Journal of Conservation Planning Vol 5 (2009) 15 — 27

Using boundary-detection methods to assess conservation corridors

John DiBari

John DiBari
Sonoran Institute
3009 Queen St.
Missoula, MT 59801
Phone: (406) 543-6858
jdibari@sonoran.org
www.sonoran.org

ABSTRACT: Identifying core habitat and corridors linking those areas is essential for species conservation. However, it is difficult to know whether corridors delineated with commonly-used geographic information system analyses may actually function in that capacity. Boundary-detection techniques were used to assess the robustness of least-cost path and corridor analyses created to identify movement routes for grizzly bears (*Ursus arctos*) in the interior temperate rainforest of western Canada and northwestern United States. Additionally, boundaries were tested to determine whether they were statistically unusual, and subsequently tested for boundary contiguity using a graph theoretic approach. The analysis identified statistically significant, contiguous boundaries bisecting least-cost paths and corridors. These results suggest barriers to movement and therefore potentially diminished functionality of conservation networks created using prospective least-cost paths and corridors. This research may help identify landscape features that affect connectivity and inform the conservation planning process.

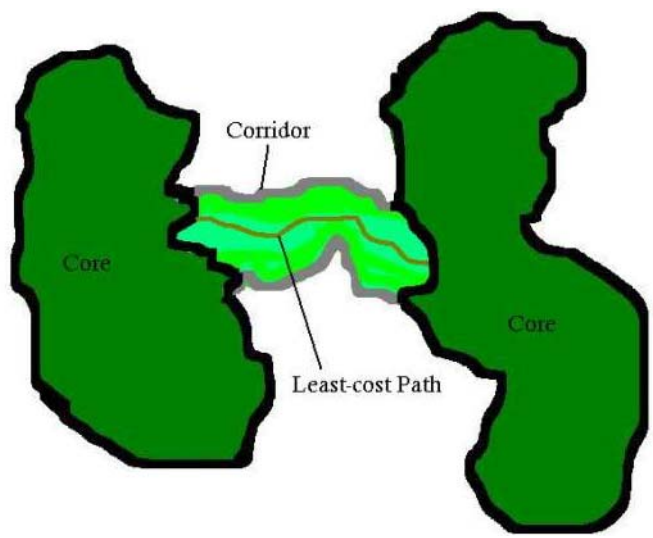
Keywords: Boundary, connectivity, core-corridor model, conservation area design, least-cost path, Wombling

INTRODUCTION

In the core-corridor conservation area design (CAD) model, cores provide the highest level of conservation protection. They are habitat for species, providing the range of resources necessary to carry out some or all of a species' life cycle. Often core areas serve as sources of individuals that disperse to populate unoccupied habitat or sustain a metapopulation (Pulliam and Danielson, 1991; Beier, 1993; Carroll et al., 2003). Alternatively, corridors act as landscape conduits through which individuals travel (Henein and Merriam, 1990; Rouget et al., 2006). The intent of the core-corridor model is to create a conservation network where cores represent high-quality habitat and corridors represent areas where movement between cores is likely given the characteristics of the landscape and ecology of the species of interest. The success of CADs developed using this model hinges on the robustness of the network (see Carroll et al., 2001; Noss et al., 2002; Carroll et al., 2003) – the conservation value of cores (Meffe and Carroll, 1997) and the amount and quality of connectivity provided by corridors (Noss and Harris, 1986; Simberloff and Cox, 1987; Simberloff et al., 1992; Perault and Lomolino, 2000). Although research has focused on delineating cores, less effort has focused on evaluating whether areas identified as corridors may function as intended (Soulé, 1991). That is, are potential corridors identified through spatial analysis useful to the species they are intended to serve, or are there landscape features that serve as potential barriers within those corridors that restrict or perhaps even prevent movement?

One method of identifying corridors within a landscape is to use a geographic information system (GIS) to undertake least-cost path (LCP) analysis (ESRI, 2005). Such analyses have formed the basis of many connectivity-oriented research projects (Bunn et al., 2000; Singleton et al., 2002; Adriaensen et al., 2003; Larkin et al., 2004; Rouget et al., 2006). LCP analysis locates the path of lowest travel "cost" (Figure 1) across a landscape cost-surface, where the cost surface is an aggregate depiction of landscape characteristics (e.g., land cover, elevation, roads) and represents a researcher's best understanding of how permeable a landscape may be for a given species or group of species. That is, costs vary based on the characteristics of the landscape for the species of interest. Areas of high quality habitat tend to have a low cost value, whereas areas of low quality habitat or non-habitat tend to have a high cost value. LCP analyses operate on the premise that animals select movement routes using similar decision-making processes as when they select habitat (Majka et al., 2007), although this assumption may not hold in all cases (Horskins et al., 2006).

FIGURE 1 Core-corridor model with least-cost path identified.



Although LCP analyses maybe useful, the term "lowest" is relative, as the lowest cost path may in some circumstances have high absolute costs. For example, an LCP may cross a large, fast-moving river in lieu of crossing a four-lane highway. An animal may be unlikely to use either path, yet due to the premise of the LCP algorithm the lowest cost alternative is identified.

Rather than identifying a single one-dimensional LCP across a landscape, a network of LCPs may be generated between cores in a pair-wise fashion. Such an effort can often illustrate redundant connections across a landscape. Additionally, it is possible to identify a low cost corridor that represents an irregularly-shaped two-dimensional area linking cores. For example, Beier et al. (2008) combine habitat maps for a suite of species and generate corridors by taking a slice of low-cost cumulative resistance values across the landscape. Each corridor is suitable for at least one species of interest.

Both LCP and corridor approaches may provide information useful in establishing conservation networks. This is especially the case in the absence of data showing routes animals actually use between core areas. However, little research has been done to evaluate the quality of corridors generated using the above methods.

In this analysis, boundary detection techniques are used to assess the quality of LCPs and corridors identified in the process of creating a CAD for grizzly bears (*Ursus arctos*) in the interior temperate rainforest (ITR) of western Canada and the northwestern United States. To date, analyses of landscape connectivity in this context have stopped once LCPs and\or corridors were delineated (see Singleton et al., 2002; Adriaensen et al., 2003; Larkin et al., 2004; Rouget et al., 2006). Yet the question remains, is this enough? The focus of this analysis is to determine if boundary-detection techniques can provide additional insight regarding connectivity with the same data used to create LCPs and corridors.

Raster Wombling (Womble, 1951; Kaufmann et al., 2001) was used to identify areas of the cost surface that exhibit high-magnitude changes in cost over space. Wombling is a statistical technique used to identify where landscape characteristics change rapidly across geographic space. Slope is such an example, where steep slopes indicate high magnitude change in elevation over a short linear distance. In this analysis, Wombling identifies high-magnitude changes in cost across the cost surface. Locations of rapid change represent "boundaries," places that separate higher from lower cost values on the cost surface. In ecological terms, boundaries can be thought of as potential barriers to movement; areas of sharp contrast which are likely too costly to move across. Using the slope example again, rapid changes in elevation (i.e., steep slopes) may indicate the presence of a cliff, a potentially non-traversable obstacle. Boundaries identified through Wombling denote these locations. Additionally, boundaries that meet a user-defined threshold of change are then statistically tested to assess, using a graph theoretic approach (see Harary, 1969), whether places of high-magnitude change form contiguous boundaries (i.e., boundaries more than one cell long). Areas where boundaries are contiguous, that is, where high-magnitude changes in cost are continuously high, indicate potential barriers (Barbujani et al., 1989) and thus a less robust conservation network. This analysis can help identify contiguous boundaries across LCPs or within corridors indicating the landscape may be impermeable or at least less permeable than LCP or corridor analyses may otherwise suggest. In other words, boundaries provide spatially explicit information regarding where permeability may be diminished in corridors or along LCPs. Additionally, this analysis may help managers identify areas within modeled corridors to investigate further for protection and\or restoration.

Lastly, cost surface characteristics, more specifically parameterization of the model creating the cost surface, affect LCP, corridor, and boundary-detection analyses. A range of cost values may be associated with each landscape characteristic comprising the cost surface. For example, cost values for land cover may vary by land cover type. Depending on the ecology of the species of interest, urban areas may be assigned a higher cost value than forested areas. Therefore, analyses are potentially sensitive to the cost values researchers assign to specific landscape characteristics. In some cases, absolute barriers to movement may exist and cost surfaces can reflect this (e.g., through the use of No Data values). The point is the structure of the cost surface dictates the utility of the landscape for the species of interest, and thus the location and characteristics of LCPs, corridors, and boundaries across the modeled landscape.

METHODS

Data

The study area encompassed the ITR of British Columbia, Canada and Washington, Idaho, and Montana, USA (Figure 2). The ITR is a rare ecosystem whose diversity compares to that of coastal temperate rainforests. Grizzlies are just one of several species of conservation concern in the ITR, where habitat destruction and fragmentation associated with human land uses threatens habitat quality and connectivity. In the US, the grizzly is considered Threatened under the Endangered Species Act (1973), whereas in British Columbia, it is considered a species of special concern due to sensitivity associated with human activities (BC Conservation Data Center, 2008). Thus, the goal of creating a CAD in the ITR is to ensure viable populations of important species, such as the grizzly (see Noss et al., 2002; Carroll et al., 2003; Carroll, 2006). Landscape and habitat suitability characteristics for the ITR were evaluated using land cover, human population density, road density, slope, and elevation data. Core habitat (Figure 2) was identified by creating a habitat suitability model for a suite of focal species including grizzly bears. An associated cost surface (Figure 3, page 19) was also created, which described landscape permeability (Table 1, page 19). Both data sets were developed in the manner used by Singleton and Lemkuhl (1999; 2000) and Singleton et al. (2002; 2004). Although the initial modeling was undertaken with more finely resolved data, the final core area, cost surface, and derivative data sets were generalized to a cell size of 1 km^2. As this work is not the focus of this paper, please consult Craighead and Cross (2004; 2005) and Craighead et al. (2008) for details regarding the methodology used to create the habitat suitability models and cost surface.

FIGURE 2 Interior temperate rainforest study area and grizzly bear core areas.

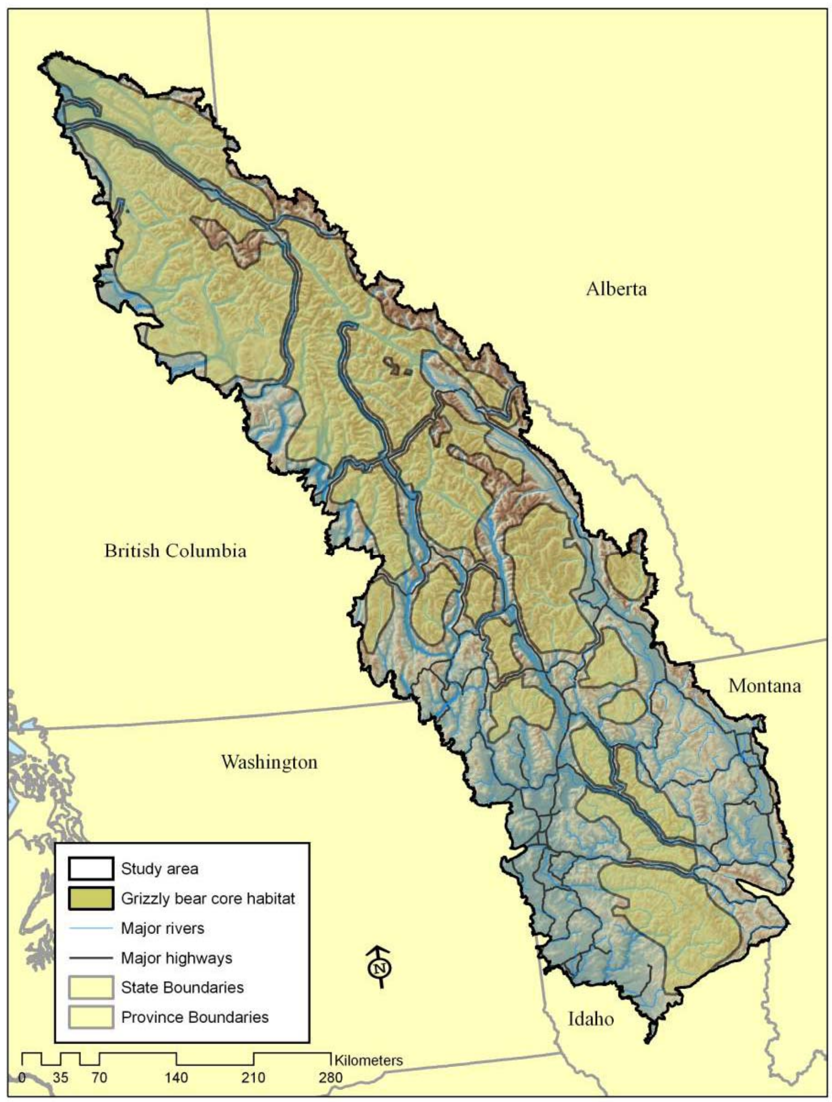


FIGURE 3 Grizzly bear core areas and cost surface.

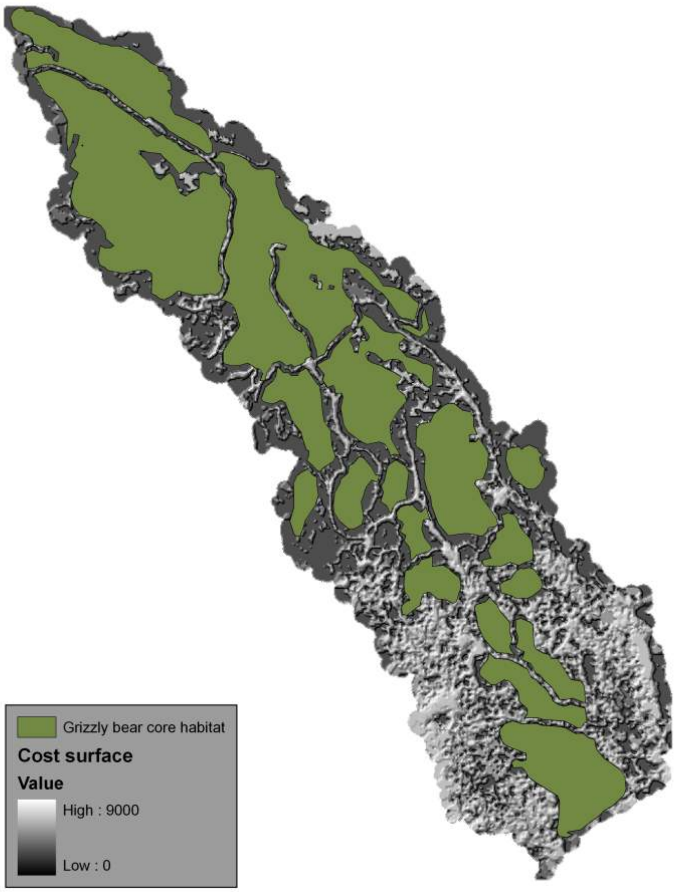


TABLE 1 Permeability values used by Craighead and Cross (2004) to derive the cost surface.

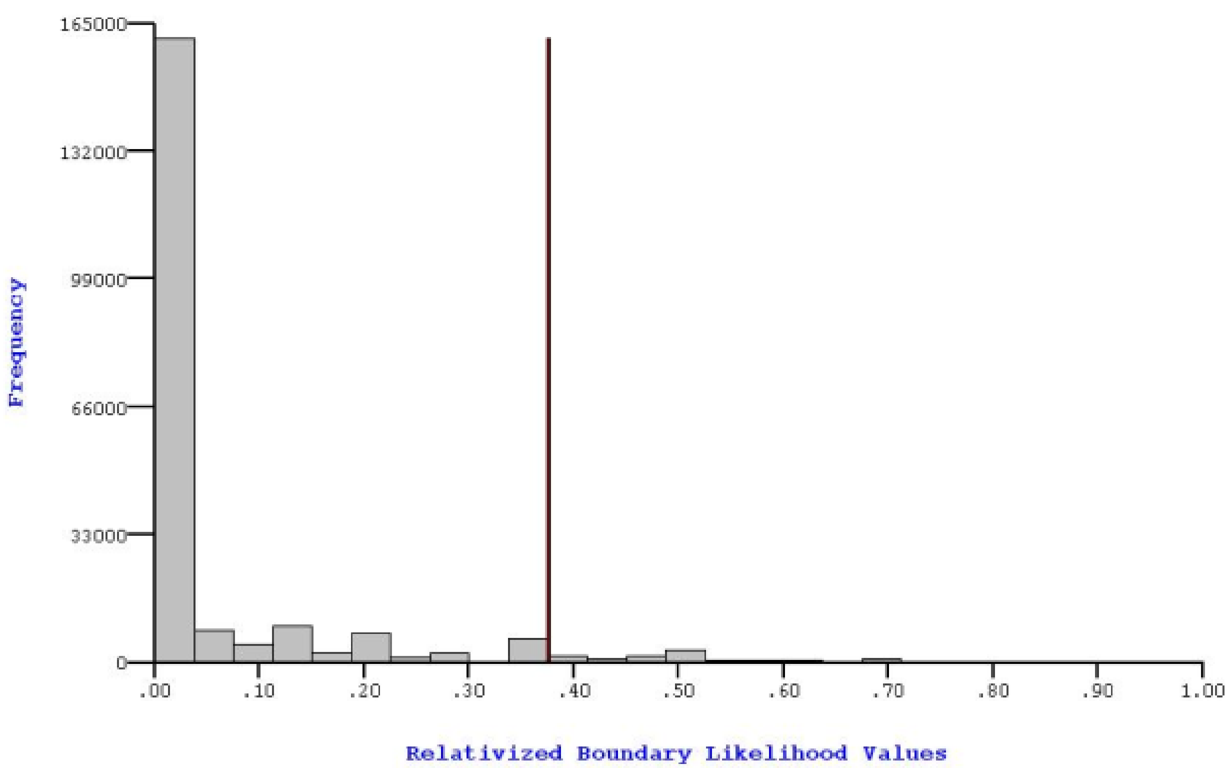
Index	Type	Value
Land cover class		
	Alpine	10
	Forest – Old/ Young	10
	Sub Alpine	10
	Ice and Snow	3
	Wetlands	4
	Water	1
	Bare ground	3
	Logged (last 40 years)	8
	Agriculture	2
	Urban	1
	Recently Burned	4
	Rangeland	10
	Shrub	8
Population density (people/mi^2)		
	0-10	10
	10-25	5
	25-50	3
	50-100	1
	100 +	1
Road Density (mi/mi^2)		
	0-0.01	10
	0.01-1	10
	1-2	10
	2-4	5
	4-6	3
	6-8	2
	8-10	2
	10-50	1
	>50	1
Elevation (m)		
	0-1000	10
	1000-1500	10
	1500-2000	10
	>2000	10
Slope (% slope)		
	0-20	10
	20-40	10
	40-60	10
	60-80	10
	80-100	10
	100-120	10
	>120	1

ANALYSIS

The COSTALLOCATION and COSTPATH commands in Workstation ArcInfo (ESRI, 2005) were used to generate LCPs between 25 core areas in a pair-wise fashion. LCPs represented the lowest-cost route, one cell wide, across the landscape on a cell-by-cell basis. Each path was converted to a line theme and all lines were combined to illustrate the network of LCPs across the study area. The CORRIDOR command in Workstation ArcInfo (ESRI, 2005) was then used to derive lowest-cost corridors, also in a pair-wise fashion, between all cost-distance maps produced in the LCP analysis. Next, the MIN command was used to identify the minimum cell values of the resulting stack of corridor maps, as this represented the lowest cost values across all pair-wise cost-distance maps. The result was a composite lowest-cost corridor map for the entire study area.

Difference boundaries were identified using BoundarySeer™ (Kaufmann et al., 2001). Difference boundaries are areas of rapid change in magnitude of the landscape characteristic being measured. In this case, difference boundaries were identified by looking for rapid changes in cost on the cost surface. Boundaries were determined using Wombling on continuous data (Fortin, 1994; Jacquez et al., 2000). Wombling is a method used to delineate difference boundaries. To identify potential boundary elements, a threshold of the upper 5th percentile (Barbujani et al., 1989; Fortin and Drapeau, 1995; Jacquez et al., 2000) was selected based on a histogram of relativized boundary likelihood values (Figure 4). This threshold is the point at which there was a large-enough change in the magnitude of cost over space, indicating a potential boundary (Fortin et al., 2000; Jacquez et al., 2000). Boundary elements with similar amounts and direction of change can be connected to form subboundaries. To test for subboundaries, a

FIGURE 4 Distribution of relativized boundary likelihood values. Vertical line delineates upper 5th percentile of values (right of line).



subboundary analysis was conducted to statistically evaluate the contiguity of the identified boundary elements. This analysis determined whether subboundaries possessed statistically significant characteristics, including length, branchiness, and diameter (Kaufmann et al., 2001). The statistics used in the subboundary analysis are drawn from planar graph theory. Each subboundary is a graph, where boundary elements are nodes and connections among subboundaries are edges or links (see Harary, 1969; Urban and Keitt, 2001). Graph theoretic methods have been used to describe landscape connectivity (Cantwell and Forman, 1993; Fortin, 1994; Bunn et al., 2000; Urban and Keitt, 2001; James et al., 2005). However, in this context the same theoretical underpinnings were used to assess the connectedness of potential landscape barriers, which in turn may affect landscape connectivity. Subboundary characteristics were evaluated based on the results of 100 Monte Carlo randomizations. The analysis tested the null hypothesis that boundaries occur randomly and are therefore no more contiguous than expected by chance. The alternative hypothesis suggests large-scale boundaries with higher boundary contiguity than expected by chance.

RESULTS

The GIS analysis produced maps illustrating LCPs on a by-cell basis across the cost surface (Figure 5, page 22). This described the potential cumulative connectivity characteristics of the landscape as viewed from the perspective of a grizzly; at least to the best of our abilities. The shortest LCP was approximately 4,969 m, whereas the longest was approximately 27,422 m. Due to the landscape characteristics and arrangement of core areas many of the gaps between cores were quite small. Additionally, many of these gaps existed in valleys which often contained roads, a river, development or some combination of the three. Thus, due to the nature of this analysis as described above, LCPs traversed, in absolute terms, some high-cost areas. Yet relatively, these areas were identified as the lowest cost routes, indicating some preference for movement based on grizzly ecology as described by the cost surface. Additionally, using output from the LCP analysis, a map was created that combined the minimum cell values of all corridors in a pair-wise fashion (Figure 6, page 22). This map illustrated a landscape permeability gradient across the ITR. The lowest cost, most permeable areas (greener shades) represented potentially preferred movement zones, whereas the higher cost, least permeable areas (bluer shades) represented less preferred zones. Again, due to the nature of this analysis, the most permeable areas may have contained landscape features such as roads, rivers, or development. However, in relative terms, these areas suggested highest potential permeability.

The boundary detection analysis produced a map of boundary elements meeting the 5% threshold of boundary likelihood values (Figure 7, page 23). Additionally, the subboundary analysis provided compelling evidence to reject the null hypothesis that boundaries occur by chance and are not contiguous. Boundary characteristics including number of subboundaries, number of singleton boundaries (i.e., boundaries consisting of only one cell), maximum subboundary length (a measure of linked boundary elements), and mean and maximum subboundary diameter (a measure of the shortest path-length between each pair of boundary elements in a subboundary) indicated that boundaries were contiguous (Table 2, page 23). Alternatively, there was inconclusive evidence of contiguous boundaries associated with mean subboundary length, and no evidence of subboundary contiguity associated with mean diameter-to-length ratio (a measure of subboundary branchiness) (Table 2, page 23).

Overlaying results from the LCP, corridor, and boundary-detection analyses indicated statistically significant boundary elements within corridors and intersecting LCPs (Figure 8, page 23).

FIGURE 5 Least-cost paths among habitat cores (cost surface in background).

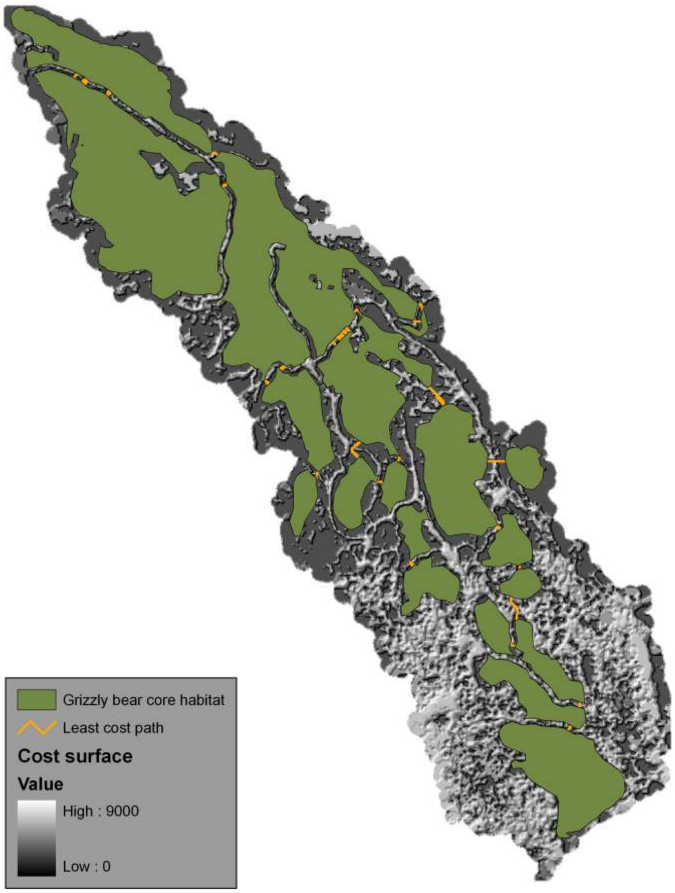


FIGURE 6 Least-cost paths in relation to corridors derived from the spatial analysis.

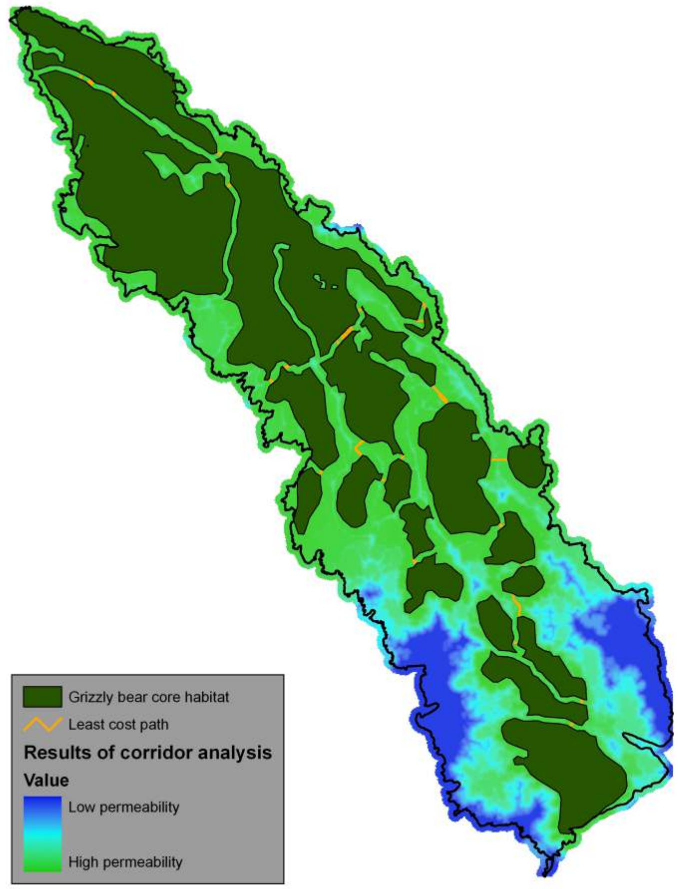


FIGURE 7 Fifth percentile boundary elements in relation to habitat cores and the cost surface.

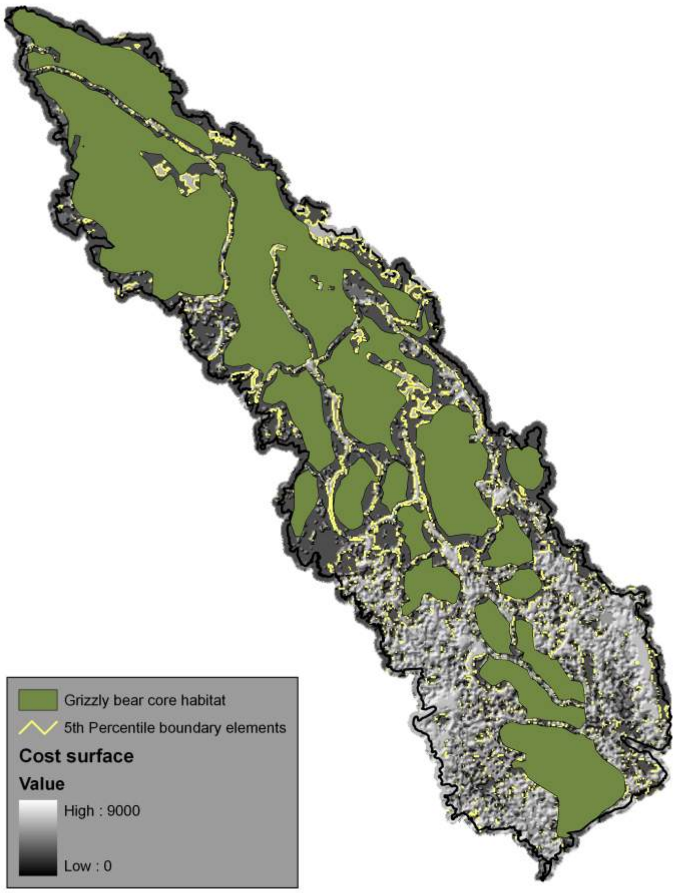


FIGURE 8 Boundary elements in relation to least-cost paths and corridors.

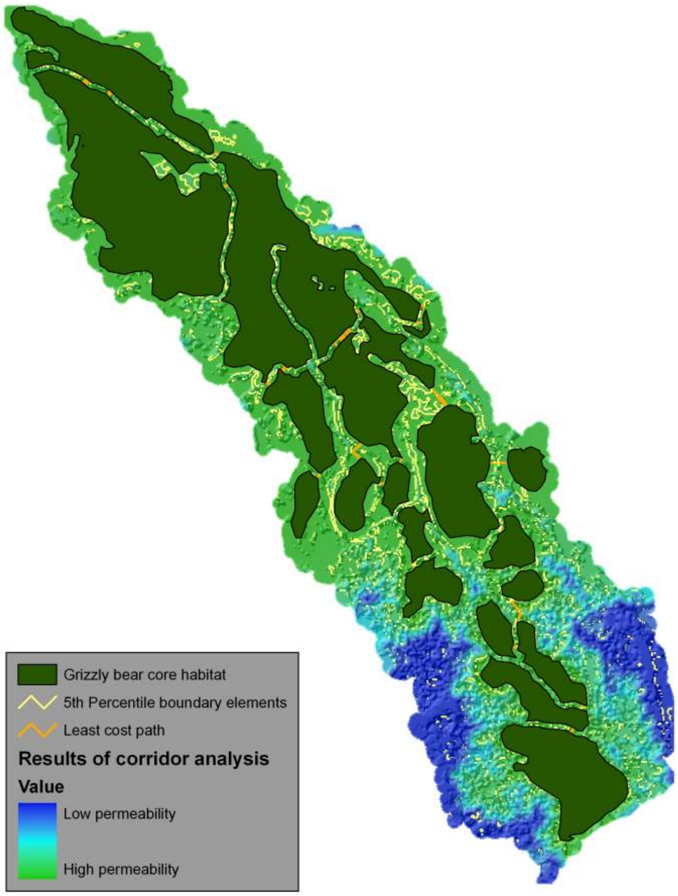


TABLE 2 Results of subboundary analysis.

NS – number of subboundaries, N1 – number of singleton boundary elements, L(mean) – mean subboundary length, L(max) – maximum subboundary length, D(mean) – mean subboundary diameter, D(max) – maximum subboundary diameter, and D/L - mean diameter to length ratio.

	NS	N1	L(mean)	L(max)	D(mean)	D(max)	D/L
Mean	1185.76	978.90	3.08	48.65	2.75	25.87	0.96
SD	123.21	107.36	0.015	6.72	0.011	2.64	0.001
Upper tail P-value	1.00	1.00	0.30	0.01	0.01	0.01	0.01
Lower tail P-value	0.01	0.01	0.71	1.00	1.00	1.00	1.00

DISCUSSION

Setting boundary-likelihood threshold values is an inexact process. From an ecological perspective, the intent is to choose a value that captures the underlying landscape conditions meaningful to the species of interest without delineating boundaries where the magnitude of change is biologically unimportant (see Jacquez et al., 2000; Fagan et al., 2003; Strayer et al., 2003). From a statistical or model fitting perspective, selecting a threshold value can be guided by the distribution of boundary likelihood values, as was the case in this analysis (Figure 4, page 20). Selecting the highest 5% of boundary likelihood values was an arbitrary, albeit conservative figure supported by the literature (see Barbujani et al., 1989; Fortin and Drapeau, 1995) in that it left 95% of the boundary likelihood values "unused". That is, if the species of interest (in this case grizzly bears) were more sensitive to landscape characteristics generating boundary likelihood values than indicated by the 5% threshold, then the number of boundary elements would increase perhaps making the landscape less permeable than indicated in this analysis. Additional work is necessary to forge a stronger link between statistically and biologically meaningful threshold values.

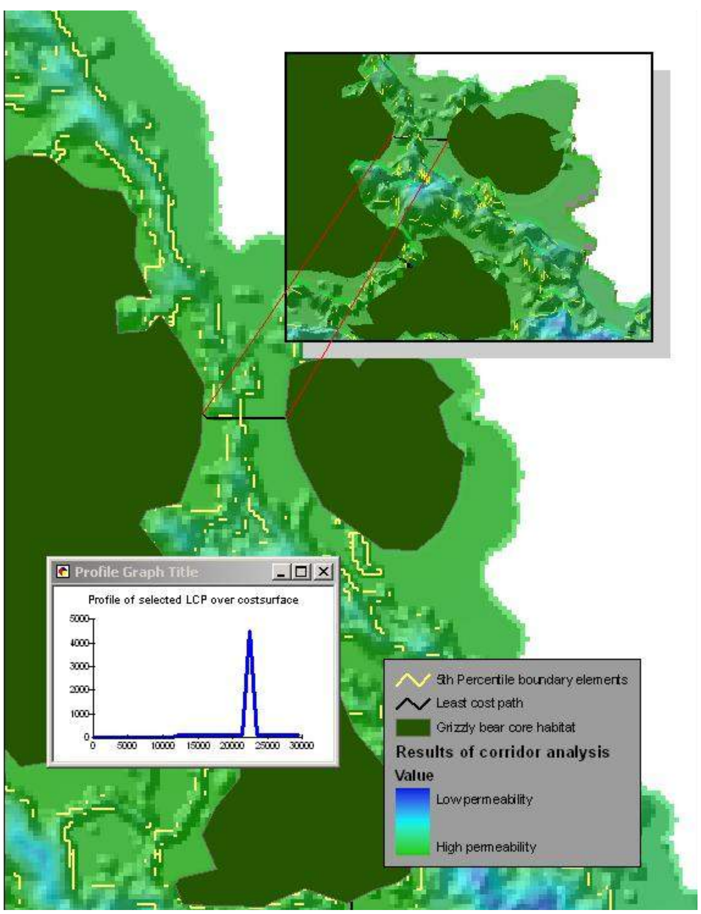
Furthermore, in addition to magnitude, it is important to consider the direction of change taking place (Barbujani et al., 1989). Even if the magnitude of change is similar, a boundary may not exist if the direction of change between boundary elements is opposite (i.e., 180°). The maximum angle for connection of adjacent boundary vectors was set at 135° – halfway between perpendicular and opposite. Thus, if the magnitude of change between a pair of boundary elements is similar and the maximum angle between gradient vectors is ≤ 135°, the boundary elements were considered connected. Adjustments in this value may be reflected in the results of the subboundry analysis.

Results from the subboundary analysis indicated that the delineated boundaries were unlikely to have occurred by chance and were contiguous (see Fortin, 1994; Fortin, 1997; Jacquez et al., 2000). Number of subboundaries and number of singleton boundaries were significant in the lower tail of the distribution (Table 2, page 23) suggesting fewer subboundaries and singletons than by chance. Alternatively, maximum subboundary length (a measure of linked boundary elements) and mean and maximum subboundary diameter (a measure of the shortest path-length between each pair of boundary elements in a subboundary) were significant in the upper tail of the distribution (Table 2, page 23) suggesting more contiguous boundaries than by chance. Mean subboundary length was inconclusive (Table 2, page 23). However, in subsequent investigation, mean boundary length was significant in the upper tail when the threshold for boundary likelihood values were set at 4% and 6%. Mean diameter-to-length ratio was not significant in the lower tail (Table 2, page 23) indicating more branch-like subboundaries than expected by chance.

Findings from this analysis suggest generating LCPs and corridors using GIS is inadequate to evaluate the condition of potential corridors in a CAD. Although boundary elements (i.e., those boundaries with likelihood values above the 5% criterion) are delineated with the same data used to delineate LCPs and corridors, the boundary-detection analysis provides information the other analyses failed to provide. Namely, boundary elements provide spatially explicit information regarding where landscape permeability may be reduced within corridors or inhibit movement along LCPs. One LCP illustrates the potential conflict that can exist along LCPs and within corridors (Figure 9, page 25). There are 89 other such instances. The GIS analysis identified an LCP between two cores and generated a corridor within the landscape. However, LCP and corridor analyses fail to provide all the information necessary to evaluate the quality of potential movement pathways as illustrated by the presence and location of boundary elements (yellow lines), profile view of the LCP (black line) across the corridor map (green to blue color ramp), and 3-dimensional representation of the LCP (inset map, Figure 9, page 25). This illustration indicates movement potential along the selected LCP remains high for several kilometers before costs increase dramatically (inset chart, Figure 9).

For this particular example, the identified subboundary indicates the edge between where land cover is good and population and road density is low, and where the opposite is the case. Presence of the intersecting boundary element may indicate an impediment to movement between these two cores at this location. In other words, just because the LCP and corridor analysis locates a low, or even lowest, cost pathway between two cores does not ensure connectivity exists. Rapid changes in cost, as indicated by the presence of a boundary, may signify a potential barrier to movement.

FIGURE 9 3-dimensional illustration and profile view of the intersection of a boundary element and a least-cost path.



Additionally, statistical evidence associated with the boundary-detection analysis indicated boundary elements produced contiguous subboundaries across portions of the landscape. Subboundaries that intersect an LCP or bisect a corridor (Figure 9) may provide evidence that movement in that location is not tenable for the species of interest. For example, subboundaries indicated locations where magnitude of change in cost was continuously high. This may represent the location of an area of otherwise good habitat that is bisected by a four-lane highway, steep slope, or the edge of an urbanized area.

Boundary-detection techniques also appear useful in identifying prospective cores and corridors. In this context, boundary detection may delineate edges of cores and corridors providing an alternative approach to methods based on landscape homogeneity (Fortin, 1994). Although the results are not presented here, such an analysis on data sets used to create cost surfaces highlight areas of substantial change in landscape characteristics including topography, land cover, and road density.

Results of this research indicate that detection of statistically significant boundaries may affect the functionality of a conservation network. In areas where travel paths or corridors have already been delineated, presence of boundaries indicates potential barriers to movement. Alternatively, in areas where such boundaries are few or absent this type of analysis may be useful in prospectively delineating corridors. Such results enhance conservation by identifying landscape features that potentially affect permeability and incorporating this information to create a functional CAD. Additionally, results from boundary-detection analyses can help managers identify potential corridors worthy of further research, protection, or restoration.

ACKNOWLEDGMENTS

Funding for this research came from the Yellowstone-to-Yukon Conservation Initiative science grant program. Thanks to my science grant colleagues: Dr. Lance Craighead, Baden Cross, Tom Olenicki, and Dr. Justin Williams. Dr. Chris Winne helped write the program to automate the GIS analysis. This manuscript was improved by the comments of two anonymous reviewers.

LITERATURE CITED

Adriaensen, A., J.P. Chardon, G. DeBlust, E. Swinnen, S. Villalba, H. Gulinck, and E. Matthysen. 2003. The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning* 64:233-247.

B.C. Conservation Data Centre. 2008. Species Summary: *Ursus arctos*. B.C. Minist. of Environment. Available: http://a100.gov.bc.ca/pub/eswp/ (accessed Dec 29, 2008).

Barbujani, G., N.L. Oden, and R.R. Sokal. 1989. Detecting regions of abrupt change in maps of biological variables. *Systematic Zoology* 38:376-389.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. *Conservation Biology* 7:94-108.

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

Bunn, A.G., D.L. Urban, and T.H. Keitt. 2000. Landscape connectivity: a conservation application of graph theory. *Journal of Ecological Management* 59:265-278.

Cantwell, M.D. and R.T.T. Forman. 1993. Landscape graphs: ecological modeling with graph theory to detect configurations common to diverse landscapes. *Landscape Ecology* 8:239-255.

Carroll, C. 2006. Linking connectivity to viability: insights from spatially-explicit population models of large carnivores. Crooks, K. and M.A. Sanjayan (eds.) In: *Connectivity Conservation*. Cambridge University Press. Cambridge, UK. Pp. 369-389.

Carroll, C., R.F. Noss, P. Paquet, and N.H. Schumaker. 2003. Use of population viability analysis and reserve selection algorithms in regional conservation plans. *Ecological Applications* 13:1773-1789.

Carroll, C., R.F. Noss, and P.C. Paquet. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. *Ecological Applications* 11:961-980.

Craighead, L. and B. Cross. 2004. A conservation area design (CAD) for the Inland Temperate Rainforest of Canada. http://www.savespiritbear.org/pdf/ITR_Conservation_Design_web.pdf. Last accessed on December 31, 2008.

Craighead, L. and B. Cross. 2005. Identifying core habitat and connectivity for focal species in the Interior Cedar-Hemlock forest of North America to complete a conservation area design: In: Watson, A., J. Sproull, and L. Dean (eds.). 2007. Eighth World Wilderness Congress Symposium; September 30-October 6, 2005. Anchorage, AK. Proceedings RMRS-P-49. Fort Collins, CO: USDA, Forest Service, Rocky Mountain Research Station. Pp. 281-296.

Craighead, L., T. Olenicki, B. Brock, and J. Williams. 2008. A Conservation Area Design for the Inland Temperate Rainforest of North America. BC's Inland Rainforest - Conservation and Community Conference Proceedings. Prince George, British Columbia, Canada. May 21-23, 2008. http://wetbelt.unbc.ca/2008-conference-Craighead-Conservation-Area-Design.html. Last accessed on December 31, 2008.

Endangered Species Act of 1973 7 U.S.C. § 136, 16 U.S.C. § 1531 et seq.

ESRI. 2005. Workstation ArcINFO. Version ArcGIS 9.1. Redlands, CA.

Fagan, W.F., M-J. Fortin, and C. Soykan. 2003. Integrating edge detection and dynamic modeling in quantitative analyses of ecological boundaries. *BioScience* 53:730-738.

Fortin, M-J. 1994. Edge detection algorithms for two-dimensional ecological data. *Ecology* 75:956-965.

Fortin, M-J. 1997. Effects of data types on vegetation boundary delineation. *Canadian Journal of Forest Research* 27:1851-1858.

Fortin, M-J. and P. Drapeau. 1995. Delineation of ecological boundaries: comparison of approaches and significance tests. *Oikos* 72:323-332.

Fortin, M-J., R.J. Olson, S. Ferson, L. Iverson, C. Hunsaker, G. Edwards, D. Levine, K. Butera, and V. Klemas. 2000. Issues related to the detection of boundaries. *Landscape Ecology* 15:453-466.

Harary, F. 1969. *Graph Theory*. Addison-Wesley Publishing Company, Reading, MA.

Henein, K. and G. Merriam. 1990. The elements of connectivity where corridor quality is variable. *Landscape Ecology* 4:157-170.

Horskins, K., P.B. Mather, and J.C. Wilson. 2006. Corridors and connectivity: when use and function do not equate *Landscape Ecology* 21:641-655.

Jacquez, G.M., S. Maruca, and M-J. Fortin. 2000. From fields to objects: a review of geographic boundary analysis. *Journal of Geographical Systems* 2:221-241.

James, P., B. Rayfield, M-J. Fortin, A. Fall, and G. Farley. 2005. Reserve network design combining spatial graph theory and species' spatial requirements. *Geomatica* 59:323-333.

Kaufmann, A., L. Muller, B. Rommel, S. Sengupta, and P. Agarwal. 2001. BoundarySeer: software for geographic boundary analysis. Version 1.0.

Larkin, J.L., D.S. Maehr, T.S. Hoctor, M.A. Orlando, and K. Whitney. 2004. Landscape linkages and conservation planning for the black bear in west-central Florida. *Animal Conservation* 7:23-24.

Majka, D.R., J. Jenness, and P. Beier. 2007. CorridorDesigner: ArcGIS tools for designing and evaluating corridors. http://www.corridordesign.org. Last accessed on December 31, 2008.

Meffe, G.K. and C.R. Carroll. 1997. *Principles of conservation biology*. Sinauer Associates, Inc., Sunderland, MA.

Noss, R.F., C. Carroll, K. Vance-Borland, and G. Wuerthner. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. *Conservation Biology* 16:895-908.

Noss, R.F. and L.D. Harris. 1986. Nodes, networks, and MUMs: preserving diversity at all scales. *Environmental Management* 10:299-309.

Perault, D.R. and M.V. Lomolino. 2000. Corridors and mammal community structure across a fragmented, old-growth forest landscape. *Ecological Monographs* 70:401-422.

Pulliam, H.R. and B.J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *The American Naturalist* 137:S50-S66.

Rouget, M., R.M. Cowling, A.T. Lombard, A.T. Knight, and G.I.H. Kerley. 2006. Designing large-scale conservation corridors for pattern and process. *Conservation Biology* 20:549-561.

Simberloff, D. and J. Cox. 1987. Consequences and costs of conservation corridors. *Conservation Biology* 1:63-71.

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

Singleton, P.H., W.L. Gaines, and J.F. Lehmkuhl. 2002. Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least-cost corridor assessment. PNW-RP-549. Pp. 89.

Singleton, P.H., W.L. Gaines, and J.F. Lehmkuhl. 2004. Landscape permeability for grizzly bear movements in Washington and Southwestern British Columbia. Proceedings of the workshop on border bears: small populations of grizzly bear in the US-Canada transborder region. *Ursus* 15:Workshop supplement:90-103.

Singleton, P.H. and J.F. Lehmkuhl. 1999. Assessing wildlife habitat connectivity in the Interstate-90 Snoqualmie Pass corridor, Washington: In: Evink, G.L., and D. Zeigler (eds.). September 13-16, 1999. Proceedings of the third international conference on wildlife ecology and transportation. Missoula, MT. Pp. 75-83.

Singleton, P.H. and J.F. Lehmkuhl. 2000. I-90 Snoqualmie Pass wildlife habitat linkage assessment: final report. WA: RD489.1. Pp. 97.

Soulé, M.E. 1991. Theory and strategy. Hudson, W.E. (ed.) In: *Landscape Linkages and Biodiversity*. Island Press. Washington D. C. Pp. 91-104.

Strayer, D.L., M.E. Power, W.F. Fagan, S.T.A. Pickett, and J. Belnap. 2003. A classification of ecological boundaries. *BioScience* 53:723-729.

Urban, D.L. and T.H. Keitt. 2001. Landscape connectivity: a graph-theoretic perspective. *Ecology* 82:1205-1218.

Womble, W.H. 1951. Differential systematics. *Science* 114:315-322.