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The Evolution of Dispersal under Demographic Stochasticity

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ABSTRACT: Temporal and spatial variations of the environment are important factors favoring the evolution of dispersal. With few exceptions, these variations have been considered to be exclusively fluctuations of habitat quality. However, since the presence of conspecifics forms part of an individual's environment, demographic stochasticity may be a component of this variability as well, in particular when local populations are small. To study this effect, we analyzed the evolution of juvenile dispersal in a metapopulation model in which habitat quality is constant in space and time but occupancy fluctuates because of demographic stochasticity. Our analysis extends previous studies in that it includes competition of resources and competition for space. Also, juvenile dispersal is not given by a fixed probability but is made conditional on the presence of free territories in a patch, whereas individuals born in full patches will always disperse. Using a combination of analytical and numerical approaches, we show that demographic stochasticity in itself may provide enough variability to favor dispersal even from patches that are not fully occupied. However, there is no simple relationship between the evolution of dispersal and various indicators of demographic stochasticity. Selected dispersal depends on all aspects of the life-history profile, including kin selection.

Keywords: dispersal, demographic stochasticity, adaptive dynamics, density dependence, viability.

In many species that live in fragmented habitats, individuals leave their natal patch and settle down in another patch of favorable habitat. This dispersal behavior creates an exchange of individuals between local habitats and influences the genetic and demographic characteristics of the population (see, e.g., Hanski and Gilpin 1997; Clobert et al. 2001). Many theoretical studies have identified spatiotemporal variations of local habitats as a key factor for the selection of dispersal. Such variations have been modeled as caused by variations in habitat carrying capacity (McPeek and Holt 1992; Olivieri et al. 1995; Lemel et al. 1997), variations in patch quality (Levin et al. 1984; Cohen and Levin 1991), or as the result of stochastic or deterministic local catastrophes (Comins et al. 1980; Olivieri et al. 1995; Gandon and Michalakis 1999; Gyllenberg and Metz 2001; Metz and Gyllenberg 2001). In all these models, the spatiotemporal heterogeneity that favors dispersal is solely due to the external environment.

However, the dynamics of the metapopulation itself may be a source of heterogeneity between habitats as well. Holt and McPeek (1996) and Doebeli and Ruxton (1997) have shown that chaotic or cyclic dynamics induced by the demographic characteristics of individuals may indeed influence the selection of dispersal (see also Parvinen 1999). Some authors have suggested that demographic stochasticity itself can induce spatiotemporal variations that modify the evolution of dispersal even in the absence of complex dynamics (Nagy 1996, in press; Cadet 1998; Ronce et al. 2001). Most metapopulation models deal with fractions of individuals rather than discrete numbers (Ronce et al. 2001) and therefore cannot be used to assess the consequences of demographic stochasticity. The approximation of local densities by continuous variables is only justified when local population sizes are sufficiently large. Where this is not the case, as can be expected for most populations living in fragmented habitats, the discrete nature of individuals and the associated demographic stochasticity cannot be neglected (Durrett and Levin 1994).

A central question is whether demographic stochasticity

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can provide enough variability between and within habitats to select for dispersal even in the absence of environmental variation in habitat quality. We address this question by studying the evolution of dispersal when the only cause of spatiotemporal heterogeneity between habitats is demographic stochasticity. A first analysis of this problem was published by Travis and Dytham (1998) and Travis et al. (1999). However, in one article (Travis and Dytham 1998), demographic stochasticity is modeled artificially instead of arising as the natural result of the discrete number of individuals per patch, whereas in the other (Travis et al. 1999), dispersal is assumed to be linearly density dependent, which is a quite strong assumption and renders the interpretation of their results difficult. Travis and Dytham's work was preceded by a more realistic tactical model (Nagy 1996, in press) that was developed to arrive at an understanding of dispersal in American pika (*Ochotona princeps*). We provide a general extension of the latter model in the framework recently developed by Metz and Gyllenberg (2001) that explicitly links stochastic local demographic processes with regional metapopulation dynamics. We use the adaptive dynamics framework (Metz et al. 1992, 1996; Geritz et al. 1998) to investigate the evolution of dispersal in this model.

Demographic stochasticity is important in particular when metapopulations are composed of small local populations. In the absence of external factors, small patch sizes are necessarily due either to density dependence (as in Levin et al. 1984; Cohen and Levin 1991; McPeek and Holt 1992; Lemel et al. 1997) or to a strict upper limit in patch capacity (as in Frank 1986, 1998; Olivieri et al. 1995; Gandon and Michalakis 1999; Perrin and Mazalov 2000; Ronce et al. 2000). To assess the relative importance of these two aspects (which, to our knowledge, has not been studied yet), we included both in our model.

When local population sizes have a fixed limit, one has to make assumptions about what happens to individuals born in saturated patches. The simplest case is where juveniles disperse with a fixed probability independent of the local circumstances (Olivieri et al. 1995; Gandon and Michalakis 1999; Perrin and Mazalov 2000; Ronce et al. 2000). In the context of this model, however, this would mean that individuals that stay in (or settle in) full patches are doomed (see, e.g., Olivieri et al. 1995; Ronce et al. 2000). Such a fixed strategy would be strongly selected against. At the other extreme, there would be fully conditional dispersal where individuals can finely gauge the local circumstances and act accordingly (van Baalen and Sabelis 1999; Metz and Gyllenberg 2001). Here, we consider an intermediate scenario in between these extremes in which individuals can detect whether a patch is fully saturated (no place available) but not the number of individuals. Therefore, we assume that juveniles will not attempt to settle in saturated patches or stay in their natal patch if it is saturated. The dispersal component that evolves in our model is therefore the voluntary dispersal of individuals from unsaturated patches, which renders our use of the word "dispersal" slightly different from the standard use.

The outline of our article is as follows. First, we determine the demographic stable regime and metapopulation viability when life-history traits and dispersal probability are fixed. Then, we will use Metz and Gyllenberg's approach (2001) to derive a fitness measure for a rare mutant and use this to analyze evolutionarily singular strategies. This allows us to assess how dispersal strategies evolve in response to different types of competition, levels of demographic stochasticity, and changes in life-history traits. In particular, we will analyze the relative roles of competition for resources and competition for space. We explain the results in terms of the conflicting selective pressures that operate in the metapopulation. Last, we discuss the possible role of kin selection in our model.

Ecological Dynamics

The Model

We consider an asexually reproducing animal species that inhabits a large number of patches. Each patch contains a number T of territories (possibly large), with each territory occupied by at most one individual. Intrinsic habitat quality is the same in all patches and does not vary in time, so each patch offers the same living conditions. However, since the number of individuals in a patch is small and discrete, local demographic processes cause the size of local populations—and, with it, the intensity of competition for space and resources—to vary stochastically. As a consequence, demographic parameters will vary in space and time because of demographic stochasticity.

In a patch with n individuals, adults give birth at rate λ_n and die at rate μ. We will assume that only the birth rate λ_n, which compounds fecundity and offspring survival, is affected by competition and decreases with local density n. This implies that our model does not contain an Allee effect, that is, positive density dependence at low densities.

Before first reproduction, juveniles born in unsaturated patches ($n < T$) either disperse with probability d or stay in their natal patch with probability $1 - d$. The dispersal probability d is assumed to be a fixed inherited quantity and, in particular, to be independent of the local density, with one exception. Juveniles born in a saturated patch ($n = T$) have no free territory available and thus cannot reproduce locally; we assume that these individuals disperse automatically (Pulliam 1988). In the following, we will refer to the latter form of dispersal as "expulsion" and will restrict the term "dispersal" to dispersal from unsaturated patches. Dispersers (of both types) enter a disperser pool, where they stay until either they die, which happens at a rate μ_D, or they find a patch that offers at least one empty territory. The rate constant of encounter of patches, α, is independent of the patch density. The density of dispersers in the disperser pool, in number of dispersers per patch, is denoted by D. Once established, individuals stay in the same territory for the remainder of their lives. Note that our assumption that juveniles are able to detect the difference between saturated and unsaturated patches affects not only their decision but also where they settle.

Assuming a large number of patches makes it possible to describe the state of the metapopulation at any time by the vector of frequencies of patches p_n harboring a local population of size n (for more details, see Metz and Gyllenberg 2001). During a sufficiently small time dt, only one out of four events may occur in a patch: arrival of a disperser, birth of a disperser, birth of a philopatric individual, or death of an adult. The temporal dynamics of frequencies p_n is then described by the system of differential equations

$$\forall n \in \{1, 2, \ldots, T-1\}$$

$$\begin{cases} \dfrac{dp_0}{dt} = -\alpha D p_0 + \mu p_1 \\ \dfrac{dp_n}{dt} = [\alpha D + (n-1)\lambda_{n-1}(1-d)]p_{n-1} - [\alpha D + n\lambda_n(1-d) + n\mu]p_n \\ \qquad + (n+1)\mu p_{n+1} \\ \dfrac{dp_T}{dt} = [\alpha D + (T-1)\lambda_{T-1}(1-d)]p_{T-1} - T\mu p_T \\ \dfrac{dD}{dt} = -\sum_{n=0}^{T-1} \alpha p_n D + \sum_{n=1}^{T-1} n\lambda_n d p_n + T\lambda_T p_T - \mu_D D. \end{cases} \tag{1}$$

How demographic and dispersal affect local population sizes is depicted in figure 1; the notation is summarized in table 1.

Note that our model includes two types of competition. First, individuals compete for space because number of territories is limited (T), as in models in the vein of Hamilton and May (1977; see, e.g., Frank 1986; Olivieri et al. 1995; Frank 1998; Gandon and Michalakis 1999; Perrin and Mazalov 2000). Second, individuals compete for local resources, which has direct demographic effects (see, e.g., Levin et al. 1984; Cohen and Levin 1991; McPeek and Holt 1992; Lemel et al. 1997). The intensity of this competition can be measured by the density at which mortality equals birth, corresponding to the classical carrying capacity, K (i.e., at density K, fecundity is such that $\lambda_K = \mu$). Local population size may fluctuate around K, but it is strictly bounded by T. The effects of each type of competition can be studied in isolation by letting K or T go to infinity.

It should also be noted that the decisions to disperse that we focus on in this article are not responsible for all dispersal that occurs in the model, since juveniles born in saturated patches are expulsed and automatically enter the disperser pool. To facilitate comparison with other studies, we will in some cases contrast dispersal, as we define it, with "overall dispersal," defined as the proportion of all juveniles that disperse, given by

$$\frac{d\sum_{i=1}^{T-1} i\lambda_i p_i + T\lambda_T p_T}{\sum_{i=1}^{T} i\lambda_i p_i}.$$

Viability and Population Dynamical Equilibrium

The viability of the metapopulation is entirely determined by the existence of a nonzero equilibrium. We show in appendix A in the online edition of the *American Naturalist* that for $T \leq 10$, this condition is

$$-(\alpha + \mu_D) + \alpha\left[\sum_{n=1}^{T-1} \frac{d(1-d)^{n-1}}{\mu^n} \prod_{k=1}^{n} \lambda_k + \frac{(1-d)^{T-1}}{\mu^T} \prod_{k=1}^{T} \lambda_k\right] > 0. \tag{2}$$

Figures 2*A* and 2*B* illustrate the two properties of this dynamical equilibrium: at the metapopulation level, the frequency of each density (0, 1, 2, …, T individuals) stays constant, but density keeps varying within each patch. The effect of the level of dispersal on viability depends highly on the other demographic parameters, as shown in figure 2*C*.

Evolutionary Dynamics

We use the adaptive dynamics framework (Metz et al. 1992, 1996; Geritz et al. 1998) to determine which dispersal strategies are favored by natural selection. In this framework, mutants are assumed to arise one at a time; that is, a metapopulation with given dispersal probability d reaches ecological equilibrium before a mutant phenotype characterized by a slightly different dispersal probability d' arises. If this mutant has an advantageous phenotype, it will invade and, typically, replace the resident population. The mutant therefore becomes the new resident and will reach an ecological equilibrium before a new mutation appears. Such "trait substitutions" (Geritz et al. 1998) are repeated until the population reaches what is called an evolutionarily singular strategy. In our study, any such

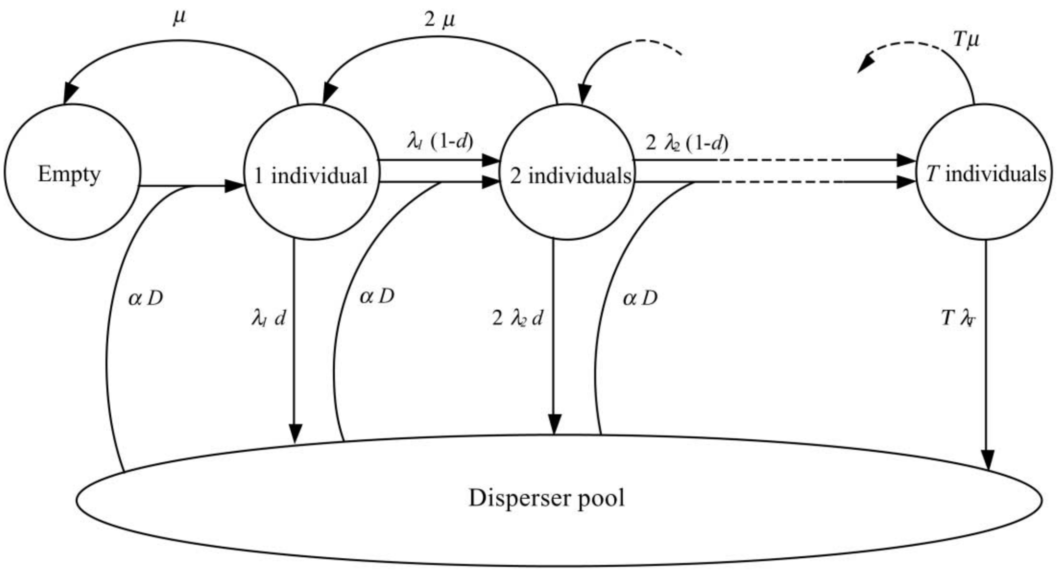

Figure 1: Transitions between sizes of a given patch and the disperser pool during the time. A patch of size n can gain an individual either by the birth of a philopatric individual (which occurs at the rate $n\lambda_n[1-d]$) or by the arrival of a disperser from the disperser pool (at rate αD). It can lose an individual through a death at the rate $n\mu$. The patch contributes individuals to the disperser pool at a rate $n\lambda_n d$. In the pool, individuals die at rate μ_D. Individuals born in a patch with no available territory ($n = T$) are automatically expelled into the disperser pool.

singularity was always found to be evolutionary stable. Hereafter, the term "selected dispersal" will therefore always refer to a continuously stable strategy (CSS), that is, a strategy that is both convergence stable and evolutionarily stable (Eshel 1983; Geritz et al. 1998).

Invasion Criterion

The capacity of a mutant to grow and replace the resident phenotype is determined by the expected number of newborn mutant dispersers resulting from a local colony founded by a newborn mutant disperser, which we denote by $R_m(d', d)$ (Metz and Gyllenberg 2001). The direction of evolution is given by the local fitness gradient

$$\frac{\partial R_m(d', d)}{\partial d'|_{d'=d}}.$$

If this gradient is positive (respectively negative), mutants with dispersal probability higher (respectively smaller) than the resident's can invade the population. Evolutionary singular strategies are defined as trait values where the fitness gradient vanishes.

Following Metz and Gyllenberg (2001), we write

$$R_m(d', d) = -\boldsymbol{A}^T \cdot \mathbf{M}^{-1} \cdot \boldsymbol{V}(0), \tag{3}$$

where $\boldsymbol{V}(0)$ is the vector of probabilities of the potential states at the moment of the founding of a mutant colony (these probabilities do not sum to 1 since a mutant may die during dispersal), $\mathbf{M}^{-1}$ is the matrix describing patch-state transitions, and $\boldsymbol{A}^T$ is the vector representing the birth rates of mutant dispersers (for details, see app. B in the online edition of the *American Naturalist*); $\mathbf{M}$ depends on the life-history parameters of mutant and resident, in particular the dispersal probabilities d and d', $\boldsymbol{A}$ depends on the life-history parameters of the mutant, and $\boldsymbol{V}(0)$ depends on the frequencies of the local densities $\hat{p}_n$ that characterize the resident ecological equilibrium.

Except in the simplest cases, equation (3) leads to complicated mathematical expressions. Therefore, our study of the adaptive dynamics of dispersal relies on a combination of analytical and numerical calculations.

Table 1: Notations

Notation	Definition
T	Number of territories within each patch
p_n	Frequency of patches with density n
d	Natal dispersal probability
λ_n	Per capita birth rate in patches of density n
μ	Per capita mortality rate within patches
μ_D	Per capita mortality rate during dispersal phase
D	Disperser pool
α	Rate constant of encounter with patches
K	Carrying capacity
λ_V, L, q	Density dependence parameters (see fig. 4)

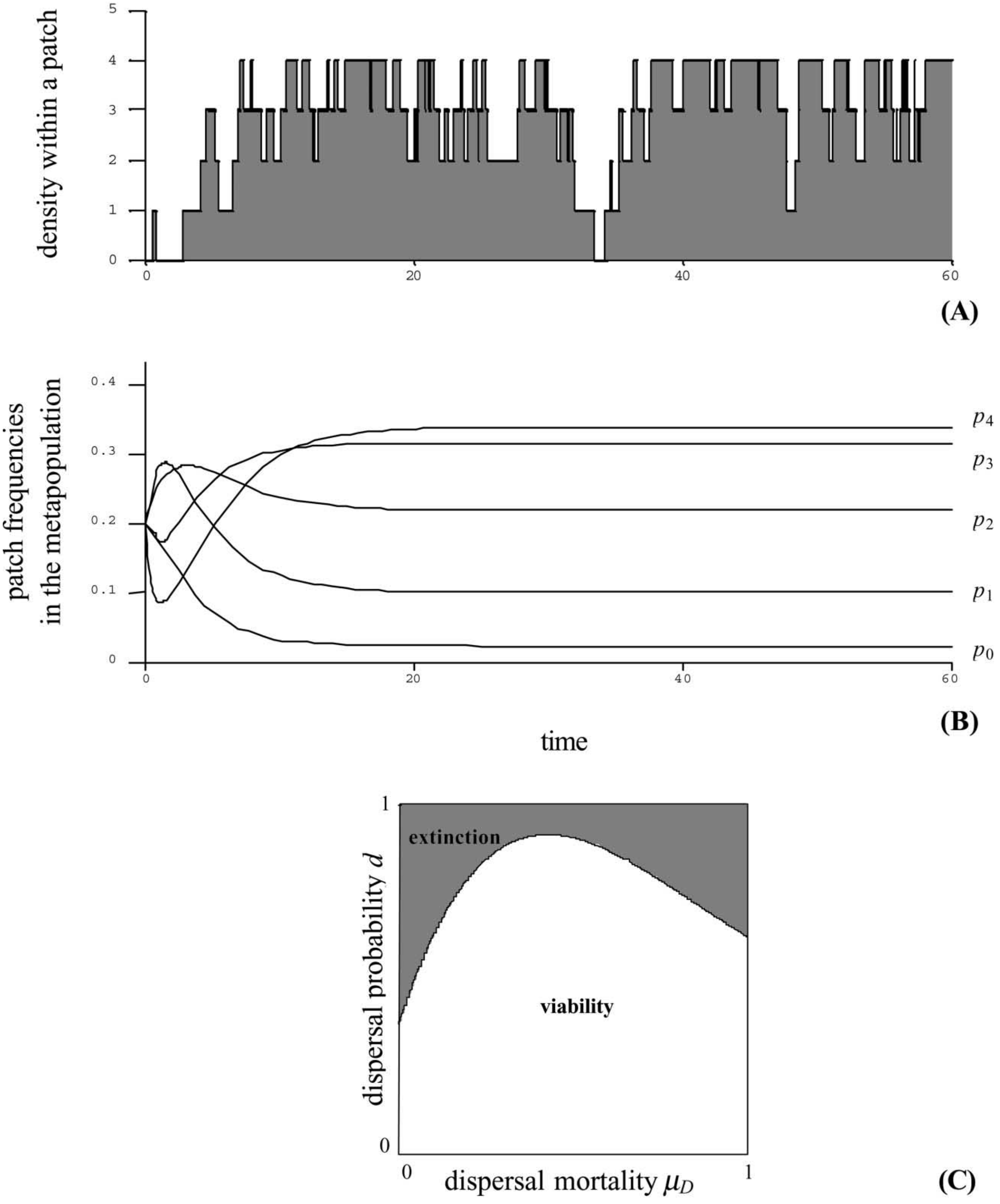

Figure 2: Ecological dynamics. An example of (*A*) local patch density and (*B*) global proportions of patches with zero, one, two, three, or four individuals as a function of time. Note that global patch occupancy converges to a stable equilibrium, whereas the density within a given patch varies permanently. Parameters: $T = 4$, $\mu = 0.5$, $\mu_D = 0.6$, $\lambda_1 = 1.5$, $\lambda_2 = 1.2$, $\lambda_3 = 1$, $\lambda_4 = 0.8$, $d = 1$, $\alpha = 1$. *C*, Area of viability of a metapopulation as a function of dispersal mortality μ_D and dispersal d ($T = 5$, $\mu = 0.8$, $\lambda_1 = 1.3$, $\lambda_2 = 1.1$, $\lambda_3 = 0.9$, $\lambda_4 = 0.7$, $\lambda_5 = 0.5$, $\alpha = 1$).

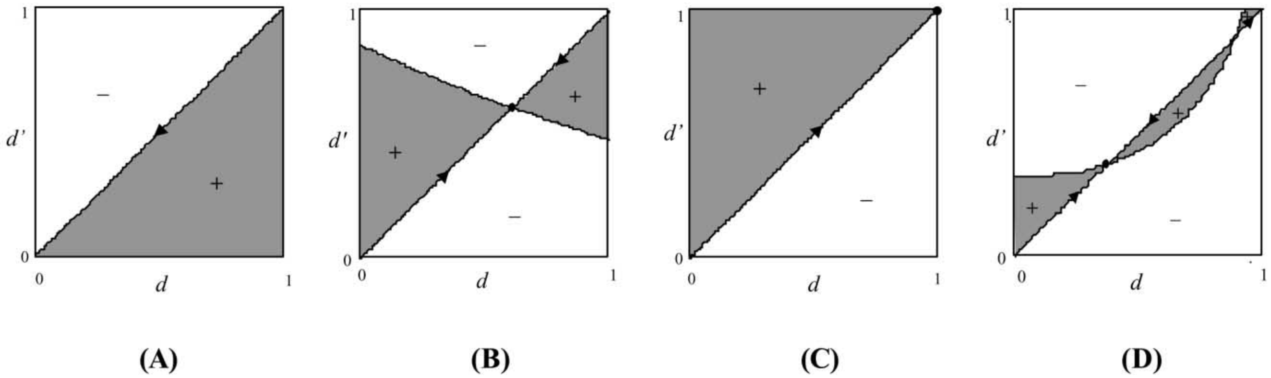

Figure 3: Four patterns of evolution of dispersal. The resident strategy is denoted by d and the mutant strategy by d'. The shaded areas indicate combinations of d and d' for which the mutant can invade the resident. The arrows indicate the direction of evolution. The points represent the selected dispersal probability, which is denoted as d_{CSS}. *A*, Philopatry is selected ($d_{\text{CSS}} = 0$). Simulations done with parameters $T = 3$, $\mu = 0.6$, $\mu_D = 0.7$, $\lambda_1 = 2$, $\lambda_2 = 0.9$, $\lambda_3 = 0.7$, $\alpha = 1$. *B*, A mixed strategy is selected ($0 < d_{\text{CSS}} < 1$). Simulations done with parameters $T = 3$, $\mu = 0.6$, $\mu_D = 0.7$, $\lambda_1 = 2$, $\lambda_2 = 0.9$, $\lambda_3 = 0.48$, $\alpha = 1$. *C*, Pure dispersal is selected ($d_{\text{CSS}} = 1$). Simulations done with parameters $T = 3$, $\mu = 0.6$, $\mu_D = 0.7$, $\lambda_1 = 2$, $\lambda_2 = 0.9$, $\lambda_3 = 0.3$, $\alpha = 1$. *D*, Depending on the initial dispersal, the population may evolve to two various outcomes: here, a mixed strategy or total dispersal. Simulations done with parameters $T = 3$, $\mu = 0.2$, $\mu_D = 0.37$, $\lambda_1 = 1.95$, $\lambda_2 = 1.2$, $\lambda_3 = 0.45$, $\alpha = 1$.

Local Competition and Demographic Stochasticity Are Necessary for the Selection of Dispersal from Unsaturated Patches

If there is no competition for space (T infinite) or for resources (K infinite, which entails that fecundity is density independent, $\lambda_n = \lambda$ at any density n, λ a constant), the evolutionary outcome can be calculated directly from the mean number of adults produced by each phenotype. A philopatric gives birth on average to λ/μ adults, whereas a disperser generates the same quantity multiplied by the probability to survive the dispersal phase, $\alpha/(\alpha + \mu_D)$, which is <1. Consequently, no dispersal strategy is able to invade, or can resist invasion by, the philopatric strategy; thus, philopatry is always selected. This result holds also when there is competition for space (T finite) but not for resources (K infinite, no density dependence); the same argument can be used with the term $\alpha/(\alpha + \mu_D)$ replaced by $\alpha(1 - p_T)/[\alpha(1 - p_T) + \mu_D]$. In this case, however, there can be much overall dispersal because of the expulsion from full patches. Expulsion then creates sufficient exchange between populations to prevent from patch isolation (that would lead in the long term to global extinction) and to allow escape from the local competition for space.

In the general case where reproduction within a patch is reduced by the presence of congeners (i.e., $\lambda_n > \lambda_{n+1}$ for any n, K finite, T finite or infinite), there are three possible evolutionary outcomes: philopatry ($d_{\text{CSS}} = 0$; fig. 3*A*), a mixed strategy ($0 < d_{\text{CSS}} < 1$; fig. 3*B*), and pure dispersal ($d_{\text{CSS}} = 1$; fig. 3*C*). Thus, under local density dependence, demographic stochasticity by itself can generate enough variability in patch density to promote the evolution of dispersal from unsaturated patches, even in the absence of any externally imposed variation of environmental quality. Actually, demographic stochasticity and density de-

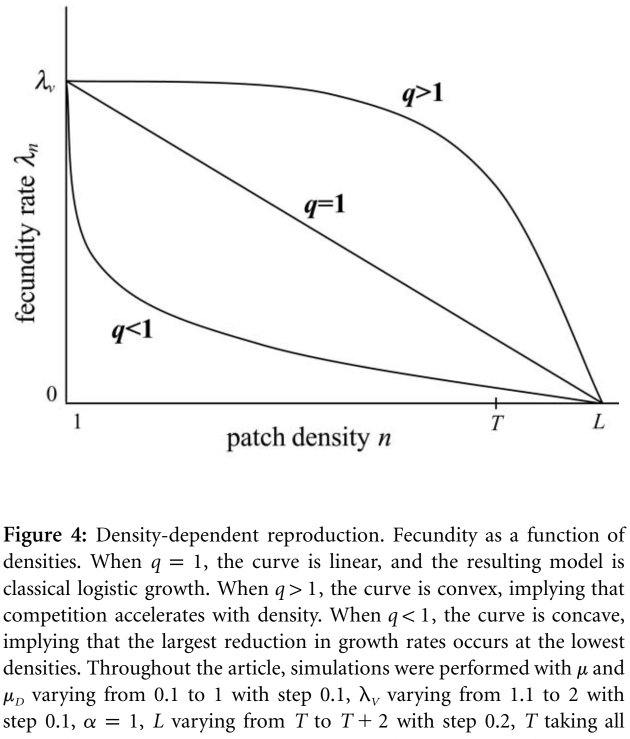

Figure 4: Density-dependent reproduction. Fecundity as a function of densities. When $q = 1$, the curve is linear, and the resulting model is classical logistic growth. When $q > 1$, the curve is convex, implying that competition accelerates with density. When $q < 1$, the curve is concave, implying that the largest reduction in growth rates occurs at the lowest densities. Throughout the article, simulations were performed with μ and μ_D varying from 0.1 to 1 with step 0.1, λ_V varying from 1.1 to 2 with step 0.1, $\alpha = 1$, L varying from T to $T + 2$ with step 0.2, T taking all values between 3 and 10 when $q = 1$, and $T = 3$, 6, and 10 when $q \neq 1$. In terms of the logistic growth rate formalism, the carrying capacity K can be written as $K = L - (\mu/\lambda_V)(L - 1)$.

pendence are complementary: demographic stochasticity provides variability in both time and space, while density dependence makes that individuals feel this variability. Except when the dependence of growth rate is highly nonlinear and bistability can occur (fig. 3*D*), the population will evolve toward a unique dispersal strategy. The actual value of selected dispersal (d_{CSS}), however, depends on demographic parameters in complex ways.

Does the Level of Demographic Stochasticity Influence Dispersal?

Intuitively, one would expect selected dispersal to decrease as demographic stochasticity decreases. However, as emphasized by Foley (1997), defining an indicator of demographic stochasticity in a metapopulation is not straightforward. The effect of demographic stochasticity is expected to fade out as the number of individuals within patches increases. As an indicator of within-patch crowding, one can therefore use the carrying capacity K, as defined for logistic regulation (fig. 4; $q = 1$). One may also characterize the level of demographic noise by the variability in the changes over time of the local population sizes, as measured by the variance-to-mean ratio (VMR); demographic stochasticity increases with this VMR. The VMR at zero dispersal for a patch with density n is

$$\mathrm{VMR} = \frac{\lambda_n + \mu}{\lambda_n - \mu}. \tag{4}$$

We chose to vary the VMR by keeping the denominator constant (which allows K to stay constant) and varying the numerator. This is done by adding the same quantity ε to both nominal values λ_n and μ (cf. Parvinen et al. 2003). This ε we used as our second indicator of demographic stochasticity.

Figure 5 illustrates how the selected dispersal varies in response to changing indicators of demographic stochasticity. As expected, dispersal decreases with an increase of K, that is, with a decrease of demographic stochasticity. In contrast, there is no simple relationship between ε and selected dispersal. Unexpectedly, the predominant pattern is a decrease of dispersal with an increase of ε, that is, with an increase of demographic stochasticity. In some cases, the response of selected dispersal is nonmonotonic (in terms of both dispersal strategy and overall dispersal). Thus, the two indicators used lead to contradictory effects on the evolution of dispersal. This is not so surprising because demographic stochasticity is a complex notion that offers several features. Moreover, changes in level(s) of demographic stochasticity are intimately tied to changes in demographic parameters. Demographic stochasticity is the necessary cause of variability, but the ensemble of demographic processes interacts to determine the effect on the evolution of dispersal.

Influence of Life-History Traits

To investigate the influence of all components of the demographic profile on the evolution of dispersal, we introduce an explicit model of density dependence acting on birth rates:

$$\lambda_n = \lambda_V \left[1 - \left(\frac{n-1}{L-1} \right)^q \right], \tag{5}$$

where λ_V is the intrinsic birth rate, that is, the birth rate of an individual in a virgin patch (in the absence of other individuals so that $\lambda_1 = \lambda_V$), L measures the intensity of competition, and q measures how sensitive the effect of competition is to an increase in density. We investigate three cases: linear decrease of birth with density ($q = 1$), accelerating decrease of birth with density ($q > 1$), and decelerating decrease of birth with density ($q < 1$). The effect of variation of life-history traits λ_V, μ, μ_D, and L on the evolution of dispersal was analyzed through extensive numerical simulations; the parameter ranges used in the computations are given in the caption to figure 3.

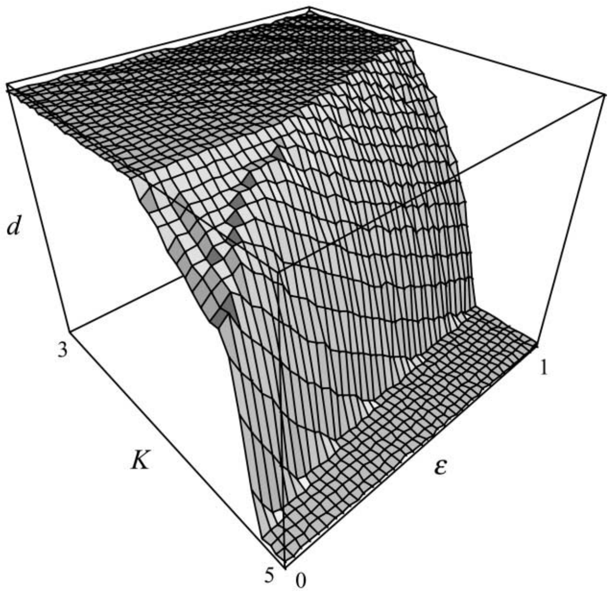

Figure 5: Demographic stochasticity and dispersal. The evolutionary stable dispersal probabilities are plotted as a function of the indicator of demographic stochasticity ε and K. Note that d_{CSS} decreases with K. In most cases, d_{CSS} decreases with ε but not invariably so. Simulations done with parameters $T = 5$, $\mu_D = 0.3$, $\alpha = 1$.

The influence of demographic parameters on dispersal from unsaturated patches is always monotonic: selected dispersal increases with an increase in mortality or in the intensity of competition and decreases with an increase in intrinsic fecundity or in dispersal mortality (fig. 6). This pattern holds even in the parameter region where bistability is possible (fig. 3*D*). It is interesting to note that the influence of dispersal mortality is minor relative to that of the other parameters (fig. 7*A*). In particular, dispersal mortality has little effect on the transition from philopatry to dispersal. Dispersal is equally sensitive to changes in mortality rate as it is to changes in birth rate (fig. 7*B*, 7*C*).

Selective Pressures

The evolution of dispersal is not a simple response to the level of demographic stochasticity but depends intricately on the species' life-history traits. To identify the selective pressures that mold the evolution of dispersal in this model, we address the case where there are few territories within patches ($T = 2$ and $T = 3$). The general patterns that emerge are tested numerically for more complex scenarios.

Simplest Cases Reveal a Decisive Influence of Local "Growth Rates"

When $T = 2$, the fitness gradient reduces to the simple form

$$\left.\frac{\partial R_m(d', d)}{\partial d'}\right|_{d'=d} = U(\lambda_2 - \mu), \qquad (6)$$

where U depends on the model parameters but is always

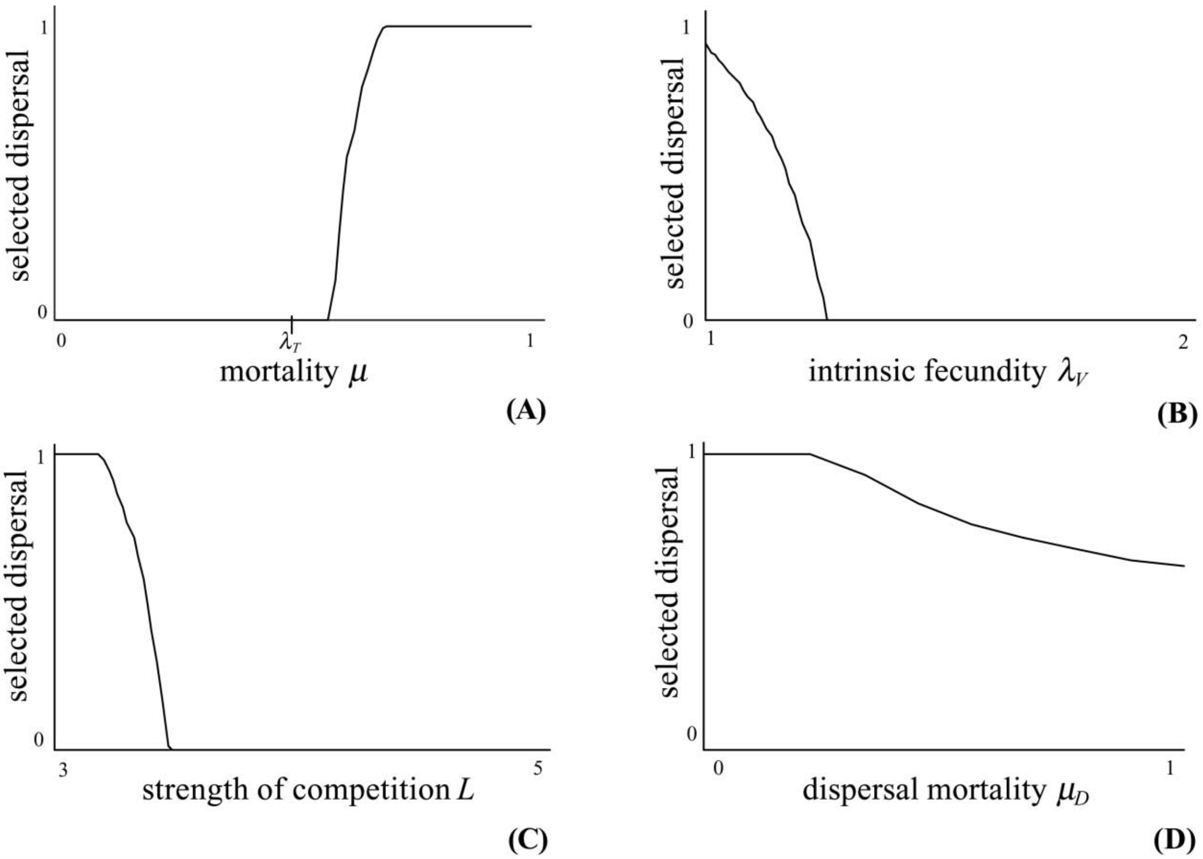

Figure 6: Effect of the life-history traits on the evolution of dispersal. Selected dispersal probability as a function of demographic parameter. *A*, Selected dispersal probability d_{CSS} when varying mortality μ. Notice that dispersal is selected when μ becomes slightly larger than λ_T. Numerical results for the pattern $T = 3$, $\lambda_V = 1.5$, $L = 4$, $\mu_D = 0.3$, $\alpha = 1$. *B*, Selected dispersal as a function of intrinsic fecundity λ_V. Numerical results for the pattern $T = 3$, $\mu = 0.5$, $L = 4$, $\mu_D = 0.55$, $\alpha = 1$. *C*, Selected dispersal as a function of L. When L increases, the strength of competition decreases. Numerical results for the pattern $T = 3$, $\mu = 0.5$, $\mu_D = 0.6$, $\lambda_V = 2$, $\alpha = 1$. *D*, Selected dispersal as a function of dispersal mortality μ_D. Numerical results for the pattern $T = 3$, $\mu = 0.3$, $\lambda_V = 1.6$, $L = 3.2$, $\alpha = 1$.

negative (see app. C in the online edition of the *American Naturalist*). The term $\lambda_2 - \mu$ is the expected instantaneous per capita growth rate in full patches. For the sake of clarity, such a quantity $\lambda_n - \mu$ will be hereafter referred to as the growth rate in patches at density n. Equation (6) indicates that the sign of $\lambda_2 - \mu$ entirely determines the direction of evolution: philopatry evolves when $\lambda_2 - \mu > 0$ (fig. 3*A*), whereas pure dispersal evolves when $\lambda_2 - \mu < 0$ (fig. 3*C*). Thus, the other parameters and the distribution of densities bear no influence on the outcome of evolution.

With $T = 3$, the fitness gradient can still be written in a relatively compact form:

$$\left.\frac{\partial R_m(d', d)}{\partial d'}\right|_{d'=d} =$$

$$Y\{(\lambda_3 - \mu)Z + (\lambda_2 - \mu)[(\lambda_2 - \mu)Q + S] + (\lambda_1 - \mu)^2 W\}. \quad (7)$$

Although Y, Z, Q, S, and W are complicated functions of the parameters, one can check that Y and W are always positive and Z, Q, and S are always negative (for details, see app. C). Equation (7) yields four main insights into the selective forces that operate on dispersal. First, if $\lambda_3 - \mu > 0$, which implies that patches are sources irrespective of their density, all terms of the gradient are negative except the last one. Therefore, there is a strong selective force against dispersal. A necessary, though not sufficient, condition for the selection of dispersal is $(\lambda_1 - \mu) > 2(\lambda_2 - \mu) + 2(\lambda_3 - \mu)$ (see app. C); that is, $\lambda_1 - \mu$ should be large and/or $\lambda_2 - \mu$ and $\lambda_3 - \mu$ should be small. Thus, the difference in growth between patches with no competition and patches with competition needs to be large. As soon as the smallest local growth rate, $\lambda_3 - \mu$, is negative, the pressure against dispersal is much lower. This suggests that the sign of the growth rate in full patches plays a key role for the selection of dispersal, as in the case $T = 2$. Second, the role of the growth rate at intermediate density, $\lambda_2 - \mu$, is more complex: when positive, it selects against dispersal, and when negative, it may select for as well as against dispersal depending. Third, the term incorporating the growth rate at lowest density, $\lambda_1 - \mu$, is always positive. This growth rate is mainly experienced by individuals that have colonized empty patches. Thus, equation (7) suggests that there is always a positive pressure for dispersal corresponding to the colonization of empty patches. Fourth, although growth rates play a key role, the precise outcome of the evolution depends in a complex way on the effect of the global structure of the metapopulation (through its effect on the factors Y, Z, Q, S, and W).

The Selection of Dispersal from Unsaturated Patches Is Conditional on the Existence of Dynamical Sinks

Extensive numerical simulations indicate that (apart from a few exceptions, discussed later), whatever the number of territories, a necessary condition for the selection of dispersal is

$$\lambda_T - \mu < 0. \quad (8)$$

Thus, dispersal from unsaturated patches evolves only if individuals experience a higher risk to die (μ) than the rate at which they reproduce (λ_T) under the most crowded conditions; in other words, full patches have to act as demographic sinks when full. This condition is a good predictor in the sense that nonzero dispersal probabilities are selected almost as soon as it is fulfilled (see examples in figs. 6, 7). Thus, the transition from philopatry to dispersal depends strongly on the consequences of competition in high-density sites. This suggests dispersal is largely determined by the need to leave specifically the worst patches.

The avoidance of crowding may explain the influence of within-patch demographic traits on selected dispersal (see “Influence of Life-History Traits”). For instance, an increase of mortality μ induces a decrease of the growth rate $\lambda_T - \mu$, or, expressed differently, the risk of dying before reproducing increases in high-density patches, thus making it unprofitable to stay in such patches so that dispersal is favored. A decrease of intrinsic fecundity (λ_V) and an increase of competition ($1/L$) have similar effects (see app. D in the online edition of the *American Naturalist*). Furthermore, the pattern of sensitivity of $\lambda_T - \mu$ to mortality and fecundity near 0 is similar to the pattern of the sensitivity of dispersal to the same parameters (app. D).

The Gain in Growth from Dispersing Modulates the Selected Probability of Dispersal

An exception to condition (8) occurs when the concavity of the density dependence (fig. 4) is very pronounced ($q \ll 1$). This makes conclusions obtained in the case $T = 3$ more general: the growth rate at lowest density, $\lambda_1 - \mu$, needs to be much higher than the other growth rates for dispersal not to evolve even when the saturated patch state is a demographic sink. Thus, the growth rate difference, evaluated as the difference between the growth rates under strong and mild competition, is a second factor involved in the selection of unsaturated patches.

In “The Selection of Dispersal from Unsaturated Patches Is Conditional on the Existence of Dynamical Sinks,” we showed how the influence of demographic parameters on

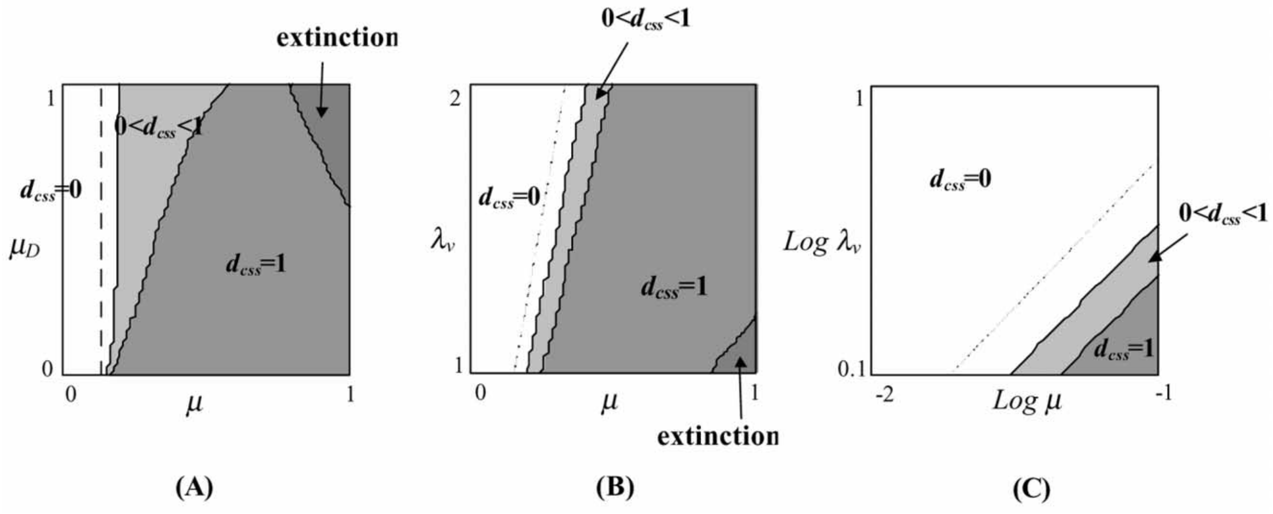

Figure 7: Relative influence of demographic parameters. In the white area, philopatry is selected; in the light grey area, intermediate dispersal is selected; in the dark grey area, pure dispersal is selected. At the right of the dashed line, $\lambda_T - \mu > 0$; at the left, $\lambda_T - \mu < 0$. *A*, Level of dispersal selected as a function μ and μ_D. Parameters used: $T = 3, \lambda_V = 1.6, L = 3.2, \alpha = 1$. *B*, Level of dispersal selected as a function μ and λ_V. Parameters used: $T = 3$, $L = 3.4$, $\mu_D = 0.2$, $\alpha = 1$. *C*, Level of dispersal selected as a function μ and λ_V. Parameters used: $T = 3$, $L = 3.4$, $\mu_D = 0.2$, $\alpha = 1$.

the evolution of dispersal may be explained by their effect on the growth rate in the saturated patch state. The effect of demographic parameters on the growth rate difference reinforces the process. An increase of mortality (respectively, a decrease of intrinsic fecundity or an increase of competition) increases the difference between the highest and the lowest growth rates and thus raises the gain in growth to disperse from high-density patches. The pressure to leave such patches is strengthened, which favors more dispersal (see app. D). Furthermore, the pattern of sensitivity of the growth rate difference to mortality and fecundity is similar everywhere to the pattern of the sensitivity of dispersal to the same parameters (app. D). Together with the results of the previous section, this suggests that whereas the level of competition in high-density patches is nearly decisive for the selection of nonzero dispersal, the growth rate difference regulates the precise value of selected dispersal.

Dispersal Mortality and Dispersal Cost

Elasticity analysis suggests that dispersal mortality has a weak influence on the selection of dispersal (see "Influence of Life-History Traits"; fig. 7). This is not surprising if one realizes that dispersal mortality does not affect the two key determinants that we identified earlier: the avoidance of competition in high-density patches and the magnitude of the growth rate difference. In addition to this, dispersal mortality μ_D has a negative effect on the frequency of full patches p_T. An increase of μ_D and the entailed decrease in full patches p_T act oppositely on the probability to find an empty territory, $\alpha(1 - p_T)/[\alpha(1 - p_T) + \mu_D]$; thus, the variation of this quantity with μ_D is weak.

Dispersal costs depend not only on the additional mortality due to not being within a patch, $\mu_D - \mu$, but also on the loss in fecundity and on the time spent in the disperser pool, linked to the probability to find an empty territory. Our calculations show that an increase of mortality μ and competition $1/L$ and a decrease of fecundity λ_V change these quantities in a way that favors dispersal. Thus, the avoidance of dispersal costs favors dispersal synergistically with the pressures described previously.

Both analytical and numerical results emphasize the key role of the avoidance of competition in high-density patches and the secondary effect of the magnitude of the growth rate difference on the precise outcome of the evolution. This suggests that local processes dominate the effects of the global dynamics in determining selective pressure on dispersal. As we have shown, this may simply be due to the almost perfect synergy between all effects (the opposite effects of dispersal mortality are the exception). An important result is that one cannot infer from the global dynamics of the system what will be the forces acting on the selection of dispersal: there is no simple optimization rule that explains the selected dispersal value (no minimization of the frequency of empty patches or maximization of the frequency of full patches or of mean density), which is not surprising given complex interaction between resident and mutant (Metz et al. 1992, 1996; Mylius 1999); moreover, for the same distribution of patch states achieved from different combinations of demographic trait values, philopatry in unsaturated patches ($d = 0$) or pure dispersal ($d = 1$) can be selected: growth rates are crucial, whereas the global density distribution is irrelevant.

Kin Selection

Our analysis primarily aims to investigate the effect of demographic stochasticity on the evolution of dispersal. However, the combination of spatial subdivision and limited dispersal that makes demographic stochasticity important also means that individuals share their environment with relatives. This, in turn, implies that our model includes a kin selection component. As Hamilton and May (1977) pointed out in their seminal article, kin selection can strongly favor dispersal when dispersing juveniles alleviate conditions for their stay-behind kin (siblings and other relatives). Unfortunately, assessing the strength of this effect in our model is not an easy task, since it requires averaging over the numbers of relatives in the patch and on how much these benefit from dispersal decisions.

For all intents and purposes, our fitness measure (R_m) is a measure of inclusive fitness (sensu Hamilton 1964) since it gives the reproductive success of a mutant colonizer via all of its local descendants. That is, our analysis is essentially about how, by varying its dispersal strategy, a clone can optimize the way it exploits its local resources (van Baalen and Sabelis 1995). In our model, it is rather the concept of "individual fitness" that is the more difficult one to define. Consider a newborn that has to decide whether to stay or not. If it stays, it will have a net birth rate of λ_{n+1} (assuming it was born in a patch with n individuals), so if the patch would stay constant, it can expect to have λ_{n+1}/μ offspring. If this value is <1, it is always better to disperse. However, it may pay to disperse also if λ_{n+1}/μ is >1. Suppose that of the n patch occupants, m are relatives. Deciding to stay would mean that all of these would see their rate of reproduction reduced from λ_n to λ_{n+1}. Taken together, the disperser would lose $\lambda_{n+1}/\mu - 1$ offspring itself, but its m relatives combined would gain $m(\lambda_n/\mu - \lambda_{n+1}/\mu)$ offspring. Under certain conditions, this condition will be fulfilled: the individual would disperse at its own cost to benefit its relatives. The frequency with which this happens would therefore give an indication about the intensity of dispersal through kin selection.

However, this reasoning presupposes that conditions in the patch stay constant, whereas in reality, they will continue to fluctuate not only in terms of overall densities but also in terms of the proportion of individuals that are related. The solution is to replace expressions like λ_n/μ by the true expected fitness of individuals in a patch containing r residents and m mutants (relatives). This can be done using a formalism very similar to the one used to derive overall R_m of the mutant (for those who are interested in this problem, see app. E. in the online edition of the *American Naturalist*), but the expressions do not generate much insight, and we do not give them here.

Discussion

Demographic Stochasticity and the Evolution of Dispersal

The metapopulation model analyzed in this article takes account of the discrete number of individuals within patches, so the effect of demographic stochasticity on population and evolutionary dynamics can be investigated. Our results show that demographic stochasticity may provide enough variability between and within habitats to favor the evolution of dispersal, even if the environment itself is homogeneous in time and space. Thus, demographic stochasticity cannot be ignored as innocent noise but may have important evolutionary consequences. This result corroborates the conclusions of Nagy (in press) in his specific model on a metapopulation of American pika (*Ochotona princeps*). It is also in agreement with the conclusions of Travis et al. (1999) based on a model of density-dependent dispersal. This conclusion is even in broad agreement with Hamilton and May's (1977) seminal article on the evolution of dispersal: even if this article is usually cited as an example of how dispersal can be favored in the absence of spatiotemporal variation, in their model, quite a bit of stochasticity results from the lottery among juveniles competing for vacated territories.

We found that the effect of demographic stochasticity on the evolution of dispersal decreases with the mean size of local populations, as expected. Therefore, its influence should diminish relative to other causes, such as environmental fluctuations, when local populations become large. In our model, which does not incorporate environmental variations, demographic stochasticity is essential to create the variability necessary to the evolution of dispersal. However, we found that the level of demographic stochasticity alone is not sufficient to predict dispersal, since the entire suite of demographic processes interacts to determine the outcome of evolution. For example, the two indicators of demographic stochasticity that we used have opposite effects on the evolution of dispersal. A comparison of the effects of environmental and demographic stochasticity on the evolution of dispersal would require a careful consideration on the different nature of the two processes. While environmental stochasticity is a priori not influenced by demography, the effect of demographic stochasticity cannot be assessed without taking into account that it is intricately interwoven with demographic events.

Multiple Pressures on Dispersal

The complex interaction between the metapopulation's ecology and evolution (involving a feedback effect of dispersal on the global structure of the metapopulation) implies that an evolutionary outcome reflects a balance of multiple forces. The benefits from dispersing or not depends on this global state. For instance, the existence of empty patches enhances the success of dispersal strategies, as shown in many studies (Comins et al. 1980; Levin et al. 1984; Olivieri et al. 1995; Gandon and Michalakis 2001). Yet, there is no simple relationship between selected dispersal and the frequency of local extinctions (generated here by demographic stochasticity only). This is in contrast with previous studies where feedback effects are ignored. This confirms that the intricate interaction between the landscape dynamics and the demography cannot be ignored (Ronce et al. 2001).

Given our assumption of automatic dispersal from saturated patches (expulsion), competition acts on the evolution of dispersal in two ways. First, dispersal from unsaturated patches will be selected only if the most crowded patch states are demographic sinks: competition needs to be so severe that, on average, less than one offspring is produced per capita at the highest level of competition. Thus, the transition from philopatry to dispersal for juveniles that have the choice depends almost entirely on a crowding effect: dispersal allows escape from the negative effect of high density within patches (Holt and Barfield 2001; Ronce et al. 2001). Second, the selected dispersal value depends quantitatively on the fluctuation of local competition in space and time expressed by the difference in growth rates. Spatiotemporal variation in local fitness has often been underlined as a key factor for the evolution of dispersal (Levin et al. 1984; Pulliam 1988; McPeek and Holt 1992; Holt and Barfield 2001). Our results suggest that such variations are less important for the selection of dispersal than the effect of crowding in high-density patches. These conclusions change if individuals cannot detect whether empty territories are available. In that case, there is an additional component in the selective pressure on dispersal to avoid staying in saturated patches. This will increase the CSS dispersal rate, but by how much depends on the frequency of patch saturation.

The role of kin selection cannot be easily disentangled from the effect of demographic stochasticity. In contrast to discrete-generational dynamics considered in models like that of Hamilton and May (1977), where local competition takes the form of a lottery among the members of one or two generations only (Comins et al. 1980; Frank 1986; Gandon and Michalakis 1999; Ronce et al. 2000), our model includes the consequences of interactions between individuals of potentially many overlapping generations. Moreover, competition is not only for space (available territories) but also for resources (modifying birth rates of all patch occupants). Last, a newborn juvenile should let its decisions depend on its estimate of how many relatives there are in its natal patch and on how its decisions affect the reproductive success of each of these. Even though kin selection certainly operates in our model, its consequences are not as easily assessed as in Hamilton and May's (1977) model. We feel that this is a fact of nature rather than a shortcoming of our model. A more extensive analysis of the relationship between demographic stochasticity and kin selection will be presented in a separate article. Here it suffices to state that the effect of kin selection on dispersal requires demographic stochasticity and that its influence on the selection of dispersal may be modulated by the mode of competition for empty sites, that is, whether it is a matter of occupying the largest proportion of sites when they become available synchronously (as in Hamilton and May 1977) or of being the first to occupy sites when they become available one at a time (as in our model).

Dispersal and Species Life Histories

Few theoretical studies have investigated the impact of demographic characteristics on the evolution of dispersal. In our study, the selected probability to disperse from unsaturated patches increases as mortality and competition increase and decreases as fecundity and dispersal mortality increase. This suggests that, under the pressure of demographic stochasticity, dispersal from unsaturated patches (or from all patches when there is no saturation) should be selected more strongly in low-fecundity species or high-mortality species as well as in highly competitive species. These results are in line with the conclusions of Comins et al. (1980) but contrasts with other previous studies (Levin et al. 1984; Olivieri et al. 1995). In these studies, variations in life-history traits occur globally and affect all patches simultaneously, whereas in our study, variations of vital rates affect the amplitude of fitness variations locally and asynchronously. A decrease of survival or of competitive ability increases the differences between high- and low-density patches, which favors dispersal. Conversely, an increase of fecundity decreases these differences, favoring low dispersal.

Many studies consider the additional mortality due to travel in a hostile environment as the main cost of dispersing (e.g., Hamilton and May 1977; Frank 1998; Travis and Dytham 1998). The role of dispersal mortality is twofold: on the one hand, it reduces the survival of dispersers compared with philopatric individuals; on the other hand, it decreases competition for empty territories. In our model, dispersers that fail to find an empty territory at once are allowed to wait a better opportunity in a disperser pool, contrary to what happens in most models (but see Kokko and Sutherland 1998; Pen and Weissing 2000). Therefore, the cost of dispersal depends also on the local demographic processes. Mortality but also the loss in fecundity due to staying outside patches are the main determinants of this cost. More generally, the global dynamics of the metapopulation influence the cost of dispersal as soon as demographic stochasticity is involved, even in the absence of a disperser pool.

Competition for Space and Competition for Resources

Our results suggest that the evolution of dispersal is strongly affected by the relative importance of the competition for space and the competition for resources. Indeed, how the number of territories per patch T, measuring the degree of competition for space (and, more importantly, a strict upper limit to patch capacity), relates to the carrying capacity K, measuring the degree of competition for resources (a nonstrict limit to patch capacity), is crucial. When there is no limit in the number of reproductive territories within a patch but competition for resources limits groups, dispersal is always favored. Thus, in contrast to what is usually predicted, we found that spatiotemporal variation of the environment is not necessary to select for unconditional dispersal (Levin et al. 1984; McPeek and Holt 1992; Lemel et al. 1997). Spatiotemporal fluctuations induced by demographic stochasticity are sufficient. In contrast, when competition is for space rather than for local resources, philopatry is favored in unsaturated patches (but note that there can still be much dispersal from saturated patches). Finally, if there is both competition for resources and space, dispersal from unsaturated patches will evolve only if the competition for resources is more intense than for space. Therefore, an explicit distinction between various causes of competition appears essential to predict the outcome of selection acting on dispersal. Since dispersal depends so strongly on the relationships between different kinds of competition, the standard way of combining all factors limiting growth and patch size in a single variable may lead to wrong assessments of the selective forces acting on dispersal (see Pulliam 1988).

This conclusion becomes all the more important when dispersing individuals have means to assess and respond to the state of their environment. This depends on the species under consideration. For example, our assumption that juveniles are capable of determining whether a patch is saturated may hold for many animals. In other organisms, in particular plants, individuals may not have the capacity to detect the presence of available sites. In such species, juveniles should disperse equally from all patches, and dispersers die when settling in full patches. This difference has no consequence on dispersal when the proportion of full patches is negligible, as is the case when the number of territories is large and local densities fluctuate around the carrying capacity induced by density dependent reproduction (K). However, when populations frequently hit the strict limit imposed by the availability of territories (T), the results will be different for the different assumptions. But note that many plants have the capacity to postpone germination if conditions are unfavorable, effectively queuing for the patch (Kokko and Sutherland 1998; Pen and Weissing 2000). The point here is that both the way carrying capacity is defined in models (strict or nonstrict) and the capacities of the species to assess the environment strongly affect the outcome. More attention should therefore be given to these aspects when studying metapopulations in which demographic stochasticity is important.

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