Contributed Paper

Effects of Weighting Schemes on the Identification of Wildlife Corridors Generated with Least-Cost Methods

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Abstract: *The importance of movement corridors for maintaining connectivity within metapopulations of wild animals is a cornerstone of conservation. One common approach for determining corridor locations is least-cost corridor (LCC) modeling, which uses algorithms within a geographic information system to search for routes with the lowest cumulative resistance between target locations on a landscape. However, the presentation of multiple LCCs that connect multiple locations generally assumes all corridors contribute equally to connectivity, regardless of the likelihood that animals will use them. Thus, LCCs may overemphasize seldom-used longer routes and underemphasize more frequently used shorter routes. We hypothesize that, depending on conservation objectives and available biological information, weighting individual corridors on the basis of species-specific movement, dispersal, or gene flow data may better identify effective corridors. We tested whether locations of key connectivity areas, defined as the highest 75th and 90th percentile cumulative weighted value of approximately 155,000 corridors, shift under different weighting scenarios. In addition, we quantified the amount and location of private land that intersect key connectivity areas under each weighting scheme. Some areas that appeared well connected when analyzed with unweighted corridors exhibited much less connectivity compared with weighting schemes that discount corridors with large effective distances. Furthermore, the amount and location of key connectivity areas that intersected private land varied among weighting schemes. We believe biological assumptions and conservation objectives should be explicitly incorporated to weight corridors when assessing landscape connectivity. These results are highly relevant to conservation planning because on the basis of recent interest by government agencies and nongovernmental organizations in maintaining and enhancing wildlife corridors, connectivity will likely be an important criterion for prioritization of land purchases and swaps.*

Keywords: connectivity, *gulo gulo*, landscape genetics, least-cost corridor, least-cost path, source-destination models, wolverine

Efectos de los Esquemas de Ponderación sobre la Identificación de Corredores para Vida Silvestre Generados con Métodos Menos Costosos

Resumen: *La importancia de los corredores para el mantenimiento de la conectividad de metapoblaciones de animales silvestres es una piedra angular de la conservación. Un método común para la determinación de localidades para corredores es el modelado de corredores de menor costo (CMC), que utiliza algoritmos en un sistema de información geográfica para buscar rutas con la menor resistencia acumulativa entre localidades en un paisaje. Sin embargo, la presentación de múltiples CMC que conectan múltiples localidades generalmente*

asume que todos los corredores contribuyen equitativamente a la conectividad, independientemente de la probabilidad de que sean utilizados por animales. Por lo tanto, los CMC pueden sobrestimar rutas largas poco utilizadas y subestimar rutas cortas utilizadas más frecuentemente. Planteamos la hipótesis de que, dependiendo de los objetivos de conservación y la información biológica disponible, la ponderación de corredores con base en el movimiento de especies, la dispersión o datos de flujo génico puede identificar corredores efectivos. Probamos si las localidades de las áreas de conectividad clave, definida como el 75° y 95° valor percentil acumulativo ponderado más alto de aproximadamente 155,000 corredores, cambia bajos diferentes escenarios de ponderación. Adicionalmente, cuantificamos la cantidad y localización de terrenos privados que intersectan áreas de conectividad clave en cada esquema de ponderación. Algunas áreas que aparentemente estaban bien conectadas, presentaron mucho menos conectividad cuando fueron analizadas con corredores no ponderados que cuando se usaron esquemas de ponderación que consideran los corredores con distancias efectivas largas. Más aun, la cantidad y localización de áreas de conectividad clave que intersectaron terrenos privados fue variable en los esquemas de ponderación. Consideramos que las suposiciones biológicas y los objetivos de conservación deben ser incorporados explícitamente para ponderar corredores cuando se evalúa la conectividad del paisaje. Estos resultados son relevantes para la planificación de la conservación porque, con base en el reciente interés de agencias gubernamentales y de organizaciones no gubernamentales por mantener e incrementar corredores para vida silvestre, la conectividad será un criterio importante para la priorización de compras e intercambios de tierras.

Palabras Clave: Conectividad, corredor de menor costo, genética de paisaje, glotón, *Gulo gulo*, modelos origen-destino, vía de menor costo

Introduction

Connectivity is critical for population and species persistence (Levins 1969; Hanski & Gilpin 1991; Corlatti et al. 2009). To this end, connectivity across extensive areas has become an important component of many political and agency conservation agendas (Tidwell 2010). For example, in the United States, the Western Governors' Association created a council to "identify key wildlife corridors and crucial wildlife habitats in the West, and preserve these lands" (WGA 2008). Furthermore, many western states, for example, Washington, have collaborated with multiple partners to identify wildlife habitat and migration corridors empirically (WWHCWG 2010). Once these essential locations are identified, land purchases, land swaps, and altered management practices may occur at unprecedented extents. Thus, it is paramount that the methods used to evaluate connectivity be unbiased, biologically relevant, and scientifically defensible.

There are several approaches for identifying corridors, including least-cost path (LCP; Larkin et al. 2004), least-cost corridor (LCC; Singleton et al. 2002), circuit theory (McRae & Beier 2007), graph theory (Pinto & Keitt 2009), and models of network flow (Phillips et al. 2008). LCP and LCC models evaluate a resistance surface and determine the lowest cumulative resistance between source and destination locations (Beier et al. 2009; Cushman et al. 2009). The lowest cumulative resistance, oftentimes termed the least cost, represents the lowest ecological cost for an organism to travel from point A to point B in a landscape. This approach acknowledges that organisms rarely travel in a straight line between locations because some landscape features have higher travel resistance (or cost) than others. Both LCP and LCC approaches identify

a route between source and destination and an associated cost; hereafter, we refer to this cost as the effective distance (cf. Adriaensen et al. 2003) (i.e., total accumulated cost between source and destination). A route identified with the LCP approach is by definition one pixel wide, whereas a route identified with the LCC approach (hereafter corridor) may be one pixel wide but can potentially be several pixels wide because there may be multiple paths from source to destination with the same effective distance corresponding to the least accumulated cost.

Least-cost resistance surfaces have been generated with a number of methods, including expert opinion (Larue & Nielsen 2008), maps of habitat quality maps (Beazley et al. 2005), step selection functions (Richard & Armstrong 2010; Squires et al. in press), or resource-selection functions (Chetkiewicz & Boyce 2009). The validity of these resistance surfaces can be tested with a variety of empirical data sources, including satellite telemetry paths or molecular genetic data. Parameterizing and validating the resistance surfaces with genetic data, which is one of the more common approaches, involves comparing a matrix of genetic distance among all individuals to a matrix of effective distance among all individuals (Coulon et al. 2004; Cushman et al. 2006; Wang et al. 2009). This comparison is generally conducted for a number of resistance surfaces, each of which is considered a hypothesis of how the organism responds to the landscape (Zielinski et al. in press). Ultimately, the effective-distance matrix with the highest correlation with the genetic-distance matrix is considered the most strongly supported by the data and, subsequently, the routes generated with that resistance surface are considered the most defensible. Furthermore, because genetic data do not always encompass the geographic range of the organism of interest, the

best supported resistance surface can be used to identify routes among a large number of source and destination locations for which genetic data are unavailable and thus provides more complete information on connectivity throughout a species' range (e.g., Schwartz et al. 2009).

There are generally 2 ways to portray routes generated with least-cost modeling. The first and most common is to display all routes between source and destination locations (Kautz et al. 2006; Larue & Nielsen 2008; Hagerty et al. 2011). The second sums the number of routes that overlap each pixel (Braunisch et al. 2010; Li et al. 2010) or with a moving window kernel (Cushman et al. 2009; Schwartz et al. 2009); this approach assumes all routes have equal weight and that pixels containing multiple routes are more important than those containing fewer routes. Neither of these methods explicitly account for the probability that an organism traveling a particular route likely decreases as the effective distance of that route increases. At the extreme, if the effective distance between source and destination exceeds an individual's dispersal capability, some of the displayed routes may not be used. Furthermore, when drawn on a map, long routes (which generally have higher effective distances) are more visible than short routes. Therefore, the visual representation of multiple routes between several locations is strongly biased toward long routes that potentially have a very low probability of being used. Although it is recognized that the probability of connectivity decreases as a function of increasing distance (e.g., Urban & Keitt 2001), we found only one study (Epps et al. 2007) that explicitly addresses, when identifying and mapping corridors, that there is a gradient of high connectivity at short distances to very little connectivity at longer distances. Epps et al. (2007) found that gene flow among populations of bighorn sheep (*Ovis canadensis*) in southern California (U.S.A.) approached zero as the effective distance increased and incorporated that information into their final corridor map.

This artifact of least-cost modeling, when used to identify and map corridors, is potentially problematic. First, there is good evidence that short-range dispersal and subsequent reproduction is, for many and perhaps most species, more common than long-range dispersal (Vekemans & Hardy 2004). Second, the fundamental assumption of least-cost modeling is that organisms are more likely to travel successfully along routes with low ecological costs. Therefore, one may incorrectly identify biologically relevant corridors because routes with large effective distances, which may be rarely or never used, are given weights equal to routes with short effective distances, which are more frequently used. However, it is argued that long routes are used for occasional long-distance dispersal events and therefore contribute to metapopulation gene flow and genetic rescue (Baguette 2003; Vila et al. 2003; Popp et al. 2011). Therefore,

when identifying corridors with least-cost approaches, one should clearly state the purpose for which corridors are being identified (e.g., corridors for long-distance dispersal events) and corridor identification should reflect biological and conservation objectives rather than an unintended mapping artifact.

Our objective was to improve understanding of the effects of the implicit assumption that all routes have equal weight in least-cost modeling. We, therefore, explored the sensitivity of connectivity maps to different weighting schemes that are based on differing dispersal assumptions or conservation objectives for wolverines (*Gulo gulo*) in the U.S. northern Rocky Mountains. We asked whether the locations of key connectivity areas substantially changed on the basis of corridor weighting. We tested 5 weighting schemes that we based on different dispersal hypotheses or conservation objectives: equally weighted, exponential decay, threshold (or step), normal, and logistic. The latter 4 schemes weight corridors on the basis of their effective distance. We then assessed changes in the locations of key connectivity areas under different weighting schemes and quantified the major land ownership types associated with these key connectivity areas. Although we examined wolverine connectivity identified with LCC modeling, these methods are applicable to many other organisms and connectivity metrics.

Methods

We used LCC methods to generate corridors for each pairwise combination of 558 locations in Wolverine habitat in the northern Rocky Mountains. We evaluated 5 schemes of weighting individual corridors and generated a connectivity map for each weighting scheme by spatially summing all weighted corridors. The value of each 5 × 5 km pixel in these connectivity maps equaled the additive value of all weighted corridors intersecting that pixel. We then identified discrepancies between the key connectivity areas of each connectivity map for each weighting scheme.

Least-Cost Modeling and Weighting

To evaluate the potential effects of climate change on connectivity of habitat for wolverine, McKelvey et al. (2011) generated connectivity maps on the basis of LCP methods and the equal-weighting approach for recent and future climate conditions. We used the inputs from McKelvey et al. (2011) to generate corridors with LCC methods. Virtually all wolverine dens occur in areas classified as snow covered through the end of the wolverine's reproductive denning period (May 15) (Aubry et al. 2007). Therefore, McKelvey et al. (2011) matched historical spring snow depth (average conditions from
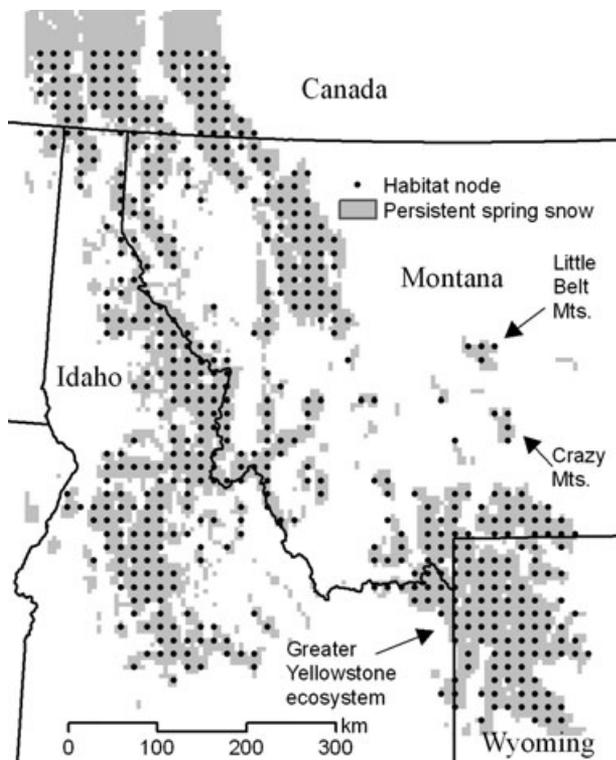
Figure 1. Areas of spring snow cover and the 558 wolverine habitat nodes for which we generated corridors between all pairwise combinations (n = 155,403 corridors).

1917 to 2006) with snow-cover maps generated by Copeland et al. (2010). McKelvey et al. (2011) then distributed 558 habitat nodes at 15-km intervals across areas identified as snow covered (Fig. 1).

We generated corridors ($n = 155,403$) by identifying and selecting those pixels with the least accumulated cost between each pairwise habitat node. Although other researchers have used larger cutoff values to identify corridors (e.g., Huber et al. [2010] identified as corridors all pixels within 2% of the least accumulated cost), we included only the absolute lowest accumulated cost to avoid arbitrary decisions on the cutoff value. A larger cutoff value would likely result in wider corridors, particularly in areas of low resistance. We used the binary habitat surface representing the presence or absence of snow to generate corridors. On the basis of genetic modeling in Schwartz et al. (2009), we considered the resistance value (i.e., the cost) for pixels with no snow to be 20 times (resistance = 0.02) that of pixels with snow present (resistance = 0.001). Therefore, a corridor traversing 20 km of snow-covered pixels had an effective distance of 20 km, whereas a corridor covering 20 km of pixels with no snow had an effective distance of 400 km. The individual corridors were created in ArcGIS 9.3 (ESRI 2008) with the cost-distance and corridor functions. Further details on the methods and rationale used to create

these corridors are in Schwartz et al. (2009), Copeland et al. (2010), and McKelvey et al. (2011).

We used 5 different schemes to weight each corridor. All weightings represented different hypotheses about species movement, dispersal, and gene flow. The equal-weighting scheme was our null model to which we compared the other weighting schemes (e.g., Li et al. 2010; McKelvey et al. 2011). In the equal-weighting scheme, the connectivity maps represented the number of corridors overlapping each pixel. The exponential-decay and threshold weighting schemes represented isolation by distance (Murphy & Noon 1992; Slatkin 1993; Cameron et al. 2011). The normal weighting scheme recognized that some species disperse intermediate distances (Soons et al. 2004; Bossuyt & Honnay 2006; Sinervo et al. 2006). The logistic weighting scheme recognized that although long-distance dispersal may be rare, it is ecologically important for metapopulation processes (Nathan 2006). We scaled the effective distances of all weighting schemes such that $0 < W \leq 1$, where W is the weight associated with the corridor. All weighting was conducted with the raster package (Hijmans & van Etten 2011) in the R statistical program (R Development Core Team 2007). We generated a connectivity map for each weighting scheme by spatially summing all weighted corridors.

Because it is likely that conservation would focus on those areas perceived to be most important (i.e., connectivity areas with the highest additive weighted values), we determined the degree to which these areas changed on the basis of different weighting schemes. Therefore, we identified key connectivity areas in each connectivity map by selecting only those pixels in the 75th and 90th percentile of the additive weighted values. For example, there were 4860 pixels in each connectivity map, so we ordered the pixels in the connectivity map by additive weighted value and selected the 1215 (75th percentile) and 486 pixels (90th percentile) with the highest values. This approach identified spatial discrepancies in the locations of key connectivity areas that may have varied as a function of weighting scheme. We identified the main land-ownership classes (Wyoming Water Resources Center 1996; BLM 2010; MTNHP 2011) of the key connectivity areas to determine the practical implications of choosing one weighting scheme over another when allocating resources toward maintaining connectivity.

Choosing a Threshold for Weighting

Schwartz et al. (2009) identified positive spatial autocorrelation (with Euclidean distance) between samples in the microsatellite DNA genotypes of wolverines. We used effective rather than Euclidean distances. Thus, we used these same nuclear genetic data presented in Schwartz et al. (2009) and evaluated autocorrelation with effective distance between samples with GENALEX (Peakall & Smouse 2006). We based variance estimates for
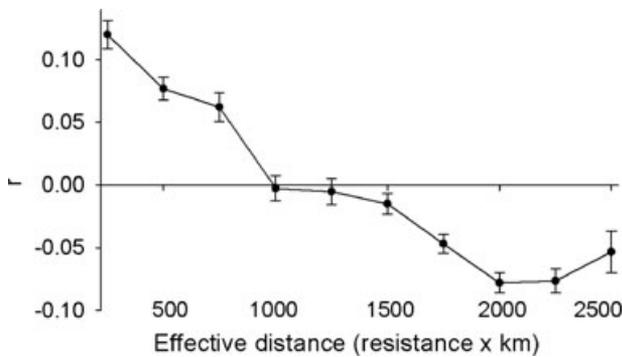
Figure 2. Correlation (r) between genetic relatedness and effective distance (i.e., lowest cumulative resistance between target locations on a landscape) generated with least-cost methods, for wolverines in the northern Rocky Mountains.

autocorrelation on 9999 permutations and 999 bootstraps. On the basis of these results, we imposed a threshold that defined the effective distance at which wolverines ceased to be genetically autocorrelated.

Results

The correlation between effective and genetic distance at distances ≤1000 effective km was positive (Fig. 2); that is, the genetic relatedness among pairs of wolverines approached zero as the effective distance approached 1000. We, therefore, used an effective distance of 1000 as a threshold for the weighting schemes. For the weighting schemes that discounted corridors with large effective distances (exponential decay, threshold, and normal), corridors with effective distances >1000 were considered to have negligible influence on connectivity (Fig. 3). For the logistic weighting scheme, corridors with effective distances >1000 contributed the most to connectivity.

The connectivity values varied markedly across weighting schemes (Fig. 3), as did the spatial locations of the key connectivity areas. The connectivity map produced with equal weighting of corridors implied there was moderate to high wolverine connectivity throughout the northern U.S. Rockies. Connectivity maps of some weighting schemes, however, indicated that some areas were not well connected. In particular, individuals in the southeastern portion of our study area (i.e., the Greater Yellowstone Ecosystem) showed limited connectivity to the rest of the wolverine population, particularly when the threshold and normal weighting schemes were used.

The proportion of pixels identified as key connectivity areas (i.e., 75th and 90th percentile) in each ownership class also varied by weighting scheme (Table 1). For both the 75th and 90th percentile pixels, the proportion of

private land was highest in the connectivity maps produced with the equal and logistic weighting schemes. In the connectivity maps for the 3 weighting schemes that discounted corridors with large effective distances, the amount of private land composed of 75th-percentile pixels was half of that associated with the equal weighting approach or less. There were also spatial discrepancies in the locations of these pixels under different weighting schemes (Fig. 4). For example, the majority of the 75th-percentile pixels overlapping private land were located in southwestern Montana in the connectivity maps produced with the equal and logistic weighting scheme, whereas such pixels were more dispersed in the corridor maps produced with the other 3 weighting schemes.

Discussion

The designation of corridors has become an important conservation tool for maintaining or increasing connectivity among populations (Haddad et al. 2003; Damschen et al. 2006; Dixon et al. 2006). However, incorporating biological information to weight individual corridors may increase the likelihood that hypothesized corridors are used by an organism of interest and make more effective use of conservation funds. In addition, weighting corridors may help alleviate concerns about corridor design and effectiveness (Hobbs 1992; Simberloff et al. 1992).

That organisms are less likely to travel long distances than short distances is a fundamental biological concept (e.g., isolation by distance). Although this relation is recognized in the connectivity literature (e.g., Urban & Keitt 2001), some researchers do not consider it when generating corridors (Hagerty et al. 2011; McKelvey et al. 2011). Others, however, recognize that some modeled corridors are too costly for an organism and set a cutoff at which corridors are not valid and exclude corridors that exceed the cutoff value (Fall et al. 2007; Richard & Armstrong 2010). This binary approach assumes all corridors are of equal value up to a particular threshold distance, at which point a corridor has no value and does not exist. For those identifying and mapping corridors, we are aware of no studies (except for this study and Epps et al. 2007) that incorporate the idea that a corridor's probability of use likely occurs on a gradient that depends on the dispersal capabilities of a species.

On the basis of different weighting assumptions, the locations of key connectivity areas for wolverine showed distinct differences in connectivity in the northern Rocky Mountains. For example, weighting schemes that discounted high-cost corridors indicated greater isolation in areas such as the Greater Yellowstone Ecosystem, which is consistent with mitochondrial DNA patterns (Schwartz et al. 2007; Schwartz et al. 2009). Thus, if the purpose of
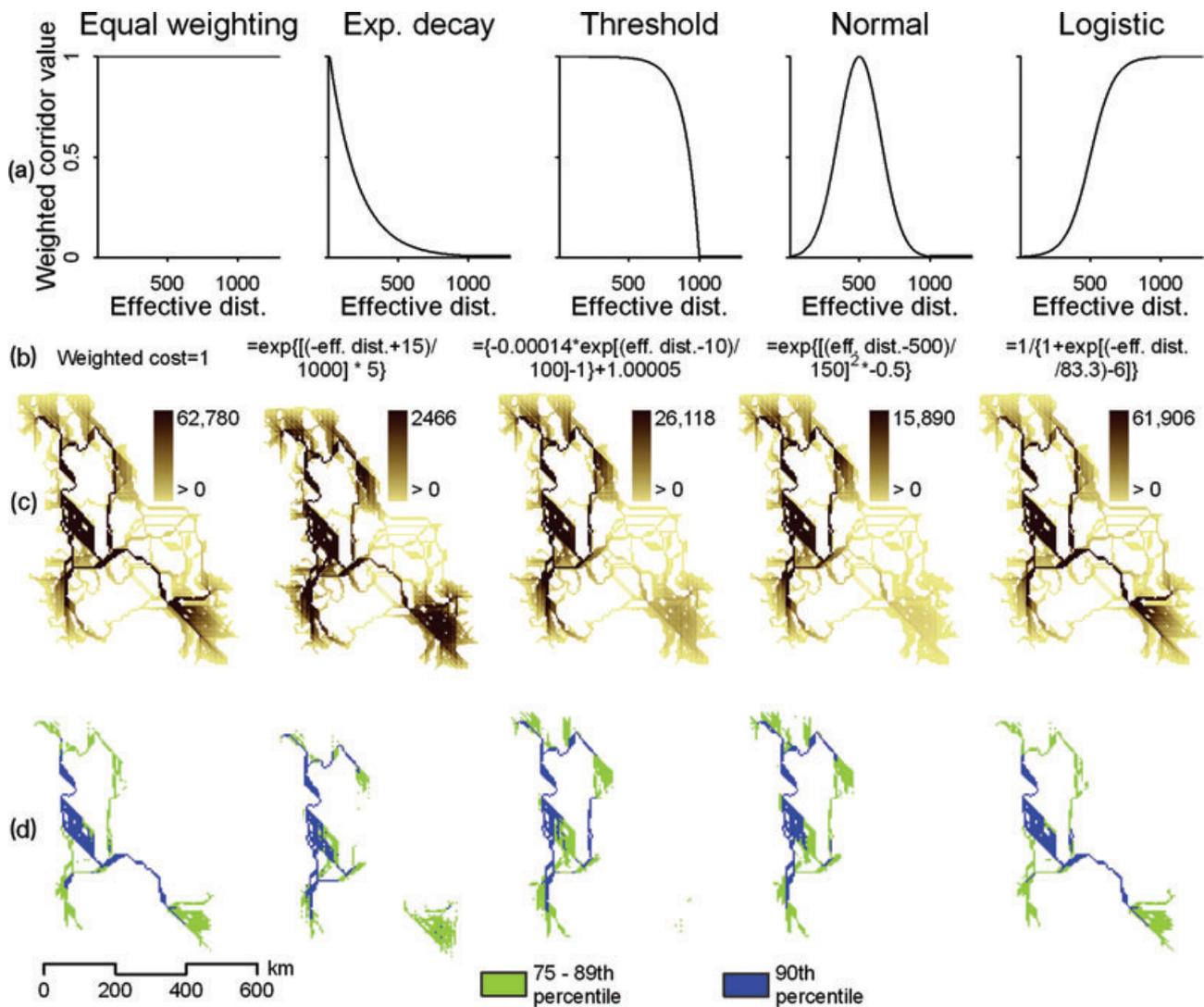
Figure 3. (a) Relation between the weighted cost and the effective distance (eff. dist.) (defined in legend of Fig. 2) of each wolverine corridor for each weighting scheme (equal weighting, exponential decay, threshold, normal, and logistic), (b) equations used to calculate each weighted corridor, (c) connectivity maps representing the 155,403 corridors for each weighting scheme from which the key connectivity areas are generated (map values represent the additive weighted values of the 155,403 corridors), and (d) key connectivity areas for each weighting scheme (i.e., the largest 75th and 90th percentiles of values in [c]) of each connectivity map.

Table 1. Percentage of key connectivity areas, defined as the 75th and 90th percentile connectivity values for each weighting scheme, for wolverine within the conterminous United States in major land ownership classes.

	75th percentile				90th percentile			
Weighting	NPS	USFS	other	private	NPS	USFS	other	private
Equal	18.3	78.7	1.2	1.8	0.4	96.5	1.4	1.6
Exponential decay	20.9	78.0	0.2	0.9	5.3	93.8	0.0	0.8
Threshold	4.0	94.9	0.6	0.6	3.7	94.0	1.1	1.3
Normal	3.6	95.2	0.6	0.7	5.0	93.7	0.2	1.1
Logistic	18.2	78.9	1.1	1.8	0.6	96.3	1.4	1.6

Abbreviations: NPS, National Park Service; USFS, U.S. Forest Service; other, other government lands (e.g., Fish and Wildlife Service and Bureau of Land Management), tribal lands, and privately owned conservation lands (e.g., The Nature Conservancy); private, privately owned, nonconservation lands.
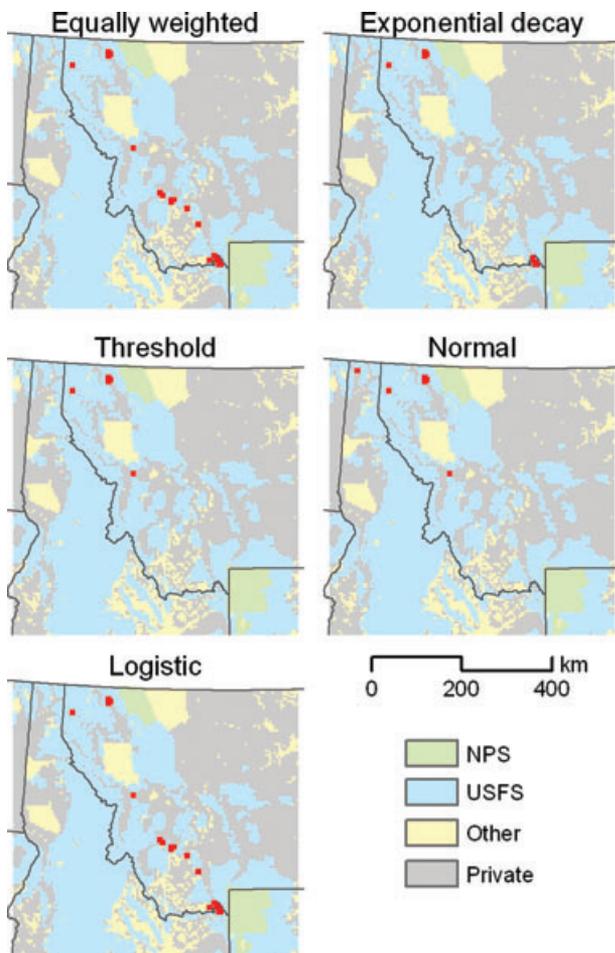
Figure 4. Locations (red) of the 75th percentile key connectivity areas (defined in legend of Fig. 3) that overlap private land for each connectivity map under each weighting scheme (graphically depicted in Fig. 3a) (red pixels enlarged for visualization purposes) (NPS, National Park Service; USFS, U.S. Forest Service; other, other government lands [e.g., Fish and Wildlife Service and Bureau of Land Management], tribal lands, and privately owned conservation lands [e.g., The Nature Conservancy lands]; private, privately owned, nonconservation lands).

the corridor analyses is to determine those areas through which there is the greatest level of gene flow, connectivity calculated on the basis of exponential decay or threshold weighting schemes is likely more biologically accurate.

The amount and location of private land that intersects key connectivity areas varied depending on the weighting scheme. For the equal and logistic weighting schemes, key connectivity areas (75th percentile) contained ≥2 times as much private land compared with schemes that discounted corridors with large effective distances. This is likely because those corridors with large effective dis-

tances, which were not discounted in the equal and logistic weighting schemes, are more likely to intersect private land. Similarly, differences in connectivity between the Greater Yellowstone Ecosystem and the remainder of the study area occurred because the majority of connecting corridors were long (judged either by effective or Euclidean distance), crossed areas of low elevation (i.e., pixels without snow), and frequently crossed private lands.

We conducted this study on wolverine because of our familiarity with this particular organism and access to existing data from previous studies (Schwartz et al. 2009; McKelvey et al. 2011). However, because wolverines can cover large distances compared with many other organisms, our results probably underemphasize the importance of weighting routes generated with least-cost models. For example, had we analyzed American pika (*Ochotona princeps*), which has a much shorter dispersal capability and more specific resource requirements than the wolverine, the effective distance threshold (Fig. 2) would have been much smaller and the subsequent connectivity maps more divergent across weighting schemes. If we had been interested in pollen or seed dispersal, we could have used weighting functions with different shapes that corresponded to our understanding of how wind carries pollen or gravity transports seeds. Generally speaking, the methods and concepts presented here are relevant to virtually all organisms providing the target landscape is large enough to encompass substantial genetic variability among organisms or populations.

Because the locations of key connectivity areas change with different weighting schemes, it is necessary to match the weighting to the intended purpose of the corridors. If the purpose is to connect populations demographically (e.g., Lada et al. 2008), then only the most highly used corridors will be valuable. For example, wolverine populations in the northern Rockies are generally small: there were an estimated 13 wolverines in the Anaconda Pintler, Flint, and Pioneer mountain ranges in southwest Montana (Squires et al. 2007). Maintaining these populations requires nearly constant demographic rescue (Lowe & Allendorf 2010), which suggests a weighting scheme that discounts long corridors is most appropriate. In contrast, there have been recent long-range dispersals of wolverines from Idaho to the Sierra Nevada (McKelvey et al. 2008; Moriarty et al. 2009) and from the Greater Yellowstone Ecosystem to Colorado (Inman et al. 2010), both areas where wolverines were extirpated in the early 20th century (Aubry et al. 2007). These movements have extremely high ecological cost for the individuals (see Schwartz et al. 2009 for cost data associated with the Yellowstone to Colorado movement) and are likely infrequent (these are the first verified wolverines in California and Colorado since 1924 and 1919, respectively [Aubry et al. 2007]). Because wolverines were extirpated from
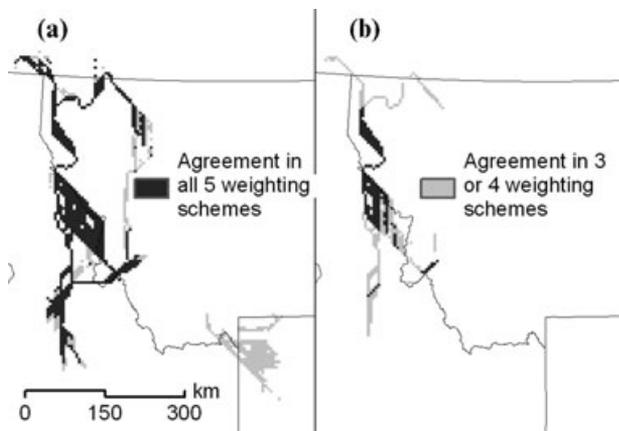
Figure 5. Overlap of locations of the (a) 75th and (b) 90th percentile key connectivity areas (defined in legend of Fig. 3) for wolverine among the 5 corridor-weighting schemes (equal weighting, exponential decay, threshold, normal, and logistic).

California and Colorado, the conservation objective is recolonization rather than demographic or genetic rescue, and meeting that objective may require maintenance or enhancement of corridors to facilitate rare, long-distance dispersal events (Baguette 2003; Popp et al. 2011). If this is the case, the equal or logistic weighting schemes may be most appropriate.

Our weighting schemes (in particular, the equal weighting scheme) are somewhat similar in concept to betweenness centrality indices in that all least-cost routes between all pairwise combinations of habitat nodes are generated (Estrada & Bodin 2008; Bodin & Saura 2010; Eros et al. 2011). We suggest that incorporating weighting schemes into betweenness centrality analyses could improve understanding of the importance of individual habitat patches in contributing to ecological flow. Other connectivity methods could also apply our weighting methods. For example, in studies involving graph theory (Minor & Urban 2007), the edges connecting habitat nodes could be weighted. Integrating the weighting concepts presented in this study with other connectivity metrics would expand knowledge in these areas.

Least-cost modeling has been criticized, primarily because the routes generated are sensitive to resistance values (Beier et al. 2009; Rayfield et al. 2011) and because corridor locations vary depending on resistance values that are often qualitatively generated (i.e., with expert opinion) (Sawyer et al. 2011). However, we believe routes generated with least-cost models are fairly robust and biologically relevant when genetic or other empirical data are used to parameterize and validate the resistance surface (e.g., Epps et al. 2007; Wang et al. 2009).

In practice, determining an appropriate weighting scheme may be difficult if relevant biological data do not exist. For wolverines in the northern Rockies, the

exponential decay weighting scheme may be most appropriate if the conservation objective involves connecting populations demographically; this scheme was also used by Epps et al. (2007) in their study of bighorn sheep in southern California. If the conservation objectives are complex, not clearly stated, or the weighting functions cannot be parameterized empirically, we suggest the use of multiple weighting schemes to test the robustness of individual corridors. Those areas that are identified under all or most weighing schemes clearly should be targeted for conservation (Fig. 5). Corridors that shift with weighting schemes should be evaluated on the basis of which weighting scheme best describes the biological rationale or conservation objective for corridor construction.

Acknowledgments

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