

The evolution of dispersal in a two-patch system: Some consequences of differences between migrants and residents

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Summary

We investigate how age-structure and differences in certain demographic traits between residents and immigrants of a single species act to determine the evolutionarily stable dispersal strategy in a two-patch environment that is heterogeneous in space but constant in time. These two factors have been neglected in previous models of the evolution of dispersal, which generally consider organisms with very simple life-cycles and assume that, whatever their origin, individuals in a given habitat have the same bio-demographic characteristics. However, there is increasing empirical evidence that dispersing individuals have different demographic properties from philopatric ones. We develop a matrix model in which recruitment depends on local population densities. We assume that dispersal entails a proportional cost to immigrant fecundity, which can be compensated by differences in survival rates between immigrants and residents. The evolutionarily stable strategies (ESS) for dispersal are identified using a combination of analytical expressions and numerical simulations. Our results show that philopatry is selected (1) when dispersal rates do not vary in space, (2) when the metapopulation is a source-sink system and (3) when dispersal rates vary in space (asymmetric dispersal) and immigrants do not compensate for their reduced fecundity. We observe that non-zero asymmetric dispersal rates may be evolutionarily stable when (1) immigrants and residents are demographically alike and (2) immigrants compensate totally for their reduced fecundity through an increase in adult survival. Under these conditions, we find that the ESS occurs when the fitnesses at equilibrium in the two habitats, measured in our model by the realized reproductive rates, are each equal to unity. A comparison with previous studies suggests a unifying rule for the evolution of dispersal: the dispersal rates which permit the spatial homogenization of fitnesses are ESSs. This condition provides new insight into the evolutionary stability of source-sink systems. It also supports the hypothesis that immigrants have adapted demographic strategies, rather than the hypothesis that dispersal is costly and immigrants are at a disadvantage compared with residents.

Keywords: dispersal; evolution; evolutionarily stable strategy; migrant; resident; survival

Introduction

Environmental heterogeneity is generally recognized as one of the main causes of dispersal (Swingland and Greenwood, 1983; Johnson and Gaines, 1990; Lidicker and Stenseth, 1992). Numerous theoretical studies have explored how dispersal could evolve in environments that are heterogeneous in space but constant in time (review in Johnson and Gaines, 1990). The results suggest that spatial variation in dispersal rates can have a profound impact on the evolution of dispersal.

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When dispersal rates do not vary in space, philopatry (i.e. non-dispersal) is always selected (Balkau and Feldman, 1973; Karlin and McGregor, 1974; Teague, 1977; Hastings, 1983; Holt, 1985; Liberman and Feldman, 1989; McPeck and Holt, 1992), except in some particular circumstances such as competition between related individuals (Hamilton and May, 1977; Comins *et al.*, 1980) or competition for breeding places (Pulliam, 1988; Morris, 1991). On the other hand, when dispersal rates are free to vary between patches (asymmetric dispersal), non-zero evolutionarily stable dispersal rates can be selected (McPeck and Holt, 1992). McPeck and Holt (1992) studied a two-habitat model, in which the carrying capacities and the dispersal rates of each population could differ, and there was no explicit cost to dispersal. They found that, at the evolutionarily stable state, the ratio of the dispersal rates is inversely proportional to the ratio of local carrying capacities; at equilibrium, the two populations exchange the same numbers of individuals and have realized fitnesses in each patch equal to 1.

There are two notable limitations to these previous models. First, the life-cycles of the organisms are very simple. Generally, only adults are described, even if juveniles are implicitly considered. Intermediate age-classes, such as subadults, are never incorporated. Second, all of the models assume that, whatever their origin, individuals in a given habitat have the same bio-demographic characteristics. There is, however, increasing empirical evidence that dispersing individuals have different demographic properties compared with philopatric animals, and that the act of dispersal itself can have important consequences for individual survival and fecundity (Johnson and Gaines, 1985, 1987; Krohne and Burgin, 1987; Clobert *et al.*, 1988, 1994; McCleery and Clobert, 1990; Pärt, 1991; Lidicker and Stenseth, 1992; Walters *et al.*, 1992; Massot *et al.*, 1994; Alberts and Altmann, 1995). Belichon *et al.* (1996) reviewed empirical studies of demographic differences between dispersers and philopatrics. They showed that dispersal negatively affects reproduction and survival, though it is not a general rule. Dispersal is essentially costly for survival during the transient and settlement phases. After the settlement phase, fecundity is more often affected than survival. For example, the fecundity of great tit (*Parus major*) immigrants to Wytham Wood, Oxford, is less than that of residents (McCleery and Clobert, 1990). Similar results were found for the common lizard (*Lacerta vivipara*), introduced into controlled resident populations (Massot *et al.*, 1994), and for white-footed mice (*Peromyscus leucopus*) (Krohne and Burgin, 1987). Julliard and Blondel (1996) have shown that this reduced fecundity of dispersers can persist during the life of blue tits (*Parus minor*). The theoretical implications of such differences between immigrants and residents have not as yet been explored. One study investigated consequences of a direct effect of dispersal on fitness (Bull *et al.*, 1987). Organisms are described by a very simple life-cycle, such that individuals are born, then either migrate or stay in their birthplace, then reproduce only once and die. Bull *et al.* found that selection for migration depended on the geometric mean fitness of migrants. The biological implications of their results are not clear, but, apparently, dispersal is selected only if there is a gain in fitness for dispersers.

In this paper, we seek an understanding of how (1) age structure and (2) differences in certain demographic traits between residents and immigrants act to determine the evolutionarily stable dispersal strategy in a two-patch environment that is heterogeneous in space but constant in time. In particular, we are interested in the extent to which (1) a complex life-cycle could modify the results of previous studies and (2) dispersal should evolve when immigrants have lower fecundities than residents in both habitats. To explore this, we develop a matrix model more particularly adapted to vertebrates (Caswell, 1989), where recruitment depends on local population densities, as often observed in these kinds of organisms (Charnov, 1990). Although a much debated question (Lidicker and Stenseth, 1992), we consider a model system where dispersal has a strong hereditary component and we identify the evolutionarily stable strategies (ESS) for dispersal using a com-

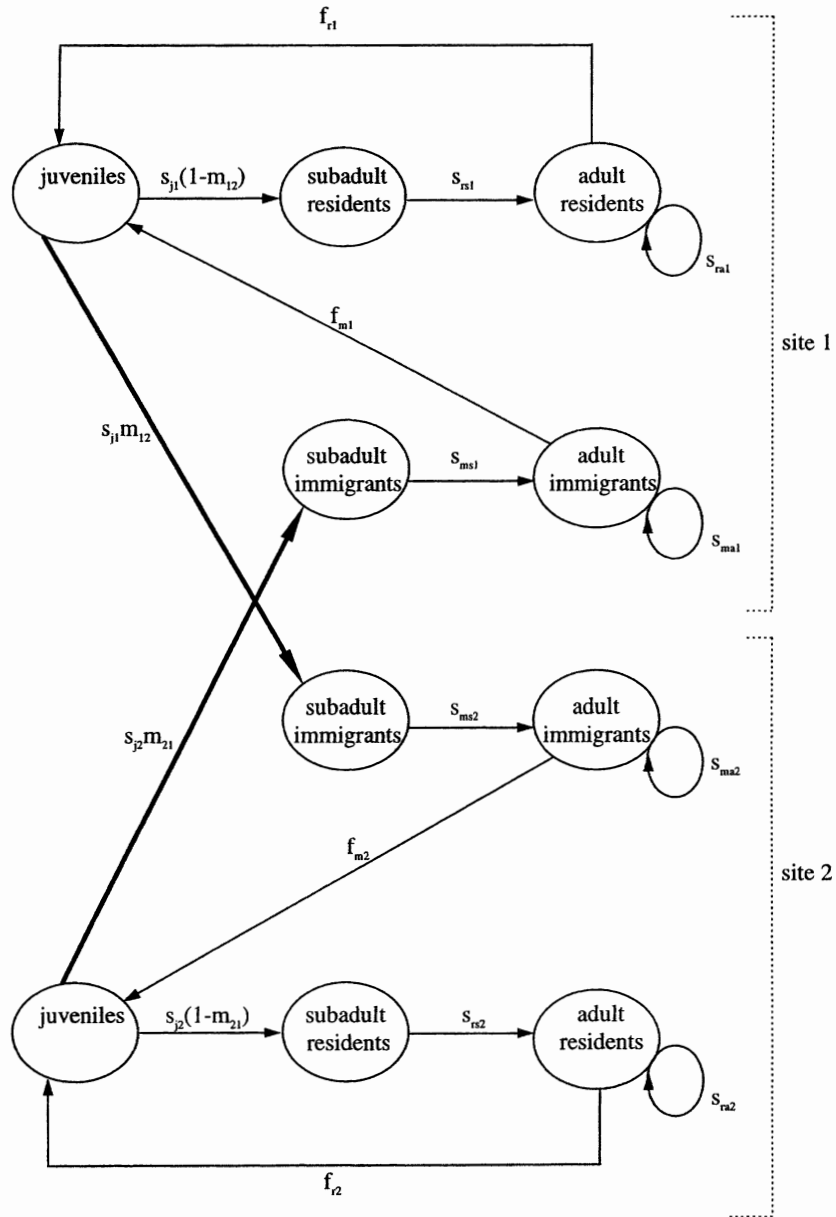


Figure 1. Life-cycle in the metapopulation. m_{ij} is the rate of movement from site i to site j . For residents (r) and immigrants (m) in patch k ($k = 1, 2$), we denote juvenile survival as s_{jk} , subadult survival as s_{rsk} and s_{msk} , adult survival as s_{rak} and s_{mak} , and adult fecundity as f_{rk} and f_{mk} . See text for details.

In vertebrate populations, density dependence often involves a main effect of adult density on fecundity or juvenile survival (Charnov, 1990). Accordingly, we assume that subadult and adult survival (s) are always constant, and we express each recruitment parameter (F) as a product of (a constant) maximum potential recruitment (\hat{F}) and density-dependent self-limitation. Self-limitation

is assumed to be 'contest' in nature, and we use the classic Beverton-Holt function (Caswell, 1989). For residents in patch k , F is:

$$F_{rk} = \hat{F}_k / (1 + c_k(y_{rk}(t) + y_{mk}(t))) \quad (3)$$

where c_k is a parameter measuring the strength of competition.

We assume that dispersal entails a proportional cost to immigrant fecundity, such that the realized recruitment of adults surviving from immigrant juveniles in patch k , F_{mk} , is linked to resident recruitment by the relationship:

$$F_{mk} = s_{jk}(1 - C_{ik}) f_{rk} = (1 - C_{ik})F_{rk} \quad (4a)$$

$$F_{mk} = (1 - C_{ik})\hat{F}_k / (1 + c_k(y_{rk}(t) + y_{mk}(t))) \quad (4b)$$

where C_{ik} is the cost of dispersal ($0 < C_{ik} < 1$) from patch i to patch k .

Dynamics generated by the model are always stable equilibrium points, due to the Beverton-Holt-type density dependence (Caswell, 1989).

Basic reproductive rates

The basic reproductive rate (R_0) is the mean number of female offspring reaching maturity, produced per adult female over her reproductive life-span, in the absence of competition. We use R_0 rather than the Fisherian rate of increase as a measure of the maximal fitness of a female. The latter is often used (for an application to a spatially heterogeneous environment, see Kawecki and Stearns, 1993), but R_0 is much easier to calculate in a discrete age-class model (Caswell, 1989). R_0 can be defined for both immigrants (R_{0m}) and residents (R_{0r}) within each patch k . R_0 for the residents in patch k is:

$$R_{0rk} = s_{rsk}(\hat{F}_k + s_{rak}\hat{F}_k + s_{rak}^2\hat{F}_k + s_{rak}^3\hat{F}_k + \dots)$$

or

$$R_{0rk} = s_{rsk}\hat{F}_k / (1 - s_{rak}) \quad (5)$$

R_0 for the immigrants in patch k is:

$$R_{0mk} = s_{msk}\hat{F}_{mk} / (1 - s_{mak})$$

or

$$R_{0mk} = (1 - C_{ik})s_{msk}\hat{F}_k / (1 - s_{mak}) \quad (6)$$

Equations (5) and (6) show that the fitness of individuals depends on subadult survival. Consequently, even if subadults are not allowed to disperse, they possibly affect the outcomes of the model. Equation (6) also shows that one dispersal event has life-long effects on fitness. To our knowledge, the persistence in time of the cost of natal dispersal has been considered in only one study (Julliard and Blondel, 1996). These authors showed that the fecundity of female blue tit (*Parus minor*) immigrants is less than that of female residents. This effect persists as immigrant females age.

Differences in survival rates between immigrants and residents can compensate (or even over-compensate) for the costs of dispersal. We examine three scenarios, leaving others for future study. The first scenario investigates the effect of age structure. The second and third investigate the effect of a difference in demographic traits between immigrants and residents. The three cases are:

1. No costs to dispersal ($C_{12} = C_{21} = 0$) and no differences between immigrant and resident survival ($s_{rsk} = s_{msk}$ and $s_{rak} = s_{mak}$). This implies that all the demographic parameters of immi-

grants and residents are equal within a site and hence so are their fitnesses ($R_{0mk} = R_{0rk} = R_{0k}$). The demographic parameters vary between sites, such that $R_{01} = R_{02}$. In essence, this corresponds to the effect of age-structure on the evolution of dispersal.

2. Costs to dispersal ($0 < C_{ik} < 1$) with total compensation by immigrants through an increase in their adult survival. The demographic parameters of immigrants and residents differ within a site, but their fitnesses are equal ($R_{0mk} = R_{0rk} = R_{0k}$). Resident fitness is found from (5) and relation (6) provides adult survival of immigrants (s_{mak}) for a given cost to dispersal (C_{ik}) and subadult immigrant survival (s_{msk}).
3. Costs to dispersal ($0 < C_{ik} < 1$) with no compensation (i.e. maximum cost to dispersal). Immigrants do not compensate their reduced fecundity, and they have the same survival as the residents ($s_{rsk} = s_{msk}$ and $s_{rak} = s_{mak}$). Under these conditions, $R_{0mk} = (1 - C_{ik})R_{0rk}$.

We equally use the basic reproductive rate to define source-sink and source-source systems. We define a patch as a 'sink' when the basic reproductive rate of either residents or immigrants is less than 1 (i.e. $R_{0rk} < 1$ or $R_{0mk} < 1$). We define a patch as a source if $R_{0rk} > 1$ and $R_{0mk} > 1$. A sink-sink system is uninteresting because the metapopulation must go extinct.

Optimization technique and numerical simulations

Any pair (m_{12}, m_{21}) constitutes a dispersal strategy. We use \mathcal{E} to refer to the current persistent dispersal strategy before the appearance of a new mutant strategy and after the elimination of any previous strategy. \mathcal{E}' is any single mutant strategy which, in our simulations, is introduced into the system at a very low density once the population of the current strategy has reached equilibrium. Finally, if \mathcal{E} cannot be invaded by any given mutant strategy \mathcal{E}' , then \mathcal{E} is an ESS, denoted \mathcal{E}^* (see Parker and Maynard-Smith, 1990, for a review).

In our model, for a given set of survival and fecundity parameters, each dispersal strategy is characterized by a transition matrix, $A(N_y(t))$, differing from others only in the dispersal rates. We employ relation (1) to determine if individuals adopting a mutant strategy (\mathcal{E}') can invade a population at equilibrium of individuals adopting a strategy \mathcal{E} . Analytical expressions for the ESSs of all possible conditions are difficult to obtain due, in part, to the complexity of the population model. Rather, we present both analytical expressions and numerical results of an algorithm to describe the ESS space. We denote, by W , the set of all possible dispersal strategies, such that $W = (\mathcal{E}_1, \mathcal{E}_2, \mathcal{E}_3, \dots, \mathcal{E}_n)$. To limit the number of strategies used in the numerical algorithm, we employ values of m_{12} and m_{21} from the set (0, 1) in steps of 0.05 (i.e. 0, 0.05, 0.1, ..., 0.95, 1.0). The first step of the numerical algorithm consists of determining if \mathcal{E}_1 is an ESS. We (1) introduce the strategy \mathcal{E}_1 (i.e. $\mathcal{E} = \mathcal{E}_1$), the number of each category of individuals being initially equal to 1 (i.e. $x_{rk}(0) = y_{rk}(0) = x_{mk}(0) = y_{mk}(0) = 1$ in each patch); (2) allow the populations in the two patches to equilibrate; and (3) introduce the strategy \mathcal{E}_2 (i.e. $\mathcal{E}' = \mathcal{E}_2$) at a density of one adult female resident in each patch, and see if it invades or displaces the resident strategy. If \mathcal{E}_1 is invaded by \mathcal{E}_2 , then \mathcal{E}_1 is not an ESS. If \mathcal{E}_1 is not invaded by \mathcal{E}_2 , we iterate steps (1), (2) and (3) until we find a mutant strategy able to invade \mathcal{E}_1 . If \mathcal{E}_1 resists invasion by any mutant strategy, then \mathcal{E}_1 is an ESS. The following steps of the algorithm consist of iterating a similar procedure to determine (1) if \mathcal{E}_2 , when established as a resident strategy, is displaced by \mathcal{E}_1 , which is introduced as a mutant strategy, or by any other mutant strategy (i.e. if \mathcal{E}_2 is an ESS), and (2) if \mathcal{E}_3 is an ESS, and so forth until \mathcal{E}_n . In our simulations, we always choose $\mathcal{E}_1 = (0, 0)$ and $\mathcal{E}_n = (1, 1)$.

Numerical simulations were conducted using the software program ULM (Legendre and Cloutier, 1995). We assume that individuals adopting a strategy \mathcal{E} compete with individuals adopting a mutant strategy \mathcal{E}' as defined by relations (3) and (4). Furthermore, we considered exclusion of the losing strategy to occur when its total abundance fell below unity before 5000 generations.

Baseline parameter values

We employed three different values (0.1, 0.5, 0.9) for subadult and adult survival, with the additional condition that $s_{rsk} < s_{rak}$ and $s_{msk} < s_{mak}$, and five different values (1.5, 5, 10, 15, 20) for the product of adult fecundity and subsequent survival of juveniles (F). Furthermore, we simulated three different values (0.1, 0.5, 0.9) of the cost of immigration to fecundity, C , and we assumed no difference between residents and immigrants in competitive ability, c , employing the single value of 0.01 in both patches.

To limit R_0 to realistic levels for vertebrates, we only considered parameter combinations for which $R_0 < 20$ (Ferrière and Clobert, 1992). This constraint creates a general trade-off, simultaneously including all demographic parameters in a unique relationship.

Results

The ESS dispersal strategies depend on a combination of three factors: (1) the spatial variation of dispersal rates (i.e. symmetric dispersal if $m_{12} = m_{21}$ and asymmetric dispersal if $m_{12} \neq m_{21}$); (2) the presence or absence of a 'sink'; and (3) the cost of dispersal with the corresponding level of fecundity compensation. More precisely, the results can be classified in three groups, corresponding to particular combinations of the previous factors. They are: (1) symmetric dispersal, (2) symmetric or asymmetric dispersal in a source-sink system, and (3) symmetric or asymmetric dispersal in a source-source system. We discuss each in detail below.

Symmetric dispersal

We found that philopatry ($m_{12} = m_{21} = 0$) is always the ESS when dispersal is constrained to being symmetric. This is the case no matter what the costs and levels of fecundity compensation (i.e. scenario 1, 2 and 3), and no matter what kind of metapopulation (i.e. a source-sink or a source-source system). Consequently, age structure and differences in demographic traits between residents and immigrants act in an identical manner on the evolution of symmetric dispersal.

Symmetric or asymmetric dispersal, source-sink system

If both symmetric and asymmetric dispersal strategies compete, philopatry ($m_{12} = m_{21} = 0$) is always the ESS in a source-sink system, whatever the cost to dispersal and the level of fecundity compensation. In this case, the effects of age structure and demographic differences between immigrants and residents are again the same.

Symmetric or asymmetric dispersal, source-source system

If both symmetric and asymmetric dispersal compete, we observe different ESSs in a source-source system, depending on the cost to dispersal and the level of fecundity compensation. We elaborate on this below.

No cost to dispersal and no differences between immigrant and resident survival

Here, the immigrants and residents are demographically alike, and we examine the effects of age structure. Consequently, within a patch k , the immigrants and the residents have the same basic reproductive rate, denoted R_{0k} ($R_{0rk} = R_{0mk} = R_{0k}$). This section is divided into two parts. First, we derive analytically the ESS by omitting the subadult class in the life-cycle of the metapopulation. Then we use our numerical algorithm to find the ESS with the complete life-cycle.

Life-cycle without the subadult class. Without the subadult class, and if the immigrants and residents are demographically alike (i.e. $s_{rak} = s_{mak} = s_{ak}$ and $F_{rk} = F_{mk} = \bar{F}_k$), the transition matrix, $A(N_y(t))$, is a 2×2 matrix and takes the form:

$$A(N_y(t)) = \begin{pmatrix} F_1(1 - m_{12}) + s_{a1} & F_2 m_{21} \\ F_1 m_{12} & F_2(1 - m_{21}) + s_{a2} \end{pmatrix}$$

\bar{F}_k is the realized recruitment in patch k and is equal to $\tilde{F}/(1 + c_k y_k)$, as defined in Equation (3), where \tilde{F} is the maximum potential recruitment. The basic reproductive rate in patch k , R_{0k} , is equal to $\tilde{F}/(1 - s_{ak})$.

At equilibrium, the realized recruitment, denoted in patch k as \tilde{F}_k , takes a constant value, and the dominant eigenvalue of the transition matrix, denoted as λ , is equal to 1. This eigenvalue is a function of m_{12} and m_{21} and, following Doebeli (1995), we have to calculate the derivatives $d\lambda/dm_{12}$ and $d\lambda/dm_{21}$ to determine the evolutionary optimum for the dispersal rates, which corresponds to the ESS. We have:

$$\lambda(m_{12}, m_{21}) = 1/2(u + v + \sqrt{(u - v)^2 + 4m_{12}m_{21}\tilde{F}_1\tilde{F}_2}) \tag{7}$$

where for notational simplicity

$$u = \tilde{F}_1(1 - m_{12}) + s_{a1} \tag{8a}$$

$$v = \tilde{F}_2(1 - m_{21}) + s_{a2} \tag{8b}$$

Using Equation (7) and $\lambda(m_{12}, m_{21}) = 1$, we get:

$$\partial\lambda/\partial m_{12} = \tilde{F}_1(\tilde{F}_2 + s_{a2} - 1)/(2 - u - v) \tag{9}$$

$$\partial\lambda/\partial m_{21} = \tilde{F}_2(\tilde{F}_1 + s_{a1} - 1)/(2 - u - v) \tag{10}$$

The evolutionary optimum is obtained when $\partial\lambda/\partial m_{12} = \partial\lambda/\partial m_{21} = 0$, which is possible if and only if $\tilde{F}_2 + s_{a2} = 1$ and $\tilde{F}_1 + s_{a1} = 1$. This global maximum corresponds to the evolutionarily stable state. Thus, if we denote the realized fitness at equilibrium in a patch k as R_k , the ESS occurs when:

$$R_k = \tilde{F}_k/(1 - s_{ak}) = 1 \tag{11}$$

We find the same patterns as McPeck and Holt (1992); that is, the ESS occurs when the realized fitnesses at equilibrium in the two habitats are each equal to unity. If $R_1 = R_2 = 1$, the sites exchange the same number of individuals and the ratio of the dispersal rates is the inverse of the ratio of the equilibrium densities of adults (y^*) in each patch.

Life-cycle with the subadult class. The immigrants and the residents have the same reproductive rate, denoted R_{0k} ($R_{0mk} = R_{0rk} = R_{0k}$). We find again the same patterns as McPeck and Holt (1992); that is, the ESS occurs when the realized fitnesses at equilibrium in the two habitats are both equal to unity. If $R_1 = R_2 = 1$, the sites exchange the same number of individuals and the ratio of the dispersal rates is the inverse of the ratio of the equilibrium densities of sub-adults (x^*) in each patch. So, \mathbf{x}^* is found from:

$$m_{12}^*/m_{21}^* = (x_{r2}^* + x_{m2}^*)/(x_{r1}^* + x_{m1}^*) \tag{12}$$

Equation (12) shows that the set \mathbf{x}^* is a straight line in m_{12}, m_{21} space (Fig. 2). Alternatively, for a given set of demographic parameters, the ESSs correspond to:

$$m_{12}^*/m_{21}^* = R_{01}\tilde{F}_2(R_{02} - 1)/R_{02}\tilde{F}_1(R_{01} - 1) \tag{13}$$

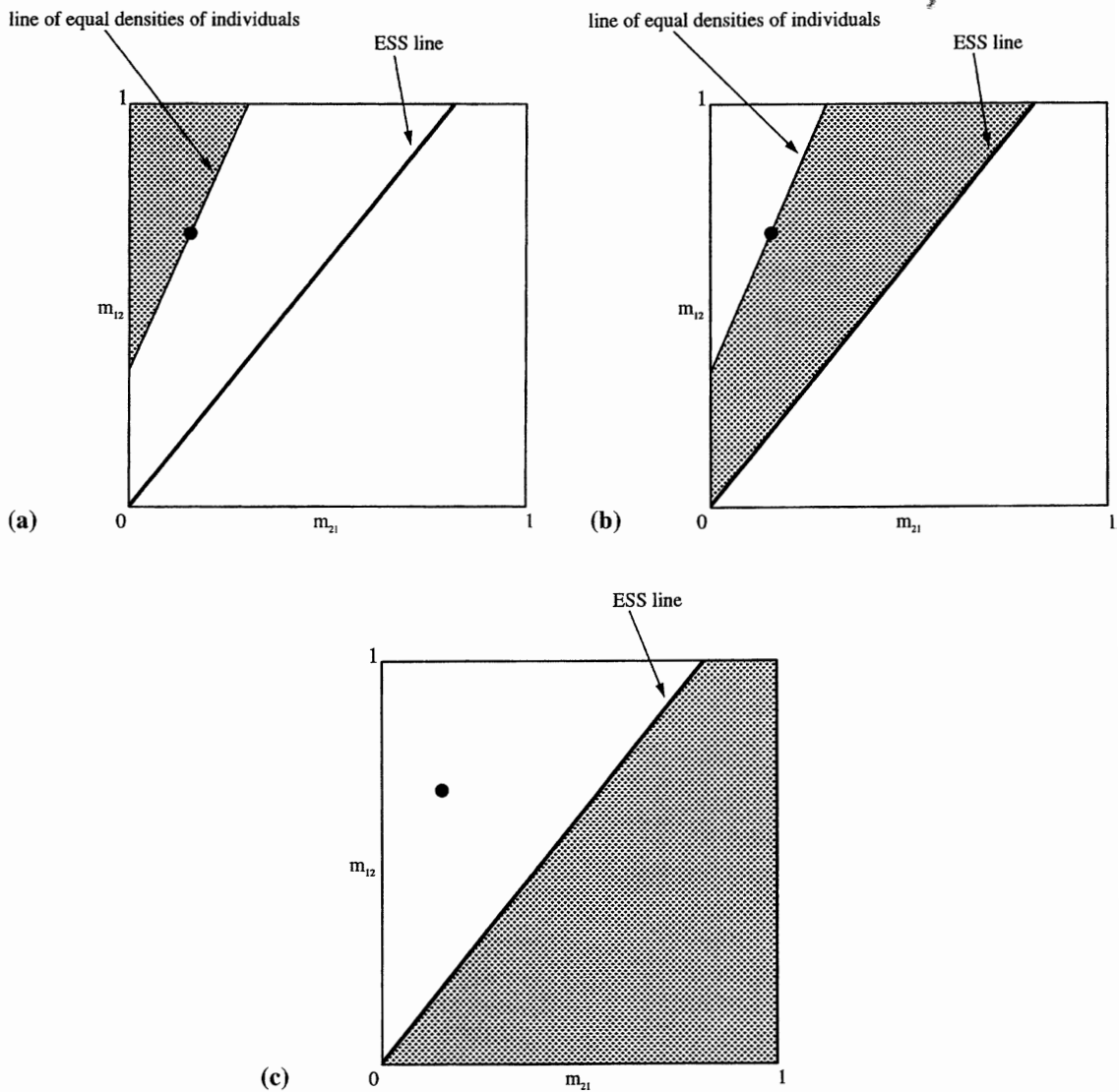


Figure 2. Results of the competition between two dispersal strategies in m_{12}, m_{21} space, when immigrants and residents are demographically alike. In m_{12}, m_{21} space, a dispersal strategy is represented by a point in this space. The ESSs are on the straight line passing through the philopatric strategy, which corresponds to the point (0, 0). The slope of the ESS line determines the corresponding set of demographic parameters, as defined by Equation (13). The symbol \bullet represents a dispersal strategy which is not an ESS and which, consequently, is not on the ESS line. All dispersal strategies along the straight line passing through \bullet are characterized by equal densities of individuals at equilibrium (i.e. the sum of adult and subadult density in each patch). We assume that the strategy represented by \bullet is a 'resident' strategy which is established in a population at equilibrium. The figure shows the results of the confrontation between the 'resident' strategy \bullet and a mutant strategy which appears in the population and which is not an ESS. Each of these two strategies corresponds to two distinct points in the m_{12}, m_{21} space. Three outcomes are possible. If both strategies occur on the same side of the ESS line (a and b), the winner is determined by the position of the mutant strategy compared to the line of equal densities passing through the resident strategy. In (a), any mutant strategy in the shaded area is outcompeted by the 'resident' strategy. In (b), any mutant strategy in the shaded area outcompetes the 'resident' strategy. If the ESS line separates the mutant strategy and the 'resident' strategy, then the two strategies co-exist (c). The shaded area in (c) represents any mutant strategy.

Our numerical simulations confirm that any \mathbf{f}^* verifying Equation (13) out-competes any mutant strategy not satisfying Equation (13) and co-exists with any strategy conforming to Equation (13). When neither \mathbf{f} nor \mathbf{f}' conform to this condition (i.e. when neither the 'resident' strategy nor the mutant strategy corresponds to an ESS), the winner depends on the relative positions of the two strategies in m_{12}, m_{21} space (Fig. 2). If both strategies occur on the same side of the ESS line, the winner is determined by the position of the mutant strategy, \mathbf{f}' , compared with a straight line passing through the 'resident' strategy, \mathbf{f} , and corresponding to equal densities of individuals at equilibrium (i.e. the sum of adult and subadult density in each patch) (Figs 2a, b). When the ESS line separates the mutant strategy and the 'resident' strategy, our simulations show that the two strategies always co-exist (Fig. 2c). No particular pattern of co-existence has been observed.

In the particular case of a spatially homogeneous environment, corresponding to identical demographic parameters in both sites, we easily obtain, using Equation (13), $m_{12} = m_{21}$ at the ESS. Consequently, in a spatially homogeneous environment, any symmetric dispersal rate is selected.

Cost to dispersal with total compensation

The cost to dispersal ($0 < C_{ik} < 1$) is totally compensated for by an increase in the survival of adult immigrants (s_{mak}). The demographic parameters of immigrants and residents are different, but their basic reproductive rates are equal ($R_{0rk} = R_{0mk} = R_{0k}$). The results of this case are very similar to the previous one: the ESS occurs when the realized fitnesses at equilibrium in the two habitats are both equal to unity. At the ESS, the sites exchange the same number of individuals and the ratio of the dispersal rates is the inverse of the ratio of the equilibrium densities of subadults in each patch. The notable difference with the previous case is the shape of the ESS line in m_{12}, m_{21} space (Fig. 3). All ESSs are found from the expression:

$$m_{12}^* = am_{21}^*/(bm_{21}^* + c) \quad (14)$$

where for notational simplicity

$$a = C_{21}C_{12}R_{01}(R_{02} - 1) \quad (15a)$$

$$b = C_{21}(1 - C_{12})\hat{F}_1R_{02}(R_{01} - 1) + C_{12}(C_{21} - 1)\hat{F}_2R_{01}(R_{02} - 1) \quad (15b)$$

$$c = C_{21}C_{12}\hat{F}_1R_{02}(R_{01} - 1) \quad (15c)$$

We used numerical simulations to test if dispersal strategies, \mathbf{f} , verifying Equation (14) were in fact the ESSs. We found that any \mathbf{f} satisfying Equation (14) eliminates any \mathbf{f}' not satisfying it and any two \mathbf{f} s conforming to this condition co-exist. So, any strategy \mathbf{f} verifying Equation (14) is an ESS.

Equation (14) is a hyperbolic function, with $a > 0$, $c > 0$ and b taking on any value. We see from the derivative of (14) with respect to either m_{12} or m_{21} that marginal increases in one are always met by increases in the other at the ESS (Fig. 3). The position of the two branches of the hyperbola depend on the value of the two asymptotes $m_{21} = -c/b$ for the vertical asymptote and $m_{12} = a/b$ for the horizontal asymptote. These branches give the maximum possible levels that each direction of dispersal can assume (within the limits (0, 1)).

The biological meaning of Equation (14) is not clear from its complex form; however, by changing the value of one parameter at a time, we can get an idea of some of the underlying properties of the ESS. Suppose that population 1 is the more productive (i.e. $R_{01} > R_{02}$). What happens if the difference between the two sites is accounted for only by the respective survival of subadult and adult residents, assuming adult maximum potential recruitment and the cost of dispersal being equal in both sites (i.e. $\hat{F}_1 = \hat{F}_2 = \hat{F}$ and $C_{21} = C_{12} = C$). Then a , b and c in Equation (14) reduce to:

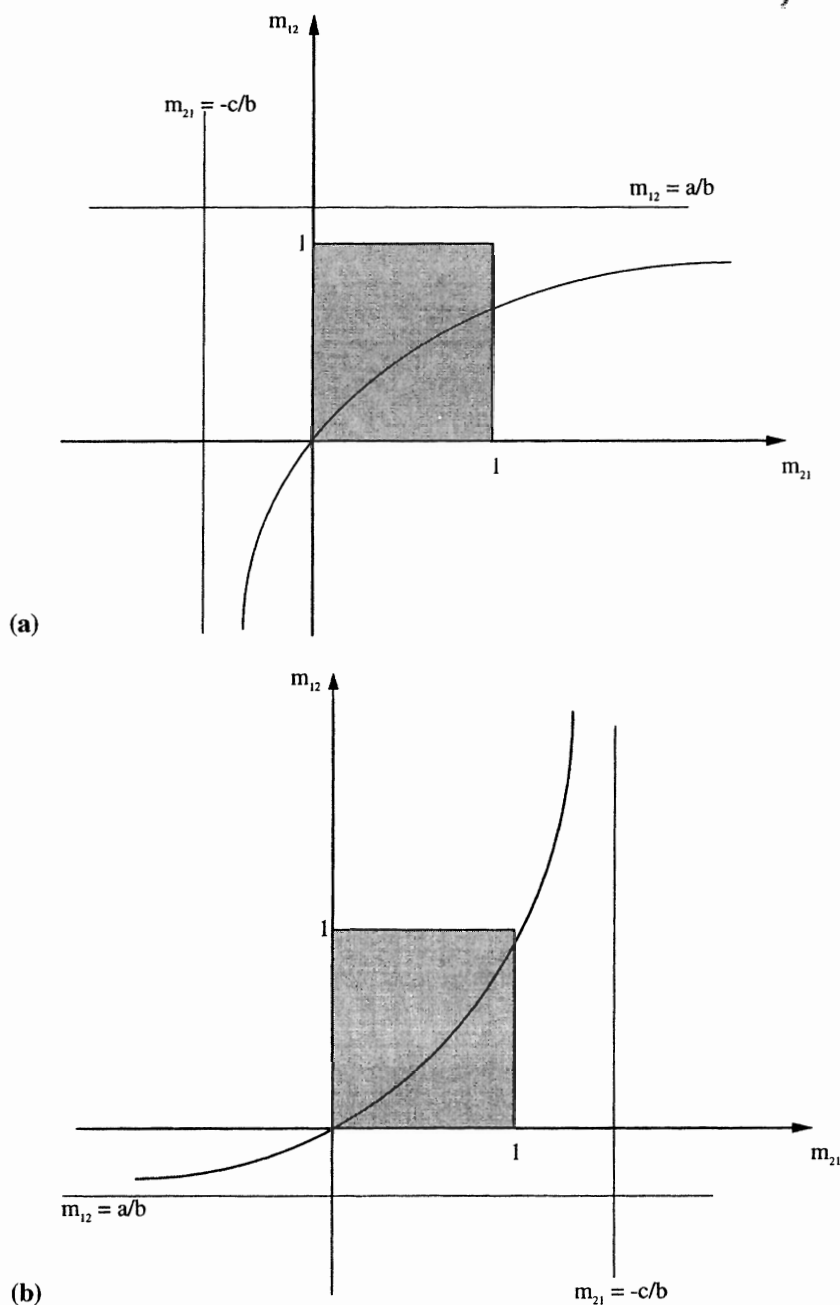


Figure 3. Shape of the ESS line in m_{12} , m_{21} space when immigrants totally compensate the cost of dispersal. The ESSs are found from the hyperbolic expression: $m_{12} = am_{21}/(bm_{21} + c)$, where $a = C_{21}C_{12}R_{01}(R_{02} - 1)$, $b = C_{21}(1 - C_{12})\hat{F}_1R_{02}(R_{01} - 1) + C_{12}(C_{21} - 1)\hat{F}_2R_{01}(R_{02} - 1)$, and $c = C_{21}C_{12}\hat{F}_1R_{02}(R_{01} - 1)$ (see text). The vertical asymptote $m_{21} = -c/b$ and the horizontal asymptote $m_{12} = a/b$ determine the positions of the two branches of the hyperbola. We only represent the branch passing through the strategy $(0, 0)$. The ESSs are on this branch, within the limits $(0, 1)$, represented by a shaded square. The figure shows the shape of the branch when $b > 0$ (a) and when $b < 0$ (b).

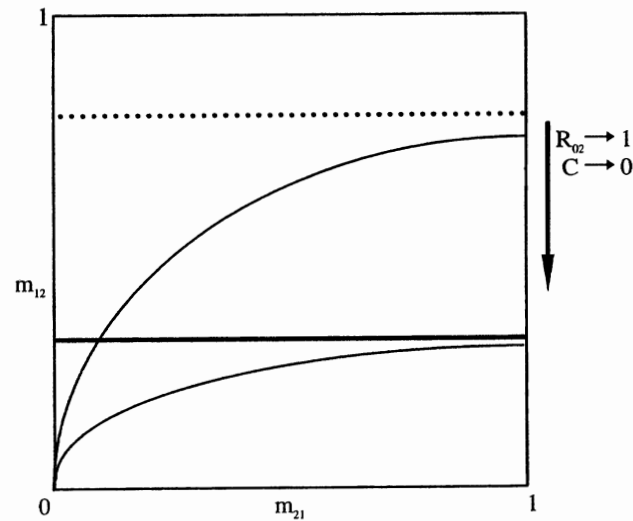


Figure 4. Evolutionarily stable dispersal strategy when the difference between the two sites is accounted for by the respective survival of subadult and adult residents only, assuming adult maximum potential recruitment and the cost of dispersal is equal in both sites (i.e. $\hat{F}_1 = \hat{F}_2 = \hat{F}$ and $C_{21} = C_{12} = C$). Fewer and fewer individuals from population 1 disperse at the ESS when the cost of dispersal (C) increases and the productivity of population 2 decreases, because the horizontal asymptote gets closer to the horizontal axis, m_{21} .

$$a = C\hat{F}(R_{02} - 1) \quad (16a)$$

$$b = (1 - C)(R_{01} - R_{02}) \quad (16b)$$

$$c = CR_{02}(R_{01} - 1) \quad (16c)$$

Because the vertical asymptote is negative, m_{21} can take on any value between 0 and 1. We find that more individuals of the less productive population disperse to the more productive population than the reverse at the ESS. As would be expected, when the cost of dispersal (C) increases and the productivity of population 2 decreases, fewer and fewer individuals from population 1 disperse at the ESS (Fig. 4). If we make the reasonable assumption that the productivity of a population reflects the quality of the habitat, the previous result only means that the better the quality of a habitat, the more it is advantageous to stay in it.

If we explicitly replace the basic reproductive rate with its components (i.e. subadult and adult survival and maximum potential recruitment), as defined in Equation (5), one obtains terms in Equations (15) equal to the product of the costs of dispersal and subadult survival. This suggests that the ESSs should not change if the cost is deducted from the survival of subadult immigrants, and not from their fecundities. Numerical simulations confirm these results.

Cost to dispersal without any compensation

Here there is a cost to dispersal ($0 < C_{ik} < 1$), but it is not compensated by an increase in the survival of adult or subadult immigrants ($s_{rsk} = s_{msk}$ and $s_{rak} = s_{mak}$). Under these conditions, $R_{0mk} = (1 - C_{ik})R_{0rk}$. We find that philopatry is always selected ($\mathbf{x}^* = (0, 0)$).

Discussion

We observed that non-zero asymmetric dispersal rates may be evolutionarily stable when (1) there are inter-patch differences in demographic parameters, but within a patch immigrants and residents are alike, or (2) immigrants compensate totally for their reduced fecundity through an increase in adult survival. Under these conditions, we found that the ESS occurs when the fitnesses at equilibrium in the two habitats, measured in our model by the realized reproductive rates, are both equal to unity. A similar pattern was also obtained numerically by McPeck and Holt (1992) and analytically by Doebeli (1995). These authors considered two populations linked by exchanges of juveniles, with no subadult class and no explicit cost to dispersal.

The general agreement of our results with these earlier studies suggests that complex age structure has little effect on the evolution of dispersal. The common finding of McPeck and Holt (1992), Doebeli (1995) and the present study is that the ESS corresponds to the spatial homogenization in fitnesses of different categories of individuals. At the ESS, the two populations exchange the same number of individuals and the ratio of the dispersal rates is the inverse of the ratio of the equilibrium densities in each patch of either subadults in our model, or just adults in the models of McPeck and Holt (1992) and Doebeli (1995). This suggests that if the immigrants disperse at age a , then, at the ESS, the ratio of the dispersal rates is the inverse of the ratio of the densities of age-class $a + 1$ in each patch. The generality of these findings, however, should be tested with more general age-structured models.

Interestingly, the condition of spatial homogenization of fitness has also been found in a different context by Fretwell and Lucas (1969), who studied the problem of habitat selection. Using a simple ecological model, they investigated how competitors should be distributed between patchy resources, under the condition that individuals move freely in the habitat. They obtained an equilibrium distribution of competitors, called the 'ideal free distribution', such that the average fitness of individuals, measured by the instantaneous rate of resource acquisition, is equal both across patches and across individuals. Interestingly, the two main assumptions of their model are similar to ours (Milinski and Parker, 1991): (1) individuals have identical competitive abilities and (2) the habitat contains a series of patches that vary in fitness values for the competitors.

Our numerical simulations show the selection of philopatry (1) when dispersal rates do not vary in space (symmetric dispersal), as has been found in almost all previous studies (Balkau and Feldman, 1973; Karlin and McGregor, 1974; Teague, 1977; Hastings, 1983; Holt, 1985; Liberman and Feldman, 1989; McPeck and Holt, 1992) (see Holt, 1985, for an analytical justification in the case of no age structure), but in contradiction with the results of Hamilton and May (1977) and Comins *et al.* (1980); (2) when one site is a sink, in contradiction with the results of Pulliam (1988) and Morris (1991); and (3) when dispersal is asymmetric and immigrants do not compensate for their reduced fecundity. In these three cases, it is straightforward to show that only zero dispersal rates (i.e. selection of philopatry) entail the spatial homogenization of fitness, thus reinforcing the general validity of this rule and suggesting that the existence of isolated populations in the wild could be subjected to at least one of the three factors. We discuss these below.

Almost all previous models of the evolution of dispersal assume symmetric dispersal between patches (Balkau and Feldman, 1973; Karlin and McGregor, 1974; Teague, 1977; Hastings, 1983; Holt, 1985; Liberman and Feldman, 1989). Empirical applications of the recent progress in the statistical estimates of dispersal rates from capture-recapture data (Brownie *et al.*, 1993) indicate that this hypothesis is overly constrained.

The literature concerning source-sink systems is growing rapidly (Shmida and Ellner, 1984; Pulliam, 1988; Howe *et al.*, 1991; Pulliam and Danielson, 1991; Davis and Howe, 1992). Theoretical studies have concentrated on the demographic viability of source-sink systems. Our study

provides insights into their evolutionary stability: a coupled source-sink system should not persist, because the philopatric strategy invades and destroys it. Pulliam (1988) and Morris (1991) have, however, argued that non-zero dispersal rates can be selected in a such system. They each assumed that there are few breeding-places within the source, such that some individuals are excluded from reproduction, whereas breeding-places are unlimited within the sink, where there is no competition. Pulliam (1988) assumed that dispersal is unidirectional, from the source to the sink. He did not look for the ESS dispersal rates. Nevertheless, he argued that dispersal is favoured simply because it is better to 'never occupy a poorer breeding site when a better one is still available'. Morris (1991) showed, with a similar model, that dispersal is an ESS only if there is reverse migration from the sink to the source. In contradiction, we found that philopatry is always selected in a source-sink system. This difference persists when immigrants and residents are demographically alike and consequently it cannot be explained by the cost of dispersal on fecundity. Pulliam and Morris both assumed that competition occurs only in the source, such that reproduction does not depend on density in the sink. By contrast, in our model, individuals are affected by competition in both patches. This difference suggests that competition has an important impact on the evolution of dispersal. Adding density-dependence in the sink creates an additional constraint which limits the possibility that non-zero dispersal rates can be selected. This point requires further research. Investigation of a real source-sink system could be subordinated to the presence of competition between individuals in the sink, or could involve factors we have not envisaged, such as temporal variability.

Many empirical studies have examined the effects of dispersal on reproduction. Their results have to be interpreted with caution because the comparison of fitness components between philopatrics and dispersers raises methodological and statistical problems which are often neglected. However, the fact that dispersal can entail a cost to fecundity is now well documented (Newton and Marquiss, 1983; Krohne and Burgin, 1987; Clobert *et al.*, 1988, 1994; Newton, 1988; McCleery and Clobert, 1990; Pärt, 1991; Walters *et al.*, 1992; Massot *et al.*, 1994; Julliard and Blondel, 1996). Belichon *et al.* (1996) reviewed empirical studies of demographic differences between philopatrics and immigrants. If we consider only natal dispersal, as in our theoretical work, 18 studies concerned differences in fecundity. There was a significant advantage for dispersers in five studies, a significant disadvantage for dispersers in eight studies, and no significant difference between dispersers and philopatrics in five studies. This effect is important in birds, whereas in mammals an advantage has generally been shown for reproduction in dispersers (Dueser *et al.*, 1981; Johnson and Gaines, 1985, 1987; Isbell *et al.*, 1990). Consequently, our model should essentially be applicable to birds. Two explanations have been proposed concerning the reduced fecundity. Either dispersal is costly and immigrants are disadvantaged compared with residents (Pärt, 1990), or dispersers compensate for their reduced fecundity (McCleery and Clobert, 1990; Pärt, 1991; Lidicker and Stenseth, 1992; Clobert *et al.*, 1994; Massot *et al.*, 1994). Our theoretical results support the latter hypothesis, since costs to dispersal which are not totally compensated for by increases in other demographic parameters prevent the evolution of dispersal. The reduced fecundity could be mechanistically compensated for by a trade-off between fecundity and adult survival.

Interestingly, our results seem to contradict those of Hamilton and May (1977) and Comins *et al.* (1980). Hamilton and May (1977) studied the evolution of symmetric dispersal in a spatially homogeneous environment in which only one adult can live within each site. They found that a non-zero symmetric dispersal rate is the ESS. In our model, when the environment is homogeneous, we find that any dispersal strategy on the straight line $m_{12} = m_{21}$ is an ESS. In a second step, Hamilton and May introduced spatial heterogeneity into their model: dispersal is still symmetric and there is still one adult at each site, but fecundities vary between sites. Comins *et al.* (1980) extended this model by having an unlimited number of adults at each site, and by having a degree

of environmental variability due to an exogeneous extinction rate. If this rate is zero, as in our model, Comins *et al.* found that the ESS dispersal rate differs from zero when the number of adults at each site is low. However, as the number of adults at each site increases, the ESS dispersal rate approaches zero. In our model, we found that dispersal is always selected in a spatially heterogeneous environment if dispersal is symmetric. The differences between our model and those of Hamilton and May (1977) and Comins *et al.* (1980) are difficult to explain, because they correspond to two distinct approaches to the evolution of dispersal. In calculating fitness, Hamilton and May and Comins *et al.* consider the relation between relatives – that is, inclusive fitness. Their models contain a genetic component, whereas our model is purely phenotypic. However, the differences between the results of our model and that of Comins *et al.* only appear when Comins *et al.* assume that the number of adults at each site is markedly reduced. Under these conditions, the relation between the relatives has great importance for identifying the ESS dispersal rate, and, consequently, kin selection is certainly an important factor in explaining the differences observed. The fact that Hamilton and May found that the ESS is a particular solution of our own solutions could indicate that kin selection creates an additional constraint which reduces the range of the dispersal strategies selected. To reconcile the approach of Hamilton and May and Comins *et al.* with our own approach, it would be necessary to develop new models, containing genetic, demographic and dynamic components.

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