
Evolution of stepping-stone dispersal rates

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We present a general model of the evolution of dispersal in a population with any distribution of dispersal distance. We use this model to analyse evolutionarily stable (ES) dispersal rates for the classical island model of dispersal and for three different stepping-stone models. Using general techniques to compute relatedness coefficients in the different dispersal models which we consider, we find that the distribution of dispersal distance may affect the ES dispersal rate when the cost of dispersal is low. In this case the ES dispersal rate increases with the number of demes that can be reached by one dispersal event. However, for increasing cost the ES dispersal rate converges to a value independent of the distribution of dispersal distance. These results are in contrast to previous analyses of similar models. The effects of the size (number of demes) and shape (ratio between the width and the length) of the population on the evolution of dispersal are also studied. We find that larger and more elongated populations lead generally to higher ES dispersal rates. However, both of these effects can only be observed for extreme parameter values (i.e. for very small and very elongated populations). The direct fitness method and the analytical techniques used here to compute relatedness coefficients provide an efficient way to analyse ES strategies in subdivided populations.

Keywords: dispersal; kin selection; isolation by distance; evolutionarily stable strategy

1. INTRODUCTION

Dispersal behaviour affects both the dynamics and genetics of species. In this respect, dispersal lies at the core of many problems in ecology and evolutionary biology. Not surprisingly, the analysis of evolutionarily stable (ES) dispersal strategies has attracted considerable attention. Three factors are classically invoked to explain the evolution of dispersal: (i) temporal variability in the environment (Van Valen 1971; Gillespie 1981; Levin *et al.* 1984; McPeck & Holt 1992), (ii) avoidance of inbreeding depression (Bengtsson 1978; Waser *et al.* 1986; Motro 1991; Gandon 1999) and (iii) kin selection (Hamilton & May 1977; Comins *et al.* 1980; Comins 1982; Motro 1982*a,b*; Frank 1986; Taylor 1988; Gandon & Michalakis 1999). In this paper we focus on the third factor. Hamilton & May (1977) showed that dispersal is an efficient way to avoid competition between related individuals. However, most of the previous models with kin selection rely on two assumptions: (i) an infinite number of demes and (ii) the island model of migration (i.e. dispersal can lead to any deme). These assumptions imply that immigrants are not related to philopatric individuals. This greatly simplifies the algebra because kin competition only occurs among philopatric individuals. To our knowledge Comins (1982) is the only author who relaxed one of these assumptions (i.e. the island model assumption) by studying the evolution of stepping-stone

dispersal rates. Here we present a reanalysis of this classic problem (Hamilton 1996, pp. 499–504) after relaxing both assumptions. We will apply the direct fitness method developed by Taylor & Frank (1996). This method has been advocated as a safe and efficient way to analyse models of kin selection. Its use in combination with Malécot's formulation of genetic models of subdivided population is further discussed in another paper (Rousset & Billiard 2000). In addition, we show that this method is useful in demonstrating some general properties of the ES dispersal rate.

We will first present a general analysis for models of spatially homogeneous dispersal with any number of demes and for any distribution of dispersal distance. Then, we will study the evolution of dispersal rates in four models: the island model, a one-dimensional (1D) stepping-stone model and two two-dimensional (2D) stepping-stone models. The comparison of these different models leads to the analysis of three effects: (i) the number of neighbouring demes (i.e. the number of demes in which a disperser can go), (ii) the size of the population (i.e. the number of demes) and (iii) the shape of the population (i.e. in a 2D population model, the ratio between the width and the length of the population).

The approach used in these analyses requires expressions for measures of genetic identity under models of 'isolation by distance' (spatially homogeneous localized dispersal). In contrast to earlier models of kin-selection under localized dispersal, we will use compact formulae giving exact solutions of Malécot's model of isolation by distance (Malécot 1975; Nagylaki 1976; Sawyer 1977; Rousset 1997). For some key results of these models an electronic appendix can be found on the Royal Society Web site.

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Table 1. *Summary of main notations*

notation	definition
N	number of adults per deme
n	number of demes
f	fecundity
c	cost of dispersal
ν	number of neighbouring demes
z_\bullet and z_i	phenotype of the focal individual and average phenotype in deme i using the focal individual as a referential
z^*	evolutionarily stable dispersal rate
w	direct fitness function
$d_{i \rightarrow j}(z)$	fraction of dispersers from deme i to deme j among all immigrants
$g_{i \rightarrow j}(z)$	number of dispersed offspring from deme i to deme j
Q'_i and Q_i	identity in state between genes from the focal individuals and a randomly chosen offspring in the deme i , before and after dispersal, respectively

2. A GENERAL KIN SELECTION MODEL

(a) *Life cycle*

The habitat consists of a finite number, n , of demes organized in a 1D or 2D torus. All of them are filled with an equal number, N , of haploid asexual individuals. We assume the following life cycle: (i) reproduction occurs; a number f of offspring are produced, but we will only consider the limit case where $f \rightarrow \infty$. (ii) Mutation occurs at rate u . (iii) Offspring dispersal occurs. Through dispersal, offspring are sent to a number, ν , of neighbouring demes. (iv) Dispersing offspring may experience a survival cost c . In this paper we assume that this cost does not depend on the dispersal distance. This assumption might be particularly relevant in the cases where dispersal is associated with the production of specific and costly organs (e.g. insect wings, pappus in plants). (v) Adults die. (vi) Offspring compete and only N of them survive to adulthood. (See table 1 for a summary of the main notations used in this model.)

In this paper we assume that individuals are haploid and asexual. The techniques used below could be applied to any kind of genetic system (sexual reproduction, diploid or haplodiploid organisms, etc.) and to study the effect of different control of dispersal (e.g. maternal versus offspring control of dispersal), but this will not be detailed here. Note that in the present case, because we assume asexual reproduction, there is no parent-offspring conflict over the evolution of dispersal.

(b) *Evolutionarily stable dispersal rate*

The phenotype of an adult is the dispersal rate of its offspring. In the following we focus on the fitness of an adult with phenotype z_\bullet . The average phenotype in deme i is written z_i where i is the coordinate of the deme i using the focal individual as a referential (e.g. the focal individual is in the population $\mathbf{0}$). We also use vector indices to cover the 2D model. Note that the z_0 variable includes the focal individual's phenotype. In general there will be within-deme variation between different

individual phenotypes, but only the expectation of these quantities must be considered to construct a fitness measure. Following the approach developed by Taylor & Frank (1996) we can write the direct fitness of the individual, w , as a function of its own behaviour, z_\bullet , and of the behaviour of all the individuals, z_i ($i = 0, \dots, n-1$), that may compete with the focal individual. The direct fitness can be expressed as

$$w = \sum_j \frac{g_{0 \rightarrow j}(z_\bullet)}{\sum_i g_{i \rightarrow j}(z_i)}. \quad (1)$$

where each of the ratios $g_{0 \rightarrow j}(z_\bullet)/\sum_i g_{i \rightarrow j}(z_i)$ is the number of offspring sent by the focal individual in a deme j relative to the total number of offspring that compete for this site. $g_{i \rightarrow j}(z)$ is defined as the number of offspring an individual with phenotype z in deme i sends to deme j . Let $d_{i \rightarrow j}(z)$ be the fraction of dispersers from deme i to deme j among all dispersing offspring. Then $g_{0 \rightarrow 0}(z) = 1 - z$, and for $i \neq j$, $g_{i \rightarrow j}(z) = (1 - c)zfd_{i \rightarrow j}$ where the latter fraction is determined by the fixed distribution of forward dispersal distance.

Rousset & Billiard (2000) show that a necessary condition for the strategy z^* to be ES may be deduced from the analysis of a genetic model with mutation rate u as $\lim_{u \rightarrow 0} S/(1 - Q_0) = 0$, Q_0 being the probability of identity of genes among offspring competing for one deme (i.e. after dispersal), and

$$S \equiv \frac{\partial w}{\partial z_\bullet} + \sum_{i=0}^{n-1} \frac{\partial w}{\partial z_i} Q'_i, \quad (2)$$

where Q'_i is the probability of identity in state of genes from the focal individual in deme $\mathbf{0}$ and a randomly chosen offspring in deme i , before dispersal (i.e. just before step (iii) in the above life cycle). Let Q_i be the probability of identity of genes from the focal individual and a randomly chosen offspring in deme i , after dispersal (i.e. step (vi) in the above life cycle). Then $Q'_i = Q_i$ except $Q'_0 = Q_0 + (1 - Q_0)/N$.

The ES strategy (ESS) condition $\lim_{u \rightarrow 0} S/(1 - Q_0) = 0$ is shown to be equivalent to the more usual ESS condition in terms of 'identity by descent' for infinite island models in Rousset & Billiard (2000). As noted there, whatever the dispersal pattern and the dispersal rates, the sum of coefficients of the Q s is null:

$$\frac{\partial w}{\partial z_\bullet} + \sum_{i=0}^{n-1} \frac{\partial w}{\partial z_i} = 0. \quad (3)$$

This follows intuitively from the fact that $w(z, z, z, \dots) = 1$ for all z , i.e. when every individual has the same phenotype z , everyone's fitness (expected number of adult offspring) is unity. As a consequence, $S = \sum_{i=0}^{n-1} (Q'_i - 1) \partial w / \partial z_i$, which is

$$S = \sum_{i=0}^{n-1} (1 - Q'_i) \sum_{j=0}^{n-1} g_{0 \rightarrow j}(z_\bullet) \frac{\partial g_{i \rightarrow j}(z_i) / \partial z_i}{(\sum_k g_{k \rightarrow j}(z_k))}. \quad (4)$$

All derivatives are evaluated at $z_{\bullet} = z_0 = \dots = z_{n-1} = z^*$. Hence, because $\sum_k g_{k \rightarrow j}(z^*) = 1 - cz^*$ is independent of j , the ESS z^* must obey

$$\lim_{u \rightarrow 0} \frac{S}{1 - Q_0} = 0 = \sum_i \lim_{u \rightarrow 0} \frac{1 - Q'_i}{1 - Q_0} \sum_j g_{0 \rightarrow j}(z^*) \left. \frac{\partial g_{i \rightarrow j}(z)}{\partial z} \right|_{z^*}. \tag{5}$$

Thus for a linear relationship $g_{i \rightarrow j}(z) = a_{i \rightarrow j} + b_{i \rightarrow j}z$,

$$z^* = - \lim_{u \rightarrow 0} \frac{\sum_j a_{0 \rightarrow j} \sum_i (1 - Q'_i) b_{i \rightarrow j}}{\sum_j b_{0 \rightarrow j} \sum_i (1 - Q'_i) b_{i \rightarrow j}}. \tag{6}$$

If $g_{i \rightarrow j}(z)$ is not linear in z we can obtain a similar expression considering only the derivatives of $g_{i \rightarrow j}(z)$ in z^* and pursue our argument as in the linear case.

It is impractical to compute this limit in equation (6) directly because both the numerator and denominator vanish (i.e. $Q'_i \rightarrow 1$ when $u \rightarrow 0$). For this reason, it is convenient first to divide the numerator and denominator by $(1 - Q_0)/N$. Let $L_i \equiv NQ_i/(1 - Q_0)$. Then z^* , which is a ratio of expressions of the form $\chi_A - \sum_i \chi_i Q'_i$ (where $\chi_A = \sum_i \chi_i$) can be rewritten as a ratio of expressions of the form $N\chi_A - \chi_0 + \sum_i \chi_i(L_0 - L_i)$. Thus, the ES dispersal rate has the same properties as the $L_0 - L_i$ -values with regard to mutation rate and deme number. This is particularly convenient because such differences of L -values have been previously studied (Rousset 1997; see the electronic appendix on the Royal Society Web site). They depend weakly on mutation rates and deme number, and have a non-trivial low mutation limit. Thus, we may expect to obtain an approximation for the ES dispersal rate at the infinite number of demes and low mutation limit which will be robust to these two assumptions.

Moreover, a result more specific to the present model is also made clear by this formulation. In the absence of dispersal cost, $\chi_A = 0$, and because L -values are independent of N (see the electronic appendix), it appears that the ES dispersal rate does not depend on N if there is no cost of dispersal.

Finally, it is possible to obtain the following ‘high cost’ approximation to the exact solution of the different dispersal models:

$$z^* = \frac{1 + c + 4cN - \sqrt{(- 32c^2N + (1 + c + 4cN)^2)}}{8c^2N}, \tag{7}$$

(see the electronic appendix). This approximation will be found to be very accurate as c and N increase.

3. SPECIFIC DISPERSAL MODELS

In the following we apply the approach presented above to study the evolution of dispersal in the island model and in stepping-stone models of migration. In each case we detail the fitness functions, and numerical examples are given below in figure 2 for the different models. The ESS can also be derived without writing any explicit expression for the fitness function, using an alternative method (see the electronic appendix), which allows an independent check of the calculations detailed below.

(a) Island model

The ‘infinite island’ version of this model has been previously studied by several authors (Hamilton & May 1977; Frank 1986; Taylor 1988). Here we study the more general case where the population contains a finite number, n , of demes, from which the infinite island model can be obtained as a limit case when $n \rightarrow \infty$. As a consequence, immigrant individuals may also experience some competition with related individuals in the $\nu = n - 1$ neighbouring demes. Following the approach described above we first write the direct fitness of an individual as

$$w(z_{\bullet}, z_0, z_1) = \frac{1 - z_{\bullet}}{1 - z_0 + (1 - c)z_1} + \frac{(1 - c)z_{\bullet}}{1 - z_1 + (1 - c)(z_0 + (n - 2)z_1)/(n - 1)}, \tag{8}$$

where z_{\bullet} , z_0 and z_1 are the phenotype of the focal individual, the average phenotype of individuals in the focal individual’s deme, and the average phenotype of individuals in other demes, respectively. This fitness function is to be understood as follows.

- (i) Philopatry: $1 - z_{\bullet}$ of an individual’s offspring do not disperse and enter in competition with $(1 - z_0)$ of the offspring in the same deme and with $(1 - c)z_1$ of the dispersing offspring from adjacent demes.
- (ii) Dispersal: $(1 - c)z_{\bullet}$ of an individual’s offspring disperse to some adjacent deme and enter in competition with $1 - z_1$ of the offspring that did not disperse out of the adjacent deme, and with $1 - c$ of the offspring that dispersed (including $z_0/(n - 1)$ from the same deme as the focal individual and $(n - 2)z_1/(n - 1)$ from other demes).

We compute S and solve equation (5) to obtain the ESS:

$$z^* = \frac{(n - 1)(Q'_0 - Q_1 + c(Q_1 - 1))}{(Q'_0 - 2Q_1 + 1 + n(Q_1 - 1))c^2 + (Q'_0 - Q_1)(n - 2c)}. \tag{9}$$

We can express the ESS in terms of much studied quantities. The well-known F_{ST} parameter is best defined as a function of probabilities of identity within and between demes, and has been defined as $F \equiv (Q_0 - Q_1)/(1 - Q_1)$ (e.g. Cockerham & Weir 1993). Then

$$z^* = \frac{F + (1 - F)/N - c}{(1 + (1 - c)^2/(n - 1))(F + (1 - F)/N) - c^2}. \tag{10}$$

With $F' \equiv (Q'_0 - Q_1)/(1 - Q_1)$, defined as a function of probabilities of identity of offspring after reproduction but before migration, we have

$$z^* = \frac{(F' - c)(n - 1)}{(F' - c^2)(n - 1) + F'(1 - c)^2}. \tag{11}$$

It is not very important which description is used provided there is no confusion between F and F' . As $n \rightarrow \infty$, z^* goes to the result of the infinite island model, $z^* = (R - c)/(R - c^2)$ (Frank 1986) for $R = F' = F + (1 - F)/N$.

The low mutation limit for F' follows from standard theory for F (Cockerham & Weir 1993, equation (1)):

$$F' \rightarrow \frac{1}{N - (N - 1)(1 - mn/(n - 1))^2}, \tag{12}$$

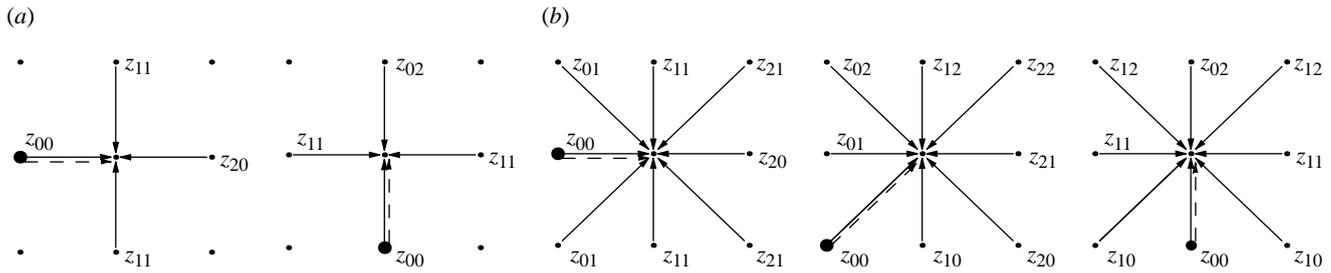


Figure 1. Derivation of the direct fitness function in different dispersal models. The dashed arrows show the dispersal of an individual's offspring from deme (0, 0). Competing offspring disperse to the same deme as this offspring, at rates depending on their relationship to the focal individual, and the appropriate z_{ij} variables can be read from these graphs: (a) in the four neighbour model, the two cases corresponding to the last two terms of equation (16) are shown. In the first case, the immigrant competitors in deme (1, 0) are 1/4 of the migrant offspring of the focal parent's deme, from deme (2, 0) and from demes (1, ±1). Note that the minus sign in deme coordinates can be dropped because the dispersal distribution is axially symmetrical. Hence the 'dispersal rate' variables to be considered in the fitness function are z_{00} , z_{11} and z_{20} , respectively. (b) In the eight neighbours model one must distinguish between an individual's offspring dispersing from (0, 0) to (1, 0), to (0, 1) and to (1, 1). These three cases correspond to the last three terms of equation (17).

where m measures the probability that an adult had its parent in another deme (i.e. after the cost of dispersal is paid and after competition). Given that m is related to the dispersal rates by $m = (1 - c)z / (1 - cz)$, this yields the following expression for the ESS:

$$z^* = (n - 1) \times \frac{(n + c(2Nn - 3) - \sqrt{((n - c)^2 + 4n(N - 1)(Nn - 1)c^2)})}{2c(c(n - 2) + n)(Nn - 1)} \tag{13}$$

This value increases with the number of demes but for $n > 10$ it gets very close to the infinite deme value which is

$$z^* = \frac{1 + 2Nc - \sqrt{(1 + 4N(N - 1)c^2)}}{2c(c + 1)N} \tag{14}$$

(b) One-dimensional stepping-stone model

We now study the case where dispersal occurs between adjacent demes on a 1D lattice (a circular population with n demes). In this case there are $\nu = 2$ neighboring demes. The derivation of the direct fitness yields

$$w(z_\bullet, z_0, z_1, z_2) = \frac{1 - z_\bullet}{1 - z_0 + (1 - c)z_1} + \frac{(1 - c)z_\bullet}{1 - z_1 + (1 - c)(z_0/2 + z_2/2)}, \tag{15}$$

where z_\bullet , z_0 , z_1 and z_2 are the phenotype of the focal individual, the average phenotype of individuals in the focal individual's deme, the average phenotype of individuals in immediately adjacent demes, and the average phenotype of individuals two steps apart on the lattice, respectively. This fitness function is to be understood as follows.

- (i) **Philopatry:** $1 - z_\bullet$ of an individual's offspring do not disperse and enter in competition with $(1 - z_0)$ of the offspring from their neighbours in the same site that did not disperse and with $(1 - c)z_1$ of the offspring of neighbours in adjacent demes that dispersed. Thus the first term is as in the island model, except that z_1 is the phenotype of a deme

adjacent to the focal individual's deme, not the phenotype of all other demes.

- (ii) **Dispersal:** $(1 - c)z_\bullet$ of an individual's offspring enter in competition with offspring competing for an adjacent deme, $(1 - c)z_0/2$ from the focal individual's deme and $(1 - c)z_2/2$ from a deme two steps away from the individual's deme.

The derivation of the ESS yields $z^* = (Q'_0 - Q_1 - c(1 - Q_1)e / (X + cY + c^2Z))$ with $X \equiv 3(Q'_0 - Q_1)/2 + (Q_2 - Q_1)/2$, $Y \equiv 2Q_1 - Q'_0 - Q_2$, and $Z \equiv Q'_0 + Q_2 - 2$. A complex expression may be obtained for d^* (not shown), which for $c = 0$ and $n \rightarrow \infty$ reduces to $z^* = 3/4$.

(c) Two-dimensional stepping-stone models

Let us now assume that the population has a 2D structure. We consider two different types of dispersal. In the first case the offspring are allowed to disperse in the nearest four neighbouring demes ($\nu = 4$) and in the second case they can disperse to the nearest eight neighbouring demes ($\nu = 8$; see figure 1).

(i) Four neighbours model

Let z_{ij} be the average phenotype of individuals in position ij relative to the focal individual on the lattice. The fitness function is

$$w = \frac{1 - z_\bullet}{1 - z_{00} + (1 - c)(z_{10} + z_{01})/2} + \frac{1}{2} \left(\frac{(1 - c)z_\bullet}{1 - z_{10} + (1 - c)(z_{00}/4 + z_{20}/4 + z_{11}/2)} \right) + \frac{1}{2} \left(\frac{(1 - c)z_\bullet}{1 - z_{01} + (1 - c)(z_{00}/4 + z_{02}/4 + z_{11}/2)} \right), \tag{16}$$

the first part of which is as in the 1D model (see the legend of figure 1 for an explanation of the weights given to the z s in the denominators of the last two parts). Evaluation of the ESS does not lead to simple analytical expressions, but some results are presented in figure 2.

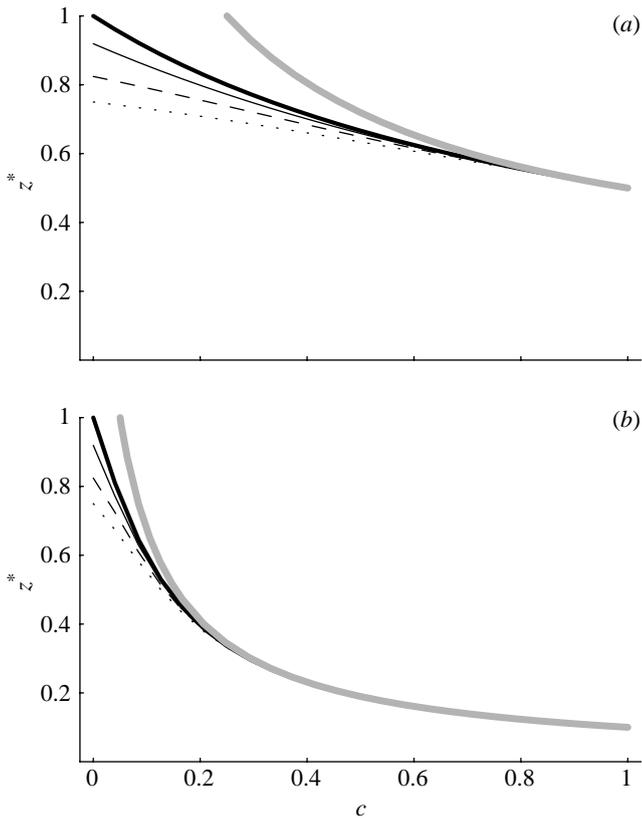


Figure 2. ES dispersal rates versus the cost of dispersal, c , for a variable number of neighbouring demes, ν , and two deme sizes ((a) $N=1$; (b) $N=5$). In each case, from top to bottom the grey curve is the approximate solution for all models (equation (7)), and the next are the exact solutions of the different models for decreasing ν : the bold curve is the ESS for the infinite island model (i.e. $\nu \rightarrow \infty$), and the three other curves are the ESS for the three stepping-stone models. Thin curve: $\nu = 8$, dashed curve: $\nu = 4$, dotted curve: $\nu = 2$. Other parameter values: $n \rightarrow \infty$.

(ii) *Eight neighbours model*

When the offspring can disperse to the nearest eight neighbouring demes the fitness function gets more complicated:

$$\begin{aligned}
 w = & \frac{1 - z_{\bullet}}{1 - z_{00} + (1 - c)(z_{10}/4 + z_{01}/4 + z_{11}/2)} \\
 & + \frac{1}{4} \left(\frac{(1 - c)z_{\bullet}}{1 - z_{10} + (1 - c)((z_{00} + z_{20})/8 + (z_{01} + z_{11} + z_{21})/4)} \right) \\
 & + \frac{1}{4} \left(\frac{(1 - c)z_{\bullet}}{1 - z_{01} + (1 - c)((z_{00} + z_{02})/8 + (z_{10} + z_{11} + z_{12})/4)} \right) \\
 & + \frac{1}{2} \left(\frac{(1 - c)z_{\bullet}}{1 - z_{11} + (1 - c)(z_{00} + z_{10} + z_{01} + z_{20} + z_{02} + z_{21} + z_{12} + z_{22})/8} \right).
 \end{aligned}
 \tag{17}$$

The first term is for philopatric offspring, the second and the third are for offspring dispersing by $(\pm 1, 0)$ and $(0, \pm 1)$ steps on the lattice, respectively, and the final term is for offspring dispersing by $(\pm 1, \pm 1)$ steps (see figure 1). Again, the exact value of d^* can be obtained numerically. The results are presented in figure 2.

(d) *Comparison of the different models*

Figure 2 shows that for a low cost of dispersal the ESS always increases with ν , the number of neighbouring

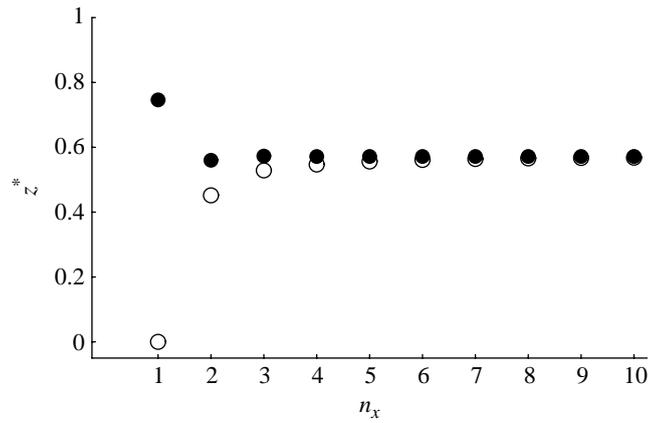


Figure 3. Effects of the shape and size of the population on the evolutionarily stable dispersal rate. The filled circles are the ESS in a population of size $n = n_x n_y = 2520$ (n_x and n_y are the width and length of the population, respectively). This shows the effects of shape for fixed size. The empty circles are the ESS in a population of increasing size $n = n_x n_x$. This shows the effect of size with a fixed shape. Other parameter values: $N = 5$, $c = 0.1$, $\nu = 4$, $u = 10^{-6}$.

demes. For example, when there is no cost of dispersal and when $n \rightarrow \infty$, z^* goes from $3/4$ in the linear stepping-stone model (i.e. two neighbouring demes) to unity in the island model (i.e. $n - 1$ neighbouring demes). This effect can be explained by the following argument. When there is no cost of dispersal, the dispersal level is determined only by the balance between kin competition at home and away. A lower number of neighbouring demes increases the level of kin competition experienced by dispersed offspring and, as a consequence, selects for lower dispersal rates. This is most evident if we count only kin competition among one's offspring, i.e. if we solve $dw(z_{\bullet}, (z_{\bullet} + (N - 1)z/N), z \dots z)/dz_{\bullet}|_{z_{\bullet}=z^*} = 0$ for z^* . In the absence of cost, the solution is simply $z^* = \nu/(1 + \nu)$, where ν is equal to 2, 4 and 8 for our three stepping-stone models. It is worth pointing out the analogy with the effect of the probability of common origin of migrants, ϕ , in an infinite island model of dispersal. Common origin increases the risk of kin competition among immigrants and, consequently, selects against dispersal. Indeed Gandon & Michalakis (1999) showed that when there is no cost of dispersal the ESS is $z^* = 1/(1 + \phi)$. This is not surprising because $\phi = 1/\nu$ when $n \rightarrow \infty$.

For a higher cost of dispersal the results for the different models converge to the same value, given by equation (7). This result indicates that the costs and benefits of dispersal become identical in the different dispersal models as c increases. Note that the convergence between the different models is quicker for larger deme sizes (figure 2).

The model also allows us to analyse other effects of the population structure (figure 3). In particular, we show that the size and shape of the population only weakly affects the evolution of dispersal. However, (i) for very small populations ($n < 10$), a lower number of demes decreases dramatically the ES dispersal rate (see equation (13) and figure 3) and (ii) elongated populations tend to increase the ESS when the width of the habitat is very small (e.g. $n_x = 1$, see figure 3).

4. DISCUSSION

Kin selection is widely accepted as a major factor in the evolution of dispersal behaviour. However, most of the investigations that have been carried out rely on the assumptions of the infinite island model of migration. Here we present a kin selection model that allows us to study the ESS for any spatially homogeneous distribution of dispersal distance. In particular, we examine the differences of the ESSs obtained in the island model and in three different stepping-stone models.

In the present paper we assume fixed distributions of dispersal distances, but these distributions are also likely to evolve. For example, if we assume that the cost of dispersal increases with dispersal distance this may select for more localized dispersal strategies. Only a few theoretical studies have addressed this question (Ezoe 1998), and they do not account for all interactions between relatives. The analytical methods used in this paper can be used to address this issue.

Our results are distinct from those of the earlier work of Comins (1982). Comins found that the ES dispersal rate is 'approximately' independent of the shape of the dispersal distribution, and exactly so in the absence of dispersal cost (Comins 1982, p. 590). We find the reverse result: the ES dispersal rate is different for the different models in the absence of dispersal cost (as one could expect from the intuitive argument given above), but that it converges to the same value as dispersal cost increases. Comins' conclusion, that dispersal rate is independent of the shape of the dispersal distribution in the absence of dispersal cost, is based on an argument not requiring explicit formulae for probabilities of identities in these models. Rather it is based on a simplification of an expression for inclusive fitness, using a recursion equation common to all models. But the expressions for inclusive fitness we have generated by the direct fitness method cannot thus be simplified, even though we have also used this recursion to simplify them (see the electronic appendix). Therefore the discrepancy is not due to different uses of mathematical models of isolation by distance. The key difference seems to be in the measures of fitness used. It is difficult to understand how Comins derives his expressions for inclusive fitness, while the direct fitness method used here is unambiguous in this respect.

We have found that having a smaller number of demes decreases the ES dispersal rate. Indeed, the difference in relatedness between individuals from different demes decreases with smaller populations. As a consequence, the marginal gain in fitness from dispersal is much lower, because dispersal is not as effective at avoiding kin competition. Actually, the assumption that the population is organized as a torus eliminates edge effects which would also select for lower dispersal rates (Travis & Dytham 1999). This may have implications in the field of conservation biology. Endangered species are, by definition, characterized by their small and, often, decreasing number of demes (i.e. suitable habitats). Because a smaller number of demes selects for smaller dispersal rates this could decrease the recolonization ability of these species and, as a consequence, increase the probability of extinction. However, a rigorous analysis of this question

requires the inclusion of additional processes in the model, such as extinction and recolonization events.

We have also studied the effect of the shape of the population on the evolution of dispersal. Crow & Aoki (1984) pointed out that the shape of the habitat could affect the evolution of altruistic traits because they noticed that 'the degree of divergence of subpopulations, and hence the opportunity for intergroup selection, is substantially increased if migrants come from nearby groups and the habitat is long and narrow' (p. 6076). Here we show that, as for the effect of the number of demes or the mutation rate, the shape of the habitat hardly affects the evolution of dispersal. This effect is only noticeable for extreme values (when the width of the population is unity) and not always in the direction predicted by Crow & Aoki (e.g. for $n_x = 2$, z^* is slightly lower than when $n_x \rightarrow \infty$).

Part of the discrepancy is due to their use of ' G_{ST} ' as a measure of relatedness. This measure involves the probability of identity for genes drawn at random from the whole population. ' G_{ST} ' gives a global estimation of the divergence between demes. However, the ESS equation (6) shows that when dispersal is localized, the cost and benefits of altruism should be weighted by identity coefficients, all of which are local (for individuals a few steps apart on the lattice, not for the whole population). Therefore ' G_{ST} ' cannot always be used to measure the strength of kin competition.

In a more general perspective our analysis raises the question of the definition of relatedness in a population with local dispersal. Following the analysis detailed in Rousset & Billiard (2000), the direct fitness approach, as described by Taylor & Frank (1996), yields the relevant measures of kin selection in terms of the identity coefficients as meant here, and these can be translated into measures involving several 'relatedness coefficients' $r_i \equiv (I_0 - I_i)/N = (Q_0 - Q_i)/(1 - Q_0)$ (see the electronic appendix). The present work demonstrates that these techniques yield a new answer to a classic problem.

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REFERENCES

- Bengtsson, B. O. 1978 Avoiding inbreeding: at what cost? *J. Theor. Biol.* **73**, 439–444.
- Cockerham, C. C. & Weir, B. S. 1993 Estimation of gene flow from F -statistics. *Evolution* **47**, 855–863.
- Comins, H. N. 1982 Evolutionarily stable strategies for localized dispersal in two dimensions. *J. Theor. Biol.* **94**, 579–606.
- Comins, H., Hamilton, W. D. & May, R. 1980 Evolutionarily stable dispersal strategies. *J. Theor. Biol.* **82**, 205–230.
- Crow, J. F. & Aoki, K. 1984 Group selection for a polygenic behavioural trait: estimating the degree of population subdivision. *Proc. Natl. Acad. Sci. USA* **81**, 6073–6077.
- Ezoe, H. 1998 Optimal dispersal range and seed size in a stable environment. *J. Theor. Biol.* **190**, 287–293.
- Frank, S. A. 1986 Dispersal polymorphism in subdivided populations. *J. Theor. Biol.* **122**, 303–309.
- Gandon, S. 1999 Kin competition, the cost of inbreeding and the evolution of dispersal. *J. Theor. Biol.* **200**, 345–364.

- Gandon, S. & Michalakis, Y. 1999 Evolutionarily stable dispersal rate in a metapopulation with extinctions and kin competition. *J. Theor. Biol.* **199**, 275–290.
- Gillespie, J. H. 1981 The role of migration in the genetic structure of populations in temporally and spatially varying environments. III. Migration modification. *Am. Nat.* **117**, 223–233.
- Hamilton, W. D. 1996 *Narrow roads to gene land*. Oxford, UK: Freeman.
- Hamilton, W. D. & May, R. 1977 Dispersal in stable habitats. *Nature* **269**, 578–581.
- Levin, S. A., Cohen, D. & Hastings, A. 1984 Dispersal strategies in patchy environments. *Theor. Popul. Biol.* **26**, 165–191.
- McPeck, M. A. & Holt, R. D. 1992 The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.* **140**, 1010–1027.
- Malécot, G. 1975 Heterozygosity and relationship in regularly subdivided populations. *Theor. Popul. Biol.* **8**, 212–241.
- Motro, U. 1982a Optimal rates of dispersal. I. Haploid populations. *Theor. Popul. Biol.* **21**, 394–411.
- Motro, U. 1982b Optimal rates of dispersal. II. Diploid populations. *Theor. Popul. Biol.* **21**, 412–429.
- Motro, U. 1991 Avoiding inbreeding and sibling competition: the evolution of sexual dimorphism for dispersal. *Am. Nat.* **137**, 108–115.
- Nagylaki, T. 1976 The decay of genetic variability in geographically structured populations. II. *Theor. Popul. Biol.* **10**, 70–82.
- Rousset, F. 1997 Genetic differentiation and estimation of gene flow from F -statistics under isolation by distance. *Genetics* **145**, 1219–1228.
- Rousset, F. & Billiard, S. 2000 A theoretical basis for measures of kin selection in subdivided populations: finite populations and localised dispersal. *J. Evol. Biol.* (Submitted.)
- Sawyer, S. 1977 Asymptotic properties of the equilibrium probability of identity in a geographically structured population. *Adv. Appl. Prob.* **9**, 268–282.
- Taylor, P. D. 1988 An inclusive fitness model for dispersal of offspring. *J. Theor. Biol.* **130**, 363–378.
- Taylor, P. D. & Frank, S. A. 1996 How to make a kin selection model. *J. Theor. Biol.* **180**, 27–37.
- Travis, J. M. J. & Dytham, C. 1999 Habitat persistence, habitat availability and the evolution of dispersal. *Proc. R. Soc. Lond. B* **266**, 723–728.
- Van Valen, L. 1971 Group selection and the evolution of dispersal. *Evolution* **25**, 591–598.
- Waser, P. M., Austad, S. N. & Keane, B. 1986 When should animals tolerate inbreeding? *Am. Nat.* **128**, 529–537.

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