

The evolution of dispersal in spatially varying environments

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ABSTRACT

We consider the evolution of dispersal in an environment that varies spatially but that is constant in time. We allow an age structure with dispersal possible in all life-stages. We suppose that demes are large enough that kin effects can be ignored. It has previously been shown that cost-free dispersal can persist over evolutionary time. However, several studies have shown that costly dispersal must in general be selected against. Here, we establish a fundamental result about stage-structured populations with stage-specific dispersal rates – that is, at evolutionary equilibrium, over each time step, the total reproductive value of the emigrants leaving each deme must equal the total reproductive value of the immigrants entering that deme. A simple consequence of this principle is that, if migration is restricted to a single stage – the same stage for all demes – then costly dispersal cannot evolve. Another corollary is that, with a ‘sequential’ age structure, over a complete life-cycle, the proportionate flow of genes out of a deme must equal the flow in. Finally, we present an example to show that dispersal may be evolutionarily stable, even when costly, if individuals can disperse more than once during their life-cycle.

Keywords: dispersal, dynamics, evolutionary stability, gene flow, spatial heterogeneity.

INTRODUCTION

Why disperse when dispersal is costly? This question has been asked many times and the discussion has centred around three main factors that may promote costly dispersal. The first of these requires kin effects: the cost to the disperser is offset by the increase in fitness, due to reduced competition, of relatives who are left behind (Hamilton and May, 1977; Motro, 1982, 1991; Frank, 1986; Taylor, 1988; Morris *et al.*, 2001). The second relies on environmental variation in both time and space (e.g. Levin and Paine, 1974; McPeck and Holt, 1992; Olivieri *et al.*, 1995). For example, stochastic variation in the carrying capacities of populations can result in selection for dispersal. Individuals are better off in populations with positive growth rates and should disperse from populations with negative growth rates. The third factor is environmental variation in space only, which appears more problematical. If the environment is constant over time, and if populations are large enough that kin effects can be ignored, can spatial heterogeneity support an evolutionarily stable dispersal pattern? This is the question we address here.

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Consider an assemblage of finite demes in a spatially variable but temporally constant terrain so that the conditions for survival or reproduction might be different from deme to deme but are constant in time. In each deme, consider a stage-structured population with the possibility of stage-specific dispersal. We will show that at evolutionary equilibrium rates of dispersal, the total reproductive value of the emigrants leaving each deme during each time step, must equal the total reproductive value of the immigrants entering that deme.

A simple corollary of this principle is that, if migration is restricted to a single stage – the same stage for all demes – then the number of emigrants who leave each deme must be equal to the number of immigrants who arrive. It follows from this that, by setting the sum of all the emigrants equal to the sum of all the immigrants, there can be no cost to dispersal. Thus a single bout of costly dispersal cannot be maintained at evolutionary equilibrium by spatial variation. Versions of this result have been obtained, for example, by Karlin and McGregor (1974), Hastings (1983), Holt (1985) and Lemel *et al.* (1997). McPeck and Holt (1992) looked at cost-free dispersal with a logistic model of population growth, and two habitats at carrying capacity. They obtained the result that, at evolutionary equilibrium, the number of immigrants into each habitat must equal the number of emigrants who leave. Their equilibrium was only neutrally stable in that the dispersal rates could drift.

Another corollary applies to ‘sequential’ life histories that consist of n stages, each with a single successor so that a complete life-cycle follows a sequence, stage 1, stage 2, stage 3, . . . stage n , stage 1, and so on. In this case, the proportion of the stage-1 genes that emigrate at some point during the life-cycle (or whose descendants emigrate) is equal to the proportion of the stage-1’ genes (one cycle later) that entered the deme at some stage during the cycle (possibly having left the deme and returned). Loosely put, the flow of genes out of a deme must equal the flow of genes in.

Finally, we provide an example of costly dispersal that is evolutionarily stable in an environment that varies in space but that is constant in time. The environment consists of two different habitats, one better suited for growth and the other better suited for reproduction. At equilibrium, some individuals in the growth phase of the life-cycle disperse to the prime growth habitat with dispersal in the opposite direction by individuals in the reproductive phase of the life-cycle.

THE MODEL

Consider an environment that consists of a finite number of discrete habitats, each supporting a single finite deme. These demes can be of variable size, although we assume that they are large enough that average within-deme relatedness can be set to zero and thus the effects of kin selection can be ignored.

Our aim is to determine the conditions for evolutionarily stable dispersal between demes. An important concept in our analysis is reproductive value. The reproductive value, v , of an individual in any deme at any stage will be its genetic contribution to a distant (limiting) future generation. Now, for this to make sense, we need to make some assumptions about future population size and structure and for this we need to assume that the population has attained an ecological equilibrium. We then look for a dispersal strategy that is at evolutionary equilibrium in the sense that a mutant individual with an altered dispersal strategy cannot increase its reproductive value. We assume that dispersal behaviour is determined by the genotype of the disperser.

Our population is both stage- and deme-structured with n stages (e.g. age classes) and N demes. We suppose that, during each time step, there is a phase of migration between demes followed by a stage-transition phase within each deme. In the migration phase, migration rates and costs are deme- and stage-specific and a stage i migrant who succeeds in finding a destination deme becomes a stage i individual in its new deme. Stage transitions within each deme k are determined by an $n \times n$ stage transition matrix \mathbf{A}_k whose entries a_{ijk} give the number of stage j ‘offspring’ of a stage i ‘parent’ in deme k . In the standard example of age structure, the a_{ijk} represent either survival probabilities or fecundities. The entries of \mathbf{A}_k will generally be density dependent. The main point to note is the dependence of \mathbf{A}_k on k – different demes can have different stage matrices. For example, one deme may have higher juvenile survival and lower adult fecundity than another.

We let

$$\mathbf{u} = (\mathbf{u}_1, \mathbf{u}_2, \dots, \mathbf{u}_N) = (u_{11}, u_{21}, \dots, u_{n1}, u_{12}, u_{22}, \dots, u_{n2}, \dots, u_{1N}, u_{2N}, \dots, u_{nN}) \quad (1)$$

be the column vector whose ik th entry, u_{ik} , is the total number of stage i individuals in deme k at the start of each time step. Then, the discrete time dynamics of the u_{ik} follow an equation of the form

$$\mathbf{u}' = \mathbf{W}\mathbf{u} \quad (2)$$

where the prime denotes numbers after one time step. The $nN \times nN$ transition matrix \mathbf{W} encapsulates all the migration and stage transition information. Its jk column tabulates the one time-step output of a stage j individual in deme k through migration, survival and/or fecundity. It can be written as the product of a stage matrix \mathbf{A} and a migration matrix \mathbf{M} as follows:

$$\mathbf{W} = \mathbf{A}\mathbf{M} = \begin{bmatrix} \mathbf{A}_1 & 0 & \dots & 0 \\ 0 & \mathbf{A}_2 & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \mathbf{A}_N \end{bmatrix} \begin{bmatrix} \mathbf{M}_{11} & \mathbf{M}_{12} & \dots & \mathbf{M}_{1N} \\ \mathbf{M}_{21} & \mathbf{M}_{22} & \dots & \mathbf{M}_{2N} \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{M}_{N1} & \mathbf{M}_{N2} & \dots & \mathbf{M}_{NN} \end{bmatrix} \quad (3)$$

where the blocks in the above matrices are $n \times n$. The matrix \mathbf{M}_{hk} specifies the migration pattern from deme k to deme h . Our assumption that individuals do not change stages during dispersal implies that \mathbf{M}_{hk} is diagonal:

$$\mathbf{M}_{hk} = \begin{bmatrix} m_{1h1k} & 0 & \dots & 0 \\ 0 & m_{2h2k} & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & m_{nhnk} \end{bmatrix} \quad (4)$$

Its entry m_{ihik} gives the proportion of the stage i population in deme k that is found in deme h after dispersal.

Our assumption of ecological equilibrium implies, from equation (2), that \mathbf{W} has a dominant eigenvalue equal to 1 with right eigenvector \mathbf{u} :

$$\mathbf{u} = \mathbf{W}\mathbf{u} \quad (5)$$

The corresponding left eigenvector is the vector $\mathbf{v} = (\mathbf{v}_1, \mathbf{v}_2, \dots, \mathbf{v}_N)$ of individual reproductive values in the equilibrium population. Here $\mathbf{v}_k = (v_{ik})$ is the vector of average reproductive value of a stage i individual in deme k at the beginning of a time step. The left eigenvector equation is:

$$\mathbf{v} = \mathbf{v}\mathbf{W} \tag{6}$$

Equation (6) tells us that the reproductive value v_{jk} of a stage j individual in deme k is equal to the total reproductive value of her next stage output in each deme: $v_{jk} = \sum_{ih} v_{ih} w_{ihjk}$.

In the following proposition, we assume that dispersal behaviour has reached an evolutionary equilibrium. By this we mean that an individual who disperses from a deme would not increase her reproductive value by staying at home, and an individual who stays at home would not increase her reproductive value by dispersing.

Proposition. Suppose that the population has reached an ecological equilibrium and that the dispersal behaviour from each deme at each stage is at evolutionary equilibrium and is not complete in the sense that m_{ikik} is never zero. Then the following must hold:

- (i) The reproductive value v_{jk} of a stage j individual in deme k is equal to the total reproductive value of her ‘offspring’ under the stage transition matrix \mathbf{A}_k . Technically, this tells us that \mathbf{v}_k is a left eigenvector of the matrix \mathbf{A}_k for the eigenvalue $\lambda = 1$.
- (ii) During each time step, the total reproductive value of the emigrants from deme k is equal to the total reproductive value of the immigrants into deme k .

Proof. (i) Consider an individual at stage j in deme k . If there are no stage j migrants from deme k , then (i) follows immediately from (6) since $w_{ihjk} = 0$ unless $h = k$ and $w_{ikjk} = a_{ijk}$. If there are stage j migrants from deme k , then the v_{jk} is the average of the reproductive value of those stage j individuals who disperse and those who remain at home. By our assumption of evolutionary equilibrium of dispersal, this is the average of two equal quantities, and thus v_{jk} is the conditional reproductive value of a stage j individual who remains at home. But this is equal to $\sum_i v_{ik} a_{ijk}$. In vector form, this means that

$$\mathbf{v}_k = \mathbf{v}_k \mathbf{A}_k \tag{7}$$

and this says that \mathbf{v} is a left eigenvector of \mathbf{A} for the eigenvalue $\lambda = 1$.

(ii) Let $\boldsymbol{\alpha}_k = (\alpha_{ik})$ be the vector of numbers of stage i individuals who emigrate from deme k during a single cycle $\alpha_{ik} = (1 - m_{ikik})u_{ik}$, and let $\boldsymbol{\beta}_k = (\beta_{ik})$ be the number of stage i individuals in deme k (after migration, before stage transition) who have immigrated into deme k during that cycle $\beta_{ik} = \sum_h m_{ikih} u_{ih}$. With this notation, the transition equation (2) can be written as

$$\mathbf{u}'_k = \mathbf{A}_k(\mathbf{u}_k - \boldsymbol{\alpha}_k + \boldsymbol{\beta}_k) \tag{8}$$

for each k .

Set $\mathbf{u}'_k = \mathbf{u}_k$ in (8), hit both sides with the reproductive value vector \mathbf{v}_k , and use (7):

$$\mathbf{v}_k \mathbf{u}_k = \mathbf{v}_k \mathbf{A}_k (\mathbf{u}_k - \boldsymbol{\alpha}_k + \boldsymbol{\beta}_k) = \mathbf{v}_k (\mathbf{u}_k - \boldsymbol{\alpha}_k + \boldsymbol{\beta}_k)$$

This implies that

$$\mathbf{v}_k \boldsymbol{\alpha}_k = \mathbf{v}_k \boldsymbol{\beta}_k \tag{9}$$

which gives us (ii).

Corollary 1. Suppose that migration is restricted to a single stage, the same stage for all demes. Then it can be at evolutionary equilibrium only if it is cost-free.

Proof. If only stage i individuals migrate, then (9) implies that $\alpha_{ik} = \beta_{ik}$ for each deme k . If we sum over all k , the total numbers of emigrants and immigrants are equal, and this implies there can be no mortality during migration.

Corollary 2. Suppose that each stage has a unique successor, so that the life-cycle follows a sequence, stage 1, stage 2, stage 3, . . . stage n , stage 1, and so on. Then the proportion of the stage-1 genes that emigrate at some point during the life-cycle (or whose descendents emigrate) is equal to the proportion of the stage-1' genes (one cycle later) that have entered the deme at some stage during the life-cycle (possibly having left the deme and returned).

Proof. Fasten attention on a fixed deme and drop the subscript k so that u_i is the number of individuals in the deme at the start of stage i , v_i is the reproductive value of each of these individuals, and α_i and β_i are the numbers of stage i individuals who emigrate from the deme and immigrate into the deme at stage i respectively. A consequence of our assumption that the life-cycle follows a sequence is that

$$v_{i+1}u_{i+1} = v_i(u_i - \alpha_i + \beta_i) \tag{10}$$

Indeed, by our assumption of evolutionary equilibrium, the $u_i - \alpha_i + \beta_i$ stage- i individuals in the deme after dispersal all have reproductive value v_i and the total reproductive value of their stage $i + 1$ 'offspring' is $v_{i+1}u_{i+1}$ and by (i) of the Proposition these must be equal. [Equation (10) also follows directly from (8) if we use the 'subdiagonal' form of \mathbf{A}_k .]

Now for each i , the proportion of the u_i individuals at the start of stage i who are still in the deme (or whose 'offspring' are still in the deme) at the start of stage $i + 1$ is

$$\frac{u_i - \alpha_i}{u_i} \tag{11}$$

Thus the proportion of the u_1 individuals at the start of stage 1 who are still in the deme (or whose 'offspring' are still in the deme) at the start of stage 1' (one cycle later) is the product of the above terms over all i from 1 to n . Similarly, for each i , the proportion of the u_{i+1} individuals at the start of stage $i + 1$ who were in the deme (or whose 'parents' were in the deme) at the start of stage i is

$$\frac{u_i - \alpha_i}{u_i - \alpha_i + \beta_i} = \frac{u_i - \alpha_i}{u_{i+1}} \frac{v_i}{v_{i+1}} \tag{12}$$

(using equation 10), and thus the proportion of the u_1 individuals at the start of stage 1' who were in the deme (or whose 'parents' were in the deme) at the start of stage 1 (one cycle ago) is the product of the above terms over all i from 1 to n . Now, since $u_{n+1} = u_1$ and $v_{n+1} = v_1$ (by ecological equilibrium), the products of the terms in (11) and (12) are the same and we have the result.

An example of an evolutionarily stable dispersal pattern

We now construct an example of an evolutionarily stable dispersal pattern with cost. To do so, it is necessary to include at least two stages of dispersal. We choose the simplest scenario, which involves dispersal between two demes with two stages. At evolutionary equilibrium, an individual that does not disperse must have the same reproductive value as one that does. Thus, since we have only two demes, it follows that, at evolutionary equilibrium, dispersal must be one-way at each stage. For simplicity, we consider a haploid, asexual organism. The two demes we work with have a similar life-history pattern with a juvenile and an adult stage, and a single bout of dispersal at each stage. In deme k , the probability that a juvenile survives to adulthood is given by the density-dependent function S_k , and the expected number of offspring per adult is given by the density-dependent function F_k . The idea is that, in the absence of dispersal, juvenile survival to adulthood is higher in deme 2, whereas adult fecundity is higher in deme 1. As a result, it is advantageous for juveniles to disperse from deme 1 to deme 2 and for adults to disperse from deme 2 to deme 1. For ease of notation, we denote these dispersal rates by d_1 (juveniles from deme 1 to deme 2) and d_2 (adults from deme 2 to deme 1), and we denote the deme k juvenile population sizes as $u_{1k} = J_k$ before migration and J'_k after migration, and the adult population size as $u_{2k} = A_k$ before migration and A'_k after migration. The configuration is shown in Fig. 1 and a numerical example is provided in Fig. 2.

Below we investigate the dynamic stability of the system, but first we examine the equilibrium conditions (5) and (6). At evolutionary equilibrium, it must be that the total reproductive value of the emigrants from deme k is equal to the total reproductive value of the immigrants into deme k . This gives us:

$$d_1 J_1 v_{11} = (1 - c_2) d_2 A_2 v_{21} \tag{13a}$$

$$d_2 A_2 v_{22} = (1 - c_1) d_1 J_1 v_{12} \tag{13b}$$

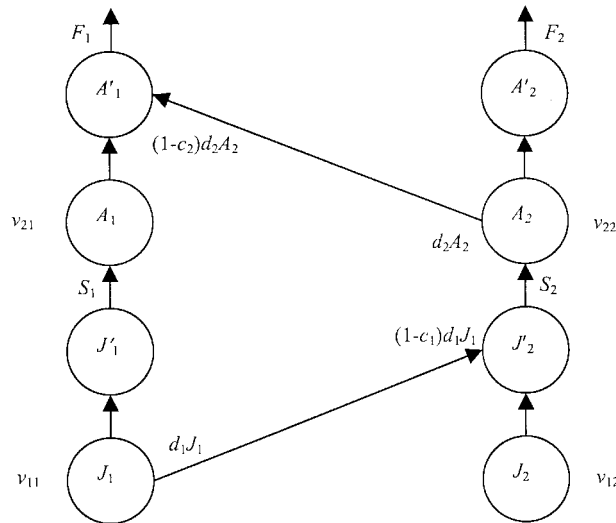


Fig. 1. Population size at different stages in deme 1 and deme 2 showing individual reproductive value v_{jk} at each stage.

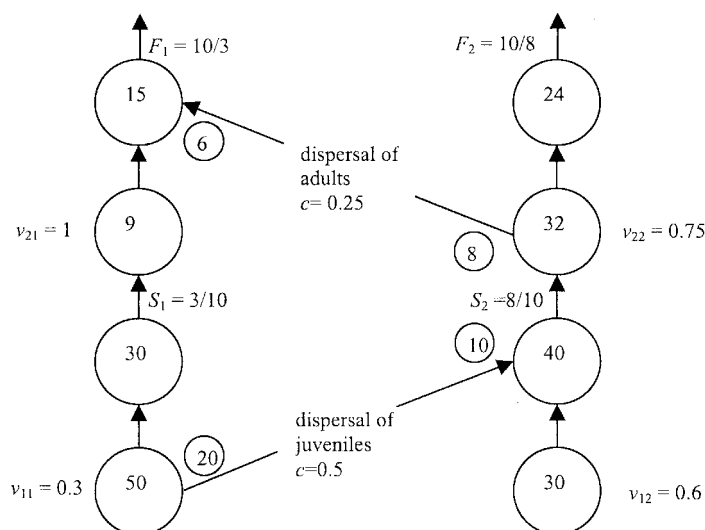


Fig. 2. A numerical example of a stable two-stage dispersal pattern. Numbers shown in the circles are population sizes. The dispersal rates are $d_1 = 0.4$ and $d_2 = 0.25$. The small circles at the beginning of the arrows represent the number of migrants leaving the population of origin, and the small circles at the end of the arrow represent the number of migrants that arrive at the destination population. Observe that these numbers illustrate our main results. The total reproductive value of those leaving deme 1 is $20(0.3) = 6$ and the total reproductive value of those entering deme 1 is $6(1.0) = 6$, giving us Proposition (ii). Also, we have the sequential life-cycle of Corollary 2 and we observe that $20/50 = 40\%$ of the genes of deme 1 leave as juveniles and $6/15 = 40\%$ of the adult genes of deme 1 have immigrated.

Also, at evolutionary equilibrium, $S_1 v_{21} = v_{11}$ and $S_2 v_{22} = v_{12}$ [by (7) and (16) below]. If we combine the two expressions from (13), we have that

$$S_2(1 - c_1)(1 - c_2) = S_1 \tag{14}$$

Note that there are two ways for a deme-1 juvenile to become a deme-1 adult – either to stay at home or to disperse twice – and condition (14) says that its survival must be the same along both paths. Using the symmetry of the population structure, we interchange 1 and 2 and S and F to get

$$F_2 = (1 - c_1)(1 - c_2)F_1 \tag{15}$$

This says that, at evolutionary equilibrium, the fecundity of a deme-2 adult is the same whether it remains in deme 2 to breed or disperses to deme 1 with all its offspring migrating back to deme 2 as juveniles.

Evolutionary dynamics

There are a number of different formulations of evolutionary dynamics with two interacting traits. The standard approach we use here (Abrams *et al.*, 1993) considers a rare mutant strategy (d_1, d_2) in an essentially monomorphic (d_1^*, d_2^*) population, obtains a

fitness function and constructs the trait dynamic from the fitness gradient. The stability conditions are then obtained by requiring the Jacobian matrix of the system to be a stability matrix.

We begin by writing the matrices **A** and **M** of (3):

$$\begin{aligned}
 \mathbf{A}_1 &= \begin{bmatrix} 0 & F_1 \\ S_1 & 0 \end{bmatrix} & \mathbf{A}_2 &= \begin{bmatrix} 0 & F_2 \\ S_2 & 0 \end{bmatrix} \\
 \mathbf{M} &= \begin{bmatrix} 1 - d_1 & 0 & 0 & 0 \\ 0 & 1 & 0 & d_2(1 - c_2) \\ d_1(1 - c_1) & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 - d_2 \end{bmatrix} \\
 \mathbf{W} = \mathbf{AM} &= \begin{bmatrix} 0 & F_1 & 0 & d_2(1 - c_2)F_1 \\ (1 - d_1)S_1 & 0 & 0 & 0 \\ 0 & 0 & 0 & (1 - d_2)F_2 \\ d_1(1 - c_1)S_2 & 0 & S_2 & 0 \end{bmatrix} \tag{16}
 \end{aligned}$$

Here, we assume that survival S_k and fecundity F_k depend only on the d_i^* , but we have not displayed this dependence. The mutant's fitness is given by the dominant eigenvalue of **W**, $\lambda(d_1, d_2, d_1^*, d_2^*)$ (Metz *et al.*, 1992), and the dynamic system by

$$\begin{bmatrix} \frac{dd_1^*}{dt} \\ \frac{dd_2^*}{dt} \end{bmatrix} = \mathbf{G} \begin{bmatrix} \frac{\partial \lambda}{\partial d_1} \\ \frac{\partial \lambda}{\partial d_2} \end{bmatrix}^* \tag{17}$$

(Abrams *et al.*, 1993), where **G** is the additive covariance matrix between the dispersal rates, and the partial derivatives of W are evaluated at $d_i = d_i^*$. Our argument requires that the additive covariance between d_1 and d_2 is small compared with the additive variance in each trait.

In the Appendix, we show that equations (14) and (13b) determine a unique dynamically stable evolutionary equilibrium (d_1^*, d_2^*) provided the S_k are negatively density dependent (an increase in J'_k causes a decrease in S_k). In fact, for the stability of this equilibrium, all we need is that the quotient S_2/S_1 is a decreasing function of d_1 . Alternatively, using the symmetry of life-cycle as described above, one can show that a stable evolutionary equilibrium is determined by equations (15) and (13a).

This stability result has a simple heuristic argument. Suppose that the S_k are negatively density dependent. Consider the effect of increasing the juvenile dispersal rate d_1 (Fig. 1). This will decrease the juvenile population J'_1 in deme 1 and increase the juvenile population J'_2 in deme 2. This results in an increase in S_1 , increasing the reproductive value of a deme-1 juvenile, and a decrease in S_2 , decreasing the reproductive value of a deme-2 juvenile. This makes juvenile dispersal from deme 1 less advantageous, and the dispersal rate should decrease. Similarly, if the adult dispersal rate d_2 is increased, this will decrease the adult population A'_2 in deme 2 and increase the adult population A'_1 in deme 1. Since the starting populations J_k are fixed, the fecundity and hence the reproductive value of a deme-2 adult

will increase, and the fecundity and hence the reproductive value of a deme-1 adult will decrease. This makes adult dispersal from deme 2 less advantageous, and the dispersal rate should decrease. In summary, juvenile dispersal is stabilized by density-dependent survival rates, and adult dispersal is stabilized by density-dependent fecundity rates.

So far we have only considered interior equilibria in which we have partial dispersal. However, under our scenario it is possible that dispersal can be selected against or, alternatively, that there is selection for complete juvenile dispersal. Suppose the cost of dispersal is high enough (at one stage or the other) that it cannot be offset by the increase in juvenile survival or adult fecundity. Our intuition tells us that, in such circumstances, dispersal should not evolve. And, of course, following our first result, if there is no dispersal at one stage there can be none at the other. In fact, we show in the Appendix that $(0,0)$ will be a stable point provided that $S_1 \geq (1 - c_1)(1 - c_2)S_2$ at this point. Second, we look at the cases $d_i = 1$. First, we expect a stable point with $d_1 = 1$ if at this point S_1 is small enough compared to S_2 and the costs of dispersal are small. In fact, we show in the Appendix that a sufficient condition for this is that $S_1 < (1 - c_1)(1 - c_2)S_2$ when $d_1 = 1$. On the other hand, because we have fixed the values J_k of the starting populations, we never expect a stable point with $d_2 = 1$, because a small number of non-dispersing individuals in A_2 would have very high reproductive value.

DISCUSSION

Our results here concern a large randomly mating population in an environment that is spatially heterogeneous but temporally constant. We suppose the population is broken up into demes, among which there might be some dispersal. We show that, at evolutionary equilibrium, the total reproductive value of the emigrants leaving a given deme must equal the total reproductive value of the immigrants entering that deme. This result should be interpreted as a gene flow result. However, it is more complicated than just saying that the flow of genes into a deme must be equal to the flow of genes out of that deme. Rather, it says that the genetic contribution to a distant (limiting) future generation of those individuals that emigrate from a given deme must equal the contribution to a distant (limiting) future generation of those individuals that immigrate to that deme.

As a corollary, we show that, if there is only one bout of dispersal in each generation, then dispersal can occur only if it has no cost. Now, one must be careful when interpreting our notion of cost. Here, cost is simply the reduction in an individual's reproductive value measured after dispersal. It is possible to partition cost into separate components measuring survival and competitive ability. For example, consider the case where a disperser survives with probability s and has competitive weighting r_k relative to a native of the k th deme, so that its reproductive value measured after dispersal to the k th deme is $sr_k v_k$ (Lemel *et al.*, 1997). Then, our result says that, at evolutionary equilibrium, $sr_k = 1$. Thus if there is a survival cost ($0 < s < 1$), then there will be selection for philopatry unless immigrants have a higher competitive weighting than natives. In nature, this might occur when male immigrants are unlike natives and, as a result, are chosen preferentially by females, but in most cases we expect immigrants to have an equal or lesser competitive weighting. Thus, at evolutionary equilibrium, we can have a single bout of dispersal per cycle only when immigrants have equal competitive weighting and guaranteed survival ($s = 1$). And, in this case, dispersal can have no effect on deme size in the sense that, in each deme, the number of immigrants must equal the number of emigrants.

It is important to note the generality of this result. It assumes only that the environment is at ecological equilibrium, that there is only a single bout of dispersal per cycle and that immigrants and residents are indistinguishable. We make no assumptions about the dispersal pattern or environmental landscape; dispersal may be either passive or directed.

For life histories that consist of n stages, each with a single successor so that the life-cycle follows a sequence, stage 1, stage 2, stage 3, . . . stage n , stage 1, and so on, we have a stronger result – the proportion of genetic material that emigrates from the deme during a complete cycle (including any genes that might emigrate but then return) must equal the proportion of the genetic material at the end of the cycle that has immigrated to the deme at some point during the cycle.

If dispersal is allowed at more than one stage, then costly dispersal can exist and be evolutionarily stable. The idea is simple enough and can be viewed as a type of optimal habitat use. If the life-history parameters differ among demes in such a way that at certain stages different demes have different individual reproductive value, and if these differences are great enough (with respect to the dispersal cost), there will be selective pressure for individuals to move to a deme with a higher reproductive value during that life-history stage. Under density-dependent fitness, this movement will be self-damping and a stable equilibrium will be attained. This sounds plausible enough, but can it actually work? We demonstrate that it can by constructing an example of two-staged dispersal between two demes. In one deme juvenile survival is much higher than in the other and this leads to juvenile migration. This raises the size of the adult population in the ‘receiving’ deme and thus lowers its individual fecundity, and this prompts a migration of adults in the direction opposite to the juvenile migration.

Holt and Barfield (2000) examine the relationship between the ideal free distribution and the evolution of dispersal. They show that, for temporally constant environments with cost-free dispersal, fitness is equalized across space such that, at evolutionary equilibrium, all individuals have a fitness of 1. So how do the ideas of ideal free distribution relate to our gene flow result for temporally constant environments? Typically, we think of a population as being ideal-free distributed when individual fitness is equalized across space (see Fretwell and Lucas, 1969). If we define the dominant eigenvalue, λ_k , of the stage transition matrix \mathbf{A}_k as a measure of overall fitness in deme k , then our theorem says that, at evolutionary equilibrium, the overall fitness of deme k is unity (i.e. from equation 7, $\lambda_k = 1$). In other words, an individual that remains in its native habitat for its entire life has fitness equal to 1. Now, since at evolutionary equilibrium a non-disperser and disperser must have equal fitness, it follows that, at evolutionary equilibrium, an individual’s fitness is 1 regardless of its birthplace or dispersal pattern. Thus, the set of evolutionarily stable dispersal strategies results in an ideal free distribution with fitness equalized across space. The converse does not hold. The presence of an ideal free distribution does not imply the presence of a set of evolutionarily stable dispersal strategies. Indeed, philopatry always produces an ideal free distribution but, as we have demonstrated, philopatry need not be evolutionarily stable.

Much attention has recently focused on source–sink population dynamics. Specifically, there is growing literature addressing whether dispersal from source habitats to sink habitats is adaptive (e.g. Pulliam, 1988; Watkinson and Sutherland, 1995; Morris *et al.*, 2001). Several authors have already noted that, for dispersal from source habitats to sink habitats to be evolutionarily stable, there must be significant migration from sinks to sources (Morris, 1991; Wilson, 2001). In fact, our result shows that the reproductive value of the genetic material that has immigrated to the source in one generation must be equal to the

reproductive value of genetic material that has left the source during that generation. Again, as a corollary, we have that if there is only a single bout of dispersal per generation, and if immigrants and natives are indistinguishable after dispersal, then dispersal from source habitats to sink habitats will be selected against. If dispersal is undirected, then the mere presence of a sink habitat will result in selection for philopatry in all source habitats. The possibility of accidentally ending up in a sink habitat acts as a cost of dispersal and this prevents dispersal at evolutionary equilibrium.

Can dispersal from source habitats to sink habitats be adaptive when the life-cycle consists of two or more distinct life-stages, each with a distinct dispersal episode? Consider our example of two-stage dispersal presented above. Now suppose that, in habitat 1, juvenile survival to adulthood is low and adult fecundity is high, whereas in habitat 2 juvenile survival to adulthood is high but the habitat lacks the necessary resources for successful reproduction and thus adult fecundity is identically zero (that is, $J_2 = 0$). Here we have habitat 1 acting as a potential source and habitat 2 acting as a sink in the sense that the habitat cannot support a population in the absence of dispersal. At evolutionary equilibrium, juvenile dispersal from source to sink is observed as a result of the higher rate of juvenile survival present in the sink. Now, since adult fecundity in the sink habitat is zero, then at any time the sink population consists entirely of immigrants. Thus we observe all adults dispersing from the sink to the source. The end result is that the sink habitat is maintained through dispersal from the source to the sink. The key idea here is that individuals should make optimal use of all habitats. If the sink habitat is suited for a particular life-history stage of a given organism, then there should be migration to the sink during that life-history stage.

Note that the idea of optimal habitat use can be extended to consider the evolution of seasonal migration among habitats. Again consider our example. We observe that, if the disparity between the two habitats is large at a certain time, the corresponding dispersal bout might be complete. Now, suppose that adult and juvenile dispersal occur at distinct times during the year, say adult dispersal in the spring and juvenile dispersal in the fall. Suppose that juvenile survival is zero in one of the habitats and adult fecundity is zero in the other. Then complete adult dispersal is observed in the spring, followed by reproduction and the subsequent death of adults. Complete juvenile dispersal is then observed in the fall. The population can only exist if it moves back and forth between the two habitats at different times of the season. This pattern is of particular interest because of its similarity to that of large-scale seasonal migration observed in many natural populations. Seasonal migration has typically been differentiated from dispersal because it involves the movement of a complete population between two habitats. However, our model suggests that seasonal migration may evolve as a result of the same selective pressures that produce dispersal among demes.

Finally, a word about stability. The standard ESS treatment of continuous characters (Eshel, 1983; Taylor, 1989; Christiansen, 1991) considers two aspects: in the first (evolutionary stability, ES), the population strategy is fixed and we look at the effect of changing the mutant strategy; in the second (convergence stability, CS), we consider how varying the population-wide strategy affects the fitness of different mutant strategies. In cases in which fitness depends on individual strategy and the *average* population strategy, the first can be thought of as changing the mutant *strategy* and the second as changing the mutant *numbers*. In cases such as the model of this paper, when the strategy represents a probability of one action or another, these alternatives exhibit a type of linearity – 100 mutants with a

strategy deviation of δ has exactly the same effect as 50 mutants with a deviation of 2δ . In such a case, the ES condition is often neutral (as it is here) and the CS condition tells the story (Abrams *et al.*, 1993). That's a question of the stability of the dynamic system (17), and that's the notion of stability we have pursued here.

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APPENDIX

If we reorder the vectors \mathbf{u} and \mathbf{v} so that $\mathbf{u} = (J_1, J_2, A_1, A_2)$ and $\mathbf{v} = (v_{11}, v_{12}, v_{21}, v_{22})$, then we can rewrite \mathbf{W} in (16) in the form:

$$\mathbf{W} = \begin{bmatrix} 0 & 0 & F_1 & d_2(1-c_2)F_1 \\ 0 & 0 & 0 & (1-d_2)F_2 \\ (1-d_1)S_1 & 0 & 0 & 0 \\ d_1(1-c_1)S_2 & S_2 & 0 & 0 \end{bmatrix} \quad (\text{A1})$$

Evolutionary equilibrium

Referring to the dynamical system (17), if \mathbf{G} is non-singular (and we assume it is), then at evolutionary equilibrium the partial derivatives $\partial\lambda/\partial d_i|_*$ must equal zero.

In practice, it is difficult to solve for $\lambda(d_1, d_2, d_1^*, d_2^*)$. However, it is possible to solve for the partial derivatives making use of the corresponding right and left eigenvectors of the dominant eigenvalue $\lambda = 1$. We use the two-stage transition matrix \mathbf{W}^2 for our analysis of (A1). We have that $\mathbf{u}(\mathbf{W}^2 - \lambda^2)\mathbf{v} = 0$. Differentiating both sides with respect to d_i and then evaluating at $d_i = d_i^*$ gives:

$$\mathbf{v} \left(\frac{\partial \mathbf{W}^2}{\partial d_i} \Big|_* - \frac{\partial \lambda^2}{\partial d_i} \Big|_* \right) \mathbf{u} = 0 \quad (\text{A2})$$

At evolutionary equilibrium, $\partial\lambda/\partial d_i|_* = 0$ and we must have that:

$$\mathbf{v} \frac{\partial \mathbf{W}^2}{\partial d_1} \Big|_* \mathbf{u} = 2J_1[(1-c_1)v_{12} - S_1v_{21}] = 0 \quad (\text{A3})$$

and

$$\mathbf{v} \frac{\partial \mathbf{W}^2}{\partial d_2} \Big|_* \mathbf{u} = 2A_2[(1-c_2)v_{21} - F_2v_{12}] = 0 \quad (\text{A4})$$

Reproductive value

We now calculate reproductive value. The vector of individual reproductive values is given by the dominant left eigenvector of the transition matrix \mathbf{W} . Here we first calculate the *class* reproductive value r_{jk} of the j th class of deme k , and then derive the *individual* reproductive value v_{jk} from these. It is convenient to define e_2 as the proportion of the adult class of deme 2 made up from the juvenile class of deme 1 and e_1 as the proportion of the juvenile class of deme 1 made up from (offspring of) the adult class of deme 2. Then

$$e_1 = \frac{d_2(1-c_2)A_2}{A'_1}$$

and

$$e_2 = \frac{d_1(1-c_1)J_1}{J'_2}$$

and Corollary 2 tells us that, at evolutionary equilibrium, $e_k^* = d_k^*$.

The equilibrium equations for class reproductive value are:

$$\begin{aligned} r_{11} &= r_{21} + e_2 r_{22} \\ r_{21} &= (1 - e_1) r_{11} \\ r_{12} &= (1 - e_2) r_{22} \\ r_{22} &= r_{12} + e_1 r_{11} \end{aligned} \tag{A5}$$

For example, the first equation writes the total value of deme-1 juveniles as the sum of the total values of their two possible destinations: adults in deme 1 and adults in deme 2. Substituting the last expression of (A5) into the second last expression and simplifying gives:

$$r_{12} = \frac{(1 - e_2)e_1}{e_2} \quad r_{11} = \frac{J_2}{J_1 d_1 (1 - c_1)} \frac{A_2 d_2 (1 - c_2)}{A'_1} r_{11}$$

Now, let $r_{11} = A'_1 (1 - c_1) d_1 J_1$ and $r_{12} = J_2 (1 - c_2) d_2 A_2$, then $r_{21} = A_1 (1 - c_1) d_1 J_1$ and $r_{22} = J'_2 (1 - c_2) d_2 A_2$. Finally, the relative values of individual reproductive values are obtained from these by dividing by the class size:

$$\begin{aligned} v_{11} &= A'_1 d_1^* (1 - c_1) \\ v_{21} &= (1 - c_1) J_1 d_1^* \\ v_{12} &= A_2 d_2^* (1 - c_2) \\ v_{22} &= J'_2 (1 - c_2) d_2^* \end{aligned} \tag{A6}$$

where the asterisk emphasizes that all this is at evolutionary equilibrium.

Evolutionary stability

We now examine the stability of the interior equilibrium. For notational simplicity, we will write $\lambda_i = d\lambda/dd_i|_*$. The convergence stability (Eshel, 1983; Christiansen, 1991) conditions are obtained by requiring the Jacobian matrix

$$\mathbf{J} = \begin{bmatrix} \frac{\partial \lambda_1}{\partial d_1^*} & \frac{\partial \lambda_2}{\partial d_1^*} \\ \frac{\partial \lambda_1}{\partial d_2^*} & \frac{\partial \lambda_2}{\partial d_2^*} \end{bmatrix}_* \tag{A7}$$

to be a stability matrix, and this will hold if the trace of \mathbf{J} is less than 0 and the determinant of \mathbf{J} is greater than zero (Edelstein-Keshet, 1988, p. 142). Let $W_i = \mathbf{v} \cdot \partial \mathbf{W}^2 / \partial d_i \mathbf{u}$. From (A2) we have that, at evolutionary equilibrium, $W_i = \mathbf{v}(\partial \lambda^2 / \partial d_i) \mathbf{u} = \mathbf{v}(2\lambda \lambda_i) \mathbf{u}$. Differentiate:

$$\left. \frac{\partial W_i}{\partial d_j^*} \right|_* = \left. \frac{\partial \mathbf{v}}{\partial d_j^*} \right|_* (2\lambda\lambda_i)\mathbf{u} - \mathbf{v} \left(2\lambda \left. \frac{\partial \lambda_i}{\partial d_j^*} \right|_* \right) \mathbf{u} - \mathbf{v} (2\lambda\lambda_i) \left. \frac{\partial \mathbf{u}}{\partial d_j^*} \right|_*$$

Since at evolutionary equilibrium $\lambda_i^* = 0$, it follows that

$$\left. \frac{\partial \lambda_i}{\partial d_j^*} \right|_* = \frac{1}{\mathbf{v} \cdot \mathbf{u}} \left. \frac{\partial W_i}{\partial d_j^*} \right|_*$$

Let

$$\mathbf{D} = \begin{bmatrix} \left. \frac{\partial W_1}{\partial d_1^*} \right|_* & \left. \frac{\partial W_2}{\partial d_1^*} \right|_* \\ \left. \frac{\partial W_1}{\partial d_2^*} \right|_* & \left. \frac{\partial W_2}{\partial d_2^*} \right|_* \end{bmatrix}$$

Then $\mathbf{J} = (1/\mathbf{v} \cdot \mathbf{u}) \mathbf{D}$ and the dynamical system (17) is stable if the trace of $\mathbf{D} < 0$ and the determinant of $\mathbf{D} > 0$. We now show that this is true.

We begin with the substitution of the appropriate reproductive values into (A3) and (A4), noting that $A_2 = S_2 J_2'$ and that $J_1 = F_1 A_1'$. This gives us

$$W_1 = J_1 J_2' \left[S_2(1 - c_2)(1 - c_1)d_2^* - \frac{S_1(1 - c_1)J_1 d_1^*}{J_2'} \right] \tag{A8}$$

and

$$W_2 = A_2 A_1' \left[F_1(1 - c_2)(1 - c_1)d_1^* - \frac{F_2(1 - c_2)d_2^* A_2}{A_1'} \right] \tag{A9}$$

from which we now obtain the entries of the matrix \mathbf{D} . Again, we introduce another useful piece of notation. Let $Q = S_2/S_1$, then (A8) can be rewritten as:

$$W_1 = S_1 J_1 J_2' \left[(1 - c_1)(1 - c_2)d_2^* Q - \frac{(1 - c_1)J_1 d_1^*}{J_2'} \right]$$

Differentiating with respect to d_1^* and evaluating at evolutionary equilibrium, (d_1^*, d_2^*) , gives

$$\left. \frac{\partial W_1}{\partial d_1^*} \right|_* = S_1 J_1 J_2' \left[(1 - c_1)(1 - c_2)Q'd_2^* - \frac{(1 - c_1)J_1 J_2'}{J_2'^2} \right] \tag{A10}$$

In this calculation, we use the fact that the expression in the square brackets in the above formula for W_1 is zero at equilibrium, and that the derivative of J_2' is $(1 - c_1)d_1^*$. Similarly,

$$\left. \frac{\partial W_1}{\partial d_2^*} \right|_* = S_1 J_1 (1 - c_1)(1 - c_2)QJ_2' = S_1 J_1 J_2' \tag{A11}$$

since $(1 - c_1)(1 - c_2)Q = 1$. Because $J_1 = F_1 A_1'$, $A_2 = S_2 J_2'$ and $J_2 = F_2 A_2 (1 - d_2)$, we can rewrite (A9) as:

$$W_2 = S_2 J_2 \left[(1 - c_1)(1 - c_2) J_1 d_1^* - \frac{(1 - c_2) J_2 d_2^*}{(1 - d_2^*)} \right]$$

A similar calculation to the above gives

$$\left. \frac{\partial W_2}{\partial d_1^*} \right|_* = S_2(1 - c_1)(1 - c_2) J_1 J_2' = S_1 J_1 J_2' \tag{A12}$$

using (14). Finally,

$$\left. \frac{\partial W_2}{\partial d_2^*} \right|_* = -S_2 J_2' \frac{(1 - c_2) J_2}{(1 - d_2^*)^2}$$

and since (Corollary 2) $1 - d_2^* = 1 - c_2^* = J_2/J_2'$, we can write

$$\left. \frac{\partial W_2}{\partial d_2^*} \right|_* = -\frac{S_2(1 - c_2) J_2'^3}{J_2} \tag{A13}$$

It is easy to verify that when $Q' < 0$ then the trace of $\mathbf{D} < 0$. We now show that the determinant of $\mathbf{D} > 0$ if, and only if, $Q' < 0$. By substitution we have

$$\text{Det } \mathbf{J} = -S_1 J_1 J_2' \left[(1 - c_1)(1 - c_2) Q' d_2^* - \frac{(1 - c_1) J_1 J_2}{J_2'^2} \right] \frac{S_2(1 - c_2) J_2'^3}{J_2} - S_1^2 J_1^2 J_2'^2$$

Using the equilibrium condition (14) we have

$$\text{Det } \mathbf{J} = -S_1^2 J_1 J_2' \left[\frac{(1 - c_2) Q' d_2^* J_2'^3}{J_2} - J_1 J_2' \right] - S_1^2 J_1^2 J_2'^2$$

Finally, with some rearrangement we have

$$\text{Det } \mathbf{J} = -\frac{(1 - c_2) S_1^2 J_1 J_2'^4 Q' d_2^*}{J_2} \tag{A14}$$

and it follows that the determinant of $\mathbf{J} > 0$ if, and only if, $Q' < 0$.

The stability argument has assumed that \mathbf{G} is the identity matrix. A close look at the inequalities will show they continue to hold if \mathbf{G} is diagonal. Since the inequalities are strict, they will also continue to hold for matrices \mathbf{G} that are close to diagonal and, therefore, they will hold if the covariance between d_1 and d_2 is small.

Finally, we consider points that fall along the boundary of the dispersal space $(d_1^*, d_2^*) \in [0, 1] \times [0, 1]$, and again we assume that \mathbf{G} is the identity matrix. First, recall that if either $d_i^* = 0$, they must both be zero and consider the point $d_1^* = d_2^* = 0$. We show that this will be stable provided that $S_1 > (1 - c_1) S_2(1 - c_2)$ at this point. In (d_1^*, d_2^*) phase space, draw the curve $e_2^* = d_2^*$. Since $e_2^* = J_1 b_1 d_1^* / J_2'$, this curve will pass through the origin and the tangent at this point will have slope $J_1 b_1 / J_2$. Take any point (a_1, a_2) on that curve near the origin and consider the box $0 \leq d_1^* \leq a_1, 0 \leq d_2^* \leq a_2$. We assert that the dynamical system (17) cannot leave this box, and from the boundary always moves inside. Indeed, on the top boundary $e_2^* < d_2^*$ and from (A9) $W_2 < 0$ and the trajectory points down into the box, and on the right boundary $e_2^* > d_2^*$ and from (A8) $W_1 < 0$ and the trajectory points left into the box. And from the top right corner (a_1, a_2) , the trajectory points left along the top boundary

and thence moves down into the box. This is enough to at least establish the neutral stability of the point.

Now we examine the line $d_1^* = 1$ and show that, if $S_1 < (1 - c_1)S_2(1 - c_2)$ on this line, then the point $(1, d_2^*)$ determined by the condition $d_2^* = e_2^*$ will be a stable equilibrium. Indeed, from (A9) we get that $W_2 = 0$ [use equation (15) and the fact $e_1^* = 1$] and from (A13) $\partial W_2 / \partial d_2^* < 0$. Second, from (A8) we get that $W_1 > 0$, noting that the last term in the brackets in that expression can be written $S_1 e_2^*$ and that establishes the stability of the point.

Finally, we argue that there can never be a stable point with $d_2^* = 1$. Indeed, in this case, $A_2' = 0$ and since we fix J_2 as a constant, a mutant with $d_2 < 1$ will have arbitrarily high reproductive value and will invade.

