Review

Do Habitat Corridors Provide Connectivity?

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Abstract: *Skeptics have questioned the empirical evidence that corridors provide landscape connectivity. Some also have suggested dangers of corridors. We reviewed published studies that empirically addressed whether corridors enhance or diminish the population viability of species in habitat patches connected by corridors. A randomized and replicated experimental design has not been used—and we argue is not required—to make inferences about the conservation value of corridors. Rather, studies can use observational or experimental analyses of parameters of target populations or movements of individual animals. Two of these approaches hold the greatest promise for progress, especially if the shortcomings of previous studies are remedied. First, experiments using demographic parameters as dependent variables—even if unreplicated—can demonstrate the demographic effects of particular corridors in particular landscapes. Such studies should measure demographic traits before and after treatment in both the treated area (corridor created or destroyed) and an untreated area (habitat patches isolated from one another). This approach is superior to observing the demographic conditions in various landscapes because of the tendency for corridor presence to be correlated with other variables, such as patch size, that can confound the analysis. Second, observations of movements by naturally dispersing animals in fragmented landscapes can demonstrate the conservation value of corridors more convincingly than can controlled experiments on animal movement. Such field observations relate directly to the type of animals (e.g., dispersing juveniles of target species) and the real landscapes that are the subject of decisions about corridor preservation. Future observational studies of animal movements should attempt to detect extra-corridor movements and focus on fragmentation-sensitive species for which corridors are likely to be proposed. Fewer than half of the 32 studies we reviewed provided persuasive data regarding the utility of corridors; other studies were inconclusive, largely due to design flaws. The evidence from well-designed studies suggests that corridors are valuable conservation tools. Those who would destroy the last remnants of natural connectivity should bear the burden of proving that corridor destruction will not harm target populations.*

Proveen Conectividad los Corredores de Hábitat?

Resumen: *Algunos escépticos han cuestionado la evidencia empírica de que los corredores proveen conectividad al paisaje. Otros han sugerido los peligros de los corredores. Revisamos estudios publicados que abordaron empíricamente si los corredores fomentan o disminuyen la viabilidad de poblaciones de especies en parches de hábitat conectados por corredores. A la fecha no se ha llevado a cabo un diseño experimental randomizado y con réplicas para realizar inferencias sobre el valor de los corresdores en la conservación—y nosotros argüimos que no es necesario. En cambio, los estudios pueden emplear análisis observacional o experimental de parámetros de poblaciones de interés o movimientos individuales de animales. Dos de estas aproximaciones son muy prometedoras y pueden progresar, especialmente si las limitantes de los estudios previos son remediadas. Primero, los experimentos que usan parámetros demográficos como variables dependientes—aún si no son replicados—pueden demostrar efectos demográficos de corredores en paisajes particulares. Estos estudios deberán medir características demográficas antes y después del tratamiento, tanto en el área tratada (corredor creado o destruído) como en un área no tratada (parches de hábitat aislados unos de otros). Esta aproximación es superior a observar las condiciones demográficas en varios paisajes puesto que la presencia de un corredor tiende a estar correlacionada con otras variables, como lo es el tamaño del*

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parche lo que puede confundir el análisis. Segundo, las observaciones de movimientos de animales que se desplazan normalmente en paisajes fragmentados puede demostrar el valor de los corredores en la conservación de manera mas convincente que los experimentos controlados sobre animales en movimiento. Este tipo de observaciones de campo están directamente relacionades con el tipo de animal (e.g., juveniles de la especie de interés dispersándose) y con el tipo de paisajes que están sujetos a las decisiones de preservación de corredores. Los estudios observacionales de movimientos de animales a futuro deberán tratar de detectar movimientos extra-corredores y enfocarse a especies sensitivas a la fragmentación y para las cuales los corredores son factibles a ser propuestos. Menos de la mitad de los 32 estudios revisados provee datos persuasivos referentes a la utilidad de los corredores; otros estudios fueron inconclusos, mayormente debido a diseños defectuosos. Las evidencias de estudios bien diseñados sugieren que los corredores son herramientas valiosas de conservación. Aquellos que intentan destruir los últimos remanentes de conectividad natural deberían sustentarse demostrando que la destrucción de los corredores no afectará a poblaciones de interés.

Introduction

Conservation biologists generally agree that landscape connectivity enhances population viability for many species and that, until recently, most species lived in well-connected landscapes (Gilpin & Soulé 1986; Noss 1987; Primack 1993; Noss & Cooperrider 1994; Hunter 1996; Meffe & Carroll 1997). Because urbanization and other human activities often sever natural connections among landscapes, many conservationists have advocated the retention of habitat corridors. In part, this approach has been justified by theoretical population models (e.g., metapopulation models, Gilpin & Hanski 1991). Such models demonstrate the utility only of habitat connectivity, however, which benefits population viability via the rescue effect (Brown & Kodric-Brown 1977) or other mechanisms. Conservation value accrues to corridors only if animals in real landscapes use corridors to bring about connectivity. Simberloff et al. (1992) argued that such evidence is lacking. Simberloff and Cox (1987), Simberloff et al. (1992), and Hess (1994) also argued that corridors might promote the spread of diseases, catastrophic disturbances (such as wildfires), or exotic species into the areas connected by corridors or might lure animals into areas—including the corridors themselves—where they experience high mortality (for a review see Hobbs 1992). A central concern is that funds spent acquiring corridors of questionable or unproven value might be better spent acquiring habitat areas for imperiled species, even if such areas are isolated (Simberloff et al. 1992).

We reviewed empirical papers that appeared relevant to the question, "Do corridors enhance or diminish the population viability of target species in the habitat patches connected by corridors?" Our goals were to make suggestions for future research on these issues and to evaluate scientific evidence that corridors serve as conduits for movement in a way that justifies their use as a conservation tool or that corridors have negative effects on target species.

Methods

We gathered papers on corridors (excluding modeling exercises) by searching for the word *corridor* in titles, abstracts, and keywords in all 1980–1997 volumes of *Auk, Biological Conservation, Condor, Conservation Biology, Ecological Applications, Ecology, Journal of Mammalogy, Journal of Wildlife Management, Wildlife Society Bulletin, Wilson Bulletin*, and recent monographs (e.g., Saunders & Hobbs 1991). We gleaned additional citations from relevant papers.

We define *corridor* as a linear habitat, embedded in a dissimilar matrix, that connects two or more larger blocks of habitat and that is proposed for conservation on the grounds that it will enhance or maintain the viability of specific wildlife populations in the habitat blocks. We define *passage* as travel via a corridor by individual animals from one habitat patch to another. Our definition of *corridor* explicitly excludes those linear habitats—such as riparian areas in agricultural landscapes—that support breeding populations of many species but do not connect larger habitat patches (e.g., Spackman & Hughes 1995). There are important conservation issues regarding nonconnective linear habitats, but we restricted our attention to linear patches of land whose conservation value is to allow passage between more significant habitat patches.

Nicholls and Margules (1991) and Inglis and Underwood (1992) discussed the formidable difficulties involved in designing a randomized and replicated experiment to test whether corridors enhance recolonization of habitat patches after local extinction. For such an experiment to be realistic, each experimental unit is an entire landscape, and there must be several replicate landscapes for each combination of treatments. Furthermore, we suggest that the species studied must be those that require connectivity on a landscape scale—fragmentation-sensitive species such as mammals with large home ranges—and that each species be studied individually. These requirements present staggering logistical and financial obstacles. Furthermore, to preclude confounding of corridor effects with other landscape effects, simple observation of various natural and anthropogenic landscapes is insufficient; the treatments must be applied randomly to those landscapes. The two essential "treatments" of the experiment, however, are creating and destroying corridors and causing local extinctions so that recolonization can occur. Randomly applying these treatments to replicate landscapes would be ethically questionable. Although one might argue that such an approach may be ethically acceptable for some abundant species, these are not the species for which conservation biologists design corridors, so the results would be of limited value.

Similar logistical, financial, and ethical problems would also bedevil any randomized and replicated experiment to determine the utility of corridors in enhancing population viability. Thus, it is not surprising we did not find a single paper that used a randomized and replicated experimental design and measured either recolonization rate or population viability as a dependent variable. Such a rigorous experiment may be unnecessary (cf. Hurlbert 1984), however. Even the most demanding critics of corridors concede that any habitat configuration that promotes immigration among patches will enhance population viability and likelihood of recolonization; the real issue is whether corridors allow such immigration in landscapes that would otherwise be fragmented (Simberloff et al. 1992). Thus, a researcher can shed light on the debate by conducting either experimental or observational analyses of parameters of target populations or parameters related to the movement of individual animals.

Parameters of target populations, such as immigration or individual survival rates, can be compared between habitat patches connected and unconnected by corridors or between landscapes where corridors are present or absent. Such studies should attempt to show that patch occupancy, abundance, colonization rate, immigration rate, disease rates, individual survival rate, frequency or intensity of disturbance, species richness, or occurrence of deleterious exotics increase or decrease in the presence of corridors relative to a landscape without corridors. Results can be meaningful only if they include a comparison to a landscape without corridors. Several widely cited papers (most notably MacClintock et al. 1977) are not helpful because they describe only a single landscape with corridors.

Because there is general agreement that landscape connectivity has at least the potential to enhance population viability, a study can simply attempt to show that animals use corridors in a way that provides such connectivity. Studies of parameters related to the movement of individual animals should attempt to confirm that animals (or diseases, disturbances, or exotic species) use corridors to move from one patch to another often enough to influence the population viability of the target species and that without corridors such movements would occur too rarely to influence the population.

We categorized each paper by the types of parameters it measured (population parameters, movements of individual animals, or the putative hazards of corridors) and whether the study used an observational or experimental approach. We then evaluated how each paper answered our research question of whether corridors enhance or diminish the population viability of species in habitat patches. In fairness, we note that the conservation value of corridors may not have been the research question of the investigations we reviewed.

Results and Discussion

Observational Studies Measuring Demographic Parameters

Seven studies (Table 1) measured either demographic parameters in relation to corridors or claimed to do so—six on birds and one on kangaroos. Five reported that corridors were beneficial for birds, one that corridors were not important for birds, and the seventh that corridors were not important for kangaroos. The main problem with this approach is severe risk of confounding; in addition, the dependent variable (especially in studies on birds) often was not closely tied to population viability.

Because each study in this group simply made observations in landscapes that were not designed to test the utility of corridors, all such studies risk the confounding of corridor effects with the effects of other factors that are highly correlated with corridors. For example, habitat patches lacking riparian corridors usually are more xeric, smaller, and further from large source populations than patches that abut such corridors. Patches without corridors may also be closer to homes, farms, cities, and human-subsidized predators. If patches with corridors are "better," it is difficult to determine whether the benefits are due to corridors or some other factors. Confounding is an inherent risk in any observational study because the treatments (corridors) are not randomly allocated to the experimental units. In studies for which randomization and true replication are impossible, investigators can minimize confounding in three ways. First, they should carefully select sites with and without corridors which are as similar as possible with respect to patch size, vegetation, moisture, distance to source populations, and proximity to disturbance. Second, they should forthrightly acknowledge and discuss plausible types of confounding. Third (and optionally), the investigator can collect ancillary data on movement routes of individual animals, especially on actual or potential extra-corridor movements. Such data can suggest whether observed differences are due to corridors or other factors correlated with corridors.

Table 1. Observational studies that compare patch occupancy, abundance, or other demographic parameters in habitat patches (or landscapes) with and without corridors.

Study[a]	*Dependent variable*	*Result*	*Treatment of confounding factors*	*Replication*	*Data on individual travel paths*
Arnold et al. 1991. Distribution and abundance of kangaroo in remnants of native vegetation in the central wheatbelt of Western Australia and the role of native vegetation along road verges and fencelines as linkages	patch occupancy and abundance	corridors not important	corridors, patch size, and proximity to next patch all highly correlated	yes	no
Date et al. 1991. Frugivorous pigeons, stepping stones, and weeds in northern New South Wales	patch occupancy and abundance	corridors not important for 5 spp of pigeons	elevation, corridors, patch size, and proximity to next patch all highly correlated	yes	no
Dmowski & Kozakiewicz 1990. Influence of a shrub corridor on movements of passerine birds to a lake littoral zone	numbers of forest birds visiting littoral zone near or away from a corridor[b]	increased number of birds in vicinity of corridor and in patch with a corridor	factors not discussed; only one corridor in the study	no	no
Dunning et al. 1995. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland	colonization rate	increased short-term colonization rates in landscape with corridors	sites well matched for landscape configuration and proximity to source patch; potential confounding factors discussed at length	no	no
Haas 1995. Dispersal and use of corridors by birds in wooded patches on an agricultural landscape	immigration rate (occupancy rates not reported)	immigration 15 times greater into patches connected by corridors (two wooded creeks); immigrants did nest in recipient patch	connected and unconnected pairs were separated by similar distances; no discussion of patch size, but map suggests that size and corridors are uncorrelated	yes	no
MacClintock et al. 1977. Evidence for the value of corridors and minimization of isolation in preservation of biotic diversity[c]	occupancy and species diversity	single 35-acre parcel connected by a short corridor was similar to "mainland"	no isolated fragment was studied	no	no
Saunders & de Rebeira 1991. Values of corridors to avian populations in a fragmented landscape	"immigration" rate (actually numbers of movements among patches by banded birds)	more "migration" between patches connected by corridors than between isolated patches	corridors, patch size, and proximity to next patch all highly correlated	yes	no

[a] *Abbreviated title; see literature cited for complete citation.*
[b] *Although not a demographic parameter, the inferred "visitation rate" might be correlated with dispersal or immigration rates, so this study (which did not assess animal travel in the single corridor) is included here.*
[c] *Although this study did not compare the single connected fragment to any corridorless fragment, it is widely cited as supporting the value of corridors as conduits.*

Because of how corridors and other factors are correlated in most fragmented landscapes, confounding is a less serious problem for studies that find corridors unimportant. Of the five studies claiming to show demographic benefits of corridors, only two (Dunning et al. 1995; Haas 1995) attempted to match the landscapes or patches with and without corridors with respect to potentially confounding factors and then discussed such confounding at some length. Although observational studies can never completely exorcise themselves of confounding, the careful treatment of these issues in these two papers greatly increased the credibility of the results.

Demographic parameters such as patch occupancy, abundance, and reproductive success influence the viability of populations in patches. Many observational studies, however, measured parameters less closely associated with the ability of the habitat patch to support animals. For instance, Haas (1995) reported that American Robins (*Turdus migratorius*) making a second nest attempt within a breeding season more often moved between patches connected by corridors than between unconnected sites. These data, however, do not suggest that the isolated patches had fewer robin nests or fewer second nest attempts than patches connected by corridors. Occupancy rates or nest density would have been a more direct measure of robin viability in the patches and probably could have been obtained with little or no extra field effort. In general, studies using short-term immigration rate must be interpreted with caution because, even if corridors help animals find suitable patches more rapidly, patches with and without corridors (if otherwise similar in size, vegetation, etc.) may have similar occupancy rates over the long term. An exception occurs in the case of species specializing in ephemeral habitat patches, such as the clearcuts used by the Bachman's Sparrows (*Aimophila aestivalis*) studied by Dunning et al. (1995). Because the clearcuts are suitable for only 4–7 years after creation, the colonization rate during the first 2 years after clearcutting was plausibly linked to viability in this case.

Although some bird species are reluctant to cross forest gaps (Bierregaard et al. 1992; Lens & Dhondt 1994; Desrochers & Hannon 1997), patch occupancy for birds is probably rarely influenced by the presence or lack of corridors a few hundred meters long. Bellamy et al. (1996) concluded similarly that, for birds, small gaps (mean 2.4 km, range 0.1–10 km) in forested landscapes did not "seriously hinder dispersal and recolonization opportunities," and Schmiegelow et al. (1997) found that 200-m wide clearcut barriers had less impact than expected on patch occupancy by forest birds. (This latter interpretation is ours; Schmiegelow et al. felt that 200-m barriers could isolate birds and attributed the small impact to counteracting factors.)

About half of these studies were unreplicated, consisting of one landscape with corridors and one without corridors. This fact was reported by the authors, allowing readers to make their own inferences. Although replication is desirable, it cannot ameliorate the more serious problem of confounding inherent in observational studies. As long as authors carefully address potentially confounding factors, observational studies can be valuable without replication.

Experiments Measuring Demographic Parameters in Different Landscapes

We found only four experimental studies that measured demographic parameters. Three studies (Mansergh & Scotts 1989; Machtans et al. 1996; Schmiegelow et al. 1997) destroyed or created corridors in real landscapes and collected pre- and post-manipulation data on both manipulated and unmanipulated areas. A third experiment (La Polla & Barrett 1993) measured animal abundance in highly artificial 20 × 20–m patches with and without corridors.

Perhaps the most defensible study was by Mansergh and Scotts (1989), who studied two subpopulations of a rare species, the mountain pygmy-possum (*Burramys parvus*). One subpopulation inhabited an intact landscape, whereas the formerly contiguous habitat of the second subpopulation had been fragmented by a ski development and an associated road. The fragmented area exhibited skewed sex ratios and lower survival rates than the intact area. After construction of a corridor, the population structure and survival rates in the ski resort changed to those observed in the undisturbed area. The study was not replicated, consisting of a single treated and a single control landscape. Nonetheless, Stewart-Oaten et al. (1986) demonstrate that if data are collected on both treatment and control areas before and after manipulation—as was the case here—investigators can make strong inferences regarding the effects of a particular unreplicated perturbation. Thus, although Mansergh and Scotts (1989) cannot make inferences about the utility of corridors in general, their study amply demonstrates the benefits of this particular corridor. We strongly encourage future studies to take the same vein as Mansergh and Scotts (1989) because, as such well-designed—albeit unreplicated—studies accumulate, each documenting local corridor effects, a more general pattern will gradually emerge.

The study of Machtans et al. (1996) similarly collected pretreatment and post-treatment data on both control and treatment areas, but it illustrates an important design limitation. It began with two intact landscapes, and the treatment consisted of creating a corridor out of formerly intact habitat and comparing bird movement rates across a control (intact) landscape to the landscape with a corridor. Because the study did not include a landscape without corridors, it is impossible to infer how readily birds would move through matrix habitat in the absence of a corridor (although the observations of Machtans et al. indicate that when a corridor was available, practically no forest birds were seen crossing the clearcut). Future experiments should contrast landscapes containing corridors with fragmented rather than intact landscapes. This can be achieved by either creating or destroying a corridor between two otherwise distinct patches.

In another experiment on bird response to forest fragmentation, Schmiegelow et al. (1997) reported two small but statistically significant benefits of 100-m wide riparian corridors: species turnover rate was higher in totally isolated fragments than in connected patches or in control areas, and diversity depended on fragment size only for the totally isolated fragments. This study was the most rigorous of the four in that pretreatment observations helped control for confounding (all fragments with corridors—but no isolated fragments—were adjacent to riparian areas) and because power analyses were used in the design phase to ensure adequate replication for statistical inference. Schmiegelow et al. (1997) noted, however, that the apparent benefits of corridors may have been an artifact of results from their smallest (1-ha) fragments because the effective size of each 1-ha fragment with corridors was doubled by the adjacent corridor habitat. Furthermore, the study was limited to short-term responses by the temporary nature of fragmentation (>1.5 m height growth in the first 2 years; Schmiegelow et al. 1997). This experimental design would be improved and made more relevant to conservation issues by altering it so that the area of habitat in the corridor has minimal influence on the dependent variable measured in the smallest habitat patch, by making longer-term observations (necessarily involving more-permanent fragmentation, such as by urban or agricultural activities), and by use of nonvolant focal species.

The more artificial experiment of La Polla and Barrett (1993) did not address the utility of corridors as a conservation tool. Through seeding they created uniform but artificial 20 × 20–m habitat patches that were connected or unconnected by 10-m-long corridors. They found higher numbers of voles in patches connected by corridors and attributed this difference in abundance to corridors. Nevertheless, rates of movement through their putative barriers (among "isolated" treatments and even among replicate sites) were comparable to those via corridors. In any event, the species (vole), corridor length (10 m), patch size (20 × 20 m), and matrix habitat (strips maintained in a mowed and tilled condition) suggest little relevance to real conservation problems and decisions. We see little prospect for elucidating the conservation value of corridors from experiments in settings so dissimilar to landscapes of conservation interest.

Observational Studies Measuring Movement of Individual Animals in Real Landscapes

If proponents and skeptics of corridors can agree on the value of connectivity in at least some situations, then it is not necessary to demonstrate the demographic effects of corridors. Instead, the issue is simply to document that animals will use corridors in a way that provides connectivity and that connectivity would be insufficient without the corridor. We found several studies (e.g., Catteral et al. 1991; Prevett 1991; Desrochers & Hannon 1997) that describe animal movements with respect to habitat edges, roads, suburbs, and domestic dogs, and other studies (Garrett & Franklin 1988) that anecdotally describe animal use of linear habitats. Some of these authors attempted to infer from these observations how animals might move through matrix or corridor lands. Although these studies can provide valuable understanding of the mechanisms underlying the use and avoidance of corridors and matrix, we excluded such studies as being too indirect to our question. We similarly excluded studies (e.g., Forys & Humphrey 1996) that document dispersal movements between habitat patches in fragmented landscapes but do not relate such movements to habitat corridors.

We considered in detail 17 observational studies (Table 2) that documented the presence or movements of nondisplaced animals (except for Reufenacht & Knight 1995) in landscapes that included corridors. Four of the 17 studies (Table 2, numbers 2, 4, 10, and 11) simply documented animal presence in corridors or the presence of individual animals in both habitat patches and corridors, without addressing the issue of whether animals made passages via the corridor from one habitat patch to another. Another six studies (Table 2, numbers 3, 5, 6, 9, 16, and 17) documented both presence and residence (i.e., probable breeding individuals) in the corridor. Of these, Vermeulen (1994) also documented movement rates, and Downes et al. (1997*a*) also compared corridor residents to forest-patch residents with respect to sex ratio, body mass, and reproductive potential. The occurrence of a resident population in a corridor—especially if residence occurs throughout its entire length—suggests that such corridors also would facilitate passage between patches. Maintaining resident populations of animals in wide corridors might be especially important when the distance between core populations is long, as is the case with grizzly bears (*Ursus arctos horribilis*) in much of the Rocky Mountains (Noss et al. 1996). Although territorial interactions between corridor residents and potential dispersers could inhibit dispersal by an individual from an adjacent patch, the corridor would still provide demographic benefits to the patches if there were modest immigration to and emigration from the corridor.

Reufenacht and Knight (1995) used a novel measure of corridor use—the number of midpoint crossings by displaced mice released in the corridor. They did not, however, report lengths of the corridors (aspen stringers), whether the stringers connected to any larger patches, where mice were released relative to the midpoints, or mouse travel distances. Hence, valid inferences from this study are limited.

Only 6 of the 17 studies (Table 2, numbers 1, 7, 8, 13, 14, and 15) provided strong evidence for passages by individual animals via corridors. Although all 6 suggested that such passages occur often enough to benefit the populations that interact via the corridor, only Suckling (1984) and Beier (1995) specifically reported on corridor passages by dispersing juveniles; both of these also reported the number of corridor transitions and the fraction of dispersers using corridors. Beier (1993, 1995) explicitly related this to the number of corridor passages

Table 2. Observations of animal movements with respect to potential corridors in landscapes not under control of the investigator.

Study[a]	Type of corridor use documented; measure of use	Documentation for (lack of) movement through matrix
1. Beier 1995. Dispersal of juvenile cougars in fragmented habitat	juvenile dispersal; fraction of dispersers making passages[b] and number of passages per corridor	radio-tagged animals never crossed urban matrix
2. Bennett et al. 1994. Corridor use and the elements of corridor quality: chipmunks and fencerows in a farmland mosaic	presence; number of captures in fencerows	not addressed
3. Bennett 1990. Habitat corridors and the conservation of small mammals in a fragmented forest environment	presence, residence, and movements between patch and corridor; number of marked animals caught in both patch and corridor	not addressed, but deemed improbable
4. Bentley & Catteral 1997. Use of brushland corridors and linear remnants by birds in southeastern Queensland Australia	presence; number of birds detected in corridor and in intact habitat	not addressed
5. Downes et al. 1997*a*. Use of corridors by mammals in fragmented Australian eucalypt forests	presence and residence; relative abundance, sex ratio, and body mass in corridor, patches, and matrix	nine native species did not use matrix (pasture), based on same sampling procedure used for corridor and patch
6. Henderson et al. 1985. Patchy environments and species survival: chipmunks in an agricultural mosaic	presence and residence; number of marked animals caught in both patch and corridor	not addressed; some animals moved via matrix
7. Heuer 1995. Wildlife corridors around developed areas in Banff National Park (wolf, lynx, and cougar; winter only)	passages[b] via corridor to other patches; number of passages per corridor (winter only)	deep snows and cliffs probably preclude movement outside of corridors
8. Johnsingh et al. 1990. Conservation status of the Chila-Motichur corridor for elephant movement in India	passage[b] via corridor to other patches; not quantified (implied that passage was frequent)	not addressed
9. Lindenmayer et al. 1993. Presence and abundance of arboreal marsupials in wildlife corridors within logged forest[c]	presence and residence; abundance of animals in linear habitats	not addressed
10. Lindenmayer et al. 1994. Patterns of use and microhabitat requirements of mountain brushtail possum in wildlife corridors	presence; number of detections in corridor	not addressed
11. Mock et al. 1992. Baldwin Otay Ranch wildlife corridor studies (deer, bobcat, and cougar)	presence; number of detections in corridor	not addressed; urban matrix likely impenetrable to bobcat and cougar
12. Ruefenacht & Knight 1995. Influences of corridor continuity and width on survival and movement of deermice	travel across midpoint of corridor (aspen stringers in sagebrush matrix) by displaced mouse; number of midpoint crossings	not addressed
13. Suckling 1984. Population ecology of the sugar glider in a system of habitat fragments	juvenile dispersal; fraction of dispersers using corridor for at least part of dispersal	at least 5 of 15 dispersals involved extra-corridor movement
14. Sutcliffe & Thomas 1996. Open corridors appear to facilitate dispersal by ringlet butterflies between woodland clearings	passage[b] via corridor to other patches; number of marked insects caught in both patch and corridor	indirect evidence suggests that less than 2% of movement occurs outside corridors
15. Tewes 1994. Habitat connectivity: importance to ocelot management and conservation	passage[b] via corridor to other patches; not quantified (implied that passage was frequent)	not addressed
16. Vermeulen 1994. Corridor function of a road verge for dispersal of stenotopic heathland ground beetles (nonvolant)	residence and movement; numbers of recaptures at various distances	apparently no movement via matrix, using same procedures as in corridor
17. Wegner & Merriam 1979. Movements by birds and small mammals between a wood and adjoining farmland habitats	presence and residence; number of marked animals caught in both patch and corridor	not addressed; some animals necessarily moved via matrix

[a] *Abbreviated title; see literature cited for complete citation; focal species listed if not in the title.*
[b] *A passage is when an animal enters a corridor from a habitat patch and travels to a habitat patch at other end of the corridor.*
[c] *This study focused on the value of linear strips as habitat, not as conduits for movement, but it has been cited as supporting the value of corridors as conduits.*

needed to enhance population viability. The greatest deficiency in such studies is that few attempted to document movements between patches via matrix land. In several studies (e.g., Wegner & Merriam 1979; Suckling 1984; Henderson et al. 1985), such extra-corridor movements clearly occurred, but the potential for such movements to connect habitat patches was not discussed or explicitly compared to corridor movements. Although several studies argued that extra-corridor movements were unlikely due to habitat unsuitability, only Beier (1995) documented this. Based on 181 overnight tracking sessions, Beier showed that the urban matrix land in his study was impermeable to the interpatch movements of cougars (*Puma concolor*).

Seven studies (Table 2, numbers 2, 4, 8, 9, 10, 12, and 15) did not attempt to document or even discuss the possibility of movements through a supposedly "hostile matrix." Other studies explicitly acknowledged the possibility of such movements but did not discuss the implications for population viability. For instance, Sutcliffe and Thomas (1996) showed that marked butterflies moved more often among habitat patches connected by corridors than among unconnected patches, and they presented indirect evidence that about 98% of movements are via these corridors. Nonetheless, might the 2% of butterfly movements through hostile habitat be sufficient to ensure the survival of isolated populations? And, if there were no corridors, might not some of the 98% find extra-corridor routes? Finally, several of the studies documented the movements of eastern chipmunks (*Tamias striatus*; Wegner & Merriam 1979; Henderson et al. 1985; Bennett et al. 1994) or other species that are unlikely to be the focus for corridor design—or even reasonable surrogates for species that are the focus—because they are relatively adaptable to anthropogenic habitats and tolerant of fragmentation.

Despite the shortcomings of many of these observational studies, the preponderance of evidence is that corridors almost certainly facilitate travel by many species. In the future this line of investigation can provide strong evidence for the utility of corridors. These studies should be improved in two ways. First, strong effort should be put into documenting actual travel paths, with equal emphasis on documenting both intra- and extra-corridor movement between patches. If extra-corridor movements do occur, their frequency relative to passages via corridors should be described quantitatively, and the implications for population viability should be discussed explicitly. Second, study species should be those most relevant to the design and implementation of corridors on real landscapes. Generally speaking, these are species that are area-dependent or fragmentation-sensitive, because they either have limited mobility or suffer high mortality moving between patches of suitable habitat.

Although lack of randomization—with its attendant potential for confounding—was a major drawback for observational studies of demographic parameters, this is not a serious issue in observational studies of animal movements because the experimental units are either individual animals or individual corridors. It is difficult to imagine that the selection of a travel path through a corridor or matrix would be correlated with an extraneous and potentially confounding factor.

Experiments on Movements of Individual Animals

We found four studies in which movements of individual animals were measured in landscapes under experimental control (Table 3). For several reasons, the results of these experiments have little or no relevance to the conservation value of corridors. First, the voles, fruit flies, mice, and salamanders in these experiments are neither the sort of species for which corridors are designed nor are they appropriate surrogates for such species. Second, all four studies used displaced animals as "simulated dispersers," usually by releasing them either directly into a corridor or into minuscule "patches" (3 × 3-m patch in Rosenberg 1994; a half-pint bottle in Forney & Gilpin 1989). These displaced animals and the environments in which they are released are at best poor indicators of how real dispersers would behave. The artificial corridors available to the animals have scant resemblance to the real landscapes across which animals must disperse. Finally, the lengths of corridors studied were 1 mm (Forney & Gilpin 1989), 40 m (Rosenberg 1994), and 300 m (Andreassen et al. 1996), and unstated (but clearly several hundred meters; Merriam & Lenoue 1990). Only Andreassen et al. (1996) explicitly compared the corridor length to the home-range diameter of the focal species (30 m), thus making the case that this distance may be relevant to dispersal movements.

We are skeptical of the arguments for "experimental model systems" (Ims et al. 1993; Wolff et al. 1997), especially when the results of studies are likely to be interpreted as lessons for conservation and land-use planning. In particular, experiments in highly controlled landscapes do not yield meaningful inferences about the conservation value of corridors in real landscapes. Nevertheless, elements of these experiments could be included in observational studies. For instance, Andreassen et al. (1996) found that movement was not inhibited by simulated competitors (caged voles) and predators (fox scats) in the corridors. Such treatments could be applied in real landscapes as well, either with true replication or in a before-after-control-impact-pair design (Stewart-Oaten et al. 1986), to yield valuable suggestions about the utility of corridors.

Studies Relevant to Negative Impacts of Corridors

Several authors have speculated on the negative impacts and other disadvantages of corridors (Noss 1987; Simberloff & Cox 1987; Simberloff et al. 1992; Hess 1994). We found only three studies with relevant results. Downes et al. (1997*b*) conducted the only study explicity designed to examine this issue: they found that exotic black rats (*Rattus rattus*) were abundant in corridors and that their abundance might affect the utility of the corridor for the native bush rat (*Rattus fuscipes*). The authors noted that black rats were matrix residents and

Table 3. Observations of animal movements with respect to potential corridors in landscapes under the experimental control of the investigator.

Study[a]	*Type of corridor use documented; measure of use*	*Documentation for (lack of) movement through matrix*
Andreassen et al. 1996. Optimal width of movement corridors for root voles	optimal width travel through 300-m-long artificial corridor by displaced voles; maximum distance, speed, and number of complete corridor transits	not addressed
Forney & Gilpin 1989. Spatial structure and population extinction: a study with *Drosophila*	transits via pinholes allowing movement between half-pint plastic bottles ("patches"); not quantified (flies not individually marked)	not addressed (no matrix available)[b]
Merriam & Lenoue 1990. Corridor use by small mammals: field measurements for three types of *Peromyscus leucopus*	presence in fencerow corridors by displaced radio-tagged mice released in farm fencerows; percentage of time traveling for 48 h, and total distance traveled in 48 h	not addressed; no corridorless landscape studied
Rosenberg 1994. Efficacy of biological corridors (for immigration movements by salamander)	travel through 40-m-long artificial corridor by displaced salamanders (released into 3×3-m patch); number of complete corridor transits	as many passages via matrix as via corridor

[a]*Abbreviated title; see literature cited for complete citation.*
[b]*Thus, this study demonstrated only that connectivity—not necessarily via corridors—enhances population persistence.*

did not use the corridors for inter-patch movement and that the bush rat would have essentially no prospect for inter-patch dispersal in the absence of corridors. Stoner (1996) found that mantled howling monkeys (*Alouatta palliata*) confined to linear habitats did have higher parasite loads than monkeys in large habitat blocks. The "corridor" site, however, was an area where the linear habitat was the only suitable habitat available, and Stoner wisely avoided making any inferences about the risks of movement corridors. Seabrook and Dettmann (1996) documented that exotic and poisonous cane toads (*Bufo marinus*) were more dense on "corridors" (roads and vehicle tracks) and probably used them to disperse. The corridors in this study (dirt roads) are certainly not the sort of wildlife movement routes that conservationists are trying to create. It has been widely observed that many pest species, including exotics and pathogens, disperse along disturbed habitats such as roads and roadsides (Noss & Cooperrider 1994). Furthermore, as was the case for most studies in Table 2, Seabrook and Dettmann (1996) provided no evidence of how fast the toad might spread through the matrix lands. In this regard, Bennett (1990) found that the exotic rodents in his study area were least influenced by lack of connectivity, being more abundant than the six native species in the smallest and most isolated patches. Hence, empirical evidence of negative impacts from corridors designed or preserved for conservation purposes has not yet emerged.

Conclusions

Generalizations about the biological value of corridors will remain elusive because of the species-specific nature of the problem. Indeed, there is no general answer to the question "Do corridors provide connectivity?" The question only makes sense in terms of a particular focal species and landscape. Nonetheless, we conclude that evidence from well-designed studies generally supports the utility of corridors as a conservation tool. Almost all studies on corridors suggest that they provide benefits to or are used by animals in real landscapes. Because most studies suffer from design limitations, only about 12 studies allow meaningful inferences of conservation value, 10 of which offer persuasive evidence that corridors provide sufficient connectivity to improve the viability of populations in habitats connected by corridors. No study has yet demonstrated negative impacts from conservation corridors. We are encouraged that the number and rigor of studies on these issues are increasing.

In comparing the approaches considered in this paper—experimental or observational analyses of target populations or individual animals—we suggest that progress will most rapidly proceed with one or both of two approaches. First, experiments using demographic parameters as dependent variables—even if unreplicated—can demonstrate the demographic effects of particular corridors in particular landscapes. Such studies should measure demographic traits before and after treatment in both the treated area (where a corridor was created or destroyed) and an untreated area (where habitat patches apparently are isolated from each other). Second, observations of movements by naturally dispersing animals in already fragmented landscapes can demonstrate the conservation value of corridors if efforts are made to document actual travel routes in both corridors and matrix land. Because corridor presence tends to be correlated and confounded with other variables, such as patch size and presence of riparian habitat, observations of demographic conditions in various landscapes is problematic, but careful selection of sites can reduce this risk.

We were surprised that most studies using birds as a focal species involved corridors and barriers that were small relative to their movement ability. We suspect that birds were selected at least in part because they are relatively easy to census, and we recognize that landscape scale is often beyond the control of the investigator. We urge greater attention to species with limited mobility and low population density, and, whenever possible, we urge observation on landscape scales relevant both to the focal species and to real conservation decisions.

The two approaches we advocate also can be used to evaluate proposed alternatives to corridors, such as "stepping stones" or managing "the entire landscape. . .as a matrix supporting the entire biotic community" (Simberloff et al. 1992). Controlled and replicated experiments on animal movement in artificial corridors have scant utility because they have little relevance to the kinds of landscapes and species for which decisions on conservation corridors will be made. Extrapolation across dissimilar species and spatial scales is generally unfounded. On the other hand, greatly lacking in the literature are studies of the community- or ecosystem-level effects of corridors. For example, rigorous studies of the effects of corridors on disturbance risk and spread, exotic species invasions, predation rates, and species richness or composition are absent.

Corridor skeptics have objected to the financial cost of corridors (Simberloff & Cox 1987; Simberloff et al. 1992). Because conservation funds are limited, each project should be considered carefully in terms of costs and benefits, including the alternative uses for the dollars that might be spent on corridors. There are certainly cases in which conservation dollars would be better spent acquiring high-quality but isolated patches of habitat for imperiled species, rather than acquiring corridors of dubious value. Many conservation projects are expensive, however, so this criticism has no unique relevance to corridor projects, which can be far cheaper than some alternatives. Furthermore, the more costly corridors are expensive precisely because they occur near large and growing human populations; the additional cost should be considered in light of proximity of the benefits—semblances of intact ecosystems, recreation—to those who ultimately pay for them.

Skeptics have correctly pointed out that the scientific evidence in support of corridors as a conservation tool has been weak. Developers and other opponents of conservation, however, frequently misrepresent this healthy spirit of inquiry and scientific self-criticism as a "disagreement among the experts." Thus, they are able to persuade planning agencies that habitat loss and fragmentation should proceed unhindered and that conservationists must bear the burden of proof for preserving each remaining corridor. Our review has shown that evidence from well-designed studies supports the utility of corridors as a conservation tool. All else being equal, and in the absence of complete information, it is safe to assume that a connected landscape is preferable to a fragmented landscape. Natural landscapes are generally more connected than landscapes altered by humans, and corridors are essentially a strategy to retain or enhance some of this natural connectivity (Noss 1987). Therefore, those who would destroy the last remnants of natural connectivity should bear the burden of proving that corridor destruction will not harm target populations.

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