Linking connectivity to viability: insights from spatially explicit population models of large carnivores

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INTRODUCTION

Increasingly, conservation groups and agencies attempt to create regional reserve designs that move beyond a simple aggregation of important sites to form a biologically functional network. As natural habitats are converted for human uses, remaining natural areas simultaneously become smaller and more isolated, reflecting the twin processes of habitat reduction and fragmentation (Wilcove *et al.* 1986). Maintaining connectivity between these remnant natural habitat patches is important for several reasons (Crooks and Sanjayan Chapter 1); on a timescale of generations, a single reserve or patch of natural habitat is unlikely to be large enough to sustain populations of area-sensitive species that are subject to the processes of demographic and environmental stochasticity (Harrison 1994); on a timescale of tens of generations, a single reserve may not be large enough to sustain a population's genetic diversity and maintain evolutionary processes, or allow the species to shift its range in response to long-term environmental trends such as climate change (Frankel and Soulé 1981).

Early literature on assessing landscape connectivity (e.g., Forman and Godron 1986) focused primarily on classifying landscape structure rather than relating this structure to population dynamics of particular species (Hanski 1994; Tischendorf and Fahrig 2000; Moilanen and Hanski 2001). In contrast, functional connectivity, at the scale discussed

in this chapter, is a population-level process that implies that individuals of a species successfully disperse between connected patches and survive to breed in the destination patch. Functional connectivity depends not only on the permeability of the linkage habitat, but also upon conditions in the source and destination patches, such as the production of sufficient potential dispersers. Therefore functional connectivity is best addressed in a whole-landscape context by examining the roles of all landscape elements in promoting or hindering effective dispersal. Functional connectivity, as used here, may be further divided into potential or actual connectivity based on whether the metric is based on model results or field data (Fagan and Calabrese Chapter 12). The models described in this chapter evaluate potential connectivity, but ideally they can inform and be informed by data on actual connectivity. For example, the newly emerging field of landscape genetics provides means to test the hypotheses of connectivity models with genetic data on regional population structure and the likelihood of rare long-distance dispersal events (Proctor *et al.* 2002; Manel *et al.* 2003; Frankham Chapter 4; Neville *et al.* Chapter 13).

Large mammalian carnivores, such as the grizzly bear (*Ursus arctos*) and wolf (*Canis lupus*), are often proposed as focal species for evaluating landscape connectivity, especially in areas such as western North America where large areas remain suitable for species that avoid humans (Soulé and Terborgh 1999). Regional-scale connectivity analyses have also been performed for other taxa, including ungulates in Europe (Bruinderink *et al.* 2003). Typically, the carnivore species have large area requirements, with a population of 500 individuals encompassing tens of thousands of square kilometers (Noss *et al.* 1996), which is larger than the size of most protected areas. Human-associated mortality is an important limiting factor for the large carnivores, and their dispersal through a landscape is often limited or blocked by areas of development or high human access (Thiel 1985), due to behavioral avoidance of developed habitat or excessive mortality in those areas (Paquet and Carbyn 2003). For example, roads may be a good predictor of wolf habitat suitability not because they are physical barriers to dispersal but because they alienate habitat by increasing human access and hence wolf mortality (Mladenoff *et al.* 1995). If we assume that these landscape change processes that fragment large carnivore habitat will eventually affect a broader suite of less-sensitive species, large carnivores may be useful indicator species (Lambeck 1997) for landscape connectivity. In order to increase the generality of conservation guidelines while

retaining the link to species biology, it is often useful to compare connectivity needs of several carnivore species that differ in their area requirements, dispersal ability, and habitat associations. Carnivores may also function as keystone species (Power *et al.* 1996) in some ecosystems, so their continued presence at ecologically effective densities may be important for maintaining ecosystem processes (Soulé *et al.* 2003).

Conservation biologists have long debated whether resources devoted to corridors might be better spent on other goals (e.g., Noss 1987; Simberloff and Cox 1987; Crooks and Sanjayan Chapter 1). Because assessing the trade-off between connectivity and other design goals is difficult without long-term field data on dispersal and demographics, this may be where mechanistic models are most useful. Spatially explicit population models can help planners decide when to allocate resources to protect relatively secure core areas, to stem the degradation of threatened buffer zones, or to restore linkages that are already degraded but might contribute to long-term persistence of metapopulations. This chapter reviews examples of the use of spatially explicit population models to evaluate connectivity for large carnivores in the Rocky Mountains of the USA and Canada and elsewhere in North America. I examine what distinguishes priorities derived from such complex models from those suggested by simpler connectivity metrics, and whether model results are robust enough to our uncertainty about biological processes such as dispersal to provide reliable insights for conservation planners.

WHY USE SPATIALLY EXPLICIT POPULATION MODELS TO EVALUATE CONNECTIVITY?

Spatially explicit population models (SEPMs), (Table 15.1) can be broadly defined as models that represent population processes in combination with the spatial location of individuals and landscape features (Dunning *et al.* 1995; South *et al.* 2002). SEPMs can be divided into those that map an individual's spatial location onto a lattice of cells and those in which a population's or individual's location is independent of any grid structure. The former type of lattice-based models can then be divided by their resolution, such that each grid cell may hold a population, an individual's home range, or be only a portion of a single home range (South *et al.* 2002). Among the latter type of non-lattice-based models are so-called "pseudo-spatial" models that follow aggregate populations that inhabit patches that have a location and distance from other patches, but no internal landscape structure or shape (e.g., VORTEX: Lacy 1993).

Table 15.1. *Definitions of model acronyms used in this chapter*

Acronym	Term	Explanation
ESLI	Ecologically scaled landscape index	Landscape indices based on patch area and isolation scaled to species-specific data on home range size and dispersal distance.
IFM	Incidence function model	A metapopulation model that predicts patch occupancy based on extinction and colonization dynamics dependent on patch area and isolation as well as more complex factors such as Allee and rescue effects.
LCP	Least-cost path model	A model developed in a geographic information system (GIS) that identifies the path between two patches that carries the least total cost. Total cost is based upon the sum of the cost of every cell in the path, with a cell's cost being based on various environmental factors such as slope that impede or facilitate movement or survival.
SEPM	Spatially explicit population model	A model that represents population processes in combination with the spatial location of individuals and landscape features, often by mapping an individual's spatial location onto a lattice of cells.
SPOM	Stochastic patch occupancy model	Patch-based metapopulation models similar to IFMs that incorporate the effect of stochastic processes on patch occupancy.

The lattice-based SEPM considered in depth in this chapter, PATCH (Schumaker 1998; Schumaker *et al.* 2004), represents each home range as a single hexagonal cell. Designed for studying territorial vertebrates, PATCH links the survival and fecundity of individual territory-holders to geographic information systems (GIS) data on mortality risk and habitat productivity measured at the location of the individual's home range by scaling the values in a demographic matrix (Schumaker 1998). Lower GIS habitat scores translate into lower survival rates or reproductive output. Because SEPMs of this type address species distribution and demography on a spatial scale that encompasses many home ranges, they are not suitable for evaluating conservation issues that depend on within-home-range movements, for example, response of carnivore

foraging movements to a small development project or road barrier (Clevenger and Wierzchowski Chapter 20).

Spatially explicit population models may be further categorized based on whether dispersal of individuals is dependent on habitat characteristics of the originating cell, the intervening matrix, or density dependence (triggered by the number of individuals in the originating patch) (South *et al.* 2002). In the PATCH model, users can choose the level of search "intelligence" that dispersers will exhibit. Intelligence options include: (1) a simple random walk with varying degrees of linearity and with increased tendency to settle as the disperser approaches a maximum number of steps; (2) the ability to sense and ascend habitat gradients; or (3) knowledge of habitat beyond immediately adjacent cells, such as the ability to settle on the closest vacant territory or the highest-quality territory within a search radius (Schumaker 1998). Moreover, adult organisms are classified as either territorial or floaters. The movement of territorial individuals is governed by a site fidelity parameter, but floaters must always search for available breeding sites (Schumaker 1998). In contrast to other SEPMs (see Lamberson *et al.* 1992), PATCH has no explicit mortality associated with dispersal beyond that which dispersers experience at the site where they are located at the end of each yearly time step. PATCH was originally developed for study of the northern spotted owl *(Strix occidentalis caurina)*, and this formulation of dispersal mortality may be more realistic for avian dispersers that can fly over habitat, rather than for less vagile terrestrial species.

Spatially explicit population models are often used to study idealized landscapes in order to elucidate general rules governing the impact of landscape structure on species distribution (With and King 2001). Alternately, SEPMs can be used to explore site- and species-specific conservation problems. Although these latter applications may be more relevant to real-world planning questions, they usually require much more biological detail, and it can be more difficult to draw from them general lessons for conservation. Spatially explicit population models that link the movement of individuals to a species dispersal ability and habitat affinity are, by their nature, well suited for analyzing functional connectivity. Besides identifying corridors whose protection has a strong effect on population viability (Carroll *et al.* 2003a), these models can also help identify the location of source and sink habitat in a landscape and evaluate the vulnerability of habitat to landscape change processes such as development (Carroll *et al.* 2004). Spatially explicit population models can help reveal non-linear responses (e.g., population viability thresholds)

of species to increasing habitat protection. However, the added complexity of SEPMs increases model sensitivity to poorly known parameters such as maximum dispersal distance (Ruckelshaus *et al.* 1997).

CONNECTIVITY IN CONTEXT: CLASSIFYING LANDSCAPES BASED ON PATCH/MATRIX CONTRAST

The relative level of connectivity between core habitat patches is one of several factors affecting the persistence of area-sensitive species in fragmented landscapes (Carroll *et al.* 2004). The importance of connectivity as compared to other factors, such as patch size and total habitat area, will vary with the dispersal ability of the species and the quality of the landscape matrix (Andrén 1994). This point is illustrated by the status of grizzly bear and wolf populations across the 750 000 km² Yellowstone-to-Yukon region (Chadwick 2000) in the Rocky Mountains of the northern USA and Canada (Carroll *et al.* 2004). The Yellowstone-to-Yukon region shows a strong contrast in the condition of landscape matrix from its more-developed southern end in the northern USA to its northern end in northwestern Canada. In the northern portion of the region, protected areas are embedded within a relatively benign landscape matrix, whereas in the south, they more closely resemble habitat islands (Carroll *et al.* 2001; Noss *et al.* 2002).

The Greater Yellowstone Ecosystem is the strongest example in the western USA of a situation that increasingly typifies protected areas throughout the world: a large core refugium is surrounded by rapidly growing human populations (Noss *et al.* 2002). In such a landscape with ''high contrast'' between protected areas and the landscape matrix, it may be so challenging to re-establish connectivity for some species that protection of linkage zones represents a lower conservation priority than protection of buffer habitat. In some areas of the Greater Yellowstone Ecosystem, protection of blocks of habitat may help achieve both goals. For example, protection of grizzly bear habitat in the buffer zone of the northwestern Greater Yellowstone Ecosystem (e.g., Madison Valley) might also help re-establish connectivity with the central Idaho core area. Protection of areas at the northern extremity of the Greater Yellowstone Ecosystem, in a proposed corridor to the more distant Northern Continental Divide Ecosystem, may be a less realistic conservation investment, since the area would likely function as sink habitat with little impact on enhancing functional connectivity or grizzly bear population persistence. Habitat restoration could move the overall regional landscape towards a condition

that would eventually recreate the historically connected grizzly bear metapopulation. However, the area of newly protected habitat necessary for this to occur is much greater (Carroll *et al.* 2003a) than that identified by analyses focused solely on linear carnivore movement corridors (Boone and Hunter 1996; Walker and Craighead 1997; Singleton *et al.* 2002).

Unlike in these high-contrast landscapes, in "low-contrast" areas such as northern British Columbia, human activities are still at sufficiently low levels that vulnerable species such as large carnivores still use much of the landscape matrix. Because species in these low-contrast landscapes are not restricted to defined corridors, the usual planning paradigm of core and buffer habitat linked by corridors (Noss and Harris 1986) may not be as useful as would be a "reversed paradigm" that maintains wild-lands as the landscape matrix with human settlements linked by "developed corridors" (Noss 1992). Thus what I categorize as "medium-contrast" landscapes remain as the situation in which connectivity may be a critical component of conservation planning. These landscapes are often located on the margin of a species' continuously inhabited range, where this continuous distribution is beginning to break up into isolated populations due to fragmentation, but enough habitat remains in the matrix that core areas are not yet comparable to islands.

Carroll *et al.* (2004) tested the applicability of the patch/matrix paradigm across the Yellowstone-to-Yukon region by predicting the ability of existing park systems to sustain carnivore populations (grizzly bears and wolves) based on both a SEPM and a simpler logistic regression model that used only data on park area and connectedness (or isolation). The patterns of persistence of grizzly bear predicted by the PATCH model for the region's parks agreed with those from the area-isolation logistic regression models for the grizzly bear in developed (northern US Rocky Mountains) and semi-developed (southern Canadian Rocky Mountains) landscapes. The area-isolation logistic regression model for the grizzly bear performed poorly where the landscape matrix contained large amounts of suitable habitat (northern Canadian Rocky Mountains). Moreover, park area and connectedness were poor predictors of gray wolf occurrence due to this species' broader-scale range dynamics and greater ability to inhabit the landscape matrix. Based on the logistic regression results, a doubling of park area corresponded to a 47% and 57% increase in projected grizzly bear population persistence in developed and semi-developed landscapes, respectively. In comparison, a doubling of a park's connectedness index corresponded to an 81% and 350% increase in grizzly bear population persistence in developed and semi-developed landscapes,
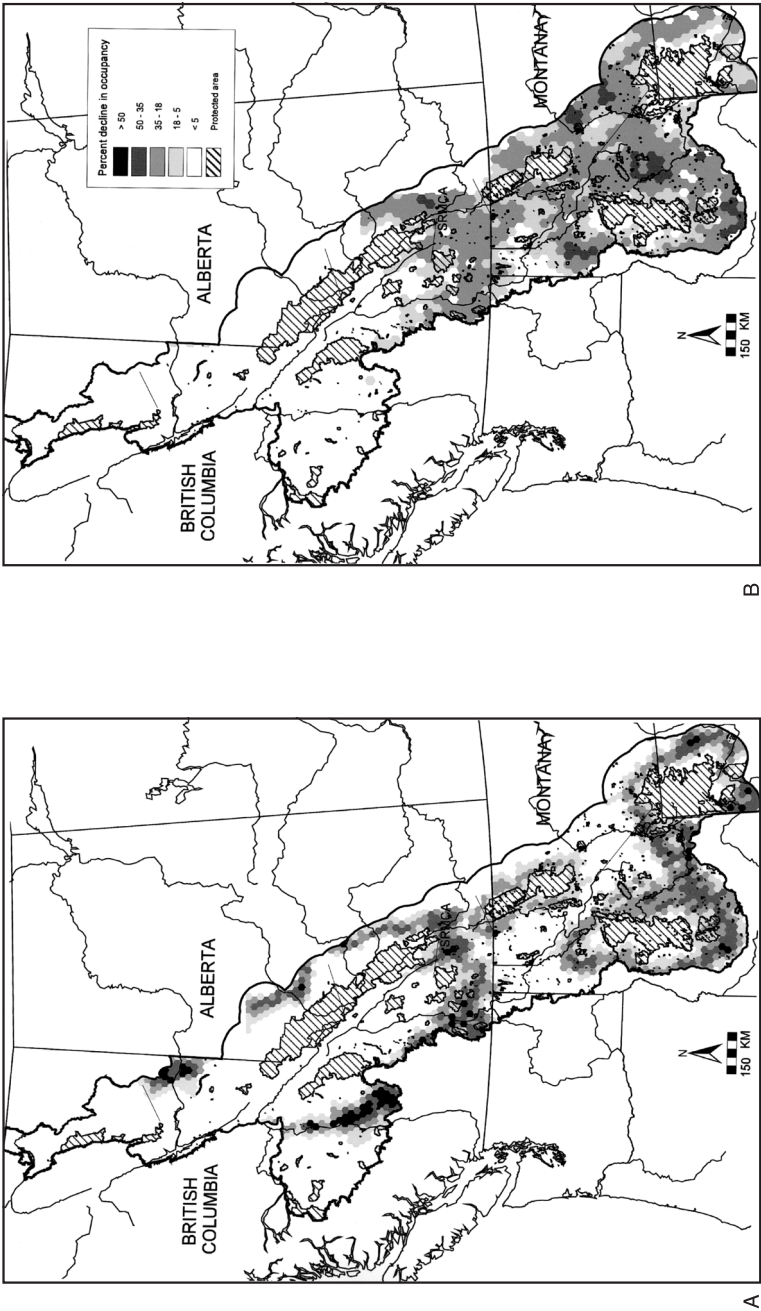
Fig. 15.1. Reduction in potential carrying capacity as predicted by the PATCH model due to landscape change from 2000–2025 for (A) grizzly bear and (B) gray wolf in the Rocky Mountains of Canada and the United States. (Adapted from Carroll *et al.* 2003a.)

respectively, suggesting that conservation planning to enhance connectivity may be most effective in the earliest stages of landscape degradation (Carroll *et al.* 2004). The PATCH results suggest that the role of the landscape matrix for sustaining connectivity varied between the two species, causing parks in the US Northern Rockies to support a functionally connected metapopulation of gray wolves, versus several disjunct populations of grizzly bears. However, in these model scenarios, landscape change trends move the US Northern Rockies landscape towards a condition where the wolf subpopulations would also become increasingly isolated (Carroll *et al.* 2003a) (Fig. 15.1). This is due not only to increasing barriers to movement (e.g., highways), but also to degradation of source habitat and consequent reduction in the numbers of dispersers and the area of sink habitat that can be sustained by this dispersal (Fig. 15.1). Range contraction (decrease in probability of occupancy in Fig. 15.1) occurs primarily on the edges of core habitat for the grizzly bear, but throughout the landscape matrix for the wolf.

CORRIDOR PLANNING IN MEDIUM-CONTRAST LANDSCAPES: AN EXAMPLE

Although SEPM results may be most informative for conservation planning at regional scales, these models may also aid corridor design at the finer subregional scales more commonly considered by planners. For example, Carroll *et al.* (2002) used the PATCH model to compare the effects on connectivity of contrasting conservation proposals in the semi-developed, medium-contrast landscape along the Highway 3 area in southwestern Alberta and southeastern British Columbia (Canada/USA transboundary region), which separates the large parks and undeveloped areas to the north from more isolated southern refugia that range in size from Glacier/Waterton Parks (4500 km²) in the Northern Continental Divide Ecosystem to smaller areas of around 1000 km² in Idaho's Selkirk Mountains, and the Cabinet/Yaak (Montana) and Granby (British Columbia) areas (Proctor *et al.* 2002).

The land-use scenarios considered by Carroll *et al.* (2002) include:

(1) current carrying capacity
(2) current trends to 2025, assuming development on both public and private lands
(3) current trends to 2025, assuming no further road construction on public lands

(4) creation of an absolute barrier or zone of inhospitable habitat along the Highway 3 area

(5) proposed Waterton Park expansion, enlarging the park to encompass areas primarily in the North Fork of Flathead (British Columbia) (Weaver 2001)

(6) proposed Southern Rocky Mountains Conservation Area, connecting the Northern Continental Divide Ecosystem to the Rocky Mountains parks across the Highway 3 area in the area of Fernie, British Columbia (Weaver 2001).

Under current landscape conditions, the SEPM results predicted that the probability of maintaining a continuously distributed population of grizzly bears across the Highway 3 area over the long term is low. Importantly, these simulation results are equilibrium predictions, in that current predictions depict the current capacity for an area to support a carnivore species over the long term (200 years), which may be lower (e.g., grizzly bears in southeastern British Columbia) or higher (grizzly bears in central Idaho) than the number of animals currently inhabiting that area. Field data suggests that the highway area currently functions as a semi-permeable sex-biased ''filter,'' with lack of female grizzly bear dispersal creating genetic divergence between bear populations to the north and south of the highway (Proctor *et al.* 2002). In the SEPM results of Carroll *et al.* (2002), landscape change through 2025 made this connection even more tenuous due to the retreat of grizzly bear range to the south and north. Because of a negative ''ripple effect'' of habitat loss in other parts of southeastern British Columbia on grizzly bear distribution to the north of Highway 3, connectivity in this area will be more difficult to maintain. Assuming no further road construction on public lands greatly reduced range loss in the model, but range contraction was still extensive in the Rocky Mountain Front, the immediate Highway 3 area, and the Columbia Trench. The effect of an absolute barrier (e.g., expanded multi-lane highway) in the Highway 3 area was noticeable under current conditions, but minor under 2025 conditions, as projected development already effectively excluded bears from the highway zone. For grizzly bears, the Waterton Park expansion was effective at counteracting the effects of landscape change to the south of the highway, but the larger Southern Rocky Mountains Conservation Area proposal was most effective at retaining a level of connectivity at or higher than the current condition, despite increasing development in other parts of the transboundary region (Fig. 15.2A). The positive ripple effect for both
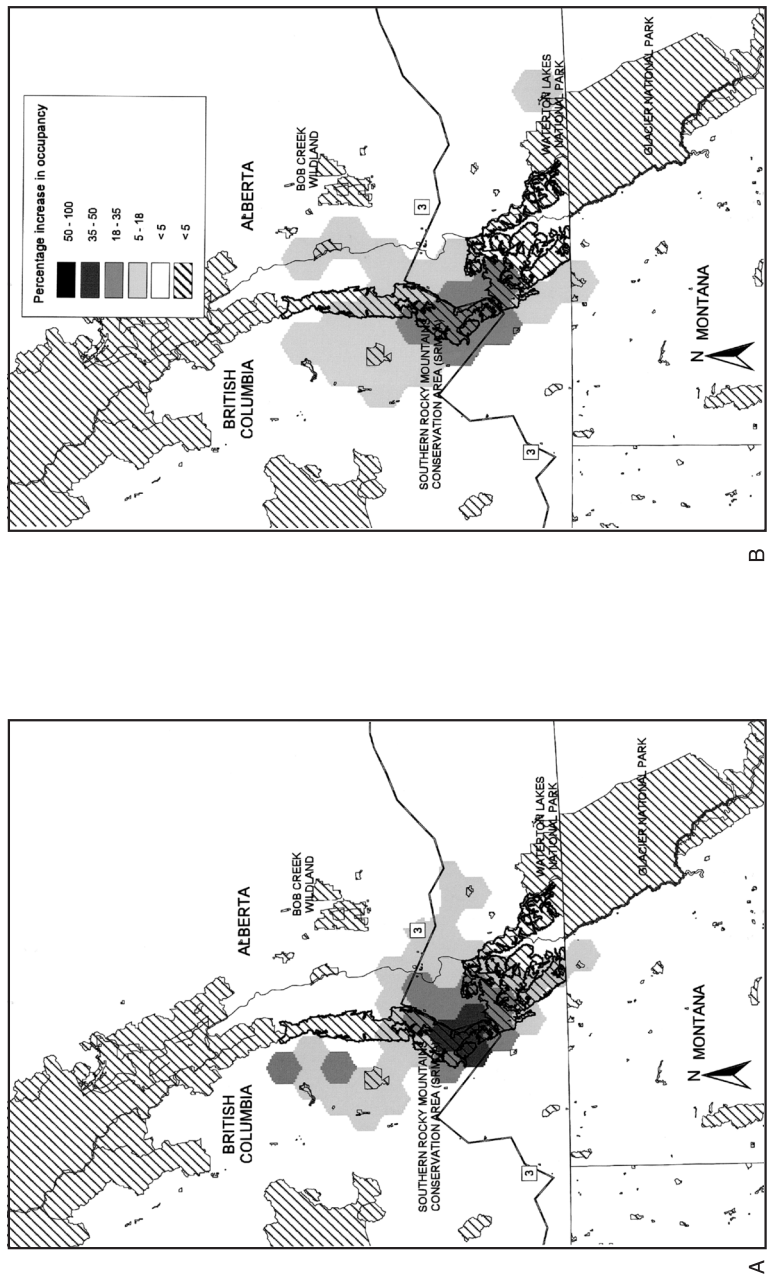
Fig. 15.2. Increase in potential carrying capacity in response to proposed park expansion within the Southern Rocky Mountains Conservation Area as predicted by the PATCH model for (A) grizzly bear and (B) wolf in the Canada/USA transboundary region under future landscape conditions (2025). (Adapted from Carroll *et al.* 2002.)

the Waterton expansion and the Southern Rocky Mountains Conservation Area on bear distribution was extensive beyond the boundaries of the proposed park areas in both Alberta and British Columbia.

For the wolf, the PATCH model predicted a continuous distribution across the Highway 3 area throughout the area under current landscape conditions (Carroll *et al.* 2002). Connectivity was most pronounced on the Alberta side of the border. However, with landscape change, long-term connectivity was effectively lost by 2025. When compared to the situation for grizzly bears, loss in carrying capacity for wolves was more widespread throughout the region because wolves are more tolerant of human impacts and hence use more areas in the landscape matrix that are at risk from development. Loss in demographic potential for wolves was greatest along the Rocky Mountain Front. In the model results, the Southern Rocky Mountains Conservation Area preserved connectivity both within its boundaries and via a ripple effect in the Alberta Highway 3 area (Fig. 15.2B).

In summary, greater dispersal ability and subsequent interlinkage of populations in the wolf versus the grizzly bear makes the effect of the Highway 3 barrier scenario more noticeable, but still of little more impact than predicted future conditions in which development trends alone approximate a barrier there. For the wolf, the positive ripple effect of the Conservation Area is similar, but not as strong as it is for the grizzly bear. The effect of the Waterton expansion is also less pronounced for the wolf than for the bear.

CORRIDOR PLANNING AND PATTERNS OF DISPERSAL

The pattern of range expansion in response to habitat restoration scenarios shown in the above SEPM simulations for the Highway 3 area can help in siting corridors where they are most likely to exhibit functional connectivity. These simulations can similarly be used to rank various restoration proposals by measuring the relative magnitude of their effect on species distribution. The SEPM-based evaluation of the Highway 3 area (Carroll *et al.* 2002) shows similarities with earlier work using static models of habitat suitability (Apps 1997). Similarly, a SEPM-based analysis of wolf viability in the northeastern USA and southeastern Canada (Carroll in press) identified a key linkage area between Adirondack (New York) and Algonquin (Ontario) parks that had been described previously using the least-cost path (LCP) analysis (Quinby *et al.* 2000; for a description of the least-cost path technique see Theobald Chapter 17). The SEPM

analysis, in addition to identifying the linkage zone, rated its relative probability as a dispersal route as similar to linkages to the east from Quebec to northern Maine, but highlighted risks of a rapid decline in functional connectivity over time, as well as threats to the viability of the extant source population (Algonquin) and potential destination population (Adirondacks) (Carroll 2003). These results suggest that the level of conservation effort required to protect the narrow Algonquin-to-Adirondacks linkage was much greater than that necessary to protect any intraregional connectivity (e.g., between a reintroduced wolf population in Maine and adjacent New Brunswick). Since a reintroduced Maine wolf population was found to be demographically viable without dispersal from Canada, intra-regional linkages may be a higher priority than inter-regional connectivity in this situation.

In contrast to the Algonquin-to-Adirondacks results, a study using a SEPM to assess wolf viability in the southern Rocky Mountains (USA) failed to identify a likely corridor from Yellowstone south to Colorado (Carroll *et al.* 2003b). (More recently, wolves have dispersed across this distance but have been killed before establishing territories due to livestock conflicts or road mortality.) In some regional landscapes such as southern Wyoming, the pattern of dispersal as simulated in PATCH is fairly uniform, whereas in other regions, such as the Adirondacks, it is channeled into corridor-like paths. This pattern is due to both the level of habitat contrast in the landscape, and the overall likelihood of effective dispersal between source and destination area. In the Algonquin-to-Adirondacks example, the source and destination areas were relatively close (~250 km) and the intervening landscape was highly modified by agriculture except in one area. In the Colorado example, source and destination area were more distant (~500 km), and the intervening landscape was sparsely settled and characterized by extensive land use such as grazing (Carroll *et al.* 2003b). The channelization of dispersal paths in the Algonquin-to-Adirondacks region was accompanied by a high sensitivity of model results to variation in dispersal parameters. This sensitivity may occur because this regional landscape is currently at a threshold for effective wolf dispersal (Carroll 2003). The narrow dispersal corridor predicted for Algonquin-to-Adirondacks cause the least-cost path results to mimic more complex SEPM results better than they would match the broad wave of dispersal predicted by SEPMs in many regions.

The regional contrasts in SEPM results may be, in part, an artifact of how dispersal mortality is treated in the PATCH model. Because there is no explicit dispersal mortality except at the end of each yearly time step

(Schumaker 1998), the likelihood of a disperser traversing a short but highly hostile landscape may be overestimated. Sensitivity of results to poorly known parameters, particularly dispersal distance, is an often-cited weakness of SEPMs (Ruckelshaus *et al.* 1997; Coulson *et al.* 2001). Other authors have identified this behavior as most typical of simple SEPMs that lack a demographic context, or that use a dispersal function that is not sensitive to landscape structure (Mooij & DeAngelis 1999; South 1999). In several SEPM-based studies of wolf population dynamics across a range of North American landscapes (Carroll *et al.* 2003a, 2003b, in press), probability of recolonization of distant habitat varied with the parameter used for maximum dispersal distance (Table 15.2). However, model results, and the resulting conservation recommendations, were qualitatively similar across the biologically plausible range of dispersal distances for this species (Table 15.2).

Compared to other SEPM parameters, the importance of dispersal varies with landscape context and appears to be most important at moderate levels of fragmentation (Rushton *et al.* 2000; Carroll *et al.* 2004). Furthermore, dispersal parameterization is rarely a significant factor in determining population persistence in SEPMs (Macdonald and Rushton 2003). The inherent uncertainty attached to predictions of rare dispersal events suggests that SEPMs may not provide useful estimates of the probability of natural recolonization of a patch of potential habitat from a distant source population (Carroll *et al.* 2003b). Of more concern than the dispersal distance parameter itself may be the differences in pattern between actual dispersal paths and the simplified rules, such as correlated

Table 15.2. *Sensitivity of wolf dispersal success in different study regions to different parameters for maximum dispersal distance using the PATCH model*

	Wolf dispersal distance (km)		
	250	500	1500
Recolonization probability (%)			
Maine	0.42	3.54	10.62
Adirondacks	0.30	12.33	43.68
Colorado	0.34	0.95	2.20
Adirondacks (2025)	0	0	0
Colorado (2025)	0	0	0

Source: Unpublished data from studies reported in Carroll *et al.* (2003a) and Carroll (2003).

random walks, used in SEPMs; dispersing animals likely respond to complex environmental cues, including conspecific attraction and fine-scale habitat structure (Lindenmayer *et al.* 2003; Tracey Chapter 14). Heterogeneity between individuals and contrasts between the same individual's behavior in the initial and later stages of a dispersal path (Morales and Ellner 2002) may add additional complexity. Although much of this complex behavior may not result in qualitative contrasts in the distribution of dispersers, they must be considered in SEPMs if they are to provide realistic estimates of dispersal success. Unfortunately, it is the few longest-distance dispersers that most influence model results, and these individuals are often unrecorded by field studies (Shigesada and Kawasaki 2002).

COMPARING SPATIALLY EXPLICIT POPULATION MODEL RESULTS TO THOSE FROM SIMPLER LANDSCAPE INDICES AND MODELS

Least-cost path techniques (Theobald Chapter 17) are one example of methods relating landscape structure to connectivity that are easier to calculate and less "data hungry" than are SEPMs, and that are more capable of being generalized to new situations (Table 15.1). Ecologically scaled landscape indices (ESLIs) (Vos *et al.* 2001) also attempt to make simple landscape indices, such as patch area and isolation, more biologically relevant by scaling them based on species-specific data on home range size and dispersal distance. Although it might be possible for SEPM results to be generalized into rules or indices that approximate simulation results in novel landscapes, comparisons of most landscape metrics against predictions of connectivity (i.e., dispersal success) from SEPMs have shown that the two match poorly (Schumaker 1996). As demonstrated above, representing a landscape mosaic of diverse habitat types as a binary system of discrete habitat patches, embedded in a non-habitat matrix, works best in highly fragmented landscapes (Carroll *et al.* 2004). These types of landscapes are increasingly common in conservation planning for endangered species, especially in regions with high human population density. However, it is important to avoid sacrificing biological relevance in the quest for model generality, and it remains unclear how informative simpler models such as least-cost paths are in the many regions and species contexts with intermediate levels of landscape contrast.

Metapopulation models (Moilanen and Hanski Chapter 3) are structurally more complex and potentially more biologically realistic than least-cost path techniques. However, the populations of large carnivores treated in this chapter often do not strictly conform to a classic metapopulation model. Some use is made of matrix habitat, and thus populations are not confined to island-like patches that experience repeated extinction and recolonization (Carroll *et al*. 2004). Habitat structure within patches is also important to the likelihood of population persistence. For poor dispersers such as grizzly bears, if "matrix" habitat is benign enough to allow dispersal, then it is likely to also occasionally support territorial individuals, and thus should be considered for its demographic role as sink habitat. If it is not benign enough to allow dispersal, then area effects alone, rather than connectivity, will be sufficient to predict viability. For many species, such as grizzly bears, the regional metapopulation is in a non-equilibrium state (Harrison 1994), and extinction events occur in small patches but few colonization events occur. For other species, such as wolves, both extinction and colonization events are common, so in landscapes that are fragmented to the degree that wolves no longer constitute a single patchy population, metapopulation concepts in the strict sense may indeed be relevant.

While the classic division of landscapes into patch and matrix is attractive due to its simplicity, biologists are increasingly moving towards more variegated habitat models that portray landscapes in shades of gray rather than black and white (Fischer *et al*. 2004). Least-cost path and more recent metapopulation models can incorporate varying levels of matrix permeability but cannot expand the patch-matrix model to allow for the demographic effect of poor but suitable (i.e., sink) habitat (Possingham *et al*. 2005). In addition, least-cost path techniques do not explicitly incorporate population viability. Irrespective of a species' dispersal ability, a least-cost path model will always identify a "best" linkage between source and destination patch. A least-cost path model assumes that "source" populations are known and fixed, whereas an SEPM makes no such assumptions, but attempts to specify where sources and sinks are in the landscape. Linkage areas identified in an SEPM-based analysis must meet a biological threshold for effective dispersal (i.e., the path is not too costly to be used), and the core and buffer habitat that anchor the ends of a corridor must provide sufficient dispersers to make the corridor effective. An SEPM-based analysis might lead to placement of a corridor in an area with a more "costly" path but stronger anchor

habitat, or in the shifting of priorities away from linkage zones if these appeared as poorer conservation bargains.

CONCLUSION

Choosing between the various models of connectivity depends on an assessment of what level of model complexity might provide better guidance in a particular conservation planning context. There is a need for a typology of landscape and species combinations that can suggest to planners which types of models are most informative for their problem. I have made the case that for wide-ranging species in medium-contrast landscapes, a simple connectivity metric such as patch isolation is unlikely to substitute for SEPM-based mechanistic and context-specific predictions of the probability of functional connectivity and persistence in a patch. Spatially explicit population models may be especially useful in providing information on population vulnerability under novel future scenarios that is hard to extract from other, simpler metrics (Carroll *et al.* 2004). However, these types of scenarios are a small subset of the situations that confront conservation planners. The match between models and metrics is expected to be better for landscapes and species combinations for which the binary habitat/non-habitat landscape is a reasonable approximation. For example, a good candidate for simpler models might be a species that shows strong associations with a single type of habitat (such as the northern spotted owl with old-growth forest), in a landscape with processes (e.g., clearcut logging) that tend to produce hard edges between patch and matrix at a scale similar to that of the species' home range. Similarly, the vagility of the species should be intermediate in relation to the level of contrast on the landscape, not being so low that all patches are isolated nor so high that the intervening matrix has little effect on dispersal success. A rigorous comparison of the conservation priorities identified by ESLIs, graph theory, SPOMs, and SEPMs (Table 15.1) in such a landscape would help planners assess the strengths and weaknesses of the diverse approaches to modeling connectivity.

The most important contribution of SEPMs to connectivity planning may not be their specific predictions, but rather the way in which they link connectivity tightly to its role in promoting population viability. The separation of connectivity from viability has led to potential misuse of the former concept in conservation planning. For example, conservation organizations increasingly use the term ''corridor'' to refer to regional landscapes that would, in traditional conservation planning terminology,

be instead a planning landscape divided into components of cores, buffers, and corridors, each with distinct management regimes (Noss and Harris 1986). Use of corridors in this broad sense tends to obscure the distinct roles played by the different components, e.g., strictly protected habitat that can sustain sources of species vulnerable to human-induced mortality versus less secure habitat (corridors in the narrow sense) that may sustain movement of these species. In this case, designation of the landscape as a "corridor," which is assumed to require few restrictions on land use, may be a means of avoiding the harder challenges to slowing the loss of both core and connective habitat.

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