Habitat persistence, habitat availability and the evolution of dispersal

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Many organisms live in ephemeral habitats, making dispersal a vital element of life history. Here, we investigate how dispersal rate evolves in response to habitat persistence, mean habitat availability and landscape pattern. We show that dispersal rate is generally lowered by reduced habitat availability and by longer habitat persistence. However, for habitats that persist for an average of ten times the length of a generation, we show a clear non-monotonic relationship between habitat availability and dispersal rate. Some patterns of available habitat result in populations with dispersal polymorphisms. We explain these observations as a metapopulation effect, with the rate of evolution a function of both within-population and between-population selection pressures. Individuals in corridors evolve much lower dispersal rates than those in the mainland populations, especially within long, narrow corridors. We consider the implications of the results for conservation.

Keywords: dispersal; evolution; lattice model; metapopulations; patches; spatial structure

1. INTRODUCTION

Organisms move on a wide range of temporal and spatial scales. Movement varies from daily foraging patterns to long-distance seasonal migrations, and from movements of a few individuals between adjoining sites to shifts in the geographical ranges of entire species (see figure 1). At present, our understanding of how different movement strategies evolve in response to different patterns of habitat suitability is limited, yet this remains an area we have to understand better if we are to develop successful strategies for conserving biodiversity in the face of habitat fragmentation and climate change. In this paper, we concentrate on dispersal and how it evolves in response to different patterns of habitat availability and quality.

The evolution of dispersal in spatially structured populations has received considerable attention from theoreticians (e.g. Gadgil 1971; Comins *et al.* 1980; Comins 1982; Hastings 1983; Levin *et al.* 1984; Holt & McPeek 1996; Doebeli & Ruxton 1997; Olivieri & Gouyon 1997). The results of these studies are summarized more thoroughly elsewhere (e.g. Johnson & Gaines 1990; McPeek & Holt 1992). Generally, increasing spatial variability leads to selection for a reduction in the rate of dispersal, while increasing temporal variability increases the rate of dispersal, although Travis & Dytham (1998) demonstrate that propensity to disperse is not a neutral character even when patches are spatially and temporally constant.

Until recently, models investigating the evolution of dispersal were not spatially explicit (but see Hamilton & May 1977) and thus excluded the possibility of looking at the effect of different patterns of habitat quality. Previous approaches to the inclusion of spatial realism into cellular

models have been attempted by random patch removal (e.g. Dytham 1994), patterned habitat destruction (e.g. Dytham 1995a), or using landscapes generated using fractals (e.g. With *et al.* 1997). Corridors have been widely discussed as a management tool for conservation (e.g. Verkaar 1990; Hobbs 1992) and a variety of models have been used to investigate movements along corridors using both plant (vanDorp *et al.* 1997) and animal (Tischendorf & Wissel 1997) examples. Understanding how the evolution of dispersal will respond to deliberate human attempts to restore connectivity may help in designing effective corridors.

In this paper we extend the spatially explicit model developed by Travis & Dytham (1998) to investigate the effect of different patterns of habitat availability and habitat persistence on the evolution of dispersal.

2. THE MODEL

The model we developed is an extension of that used by Travis & Dytham (1998) and Johst & Brandl (1997). For simplicity, we considered an asexual species. We used an 11-genotype system in which genotypes differ in their probability of dispersal. The probability of dispersal is 0.0 (i.e. individuals never move) for genotype 0, and increases in 0.1 increments up to a probability of 1.0 for genotype 10. We incorporate no trade-off between dispersal and competitive ability. The within-population dynamics consist of reproduction and competition between juveniles. Dispersal follows competition.

As before (Travis & Dytham 1998), the metapopulation is made up of $n \times n$ subpopulations on a square lattice. Importantly, the model is spatially explicit: dispersers can move only to neighbouring patches. This work extends previous studies by incorporating patterns of habitat availability. In
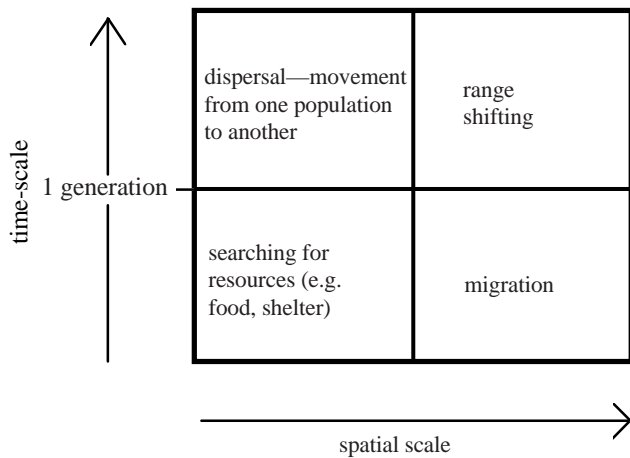
Figure 1. The forms of movement important at different spatial and temporal scales.

Figure 2. A representation of the spatial variation in patch quality with a Hurst exponent of 0.9. Vertical scale indicates patch quality.

any one generation, only a proportion of all patches is suitable for the survival and reproduction of a population. Individuals dispersing into an unsuitable patch, or remaining in a patch that becomes unsuitable, die.

(a) *Within-population dynamics*

The within-population dynamics used are based on the model of Hassell & Comins (1976) and are identical to those described for the individual-based formulation by Travis & Dytham (1998). The population size, N, in a patch, x, at time $t + 1$ is determined by the expression

$$N_{x,t+1} = \text{floor}[\lambda N_{x,t}(1 + aN_{x,t})^{-b}],$$

where λ is the intrinsic rate of increase, and a and b relate to patch quality and the type of competition, respectively. The result is floored so that an integer result is produced (it is not possible to have part of an individual). Here we assume contest competition ($b = 1$). The use of higher values of b would describe more scrambled forms of competition. The parameter a is calulated from the expression

$$a = (\lambda^{1/b} - 1) - N^*,$$

where N^* is the local equilibrium population density (a measure of patch quality).

Every individual present at time t contributes λ offspring to a pool. Offspring in this pool then compete until N_{t+1} (given by the expression above) remain to make up the next generation's adult population. Most offspring have identical genotype, and hence propensity to disperse, as their parent. However, there is a small probability of mutation, m, to a genotype—one higher or lower than that of the parent.

(b) *Between-population dynamics: dispersal*

In the dispersal phase of the model each individual has a propensity to disperse, which is determined by its genotype. Whether it disperses is determined at random. Dispersal is local: dispersing individuals have an equal likelihood of moving to each of eight neighbouring patches. Cyclic (i.e. wrapped or periodic) boundary conditions are employed. Similar individual-based
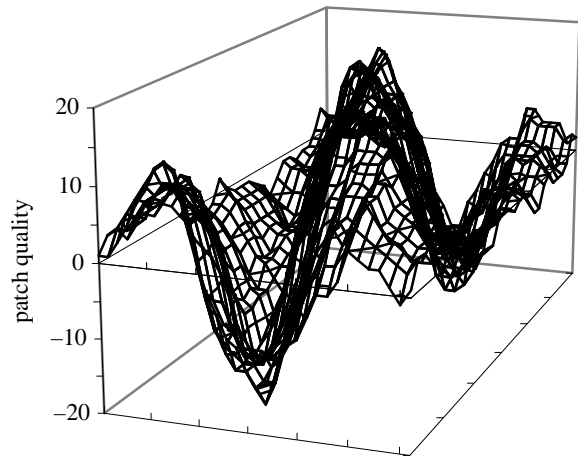
dispersal has been used previously in population models (e.g. Ruxton 1996; Wilson & Hassell 1997).

(c) *Habitat availability*

We incorporate three different patterns of habitat availability. Following dispersal, individuals which are in unavailable sites are killed. The patterns of availability used are as follows.

(i) *Static pattern*

The pattern of habitat loss is described by a fractal landscape using a similar method to that of With *et al.* (1997). We use a random fractal algorithm to generate patterns with different degrees of autocorrelation. This produces landscapes such as those shown in figure 2. We consider sites as either available or unavailable. Available sites are all of the same quality. To decide which sites are available, imagine filling the landscape in figure 2 with water until the proportion of sites uncovered is equal to the proportion that is available. This produces the type of habitat patterns shown in figure 3. Here, we look at how dispersal evolves for high, medium and low autocorrelated habitat fragmentation, with different proportions of habitat being lost. To highlight the differences caused by the types of habitat pattern used, we impose an explicit cost of not dispersing. For the model runs shown here, individuals that remain at their natal site incur a 10% risk of mortality.

(ii) *Dynamic pattern*

In reality, it is highly unlikely that habitat patches are fixed in a permanent state. Much more plausible is a dynamic mosaic with patches blinking on and off through time. In this scenario, important parameters in determining the rate of dispersal that evolves are likely to be mean habitat availability and mean habitat persistence—how much habitat is available in any one generation, and for how long a site is likely to remain available. This is incorporated into the model as follows. First, for a specified patch persistence, the mean time for which the patch is unavailable, (P_u) to give the required habitat availability is calculated as
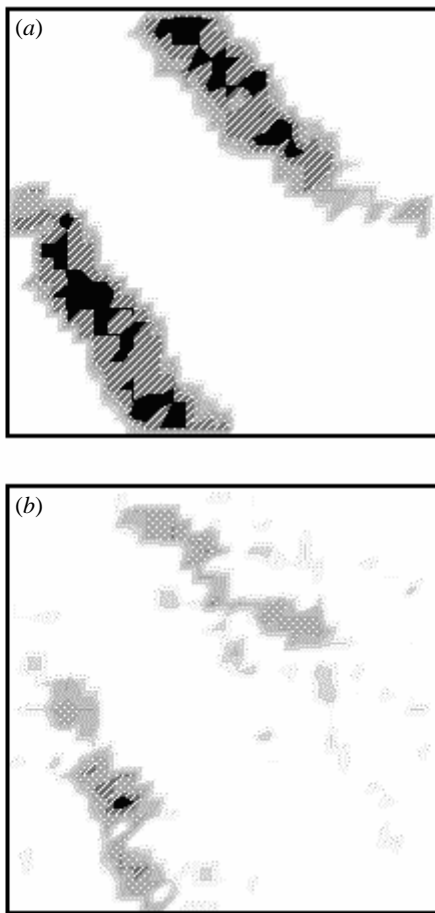
$$P_u = (P_p \times 100/A) - P_p,$$

Figure 3. Dispersal rates that evolve in landscapes with the same proportion of habitat available but different Hurst exponents: (*a*) 0.9; (*b*) 0.5. Darkest shading shows dispersal propensity >0.7; lightest shading shows dispersal propensity of <0.1. Unshaded areas are either not available for colonization or do not support a population.

where P_p is the mean persistence time, and A is mean patch availability.

The patches are initialized such that a proportion, A, are habitable. These patches are each allocated a number of generations for which they will persist, by taking a number from the Poisson distribution with mean P_a. Similarly, a proportion, $1 - A$, of patches are allocated a time for which they will remain unsuitable, by taking a number from the Poisson distribution with mean P_u. Two variables, T_a and T_u, represent the number of suitable and unsuitable generations, respectively, for each site. The following algorithm is used to update the state of patch availability during each generation.

(1) If $T_u > 0$, all individuals at that site are killed.

$\quad\quad\quad T_u$ is decremented by 1.

$\quad\quad\quad$ if $T_u = 0$, then T_a is set to Poisson (P_a).

(2) If $T_a > 0$, T_a is decremented by 1.

$\quad\quad\quad$ if $T_a = 0$, then T_u is set to Poisson (P_u).

This algorithm is iterated 1000 times before any individuals are introduced to allow the dynamic mosaic to reach an equilibrium.

(iii) *Ecological corridors*

To investigate how the rate of dispersal may evolve where habitat corridors have been provided as an attempt to connect populations otherwise isolated by fragmentation, we use the habitat patterns shown in figure 4. Here, we consider an area of land which has the same type of dynamic mosaic described above, but now has been fragmented into two blocks of habitat connected by a corridor. Habitat is either never suitable, or is suitable for a certain proportion of the time. We are interested in how the rate of dispersal may evolve locally in the region of the corridor, such that it affects the transfer of individuals and genetic information between two larger areas of suitable habitat. The length and width of the corridor was varied.

3. RESULTS

(a) *Static pattern*

There are three main results. First, as the amount of available habitat is reduced, a lower rate of dispersal evolves (figure 5). Second, for the same proportion of habitat availability, a landscape with a higher degree of autocorrelation selects for individuals with a higher dispersal rate (figure 5). Third, the propensity to disperse from a particular site depends on the position of that site in relation to other suitable habitats (figure 3). Sites towards the centre of a cluster of suitable patches contain local populations with a significantly higher mean propensity to disperse than do populations in sites at the edge. For many runs of the model, we find a distinctly bimodal distribution of dispersal strategies in the overall population. Large numbers of individuals have high or low dispersal propensity, while very few have intermediate rates (see figure 6).

(b) *Dynamic pattern*

Figure 7 shows the results obtained when a certain proportion of the environment is covered by ephemeral resources. As the percentage of habitat available is reduced, there is a general trend favouring individuals with a decreased propensity for dispersal. However, for a reduction of habitat availability between 58% and 50%, the rate of dispersal selected for actually increases (figure 7*b*) before declining again with further decreases in habitat availability. For a habitat availability higher that 35%, the results presented are the mean of 20 realizations of the model. For lower habitat availability, the results shown are for the first 20 realizations, where the population did not become extinct in 20 000 generations. In some cases, the model was realized more than 100 times before 20 results were obtained. Figure 7 also shows the effect of habitat persistence on the evolution of dispersal. When habitats persist for only short periods of time (figure 7*a*), a much higher rate of dispersal evolves than for habitats which persist for longer periods (figure 7*b,c*).

(c) *Ecological corridors*

Figure 4 shows how the rate of dispersal evolves for a simulation where two blocks of habitat are linked by a corridor. The most striking feature is the greatly reduced rate of dispersal propensity found along the length of the corridor. Selection against dispersal causes the individuals
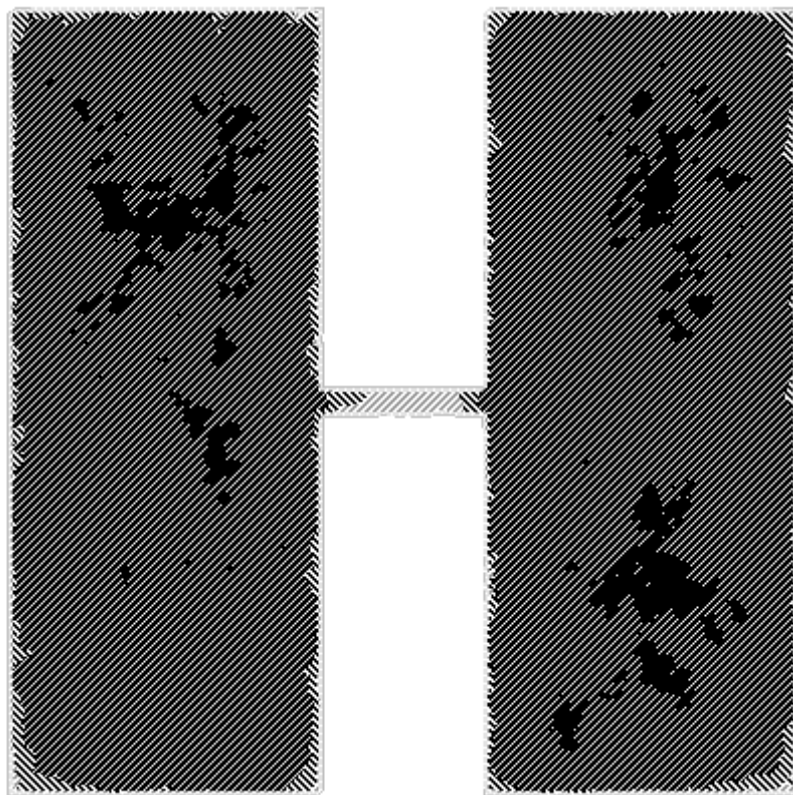
Figure 4. Dispersal rates that evolved in a landscape of two large patches of available habitat connected by a corridor. Darkest shading shows dispersal propensity of >0.7; lightest shading shows dispersal propensity of <0.1. Unshaded areas are not available for colonization. There are 10 000 subpopulations in this lattice.
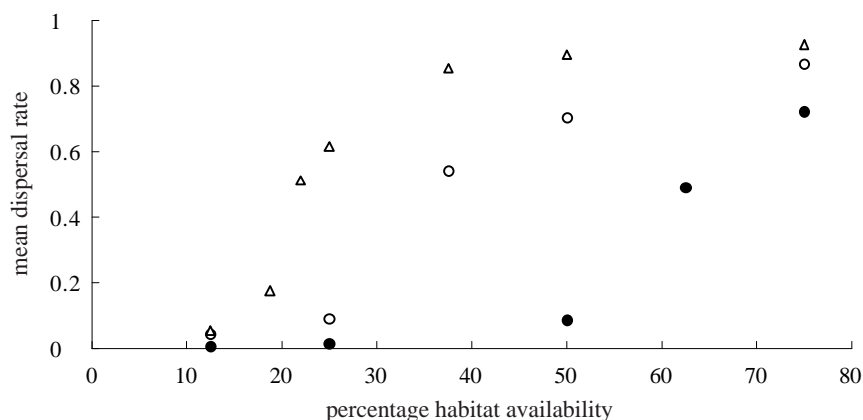

Figure 5. The effect of the amount and pattern of habitat availability on mean dispersal rate. Triangles, Hurst exponent = 0.9; open circles, Hurst exponent = 0.5; filled circles, Hurst exponent = 0.1.

found along the length of the corridor to disperse less. It is also apparent that the lowest rates of propensity to disperse evolve in the area of the corridor furthest from the main habitat blocks. Within the main populations the dispersal rate is not constant. There is a marked edge effect, with individuals near the edge of the habitat block being less likely to disperse.

We also investigated the effect of the length and width of the connecting corridors. Lower rates of dispersal evolve in longer, narrower corridors, and higher rates in short, broad corridors.

4. DISCUSSION

It is not surprising that the propensity to disperse declines as habitat is lost. Dispersal is blind so the cost of dispersing increases owing to the risk of moving into an unsuitable site. The result that a more autocorrelated pattern of habitat loss selects for higher dispersal rates is due to the same type of effect. A suitable site is more likely to be adjacent to other suitable sites in an autocorrelated landscape, so dispersal will carry a lower cost. As a habitat is fragmented, dispersal rates might be expected to decline owing to the increasing costs associated with dispersing. Fragmenting the habitat in a random fashion (as shown in figure 3) leads to the greatest decrease in dispersal rate. Previous models (e.g. Dytham 1995*b*; With & Crist 1995; Boswell *et al*. 1998) have indicated that populations will persist to lower habitat availability if the pattern is autocorrelated. Our results suggest that extinction due to habitat fragmentation might be avoided or postponed, if individuals have a plastic dispersal strategy, or if there is rapid evolution of propensity to disperse. However, a reduction in dispersal rate might have severe
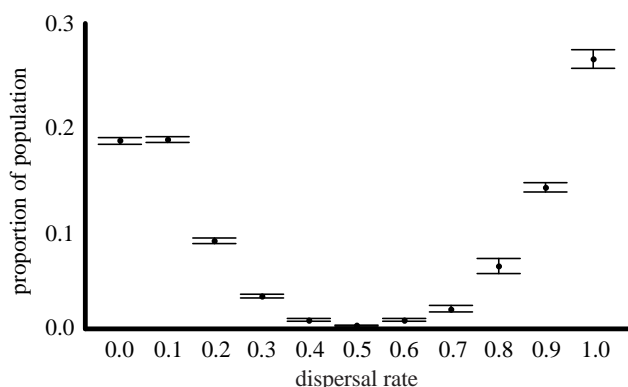
Figure 6. Mean and 95% confidence intervals for the proportion of individuals in a population with each of the 11 propensities to disperse where the Hurst exponent used to generate the landscape is 0.9 and landscape habitat availability is 22%. Results of 90 realizations. Clearly, a population with bimodal distribution of propensity to disperse has developed.

and damaging consequences for the persistence of a meta-population by reducing the chance of patch colonization. Clearly, both the amount and the pattern of habitat fragmentation cause the rate of dispersal to evolve.

The bimodal distribution of dispersal strategies found within populations for most runs of the model is intriguing. At the edge of a cluster of suitable sites individuals with very low propensities to disperse are favoured, whereas in the middle of clusters individuals with high dispersal rates are selected. Very few individuals have an intermediate dispersal rate. These results indicate that edge effects can be a powerful force driving dispersal polymorphisms in nature.

The non-monotonic relationship we found between the rate at which dispersal evolves and habitat availability was initially somewhat surprising. We had anticipated that the rate of dispersal would decline linearly as a habitat was removed because of the increased cost of dispersing due to the higher probability of moving into an unsuitable site. The results obtained (figure 7b) can be explained by the existence of a trade-off between the costs involved in being a disperser, due to the risk of moving into an unsuitable cell, and the costs of being a non-disperser (and having non-dispersing offspring) caused by a habitat having limited persistence. As habitat availability decreases both these costs increase. More sites are unsuitable so the cost of dispersing increases. Also, the cost incurred by 'low dispersal' genotypes increases. Low dispersing genotypes will be less able to track the changing habitat pattern as the number of available sites declines. Having offspring with a higher propensity to disperse is the best way for an individual to ensure that at least one of them moves to a suitable neighbouring site. This becomes increasingly important as fewer sites are suitable. The results demonstrate that, initially, as availability is reduced, the increased costs of dispersing outweigh those of not dispersing. However, this changes when habitat availability is between 58 and 50%. In this rather narrow range the opposite must be true and the increased cost of not dispersing is greater than that associated with dispersing.
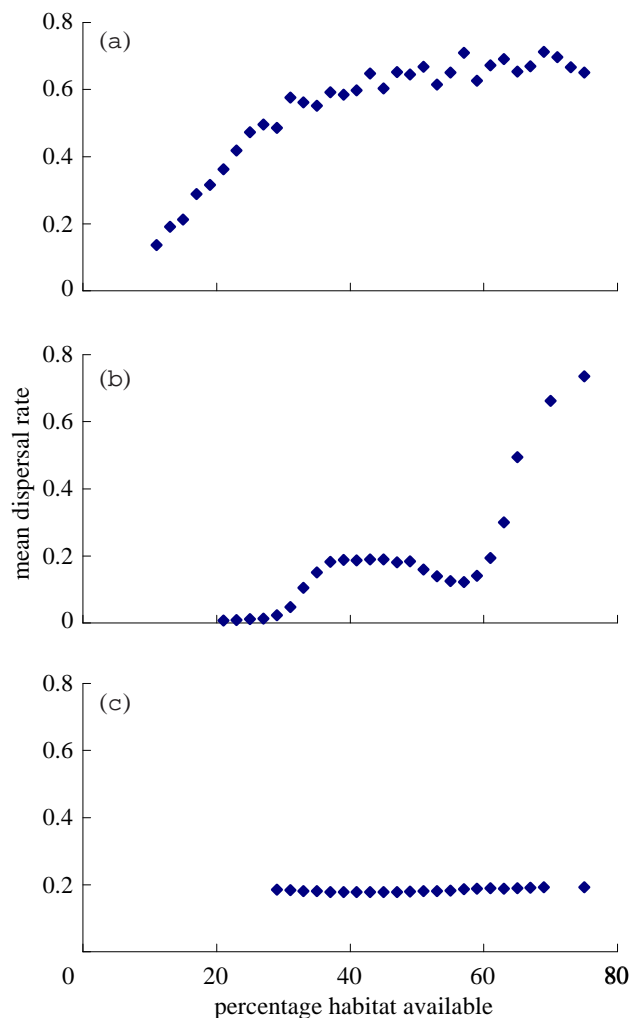

Figure 7. Mean dispersal rate across a range of habitat availabilities (20 realizations for each point). Habitat persistence is: (*a*) five; (*b*) ten; and (*c*) 20 generations.

These two selection pressures provide an example of the two levels of selection which are found within meta-populations: within-population and between-population selection (e.g. Olivieri *et al.* 1995). Indeed, Olivieri *et al.* (1995) also found a non-monotonic pattern resulting from a similar effect. Whereas, in the model presented here, a relationship between habitat availability and dispersal rate is obtained, Olivieri *et al.* (1995) produced a relationship relating the dispersal strategy to the maximal age of a subpopulation. That the rate of dispersal declines when habitat availability falls below 50% is due to the presence of a small number of sites which have a long persistence time and support a population for the duration (or most) of the simulation. If the model was run for long enough metapopulation persistence would not occur.

Habitat persistence is an important determinant of the rate of dispersal that evolves. Intuitively, dispersal is expected to be favoured in temporal habitats, as species need to be able to track a moving resource. This expectation was confirmed by the model and is consistent with empirical work (Denno *et al.* 1991). Using 35 species of plant hoppers living in habitats of varying persistence, Denno *et al.* (1991) demonstrated that flightlessness was favoured in persistent habitats while winged morphs were more common in ephemeral habitats.

Corridors have provided a focus of interest in fragmenting habitats as they could be a management tool. They can also be the agents of fragmentation when roads or power-lines cut through continuous habitats (e.g. Rich *et al*. 1994). More usually they are seen as potential movement routes for mammals (e.g. Bennett *et al*. 1994) or birds (e.g. Schmiegelow *et al*. 1997) which might be travelled many times. Our model presents a situation where the corridor is an identical habitat to the main patches, but the population takes several generations to travel along it. This is not unreasonable for plants or arthropods with 'blind' dispersal. For example, Tischendorf *et al*. (1998) showed that carabid beetles moving along a hedgerow corridor might only move 100 m per year, and thus might take several generations to travel a corridor. We predict that population densities will be lower in corridors and also, perhaps perversely, that lower propensities to disperse will evolve due to high selection against dispersal. This agrees with the model of vanDorp *et al*. (1997) who concluded, in a model where dispersal strategy was fixed, that annual plants in corridors might lose so many seeds to the unfavourable habitat that they might not be able to persist in the corridor. One example of a corridor analogous to our model is the mistletoe (*Amyema miquelii*), still locally common in woodland fragments, where a 26 km roadside of woodland contained only one individual in the whole corridor (Norton *et al*. 1995).

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