Predicting Which Species Will Benefit from Corridors in Fragmented Landscapes from Population Growth Models

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ABSTRACT: Connecting isolated patches of habitat in fragmented
landscapes with corridors is a popular conservation strategy. This
strategy is also controversial in large part because of uncertainty
about what characteristics of a species and its environment promote
corridor use. In this article we address the question, For what types
of species will populations benefit from corridors? We asked this
question using a model of two logistically growing populations con-
nected by migration in which both emigration and migration success
were determined by the presence or absence of a corridor. We found
that in the short run (e.g., during recovery from disaster), corridors
are most effective for species with fast-growing populations that have
low survivorship when dispersing through unsuitable (matrix) hab-
itat. We also found that emigration rates and habitat-specific mor-
tality rates are key determinants of the effects of corridors on pop-
ulation size. In the long term, corridors are most likely to benefit
species with slow-growing populations that have low survivorship
when dispersing through matrix habitat. Our results confirm the
major conclusions from previous empirical studies of corridor ben-
efits. However, most studies fail to consider the most appropriate
questions to determine the potential benefits of habitat corridors.
First, what is the time scale of the conservation goal? Corridors have
positive effects on different suites of species in the short and long
term. Second, is the major threat of local extinction due to sustained
population decline or boom-bust cycles? Third, what is the migration
rate through the matrix? Fourth, what fraction of migrants dispersing
through the matrix successfully immigrate to another patch?

Keywords: conservation, corridor, model, metapopulation.

Among the most popular remedies to reduce the negative
impacts of habitat loss and fragmentation is to connect
otherwise isolated patches of habitat with corridors. Cor-
ridors connect isolated populations with sources of mi-
grants that can reduce the negative effects of demographic
stochasticity, genetic stochasticity, or inbreeding that may
be associated with habitat fragmentation. In conservation,
corridors are also attractive because they are a clearly de-
fined and often achievable strategy to prevent extinction
in fragmented landscapes.

The use of corridors in conservation also has been con-
troversial. One reason for the controversy is that it is un-
clear which species will benefit from corridors. Recent
studies have confirmed that corridors effectively increase
movement rates, gene flow, and population sizes of a num-
ber of species (review in Beier and Noss 1998; Rosenberg
et al. 1998; Haddad and Baum 1999; Mech and Hallett
2001; Tewksbury et al. 2002; Haddad et al. 2003). Other
studies, however, have shown no effects of corridors on
animal movement rates or population sizes (Arnold et al.
1991; Date et al. 1991; Haddad and Baum 1999). In ad-
dition, there is the potential for corridors to affect pop-
ulations negatively by facilitating the spread of invasive
species, predators, or diseases (Hess 1994), which increases
the numbers lost during dispersal or synchronizes the dy-
namics of metapopulations (Earn et al. 2000). Unfortu-
nately, inference from existing studies to the general ques-
tion about which species corridors benefit at the
population level is limited by the number and types of
species that have been studied. Each particular study re-
ports corridor effects on one or a handful of species drawn
from a restricted pool of taxa despite the fact that corridors
may impact hundreds or thousands of species in any land-
scape. The impact of corridors will depend on species
characteristics and on characteristics of the landscape (Ro-
senberg et al. 1997; Beier and Noss 1998; Haddad 1999*b*;
Haddad et al. 2003). To sort out the cumulative effects of
corridors, conservation biologists and managers must take
a more panoramic view of corridor effects in reserve
design.

Many authors have noted that landscape conservation
will depend on the species, landscape, and scale of con-
servation concern (Weins and Milne 1989; Beier and Noss

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1998; Tischendorf and Fahrig 2000). Resolving corridor use by individual species could thus become a time-consuming and expensive endeavor. This approach raises the question, Will a particular species benefit from a particular corridor? We take a different approach and ask, What types of species, with what types of autecologies, would be expected to benefit from a corridor? This approach recognizes that corridors are often created without a particular species or the diversity of species in a landscape in mind.

The answer to this question depends on a species' habitat preferences, dispersal behaviors, and demographic and population growth rates. A number of authors have suggested that habitat specialists may benefit most from corridors (Rosenberg et al. 1997; Haddad 1999*b*; Mech and Hallett 2001). These species are the most likely to be isolated by fragmentation and the least likely to be rescued from local extinction without corridors.

Although corridor effects on plants and animals are most commonly inferred from dispersal behaviors and habitat specificity, demographic rates and population growth rates may also determine responses to corridors. Corridor effectiveness will be determined in part by habitat-specific demography, such as relative mortality rates in patch and matrix habitats. Consider the extreme example where predators occupy corridors and use them as funnels to capture dispersing prey. In such a case, prey behaviors that favor corridor use would not indicate the effects of corridors. In a contrasting example, Beier (1993, 1995) showed that differences in cougar survivorship between corridor and urban matrix habitats made corridors critical to cougar conservation in southern California.

A species' ability to respond to population loss depends not only on their movement through corridors but also on their ability to provide new colonists to repopulate newly extinct sites. The ability of a species to provide new colonists depends on its growth rate, carrying capacity, and the functional form of density dependence. For example, strong density dependence in a rapidly growing population could lead large numbers of colonists to repopulate an extinct habitat patch but may also lead to high migration losses.

Little is known about the types of species whose populations would benefit from corridors. Unfortunately, the number and breadth of species for which corridor responses are known is small, and an empirical evaluation is premature. In addition, as highlighted by the discussion above, assessing the benefits of corridors can be conceptually difficult. Yet a general approach is needed to assess the kinds of species that may respond to corridors proposed in landscape-level conservation.

Here, we present a general model to assess which types of species would be expected to benefit from corridors.

We used this approach to determine which dispersal behaviors and demographic rates, separately or in combination, lead to positive corridor effects on population sizes. To describe spatial population dynamics in fragmented landscapes, we adopted a common modeling framework in which a pair of populations exhibiting density-dependent growth within patches is connected by diffusive migration among patches (see Levin 1976; Gyllenberg et al. 1993; Hastings 1993; Amarasekare 1998; Kendall and Fox 1998). A similar approach was used by Earn et al. (2000) to demonstrate that corridors can synchronize the dynamics of patches, which makes metapopulations more vulnerable to extinction. In order to account for the effects of habitat corridors, we included an explicit accounting of dispersal-related mortality generally not found in other models of coupled population growth (but see Amarasekare 1998). Using this framework, we asked what characteristics typify species whose populations would benefit from corridors. Although we present this study in terms of the effect of corridors, our results apply to any landscape feature that modifies an organism's dispersal between patches. We discuss the implications of model results for published studies of animal populations in fragmented landscapes.

Model Description

We modeled a pair of populations within two patches that are connected by migration. The populations are assumed to grow within each patch according to a discrete logistic growth model. At the end of each generation, a fraction of the population emigrates from each patch. We assumed that migration might be either through the matrix or through a habitat corridor connecting the two patches. We further assumed that there is a survival cost to migration such that only a fraction of emigrants successfully disperse to the other patch. This model describes organisms for which fecundity and juvenile mortality are strongly density dependent while adult mortality is much greater among dispersing individuals than among those that remain within their natal patch.

We first explain specific population growth processes included in our model. We start with a single exponentially growing population:

$$N_{t+1} = N_t r. \tag{1}$$

In equation (1), r is generally thought to be the birth rate (b) minus the death rate (d) to which 1 is added to signify that an individual contributes to the next generation if it does not die ($1 + b - d$). We can separate the death rate due to mortality within the organism's habitat (d_p) and additional mortality faced by individuals that attempt to

leave their habitat (d_m). Doing so allows us to define processes that determine the population growth that occur within ($1 + b - d_p$) and outside (d_m) the organism's habitat. We now redefine r to mean the local population growth rate in the absence of emigration ($1 + b - d_p$). To ensure that an organism cannot die twice, we assume that only individuals that survive within patches emigrate. That is, dispersal-related mortality acts after within-patch mortality and only on within-patch survivors: dispersal mortality $= red_m$, where e is the fraction of the population that disperses. These assumptions fit organisms that have a short dispersal phase just before reproduction. We then define ρ to mean the population growth accounting for the additional mortality incurred by dispersing individuals:

$$\rho = r(1 - ed_m). \tag{2}$$

This parameter is the potential for a local population to contribute to the regional population size in the next generation. We will therefore call it the "contribution rate." If we now imbed the population within a landscape with multiple patches of suitable habitat, it will make a contribution to the total population in that landscape (N_{t+1}):

$$N_{t+1} = N_t\rho. \tag{3}$$

We added density dependence to our model in the form of logistic growth. We assumed that density dependence acts on the processes within a patch but not on the mortality of dispersers. The contribution of a subpopulation to the total population becomes

$$N_{t+1} = N_t r\left(1 - \frac{N_t}{K}\right)(1 - ed_m) = N_t\rho\left(1 - \frac{N_t}{K}\right). \tag{4}$$

In the absence of immigration, the focal population will grow according to the equation

$$N_{t+1} = N_t r\left(1 - \frac{N_t}{K}\right)(1 - e). \tag{5}$$

If we assume that the dispersal phase is very short, such that there is no within-patch mortality during that period, then in a system with two populations in two patches, the population growth in each patch becomes

$$N_{i,t+1} = N_{i,t}r\left(1 - \frac{N_{i,t}}{K}\right)(1 - e)$$
$$+ e(1 - d_m)N_{j,t}r\left(1 - \frac{N_{j,t}}{K}\right). \tag{6}$$

Finally, we substitute s for $1 - d_m$ to make the growth equation in each patch

$$N_{i,t+1} = N_{i,t}r\left(1 - \frac{N_{i,t}}{K}\right)(1 - e) + e(s)N_{j,t}r\left(1 - \frac{N_{j,t}}{K}\right). \tag{7}$$

Equation (7) is similar to the familiar paired logistic map. The equilibrium behavior of the paired logistic map has been thoroughly characterized in previous studies (see Levin 1976; Gyllenberg et al. 1993; Hastings 1993; Amarasekare 1998; Kendall and Fox 1998). However, only Amarasekare (1998) has allowed for dispersal-related mortality. We extended the analysis of this model by further accounting for the effects of habitat corridors on the fraction of the population emigrating from a patch (e) and success (s) of migrants between habitat patches. This extension allowed us to use the framework of a well-understood model to study the effects of habitat corridors on population dynamics and how corridor effects are influenced by specific model parameters.

We incorporated the effect of corridors into equation (7) by allowing both the emigration rate and success of migrants to depend on the habitat surrounding each patch. We assumed that the two patches are connected by a corridor of some width (c). The width of the corridor is scaled relative to the patch perimeter so that the remainder of each patch ($1 - c$) is surrounded by matrix habitat. We modeled the case without a corridor by setting $c = 0$. We separated emigration into the fraction of the population that would emigrate through the corridor (e_c) and matrix (e_m) if that habitat surrounded the entire patch. We then defined the parameters s_c and s_m as the fraction of emigrants leaving through corridor or matrix habitat that migrate successfully to the other patch. Thus, the total migration rate among the patches (μ) is

$$\mu = ce_cs_c + (1 - c)e_ms_m. \tag{8}$$

Incorporating more specific components of dispersal mortality leads to changes in both the contribution rate accounting for dispersal mortality (ρ),

$$\rho = r\{1 - [ce_c(1 - s_c) + (1 - c)e_m(1 - s_m)]\}, \tag{9}$$

and a new equation governing population growth in each patch,

$$N_{i,t+1} = N_{i,t} r \left(1 - \frac{N_{i,t}}{K}\right)\{1 - [ce_c + (1 - c)e_m]\}$$

$$+ [ce_c s_c + (1 - c)e_m s_m] N_{j,t} r \left(1 - \frac{N_{j,t}}{K}\right). \quad (10)$$

The equilibrium population sizes in a two-patch system governed by equation (10) are

$$N_j^* = N_i^*$$

$$= K \left(\frac{r\{1 - [ce_c(1 - s_c) + (1 - c)e_m(1 - s_m)]\} - 1}{r\{1 - [ce_c(1 - s_c) + (1 - c)e_m(1 - s_m)]\}} \right).$$

$$(11)$$

Substituting in ρ yields an equilibrium value at

$$N_{j,t+1}^* = N_{i,t+1}^* = \frac{K(\rho - 1)}{\rho}. \quad (12)$$

Note that equation (12) is similar to the equilibrium solution to the coupled logistic map:

$$N_{j,t+1}^* = N_{i,t+1}^* = \frac{K(r - 1)}{r}.$$

In fact, the equilibrium behavior of a two-patch system described by equation (10) with parameters such that $\rho = x$ is exactly the same as the logistic map with $r = x$, as reported by Hastings (1993).

Model Analysis

We are ultimately interested in how corridors affect population size and dynamics. As a first step, we examined two ways that corridors permit individual subpopulations to influence total population dynamics: through their contribution rate (ρ) and their migration rate (μ; i.e., the amount of population exchange that occurs among patches). The effect of a corridor on a species can be understood as the product of its effects on ρ and μ and the effect of these parameters on the total population.

The effect of a corridor on the contribution rate was determined by calculating the change in the contribution rate caused by the change in corridor width from 0 to some small fraction of the patch perimeter:

$$\frac{\partial \rho}{\partial c} = r[e_m(1 - s_m) - e_c(1 - s_c)]. \quad (13)$$

Based on inspection of this equation, we predict two patterns of corridor effects. First, a corridor will increase ρ if the risk of dispersal-related mortality is greater in the matrix than in the corridor and will reduce it otherwise. Second, the magnitude of the corridor effect on the contribution rate is proportional to the difference in the dispersal-related mortality in the matrix and in the corridor ($e_m[1 - s_m] - e_c[1 - s_c]$).

Equation (13) also leads to the novel prediction that the magnitude of a corridor's effect on a population depends directly on the local population growth rate (r; fig. 1a) regardless of the rate of migration. Populations with higher r produce more migrants, which potentially contribute to the regional population only if emigrants are successful at dispersing.
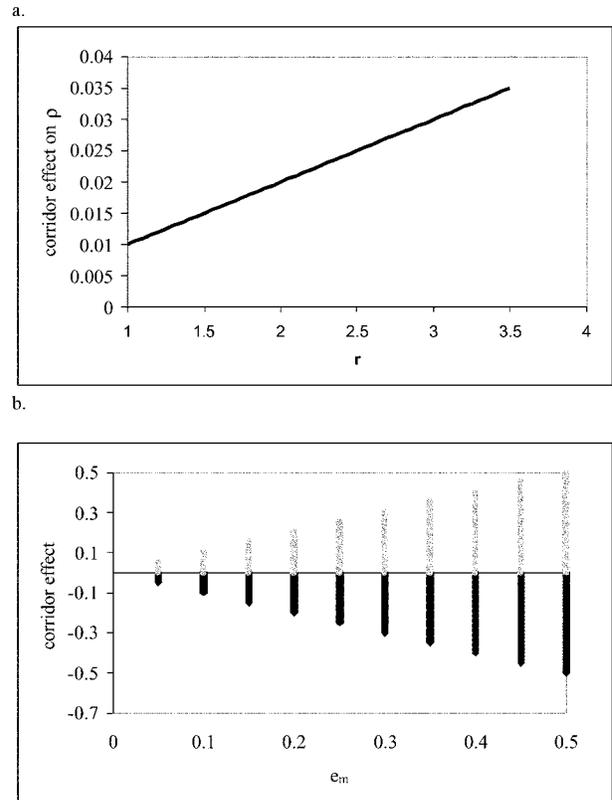
Figure 1: Corridor effects on contribution and migration rates. *a*, Relationship between local growth rate and magnitude of a corridor's effect on ρ. Other parameters are $e_m = 0.1$, $s_m = 0.75$, $e_c = 0.15$, $s_c = 0.9$. *b*, Effect of a corridor on migration and contribution rates. Each vertical line is composed of points indicating the corridor effect on μ (*dark*) or ρ (*light*) for s_m between 0.2 and 1 (from distal end to origin end of each line).

The effect of a corridor on the migration rate can be expressed as the partial derivative of μ with respect to corridor width c:

$$\frac{\partial \mu}{\partial c} = e_c s_c - e_m s_m. \tag{14}$$

A corridor's effect on the migration rate depends only on the relative emigration and success rates in corridor and matrix habitat. From equation (14) it is clear that adding a corridor will have a smaller effect on μ when emigration into the matrix is high. Note, in contrast, that adding a corridor will have a larger effect on ρ when emigration to the matrix is high (eq. [13]). Thus, those landscapes in which corridors are best for promoting migration among patches will not be the same ones in which corridors are best for promoting large contributions from local populations to regional populations (fig. 1b).

We now address how corridor-induced changes in the contribution and migration rates translate into effects on population dynamics. Because these effects depend heavily on the timescale, we examined them for three conditions. First, we examined how corridors affect the population dynamics immediately following a reduction in population size so that only one patch had a few individuals (hereafter "early dynamics"). This period determines a species' ability to spread into a landscape following a reintroduction or to recover from the brink of extinction. Second, to assess the long-term effects in a stable environment, we examined how corridors affect the equilibrium population size. Third, we examined corridor effects on species persistence in the presence of environmental or demographic stochasticity.

Early Dynamics

To determine the effects of corridors on early population dynamics, we examined the population size in both patches three time steps (N_3) after an initial population of two was introduced into a single patch. We define the corridor effect on a population as the difference in N_3 between pairs of populations that differ only in the presence or absence of a corridor between them. We chose three time steps because this was the maximum length that population size in both patches remained below equilibrium density for every combination of parameters we tested. Our results do not depend on $t = 3$ but are robust for any end point such that $t > 1$ and neither population has reached its equilibrium population size. We calculated N_3 for every combination of the parameter values listed in table 1 that resulted in $\rho > 1$ and $0 < \mu < 0.5$. When the contribution rate is <1, the population always goes deterministically extinct. When $\mu = 0$, the system behaves

Table 1: Parameter values used in numerical evaluation of corridor effects on early population dynamics

Parameter	Values tested
r	1.5, 2, 2.5, 3, 3.5
K	100
c	0, .025
e_m	0, .25, .5
e_c	e_m, e_m + .25, …, 1
s_m	0, .5, 1
s_c	0, .5, 1

Note: All combinations except those described in the text were evaluated.

as a single patch with growth rate equal to $r[1 - (ce_c + me_m)]$. When $\mu > 0.5$, the majority of individuals are migrating among patches and the system is more appropriately modeled as a single population (Harrison and Taylor 1997; Hanski 1999).

In our model, corridors that increased either ρ or μ would positively affect early population size (N_3; fig. 2). The magnitude of these effects depends nonlinearly on the value of both parameters in the absence of a corridor. Corridor-induced changes in ρ are largest when ρ and μ are large (fig. 2a). In contrast, corridor-induced changes in μ are largest when ρ is large but μ is small (fig. 2b). Both effects also scale with patch-carrying capacity (K; fig. 2a).

We have so far discussed how model parameters describing local population growth (r) and migration through the matrix (e_m and s_m) change a corridor's effect on ρ and μ and how changes in ρ and μ affect early population dynamics. We will now put these effects together to consider how the corridor's effects on early population dynamics depend on r, e_m, s_m, and K. The key results from our analysis are that r, K, and s_m predict corridor effectiveness during early dynamics.

The clearest predictions from our model are that populations with high r and large K will benefit most from corridors in the short run (fig. 2). Local growth rates (r) are positively correlated with ρ in the absence of a corridor, and ρ is positively related to population size (fig. 3). High local population growth rates also increase the effect of a corridor on ρ (eq. [13]), which, in turn, increases N_3. Large carrying capacities increase the corridor effect by increasing the number of potential migrants during the second and third time steps (eq. [13]).

There is not a clear relationship between corridor effects on early dynamics and parameters describing dispersal through the matrix (e_m, s_m). The potential for a corridor to influence ρ is greatest when emigration is high and the success of migrants through the matrix is low (eq. [13]). In contrast, corridor-induced changes in ρ have their

a.

b.
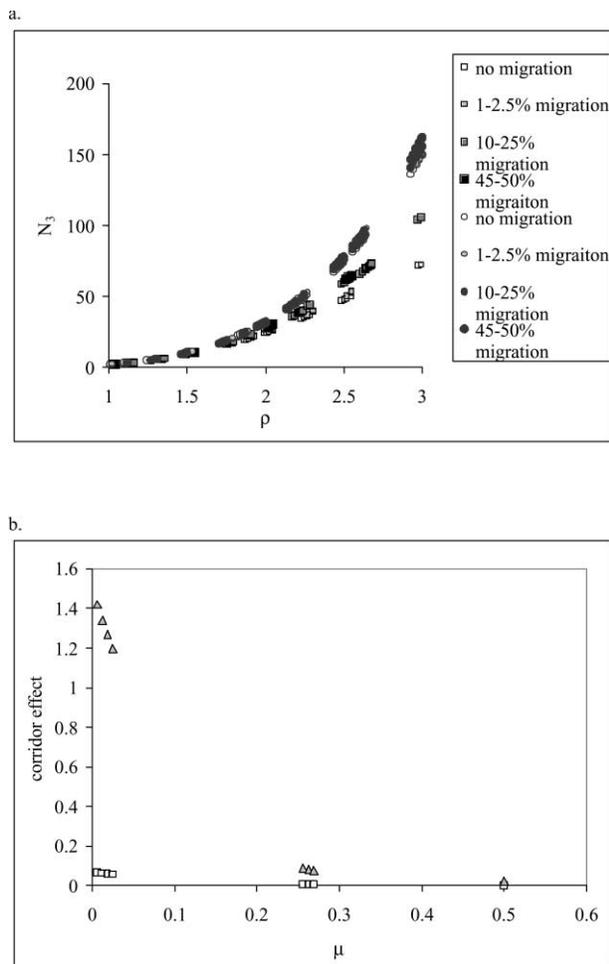
Figure 2: Total population size in both patches three time steps after initializing a single patch with two individuals (N_3). *a*, Total population size plotted against the contribution rate (ρ) for a given run. Squares correspond to runs with $K = 100$, circles to runs with $K = 1,000$. The size and shading of the points indicate the proportion of each population migrating each time step. *b*, Effect for corridors that change the migration rate (μ) by 0.01 but have no effect on ρ. *Squares*, $\rho = 1.55$; *triangles*, $\rho = 2.55$.

greatest impact on N_3 when ρ is large (fig. 2), which occurs when emigration is low and the success of migrants through the matrix is high (eq. [9]).

To better understand the complex relationship between these parameters during early population dynamics, we calculated N_3 for several combinations of e_m and s_m for logistically growing populations with $r = 2.55$ and $K = 100$, and we calculated the corridor effect as the difference in N_3 in pairs of runs that differed only in the presence or absence of a corridor ($c = 0$ vs. $c = 0.025$). In general, the effect of a corridor on N_3 decreases as s_m increases, which reflects the accelerating benefit derived with in-

creasing ρ. The relationship between e_m and the effect of a corridor on population size depended on the interaction between three variables: migration success through the matrix, migration success through the corridor, and the difference between the emigration rates through matrix and corridor habitats. As a result, emigration rates into the matrix alone provide almost no information about the potential for a corridor to benefit populations.

The conclusions above also hold if within-patch growth is modeled using Ricker, Beverton-Holt, and generalized discrete logistic equations instead of the discrete logistic equation described above.

Equilibrium Population Dynamics

To examine how corridors affect long-term average population sizes, we studied the equilibrium behavior of the model described by equation (10). As before, we examined the case of population growth within patches based on the discrete logistic, Ricker, Beverton-Holt, and generalized discrete logistic equations. Except as noted below, the results from the latter two models are qualitatively similar to those based on logistically growing populations, which we report here.

The behavior of our model at equilibrium depends entirely on ρ. When $\rho < 1$, the system has a single stable equilibrium at $N_1 = N_2 = 0$. When $1 < \rho < 3$, the system has a single positive equilibrium given by equation (12). When $\rho > 3$, the population sizes in each patch cycle between two points. If the patches are synchronized, the total population size in the two patches also cycles between two points. If the patches are not synchronized, the total population size remains at a single, unstable equilibrium. At $\rho = 3.44$, the dynamics within each patch grow more
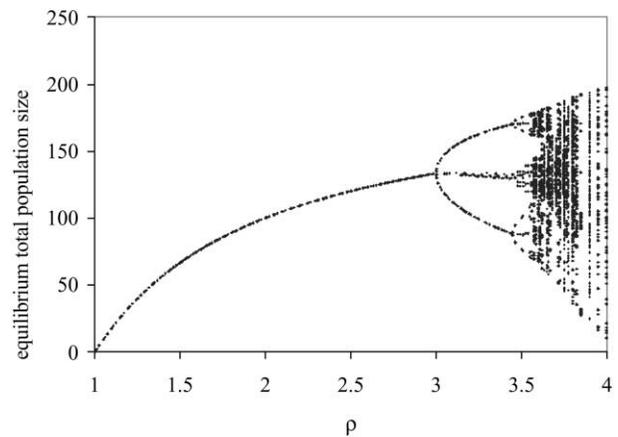
Figure 3: Total equilibrium population size in both patches graphed against the contribution rate (ρ) with $K = 100$.

complex and depend on the migration rate in a complex manner described in detail by Hastings (1993) and Lloyd (1995).

In our model, long-term corridor effects can be determined by the difference between population dynamics in patches with ($c > 0$) and without ($c = 0$) a corridor. We will consider the effect of adding a corridor between two patches when a corridor leads to deterministic extinction of a metapopulation, when $1 < \rho < 3$, and when $\rho > 3$.

When r is near unity, it is possible that connecting patches with a corridor will cause extinction. This would happen if corridors increase dispersal but also induce higher mortality. This could be the case if predators wait in corridors that funnel prey. Corridors will lead deterministically to extinction when $\rho_0 > 1$ and $\rho \leq 1$, where ρ_0 is the patch contribution rate in the absence of a corridor. If corridors are narrow relative to patches and do not have an appreciable effect on population loss through the matrix, then corridors will cause the deterministic extinction of a species when

$$r < \frac{1}{1 - M_m - M_c},$$

where M_m and M_c are the fractions of the population that are lost during dispersal through the matrix and corridor, respectively. This relationship indicates that the risk of corridor-induced extinction becomes increasingly small as r increases. This conclusion corroborates the finding below that the potential for corridors to affect equilibrium density, either negatively or positively, is greatest for slow-growing species.

When a single, stable, positive equilibrium characterizes the system ($1 < \rho < 3$), the main effect of a corridor is to change the equilibrium density in the two patches. Here, the equilibrium density increases with ρ and K. Thus, corridors that increase emigration rates without increasing migrant success will tend to lower the equilibrium density, while corridors that increase migrant success without increasing emigration rates will tend to increase equilibrium density. Because the equilibrium density is a saturating function of ρ (fig. 3), the magnitude of the effect of a corridor will be smaller when ρ_0 is larger. In other words, corridors will have a greater effect on the equilibrium abundance of species with lower growth rates, high emigration rates into the matrix, and low dispersal success through the matrix. These results are robust to the functional form of local population growth except for the case of the generalized Beverton-Holt. For the generalized Beverton-Holt model, the conclusions above do hold when $b > 1$ (notation after Bellows 1981). When $b = 1$, the equilibrium population size is a linear rather than saturating function of the contribution rate, which yields the prediction that the potential benefit of habitat corridors is affected only by patch carrying capacity (K).

When $\rho_0 > 3$, the behavior of the regional population becomes increasingly unstable as ρ increases (fig. 3). Under these conditions, corridor-induced changes in ρ may change the stability of equilibrium population. When the success of migrants through the matrix is not guaranteed ($s_m < 1$), habitat corridors that increase emigration rates without increasing migrant success rates ($e_c > e_m$, $s_c \leq s_m$) will decrease ρ and thus increase the stability of populations with $\rho_0 > 3$. In contrast, corridors that increase the success of migrants but do not increase emigration rates ($e_c \leq e_m$, $s_c > s_m$) will increase ρ and thus tend to destabilize populations with $\rho_0 > 3$. Because the transition to more complex dynamics occurs with increasingly small changes in ρ (fig. 3), the effect of corridors on population stability will be greater when ρ_0 is larger until $\rho_0 \gg 3.57$.

Species Persistence in Stochastic Environments

One of the reasons to create and maintain corridors is to reduce the extinction risk of species that experience large population fluctuations due to environmental variation. Isolated populations that experience large variation in demographic parameters always face some risk of local extinction. As a consequence, a species will tend to go regionally extinct at some rate determined by the risk of local extinction in each patch. Corridors may reduce that extinction rate by reducing the risk of local extinction through the rescue effect (Brown and Kodric-Brown 1977) or by promoting recolonization of patches following local extinction (Hanski 1999). However, corridors may increase the regional extinction rate by inducing higher rates of dispersal-related mortality, thus reducing the population growth rate within patches. We examined when corridors would have the greatest impact in reducing (or increasing) extinction rates by incorporating stochastic variation in model parameters.

We recorded the time to extinction in simulated pairs of populations with and without corridors. Each simulation began with a population of five individuals in a single patch, which then grew according to equation (10). We then allowed the populations in both patches to grow and disperse for 100 time steps or to go extinct. The parameter values used for each time step were drawn from a normally distributed random variable with a standard deviation equal to 45% of its mean. This standard deviation was chosen so that the time to extinction in most simulations was between 10 and 100 time steps.

We calculated the effect of corridors for each combination of mean parameter values listed in table 2. For each set, we recorded the difference between the mean time to extinction in 30 simulations with and without a corridor.

Table 2: Parameter values used in stochastic simulations, analyses of which are presented in table 3

Parameter	Values tested
r	1.5, 2.5, 3.5
K	50
c	0, .125
e_m	.05, .25, .45
e_c	e_m, $e_m + .05$, $e_m + .5$, 1
s_m	0, .25, .5, .75
s_c	$s_m * .9$, $s_m + .1$, 1

Note: All combinations that resulted in $\rho' > 1$ and $\mu' < 0.5$ were tested.

In each trial, we also calculated the expected contribution rate (ρ') and migration rate (μ'). We set the extinction threshold to a total population in both patches of 0.5 individuals. There are no qualitative differences in these results if the extinction threshold is set to one individual.

We analyzed the relationship between a corridor's effect on mean time to extinction and variables describing a species' survival, growth rate, and migration using a general linear model technique (PROC GLM; SAS version 8.1). We fit the corridor effect on extinction rates to a model including ρ'_0, μ'_0, the corridor effect on the contribution ($\rho'_c - \rho'_0$) and migration ($\mu'_c - \mu'_0$) rates, and all possible interactions. We simplified the model by removing all nonsignificant interactions in a stepwise fashion beginning with higher-order interactions. We repeated this analysis using both the full data set and, in order to more closely examine when corridors are most likely to benefit populations with low growth rates, only those simulations with $r = 1.5$.

In general, the larger the effect a corridor has on ρ' or μ', the larger its effect on persistence (table 3). How corridors affect a species' persistence differs for species with low and high growth rates, as indicated by a lack of a significant ρ'_m term but significant $\rho'_0 \times (\rho'_c - \rho'_0)$ and $\rho'_0 \times (\mu'_c - \mu'_0)$ interactions (table 3). When the ρ' is near 1, stochastic variation in demographic parameters is likely to cause local populations to decline toward extinction. As ρ' increases, populations become less likely to sustain declining growth rates. As a result, the impact of a corridor on persistence declines as ρ'_0 increases (indicated by a significant effect of ρ'_0 when only simulations with low intrinsic growth rates are considered; table 3). High μ' also helps to prevent sustained population declines. This is because immigrants from the faster-growing patch act as a buffer against stochastic decreases in local demographic parameters such as r. Thus, when $\rho'_0 \ll 2$, corridor-induced increases in ρ' or μ' will tend to increase persistence (fig. 4). This is the rescue effect. When there are very low levels of migration through the matrix, even corridors that reduced ρ' are likely to benefit populations through the rescue effect (table 4).

In contrast, when ρ' is large, local extinction is caused by populations overshooting their carrying capacity and subsequently crashing. When $\rho' \gg 2$, larger growth rates mean that good years are more likely to lead to large population booms and subsequently to severe population crashes. Furthermore, when migration rates are high, then a population that overshoots its carrying capacity during a good year produces immigrants that may cause the slower-growing population to also overshoot its carrying capacity. As a result, high migration rates will tend to synchronize population crashes among patches and increase the chance that both patches go extinct simultaneously. Thus, when $\rho'_0 > 2.5$, increases in ρ' or μ' caused by adding a corridor will tend to decrease persistence time (fig. 4). Corridor effects are greatest when there is little or no migration through the matrix (indicated by a significant effect of μ'_0; table 3).

Discussion

In many respects, our results confirm previous corridor studies and conventional wisdom regarding corridors. However, no "corridor theory" has been developed to date. The strongest case for conservation action will be when observations, experiments, and theory converge (Haddad et al. 2000), and our results provide some consensus among empirical and theoretical work. Our results also highlight that whether and how much a corridor benefits a population depend on the timescale under consideration, the population growth rate, the carrying capacity, the emigration rate, and the dispersal success rate of the target species. In the discussion below, we will review the conclusions drawn from our model results and discuss the implication of these results for short- and long-term recovery goals. We will then place our results in the context of recent empirical work on animal dispersal and make suggestions for future empirical studies. Finally, we offer a framework to determine the appropriateness of corridors as a strategy to meet conservation goals.

General Conclusions

One characteristic that was consistently associated with corridor benefit was patch carrying capacity. In all cases, a corridor's potential benefit was greater when the carrying capacity of the two patches was larger. Carrying capacity will vary among species within the same landscape and within a species among different landscapes. For example, all else being equal (including population growth rates), smaller-bodied species would receive greater benefit from the addition of a corridor than larger-bodied species. Fur-

Table 3: Factors affecting a corridor's effect on persistence

Parameter	Estimates for full data set	Estimates for $r = 1.5$	Correlation between parameter and				
			r	e_m	s_m	e_c	s_c
ρ_0'	.49	25.8*	+	−	+	0	0
μ_0'	−10.6***	220.5*	0	+	+	0	0
$\rho_c' - \rho_0'$	147.0***	1,191.6***	0	0	0	−	+
$\mu_c' - \mu_0'$	89.1**	NI	0	0	0	+	+
$\rho_0' * \mu_0'$	NI	−174.9*	+	0	+	0	0
$\rho_0' * (\rho_c' - \rho_0')$	−68.2***	−815.5***	+	−	+	−	+
$\rho_0' * (\mu_c' - \mu_0')$	−34.7**	NI	+	−	+	+	+
$\mu_0' * (\rho_c' - \rho_0')$	NI	−438.4*	0	+	+	−	+
$(\rho_c' - \rho_0') * (\mu_c' - \mu_0')$	−1,679*	NI	0	0	0	0	+
$\rho_0' * (\rho_c' - \rho_0') * (\mu_0' - \mu_0')$	725**	NI	+	−	+	0	+

Note: For each term, the best estimate of the parameter value in the reduced model and whether it was a significant factor in the full model are presented. NI = not included in reduced model. The sign of the correlation between each parameter and component parameters is determined from equations (8) and (9).

* $P < .05$.

** $P < .01$.

*** $P < .001$.

thermore, for a given species, carrying capacity would usually be higher in a large rather than a small patch. Thus, the corridor benefits are predicted to increase with patch size. An important caveat to this conclusion is that we only simulated environmental stochasticity for relatively small populations ($K = 50$) and did not include the effects of demographic or environmental stochasticity in our analysis. Since these factors are more likely to cause local extinction of small populations than large ones, corridor effects may be greater for organisms with low carrying capacity than is suggested by our analysis of deterministic models.

Another consistent finding of our model was the relationship between migration through the matrix and corridor benefits to populations. As expected from many previous studies, our model results supported the empirical finding that the benefit of a corridor was greatest when there was very little migration through the matrix. When there is little or no successful migration through the matrix, a corridor might benefit a population simply by providing modest amounts of migration among patches (figs. 2, 4). In such situations, corridors provide a benefit simply by promoting the transfer of individuals among patches. As is self-evident, in the absence of migration through the matrix, corridors would be necessary for the colonization of unoccupied patches. Such colonization facilitates population spread from low densities in one or a few patches. Corridor-induced increases in colonization rates will also increase the equilibrium population size of a species by increasing the number of patches, and thus area, that the species can occupy. In the absence of migration through the matrix, corridors may also provide a mechanism for

immigration to rescue slow-growing populations from extinction.

In most cases, however, low levels of migration among patches are sufficient to cause these phenomena (Harrison and Taylor 1997; Hill et al. 2002). Thus, when a species cannot migrate through the matrix, its population is likely to benefit from corridors that connect patches even if such corridors result in an increase in dispersal-related mor-
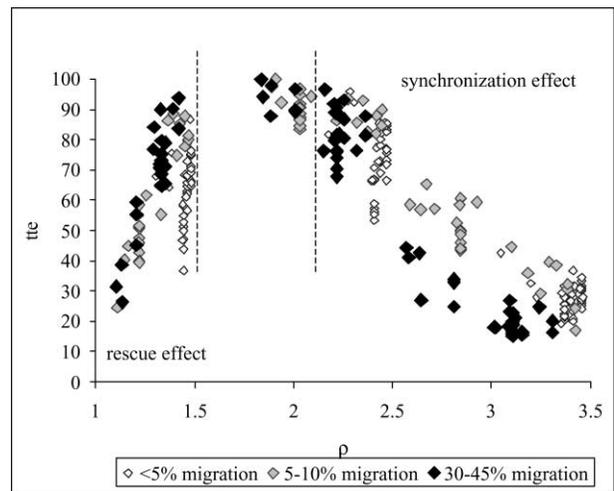
Figure 4: Mean time to extinction for sets of 30 simulations plotted against the expected modified growth rate for each set. The size and shading of each point indicates the expected migration rate (μ) for each set. *Small open diamonds*, simulations with <5% migration; *medium gray diamonds*, simulations with 5%–10% migration; *large solid diamonds*, simulations with >25% migration per time step.

Table 4: Percent of simulations where corridors increased persistence despite causing a reduction in the contribution rate

μ_0	%
$\mu_0 \leq .0625$	70.8 (24)
$0.0625 < \mu_0 < .3375$	40.0 (15)
$\mu_0 \geq .3375$	20.0 (5)

Note: Entries are separated by the migration rate in the simulation without a corridor (μ_0), with the total number of paired simulations where corridors reduced the contribution rate in parentheses. Separation points represent natural breaks in the data determined by visual inspection.

tality. For example, consider the effect of corridors in simulations of populations with low growth rates. In these situations, an increase in dispersal-related mortality is expected to reduce ρ' (eq. [9]) and thus reduce the time to extinction (fig. 4). But when migration rates through the matrix are extremely low, the rescue effect caused by corridor-induced migration is great enough to increase time to extinction (table 4).

In addition to highlighting the importance of matrix dispersal rates in determining corridor success, an important result of our analysis is to focus attention on the importance of migration success, which includes mortality during dispersal. When there is even moderate migration through the matrix, corridors no longer affect populations by increasing migration rates per se. Rather, the major impact of a corridor is to change the contribution rate, mainly by affecting the survival of dispersers. Corridor-induced changes to the contribution rate are also particularly important when growth rates within patches are near 1. In these cases, corridors that increase dispersal-related mortality (so-called death traps) pose an extinction threat.

Corridor Use for Short-Term Recovery Goals

In early dynamics following the recovery from disturbance, corridors are most beneficial for species with high population growth rates and with low survivorship in the matrix. Thus, in a frequently disturbed system, species with high population growth rates would be expected to benefit most from management corridors. These species would also recover most rapidly following extinction and recolonization. This result suggests that in the short term, corridors would most benefit species adapted to colonizing new habitats. For example, butterflies, such as the Glanville fritillary (*Melitaea cinxia*), that escape heavy parasitism through colonizing new habitats (Hanski 1999) would be strong candidates as corridor beneficiaries. This finding also points out one potential negative consequence of corridors, which is their potential to benefit invasive species, especially in heavily disturbed areas (Simberloff et al. 1992).

Corridor Use for Long-Term Recovery Goals

In contrast to short-term recovery goals, the species benefiting most from corridors over long timescales were those with slow-growing populations. Equilibrium population size is a saturating function of the contribution rate (fig. 3). Thus, when the contribution rate is small, the potential change in equilibrium density with a small change in ρ is large. This conclusion depends on the relationship between the population growth rate and the equilibrium population size within patches.

Corridors also offer the greatest benefits to species persistence in a landscape when ρ is small. Because the chance of sustained population decline decreases as ρ increases above 1, corridors should have the greatest benefit on the persistence of slow-growing species.

At first glance, these results appear to contradict the conclusions of Earn et al. (2000) that corridors will be least likely to detrimentally affect fast-growing populations through synchronizing their dynamics. However, populations need not be perfectly or even nearly perfectly synchronized to experience correlated boom-bust cycles. All that is required for correlated cycles is that migration from higher density patches is sufficient to push lower density patches substantially above their carrying capacity. There are three reasons why we find this occurs frequently at high growth rates in our model while Earn et al. (2000) did not. First, we considered only two patches while they considered 10, which makes global extinction less likely. Second, we applied environmental stochasticity to the growth process before migration rather than after migration so that corridors would tend to propagate boom growth in high-density patches before density dependence caused populations to crash during subsequent generations. Third, we considered corridors that increase successful migration by reducing dispersal mortality and simultaneously increase ρ and μ. Although corridors are less likely to synchronize dynamics in a large network of patches when local population growth rates are high, they are more likely to couple a boom-bust cycle among neighboring patches.

Implications for Conservation

Although there are a number of other articles that have focused on corridor effects on animal movement rates between patches (e.g., Beier and Noss 1998; Haddad et al.

2003), there has been no research on the impact of corridors on migration loss (i.e., contribution rate). Thus, the potential benefits offered by corridors in previous studies are assumed to operate through increased migration among patches. However, under conditions that allow even a moderate amount of migration through the matrix, the primary benefit of a corridor stems from reduced losses during dispersal. There is a need for greater empirical efforts to determine the effectiveness of corridors at preventing dispersal-related loss by reducing migrant mortality.

Only a small number of studies reported movement rates that were sufficiently low through matrix habitat to suggest corridors are likely to influence population sizes through increased migration rates alone. Radio-tagged cougars never entered urban matrix and would probably never make it through if they entered (Beier 1995). In a behavioral study, ringlet butterflies were found to leave a small opening via the woods 2% of the time even though the woods comprised 77% of the exit routes (Sutcliffe and Thomas 1996). Eight species of arboreal mammals were found in forest and forested corridors, but urban or agricultural areas were probably impenetrable (Downes et al. 1997). In other studies that showed corridor use by American robins (Haas 1995), chipmunks (Henderson et al. 1985), and sugar gliders (Suckling 1984), movement rates were not sufficiently low through matrix that corridor migration alone is unlikely to impact population sizes.

A cross-taxonomic study of corridor effects was conducted at the Savannah River site, South Carolina (Haddad et al. 2003). Of nine species studied, including butterflies, small mammals, bird-dispersed seeds, and carpenter bees, five were shown to move more frequently between connected than unconnected patches, and all may have used corridors (sample size was low, which precluded analysis in the other cases). However, only butterflies separated by the largest distances (>200 m) showed movement rates between unconnected patches low enough to suggest that increased migration alone is likely to cause corridors to increase population sizes (Haddad 1999a). In behavioral studies of butterflies and cotton rats, a minimum of 70% of individuals left open patches through forest (Bowne et al. 1999; Haddad 1999b). Although this was often less than expected by random movement, it was not low enough for migration alone to have a probable impact on population sizes. The butterflies were the only species for which population sizes were examined, and they did show higher abundances in connected patches. However, most patches were <200 m from any other patch, so the most likely contribution of corridors to butterfly populations was through a reduction in dispersal-related loss and not increased migration. In this case, corridors may have reduced dispersal-related loss by reducing emigration from the ex-

perimental area rather than increasing migrant survivorship. Patch size and shape must also have contributed to the differences (Haddad and Baum 1999).

Of course, migration rates through matrix habitat depend on landscape context. For example, previous studies have found that as distances between patches increase, movement rates between connected and unconnected patches decrease (Haddad 1999a). Thus, the potential migration-related benefit of corridors becomes larger as distances between patches increase. Matrix type may impact the importance of corridors in directing movement. For example, Ricketts (2001) showed that different butterfly taxa move through matrix habitats at different rates. Of the groups that he examined, only for the Lycaenini would increased migration rates alone have been likely to impact population sizes when the matrix was either conifer or willows surrounding open patches (deduced by multiplying the matrix movement rate by the total recapture rate). The Pierinae and Melitaeini, and perhaps the Polyommatini and Satyrinae, should benefit from corridors in conifer landscapes but not in willow landscapes. In another study, Ries and Debinski (2001) showed that different matrix types had different impacts in limiting butterfly emigration from prairies, but no butterfly had sufficiently low emigration rate to justify corridors based on migration alone.

Since most of the studies above indicate that focal species do migrate through noncorridor habitat in moderate amounts, there is a strong indication that further research must focus on the role of corridors in increasing migrant success. Although this question is difficult to answer and has not been addressed in the literature, it appears to be a key determinant of how a corridor will affect a particular species. Likewise, most corridor studies focus only on dispersal and do not consider local demographic parameters such as population growth rate or patch carrying capacity, although these also appear to play important roles in determining how a corridor will affect a particular species. We suggest that future studies should focus on the links between corridors and dispersal success and between local demographic parameters and corridor benefits to populations.

Suggestions for Determining Corridor Potential

When evaluating the potential for corridors as part of a conservation program, our results suggest the following questions should be asked during the development of conservation plans involving corridors.

What Is the Timescale of the Conservation Goal? The answer to this question determines the kinds of species most likely to benefit from corridors, with fast-growing species more

likely to benefit in the short term but slow-growing species more likely to benefit in the long term. Because fast-growing species are unlikely to be of major conservation concern, corridors will probably have less impact in short-term than in long-term conservation planning. There are two exceptions for which corridors are likely to have a large impact in the short term. Corridors will probably have a large short-term impact on the conservation of species that suffer high mortality from dispersal through the matrix but are highly successful at dispersing through a corridor, even if these species are slow growing. Corridors are also likely to have a large impact on species that persist in highly ephemeral habitats or rapidly changing landscapes. Many species of concern that depend on short-lived successional stages, such as the Saint Francis Satyr butterfly (*Neonympha mitchelli fransiscii*) or Bachman's sparrow (*Aimophila aestivalis*; Haggerty 1992; Pulliam et al. 1992; Dunning et al. 1995), might fit this category.

Is the Major Threat of Local Extinction due to Sustained Population Decline or Boom-Bust Cycles? The answer to this question determines whether or not a corridor that increases migration rates and reduces dispersal-related mortality is appropriate. A corridor would likely reduce the threat of extinction due to sustained population decline but could increase the threat of extinction when local population dynamics are characterized by large cycles.

What Is the Migration Rate through Matrix? The answer to this question determines the mechanism of corridor benefit. If there is negligible migration through the matrix, the potential benefit may be surmised from movement through the corridor and matrix alone.

However, if there is moderate migration through the matrix, corridors must act to reduce dispersal-related mortality in order to benefit connected populations. Traditionally, corridors are proposed with respect to one or a few species. However, corridors may impact many species within any landscape. Our model results give some context for thinking about which species would benefit—and which species would be harmed—by the addition of a corridor. In doing so, we hope to move the debate over corridor utility to a more fruitful discussion of the biological processes that determine the conservation value of habitat corridors.

Acknowledgments

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