

Corridors for Conservation: Integrating Pattern and Process

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Key Words

behavior, habitat selection, movement, resource selection
functions, scale

Abstract

Corridors are commonly used to connect fragments of wildlife habitat, yet the identification of conservation corridors typically neglects processes of habitat selection and movement for target organisms. Instead, corridor designs often are based on binary patterns of habitat suitability. New technologies and analytical tools make it possible to better integrate landscape patterns with behavioral processes. We show how resource selection functions can be used to describe habitat suitability with continuous and multivariable metrics and review methods by which animal movement can be quantified, analyzed, and modeled. We then show how the processes of habitat selection and movement can be integrated with landscape features using least-cost paths, graph theory, and step selection functions. These tools offer new ways to design, implement, and study corridors as landscape linkages more objectively and holistically.

Corridor: regions of the landscape that facilitate the flow or movement of individuals, genes, and ecological processes

Matrix: component of the landscape that is neither patch nor corridor

INTRODUCTION

Corridors are cornerstones of modern conservation. Traditionally, corridors have been viewed as linear strips of habitat that facilitate the movement of organisms through landscapes (Puth & Wilson 2001). Corridors, often in association with the charismatic megafauna whose populations they are designed to conserve, are a fundamental component of wildland conservation, particularly in North America where many regional and several continental-scale corridor initiatives are underway (Nelson et al. 2003, Noss 2003). International corridors foster new levels of transboundary conservation, elevating corridors from an ecological to a political and socioeconomic tool (Zimmerer et al. 2004). Despite the widespread application of corridors, much current practice causes them to fall far short of their conservation promise. On-the-ground applications of corridors usually are based on simplistic depictions of habitats that are assumed to provide the associated ecological processes. Typically, corridor applications proceed with little species-specific information and limited evaluation, and they are rarely published or reviewed in scientific journals (Vos et al. 2002; but see Beier et al. 2006). In some cases, corridors, selected for their political appeal, are being plunked down willy-nilly on landscapes that already have been carved up for other purposes. This makes the provision of practical corridor guidelines for managers as big a challenge today as it was over a decade ago (Hobbs 1992).

A grizzly bear (*Ursus arctos*) tagged as "99" and his victim provide a compelling study in the failings of this approach. This young male bear wandered into the fringes of the burgeoning town of Canmore, Alberta, in late May, 2005. After showing indifference to human encounters, it was captured on a local golf course and relocated by government conservation officers. A week later, "99" was detected in a designated wildlife corridor above the town of Canmore, one that was a scant 1000 m wide, perforated with human-use trails, and sandwiched between a recently built golf course and steep slopes above the townsite. By day's end, both the bear and a young woman were dead, and the world tuned in to Alberta's first grizzly-caused human fatality in seven years. Critics were quick to blame the wildlife policy that relocated the bear. But the bigger failing occurred years previously with the designation of the corridor. Corridors based on scant biological data supported Canmore's rapid development during the 1990s, obliterating much of the wildlife habitat in this montane valley. Too little fertile and connected habitat remains in the valley that contains Canmore to support grizzly bear movement to adjacent protected areas in the Canadian Rocky Mountains (Herrero 2005). Indeed, examining movements of three other grizzly bears in this area suggests that the designated corridors actually are avoided, and the oft-assumed distinction between corridor and matrix is not apparent (**Figure 1a**). Despite various planning guidelines supporting corridor designations (BCEAG 1999), the corridor designs in Canmore require important modifications, at least for grizzly bears. We suggest that more sophisticated approaches to corridor designs not only are possible but essential if corridors are to realize their potential for conserving biodiversity.

Although they have limitations (reviewed by Hilty et al. 2006), corridors have been promoted widely as a conservation strategy. Since their introduction as a tool for game management in the 1940s (reviewed by Harris & Scheck 1991), over 700

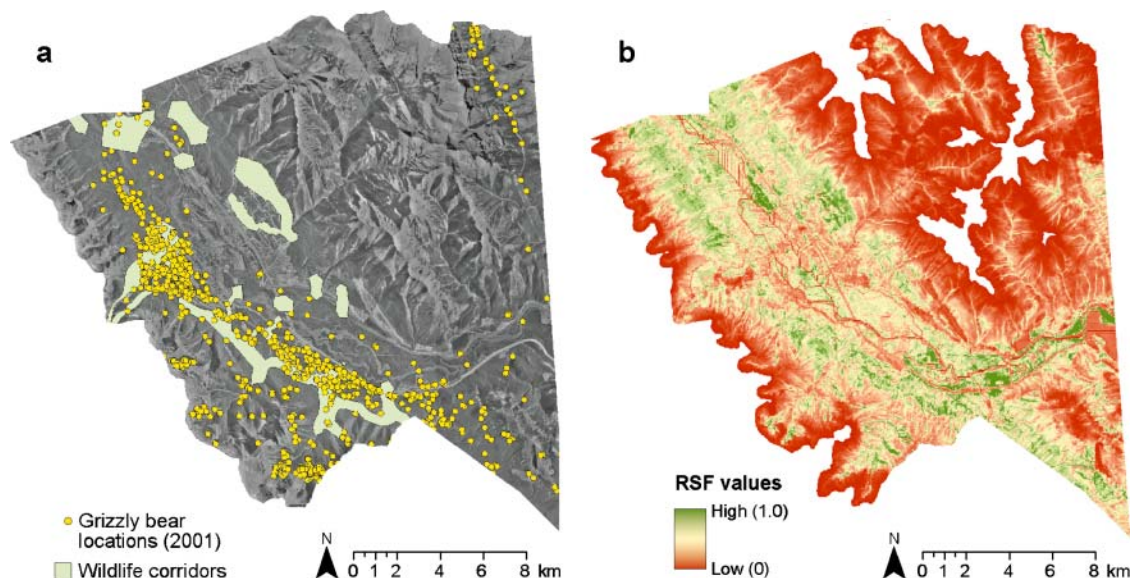


Figure 1

Telemetry locations for three grizzly bears during 2001 and designated wildlife corridors in the Canmore region of the Bow Valley, Alberta, Canada (*a*) were used to generate a resource selection function (RSF; *b*) (BCEAG 1999; C.-L. Chetkiewicz, unpublished data). An RSF was created using logistic regression to compare topographic and vegetation variables at grizzly bear telemetry locations obtained during 2001 with those at random points within the combined home ranges of the three bears. Applying the RSF in a geographic information system (GIS) identifies areas likely to support grizzly bear occupancy. Areas of high relative probability of occurrence (*green*) could be used to evaluate or amend corridor designations or guide recommendations to amend current corridor designations.

scientific papers concerning corridors have been published. Most acknowledge that the purpose of corridors is to counter the effects of habitat loss and fragmentation, which are important causes of biodiversity loss worldwide (Dirzo & Raven 2003, Sih et al. 2000). Corridors are expected to slow these effects by increasing the movement of individuals among otherwise-isolated populations (e.g., Gilbert et al. 1998, Gonzalez et al. 1998), thereby rescuing populations from stochastic local extinctions (e.g., Brown & Kodric-Brown 1977, Reed 2004), maintaining genetic diversity (e.g., Hale et al. 2001, Mech & Hallett 2001), and retaining ecological processes (Bennett 1999, Haddad & Tewksbury 2006, Hilty et al. 2006, Levey et al. 2005, Soulé & Terborgh 1999). Additionally, corridors might serve to provide routes and habitats for movement of organisms responding to climate change (Channell & Lomolino 2000). Other approaches to conserving biodiversity might be more effective than corridors (Hannon & Schmiegelow 2002, Schultz 1998) or offer better return on the investment of limited conservation dollars (Hobbs 1992, Simberloff & Cox 1987, Simberloff et al. 1992). We do not address these issues here. Rather, we assume that corridors will continue to occupy the conservation toolbox and ask how that tool can be used most effectively.

Pattern: spatial relationship between components within a landscape or ecosystem

Process: interaction between spatial components and the flow of energy, individuals, or genes

Functional connectivity: the degree to which a landscape facilitates or impedes movement among resource patches

Scale: the spatial or temporal dimension of an object or process, characterized by both grain (resolution) and extent

One important impediment to the effective use of corridors is the gap between their intended purpose and actual application, which generates a dichotomy between pattern and process. By pattern, we mean the composition and spatial configuration of habitats (Turner et al. 2001, Wiens 1995) and snapshots of organism distribution derived from censuses. By process, we mean the ways animals actually move within landscapes to cause patterns of distribution and drive related ecological processes. Probability of movement then determines the functional connectivity of landscapes (Taylor et al. 1993, Tischendorf & Fahrig 2000a,b). Despite the fact that the process of animal movement provides the impetus for corridor design and application, it is the pattern of landscape structure that dictates most of the research, planning, and application of corridors (Beier & Noss 1998, Vos et al. 2002). Extensive review (Beier & Noss 1998) found corroboration between corridor patterns and process-based metrics such as immigration and colonization rates in fewer than half of the studies. Since that time, dozens more observational and experimental studies have focused on corridors. A few emphasize processes (e.g., Berggren et al. 2002, Levey et al. 2005, Sieving et al. 2000). More often corridor designations are based—as they were in Canmore—on patterns of remaining habitat that appear (to human observers) to be connected in a simplified and binary depiction of the landscape.

The enduring bias of binary landscapes in corridor plans and studies stems partly from the ecological theory supporting corridor designs. Island biogeography (MacArthur & Wilson 1967) offered the stepping stones that others generalized to corridors (Diamond et al. 1976, Wilson & Willis 1975). Metapopulation theory (Hanski & Gilpin 1997) inferred the processes of dispersal, colonization, and local extinction in binary habitat patches with different spatial configurations (Dunning et al. 1992, Fahrig & Merriam 1994). Landscape ecology (Turner 2005) reinforced the patch-corridor-matrix paradigm by quantifying habitat configuration and composition patterns mainly with tools that juxtapose habitat and nonhabitat (e.g., McGarigal et al. 2002, Turner & Gardner 1991). Together, these theories have vastly increased appreciation of the relationships between habitat patterns and populations, but they have done so in a way that promotes corridors as archetypically linear and static features (Beier & Noss 1998, Hobbs 1992, Saunders & Hobbs 1991) in binary landscapes.

This simplistic, pattern-based view of corridors as habitats has resonated with ecologists because of its tractability (Goodwin 2003, Goodwin & Fahrig 2002) and scale versatility (Calabrese & Fagan 2004), but it has important limitations. First, it assumes that movement is categorically facilitated by corridors and impeded by the matrix (Baum et al. 2004, Rosenberg et al. 1997, Simberloff et al. 1992), whereas real landscapes create a continuum of influences on movement (Puth & Wilson 2001). Second, this simplified, categorical view of corridors homogenizes species and spatial scales for corridor planning, whereas functional connectivity is inevitably species-specific (Goodwin 2003, Lidicker 1999, Puth & Wilson 2001). In fact, corridors may not be beneficial to some species (Boswell et al. 1998, Collinge 2000, Hannon & Schmiegelow 2002, Schmiegelow et al. 1997, Schultz 1998), but even the potential disadvantages of corridors—e.g., disease transmission (Hess 1994)—may be outweighed by their benefits (McCallum & Dobson 2002). Thus, pattern-based

approaches to corridor planning may not make appropriate provisions for all or even most of the species for which a corridor is designed, and corridor structure may be both insufficient and unnecessary to promote movement. Better integration of pattern and process is critically important to corridor design.

Several researchers have distinguished the pattern and process components of corridors (Bennett 1999, Rosenberg et al. 1997) and landscape connectivity more generally (Bélisle 2005, Fahrig 2003, Tischendorf & Fahrig 2000b). Others have acknowledged that corridors are more than linear structures in binary landscapes (Beier & Noss 1998, Hobbs 1992) and instead are places on the landscape that facilitate the movement of individuals, promote genetic exchange, and support ecological processes (Forman 2002, Puth & Wilson 2001). Broadening the concept of corridors to "linkages" allows them to support these processes without being linear, continuous, or even structurally distinct from the surrounding landscape (Bennett 1999). We amplify these views by suggesting that a greater emphasis on the processes of habitat selection and movement could address several fundamental questions that pattern-based approaches tend to neglect. We do not attempt to answer these questions but review new approaches and tools that can be used to identify, design, and test corridors for conservation more effectively.

First, should corridors promote certain types of movement? Corridors often are assumed to facilitate dispersal but this might not be the only movement type relevant to corridor designs. Moreover, it is frequently difficult to know the motivation of moving organisms (Lima & Zollner 1996). Instead of assuming this motivation, we could identify habitats that are associated statistically with short-range foraging movements versus longer-distance movements (e.g., Johnson et al. 2002). This approach makes it possible to separate movement into types, some of which might be targeted by corridor designs, even without identifying their underlying motivation.

Second, should corridors increase movement rates relative to movement in other habitats (Haddad & Tewksbury 2005, Puth & Wilson 2001)? Individuals have more tortuous pathways in good quality habitat and move further and faster over unfavorable terrain (Crist et al. 1992, Johnson et al. 1992, With 1994). However, individuals that move more sometimes suffer higher mortality (Biro et al. 2003; J.L. Frair, E.H. Merrill, J.R. Allen & M.S. Boyce, submitted). Moreover, high movement rates in corridors may not correlate with the functional connectivity of a landscape (Bélisle 2005).

Third, is habitat quality as important as movement characteristics in designing corridors? Even if animals use corridors only to travel between suitable patches, they are unlikely to do so if they perceive that habitats within the corridor are unsuitable. Organisms use a wide variety of mechanisms to select suitable habitats (Danchin et al. 2001, Stamps 2001) and knowing the details of habitat selection might be as important to corridor design as it is to identifying suitable habitats for other purposes.

Fourth, if corridors result in ecological traps or sinks (e.g., Weldon & Haddad 2005; but see Little et al. 2002), is their corridor function necessarily compromised? Only occasional movement is necessary to maintain gene flow (Mills & Allendorf 1996), and infrequent dispersal may be sufficient to sustain demographic rescue

Model: a way of describing the behavior of a process in order to predict its future or understand its past

GIS: geographic information system

(Hanski 2001). Corridors might provide these benefits to adjacent populations over large timescales, even if they lessen the survival and reproductive success of most of the individuals that use them.

Despite more than 20 years of research on corridors, few corridor studies lend insight into these questions. Rather than review the latest empirical studies that focus on corridors, we explore recent advances in technology and quantitative methods that make it easier to answer these questions by integrating pattern and process. These tools could revolutionize our ability to design and manage corridors to ensure that they are accomplishing conservation objectives. This review is intended to identify those opportunities by showing how we can develop gradient-based habitat selection models and probabilistic movement models to identify corridors in complex, real-world landscapes.

HABITAT SELECTION PROCESSES

Habitat selection is the behavioral process used by individuals when choosing resources (Johnson 1980) and habitats. These choices occur at a variety of spatial and temporal scales that range from finding food resources within a season, to defining home ranges during a lifetime, to expansion of ranges across generations (Johnson 1980; **Table 1**). The motivation for habitat selection is presumably to maximize individual fitness (Garshelis 2000) with consequences for distribution and density across different habitats (Morris 2003). The behavioral mechanisms that play a role in habitat selection for residency, such as conspecific attraction, habitat imprinting (reviewed by Stamps 2001), natal home range cues (Cooper et al. 2002), and public information (Danchin et al. 2001), logically apply to the selection of habitats for movement (i.e., corridors) as well. Even during dispersal movements, animals must forage, sleep, avoid predators, and either seek out or avoid conspecifics. They do not have the omniscience that a geographic information system (GIS) provides us for visualizing corridors and must instead continuously assess habitat for its suitability.

Table 1 Movement and habitat selection processes in relation to spatial scales and structures (adapted from Ims 1995, Johnson 1980)

Spatial scale	Habitat selection (after Johnson 1980)	Movement type (after Ims 1995)	Spatial structure
Resource Patch	Food items within the patch (fourth order)	Food items search (foraging)	Food item distribution Food patch shape and size Small-scale obstructions
Habitat Patch	Patches within home range (third order)	Patch searching, traplining, territory patrolling	Food patch configuration Shelter Abiotic factors and topography
Patch Mosaic	Selection of home range (second order)	Dispersal	Patch distribution Landscape features
Region	Geographical Range (first order)	Migration	Large scale topography barriers

The assumed dichotomy between patch and corridor is likely perceived by animals as a continuum.

A second false dichotomy applies to the way corridors are typically viewed as connecting areas of habitat, in a “sea” of inhospitable matrix. We know that organisms often use the so-called matrix as habitat (Berry et al. 2005, Haila 2002, Rosenzweig 2003) and that it can increase the viability of adjacent populations (e.g., Vandermeer & Carvajal 2001). Moreover, the matrix can affect interpatch movements, particularly for species that respond to boundaries between habitat types (Bender & Fahrig 2005), and determine the use of embedded corridors and stepping stones (Baum et al. 2004). Thus, organisms actually occupy a spectrum of habitats in nearly every landscape type. The artificial dichotomy of patch and matrix creates fundamental difficulties for understanding species responses to fragmented habitats (Fischer et al. 2004, McIntyre & Hobbs 1999). Fortunately, habitats can be described instead as probabilistic functions of multiple landscape attributes.

Resource Selection Functions

Habitats can be characterized using resource selection functions (RSFs), defined to be any function that is proportional to the probability of use of a resource unit (Manly et al. 2002). A resource unit is a sampling unit of the landscape, e.g., a pixel or grid cell. Predictor variables (covariates) are habitat attributes that can be used to predict the relative probability of use for a resource unit (Manly et al. 2002).

A number of sampling designs can be used to estimate an RSF, e.g., a random sample of resource units could be drawn and examined for the presence or absence of an organism (Boyce & McDonald 1999). Model coefficients can be estimated using logistic regression if occurrence is recorded as absence-presence (0, 1), or an alternative link function might be used for count data, such as Poisson regression or zero-inflated Poisson (ZIP) regression (Nielsen et al. 2005). Alternatively a sample of occupied resource units could be contrasted with a random sample of landscape locations using a logistic discriminant function (Johnson et al. 2006). Predictive ability of an RSF can be assessed using k -fold cross-validation methods outlined by Johnson et al. (2006).

Such an RSF can be applied in a GIS to map the relative probability of use across the landscape, in contrast with binary maps of habitat versus nonhabitat. For most organisms, patterns of use of a landscape are much more complex than simple binary characterizations of habitat. These models can be used to identify habitat associations for animals at multiple scales (e.g., Boyce 2006, Carroll et al. 2001).

Using Resource Selection Functions to Delineate Corridors

By depicting landscapes as probabilistic functions, RSF models offer an important departure from categorical representations of corridors, patch, and matrix habitat. Although RSF models tell us nothing about the movement of animals per se, they allow us to identify habitats that are likely to support occupancy. For example, we used the telemetry locations for three grizzly bears in the Canmore region of the Bow Valley, Alberta, Canada (**Figure 1a**), to generate an RSF that compared topographic

Resource selection

function (RSF): statistical models defined to be proportional to the probability of use of a resource unit

ZIP: zero-inflated Poisson

and vegetation variables at telemetry locations with those at random locations in their combined home ranges (**Figure 1b**). Applying the RSF in a GIS illustrates areas of high probability of occupancy (*green*) and their proximity to one another as well as to areas of lower probability of occupancy (*red*). This approach provides a powerful framework for locating potential corridors or evaluating current corridor designations (**Figure 1a**).

Although characterizing habitats used by organisms would appear to be a fundamental first step in identifying corridors, caveats are appropriate. Use of habitats does not necessarily mean that the habitats are productive ones, and in the worst case used habitats might be sinks or traps (Kristan 2003, Pulliam 1988). Yet, 85% of avian studies have found that habitats used more intensively by a bird species were also those in which reproductive success was highest (Bock & Jones 2004). Nonetheless, corridors may sometimes represent poor-quality habitats that still facilitate movement (Haddad & Tewksbury 2005).

MOVEMENT PROCESSES

Organisms are motivated to move to forage, avoid predators, find breeding opportunities, access seasonal or ephemeral resources, and expand ranges (Bennett 1999, Ims 1995), generating movements scaled within foraging patches of a few square centimeters to transcontinental migrations. Ims (1995) offered four categories of movement—*foraging, searching, dispersal, and migration*—that are strikingly similar to a hierarchy of habitat selection described earlier by Johnson (1980; **Table 1**). All of these categories are relevant to corridors (Bennett 1999), but dispersal tends to be emphasized as most pertinent (reviewed by Vos et al. 2002), particularly for spatially structured populations (reviewed by Clobert et al. 2001). Yet corridors also may be critical for maintaining seasonal migrations (e.g., Powell & Bjork 1995) or for access to resources within a home range (e.g., Nielsen et al. 2004a). With so many contexts for movement and such a fundamental role in population dynamics, it is surprising that movement as a process is seldom explicit in corridor planning. This lack of emphasis has been caused, in part, by the difficulty of quantifying movement.

Techniques for Measuring Movement

Turchin (1998) identified two empirical approaches for measuring movement: Eulerian and Lagrangian. Eulerian approaches measure population metrics by recording the redistribution of large numbers of marked or unmarked individuals at specific locations. Individuals have been marked using leg-bands in birds, radioisotope labels and dyes in insects, or otolith dyes in fish (reviewed by Southwood & Henderson 2000). Subsequent recaptures, resightings, or recovery provide an estimation of movement rates (reviewed by Bennetts et al. 2001). In contrast, Lagrangian approaches characterize the magnitude, speed, and directionality of individual movements with a variety of techniques. For insects, movement paths have been recorded using numbered flags (e.g., Schultz 1998) or harmonic radar systems (e.g., Cant et al. 2005), whereas movement pathways for vertebrates can be recorded using snow tracking

(Whittington et al. 2005) or radiotelemetry (Millsaugh & Marzluff 2001). Movement paths are quantified by velocity, step lengths, degree of directionality, and measures of tortuosity (Turchin 1998). Eulerian and Lagrangian approaches provide different but complementary methods for understanding animal movements across a landscape.

In general, Eulerian approaches do not provide the same detail of movement information as Lagrangian approaches, but they make it possible to describe movement over much larger spatial and temporal scales. Eulerian approaches employing genetic techniques (Nathan 2005, Nathan et al. 2003, Webster et al. 2002) or stable isotopes (reviewed by Hobson 2005, Rubenstein & Hobson 2004) are rapidly evolving and offer particular promise to reveal landscape connectivity for populations. Because individuals are “marked” with a unique genotype or isotopic signature, the frequency of various markers from different sources can be identified. Genetic techniques offer enough precision to provide an estimate of dispersal movements within one or more generations (Waser & Strobeck 1998). For example, Proctor et al. (2004) measured genetic similarity to estimate dispersal distances for grizzly bears and showed that animals moved with a series of short stepping stone-like movements rather than a few long-distance dispersal movements. Genetic approaches also can be used to measure the effect of corridor patterns on gene flow (e.g., Aars & Ims 1999, Mech & Hallett 2001) or to document that some organisms moved through corridors (e.g., Coffman et al. 2001). These methods may be complemented with Lagrangian approaches to show how individual movements influence gene flow (e.g., Keyghobadi et al. 2005).

Many applications of Lagrangian approaches have involved small organisms (e.g., Schultz 1998) and experimental systems (e.g., Haddad 2000), but global positioning systems (GPSs) radiotelemetry can provide detailed movement information over much broader spatial and temporal scales (reviewed by Millsaugh & Marzluff 2001). Obviously, GPS radiocollars increase the practicality of collecting movement information for wide-ranging organisms, but handheld GPS also can be combined with field observations or conventional telemetry to support equivalent spatial grain and extent for animals that are too small to wear GPS collars or to offset the relatively high costs of GPS radiotelemetry. GPS technology provides exciting new potential to use Lagrangian data to design and evaluate corridors. The ideal approach might engage both Eulerian and Lagrangian methods.

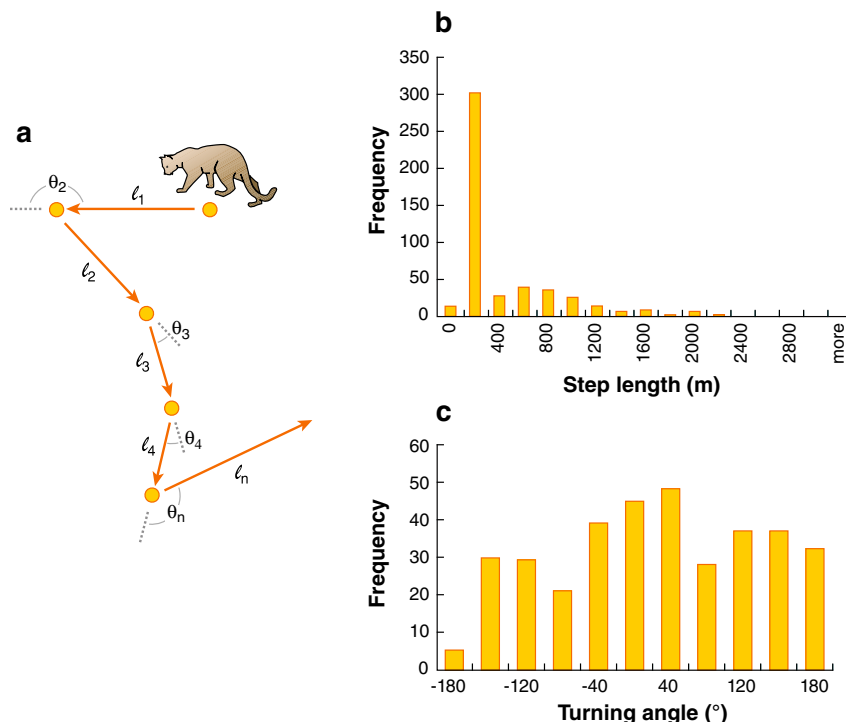
Quantifying Movement Processes

Kernohan et al. (2001) described three nonexclusive categories of quantitative approaches for characterizing movement: (a) summarizing movement pathways with turning angles, fractal dimensions, and step lengths; (b) modeling movement with random walks or their variations (Turchin 1998); and, (c) identifying patterns in movement data retrospectively to distinguish different movement types (e.g., Morales et al. 2004). The first approach, quantifying movement pathways as turning angles, step lengths (**Figure 2**), and fractal dimensions offers several advantages. First, these metrics can be used to associate movement types with landscape features. For example, cougars (*Puma concolor*) moving more than 100 m at any one time tended to

GPS: global positioning system

Figure 2

Example of how a movement pathway (*a*) can be quantified into step lengths (*b*) and turning angles (*c*) for a cougar, CACO1, during 2000–2001 in the Canmore region of the Bow Valley, Alberta, Canada (C.-L. Chetkiewicz, unpublished data).



have straighter movements and moved faster through urbanized areas (Dickson et al. 2005). Second, these metrics can be used to parameterize movement rules for spatially explicit models. Such a model was created from movement data for beetles to evaluate the effect of hedgerow width on movement rates (Tischendorf et al. 1998). A final advantage of quantifying movement pathways is they can be used to examine responses to edges or habitat boundaries. For example, eastern bluebirds (*Sialia sialis*) typically flew parallel to edges in an experimentally fragmented field system emphasizing the role of edges in directing and channelling flight pathways (Levey et al. 2005).

The second approach characterizes movements according to a mechanistic model, typically derived from diffusion theory and approximations of random walks (Turchin 1998). For example, Gustafson & Gardner (1996) simulated self-avoiding random walkers to explore the effects of landscape heterogeneity on movement patterns and identify frequently traversed portions of the landscapes that might denote corridors. In another application, a correlated random walk (CRW) diffusion model was used to simulate movements by grizzly bears to illustrate how land ownership and habitat information could reveal potential dispersal routes (Boone & Hunter 1996). Even if real organisms usually violate some of the assumptions of general movement models (Bergman et al. 2000), CRWs can be useful null models for distinguishing different movement types (Austin et al. 2004) and identify opportunities for corridors.

The third approach for quantifying movement is to identify types of movement retrospectively. An early method for achieving this was fractal dimension (fractal *D*),

CRW: correlated random walk

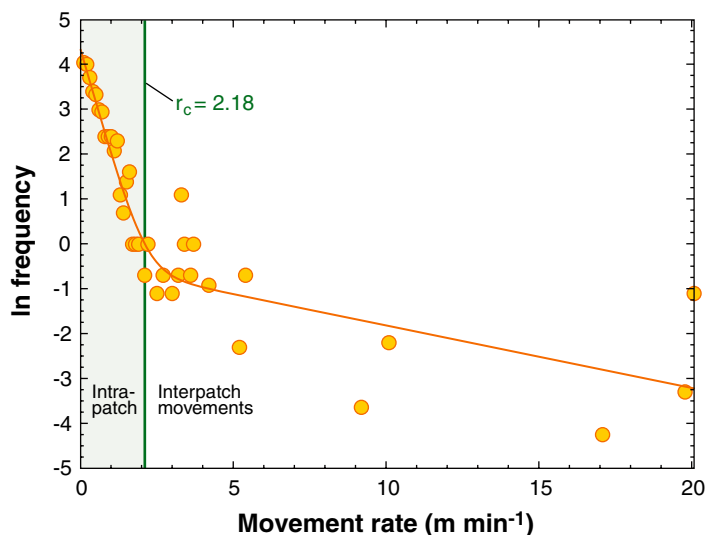


Figure 3

The \log_e frequency distribution of movement rates for a caribou is assessed using a broken-stick method to calculate a scale criterion (r_c). Movement rates less than r_c represent intrapatch movement behaviors, whereas movement rates greater than r_c represent interpatch movement behaviors (C. Johnson, unpublished data).

but this technique was typically applied to small organisms at limited spatial scales (reviewed by Nams 2005). GPS technology makes it possible to apply similar approaches at much broader spatial and temporal scales. For example, Johnson et al. (2002) used a nonlinear (“broken stick”) curve-fitting procedure to define two types of movement behavior for caribou (*Rangifer tarandus*) in British Columbia. This approach used variation in the frequency of movement rates to define a threshold value that could differentiate between intrapatch movements (short, high-frequency moves below the threshold) and interpatch movements (larger, less-frequent moves greater than the threshold) (**Figure 3**). We might expect that longer-step, interpatch movements would better characterize habitats used as corridors.

Once different movement states are identified, they can be combined with RSF-based habitat characterizations to align behavioral states with landscape features. Morales et al. (2004) used a latent model structure based on turn angles and step lengths to identify two behaviors: “encamped” (step lengths were small, turning angles were high) or “exploratory” (step lengths were several kilometers long, turning angles were low) for wapiti (*Cervus elaphus*) in Ontario. They then identified landscape features correlated with these states. Frair et al. (2005) used a similar approach to identify three types of movement behavior in wapiti and then related these behaviors to landscape conditions including wolf (*Canis lupus*) predation risk and cover.

The three approaches to quantifying movement we have described here have two important attributes. First, all are readily applied to a variety of temporal and spatial scales. Previous use of different approaches for small and large organisms has polarized the corridor literature (Haddad et al. 2000, Noss & Beier 2000). Although generalizations that transcend spatial scales for management are challenging (Boyce 2006), it is sometimes possible to derive movement mechanisms at one scale and apply them to other scales (e.g., Ims et al. 1993). In other cases, movement processes may not generalize across scales (e.g., Fortin et al. 2005b). For example, highway-crossing

structures designed as corridors for grizzly bears are frequently used by large animals (Clevenger & Waltho 2005), but almost completely avoided by microtine rodents (McDonald & St. Clair 2004).

A second useful attribute of quantifying movement is that it provides a means of identifying important differences among individuals. For example, female grizzly bears appear much less willing to cross barriers than males (Gibeau et al. 2002). Individual variation generally has been viewed as an inconvenience in wildlife studies but might be profitably examined and incorporated in studies of both habitat selection and movement with random effects (Gillies et al. 2006). Similarly, latent class models (McCulloch et al. 2002) can be used to identify how individual motivation affects both habitat selection and movement. Understanding individual variation in movement and habitat selection may be an important aspect of corridor planning, particularly if the individuals targeted for conservation (e.g., adult females) exhibit specific preferences or behaviors.

MARRYING PATTERN AND PROCESS TO CORRIDOR DESIGNS

A main impediment to advancing corridor study and planning is the missing integration between patterns of landscape composition and configuration, and the processes of habitat selection and movement. In this section we review what we consider to be the most promising approaches for advancing that integration. One of the earliest applications of this sort is percolation theory (With 1997, 2002), which examines movement within spatially structured systems representing neutral landscapes. In these landscapes, a lattice grid of "habitat" cells can be connected structurally (lattice percolation) or via movement rules (bond percolation) (With 2002). Species-specific responses to real landscapes, such as gap-crossing abilities (e.g., Desrochers 2003, St. Clair et al. 1998) and responses to edges (e.g., Haddad 1999, Schultz 1998), can be used to define movement rules for percolation models (With 2002). For example, Williams & Snyder (2005) used common "neighbor rules" from percolation theory to evaluate how habitat corridors could be restored to maintain percolating clusters, an assemblage of connected habitat cells, across the extent of simulated neutral landscapes. This application showed how landscape connectivity could be optimized to maintain percolating clusters while minimizing both corridor length and the number of nonhabitat cells that needed to be restored. Surprisingly, a meandering corridor sometimes generated lower costs (measured with both the number of restored cells and corridor length) than the shortest straight-line corridor between habitat cells. In this case, percolation theory based on movement rules identified a nonintuitive approach to corridor design.

Least-cost path analysis is a GIS-based approach similar to percolation theory except it involves estimating movement costs between two points from the suitability of intervening habitat. Parameters are based on descriptions for suitable habitats derived either from the literature or expert opinion (e.g., wolves are unlikely to occur above 1500 m; Singleton et al. 2002), and a raster grid based on accumulated distance weighted such that suitable habitats have lower movement costs than unsuitable

habitats. The least-cost path analysis evaluates the costs of moving between two habitat nodes by comparing the cumulative weighted distance between the cell and the two nodes. This approach has been used to map and visualize corridors (e.g., Rouget et al. 2006, Singleton et al. 2004) but is typically based on assumptions about movement and habitat suitability that are rarely validated (Clevenger et al. 2002). Tools like RSF offer new ways to quantify landscapes for least-cost path models. For example, inverse values generated from RSF models based on sighting data for three carnivores in the Rocky Mountains (Carroll et al. 2001) could be used to generate a cost surface to explore regional corridors between protected areas. Similarly, landscape features that characterized the risk of mortality for grizzly bears in Alberta (Nielsen et al. 2004b) could be used to generate a cost surface to explore local corridor designations. If these multivariable characterizations of habitats could be combined with movement processes, a better measure of functional landscape connectivity (sensu Taylor et al. 1993) would result.

Graph theory offers particular promise for measuring landscape connectivity holistically by combining the movement emphasis of percolation theory and the habitat modeling potential of least-cost path modeling. Graph theory evolved for transportation and computer networks (Cantwell & Forman 1993) and only recently has been applied to assessments of landscape connectivity (Urban & Keitt 2001). Graph-theoretic approaches combine landscape data, typically derived from a GIS, with movement data measured as either a dispersal distance (D'Eon et al. 2002) or a random draw from a dispersal kernel generated as a function of dispersal probability with distance (Havel & Medley 2006). A lattice describes the connections between pairwise combinations of resource patches (nodes), which can be quantified as dispersal distances (edges) or weighted by other movement metrics such as tortuosity. If the distance between a pair of nodes is less than or equal to the movement threshold used, the nodes are connected. The sum of these connections can be scaled up to assess the connectivity of the entire network using a variety of metrics such as correlation length and distance to cluster edge (Calabrese & Fagan 2004). Greater correlation lengths, for example, result from an increase in the sizes of clusters suggesting greater landscape connectivity. Best of all, these process-based metrics of connectivity are readily visualized on maps to explore the effects of adding or removing connections between nodes (e.g., corridors) or resource patches (Bunn et al. 2000, Urban & Keitt 2001). For example, Urban (2005) created a graph for the wood thrush (*Hylocichla mustelina*) in North Carolina using habitat patches as defined in a GIS as nodes and movement thresholds of 2500 m to define graph edges (**Figure 4**). The resulting graph effectively identified functional corridor locations by showing how the loss of two small patches would break the single connected graph into three separate components. Importantly, these locations did not fit a conventional corridor description of linear and connected habitat and their identification was driven by information about bird movement. A pattern-based approach to corridor designation would have been less likely to have identified these corridor locations.

Although graph theory typically relies on a binary depiction of habitat (nodes), it is possible to identify these nodes probabilistically with an RSF (B.L. Schwab, C. Woudsma, S.E. Nielsen, G.B. Stenhouse, S.E. Franklin & M.S. Boyce, submitted).

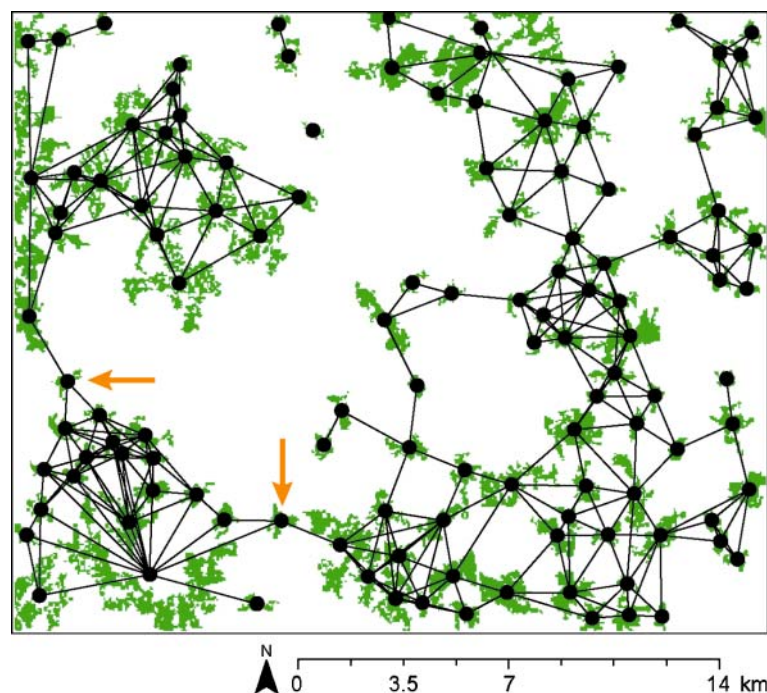


Figure 4

Graph depicting connectivity for wood thrush in a North Carolina landscape. The graph was generated using nodes generated from forest patches in a geographic information system and edges based on a dispersal distance of 2500 m. Corridor locations can be visualized between nodes where the loss of a single forest patch (*arrows*) would alter connectivity across the landscape by breaking the graph into separate components. Figure adapted from Urban (2005).

LZP: linkage zone prediction

Schwab and colleagues developed an RSF for grizzly bears in Alberta to locate areas where bears were more likely to occur (high RSF). These areas were then used to generate nodes (habitat patches) and the inverse of the RSF (i.e., $1/\text{RSF}$) was used to generate a cost surface as a surrogate for movement. Least-cost path modeling was then applied to this $1/\text{RSF}$ cost surface and the resulting paths were compared to paths created with out-of-sample GPS location data. These data aligned with the cost surface estimated from $1/\text{RSF}$ showing that it performed well as a predictor of movement. This approach provides an exciting advance over previous least-cost methods such as linkage zone prediction (LZP) models. LZP models typically predict the relative probability of movement through an area by integrating qualitative scores for a number of GIS layers. For example, an LZP model for grizzly bears integrated human features, linear disturbance elements, visual cover, and riparian habitat (Singleton et al. 2002). However, an LZP model does not incorporate quantitative information about habitat or movement and generally is not validated with empirical data (Carroll et al. 2001).

Combining graph theory with RSF models offers a technique for quantifying connectivity in general and corridors in particular because it explicitly combines spatial topology with resource selection (Wagner & Fortin 2005). Because graph theory summarizes the spatial relationships between landscape elements (configuration and composition) in a concise way (Calabrese & Fagan 2004, D'Eon et al. 2002, Urban & Keitt 2001), it is especially helpful in anticipating the effects of adding or deleting particular landscape elements. Graphs also may be used to model effects of landscape on movements in two ways. First, if one uses qualitative measures or values derived from movement data in different habitats (Manseau et al. 2002), nodes can be assigned with different weights or resistance to movement (Cantwell & Forman 1993). Second, directionality can be applied to the graph edges in the form of vectors (Urban & Keitt 2001), overcoming the enduring problem of ignoring anisotropy in landscape connectivity (Bélisle 2005). And finally, graphs can be constructed with fairly modest data (Urban 2005) to provide a useful visual tool for considering corridor placement for several species simultaneously or evaluating their associated land costs (Williams 1998).

A second new approach for integrating landscape pattern and movement processes uses conditional logistic regression to quantify movement probabilities across landscapes using step selection functions (SSF), a technique similar to RSF. Instead of characterizing telemetry locations in an RSF, Fortin et al. (2005a) compared each step (i.e., a segment between locations on the landscape) made by wapiti with random steps having the same starting point to model the effects of landscape heterogeneity on movement. They found wapiti movements were influenced by distance to roads, cover, and wolf predation risk. With this approach, areas of high movement probability quantified by the SSF could be used to predict movement distance and direction in the context of a specific landscape, which is the essence of corridor design (*sensu* Haddad & Tewksbury 2006). SSF also could be used in combination with information on movement behavior at boundaries or edges to provide stronger support for corridor designations, without reliance on categorical landscape depictions.

Graph theory and SSFs are two ways that pattern and process can be integrated better in corridor designs and studies, but many other approaches are likely possible. For example, the currency of travel cost, so extensively employed in analytical models of optimal foraging behavior (Stephens & Krebs 1986), has barely been investigated in the context of landscape connectivity (Bélisle 2005). More generally, we advocate using behaviorally informed or process-driven methods to model habitat use and movement to identify landscape locations with high need or potential for corridor functions, rather than assuming these functions based on perceptions of habitat structural connectivity. We suggest that this approach offers several important advantages for designing and assessing corridors. First, movement processes reflect an organism's perception of landscape (Lima & Zollner 1996, Olden et al. 2004), which undoubtedly varies among individuals as well as species. Second, a focus on movement behavior lets one identify whether or not corridors alter movement rates, a critical dimension of corridor efficacy (Simberloff & Cox 1987, Simberloff et al. 1992). Finally, a better understanding of movement processes can be used to evaluate the effect of

Step selection function (SSF): statistical models of landscape effects on movement probability

corridors on related key processes for individuals (dispersal, reproduction, and survival, e.g., Dzialak et al. 2005), populations (rates of immigration, emigration, persistence, and recolonization, e.g., Berggren et al. 2002, Coffman et al. 2001), and communities (biodiversity, predator-prey interactions, trophic cascades, e.g., Haddad & Tewksbury 2006).

CONCLUSIONS

“Corridors are not *the* answer to our conservation problems” (Noss 1987), but they could be used better to fulfil the promise they offer to conservation. We believe that the limitations to identifying and designing effective corridors can be traced to insufficient understanding of the processes that govern use of corridors by species of conservation interest. Behavioral processes of habitat selection and movement determine how animals use landscapes and thereby are fundamental to the identification and evaluation of corridors. We have reviewed a new generation of technological and analytical tools that allow us to quantify both habitat selection and movements with the expectation that these will allow us to approach corridors more holistically and objectively.

The Canmore example given in the introduction provides an illustration of the approach we advocate and, indeed, are attempting (C.-L. Chetkiewicz, unpublished data). There, we could conduct an RSF analysis for grizzly bears using sightings, mortality locations, and data from telemetered animals (e.g., **Figure 1a**) to identify habitats with high probabilities of use. Then we could use SSF to identify factors that promote movement across the landscape. RSFs would identify landscape characteristics supporting grizzly bear occurrence outside designated corridors (e.g., **Figure 1a,b**) and an SSF could be used to identify habitat characteristics that promote different movement behaviors. We could also use RSF and SSF models to explore important variation among individuals (e.g., habituated versus nonhabituated animals) in habitat selection and movement processes. Together, this information could be used to identify locations for mitigation (e.g., enhancing habitat, removing attractants, limiting human use or infrastructure) both inside and outside currently designated corridors. For example, the removal of human infrastructure and associated human use was highly successful in restoring connectivity for wolves on the outskirts of the town of Banff, Alberta (Duke et al. 2001). These approaches might also make it possible to combine humans and wildlife more safely in areas that appeal to both groups because of the wild areas they still contain.

We believe that more attention to the processes of habitat selection and movement will greatly strengthen our ability to identify and design effective corridors for conservation, and we suggest that this attention will bear importantly on the four fundamental questions we posed in the introduction. There we asked (*a*) if certain types of movement were more pertinent to corridors, (*b*) if corridor designs should promote faster movement, (*c*) if habitat selection is as important as movement parameters in identifying corridors, and (*d*) if corridors can promote gene flow and rescue effects even if they function as ecological traps and sinks? Answers to these questions are just beginning to emerge.

Unfortunately, even with these answers, we are unlikely to have general prescriptions for corridor designs for multiple species (e.g., Beier & Loe 1992). When Bunn et al. (2000) used a graph-theoretic approach to show that American mink (*Mustela vison*) perceived the landscape as connected, they could not generalize this result to prothonotary warblers (*Protonotaria citrea*) in the same landscape. By contrast, Haddad et al. (2003) found that corridors created in their experimental field system facilitated movement for a number of species. Thus, the best features for corridors are unknown and, even when they can be identified, may not translate well to other species, locations, and scales. That corridors have no universal rules should not really surprise us; it is a fact of most of ecology (Lawton 1999). Habitat needs for charismatic umbrella species (Simberloff 1998) like grizzly bears might encompass the needs of some species within the ecosystem (Carroll et al. 2001) and can be helpful in lobbying public support needed to meet those needs. A reasonable approach might be to identify the species and their source habitats that likely matter most in a given system (Beier et al. 2006), learn something about their actual processes of habitat selection and movement, and then use this information to restore, retain, or manage habitat in a way that will promote functional connectivity. This general approach appears to work well, but it could work better with more information about the critical processes with which animals use and move through habitat. In-depth study in the countries that can afford to support this level of investigation may well produce some guidelines, if not prescriptions, for the many countries in the world where biodiversity is being lost very rapidly and where there is neither time nor resources to spare.

In sum, we hope we have provided some new ideas and tools for sagacious input into the design and evaluation of corridors for conservation. Although they may seem daunting, many of the analytical techniques we describe are becoming quite tractable and could be used by land managers and planners now. We hope that the more process-based examination of habitat and movement we espouse can function to integrate humans better with other animals, particularly in the interface between urban and rural, and semirural and wilderness areas where many of these problems occur (McKinney 2002). Anticipating future landscapes by acknowledging how humans will directly and indirectly (e.g., climate change) affect them is critical if we are to retain our biological heritage. Conservation corridors could play an important role in ameliorating these effects and bring us closer to integrating the needs of humans and other organisms so that, at least sometimes, both parties win (*sensu* Rosenzweig 2003).

SUMMARY POINTS

1. Corridors are commonly applied in conservation and land-use planning to structurally connect otherwise noncontiguous patches, typically within a binary landscape.
2. Ecological processes such as habitat selection and movement are often assumed to occur via these connections, yet process-based metrics are rarely used to evaluate designated corridors. Process-based approaches to designing and planning corridors are lacking.

This review on corridor effects found that experiments and observations of moving individuals supported the efficacy of corridor designs for connectivity.

3. Resource selection functions describe habitat selection patterns in a continuous and multivariate way, and movement patterns can be quantified to examine movement behavior across the landscape.
4. Processes of habitat selection and movement can be integrated with landscape features using a variety of approaches. These tools offer new ways to design, implement, and study corridors as landscape linkages.

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Contents

Birth-Death Models in Macroevolution <i>Sean Nee</i>	1
The Posterior and the Prior in Bayesian Phylogenetics <i>Michael E. Alfaro and Mark T. Holder</i>	19
Unifying and Testing Models of Sexual Selection <i>Hanna Kokko, Michael D. Jennions, and Robert Brooks</i>	43
Genetic Polymorphism in Heterogeneous Environments: The Age of Genomics <i>Philip W. Hedrick</i>	67
Ecological Effects of Invasive Arthropod Generalist Predators <i>William E. Snyder and Edward W. Evans</i>	95
The Evolution of Genetic Architecture <i>Thomas F. Hansen</i>	123
The Major Histocompatibility Complex, Sexual Selection, and Mate Choice <i>Manfred Milinski</i>	159
Some Evolutionary Consequences of Being a Tree <i>Rémy J. Petit and Arndt Hampe</i>	187
Late Quaternary Extinctions: State of the Debate <i>Paul L. Koch and Anthony D. Barnosky</i>	215
Innate Immunity, Environmental Drivers, and Disease Ecology of Marine and Freshwater Invertebrates <i>Laura D. Mydlarz, Laura E. Jones, and C. Drew Harvell</i>	251
Experimental Methods for Measuring Gene Interactions <i>Jeffery P. Demuth and Michael J. Wade</i>	289
Corridors for Conservation: Integrating Pattern and Process <i>Cheryl-Lesley B. Chetkiewicz, Colleen Cassady St. Clair, and Mark S. Boyce</i>	317

The Population Biology of Large Brown Seaweeds: Ecological Consequences of Multiphase Life Histories in Dynamic Coastal Environments <i>David R. Schiel and Michael S. Foster</i>	343
Living on the Edge of Two Changing Worlds: Forecasting the Responses of Rocky Intertidal Ecosystems to Climate Change <i>Brian Helmuth, Nova Mieszkowska, Pippa Moore, and Stephen J. Hawkins</i>	373
Has Vicariance or Dispersal Been the Predominant Biogeographic Force in Madagascar? Only Time Will Tell <i>Anne D. Yoder and Michael D. Nowak</i>	405
Limits to the Adaptive Potential of Small Populations <i>Yvonne Willi, Josh Van Buskirk, and Ary A. Hoffmann</i>	433
Resource Exchange in the Rhizosphere: Molecular Tools and the Microbial Perspective <i>Zoe G. Cardon and Daniel J. Gage</i>	459
The Role of Hybridization in the Evolution of Reef Corals <i>Bette L. Willis, Madeleine J.H. van Oppen, David J. Miller, Steve V. Vollmer, and David J. Ayre</i>	489
The New Bioinformatics: Integrating Ecological Data from the Gene to the Biosphere <i>Matthew B. Jones, Mark P. Schildbauer, O.J. Reichman, and Shawn Bowers</i>	519
Incorporating Molecular Evolution into Phylogenetic Analysis, and a New Compilation of Conserved Polymerase Chain Reaction Primers for Animal Mitochondrial DNA <i>Chris Simon, Thomas R. Buckley, Francesco Frati, James B. Stewart, and Andrew T. Beckenbach</i>	545
The Developmental, Physiological, Neural, and Genetical Causes and Consequences of Frequency-Dependent Selection in the Wild <i>Barry Sinervo and Ryan Calsbeek</i>	581
Carbon-Nitrogen Interactions in Terrestrial Ecosystems in Response to Rising Atmospheric Carbon Dioxide <i>Peter B. Reich, Bruce A. Hungate, and Yiqi Luo</i>	611
Ecological and Evolutionary Responses to Recent Climate Change <i>Camille Parmesan</i>	637

Indexes

Cumulative Index of Contributing Authors, Volumes 33–37	671
Cumulative Index of Chapter Titles, Volumes 33–37	674