LOW-QUALITY HABITAT CORRIDORS AS MOVEMENT CONDUITS FOR TWO BUTTERFLY SPECIES

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Abstract.   Corridors are a primary conservation tool to increase connectivity, promote individual movement, and increase gene flow among populations in fragmented landscapes. The establishment of effective conservation corridors will depend on constructing or preserving connecting habitat that attracts dispersing individuals. Yet, it remains unclear whether corridors must necessarily be composed of high-quality habitat to be effective and promote dispersal and gene flow. We address this issue with two mobile, open-habitat butterfly species, *Junonia coenia* Hübner and *Euptoieta claudia* Cramer. Using experimental landscapes created explicitly to examine the effects of corridors on dispersal rates, we show that open-habitat corridors can serve as dispersal conduits even when corridors do not support resident butterfly populations. Both butterfly species were rare near forest edges and equally rare in narrow corridors, yet both species dispersed more often between patches connected by these corridors than between isolated patches. At least for species that can traverse corridors within a generation, corridor habitat may be lower in quality than larger patches and still increase dispersal and gene flow. For these species, abundance surveys may not accurately represent the conservation value of corridors.

Key words: butterfly; connectivity; conservation; corridor; dispersal; Euptoieta claudia; *fragmentation; gene flow; habitat quality;* Junonia coenia; *landscape experiment; small populations.*

INTRODUCTION

Corridors are among the most promising landscape management strategies for conservation of biodiversity (Mann and Plummer 1995). These relatively long, thin strips of habitat connect otherwise isolated areas in fragmented landscapes. Corridors are intended to function by increasing movement rates of individuals and genes between otherwise isolated habitat areas. This provides the means for colonists to rescue small populations from extinction (Brown and Kodric-Brown 1977), increases gene flow, and reduces inbreeding and genetic drift. In this way, corridors may reduce extinction risk for small, isolated populations. A number of studies have shown that corridors do increase movement rates between patches (Haas 1995, Sutcliffe and Thomas 1996, Beier and Noss 1998, Haddad 1999*a*, Tewksbury et al. 2002, Haddad et al. 2003) and increase gene flow (Aars and Ims 1999, Hale et al. 2001, Mech and Hallett 2001), supporting the intended function of corridors.

Another potential benefit of corridors is that they may also serve as habitat. There are many benefits of increasing the area of habitat dedicated to conservation. Most importantly, larger habitat areas typically support larger populations that are less prone to extinction (Rosenzweig 1995). Numerous studies have supported the role of corridors as habitat, showing that animals are more abundant in corridors than in unsuitable matrix habitat (e.g., Machtans et al. 1996, Laurance and Laurance 1999, Perault and Lomolino 2000, Mönkkönen and Mutanen 2003).

To function as intended in fragmented landscapes, corridors must increase the exchange of individuals and genes between patches. If not, then other areas of habitat besides corridors that may or may not enhance connectivity would equally satisfy conservation needs. Yet, corridors need not necessarily provide high-quality habitat to be effective at promoting movement or gene flow. This is especially true if establishment and reproduction are not required within a corridor for plants or animals to traverse it. In fact, corridors may inherently provide low-quality habitat for many animals and plants, because they are typically narrow strips with high edge-to-area ratios. Edges may create many costs for dispersing organisms, including increased predation or suboptimal abiotic conditions (e.g., more or less light; Sisk and Haddad 2002). In addition, if edges do not direct dispersers or retain individuals within a population (Kuussaari et al. 1996), there is high likelihood that dispersers may be lost from corridors to the unsuitable matrix. Several studies have found that lower quality corridors actually promote higher dispersal rates than higher quality corridors because of compensatory movement through low-quality habitats (Andreassen et al. 1996, Rosenberg et al. 1998, Gilliam and Fraser 2001).

In this paper, we examine the role of corridors as movement conduits and as habitat for two butterfly
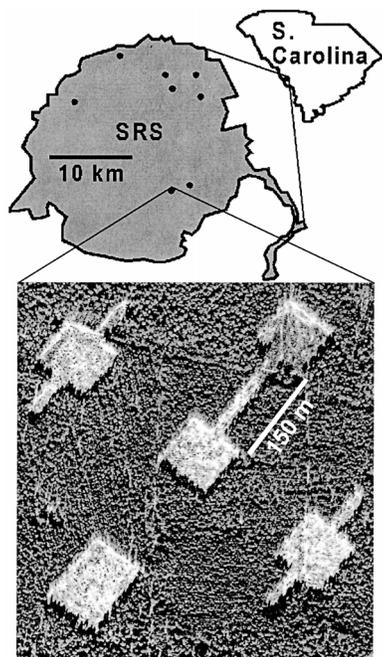
FIG. 1. Corridor experiment at the Savannah River Site (SRS), South Carolina, USA. Eight experimental blocks each had five patches. The center patch was 1 ha and was connected to one peripheral patch by a corridor 150 m long and 25 m wide. The other peripheral patches were unconnected and were all the area of the center patch plus a corridor (total area = 1.375 ha). Unconnected patches were either rectangular or winged, with corridor-shaped extensions that did not connect to any other patch.

species, *Junonia coenia* Hübner and *Euptoieta claudia* Cramer. These butterflies have been shown in previous experiments to move preferentially between connected patches (Haddad 1999a). We examine whether the corridors that increase butterfly movement rates are suitable habitat for these butterflies. In doing so, we examine factors that influence corridor suitability for the butterflies, including availability of host and nectar food resources.

Methods

Study site and experiment

We conducted our experiment at the Savannah River Site, a National Environmental Research Park near Aiken, South Carolina, USA. In eight large (50-ha) areas of pine plantation forest composed of loblolly (*Pinus taeda*) and longleaf pine (*P. elliotii*), we created replicate experimental blocks, each consisting of five experimental patches. In every block, four peripheral patches were 150 m from one central patch (Fig. 1). One peripheral patch was connected to the center patch (area = 1 ha) by a 25 m wide corridor. The unconnected patches varied in shape, but each was equal in area to the center patch plus a corridor (area = 1.375 ha). Unless otherwise stated in this paper, we consider patch connectivity as a factor in analysis, but not patch shape.

In a previous study, we found no effect of patch shape on butterfly movement rates (Tewksbury et al. 2002). Open patches and corridors were created by harvesting pine forest and then by burning. Low-intensity logging was used to minimize logging impacts and to preserve closed-canopy pine forest in the matrix. To create homogeneous patches and corridors, all trees were removed from the patches. A forested buffer was preserved around each experimental block, separating patches from other clearings (roads, utility right-of-ways, clearcuts) by at least 150 m. Within the constraints of the orientation of pine forest stands, corridor direction was determined at random.

Study species

The two study species, *Junonia coenia* (common buckeye) and *Euptoieta claudia* (variegated fritillary) are both mobile and move more frequently between connected than unconnected patches (Haddad 1999a, 2000, Tewksbury et al. 2002, Haddad et al. 2003). In addition, both butterflies reach higher population densities in connected patches (Haddad and Baum 1999). Both butterfly species use a variety of early-successional host plants, including *Linaria canadensis*, *Plantago* sp., and *Gerardia purpurea* for *J. coenia*, and *Passiflora incarnata* and possibly *Viola* sp. for *E. claudia*. During our early/midsummer study periods, host plants were *L. canadensis* and *P. incarnata*. Both butterflies are generalists with respect to nectar resources, although both species showed a preference for *Asclepias tuberosa*, and *J. coenia* also frequently nectared at *L. canadensis*.

Butterfly and plant sampling

Butterfly movements and population densities were measured through capture–recapture studies in June and July of 2000 and in May and June of 2001. Each patch was surveyed daily from Monday through Friday during the entire study period (23 times in 2000 and 39 times in 2001). The entire area of every patch and corridor was surveyed by dividing areas into 12.5 m wide transects. The length of each transect was surveyed at a rate of 1 min/25 m until the entire patch was covered. Attempts were made to capture all butterflies observed during a survey. If captured, butterflies were marked on the underside of the wing in a binary code that assigned each butterfly a unique number, and the number and location of each butterfly were recorded. Each day, the order in which patches were surveyed was randomized and field technicians were rotated through the experimental blocks to prevent observer bias. Butterfly movement rates were measured as the proportion of butterflies marked in the center patch that moved to each of the four peripheral patches within a block. We used the number of unique, daily butterfly observations to create an index of daily butterfly density. Butterfly densities were estimated as the number of individuals observed per day per hectare in

each patch or landscape type (i.e., corridor) through the flight season. Other estimates of density, such as the total number observed and the total number marked, produced qualitative results similar to the analyses presented here. We used an index of population size rather than an estimate generated from mark–recapture statistics because we did not allocate equal effort to forest habitat and because we divided data within patches for further tests.

To estimate butterfly densities in the forest matrix, we conducted surveys for five consecutive days in 2001 in areas equal to the area of the corridor between the center patch and each of the three unconnected patches. These surveys were conducted during the peak of butterfly activity to estimate the maximum density of the study species in forest. We estimated butterfly densities in the forest by averaging the densities from each of the five surveys in the forest. Because densely planted pine forests shade the understory and create a thick litter layer of pine straw on the forest floor, there are virtually no host or nectar resources for these butterfly species in the forest.

Once during each field season, we measured the abundance of important host and nectar plants in each patch and corridor. In 2000 and 2001, we counted the number of *Linaria canadensis* by walking the same transects that were walked for butterflies and counting each *L. canadensis* stem within all 12.5×12.5 m areas in each patch and corridor. We set a two-minute time limit for counting in each area. Unlike *L. canadensis*, *Asclepias tuberosa* and *Passiflora incarnata* are perennials, and we measured their densities in one year for each species. In 2000, the number and location of *A. tuberosa* flowering stems were recorded during every butterfly survey. From these data, we determined the total number of flowers per patch. In 2001, the area occupied by *P. incarnata*, a vine, was determined during one butterfly survey at the peak of the flight. The area covered by *P. incarnata* was measured in each 12.5×12.5 m area within each patch, and then was summed to determine the total area of coverage within a patch.

Analysis

To determine the effects of corridors on interpatch movement rates, we estimated the proportion of marked individuals that moved from the center patch to a connected or unconnected peripheral patch. We used a randomized-block design, with each treatment (connected or unconnected) contained within each of eight experimental blocks, and with year treated as a repeated measure. Because of previous results supporting positive corridor effects on movement for these species (Haddad 1999*a*, Tewksbury et al. 2002), we tested a directional hypothesis and used a one-tailed test for this response variable only. To assess butterfly population responses to habitat types, we created an index of butterfly density by averaging counts from each day

across the field season, and then dividing by the area of the habitat type (center patch, corridor, and forest segment) for each year. We then tested for differences in densities between habitats using a randomized-block design, with each block containing each of the two (in 2000) or three (in 2001) habitat types. We did not survey forested areas in 2000, so only patches and corridors were included in the model in that year. Because less effort was allocated to forest surveys (only 5 days), we conducted a separate analysis including only those days from all habitats. Although abundances in the patches were relatively higher during this part of the adult butterfly flight period, the analyses yielded qualitatively identical results and are not presented.

Past studies have shown that both of the butterfly species in this study avoid edges (Haddad and Baum 1999), potentially reducing the efficacy of our connecting corridors that were only 25 m wide. We examined the effects of edges on butterflies by treating butterfly density (estimated as previously described in equal distance intervals from the forest edge in the center patches) as the dependent variable, and by treating block and distance from the edge as independent variables. Using a randomized-block design, we also analyzed butterfly densities at center–patch edges, corridors, and (in 2001) forest to determine whether edge effects alone could explain population responses to corridors.

To further examine the effects of habitat quality on butterfly movements and abundances, we included densities of important butterfly host and nectar resources as covariates in analyses of habitat and edge effects. We examined correlations between plant and landscape attributes to determine whether to include all factors in the analysis, and we considered only positive relationships between plant and butterfly densities because we only considered plants that butterflies used as resources. In addition, we analyzed plant responses to habitat types and edges by including them as dependent variables in the same analyses as described previously. To homogenize variances across treatments, we used square-root transformations on butterfly and plant count data.

Results

As has been reported previously (Haddad 1999*a*, Tewksbury et al. 2002), both *Junonia coenia* and *Euptoieta claudia* moved more frequently between connected than unconnected patches. Both species were about 2–3 times more likely to move between connected patches, even after we controlled for the effects of patch area on movement rates in our experimental design (Fig. 2).

The butterflies that we studied were more likely to move between connected patches, despite the fact that corridors supported butterfly densities that were low and statistically indistinguishable from densities in forest (Fig. 3). *J. coenia* was six times more abundant in
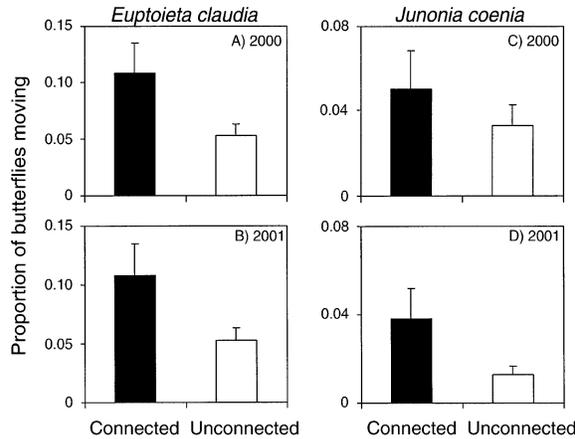
FIG. 2. Proportion (mean + 1 SE) of (A, B) *Euptoieta claudia* and (C, D) *Junonia coenia* that moved from the center patch to either connected or unconnected patches in 2000 and 2001, as estimated from capture–recapture studies (for *E. claudia*, df = 8,23, $F_{con} = 7.46$, $P_{con} = 0.005$; for *J. coenia*, df = 8,23, $F_{block} = 4.67$, $P_{block} = 0.002$; $F_{con} = 4.82$, $P_{con} = 0.02$ [subscript "con" represents connectivity]). The effects of year were not significant in either model.

patches than in corridors in 2000, and four times more abundant in patches in 2001. *E. claudia* was four times more abundant in patches than in corridors in 2000, and three times more abundant in patches in 2001. Despite trends toward higher butterfly abundances in corridors than in forest (Fig. 3), densities in corridors and forest did not differ statistically for *J. coenia* and *E. claudia* (Tukey comparison of means). In no case was block or plant abundance significant at the $P = 0.05$ level.

Proximity to forested edges may have affected habitat quality for both butterfly species. Both showed significant, positive relationships between distance from the forest edge and density. *J. coenia* density at the patch center was 13 times the density at the edge of patches in 2000, and 22 times the density of patch edges in 2001 (for 2000, $F_{9,22} = 7.34$, $P = 0.001$, $F_{block} = 2.08$, $P_{block} = 0.09$, $F_{edge} = 49.06$, $P_{edge} = 0.001$; *A. tuberosa* was dropped from the analysis because of a significant correlation with *L. canadensis* densities; for 2001, $F_{9,22} = 9.28$, $P = 0.001$, $F_{block} = 2.45$, $P_{block} = 0.05$, $F_{edge} = 61.62$, $P_{edge} = 0.001$). *E. claudia* density at the patch center was 5–7 times the density at the edge of patches (for 2000, $F_{9,22} = 5.73$, $P = 0.001$, $F_{block} = 4.31$, $P_{block} = 0.004$, $F_{edge} = 20.45$, $P_{edge} = 0.001$; for 2001, $F_{10,21} = 5.65$, $P = 0.001$, $F_{block} = 3.74$, $P_{block} = 0.009$, $F_{edge} = 28.14$, $P_{edge} = 0.001$). Again, after including edge effects, there were no significant effects of plant abundances.

To test whether edge effects explained corridor quality for the butterflies, we conducted a separate analysis comparing butterfly densities in the center patch, but only within 12.5 m of the edge, to densities in corridors and forest. In 2000, butterfly densities were signifi-

cantly higher at the patch edge than in the corridor for *Junonia coenia* ($F_{8,7} = 4.31$, $P = 0.03$, $F_{hab} = 7.98$, $P_{hab} = 0.03$; subscript "hab" is habitat), but not for *Euptoieta claudia*. For both species in 2001, butterfly densities were not different between patch edges and corridors or between forest and corridors; however, densities were higher at patch edges than in forest (Tukey comparison of mean; for *J. coenia*, $F_{9,14} = 1.69$, $P = 0.18$, $F_{hab} = 5.26$, $P_{hab} = 0.02$; for *E. claudia*, $F_{9,14} = 1.18$, $P = 0.38$, $F_{hab} = 3.89$, $P_{hab} = 0.05$). Considering the analyses of both species in both years, edge effects explain most of the low densities in corridors.

To verify that the low butterfly densities in corridors were caused by the linear nature of the habitat and proximity to habitat edge, we conducted a separate analysis comparing butterfly densities between the core area of "winged" patches (the 1-ha squares with the same shapes as the center patches) and the "wings," or corridor-shaped extensions that do not connect to any other patch (see Fig. 1). The results were qualitatively identical to the comparisons of patches and corridors. Consistent with results from connected patches, densities in patches were between three (for 2000, $F_{8,7} = 5.98$, $P = 0.01$, $F_{hab} = 23.70$, $P_{hab} = 0.002$) and nine (for 2001, $F_{8,7} = 7.21$, $P = 0.009$, $F_{hab} =$
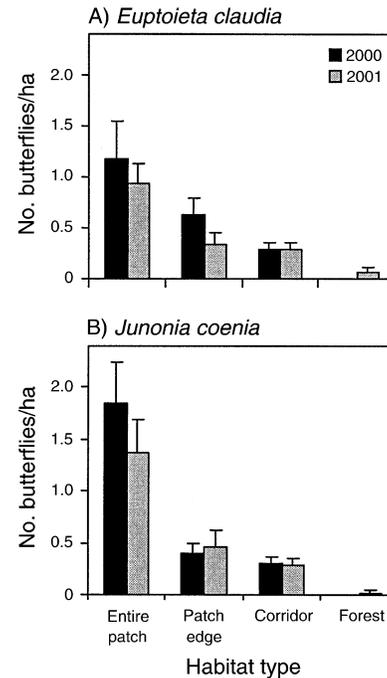

FIG. 3. Density per hectare (mean + 1 SE) of (A) *Euptoieta claudia* and (B) *Junonia coenia* in center patches, center patch edges only, corridors, and forest in 2000 and 2001. Results of habitat comparison (subscript "hab" is habitat): for *E. claudia* in 2000, $F_{8,7} = 2.09$, $P = 0.17$, $F_{hab} = 7.98$, $P_{hab} = 0.03$; for *E. claudia* in 2001, $F_{9,14} = 3.64$, $P = 0.02$, $F_{hab} = 14.33$, $P_{hab} = 0.001$; for *J. coenia* in 2000, $F_{8,7} = 7.86$, $P = 0.007$, $F_{hab} = 45.84$, $P_{hab} = 0.001$; for *J. coenia* in 2001, $F_{9,14} = 5.56$, $P = 0.002$, $F_{hab} = 21.20$, $P_{hab} = 0.001$.
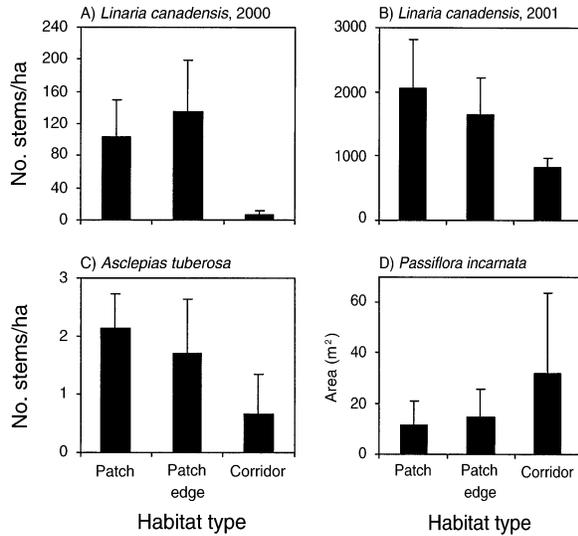
Fig. 4. Density (mean + 1 SE) of (A, B) *Linaria canadensis* stems in 2000 and 2001 and (C) *Asclepias tuberosa* flowering stems; and (D) cover (mean + 1 SE) of *Passiflora incarnata* in center patches, center patch edges only, and corridors in 2000 and 2001. Habitat comparisons: for *L. canadensis* in 2000, $F_{8,7} = 2.73$, $P = 0.10$, $F_{hab} = 8.27$, $P_{hab} = 0.02$; for *A. tuberosa* in 2000, $F_{8,7} = 4.31$, $P = 0.03$, $F_{hab} = 9.72$, $P_{hab} = 0.02$. There were no significant differences for *P. incarnata*.

48.71, $P_{hab} = 0.001$) times higher in patches than in wings for *J. coenia*, and about five times higher in patches than in wings for *E. claudia* (for 2000, $F_{8,7} = 4.63$, $P = 0.03$, $F_{hab} = 11.68$, $P_{hab} = 0.01$; for 2001, $F_{8,7} = 6.03$, $P = 0.01$, $F_{hab} = 22.99$, $P_{hab} = 0.002$). In no case was block or the abundance of particular plant species significant at the $P = 0.05$ level.

Although host and nectar resources were not identified as significant variables in statistical models of butterfly densities, some host and nectar resources did differ in abundance among habitat types. *Linaria canadensis* was more abundant in patches than in corridors in 2000, but not 2001 (Fig. 4). *Asclepias tuberosa* was also more abundant in patches than in corridors. The density of *Passiflora incarnata* was not related to habitat type. None of the densities of plant species that we measured was significantly related to distance between the forest edge and patches (Fig. 5). In all cases, after controlling for plant abundances, the edge effect on butterfly densities was still significant.

DISCUSSION

We found that two mobile butterfly species were dramatically less common in corridors than in patches, but these corridors still function as movement conduits. Effects of corridors on movement rates are consistent with those in previous studies on these species (Haddad 1999a, Tewksbury et al. 2002). Regardless of mechanism, corridors were low in quality for these butterflies. Here, we define corridor quality in terms of where adult

butterflies are found, although other corridor attributes, such as lower host and nectar resources and aversion of butterflies to edges, independently support the claim that corridors are low-quality habitat.

The most obvious causes of low habitat quality in corridors were the presence of habitat edges and, perhaps independently, the lower abundance of certain plant resources. Reduced densities of host and nectar plants may cause dispersing adults to pass through corridors without stopping. Although most plants that we measured were not rare in corridors, lower host plant densities there (with the exception of *Passiflora incarnata*) suggest that corridors may be low-quality habitat for larvae as well as adults. Unlike butterfly abundances, plant abundances did not respond significantly to habitat edges. Interestingly, food plant covariates were not usually significant in statistical models. It is possible that other plant resources that we did not measure, such as the abundances of host plants used in other seasons, influenced butterfly abundances. Our fieldwork, however, spanned multiple adult generations each year, and our choice of host and nectar resources to monitor was informed by the behavior of the butterflies. Thus we are reasonably certain that the host and nectar resources that we measured were appropriate indicators of resource abundance for the butterflies we studied.

Both butterfly species avoided forest edges independent of the distribution of host plants and nectar sources. Within our 25 m wide corridors, all areas were <12.5 m from an edge. The close correspondence between densities at patch edges and in corridors appears to explain the low butterfly density in corridors. A num-
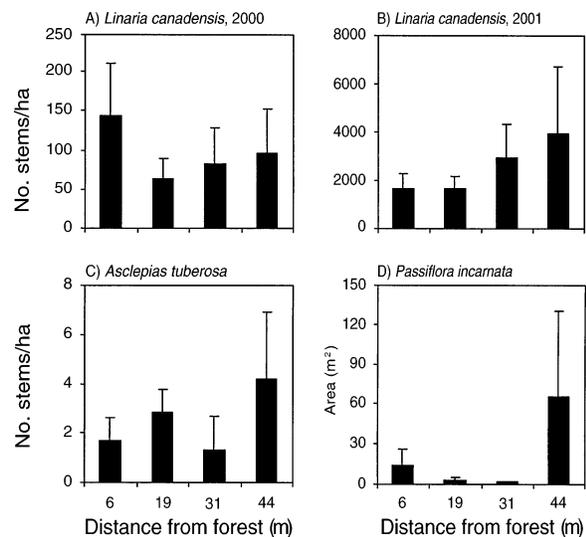

Fig. 5. Density (mean + 1 SE) of (A, B) *Linaria canadensis* stems in 2000 and 2001 and (C) *Asclepias tuberosa* flowering stems; and (D) cover (mean + 1 SE) of *Passiflora incarnata* at different distances from the forest edge toward the patch center. Densities were estimated in center patches only.

ber of mechanisms, working in concert or in isolation, could lead to edge avoidance. First, butterflies could be responding to variation in the density of egg, larval, or adult predators. Many opportunistic avian predators follow the edges in their movement within these patches (J. J. Tewksbury, *unpublished data*), potentially increasing the predation risk for adult butterflies near edges. A more complete understanding of the predators and parasites of eggs and larva is needed before we can address the potential edge effects on these life stages. Second, the quality of both larval and adult food resources may vary consistently as a function of distance from the forest edge, because nectar production and plant growth rates are both likely to be strongly influenced by temperature, moisture, and hours of direct sunlight, all of which vary predictably with distance from the forest edge (Sisk and Haddad 2002). Third, *Junonia coenia* has been shown to be ''pseudoterritorial'' (Scott 1975b), and optimal territories may be those that are surrounded by resources, and thus away from edges. Fourth, like many other butterfly species (Schultz 1998, Schultz and Crone 2001, Merckx et al. 2003, Schtickzelle and Baguette 2003), both species in this study tend to avoid crossing habitat boundaries, and these behaviors could lead to aggregation in the center of patches. We should note that the patterns we observed in patches and corridors could not be produced by shading from trees surrounding our openings. Butterflies avoided both southern (shady) and northern (sunny) edges. Corridors were oriented at random, which would affect their degree of shading. Finally, we varied the times of day when we visited each patch and corridor to account for within-day effects.

If corridors are low-quality habitat, then why do butterflies use them for dispersal? There are a number of possible answers. The most likely scenario is that the quality of the corridor is perceived to be higher than that of other surrounding habitat, thus directing dispersal. As long as the potential benefits of dispersal outweigh the costs, corridor habitat need only be higher quality than other possible dispersal routes. In addition, habitat structure itself may be a useful indicator of the availability of resources to these butterflies (Dennis et al. 2003). Their resources are commonly found in openings, so as long as butterfly movement is directed within openings or along edges, there is a high probability that they will encounter host or nectar resources (Haddad 1999b). Indeed, previous studies have demonstrated how population (Schtickzelle and Baguette 2003) and evolutionary (Merckx et al. 2003) effects of landscape structure can strengthen behavioral responses of butterflies to landscape boundaries. As with the butterflies evolving in agricultural landscapes discussed in Merckx et al. (2003), the species in our present study currently persist within landscapes dominated by hard edges, increasing the selection for strong behavioral responses to habitat boundaries.

In our study, habitat edges may serve contrasting roles in determining butterfly success: they have positive effects in directing dispersal, but negative effects on habitat quality. Edges themselves may reliably indicate boundaries between suitable and unsuitable habitat, thus directing the movement of edge-avoiding species. Yet, because forest edges modify the environment in their proximity, movement corridors such as the ones studied here may be substantially lower in quality than habitats used for breeding. To effectively evaluate the adaptive advantage of dispersing through corridors, research should focus on the relative mortality associated with dispersal along corridors vs. through or over forest (Schtickzelle and Baguette 2003). An important area of future research is the separation of corridor influence on animal emigration from corridor influence on migration mortality (Aars et al. 1999, Hudgens and Haddad 2003).

That low-quality corridors can serve as movement conduits and thereby reduce isolation highlights at least three conservation lessons. First, these results suggest that low-quality corridors may provide conservation benefit. Thus, restoring habitat structure within connecting habitats may enhance gene flow and dispersal, even if these areas do not support resident individuals. Other analyses of optimal corridor characteristics, such as corridor width, have assumed that corridors must be wide enough to permit interior species to avoid edges, or to be the width of an animal's home range (Harrison 1992). Our results suggest that corridors need not always take into account such attributes to be successful movement conduits. In several studies, animals were found to move more rapidly through poorer quality habitat than through higher quality habitat because of compensatory movement in that habitat (Andreassen et al. 1996, Rosenberg et al. 1998, Gilliam and Fraser 2001). Larger, high-quality corridors are preferable in conservation, because they provide a dual benefit as movement conduits and habitat. However, narrow corridors that may be low in quality, such as hedgerows (e.g., Dover and Sparks 2000), roadside habitats (Ries et al. 2001), and riparian or other buffers, may provide benefits by enhancing connectivity in fragmented landscapes.

A second lesson is that presence of species within a corridor is not sufficient to test their role as movement conduits. A number of studies have evaluated corridor effectiveness by the presence of animals or plants within them (Henderson et al. 1985, Lindenmayer et al. 1993, Machtans et al. 1996, Downes et al. 1997, Laurance and Laurance 1999, Perault and Lomolino 2000, Mönkkönen and Mutanen 2003). Species presence and abundance may provide a useful indicator of corridor utility in many instances, especially for sedentary species. Yet, in conservation, the role of corridors is to increase dispersal events that increase gene flow and rescue populations from extinction. Because the rate of dispersal that is needed to perform these functions

is extremely low, observation of individual organisms may be unlikely within functioning corridors. This study demonstrates how species may use corridors, even if they are encountered only rarely within these habitats in relation to other habitat types. In our study, although there was a trend toward higher abundances in corridors than in forest, densities were statistically indistinguishable between these habitats. Despite this finding, corridors were clearly preferred movement routes for both butterfly species: significantly more butterflies moved between patches connected by corridors than between patches separated by forest.

A third conservation lesson from this study is that low-quality corridors of the types discussed here will be most beneficial when organisms can move between patches via a corridor within one generation. These corridors were 150 m long, about the distance that the average butterfly of these species disperses in its adult lifetime (Scott 1975a, Haddad 1999a). However, these mobile butterflies can move much longer distances in short periods of time, potentially a kilometer or more in one to a few days (Haddad 1999a). Other more sedentary organisms in the same landscape, or the same organisms in other landscapes with more widely separated patches, would need to establish and reproduce within corridors so that their progeny could then colonize other patches. For organisms that must establish in the corridor, and for those organisms for which corridors do not direct dispersal, such as wind-dispersed plants or insects, corridor quality may have to be higher than than that of the patches themselves, so as to offset losses within corridors (Tilman et al. 1997). Two implications of these results are that (1) as interpatch distance increases, corridor quality will have to be higher; and (2) to support higher quality, longer corridors should also be wider to avoid the negative effects of edges (as documented by Beier [1995]).

This study provides some evidence that even low-quality corridors can yield conservation benefits by promoting movement between patches. This finding supports the retention and creation of many types of corridors within fragmented landscapes, including hedgerows, roadside buffers, or riparian buffers. It is important, however, not to fall into a minimalist mind-set in conservation management: the most effective corridors will be those that can serve as both movement conduits and as habitat. Such corridors, typically wider and longer than the ones discussed here, will be suitable habitat for the widest array of plants and animals that are in need of conservation in fragmented landscapes.

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