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Contributed Paper

Use of Empirically Derived Source-Destination Models to Map Regional Conservation Corridors

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Abstract: *The ability of populations to be connected across large landscapes via dispersal is critical to long-term viability for many species. One means to mitigate population isolation is the protection of movement corridors among habitat patches. Nevertheless, the utility of small, narrow, linear features as habitat corridors has been hotly debated. Here, we argue that analysis of movement across continuously resistant landscapes allows a shift to a broader consideration of how landscape patterns influence connectivity at scales relevant to conservation. We further argue that this change in scale and definition of the connectivity problem improves one's ability to find solutions and may help resolve long-standing disputes regarding scale and definition of movement corridors and their importance to population connectivity. We used a new method that combines empirically derived landscape-resistance maps and least-cost path analysis between multiple source and destination locations to assess habitat isolation and identify corridors and barriers to organism movement. Specifically, we used a genetically based landscape resistance model for American black bears (*Ursus americanus*) to identify major movement corridors and barriers to population connectivity between Yellowstone National Park and the Canadian border. Even though western Montana and northern Idaho contain abundant public lands and the largest wilderness areas in the contiguous United States, moving from the Canadian border to Yellowstone Park along those paths indicated by modeled gene flow required bears to cross at least 6 potential barriers. Our methods are generic and can be applied to virtually any species for which reliable maps of landscape resistance can be developed.*

Keywords: animal movement, black bear, connectivity, corridor, least-cost path, *Ursus americanus*, Yellowstone to Yukon

Utilización de Modelos Fuente-Destino Empíricamente Derivados para Cartografiar Corredores de Conservación Regionales

Resumen: *La habilidad de las poblaciones para estar conectadas en paisajes extensos por medio de la dispersión es crítica para la viabilidad de muchas especies a largo plazo. La protección de los corredores de movimiento entre fragmentos de hábitat es una forma de mitigar el aislamiento de una población. Sin embargo, la utilidad de elementos lineales, angostos y pequeños como corredores de hábitat se ha debatido acaloradamente. Aquí, argumentamos que el análisis del movimiento a través de paisajes resistentes permite un cambio hacia una mayor consideración de cómo influyen los patrones del paisaje sobre la conectividad a escalas más relevantes para la conservación. También argumentamos que este cambio en escala y definición del problema de la conectividad mejora nuestra habilidad para encontrar soluciones y puede ayudar a resolver disputas relacionadas con la escala y definición de los corredores de movimiento y su importancia para la conectividad de la población. Utilizamos un nuevo método que combina mapas de resistencia del paisaje derivados empíricamente con análisis de ruta de costo mínimo entre múltiples localidades fuente y destino para evaluar el aislamiento de hábitat e identificar corredores y barreras para el movimiento de organismos. Específicamente utilizamos un modelo de resistencia de paisaje basado genéticamente para osos negros americanos (*Ursus americanus*) para identificar los principales corredores y barreras de movimiento para la conectividad de la población entre el Parque Nacional Yellowstone y la frontera canadiense. Aunque*

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el oeste de Montana y el norte de Idazo contienen abundantes tierras públicas y las áreas silvestres más extensas de los Estados Unidos, el movimiento desde la frontera canadiense hasta el Parque Yellowstone a lo largo de las rutas indicadas por el flujo génico modelado requería que los osos cruzaran por lo menos 6 barreras potenciales. Nuestros métodos son genéricos y pueden ser aplicados en prácticamente cualquier especie para la que se puedan desarrollar mapas de resistencia de paisaje confiables.

Palabras Clave: conectividad, corredor, movimiento de animales, oso negro, ruta de costo mínimo, *Ursus americanus*, Yellowstone a Yukon

Introduction

Population connectivity is centrally important to many ecological processes and conservation goals and may often be a key factor affecting regional viability of animal populations (Hanski 1998; Flather & Bevers 2002; Cushman 2006). Habitat fragmentation decreases dispersal (Gibbs 1998), increases mortality (Fahrig et al. 1995), and reduces genetic diversity (Reh & Seitz 1990; Wilson & Provan 2003; Keyghobadi et al. 2005). Populations may decline if immigration is prevented (Brown & Kodric-Brown 1977; Harrison 1991) and may not be recolonized following local extinction (Semlitsch & Bodie 1998). Thus, the ability of individual animals to move across complex landscapes is critical for maintaining regional populations (Fahrig 2003; Cushman 2006).

One means often proposed to mitigate population isolation is creation and protection of movement corridors among patchy populations (Haas 1995; Beier & Noss 1998; Harrison & Bruna 1999; Crooks & Sanjayan 2006). Most prior work considered movement corridors narrow strips of habitat that facilitate movement of organisms from one large habitat patch to another (Simberloff et al. 1992; Rosenberg et al. 1997). There has been much debate regarding the utility of these small, narrow, linear features as habitat corridors and their ability to provide population subsidization and recolonization among patches (Hobbs 1992; Simberloff et al. 1992; Rosenberg et al. 1997; Hudgens & Haddad 2003).

There are a number of potential limits to this narrow definition of movement corridors and major challenges to rigorously evaluating their utility. First, there is the issue of quality. Defining corridors as linear bridges between otherwise isolated habitat patches is an unnecessary limitation of a far more general concept. Taylor et al. (1993) define connectivity as the ability of organisms to move among habitat patches. This constraint is artificial and contributes to the unnecessary controversy regarding the existence and utility of movement corridors. Instead of experiencing landscapes as categorical mosaics, it is more likely that organisms experience their surroundings as gradients of differential quality in relation to ecological and life-history characteristics (McGarigal & Cushman 2005; Cushman 2006; Cushman et al. 2006). When connectivity is considered from this perspective, the narrow focus on movement among discrete habitat patches via narrow linear corridors is subsumed as a special minor case in a more general question regarding the ability of organisms to traverse resistant landscapes (Cushman et al. 2006).

The second issue is of scale. Focus on movement across continuously resistant landscapes also allows a shift in the scale of focus from linear corridors between patches, which are usually small relative to the vagility of the organism and the distribution of its population, to a broader-scale analysis of how landscape patterns of differential resistance to movement affect connectivity at scales relevant to the population-level processes that are central to effective conservation. This expansion of scale is essential because effective conservation requires a shift in focus from local, patch-level analyses to assessments of how multiple ecological factors interact across a range of spatial scales to influence the distribution and performance of populations across complex landscapes (Berger et al. 2006; Cushman 2006). Often a change in the scale and definition of a problem can dramatically alter one's ability to find solutions and sometimes resolves long-standing disputes. We believe a shift from a narrow definition of habitat connectivity and movement corridors on the basis of discrete habitat patches to a broader gradient perspective on landscape structure has the ability to resolve the debate surrounding the utility of habitat corridors and provide more useful and robust guidance for conservation planning.

The first step in this analytical approach is to define landscape resistance as a continuous function of one to several environmental variables, rather than as categories such as patch and matrix (Cushman et al. 2006). Rather than narrow strips of habitat between patches, corridors may more generally be conceived as routes of low cumulative resistance to movement among areas of high population density. This integrates knowledge of movement behavior, movement risk, and habitat suitability, enabling inferences at broader and more relevant scales, and avoids some pitfalls of unrealistic conceptualization of corridors as narrow, binary landscape features.

Most published studies in which landscape resistance maps were used relied on expert opinion to estimate resistance to movement due to landscape features given a lack of detailed information on animal movement or gene

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flow (e.g., Compton et al. 2007). This is not surprising because it is difficult to gather sufficient sample sizes of reliable data on relationships between animal movement and multiple landscape features at broad spatial scales (McGarigal & Cushman 2002; Cushman 2006). Basing analyses on unvalidated expert opinions is not desirable (Seoane et al. 2005), and this has been a major weakness of most past landscape-resistance modeling efforts.

Recently, several approaches have been shown to be effective in developing rigorous, species-specific landscape resistance maps. If detailed data on movement paths (e.g., Cushman et al. 2009) or gene flow (e.g., Spear et al. 2005; Cushman et al. 2006; Wang et al. 2007) are available for a species of interest, it is possible to develop rigorous empirical models of landscape resistance to movement. Such resistance maps provide a key foundation for a variety of landscape-connectivity analyses.

Although resistance models can provide the foundation for applied analyses of population connectivity, they do not, in themselves, provide sufficient information to evaluate the existence, strength, and location of barriers and corridors. Where resistance is point specific, connectivity is route specific. Connectivity must be evaluated with respect to these routes and the costs associated with moving across a landscape from a source to a destination. The resistance model is the foundation for these analyses, but it is explicit consideration of movement paths across the resistance surface that provides the key information for conservation and management. By adding "source-destination" least-cost path analysis to species-specific landscape resistance mapping, it is possible to comprehensively analyze the effects of landscape structure on animal movement such that the strength and location of movement corridors and barriers can be rigorously evaluated.

Long-term viability of many wildlife species in the Rocky Mountains is believed to strongly depend on regional connectivity of habitat due to the low densities, large home range size, vulnerability to human disturbance, and low fecundity of these species (Noss 1996; Weaver et al. 1996; Carroll et al. 2001). The importance of maintaining large blocks of protected core habitat within a connected network has inspired several regional-scale conservation initiatives (Gatewood 1999; Yellowstone to Yukon Conservation Initiative reviewed in Levenesque [2001] and Chester [2003]). Most recently, the Western Governors' Association passed a major policy resolution relating to the importance of protecting wildlife migration corridors and crucial wildlife habitat in the west (http://www.westgov.org/wga/policy/07/wildlife-corridors07-01.pdf). The resolution identifies protection of wildlife migration corridors as a top priority for regional conservation efforts, noting the juxtaposition of dispersed populations of large, rare, and mobile wildlife species with rapid land-use change and development across much of the West. Nevertheless, most past work on the issue of regional-scale population connectivity has been hampered by the lack of rigorous scientific data to support identification and prioritization of core areas and corridors for species of conservation concern.

Here we demonstrate the use of "source-destination" least-cost path analyses for identifying potentially important movement routes. Our analysis evaluates and maps potential movement corridors and barriers between northern Yellowstone National Park and the Canadian border on the basis of empirical data. We used an existing resistance map developed for black bears (*Ursus americanus*) in the study area (Cushman et al. 2006) and computed least-cost paths across this surface to identify putative movement corridors and barriers.

Methods

Study Area

The study area includes Montana and northern Idaho in the U.S. Rocky Mountains (Fig. 1). It contains large areas of federally managed forest land, including extensive areas designated as Wilderness and roadless areas. The study area also includes extensive private land, mainly in the large valleys between major mountain ranges. The human population in this area is rapidly growing (up to 44% increases in some counties; 2000 U.S. Census data), and this is causing extensive changes in land-use practices on the landscape, thus necessitating the evaluation of wildlife corridors. In addition, an extensive highway network exists within the study area, potentially impeding wildlife movement.

Resistance Map

On the basis of molecular genetics, Cushman et al. (2006) mapped resistance to black bear gene flow in a subregion of the study area in a multimodel least-cost path analysis (Fig. 1). Molecular genetic methods offer a powerful approach to quantify landscape connectivity and gene flow across heterogeneous landscapes. Producing multilocus genotypes of individuals sampled across landscapes provides information to identify population units, localize genetic discontinuities (barriers), and quantify the influence of landscape features on gene flow (Manel et al. 2003; Cushman et al. 2006). Importantly, our individual-based, cost-distance approach provides a consistent framework that allows for formal evaluation of alternative models of population structure, such as isolation by distance, isolation by geographic barriers, or isolation by landscape resistance. In addition, the approach provides a rigorous framework within which to evaluate the degree of support for alternative models of landscape resistance and thus to identify the environmental factors, their relative weight, and the operative spatial scales that are most highly related to genetic relatedness. We used an

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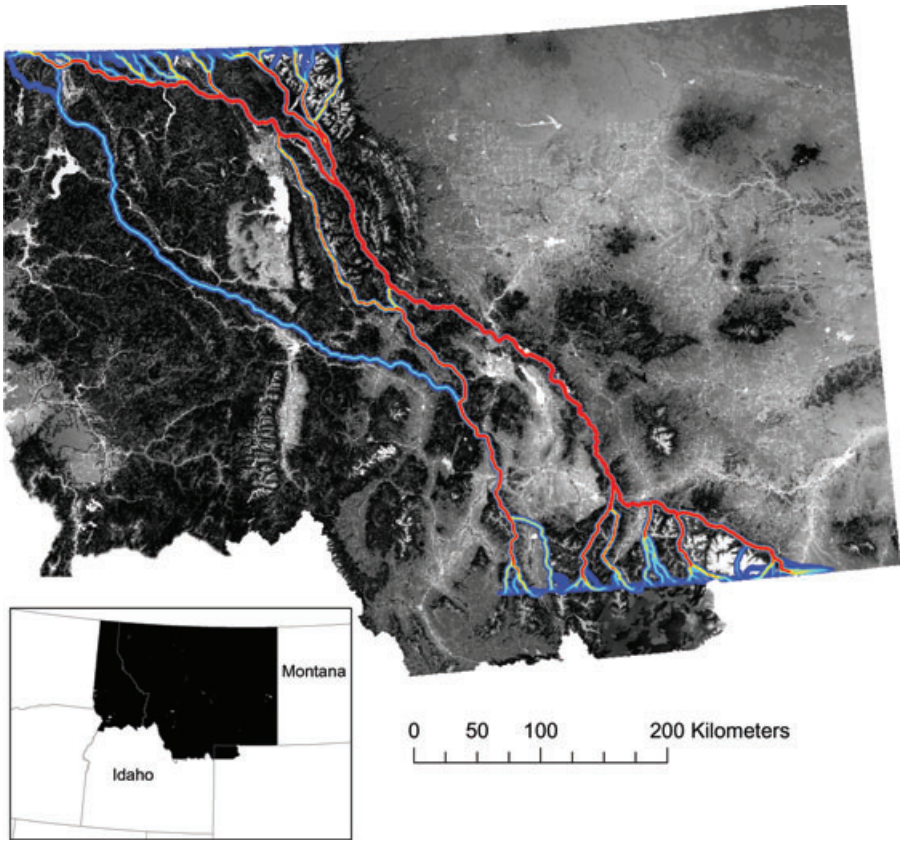

Figure 1. The movement-resistance map and source and source-destination paths for least-cost path analysis. Resistance to movement is a function of elevation, forest cover, and human developments (Cushman et al. 2006) and is scaled from black at minimum to white at maximum. The number of source-destination paths in each corridor is reflected by the color scheme, ranging from blue (few paths) to red (many paths). The extent of the analysis area is indicated in the inset orientation map and includes most of Montana and the panhandle region of Idaho.

individual-based approach for evaluating bear movement and substructure because such approaches generally are more appropriate than population approaches for organisms that are relatively continuously distributed across broad landscapes.

The main steps in the Cushman et al. (2006) landscape genetic analysis were (1) estimate genetic distance (or relatedness) between all pairs of individuals on the basis of multilocus genotypes (9-loci; 90 alleles), (2) calculate cost distance between all pairs of individuals for each of multiple hypotheses, including isolation by barriers, isolation by distance and isolation by multiple alternative models of landscape resistance, (3) use causal modeling with partial Mantel tests to reject the models that are not consistent with the observed pattern of genetic relatedness, and (4) rank the models that are supported by causal modeling to identify the landscape features, their weighting, and operative scales that most strongly predict spatial genetic structure.

In this way, Cushman et al. (2006) evaluated 110 alternative models of population substructure and identified the combination of resistance parameters that most highly influences gene flow. After removing the effects of Euclidian distance, 10 models remained significant. The significant models were all clustered in a small subregion of the 4-dimensional factorial space, with highest support for the models corresponding to strong relationships with forest cover and middle elevation, with equivocal support for the different levels of the roads factor and no relationship with slope (Fig. 5 in Cushman et al. 2006; Fig. 1). Although the degree to which roads impeded movement was equivocal, the study area had few large, busy roads and no interstate highways. The best-supported model, however, had high road resistance, and we used this model to generate corridors. The coverages used for model development extend across the entire study area and are detailed in Cushman et al. (2006).

Least-Cost Path Analysis

We modeled movement from source locations distributed at 2-km intervals along the forested portion of the Canadian border between the Idaho-Washington state border and the eastern edge of Glacier National Park (160 locations) to 160 destination locations along the northern boundary of Yellowstone National Park (Fig. 1). We then computed the least-cost paths across the best-supported resistance surface developed by Cushman et al. (2006) for all combinations of the 160 northern and 160 southern points (25,600 paths).

This was accomplished by first computing the cost distance from each source point in the north to all destination points in the south, using the "costdistance" function in ArcInfo Workstation (ESRI 2003). This function computes the cumulative cost of moving across the resistance surface from the single source point to all locations

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within the spatial extent of the resistance surface. Next, we computed least-cost paths between each of the source pixels and all destination pixels with the "costpath" function in ArcInfo Workstation (ESRI 2003). The least-cost path function maps the single path of least cumulative resistance from a specified source location to a single specified destination location. These least-cost paths are one pixel in width and record the route of a least-cost path from the source to the destination pixel. We smoothed these least-cost paths by applying a parabolic kernel with a 2500-m radius, on the assumptions that actual paths taken by bears will imperfectly follow least-cost routes due to stochastic behavioral choices of individual animals, there is a lack of perfect knowledge of the surrounding environment, and there are unmodeled fine-scale landscape attributes. This was accomplished by turning each least-cost path grid into a point file, with points spaced 90 m apart along the path and summing the cumulative kernel over all points. We summed the kernel-smoothed least-cost paths to produce density maps of least-cost routes from the Canadian border to Yellowstone National Park. Finally, we intersected these putative movement corridors with land-ownership and transportation-route maps to assess the degree to which these corridors are protected by wilderness, roadless, or federal ownership and to identify major gaps in protection and areas where the corridors intersect highways.

Results

The density of least-cost paths from the 160 source locations along the Canadian border to the northern edge of the Greater Yellowstone Area (GYA) was highly variable across the resistance map (Fig. 1). Despite the large number of combinations, all least-cost paths followed only 3 major routes. The most important route, in terms of the number of source-destination paths it contained, followed the eastern edge of the mountainous terrain along the Bridger and Belt mountains and crossed into the Bob Marshall Wilderness and then into Glacier National Park. The second major route proceeded north through the Gravelly and Tobacco Root ranges and then proceeded north roughly following the foothills along the east side of the Swan and North Fork Flathead rivers. The final route was much smaller, in terms of the number of source-destination paths it contained (Fig. 1), but was important for connectivity between the northwestern part of the study area and the GYA. This route followed the Clark Fork River and continued northward though the Cabinet and Selkirk mountains to Canada.

The majority of the length of the major paths fell within federal ownership (U.S. Forest Service [USFS] and National Park Service [NPS]). Nevertheless, only 24% of the major paths length fell within designated wilderness or national park, and less than half were in wilderness, park, or designated roadless areas (Fig. 2).

We identified 3 categories of potential barriers along the corridors: areas that are gaps in federal ownership and contain major highways (12 potential barriers of this kind); areas that are within federal land ownership where major highways cross the corridor (6 areas in this category); and areas where the major corridors parallel highways (3 areas in this category) (Fig. 2, Table 1). Gap areas usually corresponded to relatively large, privately owned breaks in forest cover. They typically had relatively high densities of human development and were most at risk of future development.

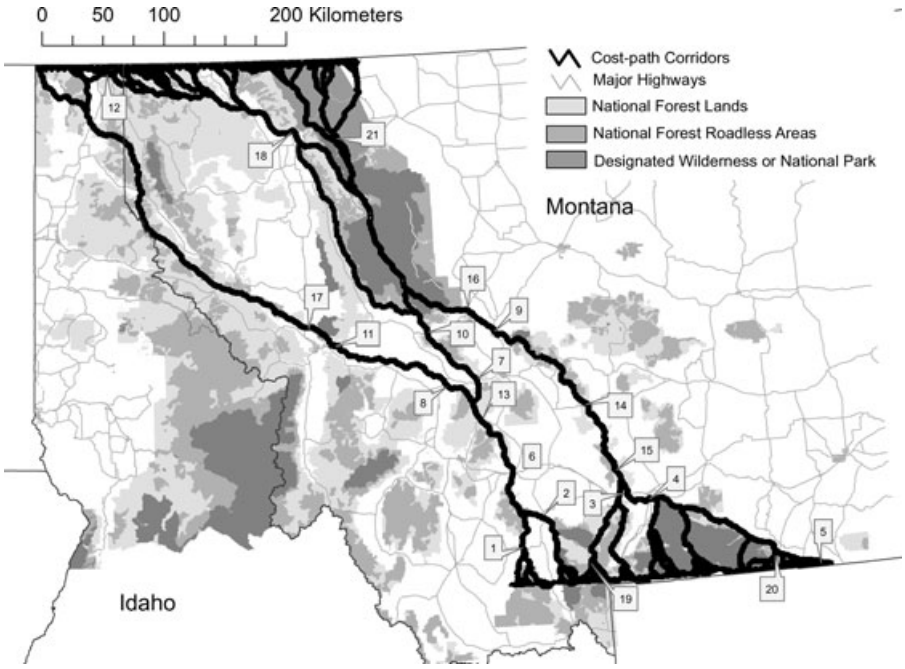

Figure 2. Intersection of least-cost path corridors for black bears with highways and nonfederal (unprotected) land ownership (bold black lines, predicted movement corridors [i.e., cost-path corridors]; light gray shading, U.S. Forest Service or National Park Service lands; numbered locations, areas that may act as barriers or be vulnerable to land-use changes that could impede movement).

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Table 1. Description of major potential barriers to animal movement along predicted wildlife corridors.*

Type	*Number*	*Description*
1	1	gap between Gravelly and Tobacco Root mountains; crossing Highway 287 just east of Virginia City
	2	gap between Madison and Tobacco Root mountains; crossing Highway 287 5 miles north of McAllister
	3	gap between Gallatin and Bridger mountains; double crossing Interstate 90, 2–3 miles west and 2–3 miles east of Bozeman Pass
	4	gap between Absaroka and Gallatin mountains; crossing Highway 89 and Yellowstone River 3 miles south of Livingston
	5	crossing Highway 72 at MT-WY border
	6	gap between Tobacco Root Mountains and Beaverhead-Deer Lodge National Forest; crossing Interstate 90 and Highway 69 8 miles east of Whitehall
	7	crossing Highway 12 just near MacDonald Pass
	8	gap between Tobacco Root Mountains and Beaverhead-Deer Lodge National Forest; crossing Highway 12 3–5 miles west of Avon
	9	gap between Big Belt Mountains and Helena National Forest; crossing Missouri River at south-westcorner of Gates of the Mountains Wilderness and Interstate 90 3–5 miles south of Wolf Creek
	10	crossing of Blackfoot River and Highway 200 4–6 miles west of Lincoln
	11	gap between Garnet and Rattlesnake mountains; crossing Interstate 90 just east of Bonner
	12	gap between Selkirk and Purcell mountains; crossing Kootenai River and Highway 95 near 12 miles north of Bonners Ferry
2	13	crossing Interstate 15 near Basin
	14	crossing Highway 12 7–9 miles east of Townsend
	15	crossing Highway 86 14–16 miles north of Bozeman
	16	crossing Highway 200 1–2 miles south of Rogers Pass
	17	crossing Highway 93 near Evaro
	18	crossing Highway 2 3–5 miles east of Columbia Falls
3	19	parallel Highway 191 for 15–20 miles, south of Big Sky
	20	parallel Highway 212 for 10–15 miles, south of Red Lodge
	21	parallel Highway 2 for 20–30 miles, West Glacier to 5 miles east of Essex

**Type refers to the type of potential barrier: 1, areas with large gaps in federal ownership and major highways; 2, areas in federal ownership but crossed by major highways; 3 areas where major highways parallel the corridor for extensive distances. Number refers to the sequential number of the potential barrier and is indicated on Fig. 2.*

Discussion

Rigorous connectivity models are critical in conservation planning for many species and ecological systems. In the U.S. Northern Rockies, long-term viability of many carnivore populations may depend on effectively maintaining connectivity among multiple, disjointed mountain ranges (Noss 1996; Carroll et al. 2001). Most past efforts to establish potential movement corridors or linkage zones have not been based on rigorous analysis of empirical data, but rather on unvalidated expert opinion. Such opinion-based models tend to perform poorly (e.g., Seoane et al. 2005). It is therefore critical that scientists provide rigorous, empirically based, spatially explicit predictions of potential corridors and barriers to movement of species of interest in this system.

Combining multimodel landscape genetics (Cushman et al. 2006) with source-destination least-cost path mapping provides a comprehensive approach to assess those factors controlling connectivity and the functional effects of landscape structure in creating movement corridors and barriers. For example, even though the study area contains extensive public lands, many wilderness areas and the largest wildernesses in the contiguous United States, our results indicate that the least-cost corridors for American black bears between the Canadian border and the GYA are few in number and concentrated along several north-south mountain ranges. Additionally, each major pathway contains multiple potential barriers. For example, to travel from Glacier National Park to the GYA following either of the 2 major least-cost path corridors requires crossing a minimum of 6 potential barriers (Fig. 2). All told, we identified 21 potential barriers along the least-cost path corridors. Twelve of these are potentially serious obstacles that combine large gaps in federally protected land, nonforested habitat, relatively high levels of human development, and major highways. Conservation efforts aimed at maintaining regional population connectivity for this species may best be served by focusing on protecting and mitigating habitat degradation and movement obstructions in these key locations.

Scope and Limitations

Our analysis was based on an inferred-landscape resistance surface (Cushman et al. 2006). The location and genetic data used in Cushman et al. (2006) were collected in the northwestern portion of the study area. Thus, the factors that drive population connectivity in the eastern

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or southern parts of the study area may differ from those identified by Cushman et al. (2006). Thus, although we believe, given the generality of the findings (forest cover, elevation, human development) and because the black bear is thought to be a forest-dependent species, it is likely our resistance model reflects landscape resistance for black bears across the full study area, these findings should be viewed as hypothetical. An important test of these hypotheses would repeat Cushman et al.'s (2006) analysis with genetic samples collected across the entire study area. Alternatively, studies with global positioning system (GPS) collars on bears (e.g., Waller and Servheen 2005) near the potential barriers and predicted corridors would help validate, refine, or refute the model. Ongoing work on this question suggests that the resistance model used in Cushman et al. (2006) is also highly supported on the basis of tests with GPS movement data instead of molecular genetic data, adding to our confidence in its reliability (S.A.C. et al., unpublished data).

Landscape resistance, movement corridors, and barriers will be experienced differently be each species due to differences in ecology, vagility, and behavior. Our results are specific to black bears and provide information about how this species' ecology may interact with landscape structure and human development to mediate population connectivity and to identify corridors and barriers to movement. Nevertheless, the analysis cannot be taken as a generalized connectivity map for the Northern Rockies. A similar analysis conducted for a species with different habitat preferences would likely produce different predictions. Thus, it is important to replicate this kind of connectivity analysis for multiple species of interest and assess the degree to which they are similar in the factors mediating connectivity and the location and strength of predicted corridors and barriers. Our methods, however, are easily generalizable and can be applied to any species for which a reliable landscape-resistance model can be developed. Given optimal path networks for multiple species, a generalized plan for multispecies connectivity could be derived empirically.

Black Bears as Surrogates for Grizzly Bears

Although no species can be used as an exact surrogate for another species, especially a common species for a rare one, it may be a worthwhile exercise to examine our results with black bears in light of grizzly bear (*Ursus arctos horribillis*) conservation. In 1975 when the grizzly bear was listed as threatened under the U.S. Endangered Species Act (Endangered Species Act 16 USC 1531–1544) its range was limited to 5 populations, 4 of which are in our study area: the GYA, the Northern Continental Divide Ecosystem, the Cabinet Yaak, and the Selkirks (USFWS 1993). In addition, a reintroduction effort had been proposed to reestablish the grizzly bear into the Bitterroot-Selway Ecosystem (USFWS 2000).

There have been several efforts to identify and evaluate grizzly bear "linkage zones," which are defined as areas between larger blocks of habitat, where animals can live, in multiple regions encompassed by our study. This has been accomplished by extrapolating understandings gained through VHF and GPS telemetry data in a Geographical Information System (GIS) framework (Mietz 1994; Sandstrom 1996; Servheen et al. 2001).

Mietz (1994) identified a linkage zone in the Evaro area of western Montana for grizzly bears with GIS modeling. We identified this area as important for connectivity between Yellowstone and Canada, although the precise location of our predicted corridor route is approximately 10 km southwest of Mietz's linkage zone (Table 1, number 17). Subsequently, Sandstrom (1996) evaluated linkage zones for grizzly bears in the Swan-Clearwater valley of western Montana and delineated 4 linkage zones across the valley, encompassing 42% of the valley. The high emphasis on the Swan-Clearwater valley by Sandstrom (1996) is supported by our resistance map for black bears, which suggests a continuous corridor could be used on the west side of the Swan-Clearwater valley (Fig. 2). Similarly, in northwestern Montana Waller and Servheen (2005) demonstrate that 52% of the monitored grizzly bears in their study crossed Highway 2 in locations we identified as important (Table 1, numbers 18 and 21).

Conclusion

Organisms may often experience their surroundings as gradients of differential quality in relation to ecological and life-history characteristics, rather than as binary mosaics of good and bad habitat. Considering connectivity from this perspective allows a shift from a narrow consideration of movement among discrete habitat patches via narrow linear corridors to a more generalized conception of the ability of organisms to traverse resistant landscapes. Analysis of movement across continuously resistant landscapes also allows a shift in the scale of focus from small features with conservation importance that is difficult to evaluate without a broader population and landscape context to a consideration of how landscape patterns of differential resistance to movement affect connectivity at scales more relevant to conservation. We argue that this change in the scale and definition of the connectivity problem improves our ability to find solutions and may help resolve long-standing disputes regarding scale and definition of movement corridors and their importance to population connectivity.

Effective conservation of wildlife species depends on broad-scale landscape connectivity. Understanding the factors that affect animal movement through complex landscapes is essential, as is the application of this

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knowledge to identify critical movement corridors and barriers. The combination of empirically derived landscape resistance mapping and source-destination least-cost path analysis provides a powerful analytical framework for assessing habitat isolation and identifying corridors and barriers to organism movement. We applied prior knowledge of the factors that affect population connectivity for American black bears in a factorial least-cost path analysis to identify major movement corridors and barriers to population connectivity. We identified several major movement routes and found that human development has likely altered regional connectivity for black bears, with highways and human development increasing isolation of portions of the study area and possibly changing the routes of least-cost movement corridors.

This information on how human development may affect regional population connectivity and detailed predictions of the location of specific corridors and barriers should be valuable in ongoing efforts to conserve wildlife populations in the Rocky Mountains. The approach may provide an effective framework for assessing population connectivity for multiple species of interest under current conditions and provide an important means to quantify expected effects of changing climate and disturbance regimes on population connectivity. This was beyond the scope of our analysis, but ongoing work shows the method effectively quantifies the degree to which alternative emissions scenarios and associated ecosystem changes alter population connectivity for habitat specialists across the western United States (S.A.C. et al., unpublished data).

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