# 6

# *On the relationship between the ideal free distribution and the evolution of dispersal*

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## Abstract

The ideal free distribution (IFD), first proposed by Fretwell and Lucas, describes how a pattern, the distribution of abundances and fitnesses across habitats, emerges from a process: evolution moulding the habitat selection strategies of individuals. Key ecological mechanisms assumed in the IFD include localized density dependence and the freedom of individuals to choose habitats so as to maximise fitness. The central prediction of the IFD is that fitnesses are equilibrated across space. Models for the evolution of dispersal in spatially heterogeneous but temporally constant environments also often predict fitness equilibration. Given combined temporal and spatial heterogeneity, there is no simple characterisation of fitness. Nonetheless, numerical studies suggest that the evolution of dispersal can produce a distribution characterised by approximate equilibration of local fitness measures (e.g., geometric means of local reproductive success, spatial reproductive values) among habitats, at least as a useful rule-of-thumb. However, there are clear counter-examples, particularly involving the use of sink habitats, or forces such as kin competition. The concept of fitness equilibration represented by the IFD describes a widespread but by no means universal outcome of the evolution of dispersal in heterogeneous environments.

**Keywords:** ideal free habitat selection, evolution in variable environments, spatial reproductive value

## Introduction

Almost three decades ago, Steve Fretwell and Henry Lucas developed a set of models to predict animal distributions, based upon the premise that organisms select habitats to maximise fitness (Fretwell and Lucas 1970; Fretwell 1972). Their simplest model led to a pattern they dubbed the 'ideal free distribution' (IFD). Roughly speaking, at an IFD individuals in different habitats have equal average fitness. Ideal free theory occupies a central position in behavioural ecology (Rosenzweig 1985; Brown 1998; Fryxell and Lundberg 1998). But what does it have to do with dispersal? The topic of dispersal includes (though not exclusively) trans-generational spatial flows among habitats. In contrast, habitat selection theory focuses more closely on within-generation patterns of habitat utilisation. Our aim is to highlight conceptual linkages between the IFD and the evolutionary theory of dispersal. We use numerical studies to suggest that the core conclusion of ideal free theory, namely that organisms should be distributed such that fitnesses are equilibrated across space, at times pertains to the evolution of dispersal.

However, in many reasonable circumstances, the evolution of dispersal does not lead to an IFD.

## A summary of ideal free habitat selection theory

It is useful to summarise the basic ideal free model (for reviews of habitat selection theory see Rosenzweig 1985, 1991; Kacelnik *et al.* 1992; Tregenza 1995; Morris 1994; Brown 1998). For simplicity, consider an environment with two habitats. Fretwell (1972) assumed that habitat 'suitability' for an individual would decrease with the abundance of conspecifics in each habitat. By 'suitability', Fretwell meant something closely related to individual fitness, as suggested by this quote: 'The suitability of a habitat is a reflection of the average genetic contribution of resident adults to the next generation and must be closely related to the average lifetime production of reproducing offspring in the habitat' (Fretwell 1972, p. 106).

Fitness is most easily characterised in species with the simple life history of discrete, synchronised generations. We assume such a life history and concentrate upon natal dispersal. As noted by Michod (1999, p. 50), it is crucial to use absolute fitnesses when concerned with evolution in spatially structured populations. We use 'local fitness' to denote absolute fitness or selective value (combining viability and fecundity into expected number of gametes produced by a newborn zygote; Roughgarden 1979) of an individual residing in a given habitat. Let $F_i(N_i)$ be local fitness in habitat $i$, given $N_i$ conspecific individuals there, and assume $F_i$ declines with $N_i$ (see Stamps, chapter 16, for implications of positive density dependence). Carrying capacity of habitat $i$ is the local population size $K_i > 0$ at which $F_i(K_i) = 1$; if no $K_i$ exists, the habitat is an intrinsic sink (Holt 1985; Pulliam 1988), where the population cannot persist without immigration. Given the behavioural assumptions that individuals are identical, perfectly assess current habitat suitability, move without cost, and do not interfere with one another's movement, ideal free theory predicts that: (i) as long as $F_1 > F_2$, individuals in habitat 2 should leave and reside in habitat 1; (ii) if both habitats are occupied, local densities should thus be adjusted such that $F_1 = F_2$ (Fretwell 1972, pp. 86–87). If the system reaches demographic equilibrium, at which average fitness equals unity, density in each habitat must match the carrying capacity of that habitat (Holt 1985). At a demographic equilibrium, no sink habitats should be occupied in an IFD. The statement that average local fitnesses are equilibrated across space at an evolutionary equilibrium appears to be the most general statement of what is meant by an 'ideal free *distribution*'. This is to be distinguished from assuming that organisms show ideal free *behaviour*, those simplifying assumptions made by Fretwell and Lucas in their original model (for a list of these assumptions, see Tregenza 1995, p. 285). If the ideal free assumptions are violated, populations of course may exhibit distributions for which local fitnesses are not spatially equilibrated. Stamps (chapter 16) points out many ways in which organisms may be neither ideal in their habitat selection, nor free in their dispersal.

There is not a one-to-one correspondence between ideal free behaviour and an ideal free distribution. Individual organisms may not be ideal or free at the level of individual behavioural traits and decision rules, yet populations may nonetheless converge on an

IFD (Houston and McNamara 1988). Hugie and Grand (1998) note that, even with unequal competitors and non-ideal free movements, the original IFD model 'may be sufficient to approximate the distributions of animals'. Conversely, organisms may not have an IFD despite having appropriate behaviours, for instance due to unstable resource–consumer interactions (Abrams 1999). Another important complication is that the local fitness measure used by Fretwell and Lucas may inadequately predict evolution in heterogeneous environments. For instance, Brown (1998) shows that, if individuals allocate time between habitats differing in risk of predation, overall fitness is a non-linear function of local fitnesses. At the evolutionarily stable state (ESS), the prevailing habitat use strategy does not equalise total fitness returns from the two habitats, but rather marginal fitness returns from each habitat.

Comparable themes arise in the evolution of dispersal. As noted elsewhere in this volume (e.g., Ims and Hjermann, chapter 14), dispersal behaviour may occur unconditionally, for example an individual's dispersal rate may be independent of the local environment, but vary by genotype, or instead may vary by habitat type, local density, or individual condition. An 'ideal free' disperser might be defined as an individual that moves between habitats only if, by so doing, it increases its realised fitness. We will show that, even if dispersers are not ideal free, a population may in some circumstances evolve toward a distribution that is approximately ideal free.

That the evolution of dispersal may have an 'ideal free' interpretation has been touched on in previous literature (Holt 1985). For instance, Levin *et al.* (1984) studied a model for evolution in a parameter $D$, the fraction of individuals that disperse from natal sites. In summarising their results they 'conjecture that the [evolutionarily stable value for $D$] is determined by the equilibration of long-term expectations from dispersing and non-dispersing individuals'. Lemel *et al.* (1997) suggest that a unifying rule for the evolution of dispersal is that 'the dispersal rates which permit the spatial homogenization of fitnesses are ESSs'. In the following pages, we focus on the suggestion that the evolution of dispersal tends towards an equilibration of fitnesses among habitats. Abstractly, dispersal is an 'assortative parameter', determining (in part) the numbers of individuals in different 'classes', which in the case of dispersal are local habitats. Slatkin (1978a) demonstrated that, given density- and frequency-dependent interactions in a population, natural selection acts on assortative parameters so 'as to equilibrate the fitnesses of those classes' and noted that this generalisation may fail in temporally varying environments.

The concept of 'fitness equilibration' should be viewed in the same spirit, we suggest, as 'fitness maximisation' in classical evolutionary genetics. In many circumstances, and in particular when individual relative fitnesses are density and frequency independent, the outcome of natural selection can be characterised as hill-climbing in an adaptive topography, or as the maximisation of a fitness function (Roughgarden 1979). This characterisation provides a compact description of the outcome of evolutionary dynamics in a wide variety of situations, and its failure in other situations (e.g., with frequency-dependent selection) highlights important features of evolution. The chapters in this volume span diverse evolutionary causes of dispersal (Ronce *et al.*, chapter 24). We will see that fitness equilibration does characterise some situations and some causal mechanisms for the evolution of dispersal, but in others fitness equilibration is not expected.

## The ideal free distribution and dispersal evolution in temporally constant environments

We first return to Fretwell's original model and cast it in a form appropriate for studying dispersal. Genetic variation is clonal and affects only dispersal rules. Dispersal strategies are defined by fixed dispersal rules, independent of population size (a non-'ideal' behaviour); however, dispersal rates may be conditional on habitat type. We first assume that the population settles into a stable equilibrium, and then consider temporal variation. Different dispersal rules give different realised fitnesses for a genotype, for a given array of local fitnesses. We consider two distinct movement scenarios: 'scalar' movement and localised dispersal.

### Scalar model

The simplest model is a 'scalar' model (terminology after Tuljapurkar and Istock 1993). Examples of the use of scalar models to study dispersal evolution include Metz *et al.* (1983), Levin *et al.* (1984), and Holt (1997b). Assume that after reproduction all newborns in a population of size $N$ enter a general dispersal pool and enter each of two habitats with a fixed probability. Thus, individuals are non-'ideal'. Genetic variability in the propensity to utilise different habitats permits dispersal to evolve. Assume the initial population uses habitat 1 with probability $p$. Expected fitness of an individual is $W = pF_1(N_1) + (1-p)F_2(N_2)$, where $N_1 = pN$, and $N_2 = (1-p)N$. We assume the population is at demographic equilibrium, so $W = 1$; hence, either $F_1 = F_2 = 1$ (so the equilibrium population $N_i^* = K_i$), or if, say, $F_1 > 1$ then $F_2 < 1$ (thus, $N_1^* < K_1$ and $N_2^* > K_2$).

A rare invading clone with a different pattern of habitat choice has an overall fitness of $W' = p'F_1(N_1) + (1-p')F_2(N_2)$. (The densities in this case are summed over both clones in a habitat.) It immediately follows that, if $F_1 > 1 > F_2$, then, given $p' > p$, the invading clone increases in frequency, whereas, if $p' < p$, the invading clone declines towards extinction; selection obviously favours increased use of whichever habitat provides higher fitness. A necessary condition for an evolutionary equilibrium with no ongoing directional selection on habitat choice is $F_1 = F_2 = 1$. In other words, an evolutionarily stable state for dispersal requires the population to exhibit an IFD, even though individuals making up the population do not have ideal free behaviours. Such an equilibrium could be monomorphic or a mix of different dispersal types, with relative abundances adjusted such that the IFD holds (McPeek and Holt 1992).

At a joint demographic and evolutionary equilibrium, each habitat is at its respective carrying capacity. Natal dispersal involves organisms born in one habitat that settle in the other. For dispersal not to affect local population size, immigrants should equal emigrants in each habitat. If $p$ is the average propensity of an individual to use habitat 1, then the number of immigrants into habitat 2 is $I = K_1(1-p)$, and the number of emigrants there is $E = K_2 p$. Setting $I = E$ implies $p = K_1/(K_1 + K_2)$. A pattern of equalised immigration and emigration has been called 'balanced dispersal' (empirical examples include Doncaster *et al.* 1997; Diffendorfer 1998). Given balanced dispersal, if there is an inverse relation between local population size and local dispersal probability,

local populations can be at carrying capacity, yet dispersal can still be ongoing (McPeek and Holt 1992; Lemel *et al.* 1997).

**Partial mixing**

The above 'scalar' model assumes the population mixes each generation, so that a single number characterises habitat use, and a single fitness measure describes the iteration of numbers through time. More generally, one expects populations in different habitats to be partially decoupled. For populations with discrete generations occupying multiple habitats, stage-structured matrix models (Tuljapurkar and Caswell 1997) provide a natural framework for analysing population and evolutionary dynamics (Holt 1996). Consider the following stage-structured model (where 'stage' = 'habitat') for a single species with discrete generations, local density dependence, and fixed habitat-specific dispersal rates, where dispersal (defined simply as movement between habitats) occurs a single time in an individual's lifetime:

$$\begin{bmatrix} N_1(t+1) \\ N_2(t+2) \end{bmatrix} = \begin{bmatrix} (1-e_{12})F_1(t) & e_{21}F_2(t) \\ e_{12}F_1(t) & (1-e_{21})F_2(t) \end{bmatrix} \begin{bmatrix} N_1(t) \\ N_2(t) \end{bmatrix} \quad (1)$$

Here $N_i(t)$ is abundance and $F_i(t)$ is realised local fitness (surviving reproductive offspring) in habitat $i$ at generation $t$. Dispersal is defined by $e_{ij}$, the *per capita* rate of movement of newborn individuals from habitat $i$ to habitat $j$. Local fitness may decrease with increasing local density (summed over clones, if there is more than one clone). If there is no density dependence in habitat $j$, we assume $F_j < 1$, so habitat $j$ is intrinsically a sink. We assume no direct cost of dispersal. Dispersal may be conditional by habitat but is not directly responsive to density; individuals are not 'ideal', because they may move from high to low fitness habitats.

To examine the evolution of dispersal, we permit clones that are identical in within-patch performance but differ in their propensity to move among habitats to compete with one another. We assume local densities are sufficiently great that kin competition can be ignored (Taylor and Frank 1996; see Lambin *et al.*, chapter 8). Several authors have used models of this basic form to examine the evolution of dispersal (Hastings 1983; Holt 1985; McPeek and Holt 1992; Holt and McPeek 1996; Doebeli and Ruxton 1997; Lemel *et al.* 1997). A general (albeit abstract) measure of fitness in populations whose dynamics are defined by a stage-structured matrix process is the dominant Lyapunov exponent of that process (Metz *et al.* 1992). In model (1), if the local fitnesses are fixed quantities (i.e., we ignore density dependence and temporal variability for a moment), the transition matrix has fixed elements, and the dominant Lyapunov exponent is simply the dominant eigenvalue of the transition matrix (Metz *et al.* 1992). The dominant eigenvalue for model (1) that provides a fitness measure is:

$$W = \frac{1}{2}\left[(1-e_{12})F_1 + (1-e_{21})F_2 + \sqrt{Q}\right] \quad (2)$$

where

$$Q = [(1-e_{12})F_1 + (1-e_{21})F_2]^2 - 4(1-e_{12}-e_{21})F_1F_2$$

For a population to be stable, one or both local fitnesses must be density dependent. We assume this is the case, so the $F_i$ values are adjusted such that $W = 1$; this requires that either $F_1 = F_2$, or if, say, $F_1 > 1$, then $F_2 < 1$. A novel clone, when sufficiently rare relative to the resident clone, experiences density dependence mainly from the resident clone; its asymptotic growth rate when rare is given by expression (2), with $F_i$ being the same local fitnesses experienced by the resident clone, but $e_{ij}$ being different between clones. With partial mixing, in contrast to the 'scalar' model, fitness in a spatially heterogeneous environment is a strongly non-linear combination of local fitnesses. Nonetheless, the evolution of dispersal tends in the same direction, towards an IFD. Rather than dwelling on algebraic details, the salient results are as follows.

(i) $F_1 > 1 > F_2$. If the dispersal parameters are free to vary, then $dW/de_{12} < 0$ and $dW/de_{21} > 0$; selection favours avoidance of the habitat with lower fitness and movement towards the habitat with higher fitness. If dispersal rates are constrained to be equal ($e_{12} = e_{21} = e$), then $dW/de < 0$. With unconditional dispersal, in a spatially heterogeneous habitat, one expects populations to evolve by selection towards very low dispersal rates (Hastings 1983; Holt 1985) at which each habitat will be at its respective carrying capacity, and fitness will converge on unity across space.

(ii) $F_1 = F_2 = 1$ (i.e., each habitat is at its respective carrying capacity). If habitats have unequal carrying capacities, an IFD is compatible with ongoing dispersal, given 'balanced dispersal' (Doncaster *et al.* 1997), i.e., dispersal that is asymmetrical and inversely related to carrying capacity: $K_1/K_2 = e_{21}/e_{12}$ (see also Lemel *et al.* 1997). McPeek and Holt (1992) note this for a special case; a simple demonstration of this necessary relationship for an equilibrium comes from adding and subtracting the two equations in (1), and evaluating them at equilibrium, with each patch at its respective $K$.

## Sink habitats and the non-equilibration of local fitnesses

So, in constant environments, the evolution of dispersal rates, given non-ideal individuals with fixed dispersal propensities, tends toward an IFD for the population as a whole. But a rich body of theory shows that a principal selective factor favouring dispersal is temporal heterogeneity (e.g., Levin *et al.* 1984; McPeek and Holt 1992). How does temporal variation affect the ideal free property of the population distribution? Analysing adaptive evolution in variable environments is a challenging problem (Haccou and Iwasa 1995), particularly in structured populations, in large measure because there is no simple characterisation of fitness (Tuljapurkar 1990). To complicate matters further, given local density dependence, dispersal alters local population size (see Hanski, chapter 20), in turn modifying fitnesses and thus selection on dispersal; in models of spatially structured populations in fluctuating environments, one cannot solve for densities through time and thus cannot analytically characterise temporal variation in fitness. The feedback between demographic functioning of populations and the selective pressure on dispersal is at the core of ESS analyses of dispersal, yet analytically finding this ESS is usually impossible.

For non-dispersing organisms with discrete generations, the appropriate measure of fitness is the geometric mean of fitness through time (Cohen 1993; Haccou and Iwasa 1995; Yoshimura and Jansen 1996). In the following paragraphs, we report numerical

studies of evolution of conditional dispersal strategies in the above scalar and matrix models. We assumed two basic spatial scenarios: a source–sink system, with density dependence in the source, or two habitats with unequal positive carrying capacities. Previous studies along these lines (e.g., McPeek and Holt 1992; Holt 1997b) have explored the issue of the evolution of dispersal *per se*. Here, we complement this earlier work by interpreting the evolutionary equilibrium in terms of spatial equilibration of two proxies for local fitness: geometric mean *local* fitness and spatial reproductive value (see Holt 1996).

Consider first the above 'scalar' model, but now assume that fitness fluctuates among generations in one or both habitats (due either to temporal variation in parameters or to unstable dynamics), so that the average fitness in generation $t$ is $W = pF_1(N_1(t)) + (1-p)F_2(N_2(t))$. K.A. Schmidt, J.A. Earnhardt, J.S. Brown and R.D. Holt (unpublished manuscript) show that if both habitats are used, the ESS value for $p$ is the solution of:

$$\sum_k \frac{q_k(F_1 - F_2)}{[pF_1 + (1-p)F_2]} = 0 \tag{3}$$

where $q_k$ is the probability that the $k$th type of generation occurs. If local fitnesses are constant, we recover the earlier result that, at the ESS, local fitnesses are equilibrated across space. But if fitnesses vary temporally, this need not hold. Consider the case where habitat 2 is a sink habitat with constant fitness $F_2 < 1$, whereas habitat 1 is a source with fluctuating fitness. Holt (1997b) and Jansen and Yoshimura (1998) demonstrate that partial use of the sink is selectively advantageous if the source is sufficiently variable in fitness, so that in some generations the source has a lower expected fitness than does the sink; this adaptive use of a sink is a 'bet-hedging' strategy (Seger and Brockmann 1987). A limiting case is for the source to alternate cyclically between good and bad years, with fitness being zero in bad years and positive (but density dependent) in good years. Nonetheless, partial dispersal to the sink can permit persistence (Jansen and Yoshimura 1998); by assuming overall geometric fitness is unity (which can be achieved by adjusting population size, and thus density-dependent fitness, in the source in good years), after manipulating equation (3), one can show that the ESS for use of the source habitat is the solution of a quadratic, $F_2^2 p^2 + 2(1 - F_2^2)p + (F_2^2 - 1) = 0$. When $F_2$ is near 1, $p$ is near 0 (most individuals should avoid the source habitat), whereas when $F_2$ is near zero, $p$ converges on 1/2. (If maximal source fitness during good years does not permit overall geometric fitness to be unity, then the population goes extinct.) Geometric mean local fitness in the source is zero; geometric mean fitness in the sink is a constant between zero and 1.

This example shows that it is certainly *not* always true that dispersal evolves so as to equalise local fitnesses (here interpreted as the geometric mean of local fitness) across space, when one habitat is an intrinsic sink (adding negative density dependence to the sink does not affect this qualitative conclusion; R.D. Holt, unpublished results). If utilisation of sink habitats were part of a bet-hedging strategy, one would not expect to see balanced dispersal, with immigrants equalling emigrants (Doncaster *et al.* 1997; Diffendorfer 1998), or an IFD.

However, if both habitats have positive carrying capacities (i.e., neither is an intrinsic sink) and do not suffer local extinctions (i.e., all $F_i(t) > 0$), numerical studies suggest

that at the ESS for dispersal the realised geometric mean of local fitness is often approximately equalised between the two habitats. We were surprised at this outcome. In our simulations, we examined a range of assumptions about temporal variation (e.g., uniform versus normal distributions) and the functional form of local density dependence. Particular forms for density dependence examined include the exponential logistic $[F_i(t) = \exp(r_i(t)(1 - N_i(t)/K_i(t)))]$, the Ricker model $[F_i(t) = \exp(r_i(t) - d_i(t)N_i(t))]$ and a flexible phenomenological model of density dependence $[F_i(t) = R_i(t)/(1 + N_i(t)^{d_i(t)})]$, where $N_i(t)$ is the summed density over all dispersal types within a patch in generation $t$. (The quantities $R_i(t)$ and $\exp(r_i(t))$ are maximal rates of increase in generation $t$; $d_i(t)$ measures the strength of density dependence; and $K_i(t)$ is the carrying capacity of habitat $i$.)

Figure 6.1 shows a representative example. Geometric mean local fitnesses were calculated over 10 000 generations for populations monomorphic in $p$ (for 101 values of $p$ uniformly distributed in [0, 1]). The ESS was then determined by clonal competition. In all cases examined, as long as each habitat patch had a positive carrying capacity in each generation, we found that the population at the ESS exhibited a distribution that was close to ideal free, as measured by realised geometric mean local fitnesses. Comparable results arise in the more general model with localised dispersal (model [1]). Again, there appears to be a qualitative difference between a system with sink habitats, and one in which all habitats have positive carrying capacities. For the source–sink system, if the population persists and is initially restricted entirely to the source, then regardless of the amount of temporal variation in fitness, very small rates of localised dispersal coupling the sink and source are disfavoured. This can be readily shown analytically for a cyclical environment of period 2. However, larger rates of dispersal can be favoured, even if small rates of dispersal are not. To find the ESS pattern of dispersal, we allowed a large

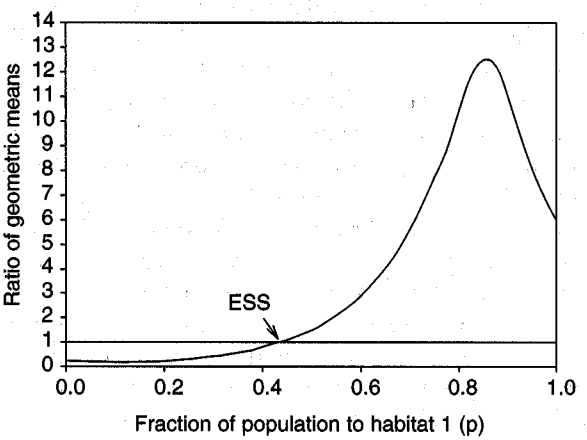


**Figure 6.1.** Relative geometric mean fitness, for two habitats coupled with scalar dispersal. In the example shown, local fitnesses were described by $F_i(t) = R_i(t)/(1 + N_i(t)^d)$. The density-independent growth parameter for each habitat was given by a sequence of independent draws from normal distributions, with a mean in habitat 1 of $R_1 = 4$, a mean in habitat 2 of $R_2 = 6$, and a standard deviation for both of 0.5. For both habitats, $d = 2$. (The simulations discarded zero and negative values of $R_i$; in our simulations with these parameters this never occurred.)

**Table 6.1.** Source–sink dynamics with unstable source and localised dispersal. A. Winning dispersal rates. Local fitness in the source is given by the Ricker model. B. Geometric mean local fitnesses for the evolutionarily stable dispersal rates

| $R_{sink}$ | 0.3 | | 0.4 | | 0.5 | | 0.6 | | 0.7 | |
|---|---|---|---|---|---|---|---|---|---|---|
| *A. Dispersal rates of persisting clone Standard deviation of r* | | | | | | | | | | |
| | $e_{12}$ | $e_{21}$ | $e_{12}$ | $e_{21}$ | $e_{12}$ | $e_{21}$ | $e_{12}$ | $e_{21}$ | $e_{12}$ | $e_{21}$ |
| 0.5 | 0.00 | 1.00 | 0.00 | 1.00 | 0.02 | 1.00 | 0.08 | 1.00 | 0.16 | 1.00 |
| 0.6 | 0.00 | 1.00 | 0.00 | 1.00 | 0.08 | 1.00 | 0.18 | 1.00 | 0.26 | 1.00 |
| 0.7 | 0.00 | 1.00 | 0.04 | 1.00 | 0.18 | 1.00 | 0.28 | 1.00 | 0.34 | 1.00 |
| 0.8 | 0.00 | 1.00 | 0.16 | 1.00 | 0.30 | 1.00 | 0.38 | 1.00 | 0.44 | 0.88 |
| 0.9 | 0.25 | 1.00 | 0.38 | 1.00 | 0.48 | 0.86 | 0.56 | 0.72 | 0.62 | 0.63 |
| *B. Geometric mean local fitness of persisting clone in source Standard deviation of r* | | | | | | | | | | |
| 0.5 | 1.000 | | 1.000 | | 0.997 | | 0.977 | | 0.943 | |
| 0.6 | 1.000 | | 1.000 | | 0.993 | | 0.972 | | 0.941 | |
| 0.7 | 1.000 | | 0.999 | | 0.987 | | 0.966 | | 0.934 | |
| 0.8 | 1.000 | | 0.993 | | 0.979 | | 0.956 | | 0.920 | |
| 0.9 | 0.999 | | 0.986 | | 0.966 | | 0.936 | | 0.894 | |

number of clones to compete, spanning all feasible values of the two dispersal rates. Table 6.1 presents a typical example (the table assumes Ricker density dependence in the source, with mean $r_1 = 1.5$, $d = 1$, and random normal deviates in $r_1$). At low sink fitness, and low fitness variance in the source, the evolutionarily stable state of the population is no dispersal, leaving the sink unoccupied. Dispersal can be favoured, given higher sink fitness or larger temporal variance in source fitness. Winning clones always disperse at a higher *per capita* rate from the sink to the source than in the reverse direction. In the source, there is often incomplete dispersal for each generation, whereas typically all individuals born in the sink immediately disperse back into the source.

Table 6.1 also shows the long-term geometric mean local fitnesses of the winning clones. As in the scalar model, natural selection does *not* equilibrate geometric mean fitness among habitats; at the ESS for dispersal, the source typically has a higher realised geometric mean *local* fitness than does the sink. In short, evolution of dispersal does not necessarily lead to an IFD, as measured by *local* (geometric mean) fitness, when the use of intrinsic sink habitats is favoured by high temporal variance in fitness in source habitats.

By contrast, as in the scalar model, if both habitats have positive carrying capacities and dispersal is localised, numerical studies suggest that the geometric mean of local fitnesses in the two habitats is typically approximately equalised at the ESS. A characteristic example is shown in Fig. 6.2, which shows a surface describing the ratio of geometric mean fitnesses for two habitats as a function of dispersal rates. The straight line defining the intersection of this surface with the plane of equal geometric mean fitnesses gives the set of dispersal rates that equilibrate geometric mean fitness; the dot is the ESS arising from competitive trials. At the ESS, geometric mean local fitnesses are very nearly equal across space. It is also clear from Fig. 6.2 that fitness equilibration does not capture all the important features of dispersal evolution. The line of intersection

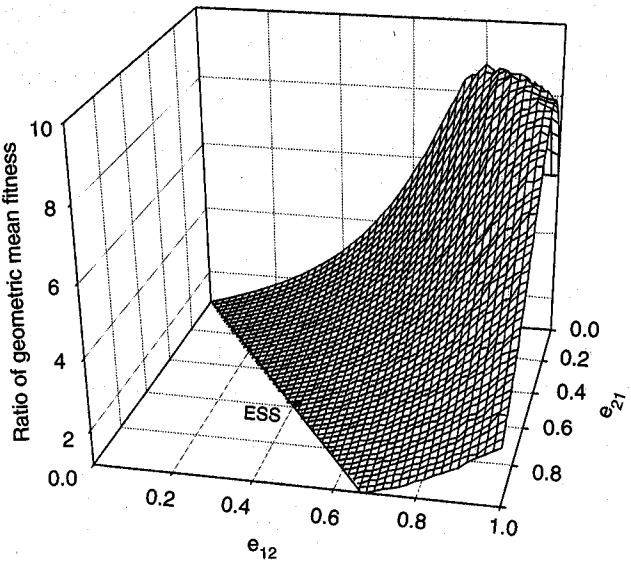


**Figure 6.2.** Relative geometric mean fitnesses in two coupled patches, as a function of dispersal rates for localised dispersal. These simulations used the expression $R_i(t)/(1 + N_i(t)^{d_i(t)}))$ for local fitnesses. The values for $R_i(t)$ were drawn from a uniform distribution, with a mean of 4 for habitat 1 and a mean of 6 for habitat 2, with a range in both cases of width 6. Independent uniform deviates between 1 and 2 were used for both the $d_i(t)$ values. Thus, the populations experienced very high levels of variation in local growth rate. The ESS was found from clonal competition trials (including pairwise competition and trials with an initially uniform distribution of all feasible dispersal clones – increments in dispersal rates of 0.02 separated clonal dispersal values). Geometric mean fitness was evaluated over 100 000 generations, after an initialisation period of 10 000 generations, with initial densities at carrying capacity in the two patches. The dot indicates the ESS for dispersal rates. At the ESS, geometric mean fitness is approximately equalized in the two habitats.

describes an equivalency class of dispersal rates, where each combination leads to fitness equilibration. When one allows these clones to compete, a unique winner emerges. Thus, there are evolutionary forces operating that are not encapsulated by this fitness equilibration rule; otherwise, these clones would be selectively neutral relative to one another.

We were puzzled by finding that geometric mean local fitness was approximately equilibrated in these simulations; given dispersal, the fitness measure relevant to predicting the course of evolution is much more complex than just the realised geometric mean fitness in each habitat. Moreover, using this measure revealed to us small (but real) discrepancies from the ESS. Fitness equilibration by this measure provides a fairly accurate 'rule-of-thumb' describing the outcome of dispersal evolution, but it is reasonable to ask whether there are other, more accurate, measures that would reveal true equilibration (if such exists).

A broad consensus has emerged that the most general definition of fitness for a structured population with non-linear dynamics in a variable environment is the dominant Lyapunov exponent of a series of random matrices, where matrix elements describe transitions among different classes or subpopulations (Tuljapurkar 1990; Metz *et al.* 1992; Ferrière and Gatto 1995). With limited dispersal, localised density

dependence, and fluctuating environments, however, analytical characterisation of this measure of fitness can be very difficult (Tuljapurkar 1997). In the absence of an analytical expression for this true fitness measure, we conjectured that evolution might tend to equalise the realised *spatial reproductive values* of each habitat. In stage-structured models with fixed coefficients (Caswell 1989), the reproductive value of a given stage is the relative contribution of an individual in that stage to eventual population size. In a spatially heterogeneous environment, 'habitat' corresponds to 'stage'. The spatial reproductive value of each habitat is the relative contribution of that habitat to the entire population (Holt 1996; Rousset 2000c). Given dispersal, an individual in one focal habitat leaves descendants across a number of habitats. The fitnesses of those descendants must enter into the calculation of the reproductive value ascribed to the focal habitat. One can abstractly define a stochastic reproductive value (Tuljapurkar 1990, 1997), but, in practice, simulation studies are required to assess reproductive value in fluctuating environments.

We assessed spatial reproductive value using neutral genetic markers. First, for any given parameter set, competitive trials determined ESS dispersal rates. Then, with just the dominant clone, the system was run for 100 generations, at which time an additional population was introduced at low density to each habitat, with dispersal parameters and

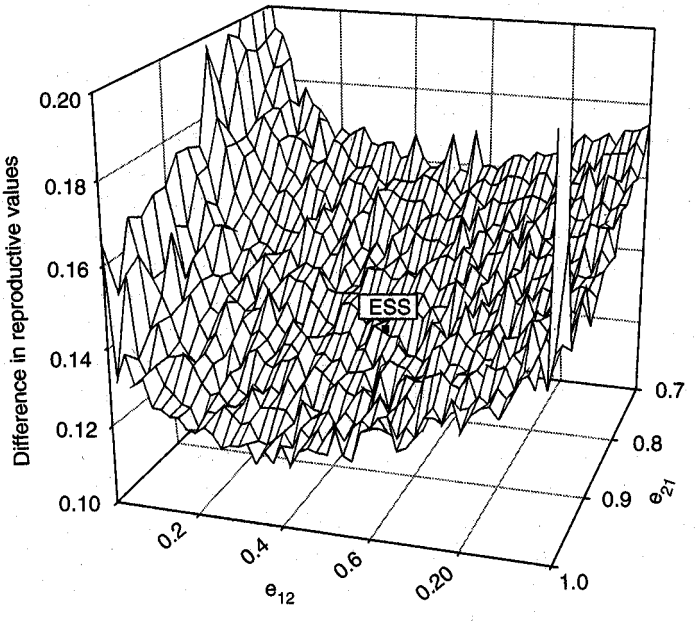


**Figure 6.3.** Differences in spatial reproductive value between source and sink, as a function of dispersal rates, given localised dispersal. The general protocol for evaluating reproductive value is described in the text. Simulations were carried out with local fitnesses described by the Ricker model in the source and a constant growth rate $< 1$ in the sink. $R_{sink} = 0.9$. The source $r(t)$ was drawn from a normal distribution, with mean $r = 1.5$, $\sigma = 0.5$, and $d = 1$. The winning dispersal strategy is $e_{12} = 0.48$, $e_{21} = 0.86$ (indicated by dot). At the ESS, spatial reproductive values are not equalised, and the winning strategy does not minimise the differences in spatial reproductive values between habitats.

local fitnesses identical to the resident clone. After 100 further generations, the total number of descendants from each new population was divided by the initial propagule size to give the reproductive value for the habitat in which that population was introduced. Because populations are fluctuating, this value can be sensitive to initial conditions and the exact pattern of environmental fluctuations; we carried out 100 000 runs for each parameter set and averaged the resulting reproductive values.

Again, numerical studies revealed a dichotomy between scenarios in which one patch was a sink and those in which both habitats had positive carrying capacities. In the source–sink system, at evolutionary equilibrium, realised reproductive value of the source did not usually equal that of the sink; Fig. 6.3 is a typical example. By contrast, given positive carrying capacities, reproductive values were approximately equalised across habitats at the evolutionary equilibrium (not shown). Our studies suggest that this equilibration among habitats is approximate, rather than exact. What impresses us is that, even in cases that involve very pronounced temporal variation in local fitnesses, equilibration of these fitness proxies provides a useful rule-of-thumb for the evolutionary outcome, deviating by less than 1–2% from the actual ESS. Thus, even though we assume organisms that are not ideal, the population as a whole converges on a near-IFD at the evolutionary equilibrium for dispersal.

## Discussion and conclusions

Given that all habitats have a positive carrying capacity, our numerical studies suggest that the evolution of dispersal tends to produce an approximate IFD, at which the quantity equilibrated across space is one of two proxies for fitness: spatial reproductive value or geometric mean local fitness. It will be an important task in future work to assess the generality of these conclusions. We are intrigued by the observation that the geometric mean *local* fitness is, to a reasonable approximation, equilibrated at the ESS for dispersal. This has practical implications: it is more likely that one could devise a reasonable estimate for local geometric mean fitness in given habitats (for a concrete example, see Boyce and Perrins 1987) than that one could directly measure spatial reproductive values – not to mention dominant Lyapunov exponents.

Our results suggest that the equilibration of local fitness measures across space can often describe the outcome of the evolution of dispersal. They also show, however, that the evolution of dispersal need not equilibrate fitnesses, even approximately, if some habitats are sinks. Natural selection favours utilisation of sink habitats if source habitats have high temporal variance in fitness (Holt 1997b; Jansen and Yoshimura 1998). Organisms with high variance in fitness in high-quality habitats might be expected not to exhibit an IFD because they are more likely to include low-quality but stable sink habitats in their habitat repertoire.

The models we examined have many simplifying assumptions. For instance, we assumed that each individual has a fixed propensity to disperse, which could vary by habitat, but in no other way. Several authors in this volume (e.g., Ims and Hjermann, chapter 14; Stamps, chapter 16; Murren *et al.*, chapter 18) discuss the importance of factors such as individual plasticity, the dependence of dispersal upon internal conditions, and density-dependent dispersal. It would be useful to assess fitness equilibration

across habitats, given more realistic assumptions about the proximal causes, conditional dependence, and costs of dispersal. Two assumptions in our models were that there was no direct cost of dispersal and that once a disperser moved it would have the same expected fitness as a non-dispersing resident. Stamps (chapter 16) suggests that evolution has favoured a wide range of mechanisms to reduce the costs of settling into new habitats. However, it is unlikely that such mechanisms will completely eliminate dispersal costs and/or differences between residents and immigrants. Incorporating these realistic features of dispersal could alter an expectation of fitness equilibration at evolutionary equilibrium.

In the models discussed above, dispersal evolved due to spatio-temporal variation in fitness, in populations large enough to consider abundance to be a continuous variable. Yet fitness variation is only one of several potential factors important in the evolution of dispersal (Johnson and Gaines 1990). Fitness equilibration is unlikely to be an evolutionary outcome for many alternative mechanisms. For instance, with highly localised density dependence and very few individuals interacting within patches, demographic stochasticity promotes the evolution of dispersal; clones with zero dispersal walk randomly to extinction in patches with low carrying capacities, leaving behind only dispersing clones (Travis and Dytham 1998). Moreover, kin competition becomes important; movement by a single individual alters fitnesses in both natal and recipient habitats, changing inclusive fitness (Taylor and Frank 1996). These two effects of individual discreteness favour intermediate dispersal rates, even in constant environments. Hamilton and May (1977) showed that this mechanism operates even if dispersal is costly. If some of this cost arises because dispersers land in low-quality sink habitats, one will observe sustained spatial variation in local fitness. Thus, kin competition (see Perrin and Goudet, chapter 9; Gandon and Michalakis, chapter 11) is an important driver of the evolution of dispersal that is not likely to lead to fitness equilibration among habitats. An absence of equilibration is also likely if parents rather than offspring govern dispersal (Murren *et al.*, chapter 18). Moreover, observing a non-ideal free distribution is compatible with a variety of evolutionary causes of dispersal; for example, such a pattern could arise from 'bet-hedging' use of sink habitats, or from kin selection with localised competition.

Despite these limitations in the scope of fitness equilibration, we believe it fair to conclude that Fretwell and Lucas's concept of the IFD provides an insight that proves surprisingly useful for characterising the population-level outcome of evolution of dispersal rates, even among organisms that are not particularly ideal in their individual habitat selection behaviour. Fitness equilibration appears to be most likely when considering movement among habitats, none of which are intrinsic sinks, and when the prime driver of dispersal evolution is spatio-temporal variation in fitness, rather than factors such as kin competition.

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