Evolution of dispersal: the importance of the temporal order of reproduction and dispersal

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SUMMARY

Dispersal is a key process in the ecology and evolution of spatially structured populations. Dispersal may occur before or after reproduction, a feature ignored in models analysing the evolution of dispersal. Using a simulation model, we examine how the temporal order of reproduction and dispersal within the life cycle affects the competition of genotypes with different dispersal strategies. We found that the evolutionary outcome in time-discrete models depends significantly on the temporal order of dispersal and reproduction, provided that: (i) density-dependent dispersal strategies are involved into competition, and (ii) the environment is temporally variable. Our results suggest that selection can act in different directions, depending on the relative timing of dispersal, reproduction and environmental fluctuations in the life cycle.

1. INTRODUCTION

Dispersal is a key factor for the persistence of spatially structured populations, facilitating the survival of species over large geographical areas. Due to this general importance in ecology and biogeography, the evolution of dispersal in response to environmental heterogeneity in space and time is a widely discussed issue (Gadgil 1971; Van Valen 1971; Roff 1975; Hamilton & May 1977; Comins *et al.* 1980; Hastings 1983; Stenseth 1983; Levin *et al.* 1984; Holt 1985; Frank 1986; Bull *et al.* 1987; Hansson 1991; McPeck & Holt 1992; Olivieri *et al.* 1995). Most previous evolutionary models used *unconditional* dispersal, that is when irrespective of local conditions, a constant fraction of individuals leaves the habitat. In these models dispersal is only favoured in temporally varying environments (Hastings 1983; Holt 1985; for a review see Johnson & Gaines 1990). However, if individuals express *conditional* dispersal, that is dispersal changes in relation to local conditions, then dispersal may also be favoured in a spatially varying but temporally constant environment (McPeck & Holt 1992).

Here we will show that conditional dispersal introduces a further trait of general importance for the evolution of dispersal strategies: the temporal order of reproduction and dispersal within the life cycle. At first this seems to be surprising and only a question of with which process one starts the simulations in time-discrete models. McPeck & Holt (1992) are, to our knowledge, the only authors who tested in their evolutionary model the effect of the temporal order of reproduction and dispersal. They found no influence on the evolutionary outcome. But we will show that the

relative timing of dispersal, reproduction and environmental fluctuations in the life cycle may influence the evolution of dispersal strategies, and we will discuss the necessary conditions. Using a simulation model we investigate the competition between genotypes that differ only in their dispersal strategy. We include unconditional and conditional dispersal strategies into the competition. There is a plethora of possibilities to model conditional dispersal. One possibility is to introduce *habitat*-specific dispersal rates. For example, McPeck & Holt (1992) assumed that individuals have higher dispersal probabilities from smaller habitats. In their model, dispersal depends on the *mean* habitat size within a temporally varying environment. Another possibility would be that dispersal depends on the *actual* environmental conditions. For example, the actual density of the individuals in the habitat may be an indicator of habitat quality, and may influence the dispersal decision of an individual, as several authors have stressed (e.g. Gaines & McClenaghagh 1980; Hansson 1991). Therefore, we used density dependent dispersal strategies, and modelled the competition between density-dependent and density-independent dispersal strategies.

2. THE MODEL

In general our model is similar to the two-patch model of McPeck & Holt (1992). We consider an asexual species where genotypes differ in their dispersal strategies, with no trade-off between dispersal and competitive ability. Dispersers have no extra mortality. However, we extend the model of McPeck & Holt in three directions: (i) we study a range of growth rates;

(ii) we use ten habitats (because with only two habitats, at large growth rates global extinctions occur due to chaotic dynamics); and (iii) we introduce – as already mentioned – density-dependent dispersal strategies. We will show that this third extension is responsible for the effect of timing. Our spatially structured population is characterized by the local dynamics within the habitats, by dispersal between the habitats, and by the spatial and temporal variability of the habitats. For simplicity, we ignore the geometry between habitats, and dispersers are distributed randomly across the habitats. We start our simulations with equal population sizes of all genotypes in each habitat, but random initial population sizes do not alter our results. Population sizes are characterized by integer values. Corresponding real numbers generated by our equations are cut to integers. Consequently, local populations as well as the global population may go extinct.

(a) Local and global dynamics

Local dynamics of genotype g in each habitat h are characterized by two processes: (1) reproduction and (2) dispersal. Population size of genotype g after reproduction and the associated regulation in habitat h is calculated by the Ricker equation:

$$N_g^h(t) = N_g^h(t) * \exp(r * (1 - N^h(t)/K^h(t))),$$

where r and $K^h(t)$ are growth rate and carrying capacity in habitat h at time t . Note that r is equal in all habitats and for all genotypes, but $K^h(t)$ differs among the habitats (habitat heterogeneity) and the times steps (temporal variability; see below). The total population size in habitat h is $N^h(t) = \sum_g N_g^h(t)$. We define the global evolutionary outcome as the relative mean number of individuals of genotype g after $t = 2000$ generations: $f_g = N_g(t)/N(t)$. $N_g(t) = \sum_h N_g^h(t)$ is the total population size of genotype g summed over all habitats, and $N(t) = \sum_h \sum_g N_g^h(t)$ is the global population size. For non-chaotic dynamics, 2000 generations proved to be sufficient for stable frequencies of genotypes. Some genotypes may go extinct during the simulations. Therefore, we routinely checked whether extinct genotypes were able to invade again. In none of our simulations could an extinct genotype invade, so our results represent one possible evolutionary stable state of the system. For a reliable characterization of the relative frequencies of genotypes in a temporally varying environment, we averaged frequencies over 100 simulations. A further complication in estimating the average frequencies of genotypes appears at large growth rates where cyclic or chaotic dynamics occur. In these cases we additionally averaged frequencies over a time interval of 200 generations.

(b) Dispersal

Dispersal is characterized in our model by the magnitude of dispersal, the functional relationship to population density and the timing of dispersal (temporal ordering of dispersal and reproduction within the life cycle). From the large number of possible dispersal

Figure 1. Dispersal strategies of the genotypes: full line – low dispersal; dotted line – high dispersal; dashed-dotted line – exponential dispersal; dashed line – threshold dispersal. These line types are also used throughout the other figures.

strategies we select the four dispersal strategies shown in figure 1, two density-independent and two density-dependent strategies. Density-independent dispersal is represented by ‘low dispersal’ (dispersal probability $m = 0.1$) and ‘high dispersal’ ($m = 0.9$). Low dispersal describes a scenario of nearly isolated local populations (see also McPeck & Holt 1992), whereas during high dispersal individuals are spread evenly across the ten habitats. We use two qualitatively different relationships to model density-dependent dispersal (figure 1): a continuously increasing and a threshold-like relationship. As an example of the former, individuals disperse with an exponentially increasing probability from $m = 0.1$ at $N^h(t) = 0$ to $m = 0.6$ at $N^h(t) = K^h(t)$, called ‘exponential dispersal’. As an example of the latter, individuals disperse only when local population size is near the carrying capacity, called ‘threshold dispersal’ (see also Hansson 1991). We assume $m = 0.1$ if $N^h(t) < K^h(t)$, but from $N^h(t) = 0.95K^h(t)$ to $N^h(t) = 1.05K^h(t)$ dispersal probability increases steeply to $m = 0.6$. By defining a range we avoid dispersal probability switches from one dispersal level to another due to just one individual. For densities larger than the carrying capacity we assume a plateau with a maximum dispersal probability $m < 1.0$, to avoid the unrealistic situation whereby all individuals of the habitat disperse. Note that our conditional dispersal strategies are only one way of modelling density-dependent dispersal. As pointed out by one referee, density-dependent dispersal may also occur when in each generation individuals may leave the habitat with a constant probability, but land in another habitat depending on the density in that habitat. The number of dispersers of a particular genotype in habitat h is

dispersal-reproduction reproduction-dispersal

Figure 2. Flow chart of the life cycle within habitat h with different ordering of dispersal and reproduction. $K(t)$ symbolizes between-generation variation of the carrying capacity, $K'(t)$ symbolizes a possible within-generation variation of the carrying capacity (as introduced in the simulations presented in figure 4). In the case of density-independent dispersal ($m = \text{const}$), the fluctuations of the carrying capacity $K(t)$ influence only reproduction and not dispersal (see dashed line), and both life cycles become identical.

calculated by $N_g^{\text{emi}} = mN_g^h(t)$. With density-independent dispersal $m = \text{const}$, whereas with density-dependent dispersal the probability to disperse is calculated by the total number of individuals within the habitat (summed over all genotypes) in relation to the carrying capacity $m = (N^h(t)/K^h(t))$. Reproduction and dispersal may be ordered in two different ways: (i) dispersal-reproduction; and (ii) reproduction-dispersal. The census is made after the completion of the life cycle (see figure 2).

(c) Spatial and temporal variability of the habitats

Spatial heterogeneity is introduced by different carrying capacities K^h of the habitats h (from 100 to 1000 in steps of 100). Temporal variations of the environment are described by (spatially-independent) variations of the carrying capacity of each habitat K^h within the limits $K^h \pm \Delta K^h / \Delta K^h$ characterizes the strength of the fluctuations. At the beginning of a new life cycle we draw random numbers from a uniform distribution, generating a special $K^h(t)$. In a first approach, this value is assumed to be constant over the whole life cycle. But environmental conditions may also alter within the life cycle. An additional variation of the carrying capacity within the life cycle can be incorporated by changing $K^h(t)$ to $K^{h'}(t)$ (figure 2). $K^{h'}(t)$ can be uncorrelated or correlated to the capacity $K^h(t)$ drawn at the beginning of the life cycle. If there is no correlation, $K^{h'}(t)$ is independently drawn from the same uniform distribution as $K^h(t)$. A temporal correlation can be generated by drawing $K^{h'}(t)$ from a uniform distribution within the limits $K^h(t) \pm \Delta K^h(t)$,

and thus be related to $K^h(t)$ instead of K^h . Also, $\Delta K^h(t) = 0$ describes a complete temporal correlation, and thus stable environmental conditions over the whole life cycle.

3. RESULTS

For a spatially heterogeneous environment, each graph in figure 3 shows the evolutionary outcome in correlation to the growth rate. Temporal variability increases from top (temporally constant habitats) to bottom (strong fluctuations of capacities), with the two columns corresponding to different timings of dispersal within the life cycle.

In a spatially varying, but temporally constant environment (figure 3a), low dispersal is superior over a wide range of growth rates. This is in agreement with other models (Hastings 1983; Holt 1985; Johnson & Gaines 1990; McPeck & Holt 1992). However, at very low growth rates, threshold dispersal dominates. The timing of dispersal has no effect on the evolutionary outcome.

With increasing temporal variability of the environment (figure 3b-d), a polymorphism of several dispersal strategies arises over a large range of growth rates. The dominance of density-dependent dispersal increases with increasing temporal variability. However, the type of density dependence which dominates the evolutionary outcome depends on the timing of dispersal. Threshold dispersal dominates when dispersal occurs before reproduction, whereas exponential dispersal dominates when dispersal occurs after reproduction (figure 3d). The importance of timing increases with increasing temporal variability.

Figure 4 shows how the assumption of stable environmental conditions within the life cycle influences the evolutionary outcome and the importance of timing (compare figure 3d for the complete temporal correlation $\Delta K^h(t) = 0$). Figure 4a shows that even at a moderate temporal correlation ($\Delta K^h(t) = 0.8K^h(t)$) timing is important for the evolutionary outcome. If the fluctuations of the carrying capacities before and within the life cycle ($K^h(t)$ and $K^{h'}(t)$) are completely uncorrelated but different in strength, ($K^h(t)$ and $K^{h'}(t)$ are drawn independently from a distribution with the same mean, but different variance) then the timing of the dispersal remains important (figure 4b). However, the effect of timing on the evolutionary outcome disappears when $K^h(t)$ and $K^{h'}(t)$ are drawn independently from each other and from the same distribution (figure 4c).

Figure 5 shows the influence of the spatial heterogeneity on the evolutionary outcome. Again we selected an environment with strong temporal fluctuations (parameters as in figure 3d). In a spatially homogeneous environment (figure 5a) high dispersal is superior over a wide range of growth rates, however, the evolutionary outcome depends on the timing of dispersal. If total carrying capacity is divided into two instead of ten habitats (a spatial situation as modelled by McPeck & Holt 1992), timing is still important in predicting the evolutionary outcome (figure 5b). Thus, figure 5 shows that the effect of timing does not depend

Figure 3. Evolutionary outcome of the competition between genotypes using different dispersal strategies versus the growth rate in a spatially heterogeneous environment. Temporal variability of the environment is described by variations of the carrying capacity of each habitat within the limits $K^h \pm \Delta K^h$. ΔK^h was assumed to be zero, $0.25K^h$, $0.5K^h$ and $0.8K^h$, characterizing a gradient from temporally constant (a) to strongly fluctuating environments (d). Each column corresponds to a different ordering of reproduction and dispersal.

on the amount of spatial heterogeneity or on the number of involved habitats.

4. DISCUSSION

Our simulations suggest that in addition to the growth rate and the temporal and spatial variability of the environment, the timing of dispersal within the life

cycle can be important in predicting the favoured dispersal strategy. Within our model low dispersal is favoured in a spatially heterogeneous and temporally constant environment, high dispersal is favoured either in a spatially homogeneous, temporally varying environment, or at large growth rates with chaotic dynamics, density-dependent dispersal dominates in spatially and temporally strongly varying environments.

Figure 4. Evolutionary outcome of the competition between genotypes using different dispersal strategies versus the growth rate in a temporally strongly fluctuating environment. (a) Moderate temporal correlation of the capacities between and within the life cycle, see figure 3d for complete correlation. (b) No correlation, different strength of the fluctuations. (c) No correlation, equal distributions; for further explanation see text. The evolutionary outcome depends on the way in which the temporal variability of the environment enters into the life cycle. Timing is only important in cases (a) and (b).

We want to note that the aim of our paper is to analyse the effect of timing of dispersal on the evolutionary outcome and not to make general predictions concerning the evolution of dispersal (global evolutionary stable strategy). Therefore, we selected only four types of dispersal strategies and analysed them within only one type of density-dependent regulation (Ricker equation). Including other dispersal strategies, a certain mortality during dispersal or using other regulation mechanisms (e.g. logistic growth) may alter the evolutionary outcome, but not the difference between the simulations using different timings of dispersal (so long as the conditions discussed below are fulfilled). For example, it can be expected that a certain mortality of dispersers gives further advantage to conditional dispersal, as well as generally favouring lower dispersal rates. Therefore,

the range of growth rates where low dispersal is favoured will increase in both life cycles. Nevertheless, our results may help to understand some general patterns in the evolution of dispersal strategies.

(a) Temporally constant environment

Previous models predicted that in a temporally constant but spatially varying environment, large, stable habitats favour individuals with low dispersal because any dispersal takes more individuals from large (good) habitats to smaller (bad) ones (figure 3a). However, these models did not include density-dependent dispersal. Our results show the same result, but when growth rates are small, threshold dispersal is superior. Thus, our results support conclusions of McPeck & Holt (1992) that under certain conditions,

Figure 5. Evolutionary outcome of the competition between genotypes using different dispersal strategies versus the growth rate in a temporally strongly fluctuating environment (see figure 3d for comparison) for other environmental settings: (a) spatially homogeneous environment, (b) spatially heterogeneous environment with only two habitats. The total carrying capacity is equal to figure 3.

even in a temporally constant environment, dispersal may be favoured if conditional dispersal strategies are involved into competition.

(b) Temporally varying environment

In a temporally varying environment the capacities of the habitats change with time. During a strong decline of the carrying capacity of a habitat the reproductive success of the individuals is low. Those individuals that leave this habitat may increase their reproductive success if temporal fluctuations are spatially uncorrelated and the mortality of dispersers is low. Thus, temporal variability drives evolution to increase dispersal (see also Johnson & Gaines 1990). In a spatially heterogeneous and temporally varying environment, density-dependent dispersal becomes superior over a wide range of growth rates (figure 3d) whereby the type of density dependence favoured depends on the timing of dispersal within the life cycle. Within threshold dispersal, individuals leave the habitat only if conditions are bad (that is when density is very high). Within exponential dispersal, the dispersal probability increases at lower densities where the growth rate is yet large. Therefore, to ensure successful reproduction, exponential dispersal is not competitive compared to threshold dispersal. If dispersal follows reproduction, the environmental conditions may alter before next reproduction. Therefore, dispersal cannot help an individual to find a habitat

with good breeding conditions. In this case exponential dispersal is superior over a wide range of growth rates. If the growth rate is large, the frequency of high dispersal increases. Then local dynamics are chaotic and local populations often decline or go extinct. Therefore, the chances of dispersing individuals hitting a sparsely occupied habitat is large, and the disadvantage of high dispersal (leaving, sometimes, a good habitat) is reduced. Moreover, local populations can be rescued from extinction due to high dispersal increasing the persistence of this spatially structured population. In a spatially homogeneous environment high dispersal is competitive also at smaller growth rates (figure 5a). If the habitats vary temporally at equal means and with equal variances, then the chance for the dispersing individuals to meet in a habitat above or below the carrying capacity is equal (in a two-patch model the favoured dispersal probability would be 0.5, see McPeck & Holt 1992).

(c) Conditions for the influence of timing on the evolution of dispersal

Aside from the influence of the growth rate and the temporal and spatial variability of the environment, our results show that the timing of dispersal within the life cycle influences the competition between different dispersal strategies. But this phenomenon arises only if special *conditional dispersal strategies* are included into competition and in a *temporally varying* environment.

(i) *Conditional dispersal strategies*

Let us consider the life cycle dispersal–reproduction in figure 2. Individuals using density-independent dispersal do not respond to the actual carrying capacity $K(t)$ by dispersal, and a constant fraction of individuals leaves the habitat. Thus, density-independent dispersal ignores environmental fluctuations. Consequently, these fluctuations affect only reproduction (see dashed arrow in figure 2): the two life cycles in figure 2 become identical. However, individuals using density-dependent dispersal are able to respond to the actual conditions within the habitat. Thus, *both* dispersal and reproduction are affected by the environmental fluctuations. Since dispersal and reproduction exhibit different processes with different functional relationships, it makes a difference which process responds first and second to the actual environmental conditions. Thus, the two life cycles shown in figure 2 are different with respect to the competition between dispersal strategies.

McPeck & Holt (1992) used a two-patch model and did not find any effect of the timing of dispersal on the evolutionary outcome, despite introducing a special type of conditional dispersal: individuals have a larger dispersal probability from the smaller habitat. But even with only two habitats our model revealed significant differences in the evolutionary outcome due to the timing (figure 5*b*). The reason is that the conditional dispersal probabilities within the model of McPeck & Holt depend on the *mean* habitat size and not on the *actual* habitat size. Therefore, the type of conditional dispersal used by McPeck & Holt is not able to respond to *actual* environmental conditions, and the effect of timing disappears.

(ii) *Temporal variability of the environment*

As long as there is a temporal variability of the environment, timing is an important factor moulding the competitive outcome (figure 3*d*). If there is an additional temporal variability of the environment within the life cycle ($K'(t)$ in figure 2) then in both types of life cycles the carrying capacity changes before reproduction *as well as* before dispersal. As long as there is some temporal correlation of the fluctuations before and within the life cycle, or as long as the distribution of the strength of the fluctuations before and within the life cycle are different, it is important which process (reproduction or dispersal) responds first and which responds second to the environmental fluctuations. Therefore, in these cases timing is important. If the fluctuations before and within the life cycle are uncorrelated and have the same distribution and strength, then reproduction and dispersal respond to the same type of environmental fluctuations and it does not matter in which sequence the life cycle is passed: the effect of timing disappears.

5. CONCLUSIONS

The importance of timing on the evolution of dispersal is caused by the way in which the temporal variability enters into a life cycle, where *both* reproduction *and* dispersal are able to respond to the

actual environmental conditions (e.g. population density). Therefore, in a temporally constant environment and for species using only unconditional dispersal strategies, the effect of timing is absent. Thus, not only the presence or absence of environmental fluctuations may be important for the evolutionary outcome, but also the timing of these environmental fluctuations in relation to the processes of the life cycle.

In the context of time-discrete models, the impact of the timing of the processes on the dynamics was only recently appreciated in the literature. For example, Doebeli (1994) found that the stabilizing effect of dispersal on the local dynamics in a two-patch model can be enhanced if the timing of dispersal differs between the two patches. In a brief review of a paper by Csilling *et al.* (1994), Ruxton (1995) noted that different rules for the relative timing of immigration and reproduction may cause different dynamics. He also suggested that the timing of events in cellular automaton models can have a large impact on model predictions (Ruxton 1996). On the other hand, Hassel *et al.* (1995) found that altering the timing of density-independent dispersal has no effect on the dynamics. The temporal order of biological processes within the life cycle may be especially important when results of time-discrete and time-continuous models are compared, or when differential equations are transformed to difference equations (see also Hassel *et al.* 1995). Contrary to time-discrete models, in time-continuous models, timing is not relevant.

Compared to the ecological discussion of Doebeli (1994) or Ruxton (1995, 1996) our results demonstrate that the temporal ordering of biological processes may also affect evolutionary considerations. Therefore, aside from the strength and the mode of dispersal, the timing of dispersal in relation to reproduction and environmental fluctuations is an additional trait that has to be considered in the discussion of the evolution of dispersal. Consequently, the timing of dispersal itself may be a trait moulded by evolution.

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