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Impacts of corridors on populations and communities

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INTRODUCTION

This chapter focuses specifically on the most popular approach to maintain connectivity in conservation and management, which is to create or maintain habitat corridors. The popularity of corridors in conservation derives from the direct and intuitive relationship to their purported function: by physically connecting otherwise isolated fragments, corridors should increase the movement of both individuals and genes. In doing so, corridors provide sources of immigrants to offset local extinction, and sources of genetic diversity to reduce harmful effects of inbreeding and drift. The most fundamental spatial models in ecology, including island biogeographic models (MacArthur and Wilson 1967) and metapopulation models (Levins 1969; Hanski 1999), predict that movement between patches will increase population size and persistence and, through the rescue of declining populations (Brown and Kodric-Brown 1977), maintain local species richness. We recognize that studies focusing on corridors represent only a small fraction of studies on connectivity, and the large literature examining effects of patch isolation on colonization and occupancy in metapopulations has been reviewed elsewhere (see Table 9.1 in Hanski 1999; Moilanen and Nieminen 2002; Molainen and Hanski Chapter 3). The goal of this chapter is to assess existing evidence for corridor effects on populations and communities, and to discuss future directions that would permit more rigorous evaluation of their use in conservation.

Connectivity Conservation eds. Kevin R. Crooks and M. Sanjayan. Published by Cambridge

We focus on population and community impacts of corridors because evidence for the necessary prerequisite – that corridors increase movement and gene flow – has been growing and has also been reviewed elsewhere. In a review by Beier and Noss (1998) of 32 published studies as of 1997, 21 studied some aspect of animal movement through or within corridors, and many supported the role of corridors in increasing movement. Since that review, a number of other studies have demonstrated that corridors enhance movement rates of plants and animals between otherwise isolated patches (e.g., Coffman *et al.* 2001; Berggren *et al.* 2002; Tewksbury *et al.* 2002; Haddad *et al.* 2003). Still other recent studies have documented the role of connectivity in enhancing gene flow (Aars and Ims 1999; Hale *et al.* 2001; Mech and Hallett 2001; Kirchner *et al.* 2003; Neville *et al.* Chapter 13). While some studies have not found evidence for corridor effects (Rosenberg *et al.* 1998; Bowne *et al.* 1999; Danielson and Hubbard 2000), no studies have shown that corridors decrease movement rates.

The growing number of studies that show how corridors affect movement between patches provide a critical base of support for the idea that corridors should enhance population viability. From this work, it follows that corridors will reduce stochastic temporal variation in local and regional population sizes by increasing the rates of immigration from high-density to lower-density patches. Another possibility that has emerged from theoretical results is that corridors may have a negative effect by synchronizing dynamics and causing simultaneous extinction (Petchey *et al.* 1997; Earn *et al.* 2000; Hudgens and Haddad 2003). However, in cases most typical in conservation where small populations have rare dispersal and low growth rates, corridors should reduce local extinctions and allow individual patches to maintain a larger number of species with stable population dynamics (Brown and Kodric-Brown 1977; Gonzalez and Chaneton 2002). Other potential negative effects of corridors that have been discussed extensively in the literature are reviewed elsewhere in this volume (Crooks and Sanjayan Chapter 1; Crooks and Suarez Chapter 18).

The link between corridor effects on movement and their effects on the demography and persistence of populations, and ultimately, the maintenance of local and regional biodiversity, is critical for the appropriate use of corridors in management. Yet, there is currently a paucity of studies addressing population or community effects of corridors. Consistent empirical evidence regarding population and community effects of corridors would support their expanded implementation in conservation.

In this chapter, we first review empirical corridor studies that focus on population and community effects, seeking synthesis across studies. We highlight deficiencies in the existing literature, describe conditions under which corridor effects are expected, and discuss problems with study scale and design. We then go on to detail how new research could more effectively test the case for conservation benefits of corridors on populations and communities.

A REVIEW OF CORRIDOR EFFECTS ON POPULATIONS AND COMMUNITIES

The literature

We reviewed all empirical studies that examined terrestrial and microcosm corridor effects on population size or persistence, or on species diversity. Ideally for conservation, population studies would focus on how corridors affect population viability, and would thus measure persistence. Population growth can also be a strong indicator of persistence, especially when corridors may tip the balance between decreasing and increasing population trends. However, these measures are often difficult to obtain as they require long-term studies for meaningful estimates. Other population-level responses to corridors, such as size and survivorship, are less useful in assessing conservation value, but are still correlated with population viability. Regarding diversity, the most relevant response variables for conservation are often those that describe change in community composition after fragmentation, such as the rate of species loss, particularly with regard to species of management concern. One commonly measured community response, species richness, could be used to assess loss. In our review, we list response variables measured in existing corridor studies.

In our analysis, we included studies of corridor effects within patches relative to similar, isolated areas. Although a number of studies have shown that corridors affect population sizes by providing habitat for plants or animals within corridors (e.g., Machtans *et al.* 1996; Laurance and Laurance 1999; Perault and Lomolino 2000; Pryke and Samways 2001; Mönkkönen and Mutanen 2003), we are interested in the effects of corridors on populations or communities within patches they connect. We also did not include corridor studies where different numbers and configurations of corridors were added (Holyoak 2000), unless there were also treatments of unconnected fragments.

We searched the following journals using ISI Web of Science: *Biological Conservation, Conservation Biology, Ecological Applications, Ecological Monographs, Ecology, Ecology Letters, Ecography, Journal of Animal Ecology, Journal of Applied Ecology, Journal of Ecology, Nature, Oikos, and Science.* We searched using the following terms: (corridor*) and (population* or communit* or biodiversity). Our search extended from 1977 to 2003, and was conducted on 15 December 2003.

We found 15 studies that tested for corridor effects on populations and five studies that tested for corridor effects on diversity (Table 16.1). Some studies were included in both categories, as they analyzed both population and community responses. Studies covered a variety of species, including population studies on mammals, insects, microorganisms, birds, and a lizard (in order of decreasing frequency), and diversity studies on arthropods and birds. No studies focused on plants. Most studies (15/19) were experimental, as they manipulated and replicated landscape pattern.

At first glance, support for the idea that corridors affect population size or persistence appears strong. Of the 15 studies focusing on population responses to corridors, 13 demonstrated some corridor effect. Yet there were often caveats along with observed effects. Some studies (Fahrig and Merriam 1985; Mansergh and Scotts 1989; Dunning *et al.* 1995) were unreplicated and others (Burkey 1997; Schmiegelow *et al.* 1997; Haddad and Baum 1999; Schmiegelow and Mönkkönen 2002) observed corridor effects that may have been caused by patch shapes, edges, or habitat types that were confounded with corridor effects (see below, section "Designing corridor studies in variable environments"). Regarding corridor effects on diversity, all measured species richness and only two microcosm experiments showed convincing positive effects (Gilbert *et al.* 1998; Gonzalez and Chaneton 2002). The only other study to report evidence for corridor effects on diversity had no replication (MacClintock *et al.* 1977).

We conclude that the empirical literature to date shows ambiguous support for corridor effects on populations or communities. In support of corridors, most studies reported some positive effect. These effects are apparent even above many other local factors that are known to impact populations (like effects of local environments and other landscape-level effects) and that might obscure corridor effects. Despite these results, evidence remains weak because of confounding effects, and because some species performed more poorly in patches connected by corridors (Holyoak and Lawler 1996; Burkey 1997). At this time, current evidence

Table 16.1. *Studies reporting responses of populations or communities within patches that are either connected by corridors or isolated*

Study	Species	Scientific name	Study type	Corridor effect	Measured population response
On populations					
Fahrig & Merriam (1985)	Mammal: white-footed mouse	*Peromyscus leucopis*	Observational	Yes	Size
Mansergh & Scotts (1989)	Mammal: mountain pygmy possum	*Burramys parvus*	Observational	Yes	Survivorship
La Polla & Barrett (1993)	Mammal: meadow vole	*Microtus pennsylvanicus*	Experimental	Yes	Size
Ims & Andreassen (1999)	Mammal: Townsend's vole	*Microtus townsendii*	Experimental	No	Growth
Coffman *et al.* (2001)	Mammal: meadow vole	*M. pennsylvanicus*	Experimental	No	Size
Hannon & Schmiegelow (2002)				Yes	Survivorship
Schmiegelow *et al.* (1997)	Birds		Experimental	Yes for 7 of 23 species	Size
Dunning *et al.* (1995)	Bird: Bachman sparrow	*Aimophila aestivalis*	Observational	Yes	Size

Boudjemadi *et al.* (1999)	Herpetile: common lizard	*Lacerta vivipara*	Experimental	Yes in rich habitats No in poor habitats	Survivorship and fecundity
Haddad & Baum (1999)	Insects: butterflies		Experimental	Yes for 3 of 4 species	Size
Forney & Gilpin (1989)	Insects: fruit fly	*Drosophila hydei, D. pseudoobscura*	Experimental (Microcosm)	Yes for 1 of 2 species	Persistence
Shirley & Sibly (2001)	Insect: fruit fly	*D. melanogaster*	Experimental (Microcosm)	Yes in polluted areas No in non-polluted areas	Persistence
Gonzalez *et al.* (1998)	Microarthropods		Experimental (Microcosm)	Yes for 18 of 21 species	Persistence and size
Burkey (1997)	Microorganisms		Experimental (Microcosm)	Yes	Persistence
Holyoak & Lawler (1996)	Microorganisms		Experimental (Microcosm)	Yes for 2 of 2 species	Persistence and size
On diversity					
MacClintock *et al.* (1977)	Birds		Observational	Yes	Species richness
Schmiegelow *et al.* (1997)	Birds		Experimental	No	Species richness, log series α, Jaccard similarity
Collinge (2000)	Insects		Experimental	No	Species richness
Gilbert *et al.* (1998)	Microarthropods		Experimental (Microcosm)	Yes	Species richness
Gonzalez & Chaneton (2002)	Microarthropods		Experimental (Microcosm)	Yes	Species richness

offers tentative support for corridors, and much more work on population and community responses is needed.

When to expect positive corridor effects

In considering why our review did not strongly support corridor effects, it is important to be clear about the mechanisms or conditions under which we expect corridors to impact populations. Certain species in any community will perceive corridor habitat as being of equal or lesser quality than other surrounding habitat. It should be clear that these species, often habitat generalists, will not respond to corridors. Thus even when corridor experiments are conducted at the appropriate scale and are well controlled and replicated, we do not expect all species to respond positively. Corridor research and application therefore should focus on species that are either specialists for the habitats and corridors of interest, or are likely to exhibit reduced survival when traveling through matrix habitat. Even for habitat specialists, patches must be separated by distances large enough to restrict movement to the rate of few or no individuals per generation without corridors. If movement rates between unconnected patches are high, then immigration does not limit population size or diversity, and corridor utility for increasing population viability depends on their capacity to reduce mortality risk relative to matrix habitat (Hudgens and Haddad 2003).

Finally, corridor effects are likely to be highly scale-specific, both in terms of the scale of the landscape relative to an organism's size or movement distances, and in terms of the timescale of study relative to an organism's movement rate and generation time. Our literature review points directly to this issue of scale. Studies focusing on smaller organisms were generally more likely to find corridor effects than studies focusing on larger organisms (Table 16.1). While just over half of the studies focusing on mammals or birds found corridor effects for a majority of species, all studies focusing on insects and on microcosms found such effects (Table 16.1). One reason for more consistent responses with smaller species is that the landscape size can be better matched to the organism's home range or ambit. Although this could be a strength of model systems, we found that researchers tended to adjust their corridor length to the size of the organism, and that the length of organisms in microcosm studies was not significantly longer relative to corridor length (Fig. 16.1A). Though again not significant, microcosm studies were conducted for many more generations (and include the four right-most points on Fig. 16.1B), allowing a greater time for population dynamics to

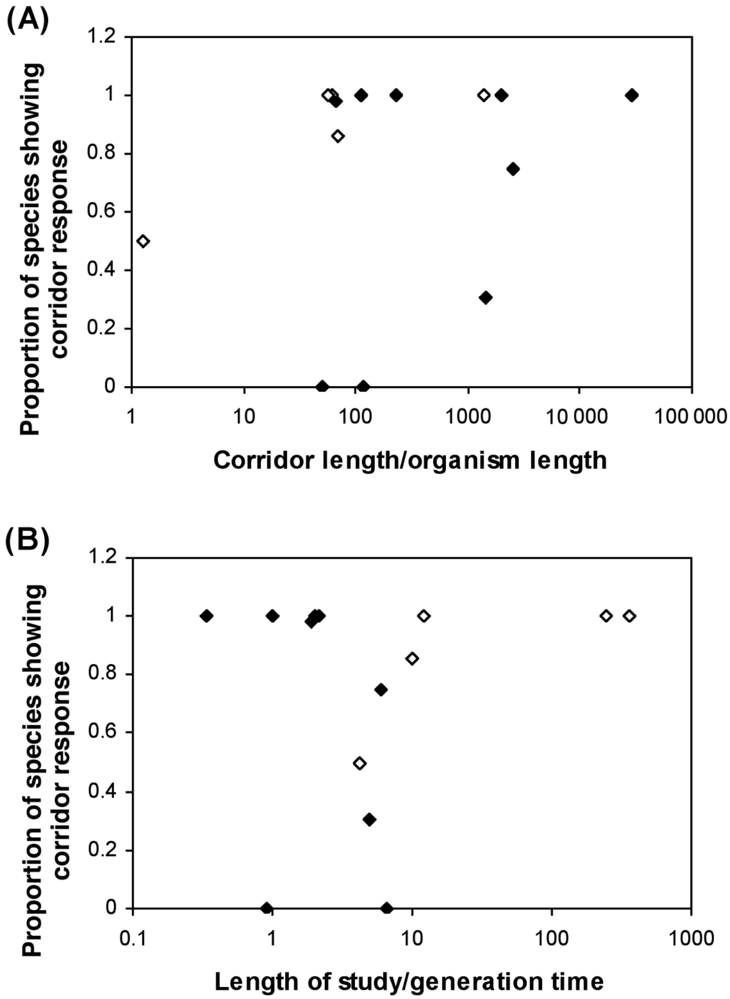

Fig. 16.1. Effects of spatial and temporal scale on population responses to corridors. Each data point represents one population study in Table 16.1, and shows the proportion of species that demonstrated population response to corridors (that is, populations performed significantly differently in connected relative to unconnected patches; $n = 14$ studies), as a function of (A) the ratio of corridor length to average organism length within a study, and (B) the ratio of study duration to the average generation time within a study. Neither relationship was significant in analyses with all studies, or excluding microcosm studies (white diamonds).

respond to corridors. Focus on scale should not become overly restrictive in the study or implementation of corridors, in that any corridor is likely to benefit many organisms, and likewise any organism is likely to respond to corridors at many scales. For example, our work with colleagues on one experiment with 1-ha patches and 150-m long corridors that was initially designed with a focus on butterflies has demonstrated corridor effects on birds, small mammals, insects, and plants (Tewksbury *et al.* 2002; Haddad *et al.* 2003; Levey *et al.* 2005). Still, more attention should be devoted to matching the scales of organisms and landscapes.

Designing corridor studies in variable environments

It is evident from our review that, in addition to issues of scale, issues of landscape variability also need more attention in the design of future studies. Corridor effects are only likely under a certain set of limited conditions, as their role is to increase the likelihood of rare events. Thus, corridors may have no effect on populations in years where dispersal is high (under density-dependent dispersal, these may be at times when populations are growing), but these same corridors may be critical in years when reproduction is lower, and dispersal is limited. Corridors may also have no effects when habitats in the landscape are stable, but be essential in the face of disturbance (Shirley and Sibly 2001). Thus, studies are needed that address the variability of effects rather than simply mean effects. These studies would be conducted for longer time periods and would more explicitly link corridor effects with population stresses.

Our review also makes clear that a critical aspect of study design is to assure that corridor effects are not confounded by other factors. These are not simply factors determined by the local environment, but rather are factors intrinsic to the landscape design. Adding a corridor affects not only connectivity, but patch size and shape, which can also affect population sizes and diversity (Harrison and Bruna 1999; Orrock *et al.* 2003). Haddad and Baum (1999) showed how the addition of a corridor changes edge effects within patches, increasing the area available to edge avoiding butterflies, and thus increasing their abundances. Schmiegelow *et al.* (1997) and Collinge (2000) both discuss how adding corridors affected the size of their experimental patches by adding the area of a corridor, and thus influenced population size and diversity. Only four experiments have controlled for the added area and change in shape caused by corridors in testing for their effects (Gonzalez *et al.* 1998; Boudjemadi *et al.* 1999; Gonzalez and Chaneton 2002;

Tewksbury *et al.* 2002). Perhaps it is because of the difficulty in separating effects of these uncontrolled variables that most studies in our review were experimental rather than observational. Of critical importance in future studies is to account for environmental and landscape variability in the design of experimental and observational studies.

FUTURE DIRECTIONS LINKING THEORY, MODEL SYSTEMS, AND MANAGEMENT

The next decade in corridor research should include an explicit focus on how corridors, and the movement they facilitate, affect populations and communities. Unlike studies of movement alone, which can usually be conducted over short time periods and at a variety of scales, studies of population and community consequences will have to more carefully incorporate into their design an understanding of isolation's impact, both in time and space. Because corridors often have their effects on extinction and on the recolonization that follows, the role of corridors is likely to be observed only after long-term studies or in particularly stressful years.

Theoretical predictions as well as some microcosm studies point to strong impacts of corridors on population and community dynamics, yet studies on macroinvertebrates and vertebrates show weaker and inconsistent effects. Why is this? While corridors may influence movement in many organisms, theory predicts stronger corridor effects on populations linked by rare events – either because the patches are sufficiently distant that migration is rare, or because the organisms are relatively sedentary. Microcosm studies appear to back this claim, with clear population effects in moss microcosm systems (patch area $= 79\,\text{cm}^2$) where the microinvertebrates in the moss are specialists on moss habitat (Gilbert *et al.* 1998; Gonzalez *et al.* 1998; Gonzalez and Chaneton 2002). In those studies, fragmentation created a matrix of completely unsuitable habitat, maximizing the barriers to dispersal between isolated patches and the benefits incurred by corridors that promote exchange. Larger-scale studies are typically leaky systems – corridors may increase movement between patches, but the degree of influence relative to movement through the matrix is often hard to determine and variable between and within species. In the following sections, we outline several research approaches to address corridor effects on populations and communities of species of management concern.

Corridors as conduits for rare events

Most corridor studies to date are small in scale, typically covering centimeters to hundreds of meters. These studies have provided a great deal of insight into how corridors function. Yet their mismatch with scales of landscape conservation is striking. This mismatch is further compounded by typical study species, which are usually common and mobile. These characteristics are convenient for obtaining results in short-term studies. Unlike species of conservation concern, common, mobile species are likely to move through inhospitable matrix, especially when distances between patches are relatively short. Higher movement rates between connected patches may not have population consequences for these species, particularly over short time periods, as movement rates between isolated patches are often sufficient to offset extinction in most years (Hudgens and Haddad 2003).

When movement events are rare and corridors buffer populations against local extinctions during stressful periods, corridors are likely to be most valuable in conservation. Perhaps that is why microcosm studies show such consistently strong effects. Gonzalez and colleagues (1998) examined microarthropod communities on moss patches for only 6 months, and demonstrated some of the strongest effects of corridors to date. While the study appears short in duration, it spanned at least several generations for all species, much greater than typical studies of corridors.

Organisms of management concern that disperse over smaller areas and have generation times of a year or less are much more likely to benefit from empirical studies of corridor effects, because small-scale studies are applicable. There are many species of plants, insects, small mammals, amphibians, and reptiles with relatively short generation times that make up much of total biodiversity and that are likely to benefit from small-scale corridors. Still, full accounting of the spatial and temporal dynamics that mediate corridor effects in these species will require studies lasting multiple generations.

For many rare species with short generation times, local extinctions and colonization dynamics are imposed by natural disturbances, and elucidating the role of corridors requires long-term studies of movement and population sizes to determine population viability. For example, our work with collaborators on an endangered butterfly, the St. Francis satyr (*Neonympha mitchellii francisci*), is designed to determine the role of corridors in facilitating colonization and maintaining viable populations. This sedentary subspecies occurs in small (0.1–0.6 ha) wetland openings

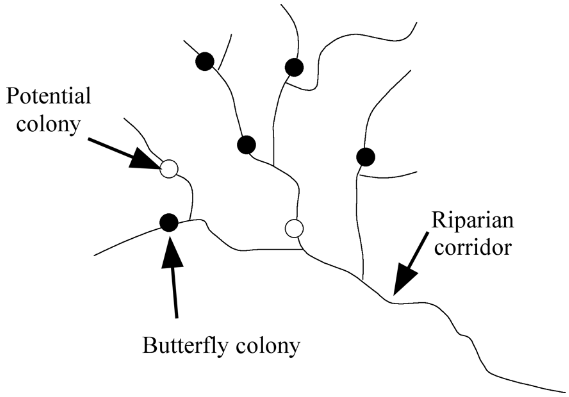

Fig. 16.2. Metapopulation structure of the St. Francis satyr. Riparian corridors may serve as movement corridors to promote colonization of habitats created by disturbance.

along streams (Fig. 16.2) that are maintained by disturbances caused by beavers and by fire, without which vegetation quickly succeeds to unsuitable riparian forest. Butterflies can survive neither the disturbance nor the succession. We believe that riparian habitats serve as corridors to promote colonization of new sites. Yet, in 3 years of research encompassing six butterfly generations, we have marked approximately 750 butterflies and observed just three movements between patches, all between the closest (separated by 300 m), connected patches.

The St. Francis satyr case study highlights an important role of corridors: their effects may be particularly important under stress or disturbance. Successional habitat dynamics for St. Francis satyr occur over many years or decades. The creation of new openings by disturbance generates the opportunity for natural experiments. We have already observed colonization of two sites that had been flooded and then abandoned by beavers (both within a couple of hundred meters of existing sites). It will take many years to observe a sample size of openings that permits conclusions that will affect landscape-level habitat restoration. Although studies of the interaction between corridors and disturbance are rare, Shirley and Sibly (2001) created a microcosm experiment with fruit flies that demonstrated the important interactions between corridors and environmental disturbance. They investigated metapopulation response under unpolluted and polluted conditions, and found that corridors increased population persistence in patches disturbed with pollution (Shirley and Sibly 2001). An important area of future research will be to further understand how the interrelationship between corridors and disturbance affects populations and communities.

Thinking big: large-scale manipulations

Conservation at the landscape scale usually involves corridors that may extend kilometers to hundreds of kilometers. At these scales, there have been only a few successful studies of movement (Beier 1995), gene flow (Hale *et al.* 2001; Mech and Hallett 2001), or population sizes (Dunning *et al.* 1995). One response variable that is not included in the corridor studies we reviewed, but is typical of connectivity studies in metapopulations, is patch occupancy (Moilanen and Nieminen 2002; Moilanen and Hanski Chapter 3). One approach to expand the number of corridor studies at larger scales may be to focus more specifically on patch occupancy in landscapes with and without natural corridors (MacKenzie *et al.* 2006).

The primary constraint on studies at large scales is the difficulty in finding replication and in controlling for variables that may confound corridor effects. In addition to the confounding factors discussed above, connected patches tend to be larger than unconnected patches (Villard *et al.* 1999; Fahrig 2003). Overcoming confounding effects of other variables will likely require a great deal of replication and/or judicious pairing of control and treatment sites, which can be difficult to find and sample at large spatial scales.

Ideally, larger-scale, longer-term studies will involve some level of controlled experimentation. Experimental manipulation of both habitat and disturbance levels allows isolation of mechanisms and greater time-efficiency by eliminating confounding variables. Long-term studies where landscapes are manipulated over large areas are much more likely to yield definitive results regarding corridor effects, and collaborative teams of researchers working at large scales may be much more effective than individual researchers working separately at smaller scales. Evidence from one long-term, large-scale fragmentation experiment, the Biological Dynamics of Forest Fragments Project in Brazil, suggests that responses accumulate over time. This experiment was created starting in 1980 in Manaus, Brazil to test the effects of fragmentation and patch size on tropical ecosystems. It is only after more than a decade of study, that major community and ecosystem impacts of fragmentation have been documented (e.g., Laurance *et al.* 1997, 2001; Bierregaard and Gaston 2001; Ferraz *et al.* 2003; see also Cook *et al.* 2005). Given the critical roles of habitat loss and fragmentation as the most important factors impacting the loss of biodiversity (Wilcove *et al.* 1998), more such studies are needed.

One approach to studying effects of connectivity at large scales is to take advantage of manipulations that occur as part of landscape management. Such manipulations occur every day through forestry, development, agriculture, and other changes in land use. Although many alterations come through habitat loss, habitat restoration should also provide opportunities for experimental assessment of responses to connectivity. Because large-scale habitat modification for scientific research alone can create serious ethical concerns, we recommend coordinating research plans along with planned habitat modifications (destruction or restoration), so that useful information can be gained in the context of adaptive management. Unfortunately, land-use manipulations are typically uncontrolled with respect to landscape factors like connectivity and other important environmental factors that might obscure landscape-level responses, thus limiting their usefulness in guiding future management. As pointed out by Beier and Noss (1998), a good example of how a study can be designed around landscape management was conducted by Mansergh and Scotts (1989). By measuring responses before and after corridor restoration at a ski resort, they demonstrated positive effects of corridors on mountain pygmy possum survivorship.

In lieu of controlled experimentation, new research will have to be creative in identifying opportunities for replicated large-scale manipulations allowing isolation of corridor effects. In our own work, we have found that academic partnerships and close collaboration with land-management agencies are critical for the success of these projects. With investigators from three additional academic institutions, we have been working closely with the US Forest Service at the Savannah River Site in South Carolina to assess large-scale effects of corridors. The Savannah River Site is an 80 000-ha site managed for plantation pine forest and as native habitat for wildlife. The Forest Service employs clearcut forestry, and creates clearings that range in size from 5 to 50 ha. These clearings vary in their connectivity, as some of the clearings are connected to others by long, straight utility rights-of-way and roads (Fig. 16.3). Because these rights-of-way are subjected to frequent, thorough disturbance (by herbicide and mowing), they are unlikely to be long-term sources of butterflies, but instead serve as corridors between suitable habitats.

To test the effects of large-scale, open corridors in landscapes managed for forestry, we have studied butterfly species that thrive in early

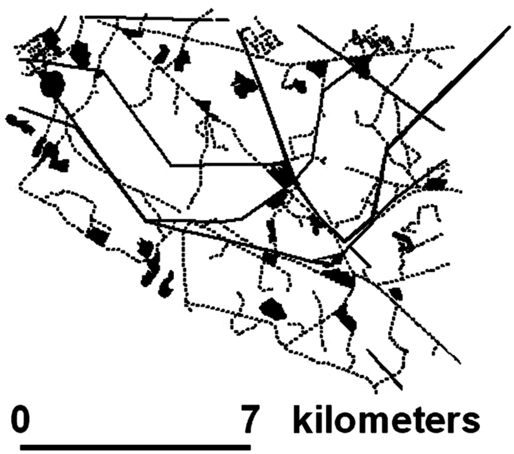

Fig. 16.3. Fragmentation of cleared patches caused by forest management at the Savannah River Site, South Carolina. Black areas are clearings 1–7 years of age. Solid black lines are utility rights-of-way that may serve as corridors for dispersing butterflies and other organisms. Dashed lines are roads, primarily small forest roads, that are less likely to serve as corridors. Cleared patches vary in isolation, both in their distance to other patches and in their connection to other patches via utility rights-of-way.

successional habitats for up to 8 years after forest harvest, when the pine canopy starts to close. After extensive studies of two of these species, the buckeye (*Junonia coenia*) and the variegated fritillary (*Euptoieta claudia*), using large, replicated, experimental landscapes, we have shown that both are more likely to move between connected patches separated by up to 400 m (Haddad 1999a; Tewksbury *et al.* 2002). To test these corridor effects at the much larger scales of operational forestry, we conducted repeated surveys for both species in all ($n = 137$) clearcut openings on the Savannah River Site (some connected by utility right-of-way corridors, others not). After controlling for potentially confounding effects such as stand type, area, and age, very preliminary analyses from the first year of a multi-year study indicate that the presence of a corridor increases population sizes of fritillaries, but not buckeyes (B. Danielson and N. Haddad, unpublished data). Thus, at least for the fritillary, results from small-scale studies appear to "scale up" to larger areas. It is worth noting that the one species whose responses did scale up – the fritillary – is more sedentary than the species whose responses did not show corridor effects at the largest scale, the buckeye (Haddad 1999a). While far from conclusive, this supports the theoretical prediction that corridor effects are more likely in situations in which migration between patches is relatively rare. This work highlights a challenge in ecology and conservation, which is to reconcile often smaller-scale experimental with often larger-scale observational data.

Linkage across life-history and trophic levels

Population- and community-level responses to corridors are potentially caused by many different mechanisms spanning trophic levels and acting on different life-history stages. This diversity of corridor effects could magnify or dampen the observed response for any particular population or community. Most often, researchers consider the effects of corridors on movement or gene flow within an individual species. Considered more deeply, however, there can be multiple stages at which movement can be important, and multiple interactions that can result in positive or negative effects of corridors on individual species. For even a single species, these may include a diversity of interactions with different groups – predators, competitors, mutualists, parasites – all of which may respond to fragmentation and corridors. For many plants, the initial effect of corridors on movement rates will be a direct function of corridor effects on pollinators and seed dispersers, and plant establishment will additionally be influenced by the response of seed-predators, parasites, and herbivores. This diversity of interactions may cause contrasting responses and can make detection of net population responses difficult. The positive effects of corridors may be dampened or reversed by negative effects (Fig. 16.4) (see also Crooks and Sanjayan Chapter 1), and more work is needed to assess the balance of positive and negative effects on population and community structure.

At both small and large scales, assessing net corridor effects on populations will most likely be done through long-term studies. In studies of short duration (i.e., the typical duration of a grant funding cycle or of a dissertation program), approaches that focus on aspects of population demography might provide more rapid assessment of corridor effects on survivorship and reproduction at key life-history stages (see Mansergh and Scotts 1989; Beier and Noss 1998; Coffman *et al.* 2001). This approach may occasionally allow researchers to model corridor effects on populations, especially if key life-history attributes and developmental stages are easily identified. With structured data, population models can be used to assess population dynamics and viability in the presence or absence of corridors (discussed below). Yet conclusions from demographic models must be approached with caution, as parameters estimated over

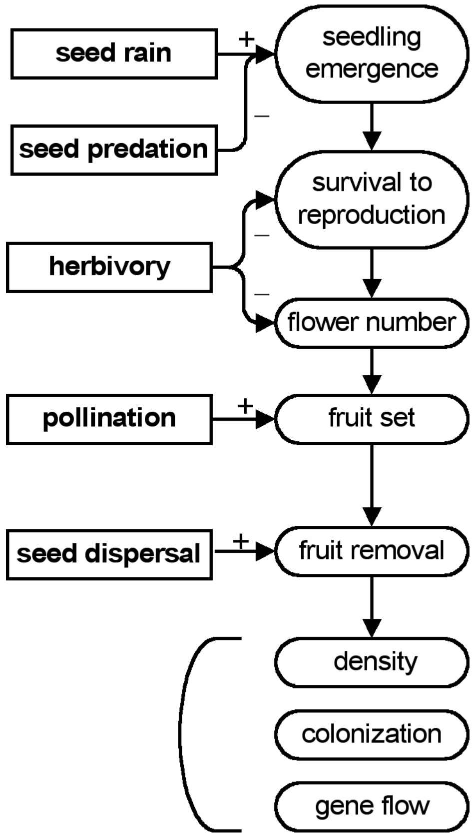

Fig. 16.4. Effects of corridors on various life stages of plants. Multiple plant–animal interactions could cancel or enhance corridor effects on a single plant species. Interactions are in square boxes, with arrows pointing to life-history stage affected (in ovals) with positive and negative signs indicating the most likely effect on plant demography. Density-dependent linkages between interactions (seed rain and seed predation, pollination, and herbivory), and feedbacks onto animal counterparts of the plants (seed predators, herbivores, pollinators, etc.), further increase the complexity of effects that may be influenced by patch isolation and connectivity.

relatively short time intervals may fail to capture corridor impacts in extreme years (catastrophes or bonanzas: Morris and Doak 2002) when corridors may be most important.

We have conducted an experimental study over the past decade where we have had some success at determining corridor effects on aspects of population demography (Tewksbury *et al.* 2002; Haddad *et al.* 2003). These experiments at the Savannah River Site have involved 1-ha experimental patches that are separated by 100 + m. The patches are open, early-successional habitat surrounded by plantation pine forest. The openings are suitable for many species of plants, insects, mammals, and birds, while the pine forest is not. Our work has focused mainly on movement of insects, small mammals, birds, and plants, but we have made some inroads into understanding effects on population demography. For example, we have found that corridors increase plant pollination rates and dispersal of fruiting plants (Tewksbury *et al.* 2002; Haddad *et al.* 2003). Both of these factors should lead to higher seed numbers in connected patches, leading to predictions of higher population sizes (Tewksbury *et al.* 2002). Yet corridor effects on plant demography are complex, and effects at one life stage may be modified or reversed by effects on other life stages. Studies with our collaborators, for example, have shown that the same corridors that increase pollination and seed dispersal (Tewksbury *et al.* 2002) also lead to increases in seed predation by mammals that use corridors as foraging conduits (Orrock *et al.* 2003; Brinkerhoff *et al.* 2005). The net impact of these corridor-related effects on whole plant population demography is unclear (Fig. 16.4). Further research should focus on integrating landscape effects across life-history stages.

Model-directed experimental research

Empirical approaches will benefit from informed models that guide targeted experiments. Three types of modeling exercises may be effective at informing future research: individual-based models, numerical models, such as demographic models linking effects at different life stages, and analytical models that determine the types of organisms most likely to respond to corridors. Models will serve to assess impacts of empirically measured responses at one life-history stage on total population size. They will also be important in determining which demographic characteristics and behaviors should be the focus of further empirical study.

Individual-based models, often spatially explicit, have the advantage of linking some of the most available data on corridor use – movement data – to impacts on populations and communities. To date, such models have had some success at linking local behavior to larger-scale distribution (Tilman *et al.* 1997; Tischendorf and Wissel 1997; Haddad 1999b; Levey *et al.* 2005). Individual-based models can incorporate understanding of fine-scale decision rules that link dispersal to landscape structure (Tracey Chapter 14). Habitat-specific data on movement distances and turning can be used to predict corridor effects on patch colonization. Of specific interest is the role of habitat boundaries, as they define corridor structure and function (Cadenasso *et al.* 2003), and vary in their permeability across species (Haddad 1999b). Other decision rules, such as the effects of density or presence of related individuals (as in Le Galliard *et al.* 2003), may also be included. One advantage to such models is that landscape characteristics can be easily varied to generate predictions about corridor impacts. For example, three different models have predicted that there is an asymptote to the effect of corridor width on movement rates (Tilman *et al.* 1997; Tischendorf and Wissel 1997; Haddad 1999b). Although this prediction has received some empirical support (Andreassen *et al.* 1996), more is needed. A disadvantage of this approach is that adapting such models to population-level questions involves a large and often intractable number of parameters. Such individual-based models may be most effective in predicting corridor effects on species with large ranges and long generation times, for which population trends are very difficult to obtain. In these circumstances, individual-based models of movement in relation to habitat boundaries, coupled with spatially explicit, habitat-specific data on reproduction and survival, may provide much needed insight into the probable effectiveness of proposed changes in land management.

Two other types of models may have greater practical applicability in determining corridor effects on population size and community structure. Numerical models, such as matrix models and structural equation modeling (Grace and Pugesek 1998; Caswell 2001), can be used to project population trends and assess population viability. The primary advantage to these approaches is that they integrate empirical estimates from research targeted at specific life-history stages. Rather than ignore all corridor effects but those on movement and on population sizes, a model-based approach integrates the impacts of corridors on species and interactions across life-history stages. In addition to determining the contribution of each stage to population growth, sensitivity analyses can be used to determine how management targeted at a specific stage might be used to increase population sizes in connected landscapes. To date, the use of these approaches has been limited, primarily because researchers have yet to gather data on the effects of corridors across life-history stages.

Another approach that can be used to predict responses to corridors is analytical modeling. Analytical models can have a closed form solution, such that the equations that describe the effects of corridors on populations can be expressed as a mathematical function. These are often much simpler than the real-world corridors they represent, but they can provide guidance about which characteristics are in need of targeted research, and which species are in need of conservation. Metapopulation models have become increasingly common in assessing effects of connectivity, including corridors (Henein and Merriam 1990; Hess 1996; Anderson and Danielson 1997; McCallum and Dobson 2002; Moilanen and Hanski Chapter 3). These models have provided some of the few analyses of how species interactions in fragmented landscapes with or without corridors may affect host populations in the context of disease dynamics (Hess 1996; McCallum and Dobson 2002; McCallum and Dobson Chapter 19).

Analytical models that assess the role of corridors on population size are less common. In simple population growth models, Earn and colleagues (2000) showed how corridors can synchronize population dynamics and lead to metapopulation extinction. Hudgens and Haddad (2003) used simple logistic population growth models to determine for what types of species and situations corridors were likely to affect populations. They modeled a two-patch system that accounted for corridor effects by including terms for corridor and matrix migration and mortality. Their results generated a number of implications for further research and future conservation. First, their results suggest that corridors are likely to benefit species with high population growth rates in the short term, whereas they are likely to benefit species with low population growth rate in the long term. Since most species of conservation concern have low growth rates, this result further reinforces the need for studies of long-term population responses to corridors. Second, their results suggest that the type of population dynamics exhibited by a species will determine corridor effectiveness. Species that have large population oscillations with years of low population size are likely to be harmed by corridors, as corridors are likely to synchronize population dynamics among patches. Corridors are likely to benefit species of conservation concern that are experiencing sustained population decline. Third, they showed that it is usually not just dispersal through corridor and matrix habitats, but also corridor and matrix mortality that determine corridor benefits. Only when species have extremely low matrix migration are corridors likely to benefit populations through their role in increasing migration. With higher matrix migration, corridors are likely to increase population viability by reducing mortality during dispersal. These results emphasize the need for demographic studies not only in patches, but in corridor and matrix habitats as well.

CONCLUSION

Over the past decade, empirical research has generated broad support for the hypothesis that habitat corridors increase movement through fragmented landscapes for many species. The effects of corridors on population viability, however, are less well studied, and the empirical understanding of corridor effects on community structure and diversity is still in its infancy. In our review of the existing evidence, we find that support for corridor effects on populations is growing, though with many caveats. There is more support for corridor effects in smaller taxa with shorter generation times. This result reflects greater ease in matching temporal and spatial scales of experiments with smaller species. Although corridors are intended to promote movement, their ultimate effectiveness in conservation must be measured by their population- and community-level effects in promoting colonization, reducing extinction, and increasing population viability.

Empirical support for corridors at the population and community level would strengthen arguments to maintain or construct corridors, rather than to allocate resources toward other conservation strategies. Empirical tests of corridor effects on populations and communities will require long-term experiments conducted at large spatial scales, coupled with creative approaches to obtaining difficult to observe events, such as rare, long-distance dispersal. While such studies require careful coordination, we believe there are opportunities for such large-scale studies in conjunction with planned habitat restoration or destruction. For rare species, purely observational studies may be the only ones that are possible to inform conservation decisions. However, they rarely can overcome the many intercorrelated factors confounding the effects of connectivity. Rather than focusing only on population abundance or species numbers, successful studies are likely to integrate research on movement, habitat-specific demography, and density-dependent interactions between species in an assessment of corridor effects on population viability. Empirical studies would be aided by insights from analytical, demographic, and individual-based models that help to focus research on specific life-history characteristics and life-cycle stages that link corridor effects to population dynamics. We are hopeful that such approaches will help stimulate more rapid progress in understanding the impacts of corridors on populations and communities, and, thus, their value in conservation.

ACKNOWLEDGEMENTS

We would like to acknowledge work by our many collaborators who have contributed to our understanding of corridor effects, including Jory Brinkerhoff, Ellen Damschen, Brent Danielson, Brian Hudgens, Daniel Kuefler, Doug Levey, John Orrock, Sarah Sargent, Patricia Townsend, Aimee Weldon, and many others. We would also like to thank our agency collaborators, including John Blake and Ed Olson at the Savannah River Site and Erich Hoffman at Fort Bragg. We thank Becky Bartel, Paul Beier, Kevin Crooks, Ellen Damschen, Bill Fagan, Andrew Gonzalez, Daniel Kuefler, Aimee Weldon, and Neal Williams for comments on this chapter. Our work on corridors has been funded by National Science Foundation DEB-9907365, the US Forest Service, Savannah River, and the Department of Defense at Fort Bragg.

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