CORRIDOR USE BY DIVERSE TAXA

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Abstract. One of the most popular approaches for maintaining populations and conserving biodiversity in fragmented landscapes is to retain or create corridors that connect otherwise isolated habitat patches. Working in large-scale, experimental landscapes in which open-habitat patches and corridors were created by harvesting pine forest, we showed that corridors direct movements of different types of species, including butterflies, small mammals, and bird-dispersed plants, causing higher movement between connected than between unconnected patches. Corridors directed the movement of all 10 species studied, with all corridor effect sizes >68%. However, this corridor effect was significant for five species, not significant for one species, and inconclusive for four species because of small sample sizes. Although we found no evidence that corridors increase emigration from a patch, our results show that movements of disparate taxa with broadly different life histories and functional roles are directed by corridors.

Key words: biodiversity; bird; butterfly; conservation; corridors; dispersal; fragmentation; frugivory; landscape experiment; movement; pollination; small mammals.

INTRODUCTION

Corridors are long, thin strips of habitat that connect otherwise isolated habitat patches. They are thought to reduce local extinction by ''rescuing'' isolated populations (Brown and Kodric-Brown 1977) and by promoting gene flow. Indeed, recent studies have demonstrated that corridors can increase animal movement between patches (Haas 1995, Sutcliffe and Thomas 1996, Gonzalez et al. 1998, Haddad 1999*a*, Mech and Hallett 2001), increase population sizes (Fahrig and Merriam 1985, Dunning et al. 1995, Haddad and Baum 1999), increase gene flow (Aars and Ims 1999, Hale et al. 2001, Mech and Hallett 2001), and maintain biodiversity (Gonzalez et al. 1998). Other studies, however, have found no corridor effects (Arnold et al. 1991, Date et al. 1991, Rosenberg et al. 1998, Bowne et al. 1999, Haddad and Baum 1999, Collinge 2000, Danielson and Hubbard 2000). In one recent review, Beier and Noss (1998) evaluated 32 corridor studies and found that, although many were inconclusive due to flaws in study design, 10 of 12 well-designed studies demonstrated positive effects of corridors. Given that habitat conservation measures such as corridors are likely to affect many species in a landscape, an important, unresolved question is: Which species in a landscape will benefit from corridors?

To date, most corridor studies have focused on single species, or on groups of closely related taxa (see recent reviews in Rosenberg et al. 1997, Beier and Noss 1998, Hess and Fischer 2001). For example, corridors have been shown to serve as movement conduits for species of birds (Haas 1995), mammals (Beier 1995), and butterflies (Sutcliffe and Thomas 1996, Haddad 1999*a*). However, for other species of birds (Date et al. 1991), butterflies (Haddad 1999*b*), and small mammals (Suckling 1984, Henderson et al. 1985, Bowne et al. 1999), as well as a salamander species (Rosenberg et al. 1998), corridors do not increase movement. In addition, many major taxa have not been considered in corridor studies. For example, there are no studies of corridor effects on the movement of plants or of many insect groups.

Using a large-scale experiment, we synthesized results from studies of the effects of corridors on movement by species from diverse taxa, including butterflies, bees, bird-dispersed plants, and small mammals. Although each taxon was studied independently, all studies took place in the same experiment. In our analysis, we incorporated new and previously published data to address two specific questions. (1) For which taxa do corridors direct movement? (2) What are the magnitudes of the effects of corridors on movement across taxa? In the discussion, using previously published data from this experiment on a subset of the taxa considered in this paper, we examine a third question: for which taxa do corridors increase emigration?
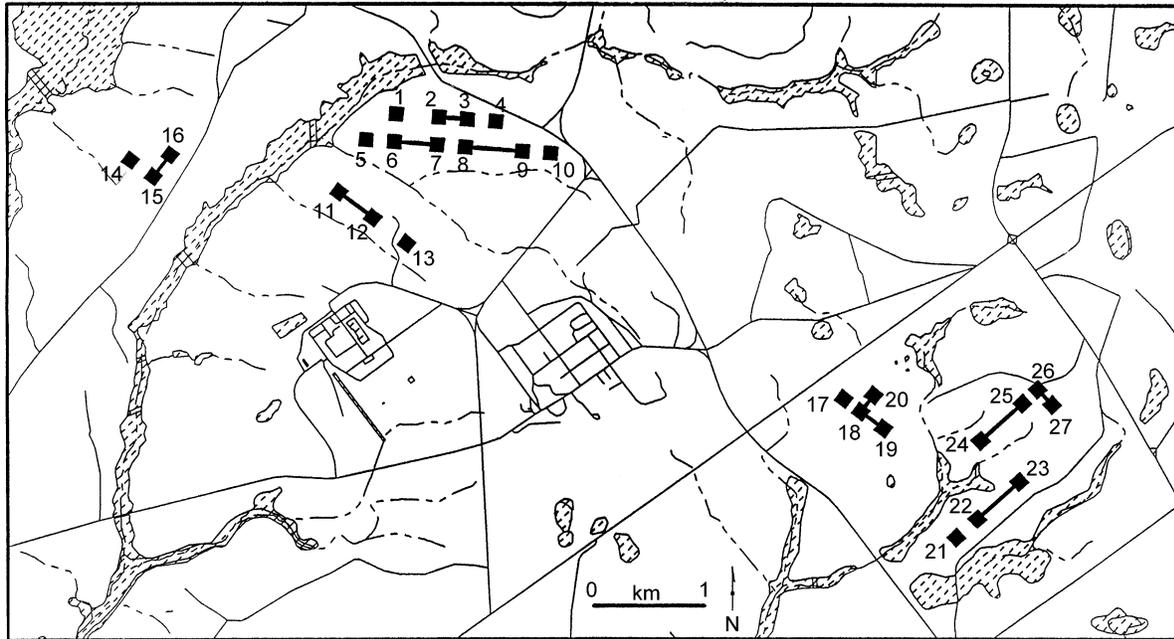
FIG. 1. Corridor experiment at the Savannah River National Environmental Research Park, South Carolina, USA. Black areas show patches (128 × 128 m, numbered 1–27) and 10 corridors (32 m wide, varying in length from 64 m to 384 m). Solid lines show roads, and stippled areas are ponds and streams.

METHODS

Our research was conducted within large-scale, experimental patches and corridors at the Savannah River National Environmental Research Park, near Aiken, South Carolina, USA. Patches and corridors were early-successional vegetation and were created by harvesting pine trees within large pine plantations. The experiment consisted of 27 128 × 128 m open patches (1.64 ha), some of which were connected by a 32 m wide, open corridor that varied in length from 64 to 384 m (Fig. 1). These patch sizes were chosen because they are large enough to prevent shading of the entire patch by surrounding trees, and because they match the scale of movement of many of the study organisms. For example, the average lifetime movement distance of two butterfly species, *Junonia coenia* and *Euptoieta claudia*, are approximately the width of a patch (Haddad 1999*a*), and home ranges of old-field mice, *Peromyscus polionotus*, are approximately one-third the area of a patch (Davenport 1964). The patches and corridors were dispersed among five different stands of pine forest (mainly *Pinus taeda* and *P. palustris*).

The landscapes of open patches and corridors surrounded by forest were the inverse of landscapes with forested patches and corridors that are typically considered in conservation. The key aspect of this system, similar to that of other landscapes where corridors are proposed, was that patches and corridors were suitable for the species that we studied and contrasted with unsuitable matrix habitat. All of our study species were common in the region and occurred naturally in the habitats that we studied. These species do not require clearcut corridors for movement in unmanaged landscapes, but are adapted to colonizing ephemeral openings within forests, some of which may be connected by strips of secondary vegetation.

Research on different taxa followed one of two approaches. In the first, movements of two butterfly species (*Junonia coenia* and *Euptoieta claudia*) and one small-mammal species (*Sigmodon hispidus*) were studied between all pairs of adjacent patches (see Fig. 1). In the second, movements of four plant species (*Ilex opaca*, *Myrica cerifera*, *Phytolacca americana*, and *Rhus copallina*), another small-mammal species (*Peromyscus polionotus*), and one bee species (*Xylocopa virginica*), as well as pollen of one plant species (*Passiflora incarnata*), were studied in "blocks" of three patches. In each block, one center patch was surrounded by two patches equidistant from the center patch. One of the two peripheral patches was connected to the center patch by a corridor, and the other was isolated from the center patch (e.g., patches 14, 15, and 16, where patch 15 is the center patch; Fig. 1). In this second approach, and except where noted, naturally occurring individuals of a study species were eliminated from patches and corridors, and newly introduced individuals were monitored. Except where noted, all research was conducted in 1996.

The results published here are a synthesis of studies for many species, and the analysis of corridor effects on movement directions of butterflies was published previously (Haddad 1999*a*). In addition, studies of *P.*

polionotus (Danielson and Hubbard 2000) and *S. hispidus* (Bowne et al. 1999) from this experiment have been published, but the analyses of the effects of corridors on movement direction are new. Although unpublished data comprise the bulk of the paper, we include the published results on corridor effects on movement directions of butterflies because they allow us to make clean cross-taxonomic comparisons.

Butterflies were studied in daily surveys of all patches between 3 April and 29 June (for detailed methods, see Haddad 1999*a*). Each butterfly was captured and marked with a unique number. An average of 124 *J. coenia* (range 38–532) and 11 *E. claudia* (range 1–38) were marked in each patch. Recaptures provided measures of movement between all pairs of adjacent patches.

Adult *Sigmodon hispidus* were captured at least 13 km from the experimental area, fitted with radio collars, and released into one of 10 different patches that were contained within one forest stand (Fig. 1, patches 1–10; detailed methods are provided in Bowne et al. [1999]). Although movement distances of released individuals were expected to be greater than those of resident individuals, there was no evidence that movement direction was biased toward the initial capture area (Bowne et al. 1999). In total, six individuals were released into each of two different patches, and their movements were monitored for 10 consecutive days. These releases were repeated until all patches had been studied once ($n = 10$ patches), and were repeated a second time in six of the same patches. Radio telemetry permitted direct observations of animal movements between adjacent patches.

Peromyscus polionotus were eliminated from three blocks of three patches, where the distance between center and peripheral patches was 128 m or 256 m. Between 16 and 27 adult female mice were ear-tagged and introduced into nest boxes in the center patch of each block (detailed methods are provided in Danielson and Hubbard [2000]). In our system, introduced *P. polionotus* move more frequently between patches than do naturally occurring individuals, but their movement orientation is not biased (i.e., by homing; J. Brinkerhoff, *unpublished data*). After acclimating to the boxes, mice were allowed to move freely. Marked individuals were recaptured in 18 Sherman traps (Sherman Traps, Tallahassee, Florida, USA) arranged in a grid in each of the nine patches. Live-trapping was conducted three days per week from 1 May to 30 August. Recaptured mice were used to estimate movement between connected and unconnected patches.

Seed dispersal of bird-dispersed plants (*Ilex opaca*, *Myrica cerifera*, *Phytolacca americana*, and *Rhus copallina*) was studied in 2–4 blocks of three patches (depending on plant species), where the distance between patches was 64, 128, 256, or 384 m. Dispersed seeds were collected from avian fecal samples in seed traps that were placed under perches positioned in a 4

× 4 grid of 16 perches in each patch. For *P. americana* and *R. copallina*, naturally occurring individuals were removed from the peripheral patches, and seeds of these species recovered in the peripheral patches were assumed to have been dispersed from the center patch, which was the nearest seed source. The two other species, *I. opaca* and *M. cerifera*, were not eliminated, and seed dispersal was tracked by marking seeds in the center patch with flourescent microspheres, which are defecated with seeds (Levey and Sargent 2000). Fecal samples were collected weekly from 26 August 1996 to 15 March 1997, and from 3 November 1997 to 10 April 1998, during the peak fruiting season of each species (fall 1996 for *P. americana*, winter 1997 and 1998 for *M. cerifera* and *R. copallina*, and winter 1998 for *I. opaca*). The numbers of seeds of each species recovered from fecal samples in each patch were summed over the entire season. When a species was studied for two years, analyses were conducted on the average numbers of seeds dispersed at each site among years.

Pollination was measured for *Passiflora incarnata*, a plant species pollinated by large-bodied bees and wasps. The experiment followed the same design as that of the seed dispersal study. After naturally occurring plants were removed from the patches and corridors, 24 individual *P. incarnata* were planted next to trellises in each patch. Pollination was estimated daily from 1 July to 14 August by marking flowers in the center patch with fluorescent powder and recording the presence of powder on flowers in peripheral patches. In addition, pollinators, including large-bodied bees and wasps, were marked during the same period with unique tags. Because one species, *Xylocopa virginica*, comprised 90% of marked individuals and was the only species recaptured, we restrict our discussion to it.

We used one-tailed *t* tests to test the hypothesis that plants and animals move more frequently between connected than between unconnected patches. For the second approach just described, where connected and unconnected patches both occurred in the same block, we used paired *t* tests. Where appropriate, we arcsine-transformed proportions or square-root transformed counts (after adding 0.375) to normalize data (Zar 1999). Because some of the studies involved small sample sizes (as low as two or three replicates), we considered a corridor effect significant if $P < 0.10$. For cases in which sample sizes were low ($n \leq 3$), we conducted power analyses to estimate the number of samples needed to detect a significant effect, given the values that we recorded (Steidl et al. 1997).

Although distances between patches were variable and replicated, many of the studies were not designed to test for distance effects on corridor function. Hence, we exclude examination of distance effects in this paper.
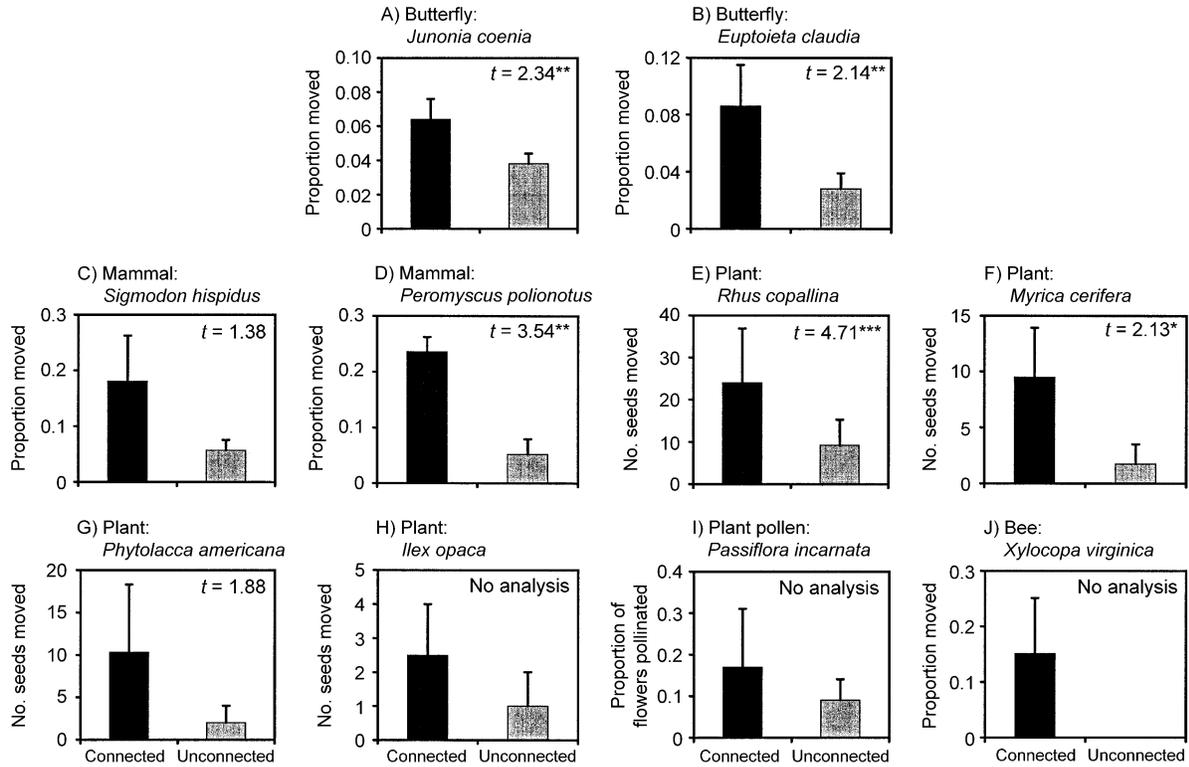
FIG. 2. Plant and animal movement between connected and unconnected patches. Panels (A)–(D) and (J) show the mean (+1 SE) proportion of individuals that were marked in one patch and moved to a connected or unconnected patch. Panels (E)–(H) show the mean (+1 SE) number of bird-dispersed seeds that moved from center patches to connected or unconnected patches. Panel (I) shows the mean (+1 SE) proportion of flowers in connected or unconnected patches with fluorescent powder. Data for butterflies are adapted from (Haddad 1999*a*). Asterisks indicate significance levels: * $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$.

RESULTS

Of the 10 species that we studied, five moved significantly more often between connected than between unconnected patches (Fig. 2), and all species showed positive corridor effects (calculated as the percentage increase in movement between connected relative to unconnected patches) >68% (Fig. 3). As shown previously (Haddad 1999*a*), both butterfly species moved more frequently between connected than unconnected patches (Fig. 2A,B; *t* test assuming equal variance: *Junonia coenia*, $n = 48$ patch pairs, $t = 2.34$, $P = 0.012$; *Euptoieta claudia*, $n = 47$, $t = 2.14$, $P = 0.019$). As in Haddad (1999*a*), one outlier was dropped from the analysis of *E. claudia* because only two individuals were marked in that patch. One rodent, *Peromyscus polionotus*, moved more frequently between connected patches (Fig. 2D; paired *t* test: $n = 3$ blocks, $t = 3.54$, $P = 0.036$). Finally, seeds of two bird-dispersed plants, *Rhus copallina* (Fig. 2E; paired *t* test: $n = 4$ blocks, $t = 4.71$, $P = 0.009$) and *Myrica cerifera* (Fig. 2F; paired *t* test: $n = 4$ blocks, $t = 2.13$, $P = 0.062$) moved more frequently between connected than unconnected patches.

For one rodent species, *Sigmodon hispidus*, the corridor effect on movement direction was not significant (Fig. 2C; *t* test assuming unequal variance: $n = 22$ patch pairs, $t = 1.38$, $P = 0.107$). The apparent large
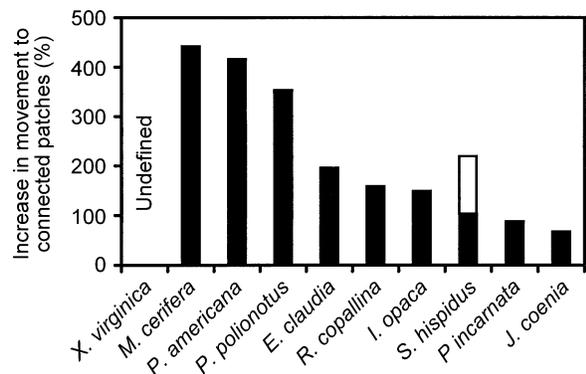

FIG. 3. The corridor effect, measured as the percentage increase in movement between connected relative to unconnected patches, presented in the rank order of the size of the effect. For *Sigmodon hispidus*, the black bar excludes one outlier, described in *Results,* whereas the white bar includes the outlier.

difference in movement into connected vs. unconnected patches (means = 0.181 vs. 0.057, respectively) was generated by a single outlier that, when removed, reduces mean movement to connected patches from 0.181 to 0.117. This statistical result, based on an analysis with large sample size, led us to conclude that this species does not move preferentially between connected patches.

Movements of four other species appeared to be directed by corridors, but our results were inconclusive, probably due to low sample size. For one plant species (*Ilex opaca*, Fig. 2H), the bee species (*Xylocopa virginica*, Fig. 2J), and the pollination study (Fig. 2I), sample sizes were two blocks each and analyses were not possible. In the pollination study, the plant, *Passiflora incarnata*, established in only two of four blocks where they were planted. For another plant species, *Phytolacca americana*, samples were gathered from three blocks and analysis was possible, yielding $t = 1.88$ and $P = 0.100$ (Fig. 2G). The importance of low sample size can be illustrated by a power analysis for *P. americana*. Despite the large corridor effect on movement (over five times as many seeds were recovered in connected than in unconnected patches), power analysis indicated that we would have needed a sample size of four to detect a statistically significant difference.

DISCUSSION

Using the results of our study on 10 taxa, we can answer two questions raised in the *Introduction* about corridor effects on movement. In answer to our first question, our results demonstrate that corridors in our experimental landscapes consistently direct the movement of diverse taxa. These results include the first demonstration that corridors affect interpatch movements of plants. Interestingly, corridor effects on movement were detected even without controlling for other known important factors that are not correlated with the presence of a corridor but that influence movement, such as abundances of butterfly host and nectar plants (Haddad 1999*a*). Even though other sources of environmental variation in our experiment may have influenced movement, the response to corridors overrode such effects.

In answer to our second question, the effects of corridors on movement direction were uniformly large. For all 10 species, at least 68% more individuals moved to connected than to unconnected patches. The low probability that 10 species would show the same positive responses to corridors by chance alone (calculated as 0.5^9, i.e., <0.01) led us to conclude that the corridor effect is generally significant. This effect was statistically significant for five species, not significant for one species, and inconclusive (because of low replication) for four species. The species that we studied spanned a large range of body sizes, locomotory modes, and trophic levels. Thus, our results suggest

that corridors influence the movement directions in these landscapes of many species with very dissimilar features.

Other previously published results from our experiment allow us to answer our third question for a subset of the taxa: for which taxa do corridors increase emigration? In those studies (Bowne et al. 1999, Haddad 1999*a*, Danielson and Hubbard 2000), corridors did not influence the number of emigrants of any species for which this response was measured, including butterflies (*Junonia coenia* and *Euptoieta claudia*) and small mammals (*Peromyscus polionotus* and *Sigmodon hispidus*). Although there are species in other landscapes that are highly restricted in habitat use and that would never leave a patch through unsuitable habitat (or would be unsuccessful emigrants if they did), our results suggest that emigration of our study species is not determined by landscape pattern.

Given the consistent patterns across most of the species that we studied, we are tempted to draw more general conclusions about the effects of corridors on movement. However, landscape connectivity is an attribute both of the species and of the landscape in which that species resides (Weins and Milne 1989, Beier and Noss 1998, Tischendorf and Fahrig 2000). Our study species, which comprise a diverse set of natural-history strategies and evolutionarily independent groups, are not representative of all of the species that occur in our landscape. In fact, we biased our selection of species toward those that we thought were likely to respond to corridors based on their habitat preferences and, in some cases, on their movement abilities relative to other species in their respective taxa. Our experiment was designed to exploit the strong contrast between openings (patches and corridors) and pine forest (the matrix). Thus, our choice of species within these landscapes probably did impact our consistent finding of corridor effects on movement direction.

In addition, the life histories and movement behaviors of individual species influence their movement through corridors. The birds that dispersed seeds in our study (primarily Yellow-rumped Warblers, *Dendroica coronata*, and Eastern Bluebirds, *Sialia sialis*) are large and highly vagile relative to the other species in our study, and frequently move across large distances regardless of corridors. However, the dispersal patterns of bird-dispersed seeds are not determined by bird dispersal ability alone. Importantly, gut retention times are typically <1 h in small (<30 g) frugivorous birds (Levey and del Rio 1999). Within this time frame, corridors appear to influence the local foraging behavior of birds, thus determining the dispersal of seeds. Likewise, large bees are able to move many kilometers between nests and foraging sites (Cunningham 2000). However, they may use corridors during short-term foraging, which will impact the plants that they pollinate. Finally, although there was a remarkably consistent and large corridor effect on movement direction across the

species that we studied, there is no obvious pattern in the relationship between taxa and the size of the corridor effect (Fig. 3).

With regard to species-specific responses to corridors, it is instructive to ask why one species, *S. hispidus*, did not show a corridor response. We propose two explanations. First, we expected species that preferred second-growth habitat to disperse through corridors of the same habitat type. *S. hispidus* is much more abundant in open habitats than in forest (Golley et al. 1965). In addition to habitat preference, however, movement behaviors, including aversion to movement through unsuitable habitat, also influence responses to corridors. Such behavioral responses were measured in another group of published studies from our experiment. The movement paths of individuals were mapped by radio-tracking *Sigmodon hispidus* (Bowne et al. 1999) and by visually tracking three butterfly species (Haddad 1999*b*). *S. hispidus* preferentially emigrated from patches through corridors (Bowne et al. 1999), although, as previously demonstrated, this behavior did not affect their ultimate destination. For butterflies, two of three species (*Phoebis sennae* and *Eurema nicippe*) were found to preferentially leave patches through corridors and to use corridors for movement (Haddad 1999*b*), whereas a third (*Papilio troilus*) showed no preference for, or use of, corridors. A second explanation for the lack of corridor use in *S. hispidus* relates to the observation that it is the largest species considered in this study, with an average home range size of 0.247 ha (Cameron and Spencer 1985). The scale of our landscape manipulations may have been too small for *S. hispidus* to have perceived corridors as a significant component of habitat heterogeneity. In short, corridor effects depend on corridor size relative to the scale at which a species perceives the landscape.

After considering the caveats associated with the types of species and landscape used in our study, we feel that our results support more general conclusions about the effects of corridors. In total, including results from this and previous studies in our experimental landscapes (Haddad 1999*b*, Haddad and Baum 1999), there were only two species of 13 (*Sigmodon hispidus* and *Papilio troilus*) for which corridors did not direct movement. All of the species in this study showed a positive effect of corridors on movement (Fig. 3), and none showed a negative response to corridors. Another result that has been consistently supported in our work, for a smaller set of species, is that although corridors do direct emigrants, they do not increase the numbers of emigrants. In sum, there appear to be consistent responses across a range of habitat-restricted taxa that may support the use of corridors in landscape planning.

Preferential movement through corridors is necessary, but not sufficient, for corridors to rescue otherwise isolated patches from extinction and to increase gene flow. In our study, we lack data on population viability and genetic diversity, and our dramatic increases in movement to connected patches strongly suggest, but do not demonstrate, the value of corridors. In the one group for which we have population data, butterfly species that used corridors for movement also had higher population sizes in connected than in unconnected patches (Haddad and Baum 1999). However, all species in our study make movements across the matrix (although not recorded in our capture–recapture studies, *Xylocopa virginica* has been observed by one of us (T. Spira) to move through the matrix). Such movements between isolated patches might be sufficient to rescue populations and maintain genetic diversity (Simberloff et al. 1992, Beier and Noss 1998). More work is needed to understand how differences in movement impact plant and animal populations.

We have shown that corridors are effective at directing the dispersal of diverse taxa. These taxa are important in a broad range of community functions, including herbivory, pollination, seed predation, and seed dispersal. Given the breadth of species that respond to corridors, our results suggest that corridors may have broader, community-wide impacts. This possibility is typically overlooked by studies of single species. Taken together, our results suggest that corridors have the potential to be valuable tools for landscape-scale conservation of diverse taxa and the biological processes that they direct.

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