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Corridor Length and Patch Colonization by a Butterfly, *Junonia coenia*

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Abstract: *Corridors have been proposed to reduce isolation and increase population persistence in fragmented landscapes, yet little research has evaluated the types of landscapes in which corridors will be most effective. I tested the hypothesis that corridors increase patch colonization by a butterfly,* Junonia coenia, *regardless of the butterfly's initial distance from a patch. I chose* J. coenia *because it has been shown to move between patches preferentially through corridors. Individuals were released 16–192 m away from open experimental patches into adjacent open corridors or forest. Neither corridors nor distance had a significant effect on patch colonization, but there was a significant interaction between the presence or absence of corridors and distance. At small distances (16–64 m),* J. coenia *was more likely to colonize open patches when released within forest than within open corridors, most likely because* J. coenia *used corridors as habitat. Nevertheless, patch colonization by butterflies released within forest decreased rapidly as distance from patches increased, as predicted by a null model of random movement. Colonization did not change with distance in the corridor, and at long distances (128–192 m), butterflies released in corridors were twice as likely to colonize open patches as those released in forest. These results suggest that one critical factor, interpatch distance, may determine the relative effectiveness of corridors and other landscape configurations, such as stepping stones, in reducing isolation in fragmented landscapes. When distances between patches are short compared to an animal's movement ability, a stepping stone approach may most effectively promote dispersal. Alternatively, the conservation value of corridors is highest relative to other habitat configurations when longer distances separate patches in fragmented landscapes.*

Extensión de Corredores y Colonización de Parches por una Mariposa, *Junonia coenia*

Resumen: *Se han propuesto corredores como una medida para reducir el aislamiento y aumentar la persistencia de poblaciones en paisajes fragmentados. Sin embargo, pocos estudios han evaluado los tipos de paisajes en los que los corredores serían más efectivos. Realicé pruebas para evaluar la hipótesis de que los corredores aumentan la colonización de parches por la mariposa* Junonia coenia *independientemente de la distancia inicial entre la mariposa y el parche. Escogí* Junonia coenia *porque ya se ha demostrado que esta especie se mueve entre parches usando corredores preferentemente. Se liberaron individuos entre 16 a 192 m de distancia de corredores adyacentes abiertos o de parches experimentales de bosque abiertos. Ni los corredores ni la distancia tuvieron efectos significativos sobre la colonización de los parches. Sin embargo, hubo una interacción entre la presencia o ausencia de los corredores y la distancia. A distancias pequeñas (16–64 m),* Junonia coenia *colonizó con más frecuencia parches abiertos cuando fue liberada dentro del bosque, que cuando fue liberada dentro de corredores abiertos, probablemente debido a que utilizó los corredores como hábitat. Sin embargo, la conlonización de parches por las mariposas liberadas en el bosque disminuyó rápidamente en correlación con el aumento en la distancia hacia los parches, tal como es establecido en predicciones de un modelo de movimiento al azar. La colonización de parches por mariposas liberadas en corredores no cambió con la distancia, y a distancias largas (128–192 m), la probabilidad de que las mariposas liberadas en corredores colonizaran parches abiertos fue doble de la de las mariposas liberadas en el bosque. Estos resultados sugieren que un factor crítico, la distancia entre parches, puede determinar la efectividad relativa de corredores y otras configuraciones del paisaje, como lo son los escalones, en la reducción del ais-*

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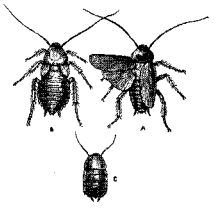

lamiento dentro de paisajes fragmentados. Cuando las distancias entre parches son cortas en comparación con la capacidad de movimiento de un animal, un enfoque de escalones puede ser más efectivo en la promoción de la dispersión. Alternativamente, cuando los parches en paisajes fragmentados son separados por distancias grandes, el valor de los corredores para la conservación es relativamente más alto que el de otras configuraciones.

Introduction

A central focus of conservation biology has been to identify landscape configurations that promote dispersal, reduce isolation, and increase population persistence within fragmented landscapes. Wilson and Willis (1975: 529) identified several habitat management strategies that might achieve this aim. Among their assertions was that "if the preserve must be divided, extinction will be lower when the fragments can be connected by corridors of natural habitat." Because corridors remain one of few tangible management options, they have become one of the most popular strategies proposed for habitat conservation in fragmented landscapes (Mann & Plummer 1993, 1995).

Since corridors were first proposed, several studies have shown that corridors may have positive effects on animal movement (Haas 1995; Sutcliffe & Thomas 1996; Haddad 1999*a*, 1999*b*) and population sizes (MacClintock et al. 1977; Fahrig & Merriam 1985; La Polla & Barrett 1993; Dunning et al. 1995; Haddad & Baum 1999). Yet, for some species, corridors have no effect on movement, whether measured as emigration from a patch (Danielson & Hubbard 1999; Haddad 1999*b*) or as colonization success (Rosenberg et al. 1998; Bowne et al. 1999). There may even be negative effects of corridors (Simberloff et al. 1992; Hess 1994; Burkey 1997). Because few generalities have emerged about which species will show positive responses to corridors, the overall conservation value of corridors remains undetermined (see reviews in Saunders & Hobbs 1991; Hobbs 1992; Simberloff et al. 1992; Meffe & Carroll 1997 [chapter 10]; Rosenberg et al. 1997; Beier & Noss 1998).

The corridor debate is now shifting. Most corridor studies have focused on how corridors influence movement or population sizes of individual animal species (review in Beier & Noss 1998). New studies are investigating for which situations and species corridors are most effective at increasing movement rates, population sizes, and population persistence. One approach to evaluating corridor use across species focuses on animal behaviors. For example, movement behaviors of butterflies may help predict whether they will use corridors (Schultz 1998; Haddad 1999*b*). Less understood are the landscapes in which corridors, as opposed to other habitat configurations, best promote conservation goals.

An alternative to corridors, a network of small patches (stepping stones), has recently emerged as an option that in some cases may better promote dispersal through fragmented landscapes (Date et al. 1991; Webb & Thomas 1994; Schultz 1998). Stepping stones may be particularly effective if animals (1) can detect a stepping stone from a source patch; (2) are not restricted or directed by habitat boundaries; (3) are reluctant to enter corridors that have a high proportion of edge habitat; and/or (4) experience higher rates of predation within corridors. Species that evolved within naturally fragmented landscapes may be most likely to benefit from stepping stones (Schultz 1998). Where these conditions do not exist, and especially at interpatch distances so long that animals do not orient toward stepping stones, corridors may most effectively promote dispersal through fragmented landscapes.

Understanding the merits of corridors relative to other management strategies in fragmented landscapes is complicated, and movement between patches can be broken into two distinct stages. First, animals must leave a patch of suitable habitat. If a corridor is similar in habitat to a patch, there may be no barrier to dispersal, and corridors may be the preferred route of emigration. In an isolated patch not connected by corridors, boundaries are more likely to limit dispersal. In a few instances, boundaries between habitats may be impenetrable to dispersing animals (i.e., Gonzalez et al. 1998); but this does not appear to be true for butterflies (Ries 1998; Schultz 1998; Haddad 1999*b*) or for most other animals. Once an animal leaves one patch, it must then move to another. This study focuses on the second stage of dispersal through patchy landscapes.

I tested the hypothesis that corridors increase colonization by a butterfly, *Junonia coenia*, regardless of the initial distance from a patch. I chose *J. coenia* because it has been shown that corridors increased its movement between patches (Haddad 1999*a*) and that higher movement rates may have contributed to higher population densities in connected patches (Haddad & Baum 1999). I conducted this experiment in the same landscape as the previous studies, which consisted of open patches and corridors within a matrix of managed pine forest. I evaluated the effectiveness of corridors by estimating patch colonization by butterflies released at equal distances from patches in corridors or in the surrounding forested habitat, which was unsuitable for *J. coenia*. The effects of habitat boundaries (edges) as barriers to dispersal were overcome in this study because butterflies were initially released outside of patches.

Methods

Patch Configuration and Study Species

I measured patch colonization by butterflies in experimentally created patches and corridors at the Savannah River Site, west-central South Carolina. The setup and configuration of the patches and corridors are presented in detail by Haddad (1999*a*; Haddad & Baum 1999). The patches and corridors were early-successional open habitats created in 1994–1995 by harvest of pine forest that was managed in monocultures of *Pinus elliotii*, *P. palustris*, and *P. taeda*. Open habitats supported the study species, *J. coenia*, and its plant resources; the densely planted pine monocultures did not. Although this landscape is the inverse of those with forested patches surrounded by agricultural fields or pastures that are typically the focus of corridor proposals, one key similarity between these types of landscapes is that patches and corridors, the preferred habitat for the study species, contrast strongly with the unsuitable matrix habitat. *J. coenia* and its resources were all strong dispersers and colonized the clearings within months after patches were harvested.

All patches were the same size (1.64 ha) and shape (128 × 128 m). Some of the patches were connected to others by a 32-m-wide corridor. I selected a subset of 13 patches from my original experiment (Haddad 1999*a*) based on the criteria that they were separated from other patches by 256 or 384 m. I chose these distances, the longest in the overall experiment, because they included the mean lifetime dispersal distance of *J. coenia* (Scott 1975; Haddad 1999*a*). Patches were contained within three different forest stands.

J. coenia is an open-habitat butterfly. Its host plants, including *Linaria canadensis* and *Gerardia purpurea*, and nectar plants, including *Rubus* sp., *Asclepias tuberosa*, and *Liatris* sp., all occurred at high densities in clearings but not in pine forest (N.H., personal observation). To successfully forage, mate, or oviposit, butterflies within forest were required to move to open habitat, whereas those in the open corridors could remain or disperse to fulfill their life-history requirements. *J. coenia* is capable of moving hundreds of meters, although its mean lifetime movements are approximately 150 m (Scott 1975; Haddad 1999*a*). Its adult lifespan is 7–10 days (Scott 1975). In mark-release-recapture studies, Haddad (1999*a*) showed that corridors increased *J. coenia* movement rates between patches, which led to higher population densities in patches connected by corridors (Haddad & Baum 1999).

Butterfly Releases and Surveys

J. coenia were collected from open habitats >5 km from experimental patches on the Savannah River Site, stored in a cooler for not more than 2 hours, and released into the experimental areas. Butterflies were released along transects perpendicular to the center of a patch edge. Each transect was replicated 10 times in the corridor and forest. Along each transect, release points were established at distances of 16, 32, 64, 128, and, in six of the longest transects in each habitat, 192 m from each patch (Fig. 1). The longest distance was half the length of the longest corridor. Although an attempt was made to establish a pair of transects from each patch (one into the corridor and one into the forest, as in Fig. 1), this was not always possible logistically because of intervening roads or boundaries between forest stands and other habitats. When it was not possible to pair transects in each habitat, one transect was located adjacent to a nearby patch such that spatial clustering of transects in each habitat was avoided and each type of transect occurred in representative locations across the study area.

At each of the 92 points, eight *J. coenia* were released in the summer of 1997, four each during two different time periods, the first from 14 June to 3 July and the second from 13 July to 6 August. During each time period, 1 week was devoted to each of the three forest stands that contained experimental patches. At the beginning of a week, butterflies were released at every point within one of the three forest stands. At each point, one butterfly was released facing each cardinal direction. All butterflies were marked with a unique code (as described by Ehrlich & Davidson 1960).

For 4 days following *J. coenia* releases, each of the patches within the forest stand was surveyed for marked butterflies. In a patch survey a researcher walked eight parallel 128-m transects that were each separated by 16 m and covered an entire patch. Each transect was walked in 6 minutes, excluding time spent capturing butterflies and recording data. An attempt was made to capture all observed *J. coenia*. If the butterfly was

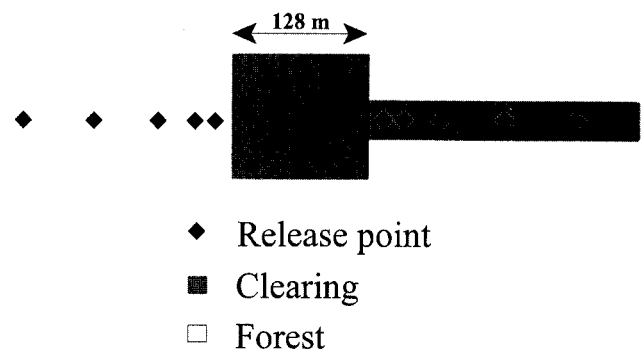

Figure 1. Example of corridor and forest treatments, where colonization of patches was measured for J. coenia *released at one of five sites on each transect that ranged from 16–192 m from an experimental patch.*

marked, the unique identification number and location were recorded. On the fourth day, corridors were surveyed for butterflies at the same rate as patches (6 minutes/128 m) in two parallel transects separated by 16 m. To prevent observer influence on colonization, corridors were not surveyed before the fourth day. The forest was not surveyed because *J. coenia* are rarely encountered there (N. H., unpublished data).

Analysis

I performed a two-factor analysis of variance in which the subjects were 192 × 32 m areas adjacent to experimental patches, the among-subject factor was the habitat (either forest or corridor), and the within-subjects factor was the distance from the patch. The analysis required that no data be missing so all distances had to be represented within each area adjacent to patches. Because of the variable length of corridors, four areas of each treatment did not contain the longest distances from a patch. Thus, all data from the 192-m release points were excluded from the analysis of variance. The dependent variable was the number of butterflies from each release point that colonized the adjacent patch. Although I did not estimate the colonization rate, the dependent variable was an index of colonization that should be proportional to actual colonization rates by butterflies released within the forest or corridor. I refer to colonization as the number of butterflies reaching an experimental patch.

To gain further insight into the effects of corridors at increasing distances from a patch, I conducted simple regressions of distance from a patch against colonization. I first analyzed the number of recaptured butterflies that colonized the patch adjacent to their release point. Butterflies could colonize any of the experimental patches, however. The number, orientation, and distance of other patches varied for each release point, and interpretation of these data are limited. Butterflies were typically released between two patches, and at the longest distances butterflies were often equidistant to two patches. So I conducted a second analysis that included all observed colonizations of adjacent or more distant patches.

I compared actual colonization with a null model that assumed straight-line movement in a randomly chosen direction. The null model was

$$\Pr[\text{colonization}] = (\text{angle subtended by a patch from the release point})/2\pi.$$

For comparison with colonization of adjacent patches, the null model included the angle subtended by the adjacent patch. For comparison with all colonizations, the null model included the angle subtended by the two nearest patches, which had the greatest effect on total colonizations. I compared the null expectation with actual numbers of colonization events by subtracting empirical measurements from predicted values. To determine whether the distribution of numbers of *J. coenia* colonizing patches was similar to the null distribution, I performed a simple regression on the difference between the empirical measurements and model predictions with respect to distance from the patch. To determine if the empirical measurements were the same magnitude as model predictions, I compared the mean of the differences with zero.

Results

Of 736 *J. coenia* released, 212 (29%) were recaptured, including 127 (60% of all recaptures) within patches adjacent to where butterflies were released, 68 (32%) in more distant patches, and 16 (8%) within corridors. Of the butterflies recaptured within corridors, 11 were initially released in the corridor and 5 were released in the forest. Of the 8 butterflies released at each point, the number of recaptures ranged from 0 to 6.

In a two-factor analysis of variance, neither corridors nor distance was significant in explaining colonization by *J. coenia* (Table 1). Because logistical factors prevented random assignment of all treatments, the degrees of freedom used to test the effects of corridors may have been inflated. This did not influence my interpretation because the effect of corridors was not significant. A completely blocked design, however, may have had better power to distinguish a potential corridor effect by accounting for spatial variability in colonization. There was a significant interaction between corridor and distance on patch colonization by *J coenia* (Table 1). At the three shortest distances between release points and patches (16–64 m), the number of *J. coenia* colonizing patches from corridors (mean ± SE = 1.5 ± 0.2) was significantly lower than the number colonizing from forest (2.5 ± 0.2; $f_{1,18} = 7.75$; $p = 0.01$). In contrast, at the two longest distances between release points and patches

Table 1. Two-factor analysis of variance testing the effects of corridors (among-subject factor) and distance (within-subject factor) on patch colonization by *J. coenia*.[a]

Variable	*df*	*Mean square*	F
Among subjects			
corridor	1	8.450	3.75
area (corridor)	18	2.253	
Within subjects			
distance	3	2.233	1.85
distance × corridor	3	5.683	4.70[b]
distance × area (corridor)	54	1.208	

[a] *Subjects were 32 × 192 m areas adjacent to patches and are labeled* area.
[b] $p < 0.01$.

(128–192 m), the number of *J. coenia* colonizing a patch from corridors was twice as high (1.6 ± 0.4) as from forest (0.8 ± 0.2). The comparison at longer distances was not significant ($f_{1,10}$ = 0.27; p = 0.61), perhaps because missing values prevented use of all data. But there was a clear trend toward lower colonization at increasing distances in the forest, whereas colonization from the corridor remained constant with distance.

Trends in colonization with distance were further clarified by simple regressions in each habitat. Patch colonization by butterflies released within corridors showed no relationship to release distance from the patch (Fig. 2a & 2c). Patch colonization by butterflies released in the forest was significantly negatively related to the distance between the patch and the release point (Fig. 2b & 2d; colonized adjacent patch, n = 46; r^2 = 0.28; p = 0.001; colonized any patch, n = 46; r^2 = 0.25; p = 0.001). I compared colonization by butterflies released within the forest and within the corridor to a null model of random movement. The empirical distributions of colonization by butterflies released within the forest showed no difference from the null model, but colonization numbers were significantly lower than zero, indicating that they were significantly lower than model predictions (Fig. 2, colonized adjacent patch, mean ± 95% CI = −0.47 ± 0.35; colonized any patch, mean ± 95% CI = −0.57 ± 0.39). Colonization by butterflies released within the corridor showed strong, significant differences from the null model: both had different distributions (colonized adjacent patch, R^2 = 0.29; p = 0.001; colonized any patch, R^2 = 0.20; p = 0.001) and lower mean colonization numbers than predicted by the model (colonized adjacent patch, mean ± 95% CI = −1.06 ± 0.45; colonized any patch, mean ± 95% CI = −0.92 ± 0.50).

Discussion

How should small areas of native habitat be arranged to promote movement and increase population persistence in fragmented landscapes? In my study, neither the presence or absence of corridors nor the distance from patches had significant effects on patch colonization by *J. coenia*, but there was a significant interaction between the presence or absence of corridors and distance. At long distances, *J. coenia* was twice as likely to colonize patches via corridors than through forested habitat. Nevertheless, I was able to reject my initial hypothesis that corridors increase colonization regardless of distance. At short distances, patch colonization by butterflies released in corridors was 40% lower than by butterflies released in unsuitable forest habitat. These results suggest that one factor—the distance between patches—may be critical in helping managers determine when to use corridors versus other landscape configurations in reserve design. When patches are separated by small distances, a network of patches that act as stepping stones may most effectively promote movement through patchy landscapes.

One surprising result from this study was that colonization via corridors did not change as the distance from a release point to a patch increased. This result emphasizes two benefits of corridors. First, at longer distances corridors effectively promoted dispersal, doubling the number of butterflies that colonized patches when released in a corridor compared with those released in forest. This corroborates previous results (Haddad 1999*a*) that showed that corridors increase interpatch movement rates of *J. coenia* at distances between 128 and 384 m but not at shorter distances. This result is a relative effect, and, with or without corridors, interpatch

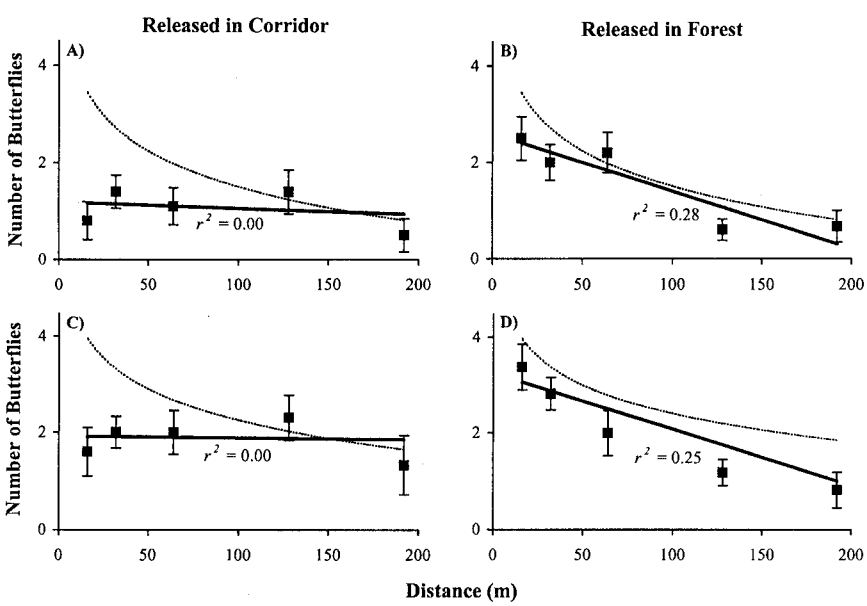

Figure 2. Patch colonization by J. coenia *(mean ± SE number of butterflies): (a) released within corridors that colonized patches adjacent to their release point; (b) released within forest that colonized patches adjacent to their release point (*p *= 0.001); (c) released within corridors that colonized any patch; (d) released within forest that colonized any patch (*p *= 0.001). The dashed lines are curves fit to predictions of a null model based on straight-line movement in a randomly chosen direction.*

movement will begin to decline at some distance. Once interpatch distances exceed a plant or animal's maximum dispersal distance, then corridor quality and the plant or animal's ability to successfully establish and reproduce within corridors become important. A second benefit of corridors in this study was that open corridors also served as habitat for *J. coenia*. This may in part explain why patch colonization by *J. coenia* released close to patches in corridors was so low. Other evidence supporting use of corridors as habitat by *J. coenia* was that, after 5 days, 13% of recaptured butterflies initially released within corridors were recaptured within a corridor. If corridors increase movement between patches and provide additional habitat, they offer a dual benefit in conservation.

Of course, use of corridors as habitat may increase settling rates and diminish their function as movement conduits (Andreassen et al. 1996; Rosenberg et al. 1997, 1998). Andreassen et al. (1996) found that intermediate-width corridors were best at promoting dispersal by small mammals because wide corridors were used as habitat. If corridors provide poor habitat or increase predation risk for dispersing animals, the habitat function of corridors may actually reduce population persistence. Under these conditions, other landscape configurations such as stepping stones may most effectively increase movement through patchy landscapes.

Nearly random movement by *J. coenia* released in forest led to higher colonization than that for butterflies released in corridors at small distances from patches (Fig. 2b & 2d); colonization by butterflies released within forest dropped quickly, however, and colonization was greater for butterflies released within corridors at distances greater than 100 m. Empirical estimates of colonization by butterflies released in forest were lower than predictions of the null model. These were probably underestimates of actual colonization because I did not adjust for butterflies that colonized a patch but were never encountered, for loss due to mortality, or for differences in age among released butterflies. This had no effect on the comparison between relative colonization by butterflies released within forest and within corridors. The close relationship between empirical estimates and model predictions for butterflies released in forest suggests that a simple model based on random movement can be used to evaluate distances at which stepping stones would be more effective than corridors at increasing movement by butterflies through fragmented landscapes.

The null model I used to predict patch colonization was simple. Although it closely approximated actual colonization rates by butterflies released within forest, other models may have been more appropriate, depending on the movement behavior of study species. One factor that may strongly influence the distance at which corridors or other management strategies such as stepping stones are most effective may be an animal's perceptual range. Lima and Zollner (1996; Zollner & Lima 1997) note that perceptual range may be a critical factor determining dispersal success and the importance of connectivity in fragmented landscapes. At short distances, animals would be capable of detecting suitable habitat, and dispersal success would be less dependent on landscape features such as corridors that are intended to direct animal movements.

To use a corridor successfully, animals must initially leave a patch of suitable habitat. This limit to interpatch movement was overcome as part of the design of this study. Corridors of suitable habitat should be less of an obstacle to emigration than a different, less suitable habitat (Ries 1998). In other landscape configurations, such as stepping stones, animals would be required to overcome any barriers to dispersal imposed by other habitats. If corridors do promote emigration, then they would have an additional, positive effect on interpatch movement rates.

The result that corridor effectiveness depends on distance should apply to other landscapes that are defined by two contrasting habitats. These include landscapes of open habitats, such as prairie or other grasslands, separated from other patches by a forest matrix, or forest patches separated by urban or agricultural landscapes. In these cases, the key ecological similarity is the contrast between patches and corridors and the surrounding matrix habitat. The conservation potential of corridors would then be determined by the nature of the unsuitable habitat as a barrier to dispersal, by the ability of an animal to detect another patch in the horizon, and by behavioral and life-history characteristics of species of management concern. Regardless of the habitat type of patches, corridors should be most effective for habitat-restricted species, especially when the matrix habitat contrasts strongly in suitability or structure with patches and corridors (Rosenberg et al. 1997; Haddad 1999*b*).

Ultimately, three factors will determine whether corridors should be created in reserve design. First, corridors must have a positive influence on population size and persistence. Several studies have shown that corridors increase population size (MacClintock et al. 1977; Fahrig & Merriam 1985; La Polla & Barrett 1993; Dunning et al. 1995; Haddad & Baum 1999). Haddad and Baum (1999) noted that three mechanisms, higher movement rates between connected patches, higher emigration into corridors from the surrounding landscape due to a "drift fence effect," and/or changes in edge effects caused by corridors, may lead to higher population sizes in connected patches. Fewer studies have shown that corridors have a positive effect on population persistence (but see Gonzalez et al. 1998).

Second, the benefits of corridors must be weighed against their economic costs in management (Simberloff et al. 1992). One problem with corridors is that they require a specific habitat area to be preserved, regardless

of cost. Other reserve designs, such as stepping stones, may provide greater flexibility in the acquisition and maintenance of habitat. Another problem with corridors, stepping stones, and other habitat arrangements proposed to reduce isolation is that they can never totally mitigate the unquestionably large effects of habitat loss (Fahrig 1997; Harrison & Bruna 1999). In most cases, the greatest possible area of habitat should be conserved. For any given area of habitat, however, corridors or other habitat arrangements may have beneficial effects on populations (Villard et al. 1999). The question in conservation biology that, once answered, will be of greatest benefit to managers is: what is the tradeoff between the relative cost of creating a corridor and the benefits it conveys to population persistence?

Third, a reserve design must have many positive and few negative consequences for the conservation of populations and biodiversity. Behaviors, habitat preferences, and life-history characteristics could be used to categorize large groups of species by their responsiveness to particular habitat management strategies. For example, behaviors at habitat boundaries may be a strong indicator of corridor use by butterflies (Haddad 1999*b*). Daily & Ehrlich (1996) suggest that diurnal species may be more sensitive then nocturnal species to habitat fragmentation. These and other attributes may simplify the task of determining appropriate management strategies for the many different species affected by habitat loss and fragmentation.

My results suggest that one critical factor for deciding between corridors and other landscape configurations, such as stepping stones, is simply the distance between patches. At least for butterflies, the distances at which these alternative management strategies are most effective may be determined from a simple model of random movement. If the distances between patches are short relative to an animal's movement ability, then stepping stones may be the most effective management strategy. At longer distances, corridors appear a promising option to reduce isolation in fragmented landscapes.

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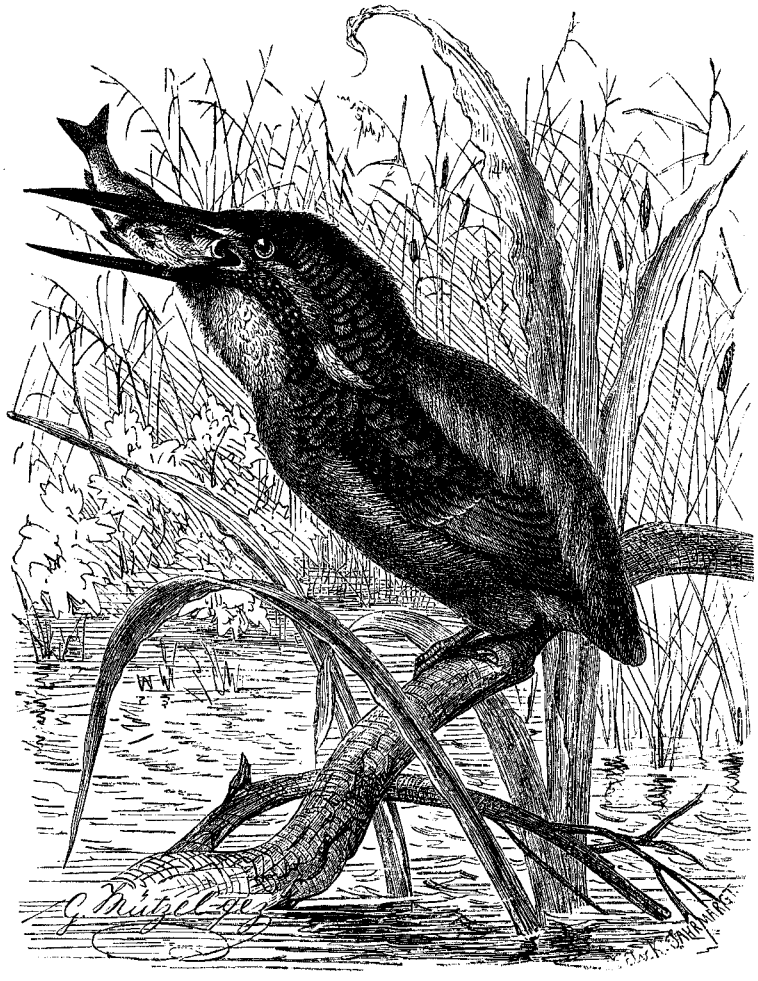
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