

Evolution of density- and patch-size-dependent dispersal rates

Hans Joachim Poethke* and Thomas Hovestadt

University of Würzburg, Ecological Field Station, Glashüttenstraße 5, 96181 Rauhenbrach, Germany

Based on a marginal value approach, we derive a nonlinear expression for evolutionarily stable (ES) dispersal rates in a metapopulation with global dispersal. For the general case of density-dependent population growth, our analysis shows that individual dispersal rates should decrease with patch capacity and—beyond a certain threshold—increase with population density. We performed a number of spatially explicit, individual-based simulation experiments to test these predictions and to explore further the relevance of variation in the rate of population increase, density dependence, environmental fluctuations and dispersal mortality on the evolution of dispersal rates. They confirm the predictions of our analytical approach. In addition, they show that dispersal rates in metapopulations mostly depend on dispersal mortality and inter-patch variation in population density. The latter is dominantly driven by environmental fluctuations and the rate of population increase. These conclusions are not altered by the introduction of neighbourhood dispersal. With patch capacities in the order of 100 individuals, kin competition seems to be of negligible importance for ES dispersal rates except when overall dispersal rates are low.

Keywords: density-dependent dispersal; metapopulation; patch size; evolutionarily stable strategy; dispersal rate; individual based model

1. INTRODUCTION

With the growing awareness of the importance of spatial aspects in ecology (Tilman & Kareiva 1997; Bascompte & Solé 1998), dispersal is increasingly considered to be an ecological key process. For example, dispersal has a significant role for the coexistence of species (Comins & Noble 1985; Rohani *et al.* 1996; Dieckmann *et al.* 1999; Hastings & Gavrilets 1999; Hovestadt *et al.* 2000). Depending on landscape structure and population parameters, dispersal also has a multitude of effects on the spatial and temporal structure of populations (Hastings 1993; Doebeli 1995; Olivieri *et al.* 1995; Ruxton 1996; Travis & Dytham 1998; Gyllenberg *et al.* 1999; Lande *et al.* 1999; Jang & Mitra 2000; Kean & Barlow 2000; Kendall *et al.* 2000). In addition, the interest in dispersal has been actuated by the needs of conservation biologists to develop strategies suited for the management of fragmented populations (Den Boer 1990; Poethke *et al.* 1996a; Appelt & Poethke 1997; Hanski 1999; Roland *et al.* 2000; Thomas 2000).

To understand the evolution of dispersal strategies, we have to investigate its consequences for the (inclusive) fitness of individuals. Theoretical models have pointed out the potential role of kin competition (Hamilton & May 1977; Comins *et al.* 1980; Gandon & Michalakis 1999; Ronce *et al.* 2000a), environmental fluctuations and habitat dynamics (Venable & Brown 1993; Travis & Dytham 1999), local extinction probability (Van Valen 1971; Olivieri *et al.* 1995; Ronce *et al.* 2000b), patch age (Ronce & Olivieri 1997) and patch capacity (McPeck & Holt 1992) for the evolution of conditional dispersal strategies. Recently, specific attention has been directed towards the evolution dispersal strategies sensitive to

population density (Ruxton 1996; Jánosi & Scheuring 1997; Sæther *et al.* 1999; Travis *et al.* 1999; Metz & Gyllenberg 2001).

The broad spectrum of model approaches and underlying assumptions often make it difficult to judge the relevance of theoretical predictions for a particular species or landscape configuration. In this paper, we focus on the evolution of dispersal rates under conditions likely to apply to insects (e.g. grasshoppers or butterflies). Many insect species survive in patchy habitats that are subject to large environmental fluctuations of patch quality (Hanski 1998); under these conditions dispersal is crucial for long-term survival of populations. The intrinsic population dynamics of insects is well studied and easy to model (Johst & Brandl 1997). In insects, migration is likely to be very risky (Den Boer 1990; Ward *et al.* 1998; Thomas & Kunin 1999; Thomas 2000), but nevertheless frequently observed (Zera & Denno 1997); i.e. there must be large benefits associated with dispersal as well. Several studies have already demonstrated that the propensity to disperse is sensitive to population density (Herzig 1995; Baguette *et al.* 1996; Rhainds *et al.* 1997; Loxdale & Lushai 1999) and patch size (Kareiva 1985; Turchin 1986; Hill *et al.* 1996; Kindvall 1999; McIntyre & Wiens 1999; Kindvall & Petersson 2000; Baguette *et al.* 2000; Roland *et al.* 2000).

Travis *et al.* (1999) focus their individual based simulation experiments on species with non-overlapping generations, a discrete dispersal phase and a type of density-dependent population growth that has been successfully used to describe the dynamics of a large number of insect populations (Bellows 1981). Thus, their approach seems to be well suited to study the evolution of dispersal in insect populations. They have shown that evolutionarily stable (ES) dispersal strategies almost always should be sensitive to population density and respond to reproductive rate, type of competition and equilibrium

* Author for correspondence (poethke@biozentrum.uni-wuerzburg.de).

population size. As we want to analyse the influence of patch size on dispersal decisions, we extend their model to allow for variance in patch capacities. In addition, we add temporal fluctuations of demographic parameters to generate environmentally induced fluctuations in population size typical for many insect populations.

A shortcoming of the analysis of Travis *et al.* (1999) lies in their *ad hoc* choice of a linear relationship between population density and dispersal probability. Thus, they restrict the outcome of their simulations to the given linear function, although they themselves suggest that a nonlinear relationship might be more appropriate. To solve this problem, we follow an approach recently presented by Metz & Gyllenberg (2001). Based on a fitness measure geared to a metapopulation, Metz & Gyllenberg present a general analytical approach to the evolution of dispersal in metapopulations and elegantly demonstrate the existence of a critical population density below which no individuals should disperse. We follow their marginal value type of argument, but restrict our analysis to the specific case of non-overlapping generations with dispersal occurring during a short synchronized phase in the life cycle. Additionally, we are only interested in the derivation of a functional relationship between dispersal rate, population density and patch size, and leave explicit numerical calculations to simulation experiments. We are thus able to simplify their analytical approach substantially.

In this paper, we first present our analytical solution for the relationship between population density, patch size and ES dispersal rates in a metapopulation with global dispersal. Our model is based on an ideal free distribution approach (Doncaster 2000) and is very similar to the marginal value considerations presented by Metz & Gyllenberg (2001). The results of the analytical model will be tested by individual-based simulation experiments. They allow us to investigate the quantitative influence of dispersal mortality and parameters affecting the population dynamics, as well as that of simplifying assumptions in the analytical approach (e.g. global dispersal, neglect of kin competition) on the evolution of dispersal rates.

2. AN ANALYTICAL MODEL FOR THE EVOLUTION OF INTER-PATCH DISPERSAL

Consider a metapopulation of a number of habitat patches. Each of these patches supports a local population of a species that reproduces in distinct generations. In common with several other studies (e.g. Johst & Brandl 1997; Ruxton & Rohani 1998; Travis *et al.* 1999), we consider the case with generations split up into two distinct phases: reproduction and dispersal. All individuals take their decision to disperse or to stay simultaneously at the start of the dispersal phase. Individuals are allowed to disperse only once. This corresponds with Travis *et al.* (1999) and with the model of Metz & Gyllenberg (2001) for the specific case of their $s = 1$. The assumption of a single dispersal event may be justified for many insects with non-overlapping generations and short periods suitable for dispersal.

We further assume that individuals can perceive and will base their dispersal decision on patch capacity (K_i) and pre-dispersal population density (C_i):

$$C_i = N_i/K_i, \quad (2.1)$$

where N_i is actual population size in patch i .

Patch capacity will depend on both patch size and habitat quality. Throughout this paper we assume that differences in patch capacity are only due to size (but see Metz & Gyllenberg 2001) and thus will use the term 'patch size'.

Each patch experiences a loss in density by emigration ($C_i \times d_i$) and an increase in density by immigration (I_i/K_i), where I_i is the expected number of immigrants arriving in patch i . Density after dispersal is thus calculated as

$$C'_i = C_i - C_i \times d_i + I_i/K_i = C_i(1 - d_i) + I_i/K_i. \quad (2.2)$$

The expected number of offspring for philopatric individuals (F_P) in patch i depends on population density at the start of the reproductive phase, i.e. on density after dispersal ($F_P = F_P(C'_i)$). We assume logistic population growth. For all types of logistic growth the reproductive success of philopatric individuals ($F_P(C'_i)$) will be a monotonously decreasing function of population density C'_i .

We assume that a fraction (μ) of individuals will die before they reach another patch of suitable habitat. For the case of global dispersal, all dispersing individuals are randomly distributed across patches. Thus, all dispersing individuals face the same dispersal mortality (μ), and the expected reproductive success of dispersing individuals (F_D) is independent of their natal patch (i). If we further assume size- and density-independent immigration, the mean number of immigrants per patch (I) will be constant and independent of patch identity. As a consequence, post-dispersal population density (C') will always decrease, and the reproductive success of philopatric individuals ($F_P(C'_i)$) will increase with the fraction of individuals leaving a patch. Following the marginal value theorem (Charnov 1976), dispersal will be more profitable than philopatry as long as $F_D > F_P(C'_i)$. For the calculation of patch-specific equilibrium dispersal rates, d_i , we have thus to distinguish the following three possible situations.

First, at very low population density, the expected success of philopatric individuals is greater than F_D at any dispersal rate. In this situation it will be more profitable for all individuals to stay

$$d_i = 0 \text{ for } F_D \leq F_P(C_i + I/K_i). \quad (2.3a)$$

Second, with increasing population density, individuals should disperse at a rate d_i equalizing the fitness of dispersing and philopatric individuals

$$0 \leq d_i \leq 1 \text{ for } F_D \geq F_P(C_i + I/K_i). \quad (2.3b)$$

Third, in some small patches the expected number of immigrating individuals (I) may already be sufficient to reduce post-dispersal fitness of philopatric individuals (F_P) below the expected fitness of dispersing individuals (F_D) regardless of dispersal rate. In this situation, it will be more profitable for all individuals born in this patch to leave:

$$d_i = 1 \text{ for } F_D \geq F_P(I/K_i). \quad (2.3c)$$

Since F_D is independent of patch identity, $F_P(C'_i)$ in patches satisfying condition (2.3b) must become independent of patch identity as well. This can either be realized in landscapes with constant population density

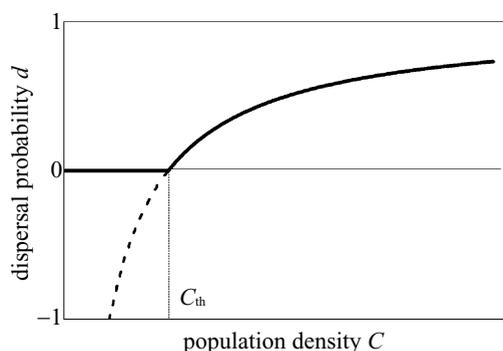


Figure 1. Predicted relationship, equations (2.3) and (2.4) in text, between population density C and dispersal probability d . With increasing density the function will asymptotically approach a probability of 1. Below the density threshold (C_{th}), the function is confined to zero. An increase in patch capacity (K_i) will elevate C_{th} .

(Parvinen 1999) or if the individual dispersal strategy (d_i) is sensitive to patch density (C_i) and patch size (K_i) in such a way that post-dispersal population density (C_i') will become independent of patch identity as well:

$$d_i = 1 - \frac{1}{C_i} \left(\hat{C} - \frac{I}{K_i} \right) \text{ for } F_P(I/K_i) > F_D > F_P(C_i + I/K_i), \quad (2.4)$$

where \hat{C} is the population density immediately after dispersal for which the reproductive success of dispersing individuals (F_D) equals that of philopatric individuals in patches satisfying condition (2.3b), i.e.

$$F_D = F_P(\hat{C}). \quad (2.5)$$

We may now extract some predictions about the principal dispersal behaviour following from equations (2.3) and (2.4).

- (i) Individual dispersal probabilities should depend on population density C_i (except for very small patches; see condition (2.3c)). As long as population density inside a patch is less than the threshold density

$$C_{th} = \hat{C} - \frac{I}{K_i}, \quad (2.6)$$

there will be no dispersal (figure 1). We predict a nonlinear increase of dispersal probability d_i with population density C_i beyond this threshold density. According to equation (2.4), for all populations satisfying condition (2.3b), dispersal will adjust post-dispersal density to \hat{C} . Threshold density C_{th} is comparable with the threshold density \tilde{x} in Metz & Gyllenberg (2001) and like these authors we expect a clumping of post-dispersal population densities around \hat{C} .

- (ii) Inspection of equation (2.6) makes clear that threshold density C_{th} declines with shrinking patch capacity K_i . Consequently, dispersal rates should increase with decreasing patch size (cf. McPeck & Holt 1992; Doncaster 2000) and reach unity in extremely small patches (condition (2.3c)).
- (iii) The influence of patch capacity (K_i) on threshold density (C_{th}) critically depends on the expected

number of immigrants (I). Consequently, the sensitivity of dispersal rates to patch size will depend on the two factors determining the number of immigrants, i.e. dispersal rate and dispersal mortality.

- (iv) With increasing dispersal mortality (μ) fewer emigrating individuals will successfully reach a new habitat and the expected reproductive success of dispersing individuals declines. Hence, due to equation (2.5), F_P must decrease, and \hat{C} increase as well. Since the number of immigrants I decreases, we can further conclude from equation (2.6) that threshold density C_{th} rises (and patch-specific dispersal probability d_i declines) with increasing dispersal mortality.

An explicit numerical solution for the dispersal probability in a specific situation must be based on a calculation of \hat{C} and the number of immigrants I , which both depend on the population dynamics of the species studied. Only for the simple case of vanishing population fluctuations, and consequently equal density in all patches, do we not need an explicit expression for the expected number of offspring $F_P(C_i)$ to estimate \hat{C} and I_i (Parvinen 1999). However, for the case of logistic growth (or other models of density-dependent population growth), equation (2.4) will lead to an implicit formulation for dispersal rates. This makes it very difficult or even impossible to derive an analytical solution. We may thus either use an iterative approach, as Parvinen (2001) has presented for the specific case of a species with continuous reproduction living in a metapopulation of indefinitely many equally sized patches, or use Monte Carlo simulations such as Travis *et al.* (1999). Additionally, simulation experiments allow us to evaluate the influence of some simplifying assumptions (such as global dispersal or the neglect of kin competition) in our analytical approach. We thus used Monte Carlo simulations: (i) to test the principal predictions of our analytical model; (ii) to quantify ES dispersal rates in specific situations; and (iii) to analyse in more detail the relationship between dispersal mortality, the specific parameters relevant for population dynamics and density-dependent fitness on the one hand, and ES dispersal rates on the other.

3. INDIVIDUAL-BASED SIMULATION EXPERIMENTS

(a) The model

Our simulation experiments are based on an individual-based model (i -state configuration model, cf. Caswell & John 1992) of insect dispersal in patchy landscapes. This model has successfully been used in studies of metapopulation dynamics in grasshoppers and butterflies (Poethke *et al.* 1996b, 1999; Amler *et al.* 1999). The landscape simulated in our model consists of a number n_{patch} of habitat patches of either constant or variable capacities K_i (see below).

Local population dynamics are governed by density-dependent reproduction of individuals according to a discrete-time logistic growth (Hassell 1998) that has successfully been fitted to the dynamics of numerous insect populations (Bellows 1981) and has also been used by János & Scheuring (1997) and Travis *et al.* (1999) in their model on the evolution of density-dependent dispersal.

According to our model, a female gives birth to Λ offspring, where Λ is Poisson distributed with mean $\Lambda_{\text{mean}}(t, \text{patch})$. Insect populations show particularly large fluctuations in population size. These fluctuations result mostly from environmentally driven fluctuations in demographic parameters. We thus extend the model of Travis *et al.* (1999) and draw the patch-specific and time-dependent value of $\Lambda_{\text{mean}}(t, \text{patch})$ from a log-normal distribution with mean λ and a standard deviation σ , the latter determining the degree of environmental fluctuations. Environmental fluctuations are assumed to be uncorrelated in space and time. Offspring develop into mature individuals with a density-dependent survival probability s :

$$s = \frac{1}{(1 + aN_i)^\beta} \quad (3.1)$$

with

$$a = \frac{\lambda^{1/\beta} - 1}{K_i};$$

β represents density dependence, N_i is the population size in patch i at the start of the reproductive phase and K_i is the carrying capacity of patch i . After all individuals have reached maturity, they disperse according to their individual dispersal probability d as outlined in the following paragraph.

Each individual is characterized by its sex, its affiliation with a specific patch i and by four alleles at two different diploid loci. The phenotype of individuals is determined by the arithmetic mean values \bar{p}_C and \bar{p}_K of the two corresponding alleles coding for density (p_C) and size dependence (p_K) of the individual's dispersal probability d . In agreement with equation (2.4), dispersal probabilities are calculated as

$$d = \left\{ \begin{array}{ll} 0 & \text{if } C_i \leq C_{\text{th}} \\ 1 - \frac{1}{C_i} (\bar{p}_C - \frac{\bar{p}_K}{k_i}) & \text{if } C_i > C_{\text{th}} \text{ and } C_{\text{th}} > 0 \\ 1 & \text{if } C_{\text{th}} \leq 0 \end{array} \right\} \quad (3.2)$$

where $k_i = K_i/K_{\text{mean}}$ is the relative capacity of patch i , K_{mean} is the mean carrying capacity of patches in the landscape and $C_{\text{th}} = \bar{p}_C - \bar{p}_K/k_i$ is the patch-size-dependent threshold density.

Since p_C is equivalent to \hat{C} in equation (2.4) we expect p_K to evolve towards the average increase in density (I/K_{mean}) induced by immigration.

In our model, individuals disperse before mating and production of offspring. Each individual has only one opportunity to disperse. Dispersing individuals die regardless of patch origin with a probability (μ) before they reach another suitable habitat. During the reproductive phase each female mates at random with one of the males present in the same patch (males can mate with several females). One corresponding allele for each locus of its descendants is then randomly drawn from each of its parents. However, any inherited parental allele can mutate with a probability m . In case of mutation, the corresponding value of p_C or p_K is modified by a value drawn with uniform probability from an interval between -0.1 and

$+0.1$ (similar to Travis *et al.* 1999). To allow for greater variability of genotypes in the first generations and to reduce the influence of mutations on the stability of the final result, we performed all simulation experiments with decreasing mutation rates

$$m(t) = 0.1 \times \exp(-2.5t/t_{\text{max}}) \quad (3.3)$$

where t is the generation number and t_{max} is the maximum number of generations.

Thus, independent of the simulated time, experiments started with mutation rates of approximately 0.1 and ended with rates below 0.001. Simulations are performed for three different scenarios, as follows.

(i) *Standard scenario*

In this scenario, all patches have the same capacity $K_i = K_{\text{mean}} = 100$. We assume global dispersal, i.e. dispersing individuals reach a patch with a probability of $(1-\mu)/(n_{\text{patch}})$. With uniform patch size the term p_K in equation (3.2) becomes meaningless and is set to zero; only p_C is free to evolve.

(ii) *Variable size*

In this scenario, patch capacities are drawn from an even distribution ($10 \leq K_i \leq 190$) with mean capacity $K_{\text{mean}} = 100$. Equation (3.2) will be used to determine dispersal probabilities.

(iii) *Nearest neighbour*

This scenario differs from the standard scenario by its dispersal mechanism. As with Travis *et al.* (1999), we also assumed that individuals only disperse to the eight neighbouring patches. To prevent edge effects we assumed our world to be a torus. To get an impression of the influence of variation in model parameters on the ES dispersal rate d , we performed simulations with all possible combinations of the following parameter values: (i) mean reproductive rate (λ) = 2, 5 and 10; (ii) intra-specific competition (β) = 0.5, 2 and 10; (iii) dispersal mortality (μ) = 0.05, 0.10, 0.20, 0.40 and 0.80; and (iv) environmental variability (σ) = 0.0, 1.0, 1.5 and 2.0. This results in a total of 180 simulation experiments ($3 \times 3 \times 5 \times 4$) for each of the three scenarios.

(b) **Results**

(i) *Standard scenario*

For all parameter combinations tested, mean dispersal rates d_{mean} as well as the density coefficient of dispersal (p_C) reached stable values after less than 3000 generations. We hence restricted simulation runs to 6000 generations, which was sufficient time to determine the evolutionary equilibrium. As shown in figure 2 for some exemplary parameter combinations, threshold density (which is synonymous with p_C in this scenario), as well as mean dispersal rate, strongly depend on dispersal mortality and strength of environmental fluctuations. While high dispersal mortality reduces mean dispersal rate due to an increase in threshold density, high environmental fluctuations have the opposite effect.

Dispersal homogenizes post-dispersal population densities between patches (figure 3). As long as population density remains below threshold density, no emigration

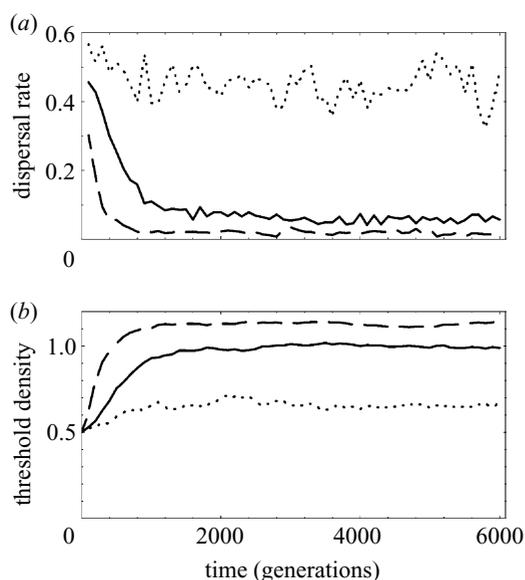


Figure 2. Evolution of (a) mean dispersal rate and (b) threshold density $C_{th}(=p_c)$ in three different simulations (standard scenario) with variable values for dispersal mortality (μ) and environmental fluctuation (σ). Density dependence ($\beta = 2.0$) and reproductive rate ($\lambda = 2.0$) were held constant. Solid line: $\mu = 0.1$, $\sigma = 0.0$; dotted line: $\mu = 0.1$, $\sigma = 2.0$; dashed line: $\mu = 0.4$, $\sigma = 0.0$.

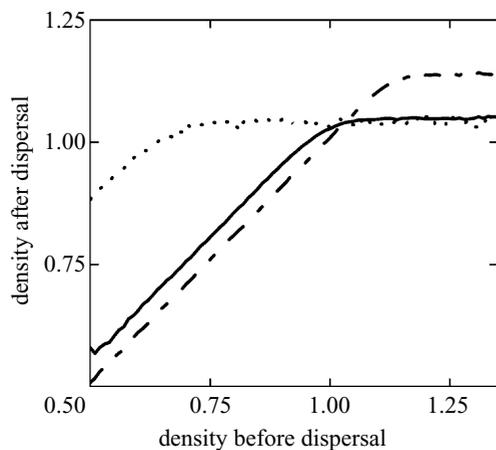


Figure 3. Mean population density after dispersal (C') as a function of density before dispersal (C). Mean values were taken over all patches and over the last 1000 generations of a simulation run. Parameters as in figure 2. Solid line: $\mu = 0.1$, $\sigma = 0.0$; dotted line: $\mu = 0.1$, $\sigma = 2.0$; dashed line: $\mu = 0.4$, $\sigma = 0.0$.

occurs, and post-dispersal population density is the sum of density before dispersal and the density increase due to immigration. As predicted by our analytical model, emigration reduces population density to a threshold for all patches with pre-dispersal density above this threshold. Post-dispersal density is thus similar in all of these patches.

A statistical analysis of the 180 standard simulations shows that all four parameters varied in our simulation experiments (λ , β , σ , μ) have a significant influence on

ES dispersal rates and account for more than 95% of the variance in evolved dispersal rates (table 1).

ES dispersal rates depend on the cost as well as the benefits of dispersal. As we do not include any investment costs of dispersal, cost of dispersal can completely be accounted for by dispersal mortality (μ) in our simulations. Excluding genetic aspects, the benefit of dispersal should be related to the amount of variation in population density that is relevant for the potential fitness improvement due to dispersal. A statistical model replacing the explanatory variables presented in table 1 by dispersal mortality and the \log_{10} -transformed coefficient of variation in population density between patches (CV_{pd}) can explain equally well the variance in the observed dispersal rates (ANCOVA: $F = 610.5$, $p < 0.001$, $r^2 = 0.97$ including a highly significant interaction term between dispersal mortality and CV_{pd} : $F = 337.3$, $p < 0.001$). An analysis of the residual variation demonstrates that the influence of the reproductive rate (λ) and environmental fluctuations (σ) on dispersal rates are almost completely accounted for by their effect on CV_{pd} (cf. figure 4); they explain only 0.09 of the remaining small variance in dispersal rates (ANOVA partial $F = 3.20$, d.f. = 11, $p < 0.01$).

According to our analytical model, dispersal rates should decrease and threshold density increase with increasing dispersal mortality. Figure 5a,b (compare separate lines) proves that both predictions are met in our simulations. As already mentioned above, we also see a positive relationship between the CV_{pd} and observed dispersal rates (figure 5a). However, as a given threshold density is more often reached at higher CV_{pd} , an increase in CV_{pd} automatically results in higher mean dispersal rates. Thus, there is no simple relationship between the threshold density and the CV_{pd} (figure 5b), at least at high dispersal mortality.

As evident from table 1, density dependence (β) has only a small positive influence on dispersal rates: β accounts for ca. 50% of the variation in dispersal rate after accounting for the effects of dispersal mortality and CV_{pd} (ANOVA partial $F = 87.46$, d.f. = 2, $p < 0.001$, $r^2 = 0.46$), with dispersal rates significantly lower at $\beta = 0.5$ compared with $\beta = 2$ or 5. Obviously, dispersal mortality defines the cost of dispersal. However, the benefit of dispersal is a function of both the expected magnitude in density reduction by emigrating from a patch with high density (dependent on CV_{pd}) and the fitness consequences of this improvement. The latter is determined by density dependence (β).

(ii) Comparison between scenarios

Results of the 'variable-size' and 'nearest-neighbour' scenarios are very similar to those of the standard scenario. The difference between scenarios in the relationship between CV_{pd} and realized dispersal rates is hardly recognizable and not statistically significant. As a limitation of dispersal to adjoining patches will principally increase the amount of kin competition after dispersal (cf. Gandon & Michalakis 1999; Gandon & Rousset 1999; Plantegenest & Kindlmann 1999; Irwin & Taylor 2000), the similarity in dispersal rates between the standard and nearest-neighbour scenario seems to contradict the relevance of kin competition for the evolution of dispersal. However, in the variable-size scenario, we find a significant

Table 1. Results of multivariate ANOVA on the relationship between evolved dispersal rate (\log_{10} transformed) and rate of increase (λ), density dependence (β), environmental variability (σ) and dispersal mortality (μ) for the standard scenario (180 simulation runs). Partial r^2 reduction indicates the reduction in total uncorrected r^2 if the term is removed from the model and + or - in the last column represents the direction of the relationship. For simplicity, weak effects ($r^2 < 0.01$) have not been included in the model.

dependent variable: \log_{10} (dispersal rate)							total $r^2 = 0.95$
source	d.f.	sum of squares (typ III)	F	p	partial r^2 reduction	effect	
constant term	1	233.86	16 527.80	< 0.001	—	—	
β	2	0.86	30.25	< 0.001	0.02	+	
$\lambda \times \sigma$	11	19.57	83.7	< 0.001	0.37	$-(\lambda), +(\sigma)$	
μ	4	30.08	531.48	< 0.001	0.57	—	
error	162	2.29	—	—	—	—	

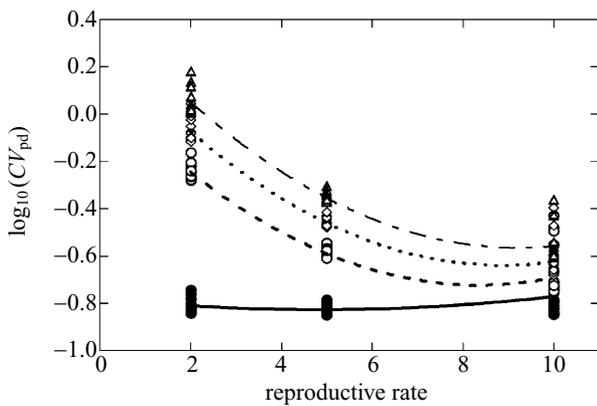


Figure 4. The effect of environmental variation (σ) and mean reproductive rate (λ) at variable density dependence (β) on the \log_{10} -transformed coefficient of variation in population density (CV_{pd}). Solid circles and line $\sigma = 0.0$; open circles and dashed line $\sigma = 1.0$; open diamonds and dotted line $\sigma = 1.5$; open triangles and long-dashed line $\sigma = 2.0$.

deviation of the size coefficient from its expected value (figure 6), i.e. the sensitivity to patch capacity is larger than predicted by our analytical model. According to equation (3.2) this especially affects dispersal from small patches. As mean dispersal rates were not altered by the introduction of variable patch sizes, this elevated size factor may indicate an effect of kin competition on dispersal strategies. This assumption is further supported by an analysis of mean offspring numbers for dispersing and philopatric individuals. In contrast to the assumptions in our analytical model and in other models ignoring kin competition (e.g. Ronce *et al.* 2000b; Metz & Gyllenberg 2001; Parvinen 2001), the mean number of offspring for dispersing individuals (F_D) is smaller than that for individuals that stay in their natal patch (F_P). This difference strongly depends on mean dispersal rates. While it is smaller than 1% for high dispersal rates ($d > 0.2$), it may increase to more than 30% in the case of extremely small dispersal rates ($d < 0.02$).

4. DISCUSSION

In our paper, we combine the simulation approach of Travis *et al.* (1999) with an analytical model similar to that

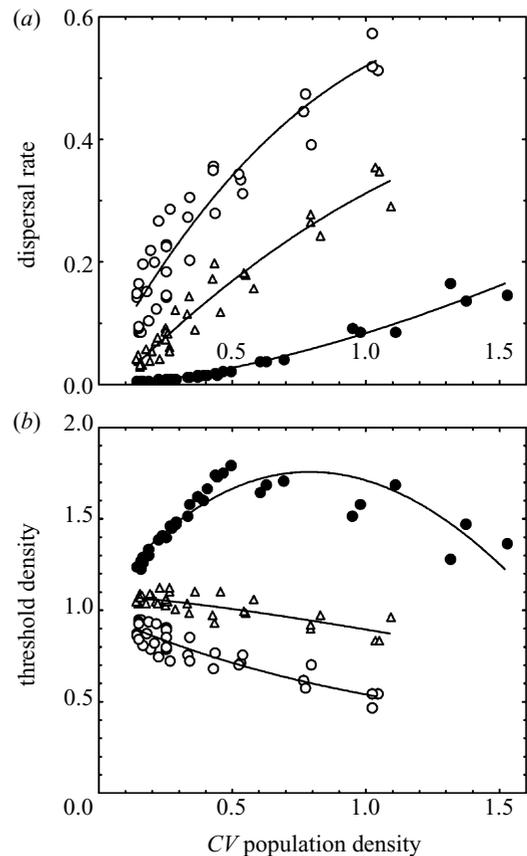


Figure 5. Population (a) mean dispersal rate and (b) mean threshold density C_{th} ($= p_c$) as functions of dispersal mortality (μ) and coefficient of variation in population density (CV_{pd}). Results of 36 replicate simulation experiments for each of the following values for mortality: $\mu = 0.05$ (open circles); $\mu = 0.2$ (open triangles); $\mu = 0.8$ (solid circles). σ , λ and β are variable across simulation experiments.

of Metz & Gyllenberg (2001). While we use the analytical approach to derive the qualitative (nonlinear) relationship between population density and dispersal rate, the simulation experiments help to test the results of this analysis and extend them to quantitative predictions. We thus combine the explanatory strength of analytical models with the greater flexibility of simulation experiments.

In our analytical approach, we did not define a specific

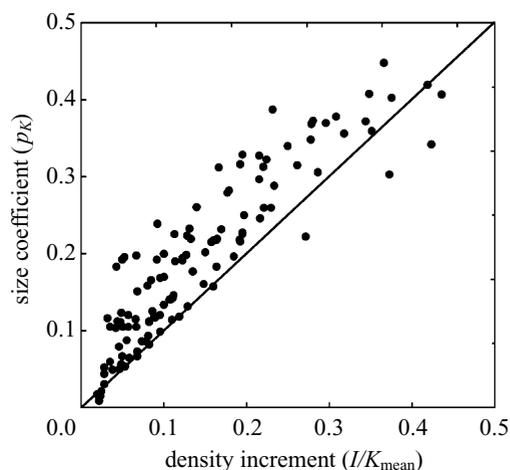


Figure 6. Relationship between evolved size coefficient (p_K) and observed mean density increase due to immigration (for patches with mean capacity) in 180 simulations with variable patch capacity ('variable-size' scenario). According to equations (2.4) and (3.2), points are expected to fall on the main diagonal. σ , λ and β are variable across simulation experiments.

relationship between population density and fitness, leaving, the investigation of specific predictions for a given population growth model (i.e. fitness function) to the simulation experiments. We thus get around many of the restrictions used in other purely analytical models, e.g. an extremely reduced strategy set (Paradis 1998), either an infinite number of populations (Gandon & Michalakis 1999) or only two (McPeck & Holt 1992; Doebeli & Ruxton 1997), the allowance of only two population states (Gandon & Michalakis 1999), limitation to global (Metz & Gyllenberg 2001) or nearest-neighbour (Jánosi & Scheuring 1997; Ruxton & Rohani 1998; Travis *et al.* 1999; Irwin & Taylor 2000) dispersal, the assumption of cost-free dispersal (McPeck & Holt 1992; Lebreton *et al.* 2000; Mathias *et al.* 2001), and the requirement for either extremely small (Ezoe & Iwasa 1997; Irwin & Taylor 2000) or infinite population size (Metz & Gyllenberg 2001).

With our model, we extend the problem posed by Olivieri & Gouyon (1997) to patch-size-dependent dispersal. We derived a nonlinear expression for the ES conditional dispersal strategy assuming that individuals can perceive both the local population density and patch size (capacity). In good agreement with previous results (e.g. Jánosi & Scheuring 1997; Ruxton & Rohani 1998; Travis *et al.* 1999; Metz & Gyllenberg 2001) our model predicts that individuals should only disperse from patches with local population density above a certain threshold and that dispersal tends to homogenize population density across patches above this threshold (cf. Ruxton & Rohani 1998; Metz & Gyllenberg 2001).

Recently, Kindvall & Petersson (2000) have demonstrated that size-dependent migration can have substantial effects on predicted metapopulation extinction rates. However, as population level (extinction risk) and individual level (fitness) considerations may lead to quite different predictions concerning optimal dispersal strategies (Comins *et al.* 1980), it is reassuring to find a positive fitness effect of size-dependent dispersal as well. For the

special case of no dispersal costs and two patches, this has already been predicted by McPeck & Holt (1992). Their model is the specific realization of our more general approach for these restricted conditions. Our analytical model, equation (2.4), also shows that the fitness relevance of size-dependent dispersal would disappear if immigration were directly proportional to patch capacity (cf. McPeck & Holt 1992). In real systems, some intermediate form of size dependence may occur, e.g. with immigration proportional to patch perimeter (Kindvall & Petersson 2000).

In particular in small populations and for small dispersal rates, kin competition may strongly influence dispersal rates (e.g. Hamilton & May 1977; Gandon & Michalakis 1999; Gandon & Rousset 1999; Irwin & Taylor 2000; Ronce *et al.* 2000a). Like most demographic models (e.g. Parvinen 1999; Ronce *et al.* 2000b; Metz & Gyllenberg 2001), our analytical model ignores this effect and eventually underestimates the sensitivity of dispersal probability to patch capacity. As individual-based models account for kin competition, this may explain the small discrepancy between the magnitude in the size coefficient predicted by the model—equations (2.4) and (3.2)—and the values realized in our experiments (figure 6). This interpretation is also supported by the observation that offspring production of dispersing individuals was substantially lower than that of philopatric individuals only when overall dispersal rate was low. Under this condition, relatedness of individuals within patches will be high and costs of dispersal can be accounted for by the benefits given to philopatric relatives. This is in good agreement with predictions from kin-selection models, which predict an increase in dispersal with increasing relatedness in local patches (e.g. Taylor 1988; Ronce *et al.* 2000a). Thus, when local populations are small and dispersal is rare, we suggest that models which ignore inclusive fitness considerations may underestimate ES dispersal rates. Further simulation experiments with smaller patch sizes, modified dispersal models and a thorough analysis of relatedness in local populations should allow to quantify the influence of kin competition in relation to demographic effects.

Of practical relevance may be the fact that the evolved dispersal rate can be accounted for by dispersal mortality and the coefficient of variation in population density only. A detailed knowledge of population parameters is thus not required to predict dispersal rates. This will ease the validation of our predictions by field experiments and allow us to extend the predictions drawn from our simulation experiments. For example, in the simulation experiments, environmental fluctuations were assumed to be uncorrelated in space and time. However, with spatially correlated fluctuations and limited dispersal distance, the variation in population density between the home patch and potential target patches will be reduced. In this case, evolution may lead to both a reduction in dispersal rates and an increase in dispersal distance (Hovestadt *et al.* 2001).

For the logistic growth model used in our simulations, the coefficient of variation mainly depends on reproductive rate (λ) and environmental fluctuations (σ). The additional effect of density dependence (β) on evolved dispersal rate is comparably small. This may be surprising and differs from the findings of Travis *et al.* (1999) and Johst *et al.* (1999). We ran additional simulations

(H. J. Poethke, unpublished data), implementing the model for population growth suggested by Maynard Smith & Slatkin (1973) and used by Ruxton & Rohani (1998) and Johst *et al.* (1999). However, they did not demonstrate a stronger influence of β on dispersal rate as long as parameter combinations did not result in chaotic local population dynamics (combinations of high β and high λ).

This project has been made possible by financial support from the Deutsche Forschungsgemeinschaft (grant PO 244/2-1) and the Bundesministerium für Bildung und Forschung (MOSAİK project, grant 01-LN0007). We thank Franjo Weissing and Stefan Messner for helpful discussions and comments during the growth of this project. Two anonymous reviewers suggested valuable improvements to the manuscript.

REFERENCES

- Amler, K., Heidenreich, A., Köhler, G., Poethke, H. J. & Samietz, J. 1999 Standardisierte Populationsprognose (SPP): eine Anwendung der zoologischen Datenbanken. In *Populationsbiologie in der Naturschutzpraxis* (ed. K. Amler, A. Bahl, G. Kaule, P. Poschlod & J. Settele), pp. 199–212. Stuttgart: Ulmer.
- Appelt, M. & Poethke, H. J. 1997 Metapopulation dynamics in a regional population of the blue-winged grasshopper (*Oedipoda caerulea*). *Insect Conserv.* **1**, 205–214.
- Baguette, M., Convié, I. & Nève, G. 1996 Male density affects female spatial behaviour in the butterfly *Proclissiana eunomia*. *Acta Oecol.* **17**, 225–232.
- Baguette, M., Petit, S. & Quéva, F. 2000 Population spatial structure and migration of three butterfly species within the same habitat network: consequences for conservation. *J. Appl. Ecol.* **37**, 100–108.
- Bascompte, J. & Solé, R. V. 1998 Spatiotemporal patterns in nature. *Trends Ecol. Evol.* **13**, 173–174.
- Bellows, T. S. 1981 The descriptive properties of some models of density-dependence. *J. Anim. Ecol.* **50**, 139–156.
- Caswell, H. & John, M. A. 1992 From the individual to the population in demographic models. In *Individual-based models and approaches in ecology* (ed. D. L. DeAngelis & L. J. Gross), pp. 36–61. New York: Chapman & Hall.
- Charnov, E. L. 1976 Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.* **9**, 129–136.
- Comins, H. N. & Noble, I. R. 1985 Dispersal, variability, and transient niches: species coexistence in a uniformly variable environment. *Am. Nat.* **126**, 706–723.
- Comins, H. N., Hamilton, W. D. & May, R. M. 1980 Evolutionarily stable dispersal strategies. *J. Theor. Biol.* **82**, 205–230.
- Den Boer, P. J. 1990 The survival value of dispersal in terrestrial arthropods. *Biol. Conserv.* **54**, 175–192.
- Dieckmann, U., O'Hara, B. & Weisser, W. 1999 The evolutionary ecology of dispersal. *Trends Ecol. Evol.* **14**, 88–90.
- Doebeli, M. 1995 Dispersal and dynamics. *Theor. Popul. Biol.* **47**, 82–106.
- Doebeli, M. & Ruxton, G. D. 1997 Evolution of dispersal rates in metapopulation models: branching and cyclic dynamics in phenotypic space. *Evolution* **51**, 1730–1741.
- Doncaster, C. P. 2000 Extension of the ideal free resource use to breeding populations and metapopulations. *Oikos* **89**, 24–26.
- Ezoe, H. & Iwasa, Y. 1997 Evolution of condition dependent dispersal: a genetic algorithm search for ESS reaction norms. *Res. Popul. Ecol.* **39**, 127–137.
- Gandon, S. & Michalakis, Y. 1999 Evolutionarily stable dispersal rates in a metapopulation with extinctions and kin competition. *J. Theor. Biol.* **199**, 275–290.
- Gandon, S. & Rousset, F. 1999 Evolution of stepping-stone dispersal rates. *Proc. R. Soc. Lond. B* **266**, 2507–2513.
- Gyllenberg, M., Hemminki, J. & Tammaru, T. 1999 Allee effects can both conserve and create spatial heterogeneity in population densities. *Theor. Popul. Biol.* **56**, 231–242.
- Hamilton, W. D. & May, R. M. 1977 Dispersal in stable habitats. *Nature* **269**, 578–581.
- Hanski, I. 1998 Spatial structure and dynamics of insect populations. In *Insect populations in theory and practice* (ed. J. P. Dempster & I. F. G. McLean), pp. 3–27. Dordrecht, The Netherlands: Kluwer Academic.
- Hanski, I. 1999 *Metapopulation ecology*. Oxford University Press.
- Hassell, M. P. 1998 The regulation of populations by density-dependent processes. In *Insect populations in theory and practice* (ed. J. P. Dempster & I. F. G. McLean), pp. 29–51. Dordrecht, The Netherlands: Kluwer Academic.
- Hastings, A. 1993 Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. *Ecology* **74**, 1362–1372.
- Hastings, A. & Gavrilets, S. 1999 Global dispersal reduces local diversity. *Proc. R. Soc. Lond. B* **266**, 2067–2070.
- Herzig, A. L. 1995 Effects of population density on long-distance dispersal in the goldenrod beetle *Trirhabda virgata*. *Ecology* **76**, 2044–2054.
- Hill, J. K., Thomas, C. D. & Lewis, O. T. 1996 Effects of habitat patch size and isolation on dispersal by *Hesperis comma* butterflies: implications for metapopulation structure. *J. Anim. Ecol.* **65**, 725–735.
- Hovestadt, T., Poethke, H. J. & Messner, S. 2000 Variability in dispersal distances generates typical successional patterns: a simple simulation model. *Oikos* **90**, 612–619.
- Hovestadt, T., Messner, S. & Poethke, H. J. 2001 Evolution of reduced dispersal mortality and 'fat-tailed' dispersal kernels in autocorrelated landscapes. *Proc. R. Soc. Lond. B* **268**, 385–392.
- Irwin, A. J. & Taylor, P. D. 2000 Evolution of dispersal in a stepping-stone population with overlapping generations. *Theor. Popul. Biol.* **58**, 321–328.
- Jang, S. R.-J. & Mitra, A. K. 2000 Equilibrium stability of single-species metapopulations. *Bull. Math. Biol.* **62**, 155–161.
- Jánosi, I. M. & Scheuring, I. 1997 On the evolution of density dependent dispersal in a spatially structured population model. *J. Theor. Biol.* **187**, 397–408.
- Johst, K. & Brandl, R. 1997 Evolution of dispersal: the importance of the temporal order of reproduction and dispersal. *Proc. R. Soc. Lond. B* **264**, 23–30.
- Johst, K., Doebeli, M. & Brandl, R. 1999 Evolution of complex dynamics in spatially structured populations. *Proc. R. Soc. Lond. B* **266**, 1147–1154.
- Kareiva, P. 1985 Finding and losing host plants by *Phylotrea*: patch size and surrounding habitat. *Ecology* **66**, 1809–1816.
- Kean, J. M. & Barlow, N. D. 2000 The effects of density-dependence and local dispersal in individual-based stochastic metapopulations. *Oikos* **88**, 282–290.
- Kendall, B. E., Bjornstad, O. N., Bascompte, J., Keitt, T. H. & Fagan, W. F. 2000 Dispersal, environmental correlation, and spatial synchrony in population dynamics. *Am. Nat.* **155**, 628–636.
- Kindvall, O. 1999 Dispersal in a metapopulation of the bush cricket, *Metrioptera bicolor* (Orthoptera: Tettigoniidae). *J. Anim. Ecol.* **68**, 172–185.
- Kindvall, O. & Petersson, A. 2000 Consequences of modelling interpatch migration as a function of patch geometry when predicting metapopulation extinction risk. *Ecol. Model.* **129**, 101–109.
- Lande, R., Engen, S. & Sæther, B.-E. 1999 Spatial scale of population synchrony: environmental correlation versus dispersal and density regulation. *Am. Nat.* **154**, 271–281.

- Lebreton, J.-D., Khaladi, M. & Grosbois, V. 2000 An explicit approach to evolutionarily stable dispersal strategies: no cost of dispersal. *Math. Biosci.* **165**, 163–176.
- Loxdale, H. D. & Lushai, G. 1999 Slaves of the environment: the movement of herbivorous insects in relation to their ecology and genotype. *Phil. Trans. R. Soc. Lond. B* **354**, 1479–1495.
- McIntyre, N. E. & Wiens, J. A. 1999 How does habitat patch size affect animal movement? An experiment with darkling beetles. *Ecology* **80**, 2261–2270.
- McPeck, M. A. & Holt, R. D. 1992 The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.* **140**, 1010–1027.
- Mathias, A., Kisdí, É. & Olivieri, I. 2001 Divergent evolution of dispersal in a heterogeneous landscape. *Evolution* **55**, 246–259.
- Maynard Smith, J. & Slatkin, M. 1973 The stability of predator–prey systems. *Ecology* **54**, 384–391.
- Metz, J. A. J. & Gyllenberg, M. 2001 How should we define fitness in structured metapopulation models? Including an application to the calculation of evolutionarily stable dispersal strategies. *Proc. R. Soc. Lond. B* **268**, 499–508.
- Olivieri, I., Michalakis, Y. & Gouyon, P.-H. 1995 Metapopulation genetics and the evolution of dispersal. *Am. Nat.* **146**, 202–228.
- Olivieri, I. & Gouyon, P.-H. 1997 Evolution of migration rate and other traits. In *Metapopulation biology* (ed. I. A. Hanski & M. E. Gilpin), pp. 293–323. San Diego, CA: Academic.
- Paradis, E. 1998 Interactions between spatial and temporal scales in the evolution of dispersal rates. *Evol. Ecol.* **12**, 235–244.
- Parvinen, K. 1999 Evolution of migration in a metapopulation. *Bull. Math. Biol.* **61**, 531–550.
- Parvinen, K. 2001 Adaptive metapopulation dynamics. PhD thesis, University of Turku, Finland.
- Plantegenest, M. & Kindlmann, P. 1999 Evolutionarily stable strategies of migration in heterogeneous environments. *Evol. Ecol.* **13**, 229–244.
- Poethke, H. J., Seitz, A. & Wissel, C. 1996a Species survival and metapopulations: conservation implications from ecological theory. In *Species survival in fragmented landscapes* (ed. J. Settele, C. Margules, P. Poschlod & K. Henle), pp. 81–92. Dordrecht, The Netherlands: Kluwer.
- Poethke, H. J., Gottschalk, E. & Seitz, A. 1996b Gefährdungsgradanalyse einer räumlich strukturierten Population der Westlichen Beißschrecke (*Platypleis albopunctata*): Ein Beispiel für den Einsatz des Metapopulationskonzeptes im Artenschutz. *Z. Ökol. Naturschutz* **5**, 229–242.
- Poethke, H. J., Griebeler, E., Appelt, E., Gottschalk, E. & Settele, J. 1999 Modelle als Instrumente der Gefährdungsabschätzung für Tierpopulationen. In *Populationsbiologie in der Naturschutzpraxis* (ed. K. Amler, A. Bahl, G. Kaule, P. Poschlod & J. Settele), pp. 126–147. Stuttgart: Ulmer.
- Rhainds, M., Gries, G. & Chew, P. S. 1997 Adaptive significance of density-dependent ballooning by bagworm larvae, *Metisa plana* (Walker) (Lepidoptera: Psychidae). *Can. Entomol.* **129**, 927–931.
- Rohani, P., May, R. M. & Hassell, M. P. 1996 Metapopulations and equilibrium stability—the effects of spatial structure. *J. Theor. Biol.* **181**, 97–107.
- Roland, J., Keyghobadi, N. & Fownes, S. 2000 Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. *Ecology* **81**, 1642–1653.
- Ronce, O. & Olivieri, I. 1997 Evolution of reproductive effort in a metapopulation with local extinctions and ecological succession. *Am. Nat.* **150**, 220–249.
- Ronce, O., Gandon, S. & Rousset, F. 2000a Kin selection and natal dispersal in an age-structured population. *Theor. Popul. Biol.* **58**, 143–159.
- Ronce, O., Perret, F. & Olivieri, I. 2000b Evolutionarily stable dispersal rates do not always increase with local extinction rates. *Am. Nat.* **155**, 485–496.
- Ruxton, G. D. 1996 Dispersal and chaos in spatially structured models: an individual-level approach. *J. Anim. Ecol.* **65**, 161–169.
- Ruxton, G. D. & Rohani, P. 1998 Fitness-dependent dispersal in metapopulations and its consequences for persistence and synchrony. *J. Anim. Ecol.* **67**, 530–539.
- Sæther, B. E., Engen, S. & Lande, R. 1999 Finite metapopulation models with density-dependent migration and stochastic local dynamics. *Proc. R. Soc. Lond. B* **266**, 113–118.
- Taylor, P. D. 1988 An inclusive-fitness model for dispersal of offspring. *J. Theor. Biol.* **130**, 363–378.
- Thomas, C. D. 2000 Dispersal and extinction in fragmented landscapes. *Proc. R. Soc. Lond. B* **267**, 139–145.
- Thomas, C. D. & Kunin, W. E. 1999 The spatial structure of populations. *J. Anim. Ecol.* **68**, 647–657.
- Tilman, D. & Kareiva, P. (eds) 1997 *Spatial ecology. The role of space in population dynamics and interspecific interactions*. Princeton University Press.
- Travis, J. M. J. & Dytham, C. 1998 The evolution of dispersal in a metapopulation: a spatially explicit individual-based model. *Proc. R. Soc. Lond. B* **265**, 17–23.
- Travis, J. M. J. & Dytham, C. 1999 Habitat persistence, habitat availability and the evolution of dispersal. *Proc. R. Soc. Lond. B* **266**, 723–728.
- Travis, J. M. J., Murrell, D. J. & Dytham, C. 1999 The evolution of density-dependent dispersal. *Proc. R. Soc. Lond. B* **266**, 1837–1842.
- Turchin, P. 1986 Modelling the effect of host patch size on Mexican bean beetle emigration. *Ecology* **67**, 124–132.
- Van Valen, L. 1971 Group selection and the evolution of dispersal. *Evolution* **25**, 591–598.
- Venable, D. L. & Brown, J. S. 1993 The population-dynamic functions of seed dispersal. *Vegetatio* **107/108**, 31–55.
- Ward, S. A., Leather, S. R., Pickup, J. & Harrington, R. 1998 Mortality during dispersal and the cost of host-specificity in parasites: how many aphids find hosts? *J. Anim. Ecol.* **67**, 763–773.
- Zera, A. J. & Denno, R. F. 1997 Physiology and ecology of dispersal polymorphism in insects. *A. Rev. Entomol.* **42**, 207–230.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.