

Evolution of dispersal in a stepping-stone population with overlapping generations

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ABSTRACT

We use Hamilton's inclusive fitness method to calculate the evolutionarily stable dispersal rate in 1- and 2-dimensional stepping-stone populations. This extends previous results by introducing a positive probability for adults to survive into the next generation and breed again. Relatedness between nearby individuals generally decreases with increasing survival, decreasing competition with kin and favouring greater dispersal rates.

Key words: altruism, dispersal, inclusive fitness, stepping-stone population, overlapping generations.

Dispersal is an important form of social behaviour which encapsulates the trade-off between cooperation and competition. Competition for resources among kin favours the evolution of dispersal. The evolutionarily stable (ES) level of dispersal can be determined from an inclusive fitness analysis of the reduction in competition with relatives and the cost of dispersal. The population structure determines the relatedness between individuals and the level of competition among kin. Populations are frequently described with a patch (Wright's infinite island) or lattice structure (e.g. stepping-stone, Kimura 1953). Carefully constructed models are necessary to discover which features of structured populations affect the evolutionarily stable level of dispersal.

The evolution of dispersal has been analysed under a variety of conditions. Hamilton and May (1977) first showed that costly dispersal in a homogeneous patch-structured environment can be favoured because it reduces the competition among relatives. Their basic model has been generalized to describe patches with more than one individual per patch, offspring control, sexual reproduction, and other genetic systems with similar results (Comins et al. 1980, Motro 1982a, b, 1983, Frank 1986, Taylor 1988). At the heart of each model is a description of the population-genetic structure which determines the relatedness between an actor and other individuals.

Many dispersal models assume all adults die at the end of every generation. Although this is a realistic reflection of many plant and animal populations, many species have overlapping generations. The degree of overlap between generations is determined by the survival probability of adults. Increasing survival of reproductively active adults affects relatedness. In a patch-structured

population, increasing survival increases the relatedness between individuals on the same patch (Pen, 2000) and promotes increased dispersal (Taylor & Irwin, 2000).

Our objective is to determine the ES dispersal rate in one- and two-dimensional stepping-stone populations with overlapping generations. We use Hamilton's (1964) inclusive fitness method to analyse the selection on a mutant gene for a deviant rate of dispersal. The method adds up the effect of the behaviour on the fitness of all individuals weighted by their relatedness to the actor; if the sum is positive, the behaviour is favoured. This approach highlights the tradeoff between the benefit of dispersal to close relatives and the cost to the disperser. We find that the ES dispersal rate in a stepping-stone population increases with increasing survival probability. In one dimension, we obtain a simple formula for the ES dispersal rate. In two dimensions the dispersal rate can't be found explicitly and we present numerical results. Olivieri et al. (1995) found an analogous result with a computer simulation of a metapopulation model and Venable & Levin (1983) found that annual plants tend to have shorter dispersal ranges than perennial species.

THE MODEL

We study a population structured by placing sites in a one- or two-dimensional square lattice. The population is infinite, with one asexually reproducing haploid adult per site. Each individual produces a large number of offspring. These disperse equally among adjacent sites with total probability d . In one dimension, there are two neighbours and a fraction $d/2$ of the juveniles disperse to each and in two dimensions, there are four neighbours which each receive a proportion $d/4$ of the individuals. Dispersal is costly; the fitness of a dispersing juvenile is reduced by increased predation or other factors. Mathematically we describe this by assuming that only a proportion $1 - k$ of dispersing juveniles arrive at a new site. We create overlap between generations by allowing adults to survive and breed again with probability s . If an adult survives, it is guaranteed to retain the breeding resources on its site. If it dies, the offspring, both native and immigrant, compete on an equal basis for the vacant site. Offspring which do not win a site die and the cycle begins again. We determine the ES dispersal rate by finding the inclusive fitness effect of a mutant with a slightly altered dispersal probability.

We make two different approximations in our calculations. We introduce an additional disper-

sal rate μ which brings in unrelated individuals from infinity and can be thought of as a mutation rate (Crow & Kimura, 1970, p. 267). This additional dispersal is necessary because in the absence of long-range dispersal or mutation the equilibrium relatednesses are all 1 on the one- and two-dimensional lattice. Our first approximation is to include terms of order $\sqrt{\mu}$ and ignore μ terms in the relatedness. This simplifies the calculation of relatedness between the actor and nearby individuals, with the effect that even in a neutral population, our relatedness coefficients are only calculated approximately. Second, we assume the mutant allele codes for a small deviation δ in the dispersal rate. The inclusive fitness result should be valid for small δ ; to be precise it is exact to first order (Taylor, 1996).

CALCULATION OF RELATEDNESS

Relatedness in one dimension.

We calculate relatedness with a one-generation recursion assuming all offspring disperse at the same rate. Let r_j be the average relatedness of an individual to one j sites to the right in the one-dimensional lattice. The relatedness in the next generation r'_j is a weighted average of relatednesses in the current generation,

$$r'_j = \begin{cases} A(r_{j-2} + r_{j+2}) + B(r_{j-1} + r_{j+1}) + Cr_j + Dr_\infty, & j \neq 0 \\ 1, & j = 0 \\ 0, & j = \infty \end{cases} \quad (1)$$

where

$$\begin{aligned} A &= p_1 p_{-1} \\ B &= p_0 p_1 + p_0 p_{-1} \\ C &= p_0^2 + p_1^2 + p_{-1}^2 \\ D &= 2p_\infty(1 - p_\infty) + p_\infty^2 \end{aligned}$$

and p_i is the probability a patch is won by an individual from a site i steps to the right. For example, the weight A is obtained by noticing that the distance between parents and their offspring can change by 2 in a generation only if offspring from each site disperse 1 step in opposite directions. The weight D is the probability individuals j sites apart are unrelated which can happen in two

ways: if one comes from infinity and the other doesn't (with total probability $2p_\infty(1-p_\infty)$) or both come from infinity (p_∞^2). With no external pressures on dispersal, we expect symmetric dispersal and set $p_{-1} = p_1$. Values for p_i are in Table I. There is a useful relationship between values of p_i for the general case and the case $s = k = 0$. Substituting \hat{d} and $\hat{\mu}$ for d and μ in the p_i for non-overlapping generations and zero-cost dispersal obtains the general p_i if the modified dispersal rates are defined by

$$\begin{aligned} \hat{d} &= d(1-s) \left(\frac{1-k}{1-k(d+\mu)} \right) \\ \hat{\mu} &= \mu(1-s) \left(\frac{1-k}{1-k(d+\mu)} \right). \end{aligned} \quad (2)$$

A standard method to analyse Eq. (1) transforms the recursion into a linear system of four first-order difference equations (Kimura & Weiss 1964, Taylor 1994). Solving the recursion for the relatedness between neighbours and next-nearest neighbours yields

$$\begin{aligned} r_1 &= 1 - \Phi \\ r_2 &= 1 - 4 \left(\frac{\sqrt{1-\hat{d}} - 1 + \hat{d}}{\hat{d}} \right) \Phi \end{aligned} \quad (3)$$

where $\Phi = \sqrt{\frac{2\hat{\mu}}{\hat{d}(1-\hat{d})}} + O(\mu)$.

The reduction to a system of first-order difference equations can't be adapted to compute relatedness in two or three dimensions. Another approach, introduced by Weiss & Kimura (1965) can be used with a regular lattice of any dimension (see also Malécot 1975). We use this method to find the relatedness between individuals on nearby sites in a two-dimensional stepping-stone population.

Relatedness in two dimensions.

We define $r_{j,k}$ to be the relatedness of a focal individual to an individual j sites away in the horizontal direction and k sites away in the vertical direction in the lattice. It's convenient to write these relatednesses in an infinite matrix $\mathbf{r} = \{r_{j,k}\}$ for all $j, k \in \mathbb{Z}$. Following the recursion above (Eq. 1), we write a recursion for relatedness in the next generation in terms of relatedness in the

present generation

$$\mathbf{r}' = \begin{cases} L^2 \mathbf{r}, & (j, k) \neq (0, 0) \\ 1, & (j, k) = (0, 0). \end{cases} \quad (4)$$

where

$$\begin{aligned} L &= p_0 + p_1(S_1 + S_1^{-1} + S_2 + S_2^{-1}) \\ &= 1 - \hat{d} - \hat{\mu} + \frac{\hat{d}}{4}(S_1 + S_1^{-1} + S_2 + S_2^{-1}). \end{aligned} \quad (5)$$

The S_i are shift operators on the relatedness matrix which move all the entries left or down one step,

$$\begin{aligned} S_1\{r_{j,k}\} &= \{r_{j+1,k}\} \\ S_2\{r_{j,k}\} &= \{r_{j,k+1}\}. \end{aligned}$$

The operator L ‘disperses’ offspring with each term; the first term keeps a fraction $p_0 = 1 - \hat{d} - \hat{\mu}$ at the natal site, and the next four terms send $p_1 = \hat{d}/4$ to each of the nearest-neighbours. L^2 appears in Eq. (4) because we need a weighted sum of relatednesses for juveniles coming from any of the five sites for each juvenile (ignoring unrelated individuals dispersing from sites infinitely far away, see Figure 1). The recursion (Eq. 4) holds for stepping-stone dispersal in a lattice of any dimension with an appropriate choice of L . For example, a recursion for one dimension can be obtained from (Eq. 4) by defining $L = 1 - \hat{d} - \hat{\mu} + \frac{\hat{d}}{2}(S + S^{-1})$ where S is the shift operator on an infinite vector of relatedness $\{r_j\}$.

We find the relatedness coefficients at equilibrium by solving Eq. (4) with $\mathbf{r}' = \mathbf{r}$. It is straightforward to verify that

$$L\{\cos(j\theta_1) \cos(k\theta_2)\} = H(\theta_1, \theta_2)\{\cos(j\theta_1) \cos(k\theta_2)\}, \quad (6)$$

where

$$H(\theta_1, \theta_2) = 1 - \hat{d} - \hat{\mu} + \frac{\hat{d}}{2}(\cos \theta_1 + \cos \theta_2). \quad (7)$$

This says that for each θ_1 and θ_2 , L has an eigenvector $\{\cos(j\theta_1) \cos(k\theta_2)\}$ with eigenvalue $H(\theta_1, \theta_2)$. We introduce a function $F(\theta_1, \theta_2)$ which is a linear combination of these eigenvectors

with the $r_{j,k}$ as weights,

$$F(\theta_1, \theta_2) = \sum_{j,k} r_{j,k} \cos(j\theta_1) \cos(k\theta_2). \quad (8)$$

The $r_{j,k}$ are the Fourier coefficients of the function F and can be recovered with the Fourier transform of F ,

$$r_{j,k} = \frac{1}{(2\pi)^2} \int_0^{2\pi} \int_0^{2\pi} F(\theta_1, \theta_2) \cos(j\theta_1) \cos(k\theta_2) d\theta_1 d\theta_2. \quad (9)$$

Now, apply $(1 - L^2)$ to Eq. (9)

$$(1 - L^2)\mathbf{r} = \frac{1}{(2\pi)^2} \int_0^{2\pi} \int_0^{2\pi} F(\theta_1, \theta_2) (1 - L^2) \{\cos(j\theta_1) \cos(k\theta_2)\} d\theta_1 d\theta_2 \quad (10)$$

and use the eigenvectors of L Eq. (6) to obtain

$$[(1 - L^2)\mathbf{r}]_{j,k} = \frac{1}{(2\pi)^2} \int_0^{2\pi} \int_0^{2\pi} F(\theta_1, \theta_2) (1 - H^2(\theta_1, \theta_2)) \{\cos(j\theta_1) \cos(k\theta_2)\} d\theta_1 d\theta_2. \quad (11)$$

The left-hand side of Eq. (11) is the vector of Fourier coefficients of $F(1 - H^2)$ and it follows from Eq. (4) that they are given by

$$[(1 - L^2)\mathbf{r}]_{j,k} = \begin{cases} 0, & (j, k) \neq (0, 0) \\ c, & (j, k) = (0, 0) \end{cases} \quad (12)$$

where c is a constant to be determined later. Since all the Fourier coefficients of $F(1 - H^2)$ are 0 except at $j = k = 0$,

$$F(\theta_1, \theta_2) = \frac{c}{1 - H^2(\theta_1, \theta_2)}. \quad (13)$$

Now combine Eqs. (9) and (13) to obtain a formal solution to the recursion

$$r_{j,k} = \frac{c}{(2\pi)^2} \int_0^{2\pi} \int_0^{2\pi} \frac{\cos(j\theta_1) \cos(k\theta_2)}{1 - H^2(\theta_1, \theta_2)} d\theta_1 d\theta_2 \quad (14)$$

with the constant c determined by $r_{0,0} = 1$. The problem now is to evaluate these integrals.

In one dimension analogous arguments show

$$r_j = \frac{c}{4\pi} \int_0^{2\pi} \cos(j\theta) \left(\frac{1}{\hat{\mu} + \hat{d} - \hat{d} \cos \theta} + \frac{1}{2 - \hat{\mu} - \hat{d} + \hat{d} \cos \theta} \right) d\theta$$

These integrals can be evaluated to obtain the results in Eq. (3).

In two dimensions the integrals must be simplified using various ingenious transformations (see appendix). Exact formulae for the first two relatedness coefficients needed in the dispersal analysis are

$$r_{0,1} = \frac{K(a_1) - K(a_2)}{a_1 K(a_1) + a_2 K(a_2)} \quad (15)$$

$$r_{1,1} = \frac{(z_1 - a_1)K(a_1) - z_1 E(a_1) + (z_2 - a_2)K(a_2) - z_2 E(a_2)}{a_1 K(a_1) + a_2 K(a_2)} \quad (16)$$

where a_i and z_i are in (Eqs. 27, 32) and K and E are complete elliptic integrals of the first and second kinds respectively (Abramowitz & Stegun 1964). Other relatedness coefficients have more complicated formulae but can be computed as indicated in the appendix.

ANALYSIS OF DISPERSAL.

We now find the ES dispersal rate in a one- and two-dimensional stepping-stone population with overlapping generations. A mutant adopts a deviant dispersal probability $d' = d + \delta$. The inclusive fitness effect of the mutant is the sum over the whole population of the fitness change due to the mutant for each individual weighted by its relatedness to the mutant:

$$\Delta w_{IF} = \sum_i \Delta w_i r_i.$$

The fitness of a breeder on site i is the expected number of its breeding descendents on all sites in the next generation. This is the sum of the probability of survival s and the expected number of offspring which obtain a breeding spot. If an adult on site i sends n_{ij} offspring to compete on site j , there will be $n_j = \sum_k n_{kj}$ juvenile competitors on site j . The probability an offspring from site i wins site j is the product of the probability the current occupant dies and n_{ij}/n_j . Thus, the fitness of the adult on site i is

$$w_i = s + (1 - s) \sum_j \frac{n_{ij}}{n_j}. \quad (17)$$

The change in fitness due to mutant behaviour on site i is

$$\Delta w_i = w'_i - w_i = (1 - s) \sum_j \left(\frac{n'_{ij}}{n'_j} - \frac{n_{ij}}{n_j} \right). \quad (18)$$

In a one-dimensional stepping-stone population, the non-zero n_{ij} are

$$\begin{aligned} n_{ii} &= 1 - d - \mu \\ n_{i,i\pm 1} &= \frac{d}{2}(1 - k). \end{aligned}$$

The mutant only affects dispersal away from the origin, so the only n'_{ij} which differ from n_{ij} in the previous generation are

$$\begin{aligned} n'_{00} &= 1 - d' - \mu \\ n'_{0,\pm 1} &= \frac{d'}{2}(1 - k). \end{aligned}$$

The mutant affects the fitness of individuals one and two steps away because it changes the number of competitors on its own site and sites one step away. The fitness changes are obtained by substituting these n_{ij} into Eq. (18),

$$\begin{aligned} \Delta w_0 &= (2 - 3d - kd) \frac{(1 - k)(1 - s)\delta}{2(1 - kd)^2} \\ \Delta w_1 &= -(1 - 2d) \frac{(1 - k)(1 - s)\delta}{2(1 - kd)^2} \\ \Delta w_2 &= \frac{-d(1 - k)^2(1 - s)\delta}{4(1 - kd)^2}. \end{aligned} \tag{19}$$

Selection is weak so we include only terms linear in δ and we ignore terms $O(\mu)$ since we only retained terms $O(\sqrt{\mu})$ in the relatednesses. The mutant gene is favoured if

$$\Delta w_{IF} = \Delta w_0 + 2\Delta w_1 r_1 + 2\Delta w_2 r_2 > 0 \tag{20}$$

using the relatedness from Eq. (3). The ES dispersal rate is

$$d^* = \frac{1}{2k} \cdot \frac{2(1 - \sqrt{1 - k(1 - k)(1 - s)}) - k(1 - s)}{1 - \sqrt{1 - k(1 - k)(1 - s)} - k(1 - s)}. \tag{21}$$

If dispersal has no cost (considering the limit $k \rightarrow 0$) then

$$d^* = \frac{3 + s}{4}. \tag{22}$$

In a patch-structured population with no cost of dispersal, the ES dispersal rate is 1 because dispersing offspring don't compete with relatives (Hamilton & May, 1977). In a stepping-stone

population, dispersers always compete with relatives, so even with no dispersal cost, only partial dispersal is favoured (Eq. 22).

In two dimensions, the method of calculation is the same, but more sites are affected by the mutant. A change in its dispersal rate affects the number of competitors on its site and on the nearest-neighbour sites. The fitness of individuals which disperse offspring to any of these 5 sites must be included in the inclusive fitness. In total, individuals on thirteen sites are affected, representing four distinct relatedness groups as shown in Figure 1. The change in fitness of individuals on these four groups of sites to first order in δ is

$$\begin{aligned}
\Delta w_{0,0} &= (4 - 5d - 3dk) \frac{(1-k)(1-s)\delta}{4(1-kd)^2} \\
\Delta w_{0,1} &= -(1-2d) \frac{(1-k)(1-s)\delta}{4(1-kd)^2} \\
\Delta w_{1,1} &= -d \frac{(1-k)^2(1-s)\delta}{8(1-kd)^2} \\
\Delta w_{0,2} &= -d \frac{(1-k)^2(1-s)\delta}{16(1-kd)^2}.
\end{aligned} \tag{23}$$

The inclusive fitness effect is obtained by adding these together, weighted by their relatedness and the number of each different site type,

$$\Delta w_{IF} = \Delta w_{0,0} + 4\Delta w_{0,1}r_{0,1} + 4\Delta w_{1,1}r_{1,1} + 4\Delta w_{0,2}r_{0,2}. \tag{24}$$

The ES dispersal rate d^* is a solution of

$$2(2d^*sk - s - 1)K \left(\frac{(1-s)(1-k)d^*}{d^*(1-s+k+sk) - 2} \right) + \pi(2 - d^*(1-s+k+sk)) = 0. \tag{25}$$

Figure 2 shows the ES dispersal rate as a function of s for one- and two-dimensional stepping-stone populations as well as a patch structure with $k = 0$ and with $k = 1/10$ (see Taylor & Irwin 2000).

DISCUSSION

We analyse the evolution of dispersal in one- and two-dimensional stepping-stone populations. Our main result is that increasing the survival rate of reproductively active adults promotes greater dispersal rates. This is a result of the effect of survival probability on the relatedness between

neighbours. As survival increases, the relatedness between neighbours decreases. Another way to think about this is that survival tends to increase the between-site genetic variance because the “mixing” effects of dispersal are reduced, even with the same offspring dispersal rate. A variety of factors affect the balance between competition and dispersal costs.

Increasing the cost of dispersal results in a smaller ES dispersal rate. A greater dispersal cost decreases the inclusive fitness due to dispersing offspring for a given dispersal rate. This provides a marginal benefit to increasing the proportion of non-dispersing offspring despite the increased competition with relatives. This is consistent with previous studies of patch-structured populations with non-overlapping generations (Hamilton and May 1977, Motro 1982a,b, Frank 1986, Taylor 1988).

In our model, competition among relatives can be reduced by increasing the dispersal rate. An interesting extension allows variable dispersal rates over a range of dispersal distances. Competition among relatives is reduced by dispersing farther and by spreading dispersed offspring over a range of sites. Preliminary results indicate that as greater dispersal distances are permitted, more offspring disperse from the natal site to more distant sites. If dispersal costs increase with distance, most of the offspring disperse to a band of sites neither adjacent to, nor very distant from the natal site.

We compare the stepping-stone populations to a patch-structured population with one individual per patch (Fig. 2, Taylor & Irwin 2000). In a patch-structured population individuals can disperse from one patch to any other, but in a stepping-stone population dispersers can only arrive from neighbouring sites (ignoring the small dispersal rate from infinity). In this sense, a patch population is the limit of a stepping-stone population as the number of neighbours goes to infinity and the relatedness between neighbours goes to zero. The ES dispersal rate in stepping-stone populations increases as the number of neighbours increases and the ES dispersal rate for the $N = 1$ patch population is greater than in either stepping-stone population. An extra difference is that the ES dispersal rate is independent of survival probability s for the $N = 1$ patch population. This is understandable because the effect of s on relatedness vanishes when the relatedness between different individuals is 0.

In one dimension, we obtain an analytic expression for ES dispersal, including a remarkably simple result when there is no cost of dispersal (Eq. 22). The two-dimensional problem is in-

herently more complicated, but we work with standard special functions and can compute exact numerical dispersal rates without requiring simulations. The two-dimensional stepping-stone population has obvious application to communities which live on a surface, but the one-dimensional lattice may be superior for examining a population in an edge habitat (e.g. alpine or coastal).

An important difference between one- and two-dimensional stepping-stone populations is that there are more interacting neighbours in two dimensions. Similar to increasing the patch size, this is expected to decrease relatedness between neighbours and favour increased dispersal and indeed our results show that the ES dispersal rate is greater in a two-dimensional stepping-stone population than in one dimension (Fig. 2).

Gandon & Rousset (1999) recently studied dispersal in the same population structures but with non-overlapping generations and finite populations, reporting results consistent with ours. Inclusive fitness calculations in finite populations present special challenges. Gandon & Rousset (1999) and Rousset & Billiard (2000) formulate relatedness in terms of the probability genes are identical in state. An alternative identity by descent formulation for a model of altruism in patch and stepping-stone structured populations is found in Taylor & Day (2000) and Taylor et al. (2000).

At the centre of the analysis of dispersal is a tension between local competition and the cost of dispersal. Offspring which remain on their natal patch are likely to compete with sibs, while those which pay the cost of dispersal are more likely to compete with more distant relatives. Dispersal can be viewed as a kind of altruism because dispersers have a reduced chance of surviving to compete and non-dispersers benefit from reduced competition. Recently it was shown that increased survival promotes altruism in a patch-structured environment (Taylor & Irwin 2000) and our results show that a similar effect holds in lattice populations, at least for dispersal behaviour.

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APPENDIX

Computing relatedness coefficients in two dimensions is technically more complicated than in one dimension. The necessary calculations appeared in Weiss & Kimura (1965) and Comins (1982) but we have simplified them for our purposes. First we rewrite Eq. (14) using a partial fraction expansion, $\frac{1}{1-H^2} = \frac{1}{2} \left(\frac{1}{1-H} + \frac{1}{1+H} \right)$ and write the two terms with a convenient notation,

$$r_{j,k} = c \left(A_{j,k}(z_1) + (-1)^{j+k} A_{j,k}(z_2) \right) \quad (26)$$

where

$$A_{j,k}(z) = \frac{1}{(2\pi)^2 \hat{d}} \int_0^{2\pi} \int_0^{2\pi} \frac{\cos(j\theta_1) \cos(k\theta_2)}{z - \cos\theta_1 - \cos\theta_2} d\theta_1 d\theta_2$$

and

$$\begin{aligned} z_1 &= 2 + \frac{2\hat{\mu}}{\hat{d}} \\ z_2 &= 2 \left(\frac{2 - \hat{\mu}}{\hat{d}} - 1 \right). \end{aligned} \quad (27)$$

The factor $(-1)^{j+k}$ comes from the substitution $\theta = \hat{\theta} + \pi$ which introduces negative signs in the denominator and a factor of $\cos(j\pi) \cos(k\pi) = (-1)^{j+k}$.

We evaluate the $A_{j,k}(z)$ in two ways. If $j = k$ then we can simplify the integrals using special functions eventually obtaining forms involving elliptic integrals. If $j \neq k$ we use trigonometric identities to express the integrals in terms of $A_{j,j}(z)$.

On the diagonal $j = k$ we transform the denominator using $\frac{1}{z} = \int_0^\infty e^{-zt} dt$ which allows us to introduce Bessel functions with imaginary argument and Legendre functions of the second kind to get

$$A_{j,j}(z) = \frac{1}{\hat{d}} \int_0^\infty e^{-zt} I_j^2(t) dt = \frac{(-1)^n}{\hat{d}\pi i} Q_{j-1/2} \left(1 - \frac{z^2}{2} \right) \quad (28)$$

(Watson 1958). This can be written using elliptic integrals as

$$A_{0,0}(z) = \frac{2}{\pi z} K \left(\frac{2}{z} \right) \quad (29)$$

$$A_{1,1}(z) = \frac{1}{\pi} \left(z - \frac{2}{z} \right) K \left(\frac{2}{z} \right) - \frac{z}{\pi} E \left(\frac{2}{z} \right), \quad (30)$$

and $A_{j,j}(z)$ for $j > 1$ can be evaluated recursively

$$Q_{n+1/2}(-z) = \frac{2z}{2n+1} \left[\left(n - \frac{1}{2} \right) Q_{n-3/2}(-z) - 2n Q_{n-1/2}(-z) \right]. \quad (31)$$

Off-diagonal elements are evaluated with algebraic manipulations and trigonometric identities.

For example, the integrand in $A_{0,1}$ can be rewritten

$$\frac{\cos \theta_2}{z - \cos \theta_1 - \cos \theta_2} = -1 + \frac{z - \cos \theta_1}{z - \cos \theta_1 - \cos \theta_2}$$

so $A_{0,1} = -\frac{1}{2} + \frac{z}{2}A_{0,0}$. Similarly, $A_{0,2}$ can be rewritten using the identity $\cos 2\theta = 2\cos^2 \theta - 1$ and the manipulation used for $A_{0,1}$ giving

$$A_{0,2} = 2zA_{0,1} - 2A_{1,1} - A_{0,0}.$$

In the text, the arguments of the elliptic integrals are abbreviated as

$$\begin{aligned} a_1 &= \frac{2}{z_1} = \frac{\hat{d}}{\hat{d} + \hat{\mu}} \\ a_2 &= \frac{2}{z_2} = \frac{\hat{d}}{2 - \hat{d} - \hat{\mu}}. \end{aligned} \tag{32}$$

Table I.

Probability the winner of a site came from a site i units away p_i ; $i = 0$ means the winner was native, $i = 1$ means the winner was a neighbour, and $i = \infty$ means the winner was not related to the previous occupant. Several sites are one unit away, each is counted separately; in one dimension there are two ($N = 2$) and in two dimensions, four ($N = 4$). The dispersal rate is d , the probability of survival is s , and the cost of dispersal is k .

i	p_i	
	$k = 0, s = 0$	general case
0	$1 - d - \mu$	$1 - \hat{d} - \hat{\mu} = \frac{1 - (d + \mu)(1 - s + sk)}{1 - k(d + \mu)}$
1	$\frac{d}{N}$	$\frac{\hat{d}}{N} = \frac{d(1 - s)(1 - k)}{N(1 - k(d + \mu))}$
∞	μ	$\hat{\mu} = \frac{\mu(1 - s)(1 - k)}{1 - k(d + \mu)}$

Figure Captions

Figure 1.

Dispersal pattern in a two-dimensional stepping-stone population. The mutant's (black) deviant dispersal rate changes the number of competitors on its own site and the 4 nearest neighbours (grey). This affects the fitness of individuals born on all the sites shown. Each different class of site is labeled with its relatedness to the mutant.

Figure 2.

Evolutionarily stable dispersal rates. Starting from the top the lines correspond to the patch model ($N = 1$, solid), the 2-dimensional stepping-stone with four neighbours (dashed) and the 1-dimensional stepping-stone (dotted). Zero-cost dispersal (A) and $k = 0.1$ (B) are shown.



