetic structure observed within the bear population and likely drivers of landscape resistance was systematically evaluated through
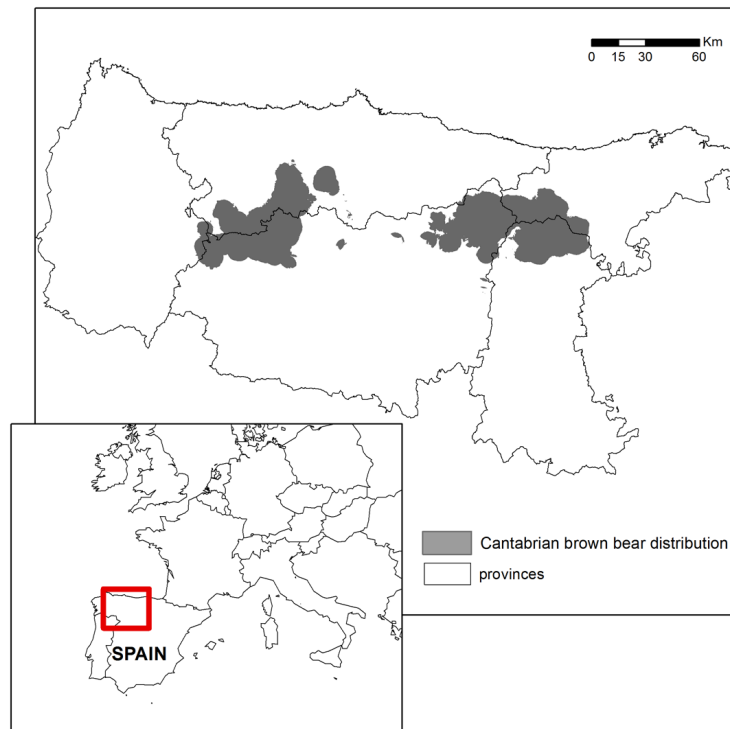
Fig. 1. Maps showing the location of the study area in Spain (small map) as well as the distribution of brown bears within the study area in Spain (large map).

reciprocal causal modeling (Cushman et al. 2006, 2013b) and the multi-model optimization approach developed by Shirk et al. (2010). The resulting resistance models included variables of landscape composition (percentage of landscape cover by mixed forest and agricultural lands), landscape configuration (cohesion of mixed forest and shrubland) and canopy cover.

One of the key questions in resistance parameterization relates to the method for combining the effects of individual landscape variables into a multivariate resistance surface (Beier et al. 2008). Hence, we explored two different ways for combining individual landscape variables: through multiplication (genetic-multiplicative scenario) and through addition (genetic-additive scenario).

Corridor identification and effective distance estimation

We used an individual-based approach to predict expected movement corridors. We considered as sources and destinations for the corridor mapping a set of 173 empirical brown

bear locations distributed across the species range for which we also counted with genetic data, which allowed meaningful comparisons between results of the different approaches (habitat vs. genetic).

We applied two different approaches: (A) least cost path modeling, using the UNICOR software (Landguth et al. 2012), in which the movement of individuals is assumed to follow the optimal (least costly) pathway between locations and (B) circuit theory, using CIRCUITSCAPE (v3.5.8; McRae and Beier 2007, McRae et al. 2008), in which multiple available pathways (including suboptimal ones) can be followed by the individuals and contribute to estimated connectivity among locations. These two approaches were used to (1) produce corridors expected to concentrate brown bear movements in the study area (least cost path density and current density map for approaches A and B, respectively; further details on our analyses can be found in Appendix A), and to (2) calculate the accumulated cost of movement between source and destination areas, corresponding to the so called
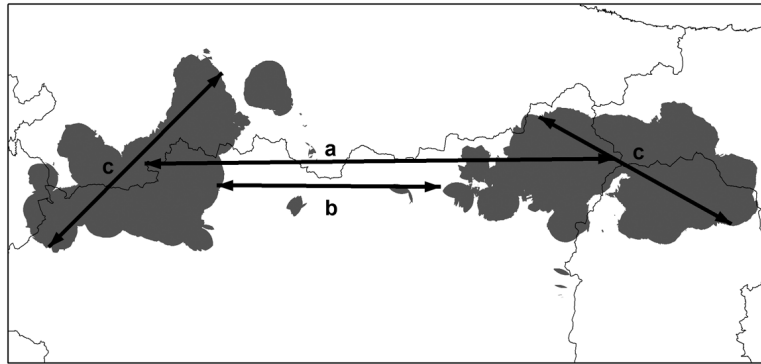
Fig. 2. Locations for effective distance and effective resistance calculations. We calculated effective distances and resistances between (a) the cores of the ranges of the two subpopulations, (b) the periphery of the two ranges, and (c) within the two ranges. See also Table 1.

effective distances in least cost path modeling and to effective resistances (or resistance distance) in circuit-based modeling (hereafter both referred to as effective distances). Higher effective distances among locations are assumed to correspond to a higher degree or likelihood of isolation among habitat areas or locations. Effective distances were calculated between (a) the western subpopulation core area and eastern subpopulation core area, (b) the western subpopulation peripheral area and eastern subpopulation peripheral area (i.e., the edge of each core population area that is closest to the other subpopulation edge) and (c) end to end within each subpopulation area (i.e., travel through the whole occupancy area) (Fig. 2). We focused on these positions due to their strategic significance in terms of connectivity between and within the two subpopulations (see also Table 1). These linkages (corridors) and effective distances were produced for each of the three landscape resistance scenarios described above. Since we aimed to compare the effective distances produced by the three resistance scenarios, each with different ranges of variation in the resistance values, we first normalized effective distances by dividing the effective distance in each scenario by the mean resistance value of all the 173 pixels with bear locations in the corresponding resistance surface.

We therefore produced and compared six sets of corridors and effective distance/resistance values, corresponding to the two analytical approaches (least cost paths and circuitscape) and the three resistance surface scenarios (Table 2).

RESULTS

Corridor comparison

The predicted movement corridor network among individuals showed substantial differences across the three resistance scenarios and two

Table 1. Definition of analyzed effective distances.

Name	Definition	Meaning
a: between subpopulation centers	Movement between two individuals located in the core of the west subpopulation and the core of the east subpopulation.	Connectivity between subpopulations, assuming most dispersers move from core to core.
b: between subpopulation edges	Movement between two individuals located in the peripheral area of the west subpopulation and the peripheral area of east subpopulation (border of each area closest to the other subpopulations). Peripheral areas correspond with the limit of both subpopulations occupancy area.	Connectivity between subpopulations, assuming that most dispersers will first try to stay within established ranges and eventually move outside currently occupied areas through the more hostile matrix to relocate into another range.
c: within subpopulations	Movement through the whole occupancy area (for each subpopulation).	Connectivity within populations.

Table 2. Sets of methods being compared for delineating corridors and estimating effective distances. These methods are based on three different approaches for parameterizing resistance models, and two different approaches for delineating corridors and estimating effective distances based on these models.

Corridor delineation approach	Resistance parameterization		
	Habitat scenario	Genetic-multiplicative scenario	Genetic-additive scenario
Least-cost path density	Corridor option 1 (Fig. 3a)	Corridor option 2 (Fig. 3b)	Corridor option 3 (Fig. 3c)
Circuit theory	Corridor option 4 (Fig. 4a)	Corridor option 5 (Fig. 4a)	Corridor option 4 (Fig. 4c)

analytical approaches (Figs. 3 and 4). Importantly, major functional links did not match among scenarios or methods (least cost path vs circuit theory). In the case of linkages defined through cumulative density of least cost paths on a resistance map derived from habitat suitability, connections between subpopulations followed two main routes that converged in the peripheral area of the East subpopulation (Fig. 3a). In contrast, for the resistance scenarios based on genetic data and least cost path analysis, connections showed more extensive networks consisting in one major route complemented by several secondary routes that converge with the principal route when using multiplicative genetic resistance (Fig. 3b). In the additive genetic resistance scenario analyzed with least cost paths, three parallel and interconnected routes coalesce in both subpopulations (Fig. 3c). When analyzing connections designated through circuit theory, potential connections identified through current maps also differed across the assessed resistance scenarios. A higher concentration of current in narrower and more clearly defined areas is found in the habitat based resistance scenario (Fig. 4a). When resistance was based on genetic data, more and wider permeable areas were detected (Fig. 4b, c), with movements less concentrated in thin strips of land. Results also show that within-subpopulation connectivity network pattern was relatively similar for all the scenarios in both approaches.

Effective distances comparison

There were strong correlations between effective distances across the three resistance scenarios assessed when all pairs of locations where simultaneously considered: Pearson's correlation coefficient r > 0.96 in all the cases for effective least cost distances and r > 0.82 in all the cases

for effective resistances based on circuit theory. However, effective distances between strategic locations showed considerably different values among scenarios (Fig. 5). Effective distances between two individuals located within different centers of the two subpopulations were 7–9% lower for genetic scenarios (multiplicative and additive) than for the habitat scenario. More importantly, when two individuals were located in the proximate peripheral areas (edges) of both subpopulations, effective distance was much higher for the habitat scenario than for genetic scenarios (47% and 79% higher for the genetic-multiplicative and genetic-additive scenarios, respectively). When comparing the multiplicative and additive genetic scenarios, the normalized effective distances were more similar than when comparing the habitat and genetic scenarios, but the additive genetic scenario showed the lowest effective distances between individuals. In contrast, effective distance between two individuals located in the same core in both subpopulations was 40–30% lower when calculated across resistance based on habitat suitability than when computed for resistance scenarios based on genetic data. Effective distances within cores were relatively similar in the two genetic scenarios, but the multiplicative approach showed higher values.

Effective distances (effective resistances) calculated through circuit theory followed the same general pattern as least-cost effective distances when considering movements between population edges and movements within populations (Fig. 5b). In these cases, effective resistances in the genetic-multiplicative and genetic-additive scenarios were again considerably lower than for the habitat-based resistance scenario (37% and 51%, respectively). Oppositely, effective resistances between the centers of both subpopulations

a) Habitat suitability

b) Genetic multiplicative

c) Genetic additive
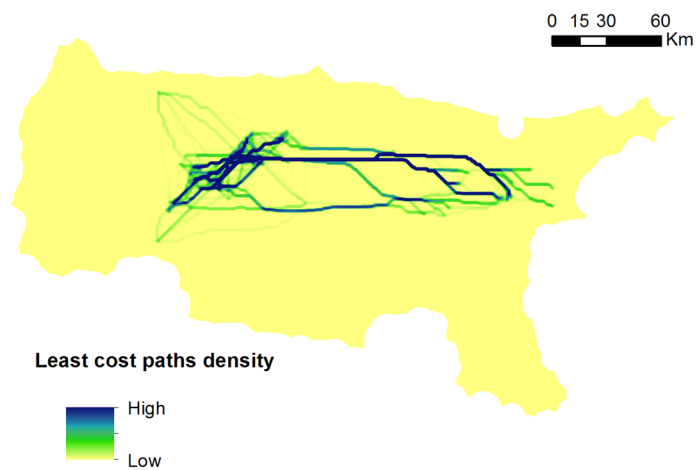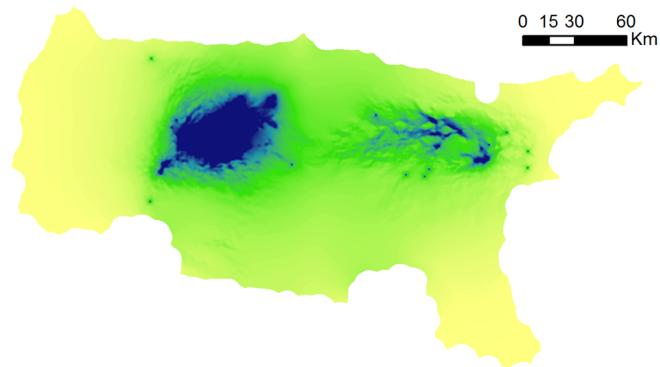
Least cost paths density

High

Low
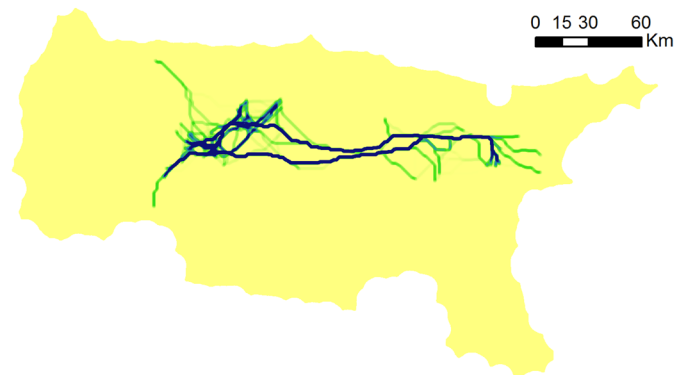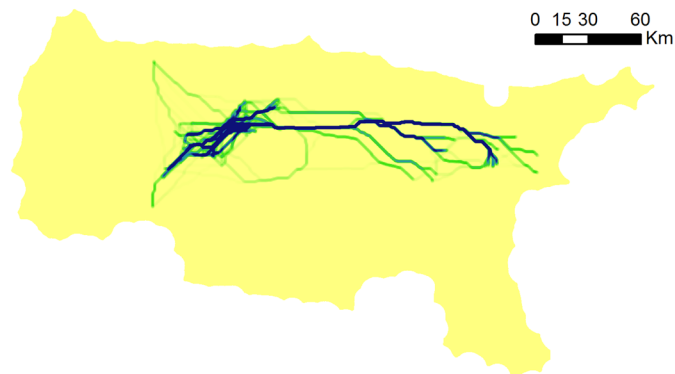
Fig. 3. Corridors defined by using least-cost paths for the three resistance scenarios: (a) Habitat suitability-based scenario, (b) genetic-multiplicative scenario, and (c) genetic-additive scenario.

a) Habitat suitability

b) Genetic multiplicative

c) Genetic additive

Current

High

Low
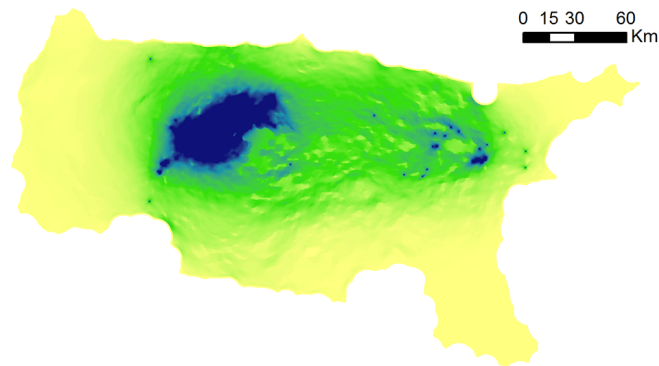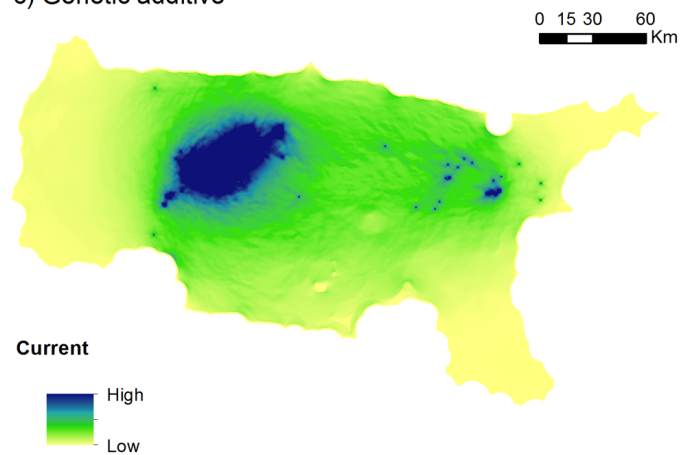
Fig. 4. Current maps defined by circuit theory for resistance scenarios: (a) Habitat suitability-based scenario, (b) genetic-multiplicative scenario, and (c) additive genetic-based scenario.

were 18% higher in the multiplicative genetic based model than in the habitat-based model. However, the additive genetic model and the habitat-based model led to very similar resistances. Remarkably, effective resistance between centers of both populations was lower than effective resistance between population edges for the habitat model (Fig. 5b).

DISCUSSION

Most current methods to predict population connectivity and to identify areas important for animal movements rely on landscape resistance surfaces (Spear et al. 2010). However, the methods and assumptions used to create these surfaces are critical for their effectiveness in guiding conservation decisions. Therefore, it is important to explore the effects that different analytical approaches have on predicted population connectivity and identified corridor routes. Here, we compared resistance surface parameterization and resulting connectivity models created by two different analytical approaches for quantifying resistances and two commonly used methods to predict likely movement paths from these resistances. Our findings showed that alternative approaches substantially affected the assessment of effective distances and largely changed the delineation of potential corridors across the study area.

Implications of multiplicative vs. additive combination of factors

The way in which factors are combined in a resistance model has important implications for resulting connectivity models. Our additive resistance surface showed denser connectivity networks and lower effective distances/resistances than the multiplicative surface. This suggests that multiplicative resistance models are more restrictive in identifying permeable areas for movement and hence indicate lower connectivity. This is because areas predicted to be highly permeable in a multiplicative model correspond to those raster cells where all the factors involved in the models have low resistance values. Thus, in a multiplicative model, even a single factor with high resistance in an area can decrease predicted landscape permeability in that area. In contrast, an additive combination of factors
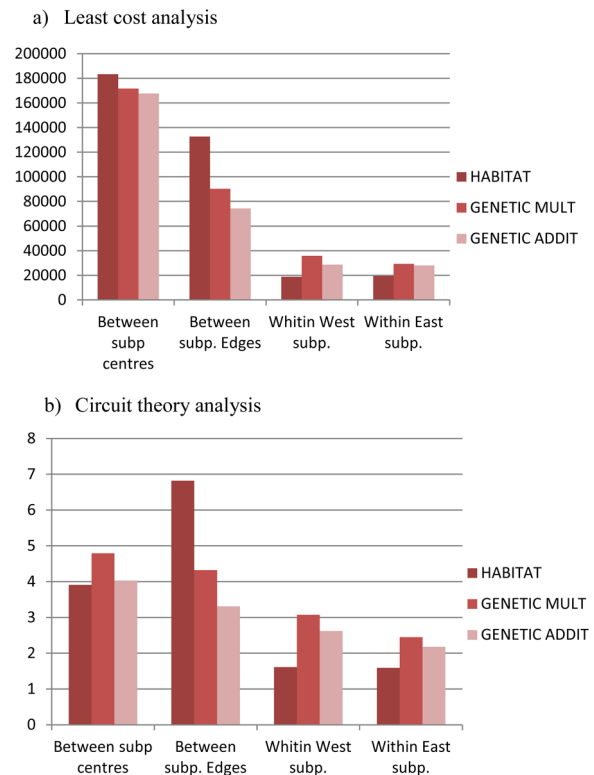
a) Least cost analysis

b) Circuit theory analysis

Fig. 5. Comparison of normalized effective distances among resistance scenarios. Distances are shown for the two analytical approaches used (a) least cost paths and (b) circuit theory. Resistance scenarios are: habitat-suitability based, genetic-multiplicative and genetic-additive. Between subpopulations centers corresponds to the normalized effective distance between two individuals located in the core of the west subpopulation and the core of the east subpopulation; between subpopulation corresponds to the normalized distance between two individuals located in the peripheral area of the west subpopulation and in the peripheral area of the east subpopulation (border of each area closest to the other subpopulation); within west and east subpopulations corresponds to the normalized effective distance between the opposite edges of that subpopulation.

allows compensation among factors and can lead to less restrictive connectivity predictions.

Comparison of least cost-path and circuit theory predictions

Least-cost path analysis and circuit theory are based on different assumptions to model con-

nectivity (Spear et al. 2010). While least-cost analyses assume animals follow a single and optimal pathway, circuit theory assumes random walks so that movement is influenced by all possible pathways. Therefore, results from both methods provide different and complementary insights about brown bear movement. For both approaches, effective distances between subpopulation centers (the individual has to cross part of the habitat area and the matrix in-between subpopulation ranges) differed from effective distances between subpopulation edges (the individual only crosses the matrix between habitat areas). However, and surprisingly, we found that circuit-theoretic effective resistance between subpopulation edges was actually higher than the effective resistance between population centers in the habitat-based resistance scenario (Fig. 5b). To have a lower effective resistance between the centers of the habitat areas than between the less distant edges of those areas is rather difficult to interpret ecologically, because bears moving away from the edges first have to reach the edges before crossing the matrix to reach the other subpopulation. This result might point out to a potential limitation of circuit theory (or of the implementation of it) to assess landscape connectivity. We ensured that our finding was not an artifact arising from some idiosyncratic and unnoted characteristic of our particular brown bear spatial data by creating a simple and purposefully controlled example depicting a resistance pattern similar to the one of the habitat-based scenario (i.e., similar extent, resolution and arrangement). This controlled example confirmed our results from the real bear data set, i.e., effective resistances were smaller between the cores than between the edges (further details can be found in Appendix A and Appendix B: Fig. B1). This finding advocates for further research to fully clarify this issue from an analytical point of view and, if possible, to provide guidelines for avoiding potentially unintended results in the application of circuit theory for connectivity analyses.

Habitat models may overestimate resistance to movement through non-optimal areas

Corridors between subpopulations predicted from habitat suitability-based resistance did not match the locations or intensity of corridors identified through genetic-based resistances. In addition, effective distances between subpopulations were substantially higher when habitat suitability was used as a surrogate for landscape resistance. These findings suggest that resistance surfaces based on habitat models may tend to overestimate landscape resistance in areas with low habitat suitability. In our analysis, this effect was dramatic when effective distance was calculated between peripheral areas of both subpopulations and individuals had to cross mostly unsuitable areas. In contrast, effective distances between individuals located within subpopulations were lowest when resistance surfaces were based on habitat suitability. Thus, congruent with results from Wasserman et al. (2010), we found that habitat suitability can predict a greater resistance to poor habitat than is suggested by genetic data. In other words, the fact that the species does not occur (permanently) in a particular habitat does not imply that it cannot move when needed (e.g., dispersal) through this area. In this sense, landscape genetics models integrate the movement of many individuals over time and thus lead to a more synoptic measure of landscape resistance (Zeller et al. 2012, Cushman et al. 2013a). This suggests that there is not necessarily a correspondence between habitat use patterns and dispersal movements. Conditions providing suitable habitat for permanent establishment and local resource may often be different than the conditions facilitating dispersal movements (Cushman et al. 2013a, Peterman et al. 2014). Since suitability models are based on occurrence data that usually represent locations within home ranges, habitat suitability models may not adequately reflect how environments affect animals during movements outside of their usual home ranges, such as dispersal or mating excursions (Cushman et al. 2013a). For our study species, results suggests that dispersing bears are more flexible in their movement behavior and less constrained by landscape conditions than suggested from their occurrence in typical bear habitats. While our analyses have only been conducted for a single species, we believe that the results may be similar for many other organisms as well, particularly for species that are highly mobile and not strictly confined to a specific type of habitat.

Genetic data estimate higher resistance to movement through suitable habitat areas

For within-population movements, the genetically-derived resistance surfaces predicted larger effective distances among individuals than the habitat suitability-based resistance surface. This is likely due to the fact that resistance models derived from landscape genetic analyses are based on comparison of genetic distances and effective distances. Such landscape genetic approaches may lead to resistance surfaces that overestimate effective distances in areas that are highly suitable (and eventually well connected to each other) when factors other than resistance to movement govern spatial-genetic structure; for instance, even when two sampled individuals are separated by a very short distance (or even located in the same raster cell), they will show some genetic differentiation, which may translate in such genetic resistance models exacerbating the effective distance estimates at short ranges to explain such genetic structure. Spatial-genetic structure within populations is likely less dependent on the resistance of the landscape matrix (Fahrig 2007), but more strongly influenced by many other biological and ecological factors acting locally, including sex-specific space-use behavior, local population density, survival, or reproductive success (Pflüger and Balkenhol 2014). Another issue related to genetic data is that in long-lived species there may be a temporal disconnection between genetic structure and the current landscape; i.e., there may be legacy effects of previous landscapes (James et al. 2007, Spear et al. 2010) that could lead to misestimate current connectivity. However, Landguth et al. (2010) showed that the legacy of past landscape features is not a particularly important problem in species with relatively large dispersal abilities. Hence, landscape legacies are unlikely to affect our conclusions about brown bear dispersal and gene flow.

The importance of inter-population movements for predicting connectivity

Movements outside of typical habitat are less frequent than within-habitat movements, but they are also critical for genetic exchange and range expansion (Nathan et al. 2003, Chetkiewicz et al. 2006). Previous research has shown that a variable but generally low number of migrants per generation can lead to a sufficient amount of gene flow between populations (e.g., Mills and Allendorf 1996, Vucetich and Waite 2000). Therefore, facilitating sufficient levels of inter-population movements should be a priority in connectivity strategies. Importantly, it is precisely in this kind of movements where, according to our results, resistance estimates and connectivity models varied most strongly between the analytical approaches we compared. Within the two subpopulations, effective distances and resistances were always low, and predicted movement paths were very consistent among the different analytical approaches. However, estimated distances and predicted movement paths differed substantially among the different approaches for connectivity between the two subpopulations. Thus, analytical choices for parameterizing and utilizing resistance surfaces will be most important when trying to predict inter-population movements, when individuals move out of established ranges and cross the unsuitable landscape matrix. Importantly, this is also the kind of analysis most relevant for corridor design, as the goal is usually the (re-) connection of different subpopulations located across a landscape or the support of species range shifts in response to climate change, rather than the facilitation of within-population movements.

Conclusions for connectivity analysis based on habitat suitability

Based on our study, it seems reasonable to question the assumption that habitat suitability models can accurately capture landscape resistance to movement for corridor design. Location data used to produce habitat suitability models tend to be dominated by habitat use (i.e., shelter, foraging) and thus by frequent routine movements within established home ranges. However, genetic structure may be strongly determined by mating movements and rare dispersal events. These types of movements are unlikely to be well-captured by occurrence data and may be therefore poorly represented in resistance models derived from such data. Thus, as already suggested by Beier et al. (2008) and Zeller et al. (2012), genetic-based studies are likely to be more useful to understand connectivity of populations. However, if genetic data are not available or when recent landscape changes are not yet

reflected in genetic data, parameterization based on habitat models, direct movement data (e.g., telemetry) or even expert opinion may be still required (Spear et al. 2010). Indeed, resistance surfaces should ideally be assessed though analyses of multiple data sources. For example, a resistance surface that is supported by independent analysis of movement and genetic data (e.g., Cushman and Lewis 2010) is much more likely to be robust than one developed from a single empirical data set. For example, recent research in telemetry data analysis provides methods that help to distinguish habitat use from dispersal locations (e.g., Dickson et al. 2005, Squires et al. 2013, Zeller et al. 2014). Compared to occurrence-based habitat models, these novel approaches could provide resistance models that more reliably reflect actual species movement across complex landscapes.

Implications for conservation

Connectivity models should accurately predict inter-population movement and gene flow, and enable researchers to reliably identify the most likely movement routes among subpopulations. As shown in this study, connectivity models and the corridors suggested by them depend strongly on the analytical methods used for creating and utilizing underlying resistance surfaces. Several published studies have suggested ways for finding optimal resistance values (e.g., Kuroe et al. 2011, Shirk et al. 2010, Graves et al. 2014), and these studies have certainly improved resistance-based connectivity modeling. However, the effects of different conceptual approaches underlying resistance models (habitat suitability vs. resistance to inter-population movement) or the analytical choices made during their creation and analysis (additive vs. multiplicative models, least-cost vs. circuit-theory) appear to be at least as important as the numerical optimization of resistance values. Indeed, our results suggest that these other aspects substantially impact the outcome of resistance-based connectivity predictions, which could be a challenge for applying resistance-based connectivity models in practical conservation. If different approaches predict vastly dissimilar areas to be important for conservation efforts (e.g., optimal locations for corridors or road-crossing structures), it will be rather difficult to objectively choose and justify a single 'best' management action.

For now, we advocate the use of genetically-derived resistance surfaces over the use of occurrence data, but agree with Zeller et al. (2012) that more comparative research is needed to fill current knowledge gaps related to landscape resistance and connectivity modeling. Indeed, we argue that research identifying the advantages and limitations of various conceptual and analytical approaches, such as those here reported, is urgently needed for assessing how meaningful and useful different resistance-based connectivity models actually are for practical conservation planning. We hope that our study has highlighted some of these future research needs and that it will motivate others to further investigate this important topic.

ACKNOWLEDGMENTS

LITERATURE CITED

Apps, C. D., B. N. McLellan, J. G. Woods, and M. F. Proctor. 2004. Estimating grizzly bear distribution and abundance relative to habitat and human influence. Journal of Wildlife Management 68:138–152.

Balkenhol, N., F. Gugerli, S. A. Cushman, L. P. Waits, A. Coulon, J. Arntzen, R. Holderegger, and H. H. Wagner. 2009. Identifying future research needs in landscape genetics: where to from here? Landscape Ecology 24:455–463.

Ballesteros, F., and G. Palomero. 2012. Conectividad, demografía y conservación del oso pardo cantábrico. Pages 19–31 in A. San Miguel, F. Ballesteros, J. C. Blanco, and G. Palomero, editors. Manual de buenas prácticas para la gestión de corredores oseros en la Cordillera Cantábrica. Fundación Oso Pardo. Ministerio de Agricultura, Alimentación y Medio Ambiente, Madrid, Spain.

Beier, P., D. R. Majka, and W. D. Spencer. 2008. Forks in the road: choices in procedures for designing wildland linkages. Conservation Biology 22:836–851.

Bowcock, A., A. Ruiz-Linares, J. Tomfohrde, E. Minch,

J. Kidd, and L. L. Cavalli-Sforza. 1994. High resolution of human evolutionary trees with polymorphic microsatellites. Nature 368:455–457.

Chetkiewicz, C.-L. B., C. C. St. Clair, and M. S. Boyce. 2006. Corridors for conservation: integrating pattern and process. Annual Review of Ecology, Evolution and Systematics 37:317–342.

Clevenger, A. P., F. J. Purroy, and M. A. Campos. 1997. Habitat assessment of a relict brown bear (*Ursus arctos*) population in northern Spain. Biological Conservation 80:17–22.

Cushman, S. A., M. Chase, and C. Griffin. 2010. Mapping landscape resistance to identify corridors and barriers for elephant movement in southern Africa. Pages 349–367 *in* S. A. Cushman and F. Huettmann, editors. Spatial complexity, informatics, and wildlife conservation. Springer, New York, New York, USA.

Cushman, S. A., and J. S. Lewis. 2010. Movement behavior explains genetic differentiation in American black bears. Landscape Ecology 25:1613–1625.

Cushman, S. A., K. S. McKelvey, J. Hayden, and M. K. Schwartz. 2006. Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. American Naturalist 168:486–499.

Cushman, S. A., B. McRae, F. Adriansen, P. Beier, M. Shirley, and K. Zeller. 2013*a*. Biological corridors and connectivity. Pages 284–404 *in* D. McDonald, editor. Conservation in theory and practice. Wiley, New York, New York, USA.

Cushman, S. A., T. N. Wasserman, E. L. Landguth, and A. J. Shirk. 2013*b*. Re-evaluating causal modeling with Mantel tests in landscape genetics. Diversity 5(1):51–72.

Dickson, B. G., J. S. Jenness, and P. Beier. 2005. Influence of vegetation, topography, and roads on cougar movement in southern California. Journal of Wildlife Management 69:264–276.

Dahle, B., and J. E. Swenson. 2003. Home ranges in adult Scandinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type. Journal of Zoology 260:329–335.

Epps, C. W., J. D. Wehausen, V. C. Bleich, S. G. Torres, and J. S. Brashares. 2007. Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44:714–724.

Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology 21:1003–1015.

Ferreras, P. 2001. Landscape structure and asymmetrical inter-patch connectivity in a metapopulation of the endangered Iberian lynx. Biological Conservation 100:125–136.

Graves, T., R. B. Chandler, J. A. Royle, P. Beier, and K. C. Kendall. 2014. Estimating landscape resistance to dispersal. Landscape Ecology. doi: 10.1007/s10980-014-0056-5

Gurrutxaga, M., L. Rubio, and S. Saura. 2011. Key connectors in protected forest area networks and the impact of highways: A transnational case study from the Cantabrian Range to the Western Alps (SW Europe). Landscape and Urban Planning 101:310–320.

James, P. M. A., M. J. Forteen, A. Fall, D. Kneeshaw, and C. Messier. 2007. The effects of spatial legacies following shifting management practices and fire on boreal forest age structure. Ecosystems 10:1261–1277.

Jongman, R. H., I. M. Bouwma, A. Griffioen, L. Jones-Walters, and A. M. Van Doorn. 2011. The pan European ecological network: PEEN. Landscape ecology 26:311–326.

Kautz, R., R. Kawula, T. Hoctor, J. Comiskey, D. Jansen, D. Jennings, J. Kasbohm, F. Mazzotti, R. McBride, and L. Richardson. 2006. How much is enough? Landscape-scale conservation for the Florida panther. Biological Conservation 130:118–133.

Kuemmerle, T., K. Perzanowski, H. Resit Akcakaya, F. Beaudry, T. R. Van Deelen, I. Parnikoza, P. Khoyetskyy, D. M. Waller, and V. C. Radeloff. 2011. Cost-effectiveness of strategies to establish a European bison metapopulation in the Carpathians. Journal of Applied Ecology 48:317–329.

Kuroe, M., N. Yamaguchi, T. Kadoya, and T. Miyashita. 2011. Matrix heterogeneity affects population size of the harvest mice: Bayesian estimation of matrix resistance and model validation. Oikos 120: 271–279.

Landguth, E., S. Cushman, M. Schwartz, K. McKelvey, M. Murphy, and G. Luikart. 2010. Quantifying the lag time to detect barriers in landscape genetics. Molecular Ecology 19:4179–4191.

Landguth, E., B. Hand, J. Glassy, S. Cushman, and M. Sawaya. 2012. UNICOR: a species connectivity and corridor network simulator. Ecography 35:9–14.

Larkin, J. L., D. S. Maehr, T. S. Hoctor, M. A. Orlando, and K. Whitney. 2004. Landscape linkages and conservation planning for the black bear in west-central Florida. Animal Conservation 7:23–34.

Mateo-Sánchez, M. C., N. Balkenhol, S. Cushman, T. Pérez, A. Domínguez, and S. Saura. *In press*. A comparative framework to infer landscape effects on population genetic structure: Are habitat suitability models effective in explaining gene flow? Landscape Ecology. doi: 10.1007/s10980-015-0194-4

Mateo-Sánchez, M. C., S. A. Cushman, and S. Saura. 2014*a*. Scale dependence in habitat selection: the case of the endangered brown bear (*Ursus arctos*) in the Cantabrian Range (NW Spain). International Journal of Geographical Information Science 28:1531–1546.

Mateo-Sánchez, M., S. Cushman, and S. Saura. 2014*b*.

Connecting endangered brown bear subpopulations in the Cantabrian Range (north-western Spain). Animal Conservation 17:430–440.

McRae, B. H., and P. Beier. 2007. Circuit theory predicts gene flow in plant and animal populations. Proceedings of the National Academy of Sciences 104:19885–19890.

McRae, B. H., B. G. Dickson, T. H. Keitt, and V. B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724.

Mills, L. S., and F. W. Allendorf. 1996. The one-migrant-per-generation rule in conservation and management. Conservation Biology 10:1509–1518.

Nathan, R., G. Perry, J. T. Cronin, A. E. Strand, and M. L. Cain. 2003. Methods for estimating long-distance dispersal. Oikos 103:261–273.

Naves, J., T. Wiegand, E. Revilla, and M. Delibes. 2003. Endangered species constrained by natural and human factors: The case of brown bears in Northern Spain. Conservation Biology 17:1276–1289.

Nores, C., and J. Naves. 1993. Distribución histórica del oso pardo en la Península Ibérica. Pages 13–33 in J. Naves and G. Palomero, editors. El oso pardo en España (Ursus arctos). ICONA, Madrid, Spain.

O'Brien, D., M. Manseau, A. Fall, and M.-J. Fortin. 2006. Testing the importance of spatial configuration of winter habitat for woodland caribou: an application of graph theory. Biological Conservation 130:70–83.

Pereira, M., P. Segurado, and N. Neves. 2011. Using spatial network structure in landscape management and planning: a case study with pond turtles. Landscape and Urban Planning 100:67–76.

Pérez, T., J. Naves, F. Vázquez, A. Fernández-Gil, J. Albornoz, E. Revilla, M. Delibes, and A. Domınguez. 2014. Estimating the population size of the endangered brown bear through genetic sampling. Wildlife Biology. doi: 10.2981/wlb.00069

Pérez, T., F. Vázquez, J. Naves, A. Fernández, A. Corao, J. Albornoz, and A. Domínguez. 2009. Non-invasive genetic study of the endangered Cantabrian brown bear (Ursus arctos). Conservation genetics 10:291–301.

Pérez, T., J. Naves, J. F. Vázquez, J. Seijas, A. Corao, J. Albornoz, and A. Domínguez. 2010. Evidence for improved connectivity between Cantabrian brown bear subpopulations. Ursus 21:104–108.

Peterman, W. E., G. M. Connette, R. D. Semlitsch, and L. S. Eggert. 2014. Ecological resistance surfaces predict fine-scale genetic differentiation in a terrestrial woodland salamander. Molecular Ecology 23: 2402–2413.

Pflüger, F. J., and N. Balkenhol. 2014. A plea for simultaneously considering matrix quality and local environmental conditions when analysing landscape impacts on effective dispersal. Molecular Ecology 23: 2146–2156.

Pullinger, M. G., and C. J. Johnson. 2010. Maintaining or restoring connectivity of modified landscapes: evaluating the leastcost path model with multiple sources of ecological information. Landscape Ecology 25:1547–1560.

Rosenberg, D. K., B. R. Noon, and E. C. Meslow. 1997. Biological corridors: form, function, and efficacy. BioScience 47:677–687.

Schwartz, C. C., S. D. Miller, and M. A. Haroldson. 2003. Grizzly bear. Pages 556–586 in G. A. Feldhammer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management and conservation. The John Hopkins University Press, Baltimore, Maryland, USA.

Segelbacher, G., S. A. Cushman, B. K. Epperson, M.-J. Fortin, O. Francois, O. J. Hardy, R. Holderegger, P. Taberlet, L. P. Waits, and S. Manel. 2010. Applications of landscape genetics in conservation biology: concepts and challenges. Conservation Genetics 11:375–385.

Shirk, A., D. Wallin, S. Cushman, C. Rice, and K. Warheit. 2010. Inferring landscape effects on gene flow: a new model selection framework. Molecular Ecology 19:3603–3619.

Simberloff, D., J. A. Farr, J. Cox, and D. W. Mehlman. 1992. Movement corridors: conservation bargains or poor investments? Conservation Biology 6:493–504.

Singleton, P. H., W. L. Gaines, and J. F. Lehmkuhl. 2002. Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least-cost corridor assessment. USDA, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Spear, S. F., N. Balkenhol, M.-J. Fortin, B. H. McRae, and K. Scribner. 2010. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Molecular Ecology 19:3576–3591.

Spear, S. F., C. R. Peterson, M. D. Matocq, and A. Storfer. 2005. Landscape genetics of the blotched tiger salamander (Ambystoma tigrinum melanosticum). Molecular Ecology 14:2553–2564.

Squires, J. R., N. J. DeCesare, L. E. Olson, J. A. Kolbe, M. Hebblewhite, and S. A. Parks. 2013. Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. Biological Conservation 157:187–195.

Storfer, A., M. Murphy, J. Evans, C. Goldberg, S. Robinson, S. Spear, R. Dezzani, E. Delmelle, L. Vierling, and L. Waits. 2007. Putting the 'landscape' in landscape genetics. Heredity 98:128–142.

Swenson, J. E., F. Sandegren, and A. Derberg. 1998. Geographic expansion of an increasing brown bear

population: evidence for presaturation dispersal. Journal of Animal Ecology 67:819–826.

Vucetich, J. A., and T. A. Waite. 2000. Is one migrant per generation sufficient for the genetic management of fluctuating populations? Animal Conservation 3:261–266.

Wasserman, T. N., S. A. Cushman, M. K. Schwartz, and D. O. Wallin. 2010. Spatial scaling and multi-model inference in landscape genetics: *Martes americana* in northern Idaho. Landscape ecology 25:1601–1612.

Zeller, K. A., K. McGarigal, P. Beier, S. A. Cushman, T. W. Vickers, and W. M. Boyce. 2014. Sensitivity of landscape resistance estimates based on point selection functions to scale and behavioral state: pumas as a case study. Landscape Ecology 29:541–557.

Zeller, K. A., K. McGarigal, and A. R. Whiteley. 2012. Estimating landscape resistance to movement: a review. Landscape Ecology 27:777–797.

SUPPLEMENTAL MATERIAL

APPENDIX A

DETAILS ON CORRIDOR IDENTIFICATION ANALYSES

Least cost path density modeling

UNICOR (UNIversal CORridor and network simulation model, Landguth et al. 2010) identifies the shortest path between every specified species location on a landscape to every other specified species location. The combination of all the movement paths produces a least cost path density map that represents the pattern of the most probable movement paths for brown bear in the study area (e.g., Cushman et al. 2013a; Mateo-Sánchez et al. 2014b). To identify putative corridors, we computed the focal density of the factorial least cost path network with a moving window of 1-km radius with a GIS (Mateo-Sánchez et al. 2014b). UNICOR also calculated effective (least cost) distance between all combinations of sources and destinations.

Circuit theory modeling

Circuitscape (McRae et al. 2008) uses circuit theory to model landscapes as conductance surfaces and predict important connections among locations. Based on the assumption of a random walk, all plausible paths between each two locations are integrated creating a current map. Analogously to the factorial least cost path density map described above, the combination of every pairwise current map allows the identify corridors with higher current flow.

This software also computes pairwise effective resistance between all combinations of locations (here brown bear occurrences). In this study we used a four-neighbor case for the calculations.

APPENDIX B

DETAILS ON THE EXAMPLE OF CIRCUITSCAPE ESTIMATES OF EFFECTIVE RESISTANCES

The simulated example consists of two habitat areas with low resistance to movement that are separated by a high resistance matrix. We computed circuit-based effective resistances between two points located in the center of both habitat areas and two points located on their closest edges (Fig. B1). Results showed that centre to centre effective resistance was lower than edge to edge (see Fig. B1), confirming our findings from the brown bear data set. This suggests that there might be a previously unreported issue related to some conceptual aspects of circuit theory or its application to model landscape connectivity, or issues related to details of the implementation of the calculations in Circuitscape.
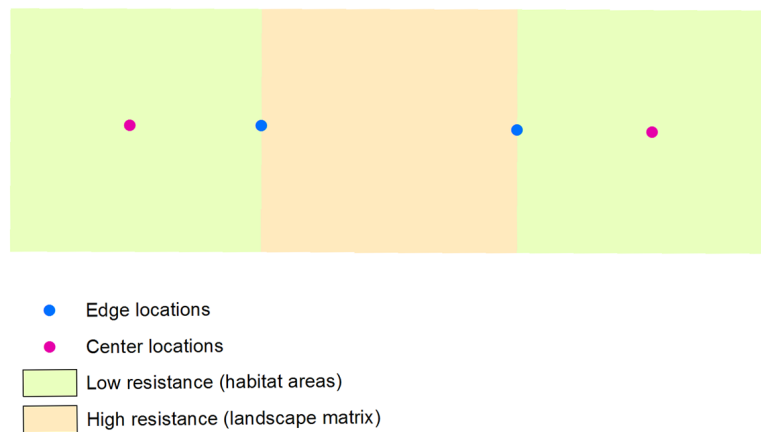
Fig. B1. Simulated landscape for illustrating the results of the effective resistances through circuit theory as implemented in Circuitscape. The landscape consists of two habitat areas with low resistance to movement (resistance score 10) that are separated by a portion of landscape matrix with a high resistance (resistance score 100). Effective resistance was calculated (1) between two points located in the center of both habitat areas (shown in magenta in the figure), resulting in 137.1 and 57.5 Ohms, respectively, for a four- and eight-neighbors case and (2) between two points located in the habitat area edges (border of one habitat area closest to the other habitat area, shown in blue in the figure), resulting in 162.3 and 69.84 Ohms, respectively, for a four- and eight-neighbors case.