

CORRIDOR AND DISTANCE EFFECTS ON INTERPATCH MOVEMENTS: A LANDSCAPE EXPERIMENT WITH BUTTERFLIES

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Abstract. The hypothesis that corridors increase animal movement between habitat fragments, a central tenet of conservation biology, has been virtually untested. This study demonstrates that corridors increase interpatch movement rates of two butterfly species. The hypothesis was tested in a large-scale, replicated experiment, in which 27 equal-sized (1.64-ha) patches of early successional habitat were created within large areas of pine forest. Patches varied in whether or not they were connected to another patch by a corridor, and in their distance from other patches (64–384 m). The results of mark–release–recapture studies showed that two open-habitat butterfly species, *Junonia coenia* and *Euptoieta claudia*, moved more frequently between patches connected by corridors than between unconnected patches. Interpatch movement was significantly, negatively related to interpatch distance. Interpatch movement rates of *J. coenia* were significantly, positively related to the density of its host and nectar resource, *Linaria canadensis*. Corridor effects were stronger for males than for females and were most pronounced within three days after butterflies were marked. Pine forest was not a complete barrier to butterfly movement; both species moved between unconnected patches, even at the longest distances. However, the results of this study suggest that corridors will increase long-distance movements of habitat-restricted species.

Key words: butterfly; colonization; conservation; corridors; dispersal; *Euptoieta claudia*; habitat fragmentation; interpatch distance; interpatch movement; *Junonia coenia*; landscape experiment.

INTRODUCTION

The corridor concept arose as a logical application of island biogeography (MacArthur and Wilson 1967, Wilson and Willis 1975, Brown and Kodric-Brown 1977) and metapopulation theory (Levins 1969, Lande 1987, Hanski and Gilpin 1991) to conservation in fragmented landscapes. Wilson and Willis (1975) first suggested the use of corridors in conservation, concluding that “. . . extinction will be lower when the fragments can be connected by corridors.” Corridors remain one of the most compelling applications of ecology to reserve design, and they have become cornerstones of local, regional, and national management strategies (Noss 1987, Mann and Plummer 1993, 1995, Meffe and Carroll 1997). As they have become more widely implemented, however, the conservation value of corridors has come into question (Simberloff and Cox 1987, Simberloff et al. 1992, Mann and Plummer 1995, Rosenberg et al. 1997). Because of difficulties in measuring movement and implementing replicated experiments at scales relevant to habitat management, few studies provide evidence that corridors fulfill their primary function and increase movement between patches

(see reviews in Simberloff and Cox 1987, Simberloff et al. 1992, Rosenberg et al. 1997).

Previous corridor studies have been limited by lack of experimental control and replication, and by the small sizes of corridors. Corridors are often much smaller than those proposed in management, and they are often too small to influence animal population dynamics. The best evidence demonstrating that corridors increase movement rates between patches comes from mark–release–recapture studies in large, non-experimental landscapes. These studies have demonstrated corridor use by small mammals (Zhang and Usher 1991), birds (Haas 1995), butterflies (Sutcliffe and Thomas 1996), and other animals (Simberloff et al. 1992, Rosenberg et al. 1997). However, low recapture rates and unreplicated landscape patterns make results difficult to interpret and generalize (Nicholls and Margules 1991). In an experimental study, Andraesson et al. (1996) showed that small mammals moved more frequently between an intermediate-width corridor (1 m wide) than between a narrower (0.4-m) or wider (3-m) corridor. In a large-scale experiment, Machtans et al. (1996) demonstrated that birds move within forest corridors more frequently than within open habitats. Two recent corridor experiments have found no evidence for corridor use by salamanders (Rosenberg et al. 1997, 1998) and small mammals (Bowne et al. 1998). Other evidence commonly cited to support corridor use by animals includes observations of higher densities in connected patches (MacClintock et al.

Manuscript received 15 January 1998; revised 8 July 1998; accepted 10 July 1998.

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1977, Fahrig and Merriam 1985, LaPolla and Barrett 1993, Dunning et al. 1995; but see Burkey 1997). However, several factors may cause higher densities in connected patches, including higher movement rates through corridors, higher immigration into corridors from the surrounding landscape, and improved habitat quality in connected patches (Haddad and Baum 1999). In summary, although increasing numbers of studies have tested the hypothesis that corridors increase interpatch movement rates, empirical support for this hypothesis remains weak.

To test the effects of corridors on animal movement rates, I created an experimental system of open patches and corridors within large stands of managed pine forest. The dimensions of landscape features, including patch area, distance between patches, and corridor length and width, were characteristic of managed landscapes in the southeastern United States. Within the experimental areas, I studied the movement of two open-habitat butterflies, *Junonia coenia* and *Euptoieta claudia*. Through mark–release–recapture studies, I measured directly the effects of corridors and distance on interpatch movement rates. A negative relationship between movement frequency and distance has been demonstrated in many empirical (e.g., Fahrig and Paloheimo 1988, Harrison 1989, Turchin and Theony 1993, Koenig et al. 1997) and theoretical studies (e.g., MacArthur and Wilson 1967, Turchin and Theony 1993, Turchin 1998). However, this is the first experimental study to examine the influence of corridors on movement rates at increasing interpatch distances.

METHODS

Study site

I tested the effects of corridors and distance on interpatch movement rates at the Savannah River Site, South Carolina. Experimental patches and corridors were open habitats, created by harvesting trees in large, forested areas managed for pine. The patches and corridors were created on sandy, upland sites. Before harvests, pine stands consisted of 30–40 yr-old loblolly (*Pinus taeda*) and slash pine (*Pinus elliotii*). Because pine were planted at high densities, closed forest canopies and dense litter prevented understory development. Host and flowering plant resources of many butterflies, even forest species, were absent or present at low densities in these forests (*personal observation*). In contrast, open habitats, created by harvesting pine forest, supported diverse and productive herbaceous vegetation. Many animals, including the butterfly species in this study, responded strongly to the contrast between open habitats and managed pine forests (Haddad 1997). Vegetation in these forests and open habitats is described in Workman and McLeod (1990).

Within the experimental patches and corridors, all trees were harvested and the remaining slash was burned. Patches were planted in loblolly pine. Harvests

were typical of those at the Savannah River Site and represented viable management alternatives in southeastern pine forests. Patches were the size of small clearcuts created in forestry, and corridors were the width of power line and road right-of-ways. Vegetation within the experimental sites developed from regrowth of established vegetation, especially trees; germination from the existing seed bank; and colonization from nearby clearings, power line right-of-ways, and roads. Because the patches, corridors, and surrounding forest were burned after experimental harvests, all butterflies were assumed to have colonized patches from surrounding habitats after patches were created.

The experiment consisted of equal-sized (1.64-ha), square patches of open habitat (Fig. 1). In total, 27 patches were created within five contiguous areas of pine forest that ranged in size from 20 to 100 ha and contained 3–10 patches each (Fig. 1). The amount of open area was 10–20% of the area of pine forest. The size of square patches was fixed at 128 m on a side, and all patches within a contiguous forest area were oriented in the same direction. Two characteristics of the patches were varied: interpatch distance and the presence or absence of a connecting corridor. Corridors were 32 m wide, or one-fourth of patch width. Distances between patches were 64, 128, 256, or 384 m (0.5, 1, 2, or 3 times the width of a patch; see Table 1). The patches were created in the following sequence: A-1 in March 1994, A-2, A-4, B-1, and the two southwestern patches in B-2 in October 1994, and the remaining B-2 patches in August 1995 (see Fig. 1). Areas A-1, A-2, and B-1 were sampled in 1995, and all patches were sampled in 1996. A grid system, described in Haddad and Baum (1999), was established within each patch to permit rapid assessment of spatial location to a resolution of 8 m.

Study species

I studied butterflies because their life history characteristics are well defined, they are generally associated with a narrow range of resources (Ehrlich and Raven 1964), and they are relatively easy to study at large spatial scales (Fahrig and Paloheimo 1988, Harrison 1989, Kuussaari et al. 1996). *Junonia coenia* (buckeye; Lepidoptera: Nymphalidae) and *Euptoieta claudia* (variegated fritillary; Lepidoptera: Nymphalidae) were selected as study species because they were common in open habitats, which they strongly preferred over pine forest (N. M. Haddad, *unpublished data*). *J. coenia*, in particular, is common in open, linear habitats like roadsides and power line right-of-ways (Clark 1932). Dense canopy cover within pine forests limited the growth of larval host plants (*Linaria canadensis* for *J. coenia* and *Passiflora incarnatum* for *E. claudia*) and flowering plants used by adult butterflies as nectar resources. *J. coenia* and *E. claudia* are vagile; Scott (1975a, b) found that average net displacement over the adult life-span of *J. coenia* was 160 m for

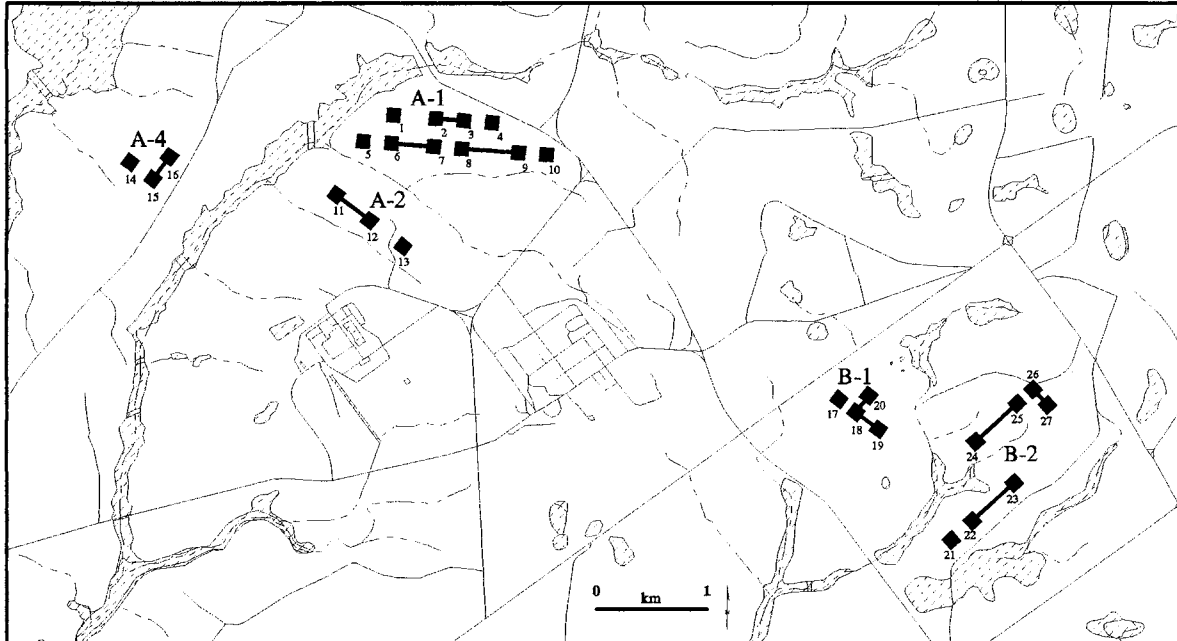


FIG. 1. Map of 27 experimental patches at the Savannah River Site, South Carolina, United States. Alpha-numeric codes (A-1, A-2, . . .) designate experimental areas that are contained within a single contiguous forest stand. The code represents the forest compartment (letter) and stand (number) used at the Savannah River Site to demarcate timber management units. Each patch was then numbered consecutively. Hatching indicates streams and other bodies of water.

males and 190 m for females, and that movement distances ranged from 0 m to 1100 m. These species rapidly colonized newly created clearings. Other species that are more restricted to a specific habitat should show stronger responses to corridors than do the species in this study.

Butterfly surveys

In 1995 and 1996, a survey covered the entire patch, was conducted in the time period 1000–1700, and was suspended during rain. However, different survey methods were used in each year. In 1995, each survey consisted of 5-min observations in nine 32×32 m areas within each patch. This method assumed detection of all butterflies within 16 m, a distance that I 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, each transect was walked in 6 min.

TABLE 1. Replication of connected and unconnected patch pairs at each distance.

Distance between patches (m)	Patch pairs	
	Corridor	No corridor
64	2	2
128	3	9
256	2	2
384	3	1

In both years, observation time excluded time spent marking butterflies and recording data. In each year, data were collected consistently among patches, permitting valid analyses of corridor effects on interpatch movements. However, differences in survey methods prevented comparisons between years.

During each survey, an attempt was made to capture every individual of the two study species with a hand-held net. Each butterfly was assigned a unique identification number by marking the ventral side of its wings with a felt-tipped pen (Ehrlich and Davidson 1960). For each individual, the identification number, time of capture, sex, age, and location to within 8 m were recorded. Individuals were released at the location of capture.

In both years, several observers were trained to perform surveys. In 1995, patches 1–13 and 17–20 were surveyed (patches 1–10 for three consecutive days, and then the other seven patches for three consecutive days). In 1996, all 27 patches were surveyed once before any patch was surveyed a second time and, on average, 23 surveys were completed each day. To prevent sampling bias, surveys of a given patch were alternated between morning and afternoon.

Supplemental releases

Data on naturally occurring individuals were supplemented by transplanting individuals of both species into the experimental patches. Transplants evened out the number of marked individuals per patch and in-

creased the potential number of recaptures. Butterflies captured outside of the study area were marked and released into one of 14 patches (2, 3, 6, 7, 8, 9, 12, 15, 18, 22, 23, 24, 25, 26; see Fig. 1) within 2 h of capture. Patches chosen for releases were adjacent to at least two other patches. Butterflies were released on six different dates in 1996: 29 April, 7 May, 16 May, 29 May, 10 June, and 18 June. On each date in every patch, 20 *Junonia coenia* and 0–5 *Euptoieta claudia* were released. Abundances of *E. claudia* were low and variable, so equal numbers of butterflies were released in each patch, rather than a specific number of butterflies. In total, 159 *E. claudia* were released. Recaptures of released butterflies were recorded as part of standard surveys.

Vegetation surveys

The abundances of important host plants and flowers were recorded in both years. Vegetation data were not used in analyses of 1995 interpatch movements because recapture data were summed across seasons, when different plant resources would have been important. In May 1996, abundances of *Linaria canadensis* (host and nectar plant for *Junonia coenia*) and *Rubus* sp. (an important flower resource for both species) were measured. To quantify abundances of those species, each patch was divided into 8 × 8 m grid cells, and the number of plants or flowers in each cell was recorded on a logarithmic scale, where 0 was 0 plants or flowers; 1 was 1–10 plants or flowers; 2 was 10–100 plants or flowers; and 3 was >100 plants or flowers. The location of each flower of *Asclepias tuberosa*, a particularly important nectar resource of *Euptoieta claudia*, was recorded during every butterfly survey. No data were collected on *Passiflora incarnatum* (the host plant of *E. claudia*), because its abundance was manipulated in the patches as part of another experiment.

Analysis

I analyzed interpatch movement rates as general linear models. Independent variables included a class variable that indicated the presence or absence of a corridor, interpatch distance, conspecific density, and plant and flower abundances. Data were tabulated into a matrix of transition probabilities for each patch pair. I only included adjacent pairs of patches in analyses, and I only counted a butterfly's first move to an adjacent patch. The response variable was the proportion of individuals marked within one patch that moved to an adjacent patch that was connected or unconnected, and separated by one of four distances. Movement in each direction between a patch pair was treated as an independent measure of interpatch movement. In addition to analyses of corridor effects on all individuals of each butterfly species, I conducted three other analyses, dividing data by: (1) sex; (2) time elapsed between when a butterfly was marked and when an interpatch move-

ment was first detected; and (3) whether butterflies occurred naturally or were transplanted.

I analyzed the effects of two additional factors that may have confounded corridor effects. First, I tested whether directionality in butterfly movements may have biased interpatch movement rates. Many insects are known to move directionally, especially when migrating. Second, I tested whether interpatch movement rates were influenced by the number of nearby patches. One potential problem with the experimental design was that each patch was adjacent to a different number of other patches (Fig. 1). To address the possibility that the number of adjacent patches influenced interpatch movement rates, I created two variables that quantified the number of patches adjacent to the patch of origin. These variables were computed for each patch, and were either the sum of all adjacent patches, or the sum of all adjacent patches weighted by the distance between patches ($1/d$).

RESULTS

In 1995, patches were surveyed 830 times (49 surveys per patch) between 2 April and 10 October. During that time, 1260 *Junonia coenia* and 189 *Euptoieta claudia* were marked. Of these, 234 *J. coenia* (19%) and 47 *E. claudia* (25%) were recaptured at least one time. Because of the low number of marked individuals, low recapture rates, and seasonal irregularity in survey intensity in 1995, I analyzed only total interpatch movement rates in 1995, and included only two independent variables: the class variable indicating the presence of a corridor and interpatch distance. In 1996, patches were surveyed 1460 times (54 surveys per patch) between 3 April and 29 June. Recapture data for 1996 are summarized in Table 2 and in Appendixes A and B.

One outlier in each year had a large impact on analyses of *Euptoieta claudia* movement rates. In both cases, patch 19 in 1995 and patch 1 in 1996, low numbers of marked individuals yielded 50% movement rates, which were $\geq 25\%$ higher than the next largest rate. I excluded these data from analyses.

Corridors increased movement rates between patches for both species in 1995 and 1996 (Table 3, Fig. 2). This result was not influenced by the number of adjacent patches (*Junonia coenia*: $F = 0.90$, $P = 0.42$; *Euptoieta claudia*: $F = 0.99$, $P = 0.38$), even when each adjacent patch was weighted by its distance (*J. coenia*: $F = 1.25$, $P = 0.27$; *E. claudia*: $F = 0.81$, $P = 0.37$). Except for *J. coenia* in 1995, interpatch movement rate was significantly, negatively related to interpatch distance (Table 3).

Interpatch movement rates of *Junonia coenia* were significantly, positively dependent on *Linaria canadensis* abundance in the patch to which the butterflies moved (Table 3). Neither the abundance of *Rubus* sp. (*J. coenia*: $F = 0.07$, $P = 0.79$; *E. claudia*: $F = 0.24$, $P = 0.63$) nor *Asclepias tuberosa* (*E. claudia*: $F =$

TABLE 2. Summary of mark–release–recapture data from 1996. Distance data were assumed to follow a lognormal distribution, and means were computed using Proc Lifereg in SAS (SAS Institute 1992). Net displacement is the distance from where the butterfly was first marked.

Variable	<i>Junonia coenia</i>	<i>Euptoeita claudia</i>
No. butterflies marked	5030	442
No. butterflies recaptured	1530 (30%)	165 (37%)
No. males recaptured	34%	46%
No. females recaptured	27%	29%
Mean distance between recaptures (m)	77.24	56.06
Mean male net displacement (m)		
After 1 d	58.08	48.17
After 3 d	85.02	50.18
After 5 d	95.24	100.05
Mean female net displacement (m)		
After 1 d	55.16	65.57
After 3 d	86.06	160.33
After 5 d	105.07	112.62
Maximum distance moved (m)	5600	935
Mean time between recaptures (d)	3.1	2.42
Maximum time between first and last recapture (d)	51	27

0.16, $P = 0.69$) had significant effects on interpatch movement rates.

The number of marked *Junonia coenia* within a patch was significantly, positively correlated with *Linaria canadensis* abundance ($n = 27$, $R^2 = 0.57$, $P = 0.001$). Because of this strong correlation, both conspecific density and *L. canadensis* abundance could not be included in analyses of *J. coenia* interpatch movement rates. However, interpatch movement rates of *Euptoeita claudia* were significantly, positively associated with

E. claudia density in the patch to which the butterflies moved (Table 3).

Interpatch movement rates of male *Junonia coenia* were significantly, positively dependent on the presence of a corridor ($F = 16.17$, $P = 0.001$; full model: $df = 3, 44$; $R^2 = 0.44$, $F = 11.60$, $P = 0.001$), and significantly, negatively dependent on interpatch distance ($F = 6.14$, $P = 0.02$; Fig. 3A). Interpatch movement rates of female *J. coenia* were significantly, positively dependent on the presence of a corridor ($F = 5.55$, $P = 0.02$; full model: $df = 3, 44$; $R^2 = 0.46$, $F = 12.59$, $P = 0.001$), but not on interpatch distance ($F = 1.85$, $P = 0.18$; Fig. 3B). Movement rates of both sexes were significantly, positively dependent on *Linaria canadensis* abundance (males: $F = 16.01$, $P = 0.001$; females: $F = 31.06$, $P = 0.001$). For *Euptoeita claudia*, only male interpatch movement rates were significantly, positively dependent on the presence of a corridor ($F = 4.82$, $P = 0.05$; full model: $df = 2, 40$; $R^2 = 0.12$, $F = 2.63$, $P = 0.08$; Fig. 3C); corridors had no effect on female interpatch movement rates ($F = 2.79$, $P = 0.10$; full model: $df = 2, 44$; $R^2 = 0.07$, $F = 1.58$, $P = 0.22$; Fig. 3D), and distance had no effect on interpatch movement rates of males ($F = 1.66$, $P = 0.20$) or females ($F = 1.10$, $P = 0.30$).

Both butterfly species exhibited the strongest response to corridors within 3 d of being marked. I separated data into three categories, based on the time elapsed from when a butterfly was marked to when its first interpatch movement was detected. These categories were 0–3 d (up to the average time to first recapture), 4–7 d (up to the average adult life-span; Scott 1975b), or >7 d. For butterflies moving between patches within 3 d of being marked, movement rates of both species were significantly, positively dependent on cor-

TABLE 3. Results of Type III analysis of covariance. The response variable was the proportion of interpatch movements for a given species and year.

Variable	Estimate	F	P
<i>Junonia coenia</i> , 1995			
Intercept	0.018		0.037
Corridor	0.021	6.52	0.016
Distance	-0.00008	2.73	0.109
<i>Junonia coenia</i> , 1996			
Intercept	0.030		0.001
Corridor	0.031	13.74	0.001
Distance	-0.00009	6.17	0.017
<i>Linaria canadensis</i>	0.0006	31.08	0.001
<i>Euptoeita claudia</i> , 1995			
Intercept	0.040		0.005
Corridor	0.068	25.05	0.001
Distance	-0.00026	12.20	0.002
<i>Euptoeita claudia</i> , 1996			
Intercept	0.021		0.380
Corridor	0.043	4.12	0.049
Distance	-0.00022	5.29	0.026
Conspecific density	0.0026	9.16	0.004

Notes: Statistics for overall models. For 1995 *J. coenia*: $df = 2, 29$, $R^2 = 0.20$, $F = 3.65$, $P = 0.038$. For 1996 *J. coenia*: $df = 3, 44$, $R^2 = 0.52$, $F = 15.95$, $P = 0.001$. For 1995 *E. claudia*: $df = 2, 26$, $R^2 = 0.52$, $F = 14.02$, $P = 0.001$. For 1996 *E. claudia*: $df = 3, 43$, $R^2 = 0.27$, $F = 5.41$, $P = 0.003$.

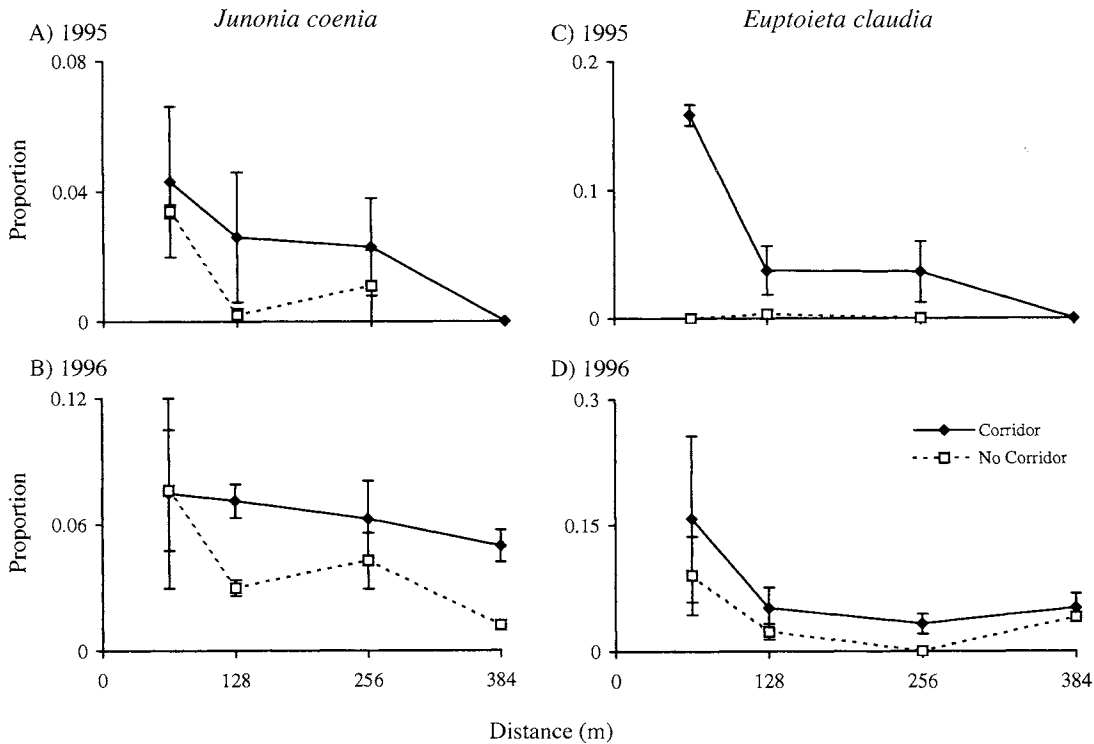


FIG. 2. Mean proportion (± 1 SE) of individuals marked in a patch that moved one of four distances to an adjacent patch. Black diamonds indicate mean proportions moving between patches connected by a corridor, and open squares indicate mean proportions moving between unconnected patches for (A) 1995 *Junonia coenia*, (B) 1996 *J. coenia*, (C) 1995 *Euptoieta claudia*, and (D) 1996 *E. claudia*.

ridors (*Junonia coenia*: $F = 4.19$, $P = 0.05$; full model: $df = 2, 45$; $R^2 = 0.12$, $F = 2.92$, $P = 0.06$; *Euptoieta claudia*: $F = 4.97$, $P = 0.03$; full model: $df = 2, 44$; $R^2 = 0.13$, $F = 3.28$, $P = 0.05$; Fig. 4A, D). *J. coenia* movement rates were also significantly, positively dependent on corridors when individuals moved between patches within 3–7 d of being marked ($F = 19.57$, $P = 0.001$; full model: $df = 2, 45$; $R^2 = 0.30$, $F = 9.86$, $P = 0.001$). In longer time periods, corridors had no significant influence on interpatch movement rates. Distance was not a significant variable in any of these analyses.

Corridors increased interpatch movement rates of butterflies that occurred naturally in the patches, but not of transplanted individuals. As in the analysis of the combined data, interpatch movement rates of naturally occurring *Junonia coenia* were significantly, positively dependent on the presence of a corridor ($F = 6.52$, $P = 0.003$; full model: $df = 3, 44$; $R^2 = 0.40$, $F = 9.79$, $P = 0.001$) and significantly, negatively dependent on interpatch distance ($F = 14.86$, $P = 0.001$). Interpatch movement rates of naturally occurring *Euptoieta claudia* were significantly, positively dependent on the presence of a corridor ($F = 5.95$, $P = 0.02$; full model: $df = 3, 43$, $R^2 = 0.16$, $F = 2.82$, $P = 0.05$), but not on interpatch distance ($F = 0.63$, $P = 0.43$). Unlike the results with naturally occurring

individuals, interpatch movement rates of transplanted *J. coenia* were only weakly dependent on the presence of a corridor ($F = 3.09$, $P = 0.09$; full model: $df = 3, 30$; $R^2 = 0.36$, $F = 5.54$, $P = 0.04$), and corridors had no significant effect on interpatch movement rates of *E. claudia* ($F = 0.15$, $P = 0.70$; full model: $df = 3, 30$; $R^2 = 0.28$, $F = 3.91$, $P = 0.02$).

Corridors may have increased interpatch movement rates in one of two ways: (1) by directing those butterflies that emigrated to connected patches, or (2) by increasing rates of emigration. The first effect of corridors was the main focus of the previous analyses. Corridors would have increased emigrants if forest boundaries had isolated butterflies, preventing them from leaving a patch. To test the hypothesis that corridors increase emigration, I analyzed the proportion of butterflies that were recaptured only in the patch where they were marked. I compared these recapture rates between connected and unconnected patches. In both years, this proportion did not differ for *Junonia coenia* (1995: $n = 17$, $F = 0.22$, $P = 0.64$; 1996: $n = 27$, $F = 0.11$, $P = 0.74$) or *Euptoieta claudia* (1995: $n = 16$, $F = 1.81$, $P = 0.20$; 1996: $n = 27$, $F = 0.15$, $P = 0.70$). Thus, I found no evidence that corridors increased emigration rates of these species.

To test for directionality in movements, I computed the average displacement in both east–west (X) and

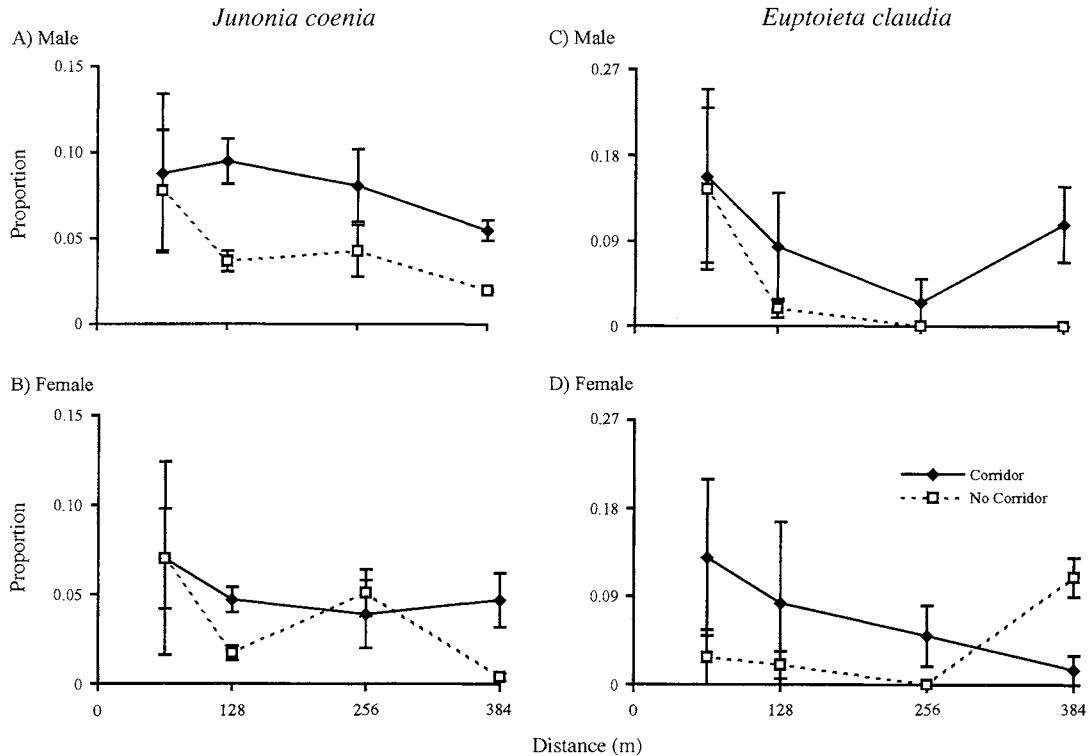


FIG. 3. Mean proportion (± 1 SE) of individuals marked in a patch that moved one of four distances to an adjacent patch, analyzed separately by sex. Black diamonds indicate mean proportions moving between patches connected by a corridor, and open squares indicate mean proportions moving between unconnected patches for (A) male *Junonia coenia*, (B) female *J. coenia*, (C) male *Euptoieta claudia*, and (D) female *E. claudia*.

north-south (Y) directions, and evaluated the mean values relative to zero (Turchin and Theony 1993). For 2507 *Junonia coenia* movements, the average displacement was: $X = -1.91 \pm 6.19$ m, $Y = 0.38 \pm 4.82$ m (mean ± 1 SE). For 342 *Euptoieta claudia* movements, the average displacement was: $X = 2.93 \pm 8.60$ m, $Y = 7.36 \pm 7.20$ m. Neither differed significantly from zero, indicating that there was no directional bias in movement.

DISCUSSION

The results of this large-scale experiment add strong support to the hypothesis that corridors increase interpatch movement rates. Both of the open-habitat butterfly species in this study moved more frequently between patches connected by corridors in two different years (Table 3). If, as theory predicts, higher interpatch movement leads to larger regional population sizes or higher biodiversity, then the results of this study suggest that corridors will be an effective strategy in conservation, at least for certain species.

This study provides some evidence that corridors may be more effective at larger interpatch distances. At the smallest interpatch distance in this study (64 m), interpatch movement rates between connected and unconnected patches did not differ (Fig. 2). At this

distance, butterflies may have been capable of visually detecting the light environment of an adjacent patch through the planted pine. At larger interpatch distances, movement rates were always greater between connected patches. Haddad (1999) simulated butterfly movement as a correlated random walk and found that, as corridor length increased, proportionately more butterflies moved between connected patches than between unconnected patches. Most corridors proposed in management are longer than any corridor study. At long distances, the importance of corridors for population dynamics is likely to hinge on infrequent interpatch movements, at rates that are still orders of magnitude higher than movement rates between unconnected patches. These infrequent dispersal events will "rescue" local populations from extinction and will increase gene flow in fragmented landscapes.

Although movement rates were higher between connected patches, the butterfly species in this study were capable of moving between unconnected patches at every interpatch distance. When doing so, they often flew over the forest canopy (*personal observation*). There was no evidence that corridors increased emigration rates, which would be expected if forest boundaries had restricted butterfly movement (Kuussaari et al. 1996). The test for effects of corridors on emigration

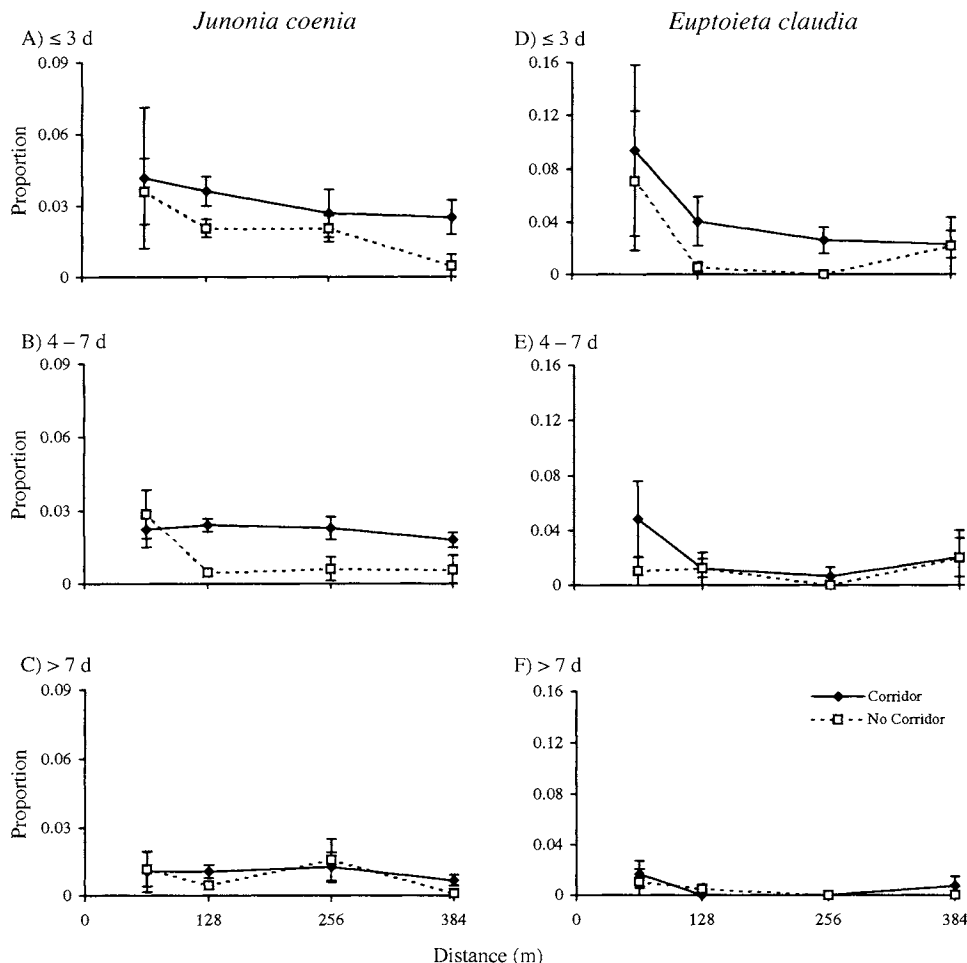


FIG. 4. Mean proportion (± 1 SE) of individuals marked in a patch that moved one of four distances to an adjacent patch, separated by the time from when a butterfly was first marked to when an interpatch movement was first detected. Black diamonds indicate mean proportions moving between patches connected by a corridor, and open squares indicate mean proportions moving between unconnected patches for (A) *Junonia coenia* (first interpatch move detected within 3 d), (B) *J. coenia* (within 4–7 d), (C) *J. coenia* (after 7 d), (D) *Euptoieta claudia* (within 3 d), (E) *E. claudia* (within 4–7 d), and (F) *E. claudia* (after 7 d).

was weak, because nothing was known about the fate of those butterflies that were never recaptured. However, these results provide further evidence that both species were strong colonists. Corridors should have even greater effects on other species that are more restricted in their movements by unsuitable habitats.

Although both species were capable of moving long distances, most observed movements were within the area of a patch (Table 2). That interpatch movements by these butterflies were dispersal events that may have influenced large-scale population dynamics can be inferred from the results that mean movement distances and mean net displacement after several days were less than the width of a patch (Table 2; Scott 1975b). For all but *Junonia coenia* in 1995, distance had a significant, negative influence on interpatch movement rates. Simple models predict lower movement rates between

patches separated by greater distances (Turchin and Theony 1993, Turchin 1998), and these predictions have been supported by several empirical studies (Fahrig and Paloheimo 1988, Harrison 1989, Turchin and Theony 1993, Koenig et al. 1997). The nonsignificant effect of distance for *J. coenia* in 1995 may have been due to low replication of distance classes in 1995, when only 17 patches were studied.

Only one food plant, *Linaria canadensis*, had a significant influence on *Junonia coenia* interpatch movement rates. No other plant resource measured in this study had a significant effect on interpatch movement rates of either butterfly species. *Euptoieta claudia* densities, which were significant in explaining *E. claudia* movement rates, may have been dependent on some combination of measured and unmeasured plant resources. Importantly, even when plant resources or con-

specific densities were included in analyses of interpatch movement rates, corridor and distance effects remained strongly significant.

Dividing the data by sex, time to first interpatch movement, and naturally occurring vs. transplanted individuals provided additional insights into the effects of corridors. For both species, males showed stronger positive responses to corridors than did females. Fewer females were recaptured (Table 2), perhaps because they were more difficult to detect, or because they moved greater distances. Corridors most strongly influenced butterflies soon after they were marked (Fig. 4). In longer time periods, the few butterflies that were not already recaptured would have had the opportunity to move greater distances. Transplanted butterflies showed no significant response to corridors. Butterflies might be expected to exhibit strong dispersal behavior immediately after being displaced, which would dampen corridors effects. However, in analyses of transplanted butterflies, sample sizes were reduced because butterflies were not released in every patch. One problem with dividing this data set by sex, time to first interpatch movement, or naturally occurring vs. transplanted butterflies was that the number of marked and recaptured butterflies in any category was quickly reduced, and estimates of movement rates were more variable.

Other factors may explain some of the additional variation in interpatch movement rates, including the abundances of unmeasured plant resources, microhabitat quality, or seasonal shifts in resources. After controlling for major landscape patterns and abundances of important resources, however, the results of this study show that corridors increase interpatch movement rates of both butterfly species.

The corridor concept is based on the assumption that higher connectivity will increase movement rates between patches. Ultimately, however, corridors will be considered effective in conservation if higher interpatch movement leads to higher metapopulation sizes or higher biodiversity. No previous study has shown that corridors increase interpatch movement rates, and that higher interpatch movement rates increase population sizes. Haddad and Baum (1999) showed that population sizes of the two butterfly species in this study were higher in connected patches. Although alternative mechanisms may have contributed to higher densities in patches connected by corridors, the combined results of this study and that of Haddad and Baum (1999) suggest that higher interpatch movement through corridors impacts the population sizes of these butterflies.

Applications to management

Habitat corridors are potentially valuable components of conservation strategies designed to combat the adverse effects of habitat fragmentation on plant and animal populations and on biodiversity. This study shows that corridors increase interpatch movement

rates for habitat-restricted species. How broadly can these results be generalized to other situations in conservation and management? The scale of experimental patches and corridors in this study falls within the range of spatial scales subjected to typical forest management in the southeastern United States. The result that corridors are effective at these scales is a promising one for current, large-scale corridor proposals (Mann and Plummer 1993, 1995, Rosenberg et al. 1997).

This experiment was created in a landscape composed of two strongly contrasting habitats: open areas that were rich in herbaceous plants, and densely planted, even-aged pine with a sparse herbaceous understory. Corridors proposed in conservation are usually the inverse of those studied here, in that forested corridors are usually surrounded by open, agricultural landscapes. The two butterfly species in this study strongly preferred open habitats and were almost never encountered within pine forests. However, the results of this study should inform proposals for forested corridors, where, as in this study, corridors contrast in suitability with the surrounding landscape for many species. For example, the results of this study lead to the prediction that forest corridors should increase interpatch movement rates of forest species through agricultural or urban landscapes. If so, then the conservation potential of corridors, especially for sensitive species, is high. One notable characteristic of species in this study that may differ from that of forest species is their adaptation to ephemeral environments. These two species were mobile and rapidly colonized newly created clearings. This characteristic may have caused the relative differences in movement rates between connected and unconnected patches to be lower than would be found for animals in more stable habitats.

At least two other concerns must be addressed before corridors are applied broadly. First, although this paper discusses corridor use by two species, corridors within any landscape will have positive, neutral, and negative effects on many different species (Simberloff et al. 1992, Rosenberg et al. 1997). Understanding interspecific responses to corridors has proven difficult. Because of the time and effort involved, mark-release-recapture techniques are unlikely to be generally used to characterize responses of different species to corridors. Other methodologies may permit more rapid assessment of the conservation potential of corridors. One common approach to evaluate corridor use is to measure population densities in connected patches (MacClintock et al. 1977, Fahrig and Merriam 1985, LaPolla and Barrett 1993, Dunning et al. 1995). An even more promising approach may be to determine corridor use from habitat associations or behaviors (Soulé and Gilpin 1991, Lima and Zollner 1996, Haddad 1997, 1999, Schultz 1998). Haddad (1999) showed that corridor use can be predicted from butterfly behaviors. In that study, butterflies that were restricted in their movements by habitat boundaries used corri-

dors, whereas butterflies that showed no behavioral response to habitat boundaries did not. Regardless of the methodology used, the conservation potential of corridors must be evaluated with regard to species that exhibit a wide range of responses to corridors.

A second important issue that must be addressed before corridors are implemented broadly is the trade-off between corridors and alternative strategies for habitat conservation, which may be less costly, but equally effective in preventing population extinction (Fahrig 1996, Rosenberg et al. 1997, Haddad and Baum 1999). In many cases, increasing habitat area, rather than creating a corridor, may be a better strategy to protect populations and biodiversity in fragmented landscapes. An empirical understanding of the broad effects of corridors on plant and animal populations can be used to measure their conservation potential, both ecologically and economically, against other management alternatives.

ACKNOWLEDGMENTS

I thank Ron Pulliam and Robert Cheney for insightful discussions about every aspect of this project. Kristen Baum, 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 provided excellent assistance in the field. Kristen Baum, Gretchen Daily, Jim Hanula, Gary Meffe, Jim Porter, Tom Sisk, and Barbara Taylor contributed helpful advice throughout this project, including suggestions on the manuscript. The experimental sites were implemented in collaboration with Robert Cheney and with support from the silvicultural, 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; an NSF predoctoral fellowship; and a University of Georgia University-wide Fellowship.

LITERATURE CITED

- Andreassen, H. P., S. Halle, and R. A. Ims. 1996. Optimal width of movement corridors for root voles: not too narrow and not too wide. *Journal of Applied Ecology* **33**:63–70.
- Bowne, D. R., J. D. Peles, and G. W. Barrett. 1998. Effects of landscape spatial structure on movement patterns of the hispid cotton rat (*Sigmodon hispidus*). *Landscape Ecology*, in press.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effects of immigration on extinction. *Ecology* **58**:445–449.
- Burkey, T. V. 1997. Metapopulation extinction in fragmented landscapes: using bacteria and protozoa communities as model ecosystems. *American Naturalist* **150**:568–591.
- Clark, A. H. 1932. The butterflies of the District of Columbia and vicinity. *Bulletin of the United States National Museum* 157. Government Printing Office, Washington, D.C., USA.
- Dunning, J. B., R. Borgella, K. Clements, and G. K. Meffe. 1995. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. *Conservation Biology* **9**:542–550.
- Ehrlich, P. R., and S. E. Davidson. 1960. Techniques for capture-recapture studies of Lepidoptera populations. *Journal of the Lepidopterists' Society* **14**:227–229.
- Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: a study in coevolution. *Evolution* **18**:586–608.
- Fahrig, L. 1996. Fragmentation and corridors: the misuse of theory in conservation biology. Supplement to the *Bulletin of the Ecological Society of America* **77**:134.
- Fahrig, L., and G. Merriam. 1985. Habitat patch connectivity and population survival. *Ecology* **66**:1762–1768.
- Fahrig, L., and J. Paloheimo. 1988. Effect of spatial arrangement of habitat patches on local population size. *Ecology* **69**:468–475.
- Haas, C. A. 1995. Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. *Conservation Biology* **9**:845–854.
- Haddad, N. M. 1997. Do corridors influence butterfly dispersal and density?: A landscape experiment. Dissertation. University of Georgia, Athens, Georgia, USA.
- . 1999. Corridor use predicted from behaviors at habitat boundaries. *American Naturalist* **153**, in press.
- Haddad, N. M., and K. A. Baum. 1999. An experimental test of corridor effects on butterfly densities. *Ecological Applications* **9**:623–633.
- Hanski, I., and M. E. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* **42**:3–16.
- Harrison, S. 1989. Long-distance dispersal and colonization in the Bay Checkerspot butterfly, *Euphydryas editha bayensis*. *Ecology* **70**:1236–1243.
- Koenig, W. D., D. Van Vuren, and P. N. Hooge. 1997. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology and Evolution* **11**:514–517.
- Kuussaari, M., M. Nieminen, and I. Hanski. 1996. An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. *Journal of Animal Ecology* **65**:791–801.
- Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. *American Naturalist* **130**:624–635.
- LaPolla, V. N., and G. W. Barrett. 1993. Effects of corridor width and presence on the population dynamics of the meadow vole (*Microtus pennsylvanicus*). *Landscape Ecology* **8**:25–37.
- Levins, R. 1969. Some genetic and demographic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**:237–240.
- Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* **11**:131–135.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- MacClintock, L., R. F. Whitcomb, and B. L. Whitcomb. 1977. Island biogeography and the "habitat islands" of eastern forest. II. Evidence for the value of corridors and minimization of isolation in preservation of biotic diversity. *American Birds* **31**:6–12.
- Machtans, C. S., M. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors. *Conservation Biology* **10**:1366–1379.
- Mann, C. C., and M. L. Plummer. 1993. The high cost of biodiversity. *Science* **260**:1868–1871.
- Mann, C. C., and M. L. Plummer. 1995. Are wildlife corridors the right path? *Science* **270**:1428–1430.
- Meffe, G. K., and C. R. Carroll. 1997. *Principles of conservation biology*. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Nicholls, A. O., and C. R. Margules. 1991. The design of studies to demonstrate the biological importance of corridors. Pages 49–61 in D. A. Saunders and R. J. Hobbs, editors. *Nature conservation 2: the role of corridors*. Surrey Beatty, Chipping Norton, New South Wales, Australia.

- Noss, R. F. 1987. Corridors in real landscapes: a reply to Simberloff and Cox. *Conservation Biology* **1**:159–164.
- Rosenberg, D. K., B. R. Noon, J. W. Megahan, and E. C. Meslow. 1998. Compensatory behavior of *Ensatina eschscholtzii* in biological corridors: a field experiment. *Canadian Journal of Zoology* **76**:117–133.
- Rosenberg, D. K., B. R. Noon, and E. C. Meslow. 1997. Ecological role of linear conservation areas for maintaining biological diversity. *BioScience* **47**:677–687.
- SAS Institute. 1992. SAS/STAT user's guide, release 6.03, fourth edition. SAS Institute, Cary, North Carolina, USA.
- Schultz, C. B. 1998. Dispersal behavior and its implications for reserve design in a rare Oregon butterfly. *Conservation Biology* **12**:284–292.
- Scott, J. A. 1975a. Movement of *Precis coenia*, a “pseudoterritorial” submigrant (Lepidoptera: Nymphalidae). *Journal of Animal Ecology* **44**:843–850.
- . 1975b. Flight patterns among eleven species of diurnal Lepidoptera. *Ecology* **56**:1367–1377.
- Simberloff, D., and J. Cox. 1987. Consequences and costs of conservation corridors. *Conservation Biology* **1**:63–71.
- Simberloff, D., J. A. Farr, J. Cox, and D. W. Mehlman. 1992. Movement corridors: conservation bargains or poor investments? *Conservation Biology* **6**:493–504.
- Soulé, M. E., and M. E. Gilpin. 1991. The theory of wildlife corridor capability. Pages 3–8 in D. A. Saunders and R. J. Hobbs, editors. *Nature conservation 2: the role of corridors*. Surrey Beatty, Chipping Norton, New South Wales, Australia.
- Sutcliffe, O. L., and C. D. Thomas. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. *Conservation Biology* **10**:1359–1365.
- Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, Massachusetts, USA.
- Turchin, P., and W. T. Theony. 1993. Quantifying dispersal of southern pine beetles with mark–recapture experiments and a diffusion model. *Ecological Applications* **3**:187–198.
- Wilson, E. O., and E. O. Willis. 1975. Applied biogeography. Pages 522–534 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Belknap Press, Cambridge, Massachusetts, USA.
- Workman, S. W., and K. W. McLeod. 1990. Vegetation of the Savannah River Site: major community types. Savannah River Site, Aiken, South Carolina, USA.
- Zhang, Z., and M. B. Usher. 1991. Dispersal of wood mice and bank voles in an agricultural landscape. *Acta Theriologica* **36**:239–245.

APPENDIX A

A table presenting the transition matrix of total interpatch movements in 1996 for *Junonia coenia* is available in ESA's Electronic Data Archive: *Ecological Archives* A009-005-A1.

APPENDIX B

A table presenting the transition matrix of total interpatch movements in 1996 for *Euptoieta claudia* is available in ESA's Electronic Data Archive: *Ecological Archives* A009-005-A2.