Landscape permeability for grizzly bear movements in Washington and southwestern British Columbia

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Abstract: Providing opportunities for grizzly bears (Ursus arctos) to move between blocks of habitat is important for the long-term conservation of grizzly bear populations. While the particulars of grizzly bear habitat selection during long-distance movements are poorly understood, some landscape characteristics such as road density and land cover type are correlated with grizzly bear habitat use at various scales. We compiled digital maps of roads, human population density, land cover class, and topography to evaluate the resistance of the year 2001 landscape to grizzly bear movement in Washington State and adjacent portions of Idaho and British Columbia (BC). We developed habitat association and dispersal habitat suitability models based on published literature and used geographic information system (GIS) weighted-distance and least-cost analysis techniques to evaluate landscape permeability for grizzly bear movement. Our analysis identified 5 blocks of potential grizzly bear habitat in Washington and adjacent areas, including the Columbia–Selkirk Mountains, the North Cascades, the Central Cascades, the South Cascades, and the Coast Range. We evaluated landscape permeability between these habitat blocks and highlighted potential linkage areas. Our models indicated the Stevens Pass fracture zone between the North and Central Cascades blocks was the most permeable, followed (in order of relative permeability) by the Fraser–Coquihalla fracture zone between the North Cascades and the Coast Range, the Okanogan–Kettle fracture zone between the North Cascades and the Columbia Mountains, and the Snoqualmie Pass fracture zone between the Central and South Cascades. This evaluation provides a consistent measure of the expected potential for grizzly movement across a broad landscape that can be used to target areas for finer-scale evaluation and help identify landscape management priorities at a regional scale.

Key words: grizzly bear, habitat modeling, highways, landscape connectivity, meta-population, North Cascades Ecosystem, Ursus arctos

Maintaining opportunities for animals to move across broad landscapes is an important conservation consideration for some sensitive wildlife species (Noss and Cooperrider 1994). Most animals are not uniformly distributed across large landscapes. They occur in populations or subpopulations centered on areas of suitable habitat. Depending on the species and the characteristics of the landscape between habitat patches, groups of populations may function as a meta-population (McCullough 1996). Providing animals opportunities to move across broad landscapes in a functioning meta-population can mitigate negative effects of genetic isolation, random disturbances (such as fire or storms), and demographic fluctuations (McCullough 1996). This is a particularly important consideration for long-lived species such as grizzly bears (U.S. Fish and Wildlife Service [USFWS] 1993, Weaver et al. 1996) and other large carnivores (Beier and Loe 1992, Noss et al. 1996, Dobson et al. 1999, Edelmann and Copeland 1999, Pierce et al. 1999, Reudiger et al. 2000).

Maintenance and restoration of landscape permeability is a particularly important consideration for ecosystems such as the North Cascades, which support relatively small populations of grizzly bears and are likely to be isolated from other populations (USFWS 1997, North Cascades Grizzly Bear Recovery Team 2001, Servheen et al. 2003). Substantial effort has been expended to assess landscape permeability for grizzly bears in the Rocky

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Mountains (Servheen and Sandstrom 1993, Meitz 1994, Boone and Hunter 1996, Walker and Craighead 1997, Servheen et al. 2003), but permeability has not been assessed in and around the North Cascades Ecosystem.

Prior to Anglo-American settlement, grizzly bears were distributed through much of western North America. By 1970 grizzly bears remained in only 2% of their former range within the contiguous United States (USFWS 1993, Servheen 1999). Though numbers have increased since their listing under the Endangered Species Act (16 U.S. Code 1531–1544) in 1975, the current distribution of grizzly bears in the contiguous United States is restricted to the Northern Rocky Mountains, the Selkirk Mountains, the Cabinet–Yaak Ecosystem, the Yellowstone Ecosystem, and the North Cascade Ecosystem (USFWS 1993, Mattson and Merrill 2002). Maintenance or restoration of connectivity both within and between these remnant populations is a key conservation concern for grizzly bears (Servheen et al. 2003) and was explicitly identified in the Grizzly Bear Recovery Plan for the United States (USFWS 1993).

Grizzly bears have been and continue to be present in the North Cascades Ecosystem in Washington and southern British Columbia (Bjorkland 1980; Almack et al. 1993; P.T. Sullivan, 1983, A preliminary study of historic and recent reports of grizzly bears in the North Cascades area of Washington, Washington Department of Game, Olympia, Washington, USA). Grizzly bear numbers in the North Cascades Ecosystem were substantially reduced following Euro-American settlement as a result of intensive killing for the fur trade and for predator reduction, followed by rapid human encroachment into grizzly bear habitat (Sullivan unpublished report 1983, Almack et al. 1993). Sullivan (unpublished report 1983) documented 425 grizzly bear hides taken around the Cascades between 1846 and 1851. Small numbers of grizzly bears continue to be present in the North Cascades Ecosystem. Almack et al. (1993) documented 20 confirmed grizzly bear observations scattered throughout the U.S. portion of the North Cascades Ecosystem between 1967 and 1991 (including 9 locations of grizzly bear tracks, 1 food cache, 6 visual observations, and a grizzly bear that was killed in 1967). L.W. Gyug (1998, Forest development plan blue-listed species inventory for mammals: assessment of grizzly bear populations, habitat use and timber harvest mitigation strategies in the North Cascades Grizzly Bear Population Unit, British Columbia; British Columbia Ministry of Environment, Southern Interior Region, Kamloops, British Columbia, Canada) evaluated grizzly bear detections and habitat conditions and estimated that the current population in the Canadian portion of the North Cascades Ecosystem consists of 17–23 adult and subadult grizzly bears, including 5–6 reproductive females. The U.S. portion of the North Cascades Ecosystem is a designated grizzly bear recovery zone (USFWS 1997). The Canadian portion of the ecosystem is an area of special management emphasis for grizzly bears (North Cascades Grizzly Bear Recovery Team 2001). Current management activities for grizzly bears in the North Cascades Ecosystem are reviewed by Gaines et al. (2000 and 2001).

While physically capable of long distance movements, grizzly bears do not frequently make such movements, particularly in the fragmented habitats of the northwestern United States and southwestern Canada (McLellan and Hovey 2001, Servheen et al. 2003). Adult male home ranges of grizzly bears in North America are 500–2,500 km² (M.N. LeFranc, M.B. Moss, K.A. Patnode, and W.C. Sugg, 1987, Grizzly bear compendium, Interagency Grizzly Bear Committee, Missoula Montana, USA), indicating the ability to move long distances. However, McLellan and Hovey (2001) found that the average natal dispersal distance of grizzly bears in the Rocky Mountains near the U.S.–Canadian border was 30 km for males (n = 18) and 10 km for females (n = 12). Maximum dispersal distances were 67 km for a male and 20 km for a female. They stated, “Our results suggest that meta-population reserve designs must provide corridors wide enough for male grizzly bears to live in with little risk of being killed” (McLellan and Hovey 2001:838).

Several models have been developed that evaluate habitat suitability or habitat effectiveness for grizzly bears (Clevenger et al. 1997, Mace et al. 1999, Merrill et al. 1999, Carroll et al. 2001). Other modeling applications evaluated habitat linkages and potential movement routes for grizzly bears. Servheen and Sandstrom (1993) developed a model to identify grizzly bear linkage zones incorporating road density, distance to developments, hiding cover, and riparian habitat. This model has been applied in a number of areas in the Rocky Mountains of Montana, Alberta, and British Columbia (Mietz 1994, Sandstrom 1996, Apps 1997, Servheen et al. 2003).

Boone and Hunter (1996) designed a diffusion model to evaluate landscape permeability in the Northern Rockies, using land cover and ownership to calculate resistance to movement. Walker and Craighead (1997) conducted least-cost corridor analysis to highlight potential movement corridors for grizzly bears in the Rocky Mountains. Their model incorporated vegetation type, edge length, and road density as predictors of landscape permeability. Kobler and Adamic (1999) developed a decision tree model from bear sighting.
locations and least-cost path analysis to predict Eurasian brown bear movement relative to highways in Slovenia. Model parameters identified from their analysis included percent forest cover, human population density, proximity to settlements, elevation, and forest type.

Based on our evaluation of previous linkage modeling efforts, we developed a modeling approach that would: (1) facilitate a multi-species analysis; (2) explicitly identify population source areas and resistance to movement between them; (3) evaluate the cumulative effects of landscape barriers to identify potential movement routes and obstructions; (4) provide a consistent measure that could be used for ranking portions of the landscape instead of placing artificial corridor boundaries on a map; and (5) provide an intuitive graphical product that can be used to communicate the problem and analysis results to individuals with diverse backgrounds. The analysis we present here emphasizes one part of a broader multi-species analysis (Singleton et al. 2001, 2002).

**Study area**

The analysis of Singleton et al. (2002) addressed landscape permeability for large carnivores in Washington and adjacent portions of Idaho and British Columbia (Fig. 1). The analysis evaluated from the Oregon–Washington border north to Revelstoke and Kamloops, British Columbia, and from the Pacific Coast east to the Idaho–Montana border, an area of 325,667 km². Results presented here emphasize the portion of that area pertinent to the evaluation of landscape permeability for grizzly bears. In particular, we focus on the Cascade Mountain Range north of Mount Rainier National Park, northeastern Washington, and adjacent portions of British Columbia and Idaho.

The gross geology of the region largely defines broad-scale landscape patterns in the study area. In particular, the crest of the Cascade Range runs from the Columbia River east of Portland, Oregon, into British Columbia east of Vancouver, meeting the Coast Range along the Fraser River in southern British Columbia. These mountain ranges substantially influence the climate, vegetation, and human development in the region. West of the Cascade Range, moist coastal conifer forest and urban development characterize the landscape of the Puget Lowlands. Southwestern Washington and the Olympic Peninsula are also characterized by moist coniferous forest, much of which is in private ownership and managed for timber production. The Olympic National Park and some surrounding national forest lands provide an isolated block of less disturbed forest and alpine habitat on the Olympic Peninsula.

East of the Cascade Range, relatively arid conditions dominate the agricultural and shrub–steppe landscapes of the interior Columbia Basin. These arid conditions extend north along the Okanogan Valley into central British Columbia. This broad valley provides some of the most temperate conditions in all of Canada and is known for its agriculture and retirement communities. Northern portions of the Okanogan Valley are heavily developed, particularly along Okanagan Lake where the cities of Penticton, Kelowna, and Vernon are located. East of the Okanogan Valley in British Columbia and northeastern Washington, the Kettle and Selkirk Mountain Ranges extend south from the Columbia Mountains to the Columbia River at Grand Coulee and the Pend Oreille River north of Spokane. These low mountain ranges are characterized by interior mixed coniferous forest, and the U.S. portions are largely within the Colville and Idaho Panhandle National Forests. Wildlife habitat conditions are described for Washington by Johnson and O’Neil (2001) and more specifically for grizzly bear by Gaines et al. (2000, 2001). Habitat conditions in British Columbia were reviewed by the North Cascades Grizzly Bear Recovery Team (2001).

**Methods**

Our analysis included 3 steps:

1. we identified concentrations of grizzly bear habitat using a regional model,
2. we evaluated landscape barriers to movement around habitat concentrations, and
3. we evaluated the potential for animal movement between habitat concentrations.

We used ArcInfo GIS (version 8.1, Environmental Science Research Institute [ESRI] 2001) to assemble regional GIS maps of road density, human population density, land cover, and slope (Table 1, base maps and complete metadata are available in Singleton et al. 2002). We compiled data that was suitable for mapping at a 1:100,000 to 1:250,000 scale. Because the analysis area spanned state and national boundaries, we combined 2 or more data sets for each layer. We used a 90-meter raster cell size for our analyses.

We identified highlighted areas with concentrations of grizzly bear habitat using a model that identified core areas with low levels of human disturbance (Puchlerz and Servheen 1994). We identified all roadless areas (road density <0.01 miles per square mile) with a mixture of forest–mesic shrub or alpine edge landcover types. We qualitatively identified the largest polygons
Fig. 1. Area evaluated for landscape permeability for grizzly bears in Washington and adjacent portions of British Columbia (southwestern Canada) and Idaho (northwestern USA), 2001.

with the highest concentrations of these habitat conditions as source areas between which we mapped landscape permeability (Singleton et al. 2002).

We conducted weighted-distance analysis to evaluate cumulative effects of landscape barriers between grizzly bear habitat concentrations. Weighted-distance analysis assigns each map cell a $c$ value that represents resistance to movement, or cost of moving across that cell, based on cell characteristics (ESRI 1992:6-63 to 6-78). The weighted-distance between each map cell and the nearest habitat concentration was calculated as the sum of $c$ for all the cells along the least-costly route between that cell and the most accessible habitat concentration. Map cells with high weighted-distance values had more landscape barriers between them and the nearest habitat concentration than cells with low weighted-distance values.

We developed an index of dispersal habitat suitability ($s$) from literature and expert opinion to calculate $c$ for each cell (Singleton et al. 2002). Dispersal habitat suitability ranged from 0 (low permeability, most costly) to 1 (most permeable, least costly), and was calculated as

$$s = \left(\frac{P_{\text{land cover class}}}{P_{\text{population density}}} \times \frac{P_{\text{road density}}}{P_{\text{slope}}}\right)$$

where $P$ is the permeability value for each landscape characteristic at that cell (Table 2). The cost ($c$) of moving across each cell was calculated as

$$c = (m(100(1 - s)))$$

where $m$ is the cell size in meters (90 for our analysis). Where $s = 1$, cells were assigned a weighted-distance of 90 meters, the minimum distance across the cell.

We identified "available areas" as those accessible to regular, intra-territorial movements for animals within habitat concentrations (areas affected least by landscape barriers) by highlighting areas within 100 km weighted-distance of a habitat concentration area. The landscapes we described as available areas were portions of the landscape with few barriers for bears moving from habitat concentrations. That these areas had few barriers for bear movement did not necessarily indicate that they were suitable habitat for grizzly bears in the sense of providing food, denning sites, or other life history requisites.

Areas between habitat concentrations with barriers to movement were identified by highlighting areas displaying a 100–1,000 km weighted-distance from habitat concentrations. We refer to such areas as “fracture zones” (Servheen and Sandstrom 1993). We assumed that areas >1,000 km weighted-distance from a habitat concentration were inaccessible to grizzly bears. We conducted least-cost corridor analysis within the fracture zones to map the portions of those landscapes with the fewest barriers to animal movement. Least-cost corridor analysis attributes each map cell with the total cost of moving between 2 habitat concentrations along the least-costly route through that cell. The most permeable portions of fracture zones were identified by stratifying the fracture zone into 10 equal-area groups that represented the most permeable 10% of the fracture zone.
Table 2. Values for habitat characteristics and permeability (P) for the grizzly bear dispersal habitat suitability index for Washington and adjacent parts of Idaho, USA, and British Columbia, Canada, 2001.

<table>
<thead>
<tr>
<th>Land cover</th>
<th>Human density (people/square mile)</th>
<th>Road density (miles/square mile)</th>
<th>Slope (degrees)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Class Value</td>
<td>Class Value</td>
<td>Class Value</td>
</tr>
<tr>
<td>alpine</td>
<td>1.0</td>
<td>&lt;1</td>
<td>&lt;20</td>
</tr>
<tr>
<td>coastal mesic forest</td>
<td>1.0</td>
<td>11–25</td>
<td>21–40</td>
</tr>
<tr>
<td>dry forest</td>
<td>1.0</td>
<td>26–50</td>
<td>&gt;40</td>
</tr>
<tr>
<td>interior mesic forest</td>
<td>1.0</td>
<td>&gt;50</td>
<td></td>
</tr>
<tr>
<td>wetland–riparian</td>
<td>1.0</td>
<td>6.1–10</td>
<td></td>
</tr>
<tr>
<td>coastal mesic shrub</td>
<td>0.8</td>
<td>&gt;10</td>
<td></td>
</tr>
<tr>
<td>interior mesic shrub</td>
<td>0.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>dry shrub–grass</td>
<td>0.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>agriculture</td>
<td>0.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>bare ground</td>
<td>0.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>snow–ice</td>
<td>0.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>urban–developed</td>
<td>0.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>water</td>
<td>0.1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

landscape (corridor value 1) to the least permeable 10% of the fracture zone landscape (corridor value 10) based on the least-cost corridor value.

Results

Five habitat concentration areas were identified based on our habitat association models for grizzly bears (Fig. 2). Our modeling indicated that the North Cascades habitat concentration area extended from Manning and Cathedral Provincial Parks (south of BC Highway 3), south to the vicinity of Glacier Peak and Lake Chelan (north of U.S. Highway 2). The BC Coast Range habitat concentration area was northwest of the North Cascades. The Coast Range habitat concentration is contiguous with occupied grizzly bear habitat extending north through coastal British Columbia and Alaska.

East of the North Cascades, the Columbia and Selkirk Mountains habitat concentration also is contiguous with occupied grizzly bear habitat to the north. South of the North Cascades, our model identified the Central Cascades (mostly within the Alpine Lakes Wilderness Area) and the South Cascades (near Mount Rainier National Park and the Norse Peak and Goat Rocks Wilderness Areas) as habitat concentration areas. The grizzly bear habitat association model did not identify habitat concentrations in the Selkirk Range in Washington and Idaho because roadless area polygons there were relatively small. However, due to the documented presence of grizzly bears in the Selkirk (W.L. Wakkinen, and W. Kasworm, 1996, Grizzly bear and road density relationships in the Selkirk and Cabinet–Yaak recovery zones, Idaho Department of Fish and Game, Boise, Idaho, USA, and U.S. Fish and Wildlife Service, Missoula, Montana, USA) and the designation of the area as a recovery zone (USFWS 1993), we felt that it was appropriate to incorporate this area into our analysis of landscape permeability for northeastern Washington. We accomplished this by appending forested, roadless polygons in the Selkirs to the modeled habitat concentration map.

The dispersal habitat modeling indicated that approximately 36% of the analysis area (Washington and adjacent portions of Idaho and British Columbia) was relatively good dispersal habitat (total permeability value >0.6), approximately 23% of the analysis area was moderate dispersal habitat (total permeability value 0.3 to 0.6), and 41% of the analysis area was poor dispersal habitat (total permeability value <0.3). The weighted-distance analysis delineated broad portions of southern British Columbia, northern Washington, and the Cascade Range as being within the 1,000 km weighted-distance that may be accessible for long-distance bear movements (Fig. 2). Most of southeastern Washington and western Washington were beyond 1,000 km weighted-distance from any habitat concentration. We expect that those areas beyond 1,000 km weighted-distance are inaccessible to any kind of movement by grizzly bears.

Available area (those areas within 100 km weighted-distance of habitat concentrations) surrounding the North and Central Cascades habitat concentrations encompassed 23,887 km² (Fig. 2). This area with few barriers connected the North and Central Cascades habitat concentrations near Stevens Pass but had a substantial bottleneck along U.S. Highway 2. Although the
Habitat Concentrations and Weighted-Distance Results

- Highways
- States and Provinces

Weighted-Distance
- 0 - 100 (Available)
- 101 - 500
- 501 - 1000 (Least Accessible)
- Habitat Concentrations and Available Areas

Scale

0 25 50 75 100 Km

Columbia - Selkirk Mountains

Coast Range

North Cascades

Central Cascades

South Cascades

Table 3. Landscape permeability within fracture zones identified for grizzly bears in Washington, USA, and adjacent portions of British Columbia, Canada.

<table>
<thead>
<tr>
<th>Fracture zone</th>
<th>Minimum ratio of linkage weighted-distance</th>
<th>Actual distance</th>
<th>Ratio of weighted-distance: actual distance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stevens Pass</td>
<td>84</td>
<td>25</td>
<td>3.3</td>
</tr>
<tr>
<td>Fraser–Coquihalla</td>
<td>348</td>
<td>23</td>
<td>14.7</td>
</tr>
<tr>
<td>Okanogan–Kettle</td>
<td>598</td>
<td>162</td>
<td>3.7</td>
</tr>
<tr>
<td>Snoqualmie Pass</td>
<td>760</td>
<td>42</td>
<td>17.9</td>
</tr>
</tbody>
</table>

Available area surrounding the South Cascades habitat concentration encompassed 5,155 km². Available area surrounding the Coast Range and Columbia Mountains encompassed 24,481 and 36,217 km², respectively. The Coast Range and Columbia Mountains are both contiguous with occupied grizzly bear habitat extending north beyond the extent of our analysis.

Weighted-distance analysis identified 3 major fracture zones between habitat concentrations, in addition to Stevens Pass (Table 3, Fig. 3). Least-cost corridor analysis indicated that Stevens Pass (between the Central and North Cascades habitat concentrations) was the most permeable fracture zone, followed by the Fraser–Coquihalla (between the North Cascades and the Coast Range), Okanogan–Kettle (between the North Cascades and the Columbia Mountains), and Snoqualmie Pass (between the Central and South Cascades).

Discussion

Our weighted-distance and least-cost corridor analysis highlighted several common features defining landscape permeability. Major transportation routes and associated urban land uses often defined the limits of habitat concentrations, areas accessible for grizzly bear movements, and landscape barriers within fracture zones. In general, our analysis identified habitat concentrations and adjacent available areas located in montane forest habitats on public lands. Fracture zones were generally located in major valleys or mountain passes where major transportation routes, human developments, and natural transitions in habitat type occurred.

The major habitat concentrations and adjacent available areas identified by our models correspond well to the documented distribution of grizzly bears in our analysis area. The North and Central Cascades habitat concentrations and adjacent available area corresponds to the North Cascades Ecosystem Grizzly Bear Recovery Area (USFWS 1997). These areas also correspond well to the distribution of confirmed grizzly bear observations recorded by Almack et al. (1993). Our modeled habitat concentration and adjacent available area for the Coast Range corresponds to the Stein-Nahatlatch and Garibaldi-Pitt Grizzly Bear Population Units, which support threatened populations of grizzly bears (North Cascades Grizzly Bear Recovery Team 2001). These population units (through adjacent units with threatened status) are contiguous with the Kinaklini-Homathko and Knight-Bute units, which have viable status and are approximately 200 km farther north and west through the Coast Range (North Cascades Grizzly Bear Recovery Team 2001). Our Columbia Mountains habitat concentration corresponds to the Valhalla, Central Selkirk, and South Purcell Grizzly Bear Population Units, which support viable populations of grizzly bears and are contiguous with viable populations extending north through the Columbia and Rocky Mountains (North Cascades Grizzly Bear Recovery Team 2001). The South Cascades was the only area modeled as a habitat concentration that does not have recent documentation of at least occasional grizzly bear presence. This is a relatively small area (5,155 km² within 100 km weighted-distance of the habitat concentration) with substantial human activity. This area is well below the 20,000 km² identified by Mattson and Merrill (2002) as characteristic of landscapes that have recently supported grizzly bears in the contiguous United States.
Major highways pass through a matrix of grizzly bear habitat in all of the modeled habitat concentrations and adjacent available areas (Figs. 2, 3). U.S. Highway 20 over Washington and Loup Loup Passes, BC Highway 3 in the vicinity of Manning Provincial Park, and WA SR 542 near Mount Baker pass through the North Cascades habitat concentration and adjacent available areas. U.S. Highway 97 over Blewett Pass intersects the Central Cascades habitat concentration and adjacent available areas. U.S. Highway 12 around White Pass, WA SR 410 near Chinook Pass, and WA SR 123 through Mount Rainier National Park pass through the South Cascades habitat concentration and adjacent available areas. BC Highway 99 between Squamish and Lillooet intersects the Coast Range habitat concentration and adjacent available areas. BC Highway 3 around Kootenay Pass, BC Highway 3a east of Nelson, and BC Highway 6 from Salmo to Nakusp pass through habitat concentrations and adjacent available areas in the Selkirk and Columbia Mountains. These routes could limit movements within landscapes that could support grizzly bears and may contribute to factors that limit resource availability and increase mortality for resident bears (Noss et al. 1996, McLellan et al. 1999). Landscapes in the Coast Range and Columbia Mountains also showed some evidence of substantial natural barriers within habitat concentrations associated with Upper Arrow, Lower Arrow, and Kootenay Lakes in the Columbia Range and extensive glacial systems in the Coast Range.

Stevens Pass Fracture Zone. With a minimum weighted-distance of 84 km, the Stevens Pass area did not meet our 100 km weighted-distance criterion to be considered a fracture zone. However, the weighted-distance map indicated a bottleneck in landscape permeability through this area, so we included it in our least-cost corridor analysis. The area east of Stevens Pass had the best potential for landscape permeability between the North and Central Cascades. Several features contribute to reduced permeability through the Stevens Pass landscape, including a large ski area at the pass, residential developments along U.S. Highway 2, and rugged terrain. U.S. Highway 2 is a 2-lane undivided highway and is 1 of 3 major east–west transportation routes over the Cascade Mountains. Because developments along this transportation route are generally limited to small recreation cabins, this landscape is relatively permeable, although levels of permeability could decline as traffic volumes and recreational developments increase along the highway.

Fraser–Coquihalla Fracture Zone. Our model showed 2 potential linkages between the Coast Range and the North Cascades. The shorter route passes from the North Cascades, northwest of Ross Lake, across the Fraser River between Chilliwack and Hope, and into the Coast Range east of Harrison Lake (Fig. 3). This is a short, 24-km linkage between modeled habitat concentrations, but it has poor landscape permeability (weighted-distance 349 km, weighted to actual distance ratio of 14.5). Poor permeability is due to the Trans-Canada Highway on the south side of the Fraser River (a 4-lane, divided highway), BC Highway 7 on the north side of the Fraser River, a 300-m water crossing through the river, and moderate to high human density in the valley bottom. The second route connects the northern portion of Manning Provincial Park to the Stein-Nahatlatch area by passing north of Coquihalla Summit and through the Anderson River drainage. This route is substantially longer, approximately 150 km, but has better overall permeability (weighted-distance 474 km, weighted to actual distance ratio of 3.1). Factors limiting permeability along this linkage include the Fraser River (a large, fast-moving river in a rugged canyon), the Trans-Canada Highway (a 2-lane highway through the Fraser River Canyon) and the Coquihalla Highway (BC Highway 5, a 4-lane divided highway). Much of the Coquihalla highway has been equipped with game fencing to reduce animal–vehicle collisions. Several underpasses provide animal crossings; however, these structures may not have the characteristics of crossing structures used by grizzly bears in other areas (Clevenger and Waltho 2000).

Gyug (unpublished report 1998) described 2 grizzly bears that were relocated into the BC portion of the North Cascades ecosystem and traveled in the Fraser–Coquihalla fracture zone. In June 1994 a female was released in the Anderson River area (north of Coquihalla Summit) and recaptured in May 1995 near Agassiz (across the Fraser River from Chilliwack, a movement of...
approximately 30 km). In October 1992 a male was released in the Pasayten River area on the east side of Manning Provincial Park. It moved about 64 km west to the Chilliwack River that fall, then returned to its original capture area in the Coast Range near Pemberton by June 1993 (a cumulative movement of at least 260 km total distance). Both bears were detected near the linkage identified by our model near Chilliwack and Hope (Gyug unpublished report 1998).

**Okanogan–Kettle Fracture Zone.** The best linkages between the North Cascades and the Columbia Mountains passed through the Okanogan Valley south of Kelowna and Penticton (Fig. 3). Both linkages involve long water crossings (>1 km) through Okanagan or Skaha Lakes. We expect that functionality of these linkages may be limited by the long water crossings. Our models also identified 2 terrestrial linkages through the Okanagan Valley; one through the Canadian portion of the valley at Vaseux Lake Provincial Park and the other through the U.S. portion of the valley near Riverside, between Omak and Tonasket. The Vaseux Lake linkage passes from the habitat concentration in the Monashee Mountains, through the Kettle and Granby watersheds, across BC Highway 33 along the West Kettle River, across BC Highway 97 at Vaseux Lake, through the Similkameen River valley north and west of Cawston, and connects with the North Cascades near Cathedral Provincial Park. This linkage extends from the Central Cascades and Mount Rainier National Park (Fig. 3). The linkage identified by our modeling corresponds to the primary linkage area along 1-90 identified by finer scale field surveys reported by Singleton and Lehmkuhl (2001) and are occasionally reported moving into the Canadian portion of the Okanagan Valley (M. Austin, British Columbia Ministry of Land, Air, and Water Protection, Victoria, British Columbia, Canada, personal communication, 2002). In 1997 a 5-year-old male grizzly bear was killed near Vaseux Lake, and in 1999 a 4-year-old male was killed northeast of Penticton (British Columbia Ministry of Land, Air, and Water Protection, Victoria, British Columbia, Canada, unpublished data). It is also noteworthy that the distance from the North Cascades to the closest viable population unit in the Columbia Mountains (the Valhalla unit) is 150 km, while the distance to the closest viable population unit in the Coast Range (the Klinaklini-Homathko unit) is 290 km.

The other linkage between the North Cascades and the Columbia Mountains passes from the Valhalla area, south across BC Highway 3 east of Christina Lake, across U.S. Highway 395 into the Kettle Range west of the Columbia River, across WA SR 20 at Sherman Pass, then west across WA SR 21 along the Sanpoil River, across U.S. Highway 97 near Riverside, and into the North Cascades northwest of Conconully (Fig. 3). This linkage was strongly channeled to the east by substantial landscape barriers along BC Highway 3, just north of the international border, between Osoyoos and Grand Forks. Agricultural land uses, high human population density, and associated urban areas combined to channel the modeled linkage into the vicinity of Christina Lake and along the crest of the Kettle Range.

**Snoqualmie Pass Fracture Zone.** Several factors limit permeability through the Snoqualmie Pass landscape. These include a major interstate highway (Interstate 90 [I-90]), extensive recreation and residential development, fragmented forest cover resulting from checkerboard federal–private land ownership, 3 large lakes, and rugged terrain along the crest of the Cascade Mountains. Interstate 90 probably reduces permeability through this area more than other features (Singleton and Lehmkuhl 1999). It is the primary east–west transportation route across the Cascades into Seattle and carries an average of 25,000 vehicles a day, with peak volumes exceeding 58,000 per day (Washington State Department of Transportation 2003). Our models highlighted a primary linkage area approximately 35 km east of Snoqualmie Pass, near Easton Lake State Park. This linkage extends from the Central Cascades habitat concentration in the Alpine Lakes Wilderness Area, across I-90 at Easton Hill, to the South Cascades habitat concentration in the Norse Peak Wilderness Area and Mount Rainier National Park (Fig. 3). The linkage identified by our modeling corresponds to the primary linkage area along I-90 identified by finer scale modeling for multi-species landscape permeability and field surveys reported by Singleton and Lehmkuhl (1999).

The Snoqualmie Pass landscape is unique for the attention it has received regarding management to restore habitat connectivity for a variety of species. This landscape was designated as an adaptive management area under the Northwest Forest Plan (U.S. Department of Agriculture Forest Service [USFS] 1997). The primary management objective was to restore habitat connectivity for species associated with late successional forest. Recent land exchanges, habitat acquisitions, and activities by non-governmental organizations (NGOs) focused on restoring habitat connectivity through the area (USFS 1999), which was also a primary objective of a large highway reconstruction project planned along I-90. Though the emphasis in this project was planned along 1-90. Though the emphasis in this project was

area has not been on restoring habitat connectivity specifically for grizzly bears, the coordination between land management agencies, NGOs, and the Washington Department of Transportation in managing the Snoqualmie Pass landscape may provide a positive example for land management emphasizing habitat connectivity in other areas.

Conclusion
The products of our approach can contribute to the management of habitat connectivity in a variety of ways. These products can be used to communicate issues associated with habitat connectivity, including identifying areas where habitat connectivity may be an appropriate management objective and highlighting factors that could influence connectivity in those areas. We view this analysis as hypothesis development in which we propose that the linkage areas we identify are more likely to provide for successful passage for grizzly bears than adjacent areas, based on the landscape characteristics we evaluated. These hypothetical linkages need to be investigated more thoroughly through the analysis of higher-resolution GIS data and field surveys.

We have attempted to develop a method that explicitly estimates landscape permeability. These estimates can be used to compare landscape permeability between different areas at various scales. However, the actual functionality of the linkage areas we identify can only be tested through empirical field studies, and even then they will be difficult to evaluate because of the challenges inherent in the study of dispersal (Nathan 2001).

These models provide a relative evaluation of landscape permeability. They highlight the most permeable portions of landscapes that could be highly disturbed. In highly altered landscapes, even the least-disturbed places may be entirely unsuitable for animal movement.

Users of this model must also consider the appropriate scales for the application of these results. These analyses were conducted using regional-scale data sets effective for evaluating broad-scale patterns; these results should not be expected to provide precise information for specific locations such as that which is required to identify locations for highway mitigation projects or to locate animal crossing structures. These analyses are not a substitute for field surveys.

This exercise is not intended to assess suitable or critical habitat. Our modeling approach emphasized evaluating resistance to animal movement, not the availability of food resources, denning habitats, or other features important for grizzly bears. Areas identified as available habitat in our analysis (areas within which movement is not restricted by substantial barriers) are not necessarily suitable habitat.

While the information presented here focuses on grizzly bears, this approach can evaluate landscape patterns for many species, identifying common patterns for those species and developing viable multi-species plans. The majority of the linkages presented here were also identified as potential linkages for other large carnivores (Singleton et al. 2002).

Successful management of broad-scale habitat linkages for large carnivores will require cooperation between resource management agencies, local governments and planning boards, NGOs, transportation agencies, public utilities, local citizens, and stakeholder groups. Planning will need to integrate land management across jurisdictional and ownership boundaries through a variety of creative mechanisms (Knight and Landres 1998). Products like those presented here can help facilitate communication between these diverse groups and contribute to the development of common goals for landscape planning.

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