

Biological Corridors: Form, Function, and Efficacy

Linear conservation areas may function as biological corridors, but they may not mitigate against additional habitat loss

Daniel K. Rosenberg, Barry R. Noon, and E. Charles Meslow

Habitat loss and fragmentation are among the most pervasive threats to the conservation of biological diversity (Wilcove et al. 1986, Wilcox and Murphy 1985). Habitat fragmentation often leads to the isolation of small populations, which have higher extinction rates (e.g., Pimm et al. 1988). Ultimately, the processes of isolation and population extinction lead to a reduction in biological diversity. Concern for this loss has motivated conservation biologists to discuss the actions that are needed to increase the effective size of local populations. Predominant among these possible strategies has been the recommendation that corridors be included in conservation plans (Figure 1) to increase the connectivity of otherwise isolated patches (Meffe and Carroll 1994).

The inclusion of corridors in reserve designs has become an important conservation tactic for protecting biological diversity. This strategy was motivated by theoretical and empirical observations demonstrating that increased interchange of in-

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dividuals among populations may increase local and regional population persistence, particularly for small, isolated populations (Fahrig and Merriam 1994, Sjögren 1991). The importance of such interchange in both reducing extinction rates and increasing colonization rates has become a paradigm in conservation biology (Doak and Mills 1994, Simberloff 1988). This understanding, together with the public interest in "greenways" (e.g., Little 1990) has led conservation biologists and land planners to advocate corridors as essential components of reserve design.

Although connectivity can be achieved in many ways, including movement through low-quality habitats surrounding reserves, corridors have been advocated as the primary means to connect isolated populations (Meffe and Carroll 1994, Noss 1983, Saunders and Hobbs 1991). Protecting naturally existing corridors likely promotes ecological processes and may benefit regional and

local biological diversity. However, the creation of linear patches intended to function as corridors as a tool to allow for further habitat removal may ultimately cause the local extirpation of species, and thus erode biological diversity. Because of these concerns, it is important to evaluate critically both the effectiveness of biological corridors and the trade-off with diminished habitat area that often accompanies habitat conservation plans.

Biological corridors may include linear patches, such as streamside riparian areas, shelter belts, forest remnants remaining from tree harvest, and, in agricultural areas, fencerows. Although all linear patches share certain structural attributes (length is much greater than width), they may function in different ways. The literature on corridors is contradictory because of the ambiguous use of the term "corridor," which is often used to describe landscape components with divergent functions. Moreover, the ability of biological corridors to ameliorate high local extinction rates remains controversial because the evidence is inadequate. In this article, we define and distinguish the two primary functions of linear patches relevant to vertebrate populations—as wildlife habitat and as biological corridors. We argue that both functions of linear patches are potentially critical to conservation of biological diversity as the landscape becomes increasingly fragmented into smaller, more isolated patches (Harris 1984, Wilcove et al. 1986).

Daniel K. Rosenberg (e-mail: rosenbed@ccmail.orst.edu) is a research associate with the Oregon Cooperative Wildlife Research Unit, Oregon State University, Corvallis, OR 97333. Barry R. Noon is a research scientist with the US Forest Service, Redwood Sciences Laboratory, Arcata, CA 95521. E. Charles Meslow is the northwestern representative of the Wildlife Management Institute, Corvallis, OR 97330. Their research focuses on the population ecology of vertebrates in managed ecosystems. © 1997 American Institute of Biological Sciences.

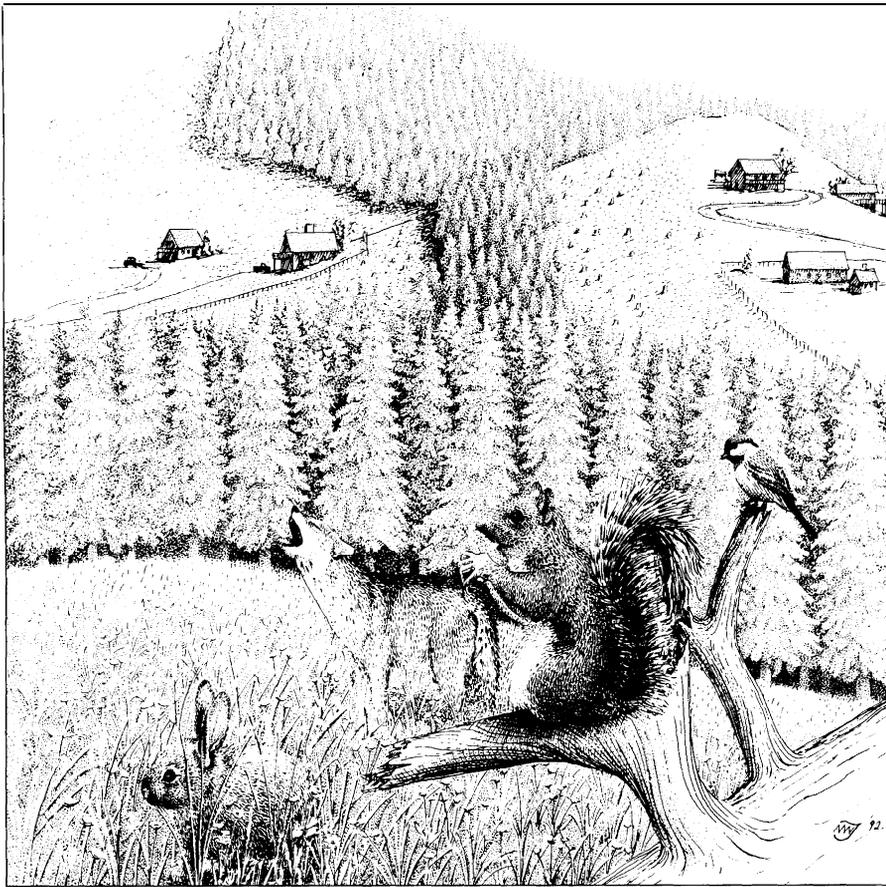


Figure 1. Representation of a linear patch of trees, a potential corridor connecting two forest patches. The surrounding area of homes, farms, and fields represents the matrix environment. Linear conservation areas connecting otherwise separated habitat patches have been suggested to facilitate movement of animals across degraded matrix environments and thus to function as biological corridors. Drawing: John Megahan.

Defining linear patches as corridor or as habitat

The use of the term *corridor* in diverse contexts has contributed to its vague and often contradictory definitions (Rosenberg et al. 1995). Landscape ecologists Richard Forman and Michel Godron (1986) characterized corridors only in terms of their shape and spatial context, defining corridors as "...narrow strips of land which differ from the matrix [the environment in which habitat and linear patches are embedded] on either side. Corridors may be isolated strips, but are usually attached to a patch of somewhat similar vegetations" (p. 123). Biological corridors have also been defined as continuous, narrow patches of vegetation that facilitate movement among habitat patches, thereby preventing isolation of populations (Merriam 1984). Although the structural definition does not preclude a functional

(i.e., enhancing movement) role for biological corridors, the different definitions suggest that the existence of either of these roles is sufficient to define a linear patch as a corridor.

One definition of a corridor thus emphasizes a movement function (i.e., passageways from one location to another), whereas the other stresses form—that is, shape, composition, and context (i.e., narrow and contrasting with the environment on its edges). Consequently, the criteria to determine if a linear patch serves as a corridor have been ambiguous. When issues such as the significance of corridors to the maintenance of biological diversity are debated (e.g., Noss 1987, Saunders and Hobbs 1991, Simberloff and Cox 1987), these different interpretations of the corridor concept may result in controversy (Rosenberg et al. 1995).

To determine whether a particular linear patch functions as habitat or as a biological corridor, the func-

tion of these two landscape elements for species that occupy them needs to be clarified. We define these two landscape elements operationally as follows (although we note that a single landscape element may be defined in either way depending on the species involved):

- A corridor is a linear landscape element that provides for movement between habitat patches, but not necessarily reproduction. Thus, not all life history requirements of a species may be met in a corridor.
- A habitat is a patch (or collection of patches) that provides resources needed for survivorship, reproduction, and movement. If average survivorship and reproduction rates allow a stable or growing population that produces emigrants, a habitat patch is a source patch; if it is dependent on immigrants to sustain its populations, it is a sink patch (Puliam 1988).

The corridor function

The primary ecological rationale for corridors in wildlife conservation is to increase population persistence by allowing continued exchange of individuals among a previously connected population. Movement of individuals among subpopulations may reduce regional extinction rates by a number of mechanisms: by decreasing variability in birth and death rates (Beier 1993, Den Boer 1981), by increasing (re)colonization rates of unoccupied patches (Hanski and Gilpin 1991), by decreasing inbreeding depression (i.e., by increasing gene flow; Shonewald-Cox et al. 1983), and by increasing potentially adaptive genetic variance for maintaining population fitness (Lande 1995).

Few studies have tested the first mechanism; however, the empirical evidence that does exist supports the notion that reduction in demographic variability will increase persistence (Den Boer 1981, Forney and Gilpin 1989). Empirical evidence also supports the second mechanism (Sjögren 1991) as important in maintaining regional persistence. The relative importance of the genetic mechanisms compared with demographic factors remains controversial (Lande 1988, Mills and Smouse 1994). How-

ever, in a large metapopulation (spatially semi-isolated populations that are linked by dispersal of individuals) the contribution of only a few immigrant individuals to local gene pools per generation is sufficient to minimize deleterious inbreeding effects and to sustain genetic diversity (Lande and Barrowclough 1987, Slatkin 1985).

In addition to connecting local populations, corridors may facilitate movement of an individual within its home range. Although the latter function has received less attention than the former, it may be important to the survival of individuals, and thus populations, in fragmented environments. Facilitation of movement may be particularly relevant for species whose home range area requirements exceed the average patch size or for species or populations whose survival requires that individuals move between discrete patches (landscape complementation; Dunning et al. 1992). For example, some species, such as migratory amphibians (e.g., red-spotted newts, *Notophthalmus viridescens*; Gill 1978) may require links among seasonally used habitats. The lack of such connectivity may cause local extirpation; it is therefore one possible mechanism for loss of biological diversity resulting from habitat fragmentation (Wilcove et al. 1986).

How well do corridors facilitate movement? Demonstrating the efficacy of corridors in promoting movement among populations and within home ranges requires knowledge of the probability of entering habitat patches that vary in configuration and landscape context. The effect of corridors on rates of immigration, a population-level process, can ultimately be explained at the level of the individual animal by asking how the individual orients its movements in the presence of a corridor. What effect does the presence of a corridor have on its movement decisions? What are the ultimate effects on the animal's fitness? Given this understanding, it is possible to scale up from an individual's pattern of movement within a patchy home range to the collective patterns of movement of individuals traveling across a patchy landscape. The first process is necessary to maintain individuals,

the second to maintain populations, in fragmented landscapes. Thus, corridors are potentially meaningful components of conservation reserve design, whether viewed at the individual or population level.

Linear patches as corridors: evidence from observational studies. Although many researchers have asserted that corridors are vital elements of conservation plans (e.g., Noss and Cooperrider 1994, Saunders and Hobbs 1991), few studies have demonstrated that corridors actually increase the rate of successful movement of animals between patches. Rather, most studies have documented animal presence in linear habitat patches lying between larger patches and have inferred that the linear patches were acting as corridors.

An early study that is often cited as evidence of the value of corridors encompassed two woodlands: one that was connected to a larger forest and one that was isolated (MacClintock et al. 1977). The connected woodland contained more forest interior bird species than the unconnected tract, and the connecting "corridor" contained several of these species as well. Although the differences in species numbers between the connected and unconnected tracts may have been the result of a corridor effect, the study was not a valid test because it lacked replication and did not directly measure the movement of individuals. Nevertheless, this study has been the basis for many of the early arguments in favor of corridors, as Simberloff et al. (1992) noted. Similar studies with parallel interpretations dominate the literature: Authors have frequently concluded that their results document the importance of corridors in connecting habitat patches even though they have not actually shown that individuals used the corridors to move between patches. Although their conclusions were not fully supported by the data, these studies have greatly influenced both the popular and scientific views of the biological value of corridors (Rosenberg et al. 1995, Simberloff et al. 1992).

Several recent studies have attempted to test more directly for increased movement of individuals between patches connected by pre-

sumed corridors. However, these studies, also not replicated, frequently did not include individuals that moved through the matrix, and outside of the corridor. For example, Dmowski and Kozakiewicz (1990) investigated the movement of birds between two pairs of patches; one pair was presumed to be connected by a corridor, the other to be unconnected. Because a higher proportion of birds from one habitat patch were subsequently found in the second patch in the connected pair than in the unconnected pair, and because movements were observed along the edge of the presumed corridor, the researchers concluded that corridors increased connectivity. However, because the authors did not directly estimate movements through matrix habitat outside of the corridor, it is unknown what effect the corridor actually had on movement rates.

Studies on small mammals, which are likely to be more selective of dispersal habitat than birds, are widely cited as evidence that linear patches function as corridors (e.g., Bennett 1990, Henderson et al. 1985, Merriam and Lanoue 1990, Wegner and Merriam 1979). Again, many of these studies lacked replication and direct measurement of movement, instead inferring movements of individuals by counting the numbers of individuals that were captured in an array of traps dispersed throughout the study area. Several studies did, however, evaluate the efficacy of corridors based on differences in movement rates. For example, Wegner and Merriam (1979) compared the number of transfers of individuals among a forest patch, fencerows, and fields; they found much greater use of fencerows than fields in movements to and from the forest patch. How the animals traveled between patches was unknown, but because few individuals were captured in fields, the authors concluded that movement across fields was unlikely. To what extent movement rates may have been reduced without the fencerows is unknown. These findings were later substantiated by the observation (Merriam and Lanoue 1990) that displaced white-footed mice (*Peromyscus leucopus*) traveled most frequently along fencerows rather than across fields.

Figure 2. Aerial view of one of the first experiments (La Polla and Barrett 1993) on the effects of biological corridors on the population dynamics of animals. Population size of meadow voles was assessed in the old-field habitat patches, which were created by mowing the surrounding vegetation. The researchers created potential corridors of different widths by maintaining strips of vegetation between patches. Three study plots with different corridor treatments were arranged by experimental units (blocks). The left plot of the lower block included a wide corridor (5 m), the middle plot no corridor, and the plot on the right a narrow (1 m) corridor. Photo: Gary Barrett; reprinted from La Polla and Barrett (1993) with permission of Kluwer Academic Publishers.



Figure 3. Oregon *Ensatina*. Animals occupying relatively small habitat patches, such as *Ensatina eschscholtzii*, have been the subjects of most of the experimental work on biological corridors. The microlandscapes-in which these animals exist or can be placed are more easily manipulated and replicated than the large landscapes needed to support more wide-ranging species, allowing a more rigorous approach to evaluating the effects of landscape attributes on animal populations.

Although there is only weak evidence that corridors increase immigration rates, it is well known that animals will repeatedly use specific routes during transit. Observations of ground squirrels moving between colonies (Garret and Franklin 1988, Wigget and Boag 1989) show that animals follow linear patches of habitat while dispersing. For example, black-tailed prairie dogs (*Cynomys ludovicianus*) often dispersed from one colony to another through vegetated ravines (Garret and Franklin 1988), and Columbian ground squirrels (*Spermophilus columbianus*) were found to use pre-existing pathways made by other colony members (Wigget and Boag 1989). However, when pathways were not available or not used for

transit, individuals moved rapidly across poor-quality habitats (Garret and Franklin 1988, Wigget and Boag 1989). These observations, together with those discussed above, suggest that corridors, when available, may be selected for movement between patches. However, these studies do not indicate how movements would be affected if corridors were not available. The observational studies conducted on movements of animals occupying landscapes with linear habitat patches lead to some interesting hypotheses, but they provide only weak evidence of how corridors affect animal movements in disturbed landscapes.

Linear patches as corridors-evidence from experimental studies. Field experimentation offers a rigorous means to test how corridors affect movement patterns of individuals and dynamics of populations. However, the large spatial and temporal scales that are appropriate to real-world conservation plans make relevant experimental studies difficult. We discuss studies from two classes of field experiments: first, manipulative and replicated experiments, and second, quasi-experimental studies, whose study design included neither randomization of manipulations nor adequate replication. Nevertheless, we included a study of this latter type because it is one of the few conducted at a spatial scale that is relevant to conservation planning and reserve design.

One of the first field experiments published on biological corridors (La Polla and Barrett 1993) tested the effects of the presence and width of linear patches of vegetation on the population dynamics of meadow voles (*Microtus pennsylvanicus*). The study design consisted of nine experimental plots that were arranged by blocks in a three-treatment x three-replicate design. Each plot consisted of two habitat patches (20 x 20 m) that were either connected by a linear patch (1 x 10 m or 5 x 10 m) of suitable habitat or separated by a continuous belt (10 x 20 m) of mowed (i.e., unsuitable) habitat, designed to be a barrier to movement (Figure 2).

The unsuitable areas separating plots failed to confine voles; animals dispersed across the habitat that had

Figure 4. (below) View of a section of a study plot from a study of biological corridors that investigated movements of the Oregon *Ensatina* salamander (Rosenberg et al. in press). Experimental treatments included pathways with narrow linear patches of vegetation retained as potential corridors, as shown here, and pathways with all surface organic matter removed. Vegetation along the perimeter of the fence was removed prior to each experiment. Photo taken at the Starker Forest site.



been assumed to be unsuitable. Male voles moved more readily between study plots over mowed areas than between habitat patches within a plot, suggesting that the linear patches intended to function as corridors probably did not stimulate or direct movement at the spatial scale of the experiments. Nevertheless, at the end of their study the authors found higher mean densities in connected than in unconnected patches, and they concluded that corridors effectively increased dispersal among patches.

The mechanisms that promoted higher average densities in connected patches were not identified; what such mechanisms might be is unclear because individuals frequently moved across habitat that had originally been considered unsuitable. One plausible explanation for the results is that the corridor increased the effective habitat area of the patch and thus allowed a greater population size. Indeed, small mammals, such as house mice (*Mus musculus*)

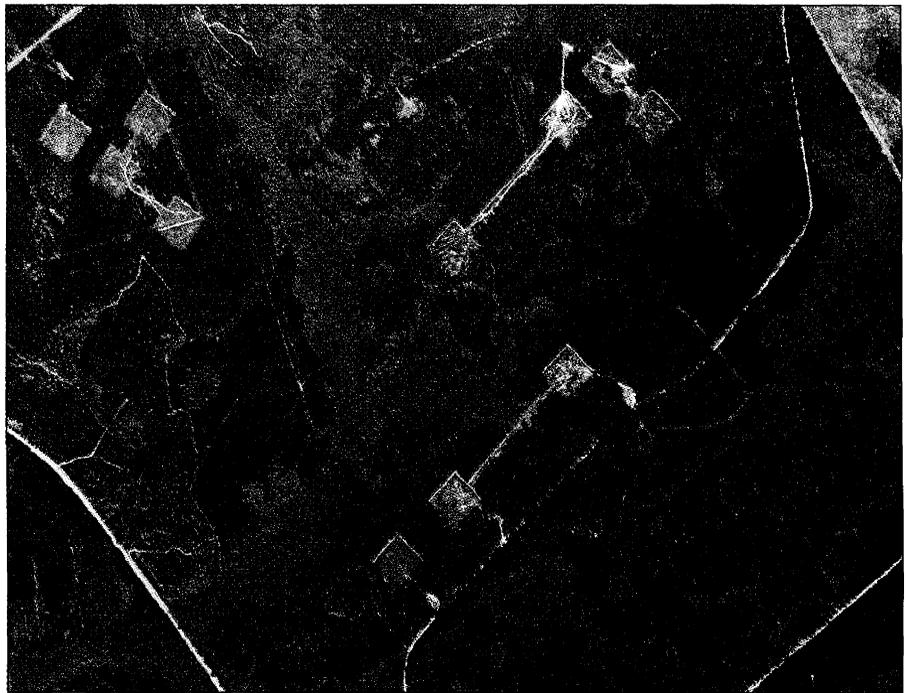


Figure 5. Aerial view of a landscape-scale experiment conducted with butterflies. Nick Haddad and Robert Cheney at the Savannah River Site in South Carolina designed experimental plots in which the US Forest Service manipulated the existence and length of pathways of clear-cuts intended to function as biological corridors connecting clear-cut habitat patches (1.6 ha). The clear-cuts provided habitat for many of the butterfly species studied by Haddad (1997). Photo courtesy of the US Forest Service.

and eastern chipmunks (*Tamias striatus*), may reside entirely within narrow linear patches (Henderson et al. 1985, Lorenz and Barrett 1990). If this residency occurred in the vole study, then similar results would have been obtained without a corridor if one of the patches was increased in size by the area of the linear patch. The mechanism that regulated vole densities at the scale of the experimental plots of La Polla and Barrett (1993) may have been related to the social structure of the vole populations (Collins and Barrett 1997). Further experiments with similar designs would need to be conducted to discriminate between the corridor hypothesis and patch-size hypothesis.

In a recent study of root voles (*Microtus oeconomus*), Andreassen et al. (1996) tested behavioral mechanisms that may be responsible for increasing immigration among patches that are connected by corridors. A fenced pathway of length 310 m and width 7.5 m was created, within which a narrower strip of grass ("corridor") of width 3 m, 1 m, or 0.4 m connected habitat patches (5 x 5 m) placed at both ends of the pathway. Vegetation was removed

from between the corridors and the fence. In addition to testing the effects of corridor widths on movement patterns, Andreassen and co-workers tested the effects of predators and conspecifics on movement behavior. The presence of predators and conspecifics was simulated by placing fox scat and voles, respectively, in enclosures placed inside the corridors. During each day of the study, two male voles were released into the habitat patches in the morning and tracked until the evening. There were no spatial replicates; instead, the different trials were conducted on the single enclosure, which was modified as needed for each trial.

Although the presence of predators (as simulated by fox scat) or conspecifics (as simulated by individually caged voles) did not affect movement patterns, corridor width had a strong effect. Immigration rates to the habitat patches were highest in the mid-width (1 m) and lowest in the widest (3 m) corridors because of differences in the resistance to and the rates of movement along the corridors. Resistance to movement was greatest in the narrowest corridor (0.4 m), as demonstrated by the high

percentage (73%) of trials in which voles did not leave the habitat patch in which they were released. Movement rates were lowest in the wide corridor, which the researchers attributed to frequent cross-directional use of the corridor.

Andreassen et al. (1996) concluded that wider corridors are not necessarily more efficient conduits for movement than narrower corridors, so long as the corridors are not so narrow that they are avoided as movement pathways. As Andreassen et al. noted, these conclusions assume that predation rates are the same, regardless of corridor width; if, however, survival rates vary among corridor types, then immigration rates (a measure of corridor efficiency) will be a function of both time spent in each corridor and corridor-specific survival rates. As the authors also noted, this study cannot be considered a "proper" experiment because there were no spatial replicates. Nevertheless, this study identified behavioral mechanisms affecting movement patterns, such as resistance to entering linear patches and rate of movement once entered, that should be considered in determining if a linear patch of habitat is likely to function as a biological corridor.

We have used a similar approach (Rosenberg et al. in press) to study movements of the Oregon *Ensatina eschscholtzii*; Figure 3). In our experiment, each study plot contained pathways with and without linear patches ("corridors") of habitat (Figure 4). This design allowed us to investigate movement patterns of displaced individuals in a setting in which they were allowed to select among pathways. Each study plot consisted of four target patches (1 x 3 m) of unmodified habitat that were connected to a central source patch (3 x 3 m) by pathways (3 x 40 m) that were enclosed by fences. These pathways were of either high quality (i.e., they contained a 1 m wide strip of natural vegetation surrounded by bare mineral soil) or low quality (i.e., all surface organic matter was removed).

We hypothesized that animals that selected a corridor pathway from the source to a target patch would be more likely to reach the target patch

than those that selected a pathway without a corridor. Pathways without corridors were selected less often than corridor pathways, and movement through noncorridor pathways was faster. The contrast between pathway types, however, was greatest following several weeks without rain. Under these conditions, animals in pathways without corridors experienced weight loss and increased mortality, but increased the rates of movement (Rosenberg et al. in press). Only under such "drought" conditions did greater numbers of *E. eschscholtzii* reach target patches connected by corridor pathways than target patches connected by pathways without corridors. Under nondrought conditions, by contrast, even though *E. eschscholtzii* preferred corridor pathways, those that selected pathways without corridors moved faster, and as a result, the immigration rates resulting from movement along both corridor and noncorridor pathways were similar.

This compensatory behavior between survival costs and movement rates contributed to the lack of consistent differences in immigration rates. The influence on immigration rates of enclosing pathways by barriers was unknown but may have contributed to similar immigration rates under nondrought conditions. Although our study did not reveal a consistent positive effect of corridors on immigration rates, it did show that behavioral mechanisms that are important to successful dispersal to target patches may be affected by compensatory behavior involving corridor selection, movement rates, and corridor and matrix quality.

A recent landscape-scale study has found increased movements of birds between forest patches connected by corridors (Machtans et al. 1996). Although few birds were observed dispersing, the authors concluded that more juvenile birds dispersed through corridors than through adjacent clearcuts. Interestingly, the authors observed a greater proportion of birds within the clear-cut areas that contained residual large trees than clear-cut areas with no trees remaining. Thus, similar to the *E. eschscholtzii* study, the likelihood of using a corridor may be a function of

the contrast between patch and matrix environments.

On the surface, this study seems to offer strong support for a functional role for corridors. However, interpretation of the results is confounded by landscape differences that were not amenable to experimental manipulation. For example, treatments (i.e., corridor or no corridor) were not located randomly—the forested linear patches were adjacent to a lake, whereas the clear-cuts were inland. Thus, the increased movement could have reflected factors other than the corridors. Moreover, different methods were used to estimate movement in the two habitat types. Nevertheless, this study is noteworthy because it is one of the few that was conducted at a scale appropriate to land management.

Preliminary results from another large-spatial scale experiment (Figure 5) that investigated the effects of landscape pattern on movement behavior of butterflies further suggests the potential of corridors to increase interpatch movement and population density (Haddad 1997). Nick Haddad and Robert Cheney used an innovative approach in which the US Forest Service created clear-cut forest patches (1.6 ha) in a predominantly pine forest matrix at the Savannah River Site in South Carolina. The study design included variation in the distance between patches and in whether or not the patches were connected by linear patches (32 m wide) of similar habitat.

For butterfly species requiring open habitats (e.g., buckeye, *Junonia coenia*), the pine forest seemed to create a partial barrier to movement because a higher proportion of individuals moved between patches connected by corridors than between unconnected patches. The proportion of transfers of all species studied decreased as distance between patches increased, regardless of the presence of a corridor. For some species, no matter what the length of the corridor (which ranged from 64 to 384 m), transfer rates between patches connected by a corridor were greater than those between unconnected patches. At all distances, these butterflies moved from one patch to another in the absence of corridors. Thus, these preliminary findings sug-

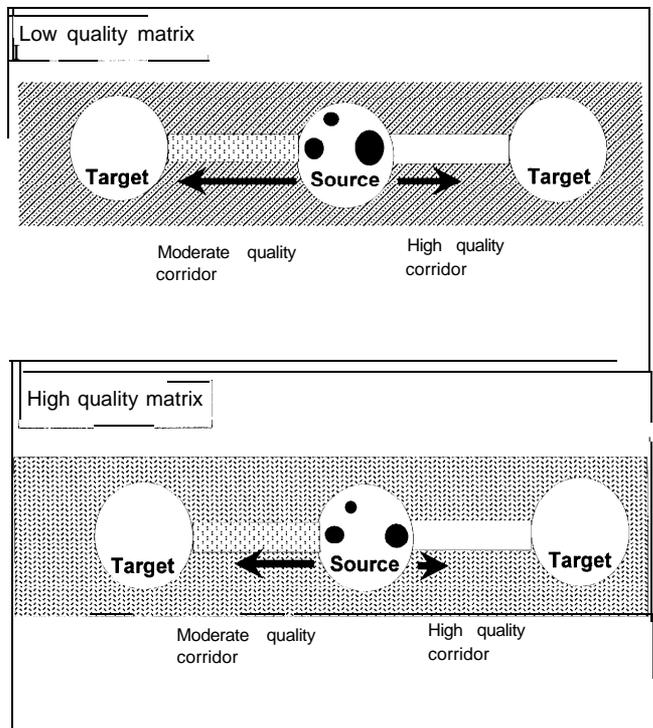
gest that linear patches did increase movement rates- for some butterfly species but that the lack of corridors did not isolate patches (Haddad 1997).

Linear patches as corridors-common patterns. The research to date shows that it is difficult to devise convincing tests of the efficacy of linear patches as biological corridors and as a means to increase population persistence. This difficulty holds even for species that are operative at limited spatial and temporal scales. Because organisms respond in species- and landscape-specific ways to potential corridors, no single study is likely to provide a definitive answer to the question of the ecological function of linear patches. Therefore, individual case studies will continue to be important in evaluating the benefits of various landscape designs as a means to increase connectivity.

Several general principles arising from the diverse array of published studies may assist in evaluating the efficacy of biological corridors. First, given a choice between habitat and nonhabitat, individual animals are more likely to select movement pathways that include components of their habitat. This behavior is particularly pronounced for individuals moving within the bounds of their home range. When movement among local populations is considered, however, most studies found that individuals were not adverse to moving through areas that did not contain suitable habitat-a typical matrix environment. Second, the relative use of the matrix as movement habitat depended on the degree to which it contrasted with patch habitat. Third, animals may show compensatory behavior in less favorable environments. For example, they may move more rapidly in low- than in high-quality habitat.

These general principles suggest a simple conceptual model for evaluating the likelihood of a linear patch functioning as a biological corridor. Assuming that once an individual reaches the target patch it remains there, then the probability of successful dispersal through a corridor can be represented by three successive events: the probability of finding the corridor, the probability of selecting the corridor, and the prob-

Figure 6. The effects on corridor use of habitat quality in the corridors and in the surrounding environment (matrix). The solid circles in the source patches represent dispersing animals; the size of the circle indicates the probability that an animal in that location will find and select the corridor, relative to the probability that it will disperse through the matrix. In the system surrounded by a low-quality matrix, animals will be more likely to select the high-quality corridor than they would when the corridor is surrounded by a high-quality matrix; however, if they do select the low-quality corridor, they will move through it more quickly. Animals adjacent to the corridor are more likely to select either corridor than to disperse through a low-quality matrix. If the matrix is composed of high-quality habitat, the chance that an animal will select a corridor instead of simply moving through the matrix decreases. Whatever the quality of the matrix, dispersing animals that enter corridors travel through them at a speed (indicated by arrow length) that is affected by the quality of the corridor and the matrix.



ability of successfully traversing the corridor (Figure 6).

The likelihood of finding a corridor is related to the distance of the animal from the corridor: As the distance increases, the probability of locating the corridor decreases. This relationship is likely to have a large effect for species that are relatively sedentary but a small effect for species that can physically assess the availability of more distant pathways. Empirical evidence supports the hypothesis that the probability of locating a landscape element is inversely related to distance. For example, movement of bark beetles (*Ips typographus*) to a pheromone trap declined with increasing distance (Helland et al. 1984), and patch selection by flea beetles (*Phyllotreta* spp.; Kareiva 1982) and cabbage butterflies (*Pieris rapae*; Fahrig and Paloheimo 1988) decreased as distance increased. Variation in distance sensitivity may be achieved by species-specific levels of exploratory movements along the periphery of a home range, as reported for wolves (*Canis lupus*; Fritts and Mech 1981).

The second critical factor is selecting a dispersal pathway. During dispersal, the difference in survival costs between the corridor and the surrounding environment (matrix) is likely to affect pathway selection; as the survival costs within a matrix increasingly exceed those within a corridor, the probability of selecting the corridor increases (Figure 6). The hypothesis that survival costs affect selectivity of a pathway is intuitively appealing and has empirical support. For example, our findings on salamanders provide evidence that the quality of the matrix surrounding otherwise isolated patches affects the efficacy of corridors that may connect them (Rosenberg et al. in press). If the contrast between patch and matrix, in terms of resistance and costs to movement, is small, then animals may be largely indifferent to the presence of corridors (Figure 6). If animals do not select a corridor, they may simply compensate for this "mistake" by moving more rapidly through matrix habitat. However, when the contrast between patch and matrix is large, the costs of failing to

select a corridor when one is present may be high. Thus, the value of corridors as landscape connectors may be dynamic, reflecting variation in the degree of contrast between patch and matrix environments. Therefore, given a choice of a pathway through a corridor or through the matrix, optimal behavior is a conditional, not an obligate, response.

The matrix environment further influences movement through the potential corridor by affecting the probability of directional movement once the animal is in the linear patch. If selectivity is low, animals may "wander" and experience high mortality rates outside of the linear patch; such a phenomenon may have occurred with dispersing cougars (*Felis concolor*) in southern California (Beier 1995). Other factors that may affect selectivity include conspecific attraction (Smith and Peacock 1990) and avoidance of conspecifics and predators (Fritts and Mech 1981, Joule and Cameron 1975); the research conducted on root voles by Andreasson et al. (1996) provided an initial investigation into these factors.

The third critical factor influencing the efficacy of a particular corridor is the likelihood that the animal can move successfully through a pathway. The probability of successfully reaching a habitat patch by moving through a corridor is a function of survival costs (mortality rates) and transit time. The rate of movement is affected by an animal's physical ability and by the environment. Average movement rate through a corridor is likely to be related to the survival cost in the corridor and to the width of the corridor. Based on evidence of the movements of salamanders (Rosenberg et al. in press), fruit flies (Dobzhansky et al. 1979), field voles (*Microtus agrestis*; Stenseth and Lidicker 1992), and flea beetles (Kareiva 1982), movement rates are likely to increase with increasing survival cost. Thus, dispersal success is a function not simply of distance, but also of velocity, a factor that is almost entirely ignored in discussions of the potential of linear patches to serve as corridors.

The habitat function

Not surprisingly, most studies of corridors demonstrate that individual

animals use linear patches as habitat, as reflected by established home ranges that are sometimes entirely within such patches (e.g., Henderson et al. 1985, Lorenz and Barrett 1990). Although there is evidence that linear patches may facilitate movements of individuals between patches, it is difficult to separate this function from that of simply adding habitat. The difficulty of distinguishing these functions has added to the controversial nature of corridors. If viewed as habitat, linear patches may provide an important component in a specific reserve design, whereas this may not be true if the linear patch is intended to function as a corridor (i.e., increase movement). Such controversy is unfortunate because it detracts from the potentially more important ecological importance of linear habitats. Furthermore, the public values linear habitats not only for their environmental quality but also for recreation and for protection of scenery; many conservation efforts have focused on their restoration and protection (e.g., Little 1990, Noss 1987). Linear habitats include streamside riparian zones, remnant habitat patches, urban greenways, and many others.

Streamside riparian areas support a wealth of biological diversity (e.g., Naiman et al. 1993) and are ecologically important regardless of their role as corridors. Areas preserved along streams include a diversity of habitats and maintain the integrity of aquatic ecosystems by providing shade, nutrients, and structure while reducing sedimentation and pollution (Gregory et al. 1991). Conservation and restoration of these habitats are, therefore, important to maintaining the biological diversity of ecosystems that include riparian habitats. Thus, the importance of streamside riparian areas as wildlife habitat is unrelated to their potential to function as corridors.

The importance of remnant habitat patches in wildlife conservation has recently been emphasized (e.g., Saunders et al. 1987, Shafer 1995). Linear patches may often be considered to be remnants; in many landscapes, they provide the only remaining habitat, thus contributing to the maintenance of local and regional biological diversity. Fencerows, small

patches of trees, and other types of vegetation that are left after land-altering activities provide habitat for many vertebrate species (Martin 1980, Wegner and Merriam 1979), and even small strips of uncultivated land between crops provide important habitat for invertebrates (Maelfait and DeKeer 1990). Many areas created as potential corridors may, in fact, realize their greatest function as remnant habitats.

Linear patches of vegetation in urban environments, often called greenways (Little 1990), may likewise serve as habitat for species that do not require extensive wild areas. Greenways play an increasing role in nature education, recreation, and scenic quality of landscapes (Saunders et al. 1987). Because greenways are increasingly popular as a means of improving urban and suburban living environments (Little 1990) and may themselves serve as important habitat, biologists should work with urban planners and community groups to design greenways that contribute to urban wildlife conservation and education, rather than arguing whether greenways function as corridors.

Much of the argument against including linear patches in reserve designs is based on the possible ill effects of attracting wildlife to areas in which a high proportion of linear patch is exposed to the surrounding environment (e.g., Simberloff and Cox 1987, Simberloff et al. 1992), a landscape component that is often referred to as "edge habitat." Corridors in which the matrix environment affects the environment of the corridor's interior are considered edge habitat. The amount of edge habitat is increasing in many human-modified environments, often at the expense of interior habitat (e.g., Robbins et al. 1989). This trend is a matter of concern because edge environments may not provide habitat for species that are most in need of protection; many edge species have high birth and survival rates in disturbed areas, and providing habitat for these species will not maintain regional diversity (Robbins et al. 1989).

Land that is allocated to corridors in conservation plans may require the size of core habitat patches to be smaller to account for the area of the corridors, thus increasing the pro-

portion of edge habitat in a landscape. This tradeoff is apparent in many forest planning alternatives (e.g., USDA 1996). If large reserves are compromised in size to allow for linear patches, regardless of whether they function as corridors or simply as habitat, then their establishment may represent a net loss to wildlife protection. Recent observational (Schmitz 1997) and theoretical (Fahrig in press) work on the importance of habitat quantity and composition (Dunning et al. 1992), rather than its configuration in the landscape, supports this hypothesis.

Compromise in connectivity and patch size

The tradeoffs in the type and size of patches in reserve designs are important considerations for conservation strategies (Figure 7). Larger, high-quality habitat patches will reduce the level of connectivity needed for population persistence. Indeed, when habitat patches are large, a low level of connectivity—just enough to allow a few individuals per generation to reach other habitat patches and reproduce successfully—may be sufficient for the population to persist. Increasing the size of the reserve or the permeability of the matrix may increase viability of the population more than adding corridors as distinct linear elements, especially if the matrix allows some movement of individuals among populations (Figure 7). Most of the work on corridors suggest that movement through the matrix occurs, especially if the matrix retains elements of the patches, such as remnant live or dead trees, as Machtans et al. (1996) demonstrated with songbirds in recently harvested forests. Increasing reserve size and enhancing the matrix for dispersal was recommended to protect Northern spotted owls (*Strix occidentalis caurina*; Thomas et al. 1990).

Although quantitative analyses to ascertain the relative benefits of alternative reserve designs that include different types of connectivity would be difficult, it is important to consider options other than corridors. In some cases, of course, few alternatives are available (e.g., highly urbanized areas), and increasing con-

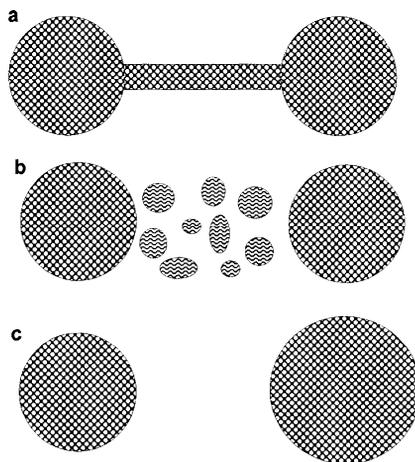


Figure 7. Comparison of tradeoffs in reserve design. Although a corridor design (a), in which the linear patch has similar vegetation as the habitat patches, is often advocated as the best means for ensuring connectivity, there are potential tradeoffs with such a design when the quality of the matrix or patch size is compromised because of land allocated to corridors. An alternative to creating a potential corridor with high-quality habitat that is otherwise surrounded by unsuitable habitat is a matrix design (b), which increases connectivity by embedding moderate-quality patches throughout the matrix. The matrix design shown here has discrete patches, but a more homogenous distribution of moderate-quality habitat within the matrix is another alternative to corridors. Creating potential corridors may also result in a tradeoff with reserve size. The patch-size design (c) demonstrates that patch size can be increased by including the area that was formerly allocated to a corridor. With increases in patch size and, presumably, in population size, there is less need for high levels of connectivity, and edge effects are minimized.

nectivity with corridors may be the most effective way to increase population viability (cf. Beier 1993, 1995). The importance of a particular linear patch as habitat for maintaining or restoring local or regional biological diversity should also be evaluated. Most important, however, elements in reserve designs must be viewed as tradeoffs, especially when the issue of creating corridors, rather than of simply retaining existing linear patches (e.g., streamside riparian areas), arises. In some cases, the creation of corridors as a tool to mitigate against habitat loss due to development activities may ultimately

cause the local extirpation of species, and thus erode biological diversity. Corridors are often advocated as a means to lessen the effects of habitat loss. If, however, population growth rates are influenced more negatively by habitat loss than positively by the creation or maintenance of corridors, the population will decline. Because of the lack of strong empirical data supporting the biological function of corridors, and because even if linear patches do have this function, they do not necessarily compensate for additional habitat loss and fragmentation, caution is necessary when incorporating corridors into reserve designs.

Conclusions

Linear patches have often been equated with biological corridors, but in fact, linear patches serve two different functions: as movement pathways and as habitats for resident animals. Distinguishing between the two requires knowledge of the life history stages that the species in question fulfills within the linear patch. Evaluation of the corridor function of linear patches should include the three stages of successful dispersal to a target patch through a corridor—finding, selecting, and moving successfully through it (Figure 6). In each stage, environmental influences, such as landscape patterns, and species-specific behavioral components must be considered when attempting to determine whether a linear patch could indeed function as a biological corridor. To evaluate the role of a linear patch as habitat, survival and reproduction rates within the patch need to be considered. Again, we emphasize that determining whether a particular linear patch serves as a biological corridor or as a habitat patch will indeed be species and landscape specific.

Although much of the literature on corridors has discussed the occurrence of animals within linear patches, differentiating between the corridor and habitat functions of linear patches requires knowing whether the patch increased animal movement to connected patches. However, even demonstrating that a linear patch has increased immigration rates over what would otherwise have been

achieved does not necessarily translate to increased viability for the population, species, or biological community; it simply shows that the linear patch functioned as a corridor. The level of connectivity needed to maintain a particular population will vary tremendously with the dynamic properties of the demography of the population, including population size, survival and birth rates, and genetic factors, such as the level of inbreeding and genetic variance. The movement and habitat functions of linear patches are clearly not mutually exclusive, but we believe that it is important to determine which is primary.

We suggest that if corridors are effective in facilitating movement among patches of habitat, then their effectiveness may be due to one of two mechanisms: increasing the probability of successful movements within the home range of an individual and increasing the movements of individuals among subpopulations through dispersal of young produced in the corridor. If these mechanisms indeed contribute to the effectiveness of corridors, then the design of potential corridors and the means for their assessment need to be refined. Attention will need to be placed on individual movements between connected patches and the demography of populations within the linear patch, and on those populations that the linear patch is assumed to be connecting, rather than on simply the numbers of individuals observed within linear patches. Future research of the efficacy of corridors will be most productive if conservation biologists and land managers focus on how corridor selectivity, survival costs, and movement rates of individuals vary among species with divergent evolutionary and life histories, in the conditions that are likely to persist in real landscapes.

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