

Corridor Use Predicted from Behaviors at Habitat Boundaries

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ABSTRACT: Through empirical studies and simulation, I demonstrate how simple behaviors can be used in lieu of detailed dispersal studies to predict the effects of corridors on interpatch movements. Movement paths of three butterfly species were measured in large (1.64 ha) experimental patches of open habitat, some of which were connected by corridors. Butterflies that “reflected” off boundaries between open patches and the surrounding forest also emigrated from patches through corridors at rates higher than expected from random movement. This was observed for two open-habitat species, *Eurema nicippe* and *Phoebis sennae*; however, edges and corridors had no effect on a habitat generalist, *Papilio troilus*. Behaviorally based simulation models, which departed from correlated random walks only at habitat boundaries, predicted that corridors increase interpatch movement rates of both open-habitat species. Models also predicted that corridors have proportionately greater effects as corridor width increases, that movement rates increase before leveling off as corridor width increases, and that corridor effects decrease as patch size increases. This study suggests that corridors direct movements of habitat-restricted species and that local behaviors may be used to predict the conservation potential of corridors in fragmented landscapes.

Keywords: corridors, conservation, simulation, movement, behavior, landscape.

One popular conservation strategy for fragmented landscapes that has emerged directly from ecological theory is to connect isolated patches with corridors (Wilson and Willis 1975; Mann and Plummer 1993, 1995; Meffe and Carroll 1997; Rosenberg et al. 1997). If corridors function as intended and increase animal movement rates between patches, they should provide a source of immigrants to prevent population extinction and inbreeding. However, little empirical evidence supports the importance of corridors in population dynamics or in conservation (Simberloff et al. 1992; Rosenberg et al. 1997). Methods are

urgently needed to assess rapidly the positive and negative effects of corridors on species that vary in behaviors and life-history characteristics. In this study, I integrate behavioral results from large, experimental landscapes with simulation models to predict corridor use by butterflies.

Behavioral approaches for assessing corridor use may be superior to other common approaches for several reasons. First, traditional approaches are extremely intensive and are not easily employed to study more than one species (Machtans et al. 1996; Haddad 1999). This is particularly true of mark-release-recapture studies, which have been used to quantify directly the effects of corridors on interpatch movement rates (Haas 1995; Andreassen et al. 1996; Sutcliffe and Thomas 1996; Haddad 1999). Second, results of many previous studies are open to alternative interpretations. In one common approach, corridor use is inferred from population densities in connected and unconnected patches. Corridors should increase average densities in connected patches due to increased rates of immigration and recolonization (Brown and Kodric-Brown 1977). While higher densities are often found in connected patches (MacClintock et al. 1977; Fahrig and Merriam 1985; La Polla and Barrett 1993; Dunning et al. 1995; Haddad and Baum 1999), higher densities may be explained by alternative hypotheses, including higher immigration into corridors from matrix habitats and improved habitat quality in connected patches (Haddad and Baum 1999). A third shortcoming of previous approaches is that they have failed to accumulate general support for corridor use. One limitation with previous studies is that they generally have not been experimental (Rosenberg et al. 1997) and that corridor effects are often confounded by other factors, such as patch size and shape, that vary in natural landscapes. Another is that corridor studies are limited in their taxonomic breadth. Yet, corridors are likely to have positive, neutral, and negative effects on many different species in a landscape (Simberloff et al. 1992; Rosenberg et al. 1997).

A new approach is needed that enables rapid evaluation of the conservation potential of corridors for many different species. Because corridors are intended to influence animal behaviors and direct animal movements, a behavioral approach may provide the best general predictions

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about corridor use (Soulé and Gilpin 1991; Lima and Zollner 1996; Tischendorf and Wissel 1997; Schultz 1998; Turchin 1998). Corridors would effectively direct animals to other patches under two conditions (Rosenberg et al. 1997). First, an animal must be more likely to leave a patch through a corridor than would be expected by random movement. Second, a greater proportion of animals must successfully disperse through corridors than through alternative, less suitable habitats.

Movement behaviors at habitat boundaries may provide particularly strong indication of corridor use (Wiens et al. 1985; Soulé and Gilpin 1991; Turchin 1991; Kuussaari et al. 1996; Tischendorf and Wissel 1997; Schultz 1998). Boundaries may bias turning behavior, reducing permeability of edges to dispersing animals (Stamps et al. 1987). Biased turning at habitat boundaries would increase the distance an animal moves within a patch, which would increase the probability that it encounters a corridor (Tischendorf and Wissel 1997). Similarly, biased turning at the edge of a corridor would direct movement along a corridor.

Here, I describe a behavioral approach to assess corridor use by butterflies. In the same, large-scale experiment as this study, I have conducted mark-release-recapture studies and shown how corridors increase interpatch movement rates of two open-habitat butterfly species (different from species in this study; Haddad 1999), and I have demonstrated that corridors increase population densities of open-habitat species but not of a habitat generalist species (two of the four species in this study; Haddad and Baum 1999). This article describes a novel approach to evaluating corridor use, and the other studies provide some validation of simulation predictions in this study.

Field Methods

Large-Scale Corridor Experiment

The experiment was conducted at the Savannah River Site, South Carolina (details of the design are presented in Haddad 1999). The experiment consisted of patches and corridors of open habitats, which were created by harvesting within large forested areas managed for *Pinus taeda* and *Pinus elliotii*. The open patches and corridors were similar, and both supported diverse and productive herbaceous vegetation (including the host and flowering plants of my study species). In sharp contrast, trees were planted at high densities in the surrounding forests, preventing the development of herbaceous vegetation.

The experiment consisted of equal-sized (1.64 ha), square patches of open habitat (Haddad 1999). A total of 27 patches were created within five contiguous stands of pine forest. The size of square patches was fixed at 128 m

on a side, and all patches within a contiguous forest stand were oriented in the same direction (though orientation varied among stands). I varied two patch characteristics: distance from other patches and connection to another patch by a corridor. Corridors were 32 m wide. Each of the 19 connected and eight isolated patches was considered an independent experimental unit in behavioral analyses. Patches were separated by 64 m (two connected, two unconnected), 128 m (three connected, nine unconnected), 256 m (two connected, two unconnected), or 384 m (three connected, one unconnected). Because observations of interpatch movements were rare, distance was not considered in behavioral analyses.

A grid system was established within each patch to permit rapid assessment of spatial locations. Sixteen meters from the edge of each patch, a 3 × 3 grid of cells was demarcated using a laser transit. Grid cells were 32 m × 32 m, and the corners were marked with a 3.3-m-tall polyvinyl chloride pipe (fig. 1). A second system of grid subcells (8 m × 8 m) was marked with two additional pipes within each cell (fig. 1). This grid allowed determination of spatial locations of individual butterflies at a resolution of 8 m. A grid system was also created within the forest. This grid consisted of permanent markers at 32-m intervals along flagged transects that were separated by 64 m. These transects extended for at least 128 m from the outermost patches and allowed determination of forest locations at a resolution of 16 m.

Study Species

I studied three butterfly species that varied in their movement abilities and in their preferences for open habitats. *Eurema nicippe* (sleepy orange) was least vagile and strongly preferred open habitats, where its host and nectar plants, *Cassia* sp. and *Crotolaria* sp., were abundant. Individuals were likely to leave patches within hours to days. *Phoebis sennae* (cloudless sulphur) was a vagile, open-habitat species. It was seasonally migratory, moving northwest in the spring and southeast in the fall. The resident population in midsummer was capable of moving long distances (on the order of many kilometers). Like *E. nicippe*, *P. sennae* used *Cassia* sp. and *Crotolaria* sp. as host and nectar resources. Unlike the other two species, *Papilio troilus* (spicebush swallowtail) was a habitat generalist. Like *P. sennae*, *P. troilus* was extremely vagile and usually left a patch within hours. Its host plant, *Sassafras albidum*, was found in open patches, corridors, and pine forests (though it was most productive in open habitats). However, its nectar resources, including *Carduus repandus* and *Gelsemium sempervirens*, were limited to open habitats. Importantly, none of the host or flower resources differed in

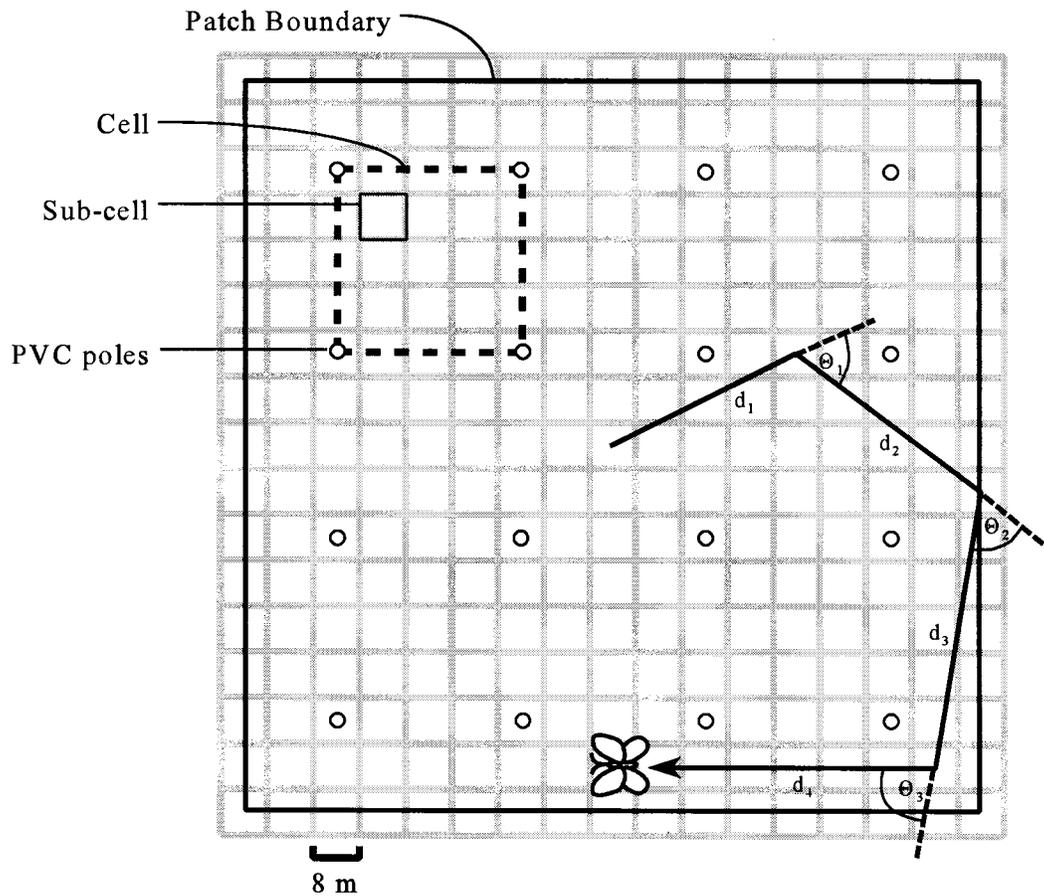


Figure 1: Example of an experimental patch and data collection. Grid cells and subcells were marked with polyvinyl chloride (PVC) poles (see text), allowing data to be recorded at a resolution of 8 m. Butterfly movement paths were recorded on maps of each patch. Measures extracted from the movement paths include movement distances (d_i 's), turning angles between two movement steps (θ_i 's), and duration of each movement step (not depicted).

densities between connected and isolated patches (Haddad and Baum 1999).

The butterflies in this study were strong colonists and were adapted to ephemeral habitats. This characteristic differs from many threatened or endangered species, which are often less vagile and more isolated in patchy landscapes. Other species that are highly restricted to a specific habitat would be expected to show higher corridor use than species in this study.

Field Studies of Butterfly Behaviors

Butterfly movement paths were recorded from April–October 1995 and April–June 1996. Each patch was surveyed between 1000 and 1700 hours, except when it rained. In 1995, each survey consisted of 5-min observations within each of nine cells (fig. 1). In 1996, patches were divided into eight 128-m-long transects, each sep-

arated by 16 m. Each transect was walked in 6 min. Survey time excluded time spent observing butterflies and recording data. While survey methods differed between years, methods for tracking individual butterflies did not, and results gathered in the 2 yr were comparable.

During each survey, an attempt was made to record movement paths of each individual of the three study species. Movement paths of individual butterflies were recorded on maps of each patch (see example, fig. 1). Once a butterfly was encountered, a handheld timer was activated, and the initial point of sighting was recorded to the nearest subcell. Movement steps were approximated in discrete vectors that ended when a butterfly turned or stopped flying to feed, to rest, or to oviposit. Turns were recorded only if the subsequent movement step extended at least 4 m beyond a line formed by the centers of grid subcells (fig. 1). This definition of a turn excluded small-scale behaviors characteristic of many butterfly species.

However, even in small-scale studies, measuring all butterfly turns is impractical (Turchin et al. 1991). Data resolution was assumed appropriate to interpret butterfly responses to large landscape features such as edges and corridors. After a butterfly stopped or turned, the next movement step consisted of the straight-line movement to the next stop or turn. The end points of movement vectors were recorded to the nearest subcell, successive movement steps were timed, and each individual was observed until it was lost from view or until it stopped for 10 min.

Statistical Analysis

Movement paths were divided into discrete movement steps. Each step was characterized by a direction, length, and duration. Turning angles were computed from pairs of movement steps (Kareiva and Shigesada 1983; Turchin et al. 1991). I analyzed several behaviors that might influence movement through patches and corridors. I analyzed symmetry and persistence in movement direction by comparing mean sines and cosines of turning angles with zero (Turchin et al. 1991). I evaluated habitat-specific changes in turning behavior. I compared movement speeds and distances between individual butterflies by first computing a mean movement speed and distance for each butterfly in each habitat. I then analyzed these means across individual butterflies using maximum likelihood estimation (Proc Lifereg; SAS Institute 1992). Because distributions of movement distances and speeds were characterized by many low values and infrequent high values, data were assumed to follow a lognormal distribution. Rates of net displacement in each habitat were compared graphically for each species.

I developed a measure of turning bias to estimate the effects of forest edges on turning. I assigned movement directions after encounter with a forest boundary to one of four 90° classes. These classes formed four quadrants, with one axis being the forest edge and the origin at the location of the turn. If butterflies do not bias their turning when moving toward the edge, the ratio of turns into or out of the patch should equal 1. I evaluated turning bias at increasing distances from the forest edge as the departure of this ratio from one using a *G*-test of goodness of fit, adjusted by William's correction for small sample sizes (Sokal and Rohlf 1981).

To determine corridor use, I compared emigration from patches through corridors to emigration from the rest of the patch. Corridor width (32 m) was 1/16 the length of the patch perimeter (512 m). If butterfly movement paths followed a random course with respect to corridors, the expected proportion of butterflies leaving the patch

through a corridor would equal corridor width/patch perimeter = $32/512 = 0.0625$.

Empirically Based Model

I developed a simulation model, parameterized with the behavioral data described above, to link local movement behaviors to landscape-level dispersal. The model was a hybrid that drew on correlated random walk models of movement (which are well developed for insects; Kareiva and Shigesada 1983; Turchin 1991, 1998) and predicted the consequences of habitat-specific variation in behaviors for interpatch movement rates. In the model, random draws were made from nonparametric distributions of empirical data for step distances and turning angles.

To model movement through patchy landscapes more realistically, the model differed from a correlated random walk in three ways. First, step distances and turning angles were sampled from habitat-specific empirical distributions. Second, because of correlations in movement parameters (Haddad 1997), the model sampled from joint distributions of movement distance and turning angle. Third, to simulate the effects of boundaries on movement more realistically, turning behavior at habitat boundaries depended on distance from and orientation to the habitat edge. The magnitude of boundary effects on movements varied with distance from the edge and corner of a patch or corridor (see "Results"; Haddad 1997). Within 20 m of the corner or 12 m of the edge, the patch was divided into three areas (0–4 m from the corner, 4–20 m from the corner, or the remaining area). The direction of the next movement step in one of these areas or in the corridor was sampled from empirical distributions of angle relative to the edge, rather than turning angle.

Simulated landscapes consisted of three patches, oriented in a line. The center patch was connected to one of the two outer patches by a corridor. Except when attributes of the patches or corridors were varied, I fixed the size of square patches at 1.64 ha, corridor width at 32 m (as in the experiment), and interpatch distance at 512 m. Three landscape attributes were varied: distance between patches, corridor width, and patch size. Only the size of the outer two patches (one connected, one isolated) changed. A buffer equal to three patch widths surrounded the outermost patches in all directions; individuals that reached the landscape boundary were absorbed. At each interpatch distance, corridor width, and patch area, 100,000 butterfly paths were simulated, beginning at the center of the center patch. For each species, the number of movement steps was fixed (1,000 steps for *Papilio troilus* and *Phoebis sennae* and 500 steps for *Eurema nicippe*). Average adult life spans are poorly known for these species, so total movement steps were order of magnitude approximations. Movement

paths were terminated once an individual colonized either of the outer patches. The model predicted interpatch movement rates to connected and unconnected patches.

I conducted two analyses of model sensitivity. First, the proportion of long, straight movements measured in the behavioral study may have been underestimated. Movement paths in the corridors and forest were often truncated when butterflies were lost from view. To explore the effects of this sampling deficiency, I simulated *P. sennae* movement paths after adding straight movements of 64 m to the empirical data from the corridors and forest. In a second sensitivity analysis, I varied more than one landscape characteristic at a time to determine if my choice of fixed landscape characteristics had a qualitative influence on model results.

Results

Behavioral Studies

Movement paths of 1,306 individual *Phoebis sennae* were recorded. Migratory *P. sennae* oriented movement paths to compass direction (Haddad 1997). Seasonal migrants (938 movement paths in the early spring and fall) were separated from nonmigrants (368 movement paths from July 1 to August 29) for analyses. Movement paths of 1,075 individual *Papilio troilus* and 141 individual *Eurema nicippe* were recorded. An average of 4.2 movement steps were recorded for each movement path. Some movement paths, especially those of migratory *P. sennae*, were represented by one step. Others were characterized by many movement steps.

Within patches, the distribution of turning angles was symmetric around zero for all species, indicating no bias in turning direction (table 1). Migratory *P. sennae*, with a relatively high mean cosine, showed the strongest persistence in direction. Mean cosines of *E. nicippe* and *P. troilus* were also significantly >0, indicating a significant forward bias in movement (table 1).

Turning angles within the corridors differed most from turning angles within the patches and forest (fig. 2). Within

patches, all species had a high proportion of 0°–90° turns. Differences between patch and forest turning behavior were small (except for nonmigratory *P. sennae*'s higher proportion of reversals). In corridors, however, *E. nicippe* and *P. sennae* moved straight ahead at higher frequencies than they did within patches (fig. 2). Speeds did not differ between habitat types (table 2). For all species, step distances were longer in corridors than in patches. For *E. nicippe* and female *P. troilus*, step distances were also longer in the forest than in patches. Movement speed and distance were significantly, positively correlated for all species (table 2).

Net displacement measured the distance traveled from the initial point of observation. I graphed net displacement for successive movement steps (fig. 3). The average time between movement steps includes time spent ovipositing, nectaring, and stopping. For all species, the rate of net displacement was slowest within patches and was similar within the forest and corridors.

Habitat Boundaries and Corridor Use

For butterflies moving toward the edge, reflective bias was calculated as the following proportion: turns into the patch/turns out of the patch (P_i/P_o ; see fig. 4). For two species, there was a strong reflective bias in turning behavior at habitat boundaries (fig. 4). *Eurema nicippe* ($G = 8.76$, $P < .001$) and *P. sennae* ($G = 30.71$, $P < .001$, migrant: $G = 12.63$, $P < .001$) were three to four times more likely to turn into the patch at the forest edge. Forest boundaries influenced movement direction at up to 8 m from the patch boundary. The turning angle of *P. troilus* was unbiased at the forest boundary ($G = 1.00$, $P > .10$).

Those butterflies with biased turning at habitat boundaries were also more likely to leave patches through corridors than expected by random movement. The mean proportion leaving patches through corridors was 2.5–4.5 times greater than expected by chance (fig. 5). *Papilio troilus* left patches through corridors at rates expected by random movement.

Table 1: Mean (\pm SE) sine and cosine of turning angles within patches

Species	N	cos (θ)			sin (θ)		
		Mean \pm SE	t	P	Mean \pm SE	t	P
<i>Eurema nicippe</i>	319	.24 \pm .04	6.50	.001	.04 \pm .04	.96	NS
<i>Papilio troilus</i>	2,825	.19 \pm .01	15.22	.001	.01 \pm .01	.84	NS
<i>Phoebis sennae</i>	1,355	.03 \pm .02	1.89	.06	.01 \pm .02	.51	NS
<i>P. sennae</i> migrant	1,637	.39 \pm .01	26.02	.001	-.02 \pm .02	-1.13	NS

Note: Mean sine never differed from 0, indicating no left or right bias in turning direction. Values of mean cosine close to 1 indicate strong directional persistence and close to -1 indicate frequent reversals. All turns, including multiple turns for each butterfly, were used in these analyses.

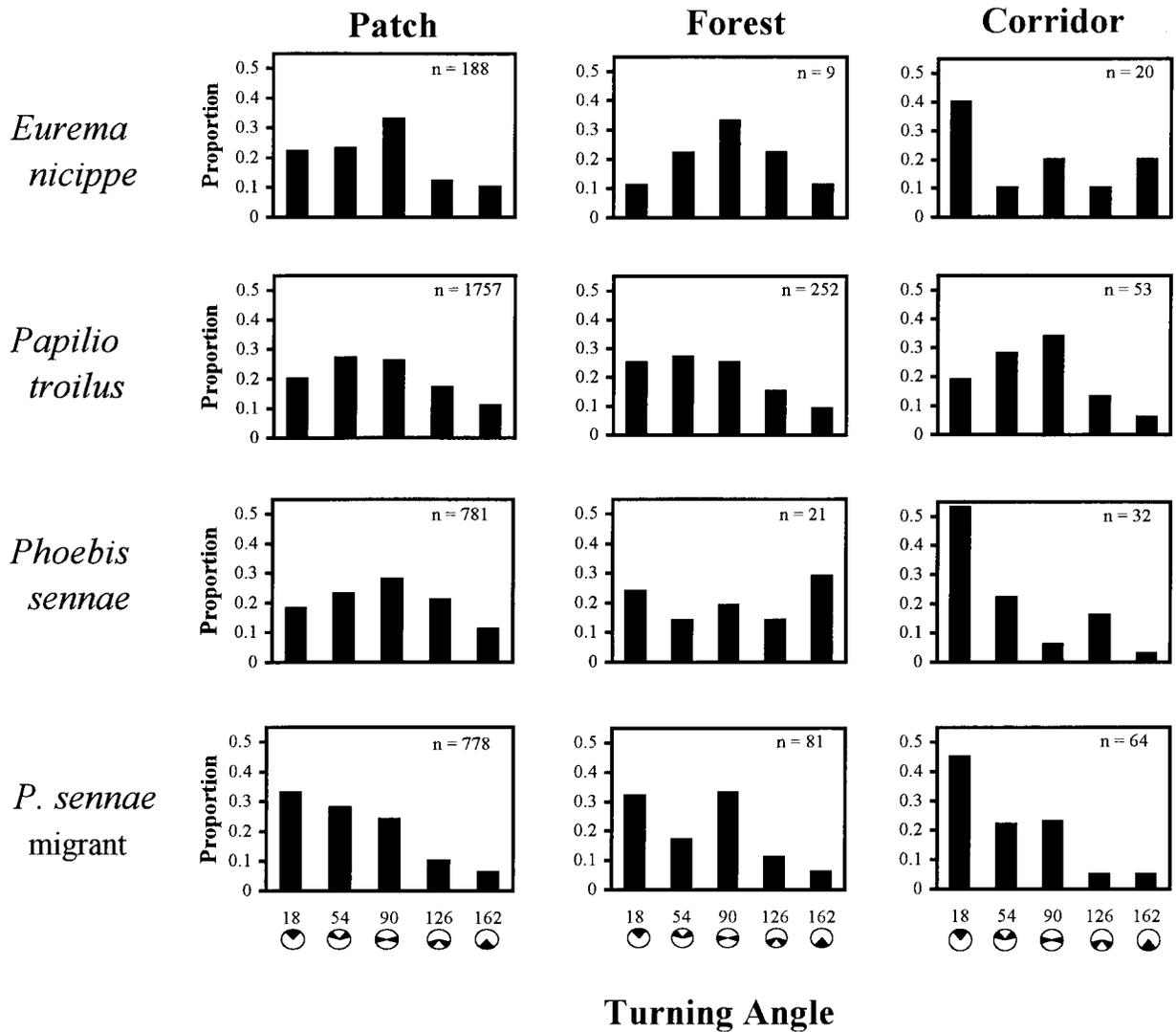


Figure 2: Frequency distributions of turning angles in patches, corridors, and forest for each butterfly species. Within-patch turning included data at distances >16 m from the forest edge. Because turning direction was not biased (see table 1), the X-axis is the absolute value of turning angles. The turning angles represented by the X-axis classes are shaded in the circular diagram below the axis.

Simulation Results—Corridors and Interpatch Movements

Simulation models predicted that corridors increase interpatch movement rates for both open-habitat butterfly species (figs. 6, 7, 8). The presence of a corridor had little effect on *P. troilus* (figs. 6C, 7C, 8C). For *P. sennae* and *E. nicippe*, corridors had a proportionately greater impact on movement rates as interpatch distance increased (fig. 6A, B), the effects of corridors increased as corridor width increased and then leveled off at a maximum (fig. 7A, B), and the effects of corridors diminished as patch size increased (fig. 8A, B).

In sensitivity analyses, adding long straight movements

in the corridor increased movement rates between connected patches, increasing total corridor effects. Adding long straight movements in the forest reduced interpatch movement rates between both connected and unconnected patches. Varying my choice of fixed landscape characteristics had no qualitative effect on model results.

Discussion

The results of this study show how simple behaviors may be used to predict corridor use by animals. A behavioral approach may have several advantages over other methods

Table 2: Mean (\pm 95% confidence interval) movement speeds and distances

	<i>Eurema nicippe</i>	<i>Papilio troilus</i>		<i>Phoebis sennae</i>	
		Female	Male	Migrant	Summer
Speed (m/s):					
Patch	1.91 (1.7, 2.1)	1.49 (1.4, 1.6)	2.31 (2.2, 2.5)	3.67 (3.5, 3.8)	2.73 (2.5, 3.0)
Corridor	1.75 (1.1, 2.7)	1.49 (1.0, 2.3)	3.89 (2.1, 4.0)	3.27 (2.9, 3.7)	3.01 (2.3, 3.9)
Forest	2.84 (2.1, 3.9)	1.64 (1.4, 1.9)	2.11 (1.8, 2.4)	3.41 (3.2, 3.6)	2.88 (2.4, 3.4)
Distance (m):					
Patch	21.88 (19.4, 24.6)	19.82 (18.8, 20.9)	23.90 (22.7, 25.2)	36.37 (34.6, 38.2)	24.77 (23.1, 26.5)
Corridor	86.97** (58.2, 130.0)	30.60* (23.7, 39.6)	37.90* (28.8, 49.9)	49.4** (42.1, 58.1)	36.61** (29.4, 45.6)
Forest	32.94* (24.6, 44.1)	25.61** (23.3, 28.1)	25.64 (23.0, 28.6)	34.59 (32.2, 37.1)	23.50 (27.1, 20.4)
Correlation	.151	.172	.167	.230	.296

Note: For each individual butterfly, one mean speed and distance was calculated for each habitat by averaging all movement steps. Means calculated across all individuals are presented (below). Data considered in these analyses were >16 m from a forest boundary. Both variables were lognormally distributed and were compared using Proc Lifereg in SAS (SAS Institute, 1992). χ^2 tests indicate differences in the speed or distance of movement steps between patches and other habitats. In every case, movement speed and distance were significantly, positively correlated ($P < .01$).

* $P < .01$.

** $P < .001$.

to assess the conservation value of corridors. First, if the relationship between simple movement behaviors and corridor use is a general one, then corridor use can be assessed quickly for many different species. Second, a behavioral approach would involve less handling and trampling, which is an important concern for threatened and endangered species and for their habitats, where corridors are typically proposed. Third, habitat specific movement behaviors provide general information that can be used to assess the effects of many different landscape configurations on animals. Behavioral methods may offer a robust approach to predict the effects of corridors, and other patterns in fragmented landscapes, on animal populations (Wiens et al. 1993; Beier 1995; Lima and Zollner 1996; Pulliam and Dunning 1997; Tischendorf and Wissel 1997; Schultz 1998; Turchin 1998).

Behavioral Evidence for Corridor Use

Several results from the empirical study demonstrated how behaviors of open-habitat butterfly species lead to corridor use. First, turning was biased at habitat boundaries, which should increase time spent and distance traveled within a patch and increase the probability that corridors were encountered. Second, butterflies that were less likely to cross habitat boundaries were more likely to emigrate from patches through corridors. Third, once open-habitat spe-

cies were in a corridor, movement distances were longer and movement directions were more persistent than in the patches or forest. Corridors, which are composed of two linear edges, may more strongly bias butterfly movements than boundaries in patches. Importantly, behavioral evidence for corridor use was consistent for each species. *Eurema nicippe* and *Phoebis sennae* turning was biased at habitat boundaries, emigration was higher through corridors than expected by random movement, and, once in the corridor, movement was more persistent. Alternatively, I detected no movement bias for *Papilio troilus* caused by corridors.

Model Predictions and Corridor Use

Results of simulated movement paths through landscapes that varied in interpatch distance, patch width, and patch size provided important messages for conservation planning. For those species that showed a behavioral response to edges and corridors, the model predicted higher movement rates between connected patches. In addition, corridors had a proportionately greater effect on movement rates as interpatch distance increased. This finding may be particularly important in conservation. Corridors are intended to increase recolonization and gene flow over generational timescales. Differences in movement rates at long interpatch distances, between very low coloni-

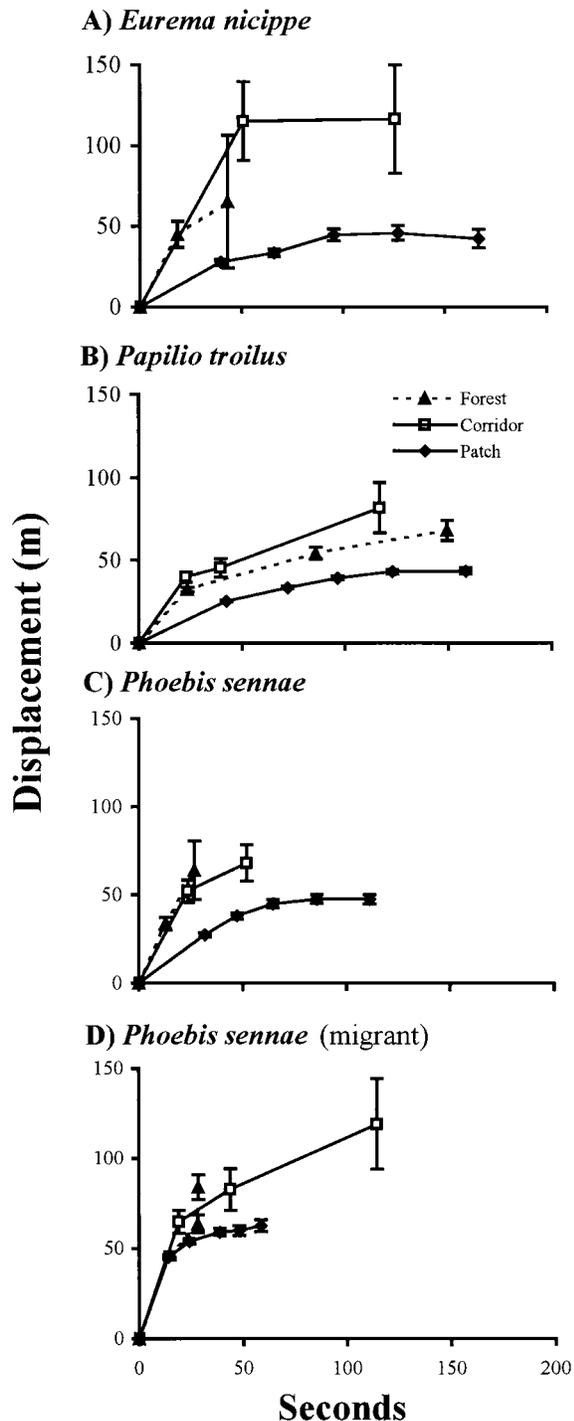


Figure 3: Habitat-specific mean displacement for successive movement steps, where steps are represented by consecutive points from 1 to n . The X-axis is mean duration of each step and includes time spent nectaring, ovipositing, or resting. The Y-axis is mean displacement, measured as straight line distance from the first point of observation to the current step. A, *Eurema nicippe*. B, *Papilio troilus*. C, *Phoebis sennae*. D, *Phoebis sennae* (migrant).

zation in the presence of corridors and no colonization in their absence, may be critical to maintaining dynamic metapopulations.

The simulation result that corridor effects on interpatch movement rates increase asymptotically as corridor width increases supports an emerging consensus that has been demonstrated in experimental, behavioral, and theoretical studies (fig. 7A, B; Soulé and Gilpin 1991; Andreassen et al. 1996; Tilman et al. 1997; Tischendorf and Wissel 1997). The maximum was determined by two factors. First, the effects of habitat boundaries on butterfly movement extended no further than 8 m from the edge. At longer distances from the forest edge, corridors had little effect on movement direction. For other species, especially habitat interior species that strongly avoid the edge, wider corridors could be more effective at increasing interpatch movement rates. A second factor determining corridor effectiveness was that wide corridors take on the characteristics of a patch and butterflies were more likely to remain within wider corridors. While the widest corridors did not appear to increase interpatch movement rates, they may provide an added benefit by serving as habitat for threatened or endangered species.

Finally, the effects of corridors diminished as patch size increased. To a dispersing individual, larger patches occupy a greater fraction of the horizon (MacArthur and Wilson 1967; Fahrig and Paloheimo 1988; Harrison 1989). As patch size increases relative to interpatch distance, the probability that it is colonized by individuals moving in random directions increases. This suggests that as patch size increases relative to the distance between patches, the benefits of corridors diminish. In such cases, enlarging habitat areas, or adding habitat "stepping stones" that promote dispersal success, should be the focus of management strategies.

The few interpatch movements observed in behavioral studies do not provide reliable validation of simulation results. In another study within the same experiment (Haddad 1999), interpatch movement rates for two other open-habitat butterfly species were estimated using mark-release-recapture techniques. As was predicted for the open-habitat butterflies in this study, the butterflies in the mark-release-recapture study also moved more frequently between connected patches. In addition, mark-release-recapture results demonstrated that corridors had stronger effects at longer interpatch distances. Compared to mark-release-recapture results, the model predicted higher interpatch movement rates. Higher rates in the model may have been due to the more sedentary nature of butterfly species in the mark-release-recapture study or to omniscient sampling in the model.

Models assumed that local movement behaviors could be used to predict landscape-level movements. While the

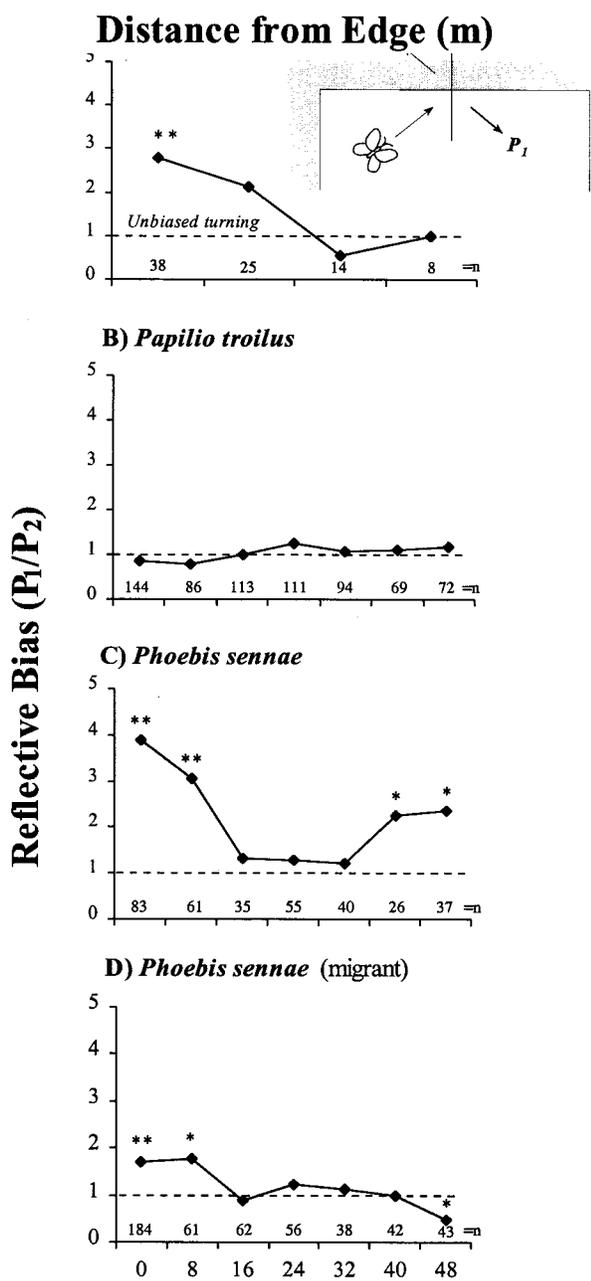


Figure 4: For butterflies moving toward the patch boundary, reflective bias is the proportion of turns away from the forest edge relative to turns toward the forest edge (P_1/P_2 ; see diagram). Butterflies moving in random directions are expected to turn left or right with equal frequency. Values >1 indicate biased movement toward the interior of the patch, while values <1 indicate biased movement out of the patch. Differences between observed and expected values were compared using a G-test for goodness of fit (** $P < .001$; * $P < .05$) for A, *Eurema nicippe*; B, *Papilio troilus*; C, *Phoebis sennae*; and D, *Phoebis sennae* (migrant).

model was supported by large quantities of movement data and the modeling approach is supported by other studies with insects within a single habitat (see Turchin 1998), two caveats should be noted when interpreting model results. First, low interpatch movement rates were caused in part by the intentionally simple nature of the simulated landscapes, which tested the effects of corridors in a direct comparison. These rates would lead to rapid extinction in the context of a metapopulation model. The butterflies in this study were vagile, and a more realistic and dynamic metapopulation model of these butterflies would simulate movements within a much larger landscape. Second, one deficiency in many movement studies is poor estimation of long-distance movements (Ruckelshaus et al. 1997). Movement data in this study included very long movements, on the order of hundreds of meters. However, especially in the forest and corridors, dispersing butterflies were often lost from view. When I added long distance movements in sensitivity analyses, the magnitude of corridor effects changed, but the qualitative predictions of the model did not.

The Conservation Value of Corridors

Ultimately, the success of corridors depends on their ability to increase population sizes, gene flow, and biodiversity in fragmented landscapes. The behavioral and simulation results from this study are corroborated by population studies within the same experiment (Haddad and Baum 1999). That study showed that *P. sennae* densities were higher in connected patches than in isolated patches, while *P. troilus* densities were not. Taken with the results of the previous study, behavioral and simulation results in this study support the idea that corridors direct interpatch

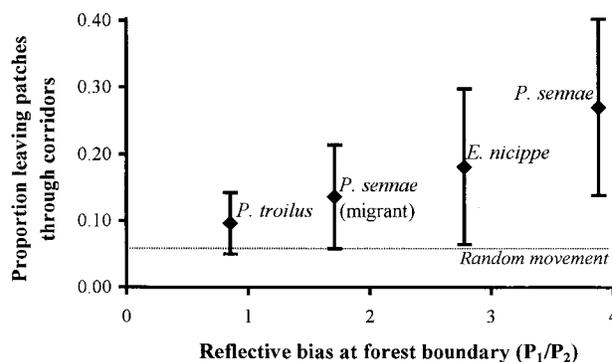


Figure 5: Mean proportion ($\pm 95\%$ confidence interval) of individuals leaving the patch through the corridor plotted against reflective bias at the forest edge (fig. 4). If movement direction was random, the expected proportion leaving the patch through a corridor equals 0.0625 (corridor width/length of patch perimeter = 32 m/512 m).

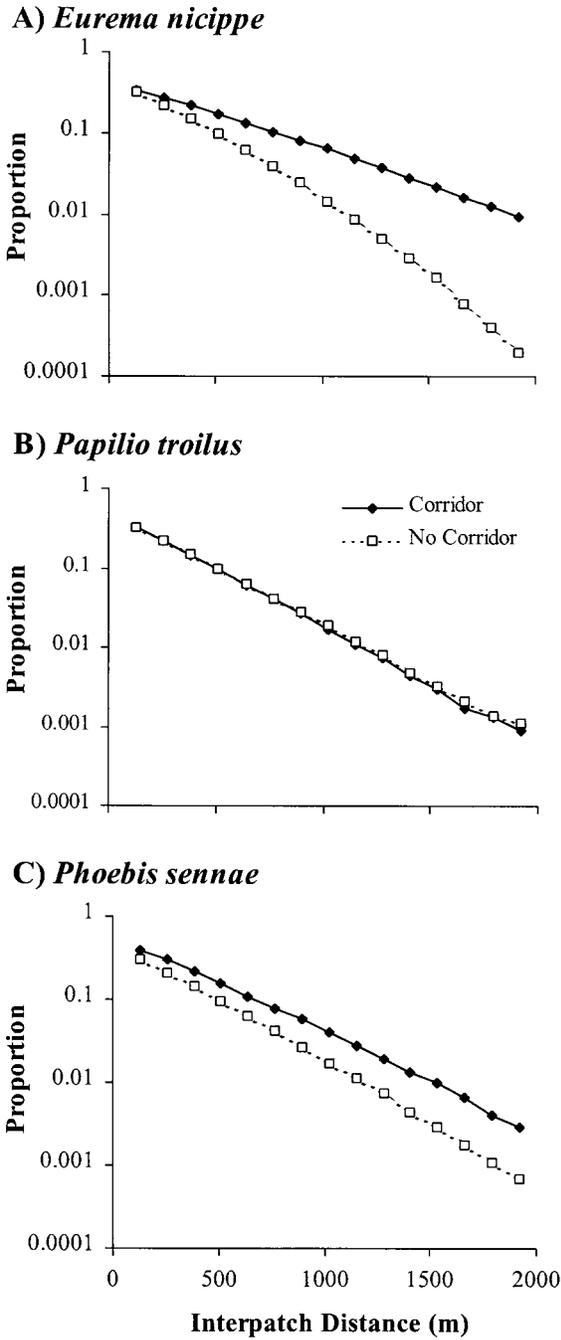


Figure 6: Interpatch movement rates predicted from simulated movement paths as the distance between patches varied. At each interpatch distance, 100,000 butterflies were released in the center of the center patch, and the path was terminated once a butterfly colonized an outer patch. Corridor width (32 m) and patch size (1.64 ha) were held constant. A, *Eurema nicippe*. B, *Papilio troilus*. C, *Phoebis sennae*.

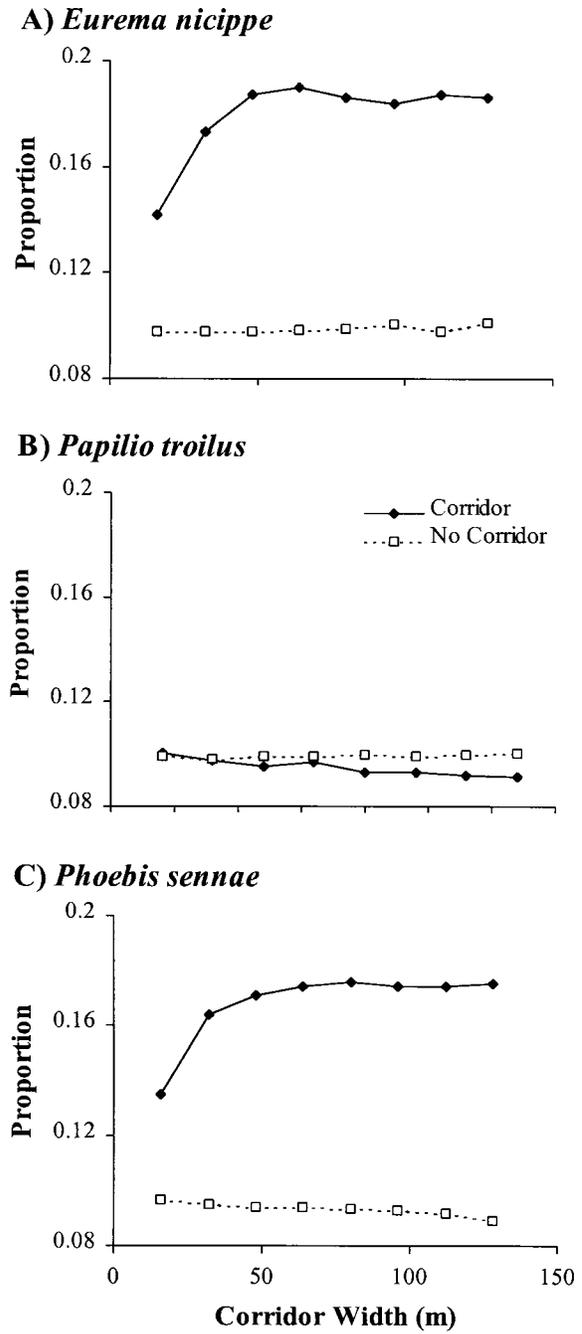


Figure 7: Interpatch movement rates predicted from simulated movement paths as corridor width varied. At each corridor width, 100,000 butterflies were released in the center of the center patch, and the path was terminated once a butterfly colonized an outer patch. Interpatch distance (512 m) and patch size (1.64 ha) were held constant. A, *Eurema nicippe*. B, *Papilio troilus*. C, *Phoebis sennae*.

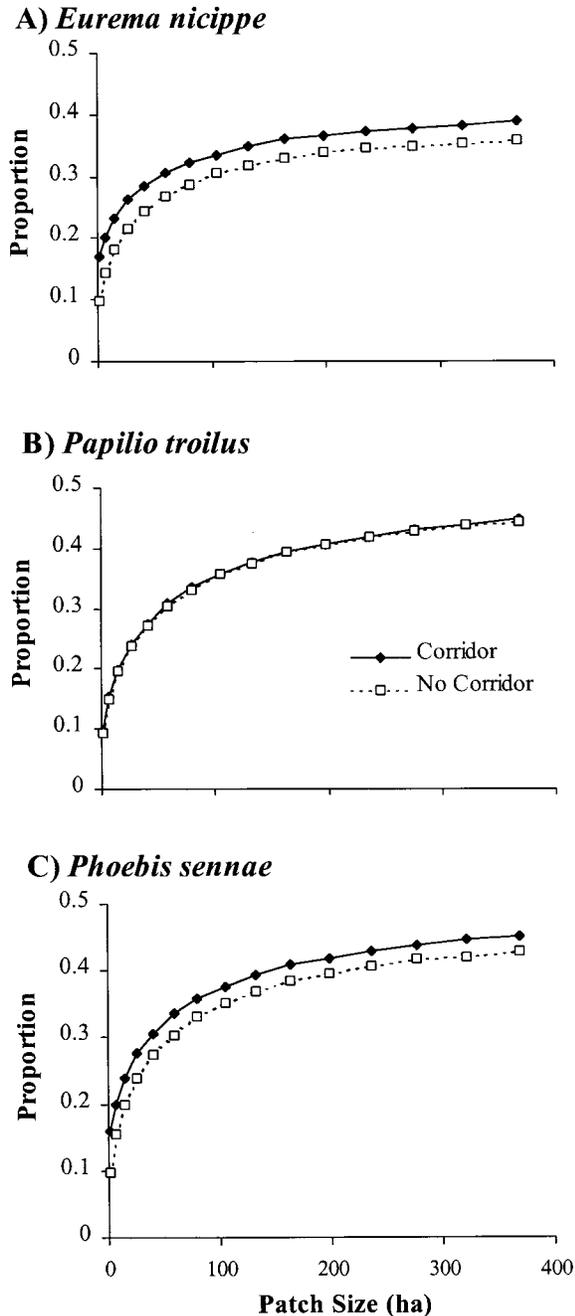


Figure 8: Interpatch movement rates predicted from simulated movement paths as patch size varied. At each patch size, 100,000 butterflies were released in the center of the center patch, and the path was terminated once a butterfly colonized an outer patch. Interpatch distance (512 m) and corridor width (32 m) were held constant. A, *Eurema nicippe*. B, *Papilio troilus*. C, *Phoebis sennae*.

movements and have a positive influence on population sizes of habitat-restricted butterfly species.

A behavioral framework for evaluating the impacts of corridors should be robust when applied to other landscapes. Forest corridors are typically proposed to connect forested patches in urban or agricultural landscapes. Behaviors of forest-restricted species would be expected to show turning biases at boundaries with urban or agricultural landscapes, just as open-habitat species responded to forest boundaries in this study (Beier 1995). In addition, the difference between suitable and unsuitable habitat need not be as structurally distinct as between open habitat and forest. Ries (1998) showed that a prairie butterfly species, *Speyeria idalia*, avoided crossing nonprairie grassland or agricultural boundaries almost as strongly as it avoided crossing forest boundaries. Schultz (1998) demonstrated that movements of an endangered butterfly, *Icaricia icarioides fenderi*, were biased away from open habitats surrounding patches of lupine. In sum, behaviors may provide adequate indication of corridor use, even at relatively subtle habitat boundaries.

Compared to other butterflies, and to other habitat-restricted animals for which corridors might be created, the species in this study were vagile, and their behavioral characteristics were well suited to shifting landscapes. Forest species, as well as threatened and endangered species that are often native to structurally stable habitats, are likely to be more restricted in their movements. The results reported here are probably conservative estimates of the effects of corridors on species that are more restricted in habitat use.

Corridors need not support animal populations to function effectively as movement conduits. Indeed, edge effects on butterflies or their plant resources may cause corridors to be of substantially lower quality than a larger habitat patch (Haddad and Baum 1999). This suggests a strong dichotomy between animals that navigate through patchy landscapes and plants that are not animal dispersed. For corridors to be effective for plants, and other species that must successfully establish and reproduce within corridors, corridor quality must be as high as or higher than the quality in larger patches (Tilman et al. 1997).

Importantly, the results of this study demonstrate that a range of different butterfly species exhibited a range of responses to habitat boundaries and corridors. In large part, differences could be ascribed to butterfly habitat preferences. Other behavioral or natural history characteristics may also influence sensitivity to habitat boundaries and movement through patchy landscapes (e.g., Daily and Ehrlich 1996). While it is not surprising that different species showed different responses to corridors, this result emphasizes a point that is typically ignored both in ecological research and in conservation planning that focus on a

single species. A behavioral approach may allow corridor effects to be evaluated more easily across many species of management concern. Corridors can then be judged effectively against alternative conservation strategies in managed landscapes.

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