

AN EXPERIMENTAL TEST OF CORRIDOR EFFECTS ON BUTTERFLY DENSITIES

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Abstract. In a large-scale experiment, we found that three habitat-restricted butterfly species reached higher densities in patches connected by corridors than in similar, isolated patches. We conducted our study in 27 equal-sized (1.64-ha) patches that varied in whether or not they were connected to another patch by a corridor. Patches and corridors were open, early-successional habitat that contrasted strongly with the surrounding pine forest. Of four butterfly species studied, three open-habitat specialists (*Junonia coenia*, *Euptoieta claudia*, and *Phoebis sennae*) reached higher densities in patches connected by corridors than in isolated patches. A fourth species, *Papilio troilus*, showed no preference for open habitat or pine forest, and its density did not differ in connected or isolated patches. Although butterfly densities were often significantly, positively associated with densities of host plant or flower resources, plant densities did not confound corridor effects on butterfly densities.

Higher densities in patches connected by corridors may have been caused by three different factors. First, species with higher densities in connected patches also moved more frequently between connected patches, and higher movement rates may have helped to sustain higher population sizes. Second, species with higher densities in connected patches also had higher densities farther from the forest edge. Corridors increased the area of a patch that was farther from the forest edge, which increased the “effective area” of connected patches and may have increased butterfly densities. Third, corridors may have acted as “drift fences,” intercepting dispersers from the surrounding forest and directing them to connected patches. We could not determine the relative contribution of each factor, and it is possible that all three contributed to higher densities of habitat-restricted butterflies in patches connected by corridors.

Key words: butterfly; conservation; corridors; edge effects; habitat fragmentation; landscape experiment; patch colonization; population densities; population dynamics.

INTRODUCTION

The primary cause of species endangerment and extinction is the fragmentation and loss of native habitats (Wilcove et al. 1998). Even when suitable habitat exists, small fragments may be isolated and inaccessible to dispersing plants and animals. Corridors that connect habitat areas might increase movement rates of plants and animals into otherwise isolated fragments (Wilson and Willis 1975, Rosenberg et al. 1997). Thus, periodic population declines and local extinctions in habitat fragments might be offset by more frequent colonization via corridors (Brown and Kodric-Brown 1977, Fahrig and Merriam 1985). Although theory and intuition suggest that corridors should prevent population extinctions, few empirical studies demonstrate that corridors increase interpatch movement and that more fre-

quent interpatch movement causes higher population sizes in fragmented landscapes.

The prediction that patches connected by corridors have higher densities than isolated patches has been tested in several studies (MacClintock et al. 1977, Fahrig and Merriam 1985, Forney and Gilpin 1989, La Polla and Barrett 1993, Dunning et al. 1995, Norton et al. 1995). Higher densities caused by corridors are ascribed to higher rates of recolonization after local extinction, or to higher rates of immigration. Because of the intense effort needed to obtain data on movement between patches at large spatial scales, however, little empirical evidence supports the hypothesis that higher densities in these studies were caused by higher movement rates between connected patches. Separate studies have shown that corridors increase interpatch movement rates (Haas 1995, Machtans et al. 1996, Sutcliffe and Thomas 1996, Haddad 1999a), but these studies do not document the effects of higher interpatch movement on population sizes.

The hypothesis that higher densities in connected patches are caused by higher interpatch movement rates remains untested. Unfortunately, this hypothesis appears to have been generally accepted without thorough consideration of other ways in which corridors might

Manuscript received 22 December 1997; revised 8 July 1998; accepted 10 July 1998.

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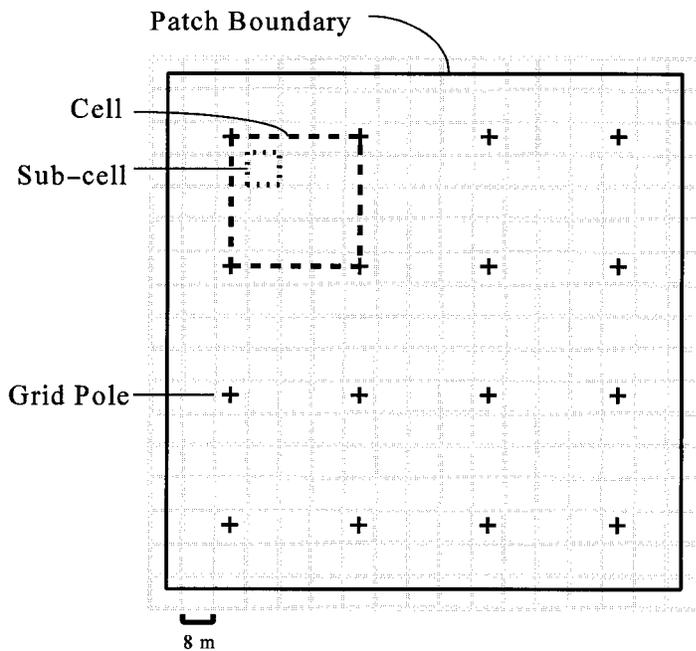


FIG. 1. Example of an experimental patch. The light gray grid indicates 8×8 m subcells used to identify butterfly locations. Large grid poles (+) were spaced at 32-m intervals.

cause higher population sizes. Higher interpatch movement rates through corridors would have a strong effect on population sizes in cases in which dispersal into isolated patches is extremely limited. However, in existing, small-scale studies of corridor effects on population sizes, animals often are not dispersal limited. Other changes to a landscape caused by corridors may also influence population sizes. In particular, a corridor increases patch area and changes the shape of a patch. These two factors have been shown to influence animal immigration and densities in numerous studies, but never in relation to corridors. Corridors alter the internal environment of a patch by increasing the area of the patch that is farther from the habitat edge. This could decrease densities of edge species, or increase densities of edge-avoiding species. Corridors also change the position and orientation of a patch in the context of the larger landscape (Anderson and Danielson 1997). For example, corridors may serve as "drift fences," intercepting dispersing individuals from the surrounding landscape and directing them toward patches connected by corridors. These additional effects of corridors may confound the interpretation that corridor effects on population sizes are caused by higher interpatch movement rates.

To test corridor effects on butterfly densities, we developed an experimental network of large patches and corridors (see Haddad 1999; Fig. 1). Within open habitat patches that were either isolated (i.e., surrounded by pine forest) or connected to another patch by an open-habitat corridor, we measured butterfly densities and evaluated the hypothesis that densities are higher in patches connected by corridors than in isolated patches. Because species may differ in their responses

to corridors, we studied four butterfly species that varied in their movement abilities and in their preferences for open habitat.

Using the results of this and other studies (Haddad 1997, 1999a, b), we evaluated five mechanisms that might change densities in patches connected by corridors. Changes in density may result from changes in: (1) interpatch movement rates (MacClintock et al. 1977); (2) the densities of essential host plants or flower resources (e.g., Kuussaari et al. 1996); (3) edge-related densities, i.e., corridors increase the area of a patch that is far from the edge, increasing the effective area of a patch for edge-avoiding species (Sisk et al. 1997); (4) immigration rates into a patch, i.e., a corridor may intercept more individuals dispersing through the larger landscape (Taylor 1987); or (5) emigration rates, which may be dependent on a patch's edge: area ratio (Kariva 1985).

METHODS

Study site

The experiment, conducted at the Savannah River Site, South Carolina, is described in detail in Haddad (1999a). Experimental patches and corridors were open habitats, created by harvesting pine trees in large stands of managed pine forest. Pine were grown at high densities, creating a strong contrast between forest that supported little understory development and early successional clearings that supported dense herbaceous vegetation. A total of 27 equal-sized (1.64-ha) square patches were created within five contiguous stands of pine forest, of which 19 were connected to other patches and eight were isolated (see Haddad 1999a; Fig. 1).

TABLE 1. Study species, their flight phenologies, and most common host plants and flower resources.

Butterfly species	Common name	Adult flight periods	Host plant(s)†	Nectar plant(s)†
<i>Junonia coenia</i>	buckeye	3 Aug–16 Sep 1995 23 Apr–3 Jun 1996 4 Jun–30 Jun 1996	<i>Linaria canadensis</i> , <i>Gerardia purpurea</i>	<i>L. canadensis</i> , <i>Rubus</i> sp., <i>G. purpurea</i>
<i>Euptoieta claudia</i>	variegated fritillary	21 May–16 Sep 1995 30 Apr–30 Jun 1996	<i>Passiflora incarnata</i>	<i>Asclepias tuberosa</i> , <i>Rubus</i> sp.
<i>Phoebis sennae</i>	cloudless sulphur	23 Jul–16 Sep 1995 4 Apr–28 Apr 1996	<i>Cassia</i> sp., <i>Crotolaria</i> sp.	<i>Cassia</i> sp., <i>Crotolaria</i> sp., <i>Gelsemium sempervirens</i>
<i>Papilio troilus</i>	spicebush swallowtail	21 May–16 Sep 1995 4 Apr–25 May 1996 26 May–30 Jun 1996	<i>Sassafras albidum</i>	<i>Carduus repandus</i> , <i>G. sempervirens</i>

† Not all host and nectar plants are available for all flight periods; these columns simply list species important to the butterflies.

Corridors were 32 m wide, or one-fourth the width of a patch. A grid system was established within each patch to enable rapid assessment of spatial locations. Sixteen meters from the edge of each patch, a 3 × 3 grid was demarcated using a laser transit (Fig. 1). Grid cells were 32 × 32 m and the corners were marked with 3.3 m tall polyvinyl chloride pipes. Within the larger grid, a second system of 8 × 8 m grid subcells allowed determination of spatial locations and estimates of butterfly densities at a resolution of 8-m intervals (Fig. 1).

Study species

We studied four butterfly species (Table 1) that varied in movement ability and habitat preference. *Junonia coenia* (Lepidoptera: Nymphalidae) and *Euptoieta claudia* (Lepidoptera: Nymphalidae), both open-habitat species, were the least vagile (Scott 1975a, b), and typically remained within an experimental patch for several days (Haddad 1999a). *Phoebis sennae* (Lepidoptera: Pieridae) and *Papilio troilus* (Lepidoptera: Papilionidae) were more vagile, and were likely to leave the patch within minutes after being encountered. *P. sennae* strongly preferred open habitats, whereas *P. troilus* showed no habitat preference (Haddad 1999b). All of the study species were able to rapidly colonize newly created experimental patches. Because the patches, corridors, and surrounding forests were burned, we assumed that butterflies colonized patches from outside the experiment after the patches were created.

Butterfly surveys

Data were collected from May to September 1995 and April to June 1996. In both years, surveys covered the entire patch, were conducted between hours 1000 and 1700, and were suspended during rain. However, census techniques differed between years. In 1995, each survey consisted of 5-min observations in each of the nine cells within a patch (Fig. 1). This method assumed detection of all butterflies within 16 m, a distance that we realized was too large to encounter all

Junonia coenia. A transect approach was implemented in 1996 that assumed an 8-m detection distance. Patches were divided into eight 128 m long transects, each separated by 16 m. During a survey, we walked each transect in 6 min. In both years, observation time excluded time spent observing and marking butterflies and recording data. In each year, data were collected consistently among patches, permitting valid analyses of corridor effects on butterfly densities. However, differences in 1995 and 1996 survey methods prevented comparisons between years.

Locations of individual butterflies were recorded at the resolution of a patch subcell (Fig. 1). To avoid double counting, we captured individual *Junonia coenia* and *Euptoieta claudia* and marked them with a unique identification code (Ehrlich and Davidson 1960, Haddad 1999a). Double-counting was not a problem with *Papilio troilus* and *Phoebis sennae*. These species were highly mobile and were usually followed until they left the patch. To obtain an unbiased estimate of spatial location for *P. troilus* and *P. sennae*, we recorded the location where the butterfly was first encountered. Because an equal amount of time was spent observing butterflies in each area of a patch, we assumed that individuals were first encountered in proportion to their density in any given area within a patch. Only 20 patches were surveyed in 1995 (10 patches for three consecutive days, followed by the other 10 patches for three consecutive days). In 1996, all patches were surveyed once before any patch was surveyed a second time; on average, 23 surveys were completed each day.

Vegetation surveys

Vegetation surveys for specific host plants and flowers (used as nectar resources by adult butterflies) were conducted several times each year. No butterfly species used more than two species or genera as larval host plants (Table 1). All were generalists with respect to nectar resources; however, each exhibited a preference for certain flowers. Data were collected on the abundances of all larval host plants and of the most im-

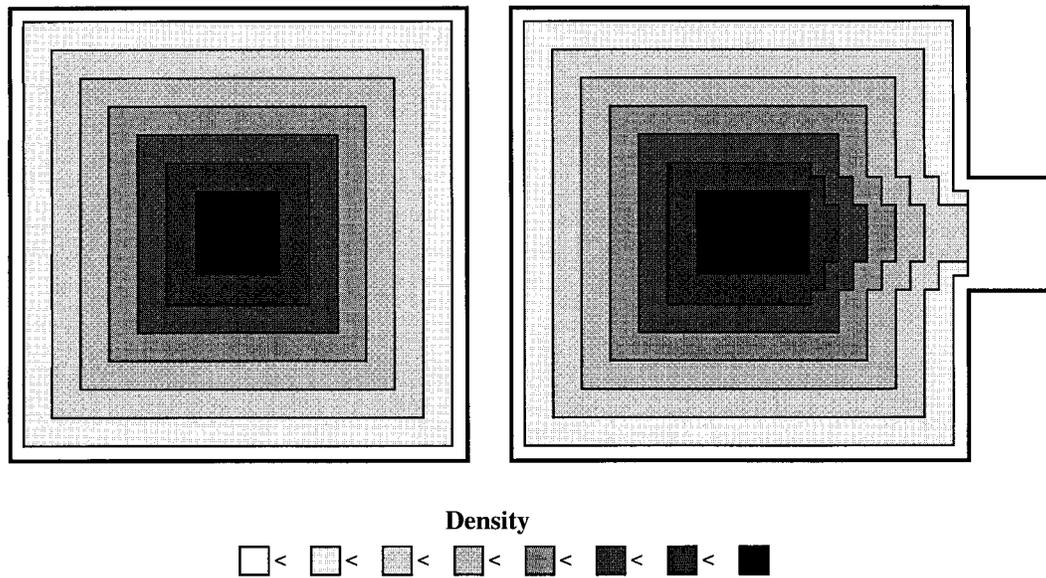


FIG. 2. Density contours in relation to the forest edge. In this example, density increases with distance from the edge to the center of a patch, a relationship similar to the one found for three open-habitat species in this study. A corridor changes the edge effects on density, as well as the distribution of densities within a patch. When integrated over the entire patch, densities are higher in the connected patch.

portant flowering plants for each butterfly species (Table 1).

For most plant species, the quantity of host plants or flowers was estimated on a log scale. Within each cell or subcell, the number of plants or flowers was recorded as: 0, 0 plants or flowers; 1, 1–10; 2, 10–100; and 3, >100 plants or flowers. In September 1995, each patch was surveyed for *Cassia* sp., *Crotolaria* sp., and *Gerardia purpurea* (see Table 1 for butterfly–plant associations), and data were recorded within each cell. In March 1996, each patch was surveyed for *Gelsemium sempervirens* flowers and data were recorded within each subcell. In May 1996, each patch was surveyed for *Linaria canadensis* and for *Rubus* sp. flowers, and data were recorded within each subcell.

For two particularly important flowers, *Asclepias tuberosa* and *Carduus repandus*, flower locations were recorded to the nearest subcell during each butterfly survey. Finally, the density of *Sassafras albidum* was measured monthly in June–August 1995 and in April and July 1996. The abundance of *Passiflora incarnatum* was manipulated as part of another study and was not measured here.

Analysis

The response variables used in statistical analyses were counts of each butterfly species within each patch at 8-m intervals from the forest edge (Fig. 1). The response variable was weighted by the area of the 8-m interval and the number of surveys per patch. Independent variables included a class variable that indicated the presence or absence of a connecting corridor, a class variable that indicated the experimental region

(one of five forest stands that contained patches), distance from the forest edge (0–56 m in 8-m intervals), and abundances of essential plant resources.

Because count data followed a Poisson distribution, we analyzed our data with Poisson regression (SAS Institute 1996). The significance of each variable was evaluated with a chi-square test. The Poisson mean was characterized by the following equation:

$$\lambda_i = E(Y_i) = t^*A_i^*\exp(\beta_0 + \beta_1x_1 + \dots + \beta_px_p)$$

where Y_i denotes the number of butterflies observed after t surveys in one of the 8-m intervals within a patch of area A_i , (x_1, x_2, \dots, x_p) were model variables, $(\beta_0, \beta_1, \dots, \beta_p)$ were estimated constants for those variables, and $(t^*A_i^*)$ was a scaling factor, which weighted the counts by the number of surveys and the area surveyed. An expanded model (i.e., one with additional independent variables) was accepted over a reduced model when the likelihood ratio statistic ($=2\{\log \text{likelihood of expanded model} - \log \text{likelihood of reduced model}\}$) was greater than $\chi_{0.05}^2$ with the degrees of freedom equal to the number of dropped variables.

Using empirical estimates of butterfly densities in connected and isolated patches, we tested the hypothesis that higher densities could be attributed to the effects of edges on patch quality for each butterfly species. The potential effects of edges on butterfly densities are diagrammed in Fig. 2. In the example, higher densities at greater distances from the forest edge indicate an edge-avoiding species (i.e., one that prefers habitat near the center of the patch). We predicted densities in connected patches by applying the Effective Area Model (Sisk et al. 1997) and using empirical data

TABLE 2. Type III likelihood ratio statistics for all significant variables retained in best-fit Poisson regressions of butterfly density for each adult flight period (SAS Institute 1996). Nonsignificant (NS) variables were not retained in the final model.

Species	Flight†	No. individuals	Forest region		Corridor		Distance to edge		Plant density	
			χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
<i>Junonia coenia</i>	1995	333	61.50	0.001	...	NS	165.47	0.001	96.65‡	0.001
	1996a	2928	45.59	0.001	4.28	0.04	403.24	0.001	86.95§	0.001
	1996b	2469	182.17	0.001	12.01	0.001	255.25	0.001		
<i>Euptoieta claudia</i>	1995	190	...	NS	...	NS	194.44	0.001		
	1996	333	54.75	0.001	11.62	0.001	255.25	0.001	8.15	0.004
<i>Phoebis sennae</i>	1995	1090	69.25	0.001	6.07	0.01	102.49	0.001	...¶	NS
	1996	103	21.78	0.001	...	NS	...	NS	...#	NS
<i>Papilio troilus</i>	1995	633	11.60	0.009	...	NS	97.22	0.001	11.24††	0.001
	1996a	680	12.41	0.01	...	NS	33.60	0.001	...#	NS
	1996b	274	27.83	0.001	...	NS	6.98	0.008	80.82††	0.001

Notes: Ellipses indicate that data were not included in the final model because they were not significant. Blank cells indicate that no data were collected.

† a, first flight period; b, second flight period.

‡ *Gerardia purpurea*.

§ *Linaria canadensis* (density > 10 plants/cell).

|| *Rubus* sp.

¶ *Cassia* sp. and *Crotolaria* sp.

Gelsemium sempervirens.

†† *Carduus repandus*.

from isolated patches. This was done by multiplying the area of each 8-m interval in a connected patch (as shown in Fig. 2) by densities estimated for that interval in an isolated patch. We summed the estimates from each interval to obtain a density estimate for the entire connected patch. Edge effects would explain the entire effect of corridors on densities if the estimate were to equal actual densities in connected patches. We predicted the influence of edge effects on butterfly densities for each flight period of each butterfly species that had higher densities in patches connected by corridors.

We also analyzed the effects of corridors on the abundances of important plant resources. The response variable was either plant or flower density, or the proportion of cells or subcells in which density was greater than or equal to 1, 10, or 100 plants or flowers. Plant and flower abundances in connected and isolated patches were analyzed as a single-classification ANOVA.

RESULTS

Butterfly densities

In 1995, 700 butterfly surveys were conducted, for an average of 35 surveys per patch. In 1996, 1464 surveys were conducted, for an average of 54 surveys per patch. To evaluate the seasonal effects of different plant resources on butterfly densities, 1996 data were divided into flight periods, based on adult emergence patterns (Tables 1 and 2). Although flight periods overlapped in some cases, we determined the beginning and end of flight periods at times when adults reached their lowest seasonal abundances.

Densities of three species, *Junonia coenia* (1996; Fig. 3B,C), *Euptoieta claudia* (1996; Fig. 4B), and *Phoebis sennae* (1995; Fig. 5A), were higher in patches

connected by corridors than in similar, isolated patches during one or more flight periods (Table 2). In 1995, the analysis of *J. coenia* density was influenced strongly by two patches, one connected and one isolated, with densities an order of magnitude higher than in other patches. We suspect that this was due to high densities of unmeasured flowers in these patches. When these patches were excluded from the analysis, *J. coenia* density was significantly, positively dependent on the presence of a corridor ($\chi^2 = 38.03$; $P = 0.001$; full model: $df = 6, 137$). Corridors also had no significant influence on *P. sennae* in 1996, when its densities were depressed by late spring frosts. No differences in density between connected and isolated patches were detected for *Papilio troilus* in either year (Fig. 6).

In several cases, butterfly densities were significantly, positively correlated with abundances of host or nectar plants (Table 2). In 1995, *Junonia coenia* density was significantly, positively related to the number of cells containing *Gerardia purpurea*. In its first 1996 flight period, *J. coenia* density was significantly, positively related to the proportion of subcells containing >10 individual *Linaria canadensis*. In 1996, *Euptoieta claudia* density was significantly, positively related to the proportion of subcells containing *Rubus* sp., and weakly, positively related to *Asclepias tuberosa* flower density ($\chi^2 = 2.78$; $P = 0.09$; full model: $df = 8, 207$). In 1995 and 1996, *Papilio troilus* density was significantly, positively related to *Carduus repandus* flower density. Other plant resources were not significant covariates in models of butterfly densities.

Except in one flight period of *Papilio troilus*, region was always a significant variable in models of butterfly densities (Table 2). Regional clusters of patches differed in soil types, histories of forest management, and

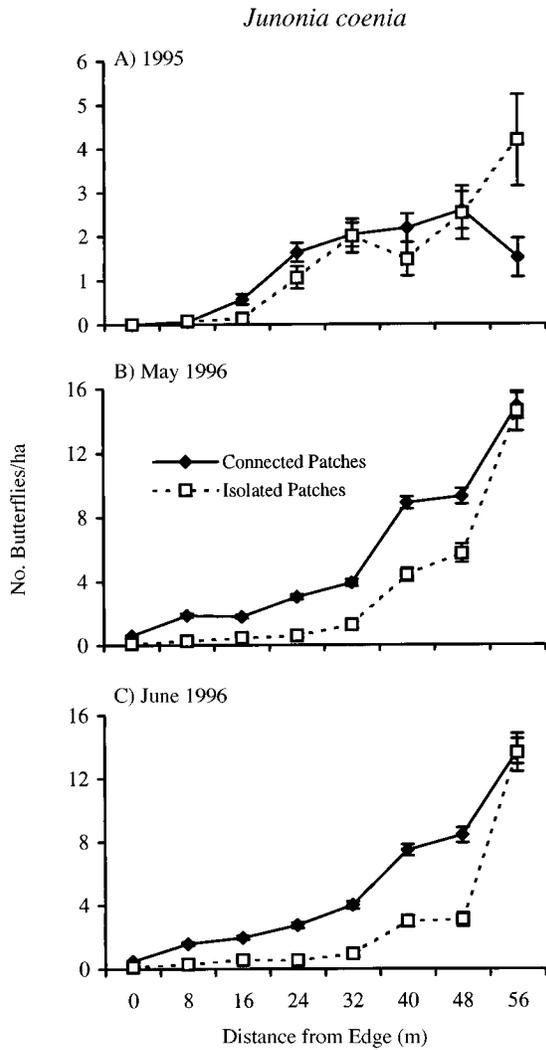


FIG. 3. Mean densities (± 1 SE) of *Junonia coenia* in connected and isolated patches. Distance from the edge is the linear distance to the nearest forest boundary.

surrounding landscapes. These factors were not quantified as part of this study. However, even after accounting for regional differences, the effects of corridors on densities were still significant for *Junonia coenia*, *Euptoieta claudia*, and *Phoebis sennae*.

Predicting the effects of edges on butterfly densities

Densities increased with distance from the forest edge for all species, except for *Phoebis sennae* in 1996 (Table 2). Densities of *Junonia coenia*, *Euptoieta claudia*, and *P. sennae* (1995) increased sharply with distance from the forest edge (Figs. 3–5). Densities of *Papilio troilus* were low near the forest edge and high near the patch center, but showed little change at intermediate distances (Fig. 6).

Using data from isolated patches, we estimated the effects of edges on butterfly densities in connected patches. In Table 3, we present the actual mean den-

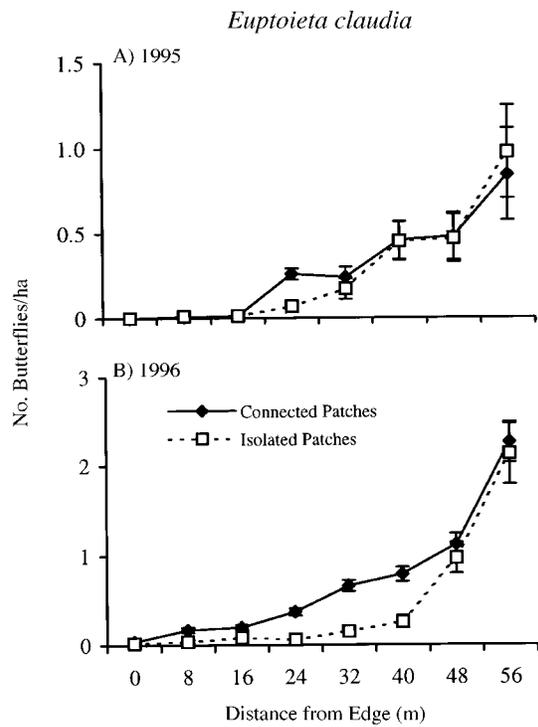


FIG. 4. Mean densities (± 1 SE) of *Euptoieta claudia* in connected and isolated patches. Distance from the edge is the linear distance to the nearest forest boundary.

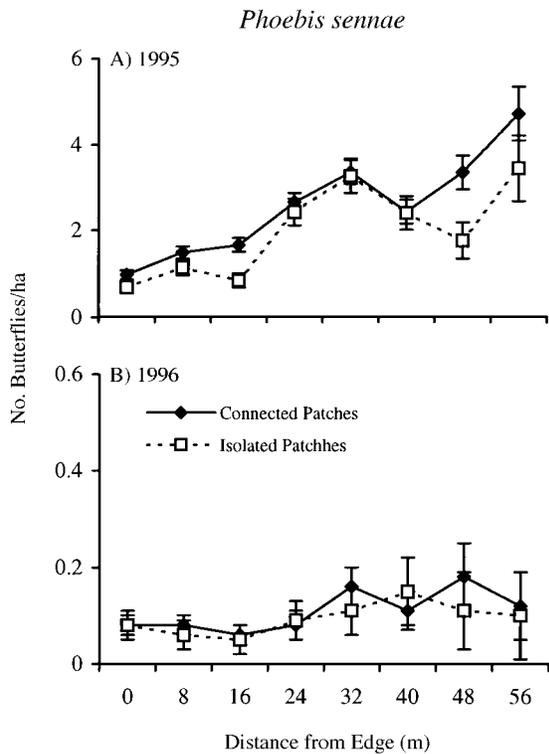


FIG. 5. Mean densities (± 1 SE) of *Phoebis sennae* in connected and isolated patches. Distance from the edge is the linear distance to the nearest forest boundary.

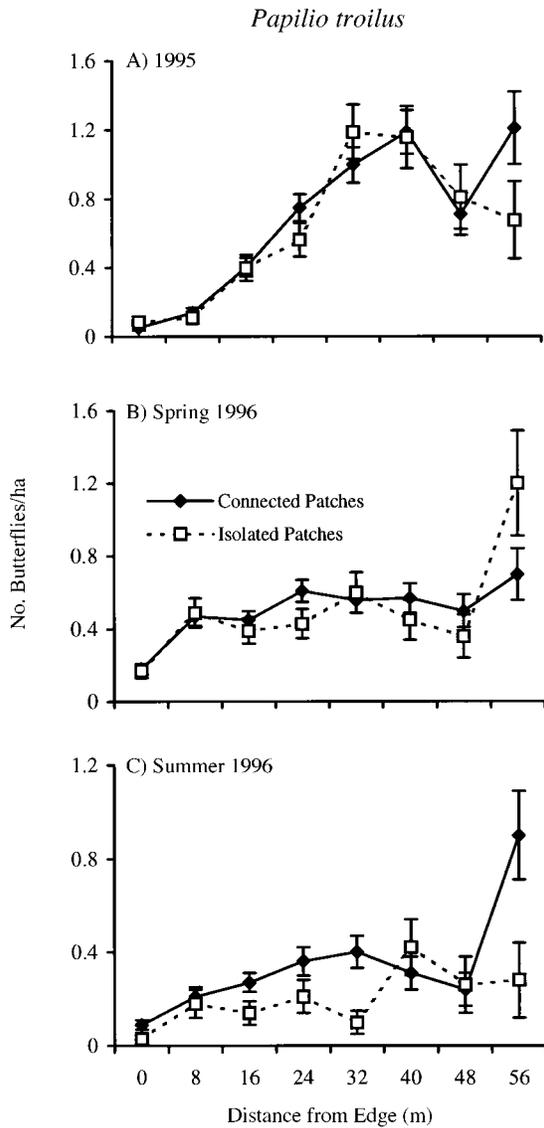


FIG. 6. Mean densities (± 1 SE) of *Papilio troilus* in connected and isolated patches. Distance from the edge is the linear distance to the nearest forest boundary.

sities in isolated and connected patches, as well as our density estimates for connected patches for all species that showed a significant, positive response to corridors. The Effective Area Model predicted densities 8–19% higher in connected patches. Actual densities were 17–155% higher in connected patches. The prediction for 1995 *Junonia coenia* density was the only case for which our prediction matched actual densities.

Vegetation densities

Although densities of several butterfly species were significantly, positively correlated with the abundances of important plant resources, only one plant species had different abundances in connected and isolated patches (Table 4). In 1996, *Gelsemium sempervirens* flowers were more abundant in isolated patches. Because the abundance of one in 20 plant species would be expected to differ by chance alone, we conclude that there was no significant effect of corridors on abundances of host or nectar plants.

DISCUSSION

This large-scale experiment demonstrates that corridors increase densities of habitat specialist butterflies. During one or more adult flight periods, densities of three open-habitat butterfly species were higher in patches connected by corridors than in similar, isolated patches. Our results corroborate most other studies that also show higher animal densities in patches connected by corridors (i.e., MacClintock et al. 1977, Fahrig and Merriam 1985, LaPolla and Barrett 1993, Dunning et al. 1995), and add support to the emerging consensus that corridors increase densities of habitat-restricted species.

For each open-habitat species, results from one flight period did not agree with the prediction that corridors increase butterfly densities. Four factors may have contributed to the variability in our results. First, in all cases when corridors had no effect on densities of open-habitat butterflies, there were far fewer individuals compared to other flight periods. For instance, total densities of *Phoebis sennae* in spring 1996 were de-

TABLE 3. Effects of edges on butterfly densities in connected and isolated patches.

Species (by flight period)	Density (no. butterflies/ha)			Predicted effect of corridors (%)	Actual effect of corridors (%)
	Isolated patches	Estimate	Connected patches		
<i>Junonia coenia</i> (1995)	0.90	1.04	1.05	16	17
<i>J. coenia</i> (May 1996)	1.71	2.03	3.80	19	122
<i>J. coenia</i> (June 1996)	1.37	1.63	3.50	19	155
<i>Euptoieta claudia</i> (1996)	0.22	0.26	0.45	18	105
<i>Phoebis sennae</i> (1995)	1.82	1.97	2.32	8	27

Notes: For all butterflies and flight periods in which density showed a positive response to corridors, we estimated densities in patches with corridors using the Effective Area Model (Sisk et al. 1997; see Fig. 2). The predicted effect of corridors = (estimated density in connected patch - actual density in isolated patch)/(actual density in isolated patch) \times 100%. The actual effect of corridors = (actual density in connected patch - actual density in isolated patch)/(actual density in isolated patch) \times 100%.

TABLE 4. Abundances of essential plant resources in connected and isolated patches. Means were compared in a single-classification ANOVA.

Plant species	Abundance (mean \pm 1 SE)		F	P
	Connected patches	Isolated patches		
1995	(n = 13)	(n = 7)		
<i>Gelsemium sempervirens</i> †	0.188 \pm 0.102‡	0.224 \pm 0.101	0.30	NS
<i>Cassia</i> sp.	0.622 \pm 0.272‡	0.571 \pm 0.289	0.15	NS
<i>Crotolaria</i> sp.	0.243 \pm 0.258‡	0.189 \pm 0.332	0.17	NS
<i>Gerardia purpurea</i>	0.217 \pm 0.300‡	0.245 \pm 0.178	0.06	NS
<i>Carduus repandus</i>	12.85 \pm 5.46§	27.86 \pm 9.88	2.11	NS
<i>Asclepias tuberosa</i>	3.92 \pm 1.53	2.14 \pm 1.35	0.59	NS
<i>Sassafras albidum</i> ¶	144 \pm 58	121 \pm 44	0.92	NS
1996	(n = 19)	(n = 8)		
<i>G. sempervirens</i> #	0.279 \pm 0.262‡‡	0.530 \pm 0.262	4.46	<0.05
<i>Linaria canadensis</i>	0.299 \pm 0.223‡‡	0.150 \pm 0.109	3.20	NS
<i>Rubus</i> sp.	0.140 \pm 0.132‡‡	0.139 \pm 0.093	0.00	NS
<i>C. repandus</i>	26.37 \pm 9.57§	30.75 \pm 11.82	0.07	NS
<i>A. tuberosa</i>	26.52 \pm 9.49§	52.5 \pm 32.57	1.50	NS
<i>S. albidum</i> ††	86.7 \pm 7.6	90.9 \pm 16.7	0.07	NS

† Corridor, n = 6; no corridor, n = 4.

‡ Mean proportion of cells per patch.

§ Mean no. flowers per patch.

|| Mean no. plants per patch.

¶ July measurements: connected, n = 11; isolated, n = 8.

df = 1, 25.

†† July measurements: connected, n = 17; isolated, n = 7.

‡‡ Mean proportion of subcells per patch.

pressed by late frosts. During that time, sampling effects may have been introduced by extremely low butterfly encounter rates. Second, outliers, caused by extremely high flower densities in two plots in fall 1995 obscured a significant, positive effect of corridors on *Junonia coenia* densities in the other patches. Third, because only 20 patches were surveyed in 1995, sample sizes may have been too small to detect real differences in densities. Finally, the results may indicate seasonal differences in responses to corridors. Seasonal differences may have arisen from changes in butterfly flight patterns, which were only observed for *P. sennae*, a migratory species (Haddad 1997), or from changes in the spatial distribution of host plants or flowers.

Studies conducted at the same time and in the same experimental patches as this study provide support for the hypothesis that higher butterfly densities were caused by higher interpatch movement rates. In a mark-release-recapture study, Haddad (1999a) demonstrated that *Euptoieta claudia* and *Junonia coenia* move more frequently between connected patches than between unconnected patches. In behavioral studies, Haddad (1999b) showed that *Phoebis sennae* use corridors more frequently than expected by random movement, whereas *Papilio troilus* do not.

Can we conclude that, by increasing interpatch movement, corridors increase densities in the patches they connect? Given the difficulty in obtaining empirical evidence for movement through corridors (Rosenberg et al. 1997), a relationship between corridor use and population density would provide a straightforward, less intensive method for evaluating the conser-

vation potential of corridors. However, the hypothesis that corridors increase densities by increasing interpatch movement rates should not be accepted without thorough consideration of alternative hypotheses. In particular, corridors have what are perhaps unintended effects: they increase the area of the patch that is far from the habitat edge and modify the shape of the patch in the context of the surrounding landscape. In doing so, corridors may have additional consequences for animals or their resources. We consider four alternative explanations for higher butterfly densities in patches connected by corridors.

Vegetation resources and butterfly densities

Densities of several plant species, particularly adult nectar resources, were important variables in explaining butterfly densities (Table 2). This finding corroborates results of several other studies that report an association between densities of adult butterflies and their nectar resources (Murphy et al. 1984, Grossmueller and Lederhouse 1987, Kuussaari et al. 1996). However, only for *Papilio troilus* was density significantly, positively related to plant density, but not to the presence of a corridor. In addition, corridors did not increase host plant or flower abundances (Table 4). Therefore, resource densities did not confound the positive effect of corridors on densities of open-habitat butterflies.

Edge effects and butterfly densities

Species with higher densities in connected patches also had higher densities at greater distances from the

forest edge (Figs. 3–5). A similar response to habitat boundaries has been shown for an endangered habitat specialist butterfly, *Icaricia icarioides fenderi* (Schultz 1998). For such species, the addition of a corridor to an otherwise isolated patch may change the density within an entire patch (i.e., by changing the “effective area” of a patch; Sisk et al. 1997), even if corridors do not increase interpatch movement rates. As exemplified by the study by Sisk et al. (1997) of birds in patchy landscapes, accounting for species-specific responses to edges may improve predictions of densities within the entire patch. Schmiegelow et al. (1997) found that changes in the effective area of small patches caused by an experimental corridor could account for higher bird diversity when compared to similar, isolated patches.

The Effective Area Model predicted higher densities in patches connected by corridors due to edge effects. However, predictions underestimated the actual changes in densities (Table 3). One explanation for this may be that a simple density estimate based on linear distance to the nearest edge may not account for more complex changes in the effective area of a patch caused by the addition of a long corridor. More likely, edge effects may be only one of several factors contributing to higher butterfly densities in patches connected by corridors.

Corridors and colonization probability

Butterflies in this study were capable of moving distances far greater than the largest interpatch distance (Haddad 1999a). Immigration into a connected patch strictly through a corridor may be far less than immigration into patches from outside the experimental areas. If immigration from the surrounding landscape is high, then corridors may act as “drift fences,” capturing more immigrants than similar, isolated patches (Taylor 1987). This effect of corridors on immigration assumes that the probability of a disperser reaching a patch is a function of the angle the patch subtends in the horizon (MacArthur and Wilson 1967:127, Taylor 1987, Fahrig and Paloheimo 1988, Harrison 1989, Turchin 1998).

Our experiment does not directly test the “drift fence effect” of corridors on immigration. However, the prediction that corridors increase immigration from the surrounding landscape can be demonstrated conceptually. Consider a dispersing butterfly that is equidistant from four equal-sized patches, where two of the patches are connected by a corridor (Fig. 7). The angle subtended by two connected patches is greater than the angle subtended by two isolated patches; in this case, the angle is proportionately greater than the area added by the corridor. The effects of corridors on immigration can be solved numerically by averaging the angle subtended by two connected and two isolated patches over all possible butterfly locations in a landscape.

The effects of corridors on immigration will translate

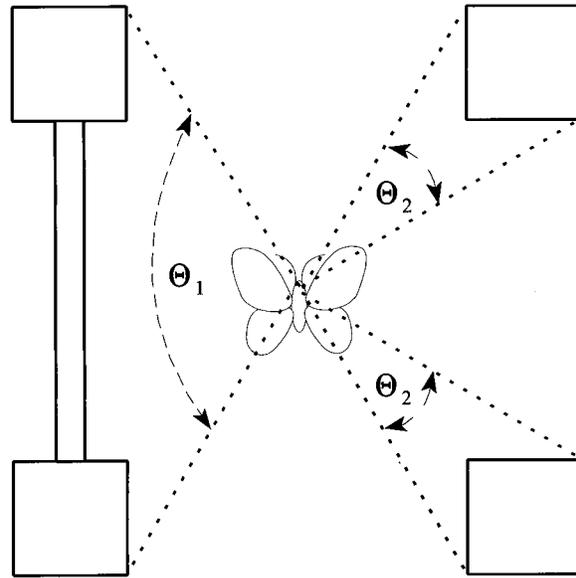


FIG. 7. Conceptual diagram illustrating the “drift fence effect” of corridors on immigration rates, assuming that immigration is proportional to the angle subtended in the horizon. The angle subtended by a single isolated patch in the horizon is less than the angle subtended by two connected patches ($\Theta_1 > 2\Theta_2$). When compared to two isolated patches, the angle subtended by two connected patches may be proportionately greater than the area added by a corridor.

into higher colonization of the patches if corridors intercept dispersing individuals and then direct them to the patches. In simulation models, Haddad (1997; *unpublished manuscript*) has shown how corridors might increase immigration into patches in this way. Butterfly movement was simulated as a correlated random walk using behavioral data for *Phoebis sennae* and *Papilio troilus*. Movement paths were initiated in the area surrounding three patches, two of which were connected by a corridor. The corridor increased immigration into patches by as much as 15%. Importantly, as corridor length increased, the effect of corridors on immigration increased. These model results suggest that the “drift fence effect” of corridors on immigration must be considered, along with increased interpatch movement and increased effective patch area, as a possible factor causing higher population sizes in connected patches.

Patch size and butterfly densities

In this study, two connected patches can be viewed as a single, larger patch. Several studies have reported higher insect densities in larger patches (e.g., Kareiva 1985, Turchin 1986, Bach 1988, Hill et al. 1996). Our previous discussion addresses two possible effects of larger patches on butterfly densities: those caused by changes in the effective area of a patch and by changes in immigration from the surrounding landscape. One conclusion from previous studies is that larger patches, due to their smaller edge : area ratios, have lower rates of emigration. Because more individuals remain within

large patches, densities are higher (Kareiva 1985, Turchin 1986, Bach 1988). In our study, the edge : area ratio of two connected patches is higher than the edge : area ratio of a single, isolated patch. Thus, viewing two connected patches as a single, larger patch does not explain higher densities in connected experimental patches in ways that are not already explained by changes in effective patch area and in immigration from the surrounding landscape.

Application to management

Corridors are typically implemented in management on the assumption that they will increase population densities by increasing movement to otherwise isolated patches. Our study suggests that corridors may increase densities by one of three mechanisms: by increasing interpatch movement, by modifying the effective area of a patch, and by increasing immigration from the larger landscape. The two final effects of corridors on density could be obtained without the addition of a corridor. Larger habitat areas could also change edge effects and immigration rates, and could increase regional population densities. In cases in which corridors do not increase interpatch movement rates, habitat areas other than corridors should be considered that are potentially less costly, but more effective at increasing animal population sizes (Fahrig 1996).

The potential for corridors to serve as habitat that supports animal populations, independent of the area and isolation of the patches that they connect, should also be considered among the benefits of corridors. Corridors in our experiment contained host and flower plant resources and probably served as habitat for our study species. However, low butterfly densities at distances <16 m from the edge suggest that narrow corridors may be less preferred habitat for our study species. Instead, butterflies may have used corridors primarily as a dispersal conduit. Andreassen et al. (1996) showed that small mammals moved more frequently through intermediate-width corridors than through narrow or wide corridors. In general, wider corridors would provide better habitat for habitat-restricted species.

The conservation value of corridors must be evaluated in the context of their effects on species that vary in movement behaviors and life history characteristics. Corridors may have positive, neutral, and even negative effects (Simberloff et al. 1992, Rosenberg et al. 1997). Most studies have focused on the positive effects of corridors on interpatch movement and population size (i.e., MacClintock et al. 1977, Haas 1995, Sutcliffe and Thomas 1996). In the same experimental patches and corridors as this study, Bowne et al. (1998) showed that cotton rats (*Sigmodon hispidus*) preferred leaving connected patches through corridors, but that corridors did not promote emigration or increase interpatch movement rates. Schultz (1998) concluded that corridors would have little if any benefit for an endangered

butterfly species, even though corridors were proposed as a conservation strategy to protect the butterfly's populations. Rosenberg et al. (1998) found that, except under drought conditions, corridors had no effect on movement rates of a salamander, *Ensatina eschscholtzii*. In a microcosm experiment, Burkey (1997) found that corridors have negative effects on predators, decreasing their time to extinction. Our study examined several different butterfly species in the same experiment, and demonstrated that corridors should increase densities of habitat-restricted species.

Our conclusion that corridors increase densities of habitat-restricted species should apply generally to different species in other managed landscapes. Corridors are most often proposed to connect forest patches in open, agricultural landscapes. In this study, corridors were effective at increasing densities of open-habitat species because of the strong contrast between the open habitat and surrounding pine forest. Similarly, forest habitats contrast strongly with open, agricultural landscapes that surround them. Based on our results, we predict that forest corridors in those landscapes should increase densities of forest species. In general, habitat-restricted species will be most likely to benefit from corridors in fragmented landscapes.

ACKNOWLEDGMENTS

We thank Ron Pulliam for advice on all aspects of this research. Data were collected with the assistance of Eric Carlin, Kathryn Haddad, Jim Gillis, Leah Gorman, Stephanie Griffen, Will Hicks, Chad Johnson, Shannon Kelley, Genevieve Kipte, Leslie Ries, Toni Smith, and Mary Sundstrom. We benefitted greatly from discussions about statistical analyses with LaTonya Rodgers and Steve Rathbun, and about mathematical analyses with Clarence Lehman. Gretchen Daily, Lenore Fahrig, Bryan Foster, Jim Hanula, Gary Meffe, Jim Porter, Leslie Ries, Tom Sisk, Barbara Taylor, and two anonymous reviewers provided helpful comments on the manuscript. The experimental sites were implemented in collaboration with Robert Cheney, as well as the timber, fire, and engineering staffs at the Savannah River Institute, especially John Blake, Ed Olson, Rick Davalos, and Gloria Nielson. Financial support for this project was provided by a cooperative agreement with the Southern Research Station of the U.S. Forest Service through the Savannah River Site's biodiversity program, a National Environmental Research Park grant from the Savannah River Ecology Lab, a Sigma Xi Grant-in-aid-of-Research, an NSF predoctoral fellowship, and a University of Georgia University-wide fellowship.

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