

Effectiveness of Corridors Relative to Enlargement of Habitat Patches

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Abstract: *The establishment of biological corridors between two otherwise isolated habitat patches is a common yet contentious strategy for conserving populations in fragmented landscapes. We compared the effectiveness of corridors with the effectiveness of an alternate conservation strategy, the enlargement of existing habitat patches. We used a spatially explicit population model that simulated population size in two kinds of patches. One patch had a corridor that connected it to a larger “source” patch and the other patch was unconnected and enlarged at the periphery by an area the same size as the corridor. Patch isolation, corridor width, patch size, and the probability that individuals would cross the border from habitat to matrix were varied independently. In general, population size was greater in enlarged patches than in connected patches when patches were relatively large and isolated. Corridor width and the probability of crossing the border from habitat to matrix did not affect the relative benefit of corridors versus patch enlargement. Although biological corridors may mitigate potential effects of inbreeding depression at long time scales, our results suggest that they are not always the best method of conserving fragmented populations.*

Keywords: corridor, patch size, population model, population size, spatially explicit simulation

La Efectividad de los Corredores en Relación con la Ampliación de Parches de Hábitat

Resumen: *El establecimiento de corredores biológicos entre dos parches de hábitat aislados es una estrategia común, pero discutible, para la conservación de poblaciones en paisajes fragmentados. Comparamos la efectividad de los corredores con la efectividad de una estrategia de conservación alternativa, la ampliación de los parches de hábitat existentes. Utilizamos un modelo poblacional espacialmente explícito que simulaba el tamaño de la población en dos tipos de parches. Un parche tenía un corredor que lo conectaba a un parche “fuente” más grande y el otro parche estaba desconectado y fue ampliado en la periferia con una superficie equivalente a la del corredor. El asilamiento del parche, la anchura del corredor y la probabilidad de que los individuos cruzaran el límite entre el hábitat y la matriz fueron variados independientemente. En general, el tamaño poblacional fue mayor en los parches ampliados que en los conectados cuando los parches eran relativamente grandes y aislados. La anchura del corredor y la probabilidad de cruzar el límite entre el hábitat y la matriz no afectaron al beneficio relativo de los corredores versus la ampliación de parches. Aunque los corredores biológicos pueden mitigar los efectos potenciales de la depresión por endogamia en escalas de tiempo largas, nuestros resultados sugieren que no siempre son el mejor método para la conservación de poblaciones fragmentadas.*

Palabras Clave: corredor, modelo poblacional, simulación espacialmente explícita, tamaño de parche, tamaño poblacional

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Introduction

Biological corridors are becoming a common conservation strategy despite debate over their effectiveness in mitigating pernicious effects of landscape fragmentation on populations (Hobbs 1992; Simberloff et al. 1992; Beier & Noss 1998). Even if corridors are effective in enhancing population persistence, it is not clear that this is the most effective strategy for conserving species in fragmented landscapes. Increasing the size of reserves or habitat patches will also improve population persistence (Simberloff et al. 1992). Rosenberg et al. (1997) identified a conservation dilemma wherein allocation of land to corridors may require a reduction in the size of habitat patches. Haddad (1999a) also noted that increasing patch area, rather than creating corridors, may be a better strategy with which to protect fragmented populations. Nevertheless, the circumstances under which the benefit of corridors exceeds the benefit of additional patch area have not been studied.

Corridors are thought to improve population persistence by enhancing movement among otherwise isolated habitat patches. Migrating individuals may “rescue” imperiled local populations (Brown & Kodric-Brown 1977), recolonize abandoned habitat (Fahrig & Merriam 1985, 1994; Hanski 1990), and enhance gene flow (Merriam et al. 1989). Thus, most studies on corridors have focused on whether corridors will indeed facilitate movement. Nevertheless, information on within-patch population responses (e.g., population size, density, persistence) is a more direct measure of corridor effectiveness than information on movement rates.

Empirical evidence suggests that corridors can increase population density (Haddad & Baum 1999). Studies on movement have controlled for area effects associated with corridors (Tewksbury et al. 2002; Haddad et al. 2003; Fried et al. 2005). The effectiveness of corridors in enhancing movement between patches increases with increasing corridor width (Tischendorf & Wissel 1997; Haddad 1999b) and increasing interpatch distance (Haddad 1999b), but perhaps there are scenarios under which population size would be improved more by enlarging patches than by creating long, wide corridors.

Increasing patch area can increase population size and persistence by providing high-quality interior habitat that corridors—with their high edge-to-area ratio—do not provide (Simberloff & Cox 1987; Simberloff et al. 1992). Average population size and persistence will increase if the minimum patch size required to sustain a viable population is reached by enlarging the patch. Furthermore, a nonlinear increase in population size with increasing habitat area, known as the density–area relationship (Matter 1997) or individuals–area relationship (Connor et al. 2000), makes patch enlargement a prudent alternative to corridor establishment.

Given limited resources available for habitat restoration, managers must decide whether it is best to assign those resources to increase connectivity between patches (e.g., create corridors or “stepping-stone” reserves) or to ensure population persistence within patches by enlarging them. Therefore, our objective was to determine whether, given a fixed amount of habitat, it would be better to create corridors or to enlarge habitat patches. We expected the relative benefit from corridors versus patch enlargement to depend on factors such as patch size and isolation, the width of the corridor and, ultimately, on species-specific traits. We developed a population simulation model in order to perform a multifactorial analysis of population responses across multiple generations.

Methods

Demographics

We developed a spatially explicit, individual-based population model that simulates density-dependent rates of movement, reproduction, and mortality. Parameter values used to establish a multigenerational population are provided in Table 1. We explored various combinations of parameter values, discarding those that resulted in populations that would not persist and those that grew to sizes requiring prohibitively long simulation times.

We used an energy-balance approach at the individual level to model population dynamics. Each individual expended energy at a constant rate while searching for food and mates. If an individual's energy reserve fell below a threshold level, then it died and was eliminated from the program. Food items were randomly located in habitat, including corridors and edges. When an individual moved into a cell containing a food item, it acquired a given amount of energy and the food item disappeared for a given regeneration time period. If an individual's energy reserve exceeded an upper energy threshold, new individuals were introduced into the program at the point of contact with an individual of the opposite sex that had also exceeded the upper energy threshold.

The energy-balance approach produced population dynamics that were governed by food availability. If the population size increased significantly, the overall rate of food consumption surpassed the rate of food regeneration, and food availability was reduced. This reduced individuals' probability of reproducing and increased their probability of mortality. Therefore, population size declined. If the population size declined significantly, the overall rate of food consumption fell below the rate of food regeneration. Food items then accumulated and individuals' probability of reproducing increased, whereas their probability of mortality decreased. Therefore, population size increased. Random mortality was also included to simulate density-independent effects of, for example, aging,

Table 1. Parameter values used to establish multigenerational population.

<i>Parameter</i>	<i>Value</i>
Initial density of individuals	5/1000 pixels of habitat
Energy reserve of new individuals	200 units
Density of food items	25/1000 pixels of habitat
Energy conferred to individual by one food item	285 units
Regeneration time of food items after consumption	400 iterations
Energy individuals expend every step	1 unit
Energy needed for reproduction	>900 units
Proximity between males and females for reproduction	<5 pixels
Number of offspring per reproduction event	5 individuals
Energy of parents after reproducing	300 units
Radius around individual where local population density is measured	10 pixels
Number of individuals in radius needed for high-density movement pattern	≥4 individuals
Number of individuals in radius needed for low-density movement pattern	<4 individuals
Probability of random mortality (all individuals)	0.0005/step
Additional probability of random mortality in matrix	0.0005/step
Probability of crossing border from habitat to matrix	0.25 & 0.5

predation, and injury. The difference between “habitat” and “matrix” in this model was the rate of random mortality (two times higher in matrix than in habitat) and absence of food items in the matrix. The spatial arrangement of habitat determined whether it was a population source or sink, but the matrix was always a population sink.

Individuals assumed one of two movement patterns. When the number of individuals within a given radius from a focal individual exceeded a threshold value, then the individual randomly selected and occupied one of three forward-facing pixels (in a Moore neighborhood with radius of one, there are eight pixels surrounding a focal pixel). Turning radius widened to include all eight surrounding pixels when the density of individuals did not exceed the threshold value, but individuals were not allowed to return to the eight most recently visited pixels. These movement patterns favored higher displacement velocities in areas where local population density was relatively high; hence, competition for resources was more severe. In relatively low-density areas, individuals tended to displace more slowly and

were prevented from frequently returning to recently visited pixels in order to simulate a more efficient foraging pattern. Simulations were repeated for populations of individuals with a 0.25 and a 0.5 probability of crossing the border from habitat to matrix when they encountered the border. This was done to model different species’ ability to perceive and avoid the relatively hazardous conditions of the matrix. The probability of reentering habitat from the matrix was always one.

Landscapes

To test for differences in population size between connected and enlarged patches, a viable population was established in a source patch of 150 × 150 pixels. Two “objective” patches were located on opposite sides of the source patch. One objective patch was connected to the source patch via a corridor, and the other objective patch had the surface area of the connected patch’s corridor added to its periphery (Fig. 1). Population size was recorded within the connected objective patch (individuals in the corridor were not counted) and within an area of equal size in the enlarged patch (individuals in the additional peripheral area were not counted).

We used a balanced, complete factorial design with four levels of patch sizes, four levels of patch isolation, three levels of corridor width, and two levels of probability of habitat-to-matrix border crossing. This resulted in (4 × 4 × 3 × 2) 96 unique parameter combinations. The levels of the factors are provided in Fig. 1. The difference in population size between connected and enlarged patches was obtained for 40 replicates of all 96 unique scenarios. The effects of patch size, patch isolation, corridor width, and border crossing probability were analyzed with analysis of variance. We used a Tukey adjustment to test each of the 96 parameter combinations for significant differences from 0 (i.e., no difference between population size in connected and enlarged patches). We observed that the initial model conditions (e.g., number of individuals present at start-up, their initial energy reserve, the number of food items available) influenced population dynamics during the first 3000 model iterations. Therefore, mean population size was calculated between the 3000th and 8000th iteration for all simulations.

Results

We observed that the minimum patch size required for population persistence in our model was approximately 75 × 75 pixels. Establishment of a corridor or patch enlargement was a necessary but not sufficient condition for population persistence when patch size was smaller. Thus, our results apply to populations with different levels of imperilment caused by patch size, including populations that can persist without intervention.

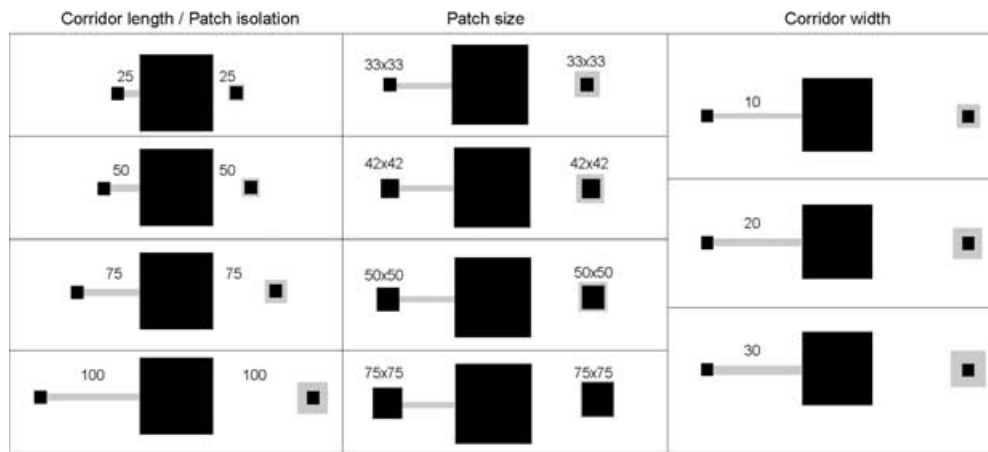


Figure 1. Four levels of corridor length and patch isolation, four levels of patch size, three levels of corridor width, and two levels of probability of habitat-to-matrix border crossing (0.25 & 0.5, not shown) were fully crossed in a multifactorial experimental design. For every simulation, the amount of habitat used to establish a corridor equaled the amount of habitat used to enlarge a patch (grey). Population size was recorded in connected patches and an area of equal size within enlarged patches (smaller black squares).

Overall, patch isolation and patch size significantly influenced the difference in population size between connected and enlarged patches, but corridor width and the probability of crossing the border from habitat to matrix did not (Table 2). In general, mean population size was greater in enlarged patches than patches connected with a corridor when the degree of isolation between the objective patch and the source patch was relatively large and when the size of the objective patch was relatively large (Fig. 2).

Increasing the width of the corridor tended to have the same effect on population size as enlarging patch area by the same amount of pixels used to widen the corridor. Thus, corridor width did not have a significant effect on the relative benefit of establishing a corridor versus using that area to enlarge the objective patch (Table 2). Similarly, changing the probability that individuals cross the border from habitat to matrix resulted in identical changes in population size within connected and enlarged patches. Thus, the probability that individuals cross the border from habitat to matrix was insignificant with respect to the relative benefit of corridors versus patch enlargement (Table 2).

Table 2. Type III analysis of variance on difference in population size between connected and enlarged patches.

Source	df	F	p
Isolation	3	147	<0.0001
Patch size	3	95	<0.0001
Width	2	1.57	0.208
Pr(border crossing)	1	2.33	0.123

Discussion

A previous model predicts that corridors become more effective in facilitating movement between patches as interpatch distance increases (Haddad 1999b). Although we do not dispute this, we contend that the effectiveness of corridors relative to patch enlargement is diminished as interpatch distance increases. Our results indicate that as interpatch distance increases, enlarging a patch may become a better strategy than creating a large corridor.

Corridors increased average population size in patches more than patch enlargement when patch size was small. For most of these scenarios, patches were too small to maintain a viable population (in general, populations in patches smaller than 75×75 would not persist without a corridor or patch enlargement). Corridors increased mean population size more than patch enlargement because of increased population supplementation through the corridor. Thus, although corridors did improve mean population size more than patch enlargement, this was achieved by directing individuals into a sink habitat. In this case a greater mean population size in the connected patch is a misleading indicator of conservation success (Van Horne 1983). Once patches were sufficiently large to approach the minimum size required for population viability, patch enlargement became more effective than corridors because increasing patch size ensured population persistence more than supplementation through a corridor. Even in large patches (75×75 pixels), where population viability was ensured without connecting or enlarging the patch, patch enlargement increased mean population size more than corridors.

Corridor width is frequently the subject of research because it is affected by (and can potentially affect)

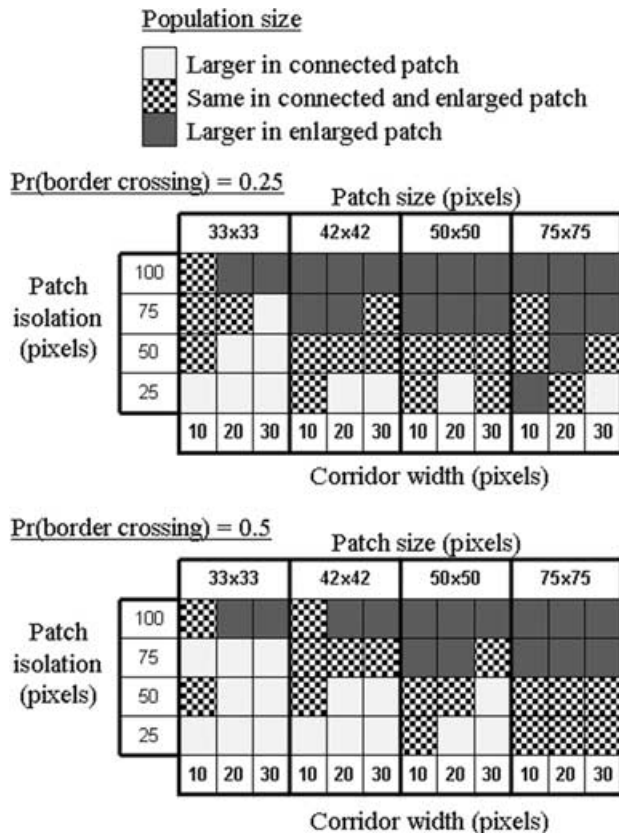


Figure 2. Results of Tukey tests ($\alpha = 0.05$) on difference in population size between connected and enlarged habitat patches. Each of the 96 cells corresponds to a unique combination of model parameters. Top and bottom panels correspond to different probabilities of habitat-to-matrix border crossing (0.25 & 0.5, respectively). Three corridor widths (bottom x-axis) are shown within four patch sizes (top x-axis). Patch isolation increases from bottom to top in each panel. Cells are shaded light grey if population size is significantly larger in the connected patch than in the enlarged patch. Cells are shaded dark grey if population size is significantly larger in the enlarged patch than in the connected patch. Cells are checked if population size is not significantly different between the connected and enlarged patch.

management decisions. Results of modeling studies indicate that movement rates between patches increases asymptotically as corridor width increases (Tischendorf & Wissel 1997; Haddad 1999b), but some empirical work suggests that an intermediate corridor width is most effective in facilitating movement (Andreassen et al. 1996). Our results do not directly address this discrepancy; however, they do suggest that potential corridor width should not influence the decision to either create a corridor or enlarge a patch, provided the same amount of habitat is available to both strategies. For example, if managers only

have enough resources available to create a dubiously narrow corridor, then the potential benefit of enlarging a target habitat patch with the same amount of resources is equally dubious.

Specialist species are more likely to avoid the matrix environment and stand to benefit more from corridors than generalist species (Haddad 1999b). In our model the probability that individuals cross the border from habitat to matrix did not influence the relative benefit of corridors and patch enlargement. Therefore, although a species' behavior at habitat boundaries may affect the effectiveness of a corridor, boundary behavior should not influence the decision to either create a corridor or enlarge a patch.

If we had explicitly induced a positive relationship between population density and patch area by, for example, reducing habitat quality in edges, then patch enlargement would have been further favored over corridor use. In this respect our estimate of the benefit of patch enlargement is conservative. (see Bender et al. [1998] and Connor et al. [2000] for reviews of the relationship between population density and patch area.)

A purported benefit of corridors is that they will enhance gene flow and potentially prevent inbreeding depression (Ars & Ims 1999). Our model does not include this potential benefit in the assessment of the two conservation strategies. Nevertheless, if population size can be significantly increased by enlarging patches, then the rate of accumulation of deleterious alleles will slow and may even be "purged" from the population (Templeton & Read 1984). This remains controversial (Ballou 1997; Allendorf & Ryman 2002).

The results of our model indicate that, for a given amount of habitat, patch enlargement can increase population size more than the establishment of biological corridors. Enlarging patches will be most effective if it causes them to surpass the minimum size required to maintain a viable population or if their degree of isolation from other patches significantly diminishes the usefulness of corridors as movement conduits. Patch enlargement will also be a prudent alternative to establishment of corridors if disease vectors (Simberloff et al. 1992; Hess 1994), predators, invasive species, or fire can use corridors to propagate through the landscape and further jeopardize the viability of focal species. Knowledge of a species' density-area relationship, the minimum patch size required for maintaining a viable population, and the degree of isolation between patches should inform decisions on whether to establish a corridor or enlarge a habitat patch.

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