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Connectivity

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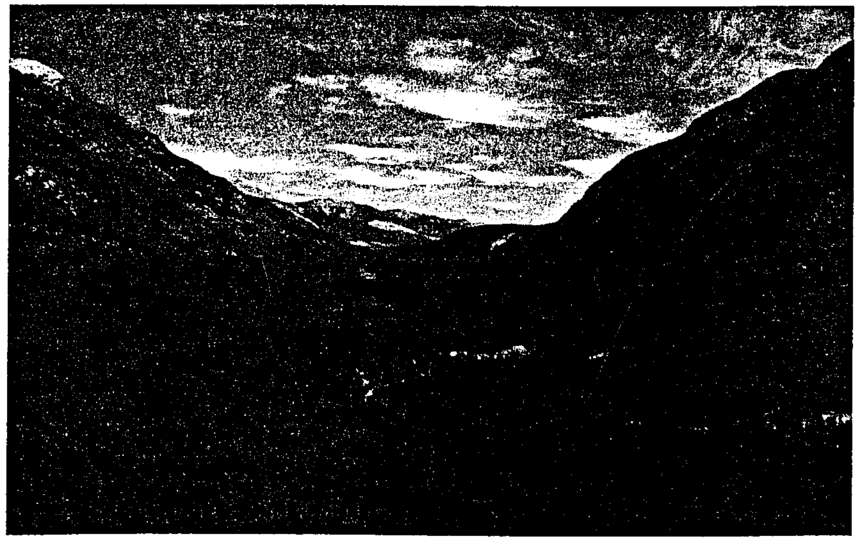
Definitions

Connectivity is an ecological term that describes connections among habitats, species, communities, and ecological processes. Connectivity enables the flow of energy, nutrients, water, disturbances, and organisms and their genes at many spatial and temporal scales (Noss and Harris 1989; Noss 1991). Connectivity for fauna can be measured as the probability that a species will move between patches in the landscape (Taylor et al. 1993). These movements depend on how close the patches are and how well the patches are connected (Taylor et al. 1993). As connectivity between patches is lost, the patches become more isolated and the landscape becomes more fragmented.



In forested landscapes, connectivity describes the linkages among areas of forest cover. In ar[illegible]a where there is no disturbance, the level of connectivity is 100%. (Photogr[illegible]cott Harrison)

Connectivity often is discussed in terms of the mechanisms used to achieve or maintain natural connectivity between patches, namely, corridors or linkages. However, corridors are not always necessary to maintain connectivity. Individual patches that are suitable for a species to move through or live in may constitute connectivity (Merriam 1991a). Corridors may be defined natural features such as riparian habitats along a water course or human-built features such as fencerows. The use of the word *corridor* often implies 'a linear remnant of naturally occurring vegetation that allows movement of individuals or genes between patches of natural habitat' (Harris and Scheck 1991). The following are other definitions of mechanisms for maintaining connectivity.

Corridor, faunal dispersal corridor, movement corridor or conservation corridor: a 'linear remnant' of vegetation, unlike the surrounding vegetation, that connects at least two historically connected patches (Saunders and Hobbs 1991a; Hobbs 1992). A naturally occurring or restored strip of landscape that connects larger patches of similar habitat; the strip functions as a movement route for individuals or for gene flow of native flora and fauna (Harris and Atkins 1991; Harris and Scheck 1991). Any habitat through which an animal has a high probability of moving (Noss 1991).

Convex corridor: a corridor that has greater height than the surrounding matrix, such as a hedgerow, forest in clearcut or agriculture, and shelterbelts (Gates 1991).

Concave corridor: a corridor that is lower in height than the surrounding matrix, such as a powerline, railroad, trail, and highway right-of-way (Gates 1991).

Strip corridor: a corridor that is wide enough to contain interior habitat (Forman 1983; Hobbs 1992).

Line corridor: a corridor that is thin enough to have an edge effect throughout (Forman 1983; Hobbs 1992).

Sink corridor: a corridor that entices animals away from one patch but fails to take them to another patch (Forman 1991; Simberloff et al. 1992).

Riparian or stream corridor: a linear landscape of natural habitat that includes the stream or waterway and the portion of landscape up to and including the level where vegetation may be influenced by high water or flooding and by the ability of soils to hold water (Naiman et al. 1993).

Utility or transportation corridor: a linear strip of development through an area of natural vegetation, such as a trail, railroad, powerline, highway right-of-way, gas pipeline, and so on.

Underpass or tunnel: human-built structures that enable faunal movement across or under utility corridors, such as highways (Simberloff et al. 1992).

Windbreak or shelterbelt: a convex corridor or linear belt of trees in an agricultural setting used to decrease wind and soil eros[illegible]able 1991).

Greenway: a linkage of natural or planted vegetation that connects open spaces such as parks, recreational areas, nature reserves, cultural areas, and historic features, and that follows natural (rivers, streams, ridges) or human-built features (roadsides, railroads, canals); trails are not considered greenways but may be part of them (Hay 1991).

Forest Ecosystem Network: linkages are created to maintain the dynamics of natural forest ecosystem processes, provide relatively undisturbed interior habitat, and aid in recolonization, dispersal, and movement (McDougall 1991).

Landscape linkage: corridor within which community and ecosystem processes occur, allowing movements to occur over generations (Csuti 1991).

Biogeographic landbridge: large linkages that aid in the intercontinental movement of complete communities, such as the Isthmus of Panama (Simberloff et al. 1992).

Stepping stone effect, discrete refuges: a series of distinct patches that may act as a corridor for such species as migratory waterfowl (Date et al. 1991; Simberloff 1992).

Background

The concept of corridors was first proposed by Simpson (1936), who used the term to describe situations in which two biogeographically separate regions came close enough to exchange fauna (e.g., the Isthmus of Panama) (Simpson 1940). His view of corridors was on a much grander, continental scale than we generally consider today. Although many ecologists are again pointing out the importance of this continental scale for maintaining connectivity for wide-ranging fauna (Noss 1992). More recent views of corridors as mechanisms to maintain connectivity within a landscape began with Preston (1962). He concluded that a park could not retain the complete inventory of fauna that would occur in a larger area, but corridors between reserves may prevent isolation and total faunal collapse.

The early corridor work was followed by MacArthur and Wilson's (1967) *Theory of Island Biogeography.* This theory states that the number of species on an oceanic island represents a balance between immigration and extinction, and is a function of the island's area and the degree of isolation. MacArthur and Wilson (1967), and later Wilson and Willis (1975), proposed that 'habitat islands,' created through habitat fragmentation, were similar to true oceanic islands. They suggested that the number of species that would reach equilibrium on these habitat islands was a function of the area and the degree of isolation from a 'mainland' source. As an area became more isolated, its natural diversity would decrease until it reached a new, lower equilibrium. Field data collected by Diamond (1975) in New Guinea and Terborgh (1974) on Barro Colorado Island in the Panama Canal supported this hypothesis.

Wilson and Willis (1975) went on to propose the use of corridors as a method to decrease the isolation of habitat fragments and thus decrease the likelihood of losing natural diversity. Wilson and Willis (1975) and Simberloff and Abele (1976) proposed that to preserve populations of unique biota and habitats, it may be better to have several small, connected reserves rather than one large reserve. They argued that species seldom become extinct in all parts of their range at the same time, and there were dangers in putting all individuals of a given species into one refuge. For example, the heath hen (*Tympanachus cupido cupido*) became extinct when a disease common to poultry infected the last remaining birds in their single refuge (Simberloff and Cox 1987). However, Simberloff and Cox (1987) acknowledge that there is a limit to how small a reserve can be. Other studies also have demonstrated that there is a limit to how small and isolated a reserve can be and still retain its natural faunal assemblage. Newmark (1987) studied 14 western North American parks. Thirteen of the 14 parks had lost 43% of their original mammalian assemblage. Only the large area linking several parks, the Kootenay-Banff-Jasper-Yoho, had managed to maintain all its original mammalian fauna.

In 1970, Levins introduced the metapopulation model. The fundamental metapopulation model is an interconnected group of populations where there is interchange of individuals. Some populations may experience local extirpations, but recolonization by connected populations prevents the overall extinction of the species (Merriam 1991a). This theory assumes that (1) more than one mainland source exists, and (2) recolonization is not a rare and limiting factor. Metapopulation theory also incorporates the effects of heterogeneity within and among patches used by different populations (Merriam 1991a).

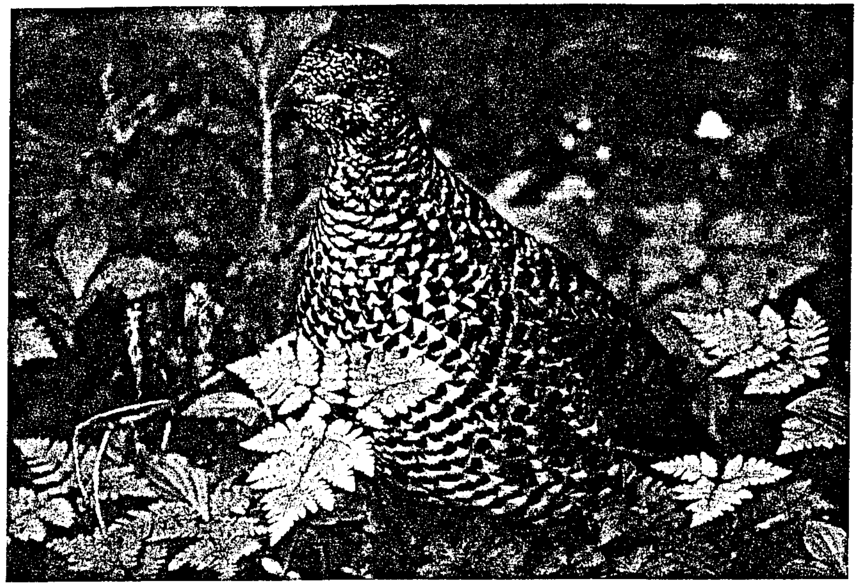
Metapopulations proved to be an attractive model upon which to base habitat management. Support for the metapopulation model increased, in part, because some ecologists became disillusioned with conservation strategies that conserved species numbers rather than species natural diversity (McEuen 1993). Fragmentation was viewed as having the effect of converting continuous, stable populations into increasingly unstable metapopulations. The conservation movement soon adopted the idea that populations require links among patches, and that the solution for the conservation of many species consisted of multiple reserves linked by corridors. Empirical data, however, reveal that there are few populations that fit the basic model. Harrison (1991) suggests that there are different, more common types of metapopulations: source-sink populations, patchy populations, and non-equilibrium metapopulations. To determine which model best describes a population, one requires an understanding of the population's dynamics, including the role of dispersal, recolonization, or gene flow.

Many studies on the use and importance of corridors have involved small mammals and birds (Bennett 1990; Merriam and Lanoue 1990; Saunders and de Rebeira 1991). Merriam and Lanoue (1990) found that white-footed mice (*Peromyscus leucopus*) preferred fencerows to other landscape types. Data from Fahrig and Merriam (1985) suggested that isolated populations of white-footed mice had lower growth rates and were more prone to extinction than connected populations. Bennett (1990) observed that small mammals frequently used corridors between forest patches and that corridors maintained continuity among isolated populations. Saunders and de Rebeira (1991) observed that as native vegetation decreased, so did native fauna. Their study indicated that linkages between patches of habitat could slow or halt faunal relaxation (decreases in the number of species in an area) caused by fragmentation of the habitat.

A study in the eastern United States (MacClintock et al. 1977) inferred that corridors were important for birds living in a fragmented habitat. MacClintock et al. (1977) indicated that fragmentation was a serious problem, and that it had detrimental effects on neomigrants and interior habitat bird species. The study demonstrated a relationship between habitat tract size and avifaunal composition. There was one exception, where a 35-acre site supported a greater number of bird species than many of the larger preserves; unlike the larger preserves, however, this site was connected by a corridor to a 400-acre site that was connected by corridors to a 10,000-acre forest. The species common in the 400-acre site were also common in the 35-acre site, which, with its corridor, also supported breeding pairs of interior habitat species. MacClintock et al. (1977) concluded that forest species could breed in fragments provided the fragments were attached to larger tracts of forest.

Similar movement patterns have been observed in other species, suggesting that connectivity enhances a population's resilience. Fifty moves by 31 voles (*Clethrionomys glareolus*) were noted between a small patch and large patch of forest along a corridor, whereas no moves were noted between a small patch and large patch of forest of similar distance without a corridor (Szacki 1987). Two mule deer herds (*Odocoileus hemionus*) in the Sierra Nevadas used a specific migration corridor that joined their fragmented seasonal ranges (Kucera and McCarthy 1988). The loss of this migration corridor was equated to the loss of deer. A study of cougars (*Felis concolor*) in the Santa Ana Range of California concluded that cougars used corridors and that the loss of the corridor would guarantee the loss of cougars in isolated areas of their range (Beier 1993).

Still, there are few data on the role of connectivity in landscapes. It is a challenge to implement studies of landscape connectivity and its effect on ecological processes. Ecologists try to balance the need to work at suitable spa les with research designs that have an appropriate level of statistical rigour. Nicholls and Margules (1991) discuss MacClintock et al. (1977) and provide options for study designs intended to test the effectiveness of connections in existing landscapes.



Female spruce grouse will make seasonal movements of up to 30 km one-way. The level of connectivity in the landscape is probably an important factor affecting where spruce grouse are found and how they get to and from these areas. (Photograph by Scott Harrison)

Harrison et al. (in press) is one example of a study that is attempting to achieve statistical rigour at a relatively large spatial scale of research. This study is examining the effects of landscape connectivity on the ecological processes of natality, mortality, movement, and dispersal. After consideration of some ecological and logistical factors, Harrison et al. (in press) are studying 100 ha patches of forest in 400,000 ha of British Columbia's sub-boreal spruce forest (*Picea glauca* x *engelmannii*). They are quantifying the level of connectivity to each of the patches as low or medium based on the percentage of connections remaining after logging. They also are interested in the effect of increases in population density; therefore, the resulting study layout is a factorial experiment with two factors and two levels. In total, they selected eight forest patches, each 100 ha, to allow for replication of all treatment units. They chose spruce grouse (*Dendragapus canadensis*) as their study species because they felt it had characteristics that made it well suited for a study of landscape connectivity.

As studies continue, so do discussions about ways to address the issue of connectivity. Simberloff and Cox (1987) present many salient points about the use of corridors for conservation efforts in Florida. T ation in Florida differs from that in most other areas of North America in that Florida is facing reconstruction of habitats to provide corridors for species movement rather than maintenance of natural connectivity. Nevertheless, the authors raise points that are applicable elsewhere, such as a concern over the increased exposure to humans and predators of animals using corridors. Another concern is economic: is it wiser to spend money on buying up land for corridors or on purchasing land for large reserves? This debate sparked a series of articles in which Noss (1987) and Simberloff and Cox (1987) presented the advantages and disadvantages of corridors (Table 3.1).

Advocates of corridors argue that linkages should be established or maintained only where such connectivity occurred in the recent past (Harris and Scheck 1991; Saunders and Hobbs 1991a). This approach defuses many of the concerns about corridors opening up dispersal pathways for exotic or 'weedy' species (McEuen 1993). Also, Hess's (1994) modelling of disease transmission demonstrated that only under very restricted conditions would corridors lead to metapopulation extinctions. He concluded that modelled patches connected by corridors generally had fewer metapopulation extinctions than isolated patches. It also was thought that outbreeding depression (caused when increased gene flow between populations leads to loss of local variants and homogenization of gene pools) in naturally connected populations was unlikely to be a problem (Coates 1991). As few as one or two individuals moving into an area each decade could be sufficient to retain genetic diversity (Mann and Plummer 1993). Conversely, studies indicated that inbreeding depression (caused by the isolation of a population) could occur in isolated populations such as the Florida panther (*Felis concolor coryi*). Of all adult panthers known, only eight were genetically unrelated, and all adult males found in recent years have exhibited 90% infertile spermatozoa (Harris and Scheck 1991).

Other biologists, such as Hobbs and Hopkins (1991), believe that there also may be a role for corridors in a changing climate, although they acknowledge that it is difficult to determine. They propose that corridors may have the potential to allow plants and animals to make landscape-scale movements along the changing climate gradient to avoid adverse environments.

Historically, ecologists studied different elements of the landscape as separate entities. Forman (1983), Noss (1983), and others (Forman and Godron 1981; Harris 1984; Franklin and Forman 1987; Saunders and Hobbs 1991a) began to promote a different approach to the study of landscape ecology that focused on the whole landscape rather than the individual parts (Forman 1988). This new discipline depended substantially on the use of corridors and connectivity (Noss 1983; Harris and Scheck 1991).

The benefit of corridors for larger landscape areas was recognized following some of the [illegible] use of corridors as streamside and [illegible]n strips designed to protect fish habitat. In Australia, a number of authors proposed the use of corridors to provide a linked forest landscape (see Saunders and Hobbs 1991b). In British Columbia, the use of Forest Ecosystem Networks

Table 3.1

Potential advantages and disadvantages of corridors

Advantages	Disadvantages
1 Increase immigration rate to a reserve, which could:	1 Increase immigration rate to a reserve, which could:
(a) increase or maintain species richness and diversity (as predicted by island biogeography theory)	(a) facilitate the spread of epidemic diseases, insect pests, exotic species, weeds, and other undesirable species into reserves and across the landscape
(b) increase population sizes of particular species and decrease probability of extinction (provide a 'rescue effect') or permit re-establishment of extinct local populations	(b) decrease the genetic variation among populations or sub-populations, or disrupt local adaptations and coadapted gene complexes ('outbreeding depression')
(c) prevent inbreeding depression and maintain genetic variation within populations	
2 Provide increased foraging area for wide-ranging species	2 Facilitate spread of fire and other abiotic disturbances ('contagious catastrophes')
3 Provide predator-escape cover for movements between patches	3 Increase exposure of wildlife to hunters, poachers, and other predators
4 Provide a mix of habitats and successional stages accessible to species that require a variety of habitats for different activities or stages of their life cycles	4 Riparian strips, often recommended as corridor sites, might not enhance dispersal or survival of upland species
5 Provide alternative refugia from large disturbances (a 'fire escape')	5 Cost, and conflicts with conventional land preservation strategy to preserve endangered species habitat (when inherent quality of corridor habitat is low)
6 Provide 'greenbelts' to limit urban sprawl, abate pollution, provide recreational opportunities, and enhance scenery and land values	

Source: Noss (1987)

(FEN) was suggested as an approach to managing biodiversity across a landscape (McDougall 1991). The purpose of a FEN was to maintain natural forest ecosystem processes, to provide interior habitat, and to allow for dispersal, recolonization, and movement. These FENs would be composed of reserves, corridors, and buffers. In 1991, Noss, Soulé, and others founded the Wildlands Project, the largest landscape plan ever proposed (Mann and Plummer 1993). This project intends to establish a network of corridors, reserves, and buffers across North America to maintain continental connectivity.

Ecological Principles

Maintaining Connectivity

Connectivity is maintained in a landscape when there is a continuity of habitats and processes along environmental gradients (Noss 1991). Connectivity of ecological processes (e.g., dispersal, predation, fire, flooding) is as important as connectivity of habitats. The collective habitat requirements of species need to be viewed as interacting, functional components of the landscape ecosystem (Noss 1991). The primary intent of management should be to maintain natural connectivity at many scales, not to reconnect recently isolated habitats (Noss and Harris 1989).

Ecological processes are fundamental components of forested landscapes. Processes are characterized temporally by rates and spatially by flows. Maintaining connecti[illegible] is intended to maintain the natural continuum of these ecological rates ar[illegible]. (Photograph by Scott Harrison)

Providing habitat and movement routes are predominant themes in maintaining connectivity. The premise is that if suitable habitats are connected, fauna will move among patches to use resources, recolonize areas, and maintain gene flow (Merriam 1991b). Dispersal and gene flow are key features of these movements. Dispersal is the movement of organisms away from their place of origin; gene flow is the movement of alleles due to the dispersal of gametes of offspring (Noss 1991). Harris and Scheck (1991) present nine reasons organisms disperse:

- to forage for resources that are patchy in space, such as food, mates, or special habitats
- to exploit resources that are sporadic in time
- to exploit seasonal environments (e.g., migrations)
- to accommodate different life stages
- to return to a birthplace
- to colonize a new, local environment
- to extend range distribution
- to accommodate climate change
- to colonize new islands or continents.

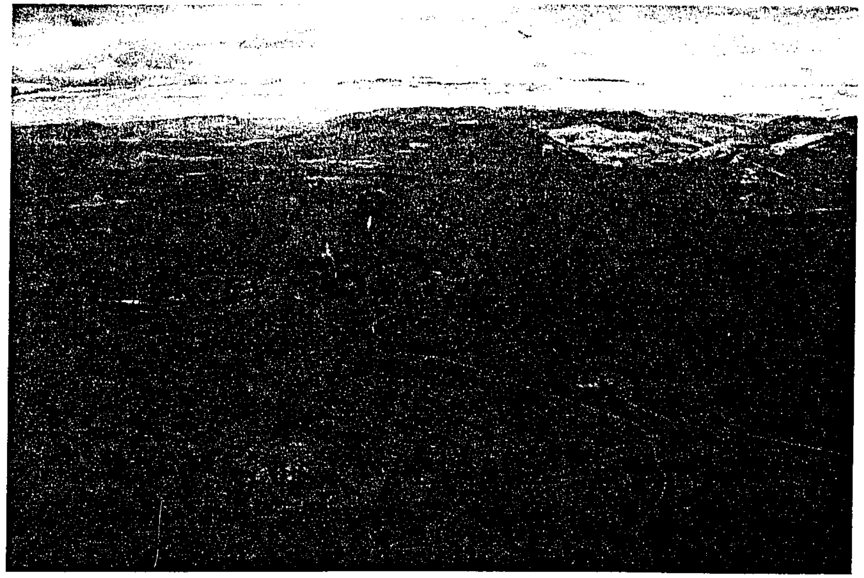
They also discuss the time and distances associated with these dispersals (see Table 3 in Harris and Scheck 1991). These spatial and temporal considerations of dispersal are important. If there are barriers to long-term movements over great distances even with corridors in place, broad-scale retention of habitat, rather than corridors, may be necessary to maintain connectivity (Merriam 1991b). Nuthatches (*Sitta europaea*) in fragmented Belgian habitats had dispersal distances several times larger than nuthatches in more forested landscapes (Matthysen et al. 1995), and young nuthatches were less likely to move through the less connected landscape once they had settled. Haas (1995) found that for adult American Robins (*Turdus migratorius*), Brown Thrashers (*Toxostoma rufum*), and Loggerhead Shrikes (*Lanius ludovicianus*), movements between patches were rare but occurred significantly more frequently when sites were connected by a corridor.

Connectivity is believed to be important for viability of faunal populations (Taylor et al. 1993). The loss of connectivity, often discussed as fragmentation, is considered by some to be the greatest threat to natural biological diversity (Harris 1984; Wilcox and Murphy 1985; Wilcove et al. 1986; Noss 1991). The loss or gain of only a few species can affect many other species and destabilize the whole community (Wilson and Willis 1975). Reductions in the levels of neotropical bird populations have been shown for fragmented habitats (MacClintock et al. 1[illegible]). These migrant birds have lower dispersal and reproductive rates a[illegible]ibit specialized insectivorous feeding strategies. As connectivity is lost and habitat patches become isolated, the neotropical migrants are outcompeted by resident birds that are feeding generalists and that have all year to recolonize fragmented habitats (MacClintock et al. 1977). Populations of white-footed mice living in isolated forest patches in agricultural landscapes have lower growth rates and are more prone to extinction than populations living in forest patches linked by fencerow corridors (Fahrig and Merriam 1985).

In areas with extensive human disturbance, natural connectivity often has been lost. In Florida no natural communities are pristine (Noss and Harris 1989), and habitat management must focus on the restoration, rather than maintenance, of connectivity. This is a different situation from areas where human disturbance and habitat fragmentation are less severe. Even authors who question the cost-effectiveness of corridors as mechanisms for restoring connectivity in Florida's severely fragmented landscapes acknowledge that natural connectivity is important and should be retained before landscapes are disturbed (Simberloff and Cox 1987).

Connectivity should be maintained at the landscape level (Harris and Scheck 1991; Merriam 1991b; Noss 1991). Taylor et al. (1993) define landscape connectivity as the degree to which the landscape facilitates or impedes movement among resource patches. A landscape unit may be a mountainous watershed of 5,000 ha or an undulating plateau of 100,000 ha. In either case, the landscape unit is a distinct, measurable unit with a recognizable and repeated cluster of ecosystems and disturbance regimes (Forman and Godron 1981). Connectivity objectives should be set for each landscape unit. Objectives should be specific and focused on issues such as the viability of specific target species (Soulé 1991); rare and threatened species must receive special consideration (Bennett 1991). Csuti (1991) states that connectivity objectives should address the stabilization of natural biological diversity, not just a reduction in the rate of species loss.

Connectivity objectives need to account for all habitat disturbances within the landscape unit (Csuti 1991). The objectives must consider the duration and extent to which different disturbances will alienate habitats. Fencerows that maintain connectivity in an agricultural landscape (Merriam and Lanoue 1990) would need to be maintained indefinitely if the surrounding land remained agricultural. Conversely, linkages that maintain connectivity in a newly logged landscape could be replaced by other areas within the landscape as the new forest grows. However, Harris (1984) states that in the managed forests of the future, reserves may be 'islands' in a sea of short-rotation plantations, and that these plantations will not act as source pools to recolonize the reserves. Thus, before corridors of old-growth habitat are replaced by younger stands, there should be evidence that the new forest will provide habitat attributes similar to those of the original linkage (i.e., complex forests [illegible]ucturally simplified plantations). In [illegible]s, the



This 1996 photograph of the Bowron clearcut in central British Columbia shows how the level of connectivity in portions of this 55,000-ha clearcut has remained low 12 years after logging. (Photograph by Scott Harrison)

objectives must acknowledge that the mechanisms used to maintain connectivity will be required for decades or centuries (Csuti 1991).

Mechanisms for Maintaining Connectivity

Linkages are mechanisms by which the principles of connectivity can be achieved. Although the definitions of linkages vary, all imply that there are connections or movement among habitat patches. *Corridor* is another term commonly used to refer to a tool for maintaining connectivity. Csuti (1991) differentiates between the functions of corridors and linkages: corridors provide only pathways for movement, whereas linkages enable ecosystem processes to continue. Therefore, the successful functioning of a corridor or linkage should be judged in terms of the connectivity among subpopulations and the maintenance of potential metapopulation processes (Merriam 1991b).

Noss (1992) uses the term *linkage* to emphasize the role of faunal movements as part of the overall ecosystem function. Linkages provide routes for movement and dispersal, and habitat for non-mobile organisms; they often encompass special habitats that are distinct in the landscape, such as riparian habitats. Linkages also provide avenues for long-distance range shifts to enable species to adapt to gradual, long-term environmental changes such as global warming. Fo[illegible] (1983) presents four major functions of corridors:

- to enhance the movement of flora and fauna
- to act as semi-permeable barriers to movement across the width of the corridor (the effects of water runoff, mineral-nutrient runoff, or winds can be moderated)
- to provide habitat for some species
- to provide sources of environmental and biotic effects on the surrounding matrix (organisms may move from the corridor to the surrounding matrix, colonizers may disperse, the corridor may moderate the local environment through shading or deposition of leaf litter).

The particular fauna that will benefit from linkage networks are often inferred from species' life histories, although data are limited on the extent to which linkages will be used. Bennett (1991) categorizes species by their ecological characteristics in order to speculate about their use of linkages and corridors:

Interior versus edge species. Species that can use habitat edges predominate among animals known to use corridors, but they may not need to use the corridor for movement. Species typical of habitat interiors have a greater need for corridors to minimize population isolation, but they are more limited in their use of corridors. Predation along habitat edges is believed to be an important influence on interior species and their ability to use corridors effectively.

Habitat specialists versus generalists. Because of specialized habitat requirements, certain species occur in low densities, and their conservation status would be enhanced by corridors that effectively link populations. However, specialized habitats may not be available or are difficult to incorporate and manage in corridors, thus limiting the value of the corridor to these species. In contrast, species with generalized habitat requirements are more likely to use corridors, but because of their wider habitat tolerance they may not need to do so.

Body size and scale of movement. Large species and those capable of longer regular movements are more likely to be able to use corridors for direct movements by individuals. They may also be less vulnerable to predation within the corridor than are small animals and those that move shorter distances per unit time. However, smaller and less mobile animals may maintain a resident population within the corridor, which in turn serves as an additional source of dispersing individuals.

In general, species that need to use corridors are those that have an obligate relationship with natural vegetation and are dependent on the remnant system of habitat (Bennett 1991). Moreover, even relatively little use of corridors may be enough. In a population model examining the status of the endar[illegible]ed Florida panther, one or two dispersals every decade was enough [illegible] the population from going extinct (Mann and Plummer 1993). MacClintock et al. (1977) felt that most forest species would sustain breeding populations in larger fragments of habitat (thousands of acres) provided the fragments were linked to larger forest tracts.

Despite gaps in our understanding of the mechanisms for maintaining connectivity within landscapes, it is better to retain corridors and then assess their role than to lose corridors and find out they were important (Saunders and Hobbs 1991a). Bennett (1991) summarizes the situation as follows:

> Despite our limited knowledge concerning the use of corridors by plants and animals, we must proceed with the designation and management of corridors on the basis that they *are* beneficial to nature conservation. Until further knowledge is available, management should endeavour to: retain existing corridors and corridor networks; maintain corridors as close to a 'natural' or 'pristine' state as is possible, in order to leave future management options open; and avoid activities or disturbance that will reduce corridor width or lead to an increase in 'edge' effects in the corridor.

Corridor Location and Design

Corridors are seldom thought of as single strips of natural vegetation but rather as an integral part of an interconnected landscape. The specific purpose of a corridor will influence its location (Harrison 1992). The location of corridors is important because corridors attempt to accommodate so many aspects of faunal ecology: species movement type and magnitude, immigration and emigration rates, movement rates, habitat requirements, and interactions among organisms (Soulé 1991).

Corridor networks should link ridgetops and valley bottoms and encompass a diversity of habitats and topographic gradients (Noss and Harris 1989; Noss 1991). Lindenmayer and Nix (1993) found that corridors that linked the valley bottom to the ridgetop had more species use than corridors located only along a midslope. Similarly, riparian habitats are often candidates as corridors because of the ecological importance of these areas and because the dendritic drainage patterns usually link midslopes and valley bottoms (Harris 1984). However, the maintenance of riparian corridors alone may not be suitable for some upland species (Noss 1991). In general, corridor location and design should reflect the ecology of an area. Corridors should be designed so that they remain functional after a human-caused or natural disturbance and until the surrounding habitat matrix can return to a pre-disturbance state.

Different organisms have different dispersal capacities (e.g., birds and bats versus terrestrial snails and plants), and a movement corridor for one species may be a barrier to another (Noss 1991). Informat[illegible] the requirements for the full gamut of native species is therefore [illegible]ed to design

In contrast to more typical alpine mountain goat (*Oreamnos americanus*) populations, some mountain goats inhabit river canyons surrounded by forested habitat. For these canyon-dwelling goats, it is unclear whether the forest acts as a corridor or a barrier. (Photograph by Georgie Harrison)

and evaluate the effectiveness of corridors on the basis of their dispersal performance (Harris and Scheck 1991). In most cases, corridors intended as pathways for movement should be continuous for maximum effectiveness (Forman and Godron 1981). Soulé (1991) believes that they should have straight sides and a constant width because animals will spend less time in edge habitats. He argues that any departure from linearity (e.g., corridors with barriers or doglegs, or shaped as cul-de-sacs) will create a maze effect that can trap animals. McEuen (1993), however, argues that if the habitat within the corridor is sufficient 'survival' habitat, being caught in this corridor is the same as being caught in a reserve.

The quality of the habitat within corridor networks is an important element of connectivity (Henein and Merriam 1990). Frequently, corridors are intended to facilitate the movement of organisms by extending interior forest habitat characteristics through areas of timber harvest (Saunders and Hobbs 1991a). Although planning decisions can be eased by simply placing corridors in 'inoperable' or 'non-productive' areas where timber harvest is not feasible, maintaining connectivity among 'productive' timber areas is probably necessary for species that prefer such habitats. Harris and Scheck (1991) emphasize that faunal dispersal corridors should maintain or enhance the habi ues for native fauna and flora; corrido uld therefore consist of r or restored native landscape features. H d Scheck

(1991) cite an example where introduced landscape features have resulted in the loss of native biological diversity: trees planted as windbreaks on the Prairies provided an unnatural corridor; Yellow-Shafted Flickers (*Colaptes auratus*) followed these corridors westward and interbred with the western Red-Shafted Flickers, resulting in the loss of the subspecies variation.

Corridor Width

The suitability of a corridor for a particular species may depend on behaviour, physical aspects of the landscape, or distance between patches. Scale also influences the definition of a corridor; for example, fencerows can provide linkages for small mammals but not for grizzly bears (*Ursus arctos*) or cougars. Saunders and de Rebeira (1991) found that birds used vegetated connections as narrow as 4 m for movement; however, wide-ranging, large mammals require landscape-scale corridors (Noss 1991). Some authors suggest that corridor width must be established in relation to the movement ability of a species, otherwise the corridor may act as a sink habitat rather than a channel (Saunders and Hobbs 1991a; Soulé 1991). Csuti (1991) points out that the concerns about wide corridors and 'sinks' is based on a view of corridors as strictly travel routes. He notes that if a corridor is wide enough, some species will maintain a population within it and will eventually die natural deaths within the corridor.

Ultimately, the effectiveness of a corridor depends on the amount of human activity in and around the corridor (Harrison 1992), and the optimum corridor width depends on the strength of edge effect (Soulé 1991). Forman and Godron (1981) outline the importance of corridors as buffers against edge effects:

> The corridor must provide protective cover for species from natural predators, domestic animals, and human effects lining each side of the corridor. The outer portions of the strip corridor have the edge effect, while the central portion contains the interior environment required for many patch interior species. For this reason, the width of a strip corridor is critical, since the interior environment must be present and sufficiently wide itself to be used by interior species.

A range of edge effects occur along the interface of interior and disturbed habitat types: (1) biological edge effects (predation, herbivory, weed invasion), (2) physical effects (light, temperature, humidity, nutrient status, hydrology changes, wind effects), and (3) human effects (pollution, hunting) (Start 1991). Importantly, the greater the difference between the corridor and the surrounding habitat matrix, the deeper the edge effect (Forman 1983; Harris 1984). Feat ng edges around reserves and corridors (e.g., partial-cut logging in of clearcutting with hard edges) is one method of mitigating some edge effects. Other authors feel that the solution is more straightforward: to minimize the edge effect, widen the corridor (Start 1991).

A single optimum width is impossible to specify. Corridor width should be assessed in relation to the life histories and requirements of the fauna for which the corridors are intended (Friend 1991). In Maine, species known to do well in edge habitats – moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and black bear (*Ursus americanus*) – used corridors 76-152 m wide (Laitin 1987). Csuti (1991) uses measures of edge effects to present minimum useful corridor widths, and suggests widths of 1.2-6.4 km to provide interior habitat within the corridor. Harris and Scheck (1991) account for spatial and temporal aspects of corridor design (capitals their emphasis):

> When the movement of individual animals is being considered, when much is known about their behaviour, and when the corridor is expected to function in terms of weeks or months then the appropriate corridor width can be measured in metres (*c.* 1-10 m).
>
> When the movement of a species is being considered, when much is known about its biology, and when the corridor is to function in terms of years then the corridor width should be in 100s of metres (*c.* 100-1000 m).
>
> When the movement of entire assemblages of species is being considered and/or when little is known of the biology of the species and/or if the faunal dispersal corridor is to function over decades the appropriate width must be measured in kilometres.

There are few data indicating how corridor width and composition may influence faunal movement, although many authors feel that these are important considerations with respect to the effectiveness of a corridor network (Friend 1991). In broad terms, for a faunal dispersal corridor to be effective, its size must be appropriate for the ecological function being asked of it; the width must be appropriate to the scale of the phenomenon being addressed (Harris and Scheck 1991). Bigger animals probably need wider corridors, and corridor networks in heavily disturbed ecosystems must provide more habitat for connectivity of ecological functions. Of course, all corridors, regardless of their width, must connect areas of useful, protected habitat (Harris and Scheck 1991).

Summary

Connectivity connotes connections among habitats, species, communities, and ecological processes. Connectivity is the antithesis of fragmentation. Corridors are tools by which the principle of connectivity is maintained. [illegible]ite some potential disadvantages, corridors are the only means of maintaining connectivity between patches for mobile organisms (Csuti 1991). One should accept the working hypothesis that wide, continuous corridors are most likely to foster movements (Saunders and Hobbs 1991a).

Research Needs

Maintaining connectivity throughout the landscape is a relatively recent conservation concern. The following are the major information gaps identified in the literature.

Monitoring of corridor use. In order to understand the success or failure of connectivity through corridors, it is imperative to monitor the species that use them (Noss 1987; Saunders and Hobbs 1991a; McEuen 1993). As well, monitoring the shift of species that use corridors when conditions change (e.g., width, length, habitat) could be significant to future corridor design (McEuen 1993). For experimental designs and statistical considerations, see Nicholls and Margules (1991) and Inglis and Underwood (1992).

Genetic studies. It is important to learn more about the effects of inbreeding and outbreeding on both target and corridor-dependent species. The effectiveness of corridors in maintaining genetic diversity and gene flow also needs to be understood (Coates 1991).

Fragmentation. Studies should be initiated on how fragmentation affects the persistence of amphibian, reptile, and mammal species during the process of fragmentation, as opposed to studies on the after-effects of fragmentation (i.e., habitat 'islands') (Verner 1984; Lehmkuhl and Ruggiero 1991). There is also a need to determine population parameters and then model population responses to fragmentation over time and space (Lehmkuhl and Ruggiero 1991).

Behaviour. Information such as behaviour, habitat requirements, and life histories is needed on 'keystone' species (large mammals, endangered species, or corridor-dependent species) to better understand their needs for connectivity (Friend 1991; Merriam 1991a).

Width and dimensions of corridors. Studies to determine the importance of width or width versus length of a corridor should be initiated (Friend 1991). Also, studies of 'keystone' species and their home ranges may help determine the minimum widths required for a corridor (Harrison 1992). If corridors are to support the movement of species over a long period, it will be important to determine the optimum dimensions needed to support resident populations of a wide range of native species (Bennett 1990).

Dispersal. Studying dispersal in natural corridors and observing species movement across unknown and unsuitable habitat may help in developing future landscape designs for connectivity (Harrison 1992). Data such as distance, rate, and frequency of species movement through corridors and the landscape should be collected (Bennett 1991).

Invertebrate studies. Understanding invertebrate assemblages in corridors may be key to corridor design, as invertebrates are an integral part of an ecosystem and an important food source for many vertebrates (Saunders and Hobbs 1991a).

Literature Cited

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology 7(1):94-108.

Bennett, A.F. 1990. Habitat corridors and the conservation of small mammals in a fragmented forest environment. Landscape Ecology 4(2-3):109-122.

–. 1991. What types of organisms will use corridors. Pages 407-408 in D.A. Saunders and R.J. Hobbs (eds.). Nature conservation 2: the role of corridors. Surrey Beatty and Sons, NSW, Australia. 442 pp.

Cable, T.T. 1991. Windbreaks, wildlife, and hunters. Pages 36-55 in J.E. Rodiek and E.G. Bolen (eds.). Wildlife and habitats in managed landscapes. Island Press, Washington, D.C. 219 pp.

Coates, D.J. 1991. Gene flow along corridors. Pages 408-409 in D.A. Saunders and R.J. Hobbs (eds.). Nature conservation 2: the role of corridors. Surrey Beatty and Sons, NSW, Australia. 442 pp.

Csuti, B. 1991. Introduction. Pages 81-90 in W.E. Hudson (ed.). Landscape linkages and biodiversity. Defenders of Wildlife, Washington, D.C. 196 pp.

Date, E.M., H.A. Ford, and H.F. Recher. 1991. Frugivorous pigeons, stepping stones, and weeds in northern New South Wales. Pages 241-245 in D.A. Saunders and R.J. Hobbs (eds.). Nature conservation 2: the role of corridors. Surrey Beatty and Sons, NSW, Australia. 442 pp.

Diamond, J.M. 1975. The island dilemma: lessons of modern biogeography and the design of nature reserves. Biological Conservation 7:129-146.

Fahrig, L., and G. Merriam. 1985. Habitat patch connectivity and population survival. Ecology 66(6):1762-1768.

Forman, R.T.T. 1983. Corridors in a landscape: their ecological structure and function. Ekologia 2(4):375-387.

–. 1988. Landscape ecology plans for managing forests. Pages 131-135 in Proceedings of the Convention for the Society of American Foresters. USDA Forest Service General Technical Report NE-140.

–. 1991. Landscape corridors: from theoretical foundations to public policy. Pages 71-84 in D.A. Saunders and R.J. Hobbs (eds.). Nature conservation 2: the role of corridors. Surrey Beatty and Sons, NSW, Australia. 442 pp.

Forman, R.T.T., and M. Godron. 1981. Patches and structural components for a landscape ecology. BioScience 31:733-739.

Franklin, J.F., and R.T.T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecology 1(1):5-18.

Friend, G.R. 1991. Does corridor width or composition affect movement? Pages 404-405 in D.A. Saunders and R.J. Hobbs (eds.). Nature conservation 2: the role of corridors. Surrey Beatty and Sons, NSW, Australia. 442 pp.

Gates, J.E. 1991. Powerline corridors, edge effects, and wildlife in forested landscapes of the Central Appalachians. Pages 14-32 in J.E. Rodiek and E.G. Bolen (eds.). Wildlife and habitats in managed landscapes. Island Press, Washington, D.C. 219 pp.

Harris, L.D. 1984. The fragmented forest: island biogeography theory and the preservation of biotic diversity. University of Chicago Press, Chicago, Ill. 211 pp.

Harris, L.D., and K. Atkins. 1991. Faunal movement corridors in Florida. Pages 117-134 in W.E. Hudson (ed.). Landscape linkages and biodiversity. Defenders of Wildlife, Washington, D.C. 196 pp.

Harris, L.D., and J. Sc [illegible] 991. From implications to applications: the di [illegible] corridor principle applied to [illegible] ervation of biological diversity. Pages 189-220 i [illegible] unders and R.J. Hobbs (eds.). Nature conservation 2: the role of corridors. Surrey Beatty and Sons, NSW, Australia. 442 pp.

Harrison, R.L. 1992. Toward a theory of inter-refuge corridor design. Conservation Biology 6(2):293-295.

Harrison, S.P. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnean Society. 42:73-88.

Harrison, S., B. Chatterson, and D. Paul. In press. Landscape connectivity and its effect on the ecological processes of spruce grouse populations. Wildlife Biology.

Hass, C.A. 1996. Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. Conservation Biology 9(4):845-854.

Hay, K.G. 1991. Greenways and biodiversity. Pages 162-175 in W.E. Hudson (ed.). Landscape linkages and biodiversity. Defenders of Wildlife, Washington, D.C. 196 pp.

Henein, K., and G. Merriam. 1990. The elements of connectivity where corridor quality is variable. Landscape Ecology 4(2/3):157-170.

Hess, G.R. 1994. Conservation corridors and contagious disease: a cautionary note. Conservation Biology 8(1):256-262.

Hobbs, R.J. 1992. The role of corridors in conservation: solution or bandwagon? Tree 7(11):389-392.

Hobbs, R.J., and A.J.M. Hopkins. 1991. The role of conservation corridors in a changing climate. Pages 281-290 in D.A. Saunders and R.J. Hobbs (eds.). Nature conservation 2: the role of corridors. Surrey Beatty and Sons, NSW, Australia. 442 pp.

Inglis, G., and A.J. Underwood. 1992. Comments on some designs proposed for experiments on the biological importance of corridors. Conservation Biology 6(4):581-586.

Kucera, T.E., and C. McCarthy. 1988. Habitat fragmentation and mule deer migration corridors: a need for evaluation. Transactions of the Western Section of the Wildlife Society 24:61-67.

Laitin, J. 1987. Corridors for wildlife. American Forests (September/October):47-49.

Lehmkuhl, J.F., and L.F. Ruggiero. 1991. Forest fragmentation in the Pacific Northwest and its potential effects on wildlife. Pages 35-46 in L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff (eds.). Wildlife and vegetation of unmanaged Douglas-fir forests, USDA Forest Service General Technical Report GTR-285.

Levins, R. 1970. Extinction. Pages 77-107 in M. Gerstenhaber (ed.). Some mathematical questions in biology: lectures on mathematics in the life sciences, vol. 2. American Mathematical Society, Providence, R.I.

Lindenmayer, D.B., and H.A. Nix. 1993. Ecological principles for the design of wildlife corridors. Conservation Biology 7(3):627-630.

MacArthur, R.H., and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J. 442 pp.

MacClintock, L., R.F. Whitcomb, and B.L. Whitcomb. 1977. Island biogeography and 'habitat islands' of eastern forest. American Birds 31(1):3-16.

Mann, C.C., and M.L. Plummer. 1993. The high cost of biodiversity. Science 260:1868-1871.

Matthysen, E., F. Adriaensen, and A.A. Dhondt. 1995. Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. Oikos 72:375-381.

McDougall, I.A. 1991. Forest ecosystem networks – a strategy for managing biological diversity. Unpublished report, B.C. Ministry of Environment, Lands and Parks. 7 pp.

McEuen, A. 1993. The wildlife corridor controversy: a review. Endangered Species Update 10(11/12):1-6/12.

Merriam, G. 1991a. Corridors and connectivity: animal populations in heterogeneous environments. Pages 133-142 in D.A. Saunders and R.J. Hobbs (eds.). Nature conservation 2: the role of corridors. Surrey Beatty and Sons, NSW, Australia. 442 pp.

–. 1991b. Are corridors necessary for the movement of biota? Pages 406-407 in D.A. Saunders and R.J. Hobbs (eds.). Nature conservation 2: the role of corridors. Surrey Beatty and Sons, NSW, Australia. 442 pp.

Merriam, G., and A. Lanoue. 1990. Corridor use by small mammals: field measurement for three experimental types of *Peromyscus* [illegible] *s.* Landscape Ecology 4(2/3):123-131.

Naiman, R.J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3(2):209-212.

Newmark, W.D. 1987. A land-bridge island perspective on mammalian extinctions in western North American parks. Nature 325:430-432.

Nicholls, A.O., and C.R. Margules. 1991. The design of studies to demonstrate the biological importance of corridors. Pages 49-61 in D.A. Saunders and R.J. Hobbs (eds.). Nature conservation 2: the role of corridors. Surrey Beatty and Sons, NSW, Australia. 442 pp.

Noss, R.F. 1983. A regional landscape approach to maintain diversity. BioScience 33(11):700-706.

–. 1987. Corridors in real landscapes: a reply to Simberloff and Cox. Conservation Biology 1(2):159-164.

–. 1991. Landscape connectivity: different functions at different scales. Pages 27-39 in W.E. Hudson (ed.). Landscape linkages and biodiversity. Defenders of Wildlife, Washington, D.C. 196 pp.

–. 1992. North American wilderness recovery project: land conservation strategy. Wild Earth special issue. 35 pp.

Noss, R.F., and L.D. Harris. 1989. Habitat connectivity and the conservation of biological diversity: Florida as a case history. Pages 131-135 in Forestry of the Frontier Convention of the Society of American Foresters, Spokane, Wash. 444 pp.

Preston, F.W. 1962. The canonical distribution of commonness and rarity. Part 2. Ecology 43(3):410-432.

Saunders, D.A., and C.P. de Rebeira. 1991. Values of corridors to avian populations in a fragmented landscape. Pages 221-240 in D.A. Saunders and R.J. Hobbs (eds.). Nature conservation 2: the role of corridors. Surrey Beatty and Sons, NSW, Australia. 442 pp.

Saunders, D.A., and R.J. Hobbs. 1991a. The role of corridors in conservation: what do we know and where do we go? Pages 421-427 in D.A. Saunders and R.J. Hobbs (eds.). Nature conservation 2: the role of corridors. Surrey Beatty and Sons, NSW, Australia. 442 pp.

– (eds.). 1991b. Nature conservation 2: the role of corridors. Surrey Beatty and Sons, NSW, Australia. 442 pp.

Simberloff, D., and L.G. Abele. 1976. Island biogeography theory and conservation practice. Science 191:285-286.

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

Simberloff, D., J.A. Farr, J. Cox, and D.W. Mehlman. 1992. Movement corridors: conservation bargains or poor investments? Conservation Biology 6(4):493-504.

Simpson, G.G. 1936. Data on the relationship of local and continental mammalian fauna. Journal of Palaeontology 10:410-414.

–. 1940. Mammals and land bridges. Journal of the Washington Academy of Sciences 30:137-163.

Soulé, M.E. 1991. Theory and strategy. Pages 91-103 in W. Hudson (ed.). Landscape linkages and biodiversity. Defenders of Wildlife, Washington, D.C. 196 pp.

Start, A.N. 1991. How can edge effects be minimized? Pages 417-418 in D.A. Saunders and R.J. Hobbs (eds.). Nature conservation 2: the role of corridors. Surrey Beatty and Sons, NSW, Australia. 442 pp.

Szacki, J. 1987. Ecological corridor as a factor determining the structure and organization of a bank vole population. Acta Theriologica 32(3):31-44.

Taylor, P.D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68(3):571-573.

Terborgh, J. 1974. Preservation of natural diversity: the problem of extinction prone species. BioScience 24:715-722.

Verner, J. 1984. Predicting effects of habitat patchiness and fragmentation – the researcher's viewpoint. Pages 327-329 in J. Verner, M.L. Morrison, and C.J. Ralph (eds.). Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, Wis.

Wilcov C.H. McLennan, and A.P. Dobson. 1986. Habitat fragmentation in the tempera Pages 237-256 in M.E. Soulé (ed.). Conservation biology: the science of scarcity ersity. Sinauer Associates, Sunderland, Mass.

Wilcox, B.A., and D.D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. American Naturalist 125:879-887.

Wilson, E.O., and E.O. Willis. 1975. Applied biogeography. Pages 522-534 in M. Cody and J.M. Diamond (eds.). Ecology and evolution of communities. Harvard University Press, Cambridge, Mass.