

Natal versus breeding dispersal: Evolution in a model system

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ABSTRACT

Dispersal may be age-specific and is often biased towards juveniles. Some explanations for this pattern assume special social or genetic advantages for juveniles. Using a model, we studied the competition of individuals using different dispersal strategies characterized by the magnitude and mode of dispersal as well as the age class where dispersal occurs. We found that the evolution of natal versus breeding dispersal is influenced by the age structure of the population. Details of population regulation and environmental fluctuations are also important because they influence the distribution of age classes. Our model shows that natal dispersal can be favoured over a wide range of conditions, either as a pure strategy or in combination with breeding dispersal, even without assuming special advantages for dispersing juveniles.

Keywords: age structure, density-dependence, dispersal strategies, spatially structured model.

INTRODUCTION

Dispersal is an important trait influencing the ecology and genetics of organisms (for a review, see Johnson and Gaines, 1990). In animals, the causes and consequences of dispersal depend on the age of dispersers. Vertebrate ecologists, therefore, divide dispersal into natal dispersal and breeding dispersal. Natal dispersal describes dispersal from the site of birth to that of first reproduction or potential reproduction, whereas breeding dispersal describes the subsequent movement of adults between sites (Greenwood, 1980; Greenwood and Harvey, 1982).

In vertebrate populations, dispersal is often biased towards juveniles (Greenwood and Harvey, 1982; Cockburn, 1992). Several explanations for this phenomenon have been suggested. Pre-reproductive juveniles may gain more by dispersing than reproductive adults because they have no fecundity costs due to dispersal (Morris, 1982). Juveniles may be at a disadvantage in the competition for breeding sites and territories because adults are more familiar with resources and are socially dominant. Therefore, adult breeding site fidelity and territorial behaviour may induce juveniles to disperse (Greenwood and Harvey, 1982).

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Furthermore, inbreeding avoidance might necessitate dispersal before first reproduction (Johnson and Gaines, 1990).

Despite the enormous interest in the theory of dispersal (e.g. Gadgil, 1971; Roff, 1975; Gaines and McClenaghan, 1980; Hastings, 1983; Stenseth, 1983; Levin *et al.*, 1984; Vance, 1984; Holt, 1985; Davis and Howe, 1992; McPeck and Holt, 1992; Stenseth and Lidicker, 1992; Doebeli, 1995; Olivieri *et al.*, 1995; Holt and McPeck, 1996; Ruxton, 1996; Johst and Brandl, 1997a,b), to our knowledge the only model to analyse the evolutionary background of natal versus breeding dispersal is that of Morris (1982). Using a model that includes spatial structure and age structure, we show that the competitive differences of natal versus breeding dispersal may be generated by the distribution of age classes. Thus natal dispersal may evolve even without assuming special advantages (e.g. social or genetic advantages, less dispersal costs) for dispersing juveniles.

THE MODEL

To determine the basic principles that influence the evolution of natal versus breeding dispersal, we make our model as simple as possible. We consider a spatially structured population of two habitats of different quality. However, the number of habitats has no influence on our general conclusions. We define asexual genotypes that compete for the same resource but differ in their dispersal strategy. A similar model was used by McPeck and Holt (1992) and Holt and McPeck (1996), but in our model a dispersal strategy is characterized by the magnitude and mode of dispersal as well as by the *age class* where dispersal occurs.

Local dynamics

We use a model with overlapping generations, a prerequisite for distinguishing between natal and breeding dispersal. The population of genotype g (see below) in habitat h at time t consists of juveniles (born in the preceding time step) and adults $N_g^h(t) = N_g^{j,h}(t) + N_g^{a,h}(t)$ (Fig. 1). Dispersal causes a redistribution of individuals and changes local population size $N_g^h(t)$ to $N_g'^h(t)$. After dispersal, local population size is influenced by reproduction and mortality.

We define reproduction by a birth rate b , including the mortality of newborn individuals. Thus, the number of newborn individuals that are able to survive to the next time step (= number of juveniles) is determined by $N_g^{j,h}(t+1) = bN_g'^h(t)$. We define mortality by a death rate d . Thus, the number of all other individuals that are able to survive to the next time step (= number of adults) is determined by $N_g^{a,h}(t+1) = (1-d)N_g'^h(t)$. For simplicity, we assume that individuals mature in the next time step. The rates b and d may depend on density, that is on the total population size in habitat h (after dispersal) summed over all genotypes $N'^h(t) = \sum_g N_g'^h(t)$.

In the following, we use a form of density-dependence originally introduced by Maynard Smith and Slatkin (1973) and proposed by Bellows (1981) to describe a wide range of data. In vertebrate populations, density often has a main effect on fecundity or juvenile survival (Charnov, 1990). Therefore, in a first approach, we assume that the birth rate is density-dependent, that is $b(N'^h(t)) = b/(1 + (b/d - 1)(N'^h(t)/K^h(t))^\beta)$. The death rate is density-independent, that is $d(N'^h(t)) = d$, assuming that $b(K^h) = d$. K^h is the mean carrying capacity of habitat h , which may fluctuate between the time steps (temporal variability

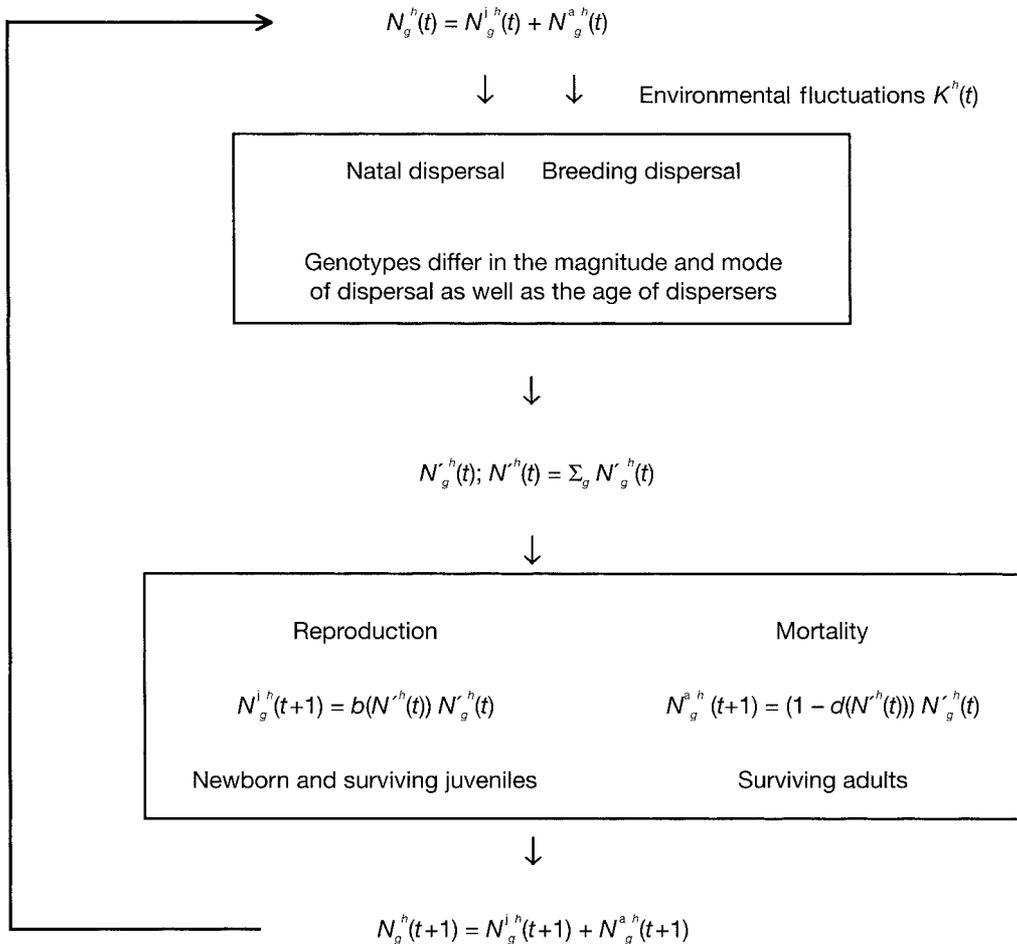


Fig. 1. Flow chart of local dynamics for a given genotype g in habitat h (for further explanation, see model section within the text).

$K^h(t)$; see below). In a second approach, we assume that both the birth rate and the death rate are density-dependent, that is $b(N^{r,h}(t)) = b/(1 + (b - d)(N^{r,h}(t)/K^h(t))^\beta)$, and the survival of adults is $1 - d(N^{r,h}(t)) = (1 - d)/(1 + (b - d)(N^{r,h}(t)/K^h(t))^\beta)$, assuming that $b(K^h) = d(K^h)$. b and d are the corresponding rates at low densities and are equal in all habitats and for all genotypes. Note that the relation between the birth rate and the death rate influences the ratio of juveniles to adults within the population and thus the age structure of the population. The parameter β determines the strength of density-dependence: small β describe compensatory density-dependence resulting in equilibrium dynamics, whereas large β describe overcompensatory density-dependence that may result in complex dynamics.

In general, b and d are positively related: the larger the possible number of juveniles, the shorter the mean lifetime of adults (Peters, 1983). At the maximum $d=1$, only

newborn individuals survive and breeding dispersal is impossible (non-overlapping generations). In our simulations, we use the (arbitrary) relationship $d = 0.2b$. Other relations between b and d do not affect our general conclusions, only the range of b that can be analysed.

Spatial heterogeneity is introduced by different carrying capacities K^h of the habitats: we consider two habitats with carrying capacities $K^1 = 5000$ and $K^2 = 10,000$ individuals. Temporal variations of habitat quality are described by (spatially independent) variations of $K^h(t)$ within the limits $K^h \pm \Delta K^h$. We draw random numbers for K^h from a uniform distribution and the quantity $\Delta K^h = 0.8K^h$ characterizes the maximum of the fluctuations.

Definition of genotypes

We define genotypes g by special dispersal strategies characterized by the magnitude and mode of dispersal as well as the age class where dispersal occurs. Dispersers experience no mortality due to dispersal.

Magnitude and mode of dispersal

We use two different modes of dispersal: density-independent and density-dependent dispersal. With density-independent dispersal, individuals decide with a constant probability m to leave the habitat. With density-dependent dispersal, the probability to disperse depends on the total number of individuals within the habitat (summed over all genotypes) in relation to the carrying capacity: $m = f(N^h(t)/K^h(t))$. We used two qualitatively different functional relationships: a continuously increasing and a threshold-like relationship (Hansson, 1991; Johst and Brandl, 1997a). As an example of the former, individuals disperse with an exponentially increasing probability from 0.1 at $N^h(t) = 0$ to 0.5 at $N^h(t) = K^h(t)$. We call this strategy ‘increasing dispersal’. As an example of the latter, individuals disperse only when local population size is near the carrying capacity, which we call ‘threshold dispersal’. We assume a dispersal probability of $m = 0.1$ if $N^h(t) < K^h(t)$, but from $N^h(t) = 0.95K^h(t)$ to $N^h(t) = 1.05K^h(t)$, the dispersal probability increases steeply to 0.5.

Age of dispersers

Dispersal may occur within the age class of juveniles and/or adults. Thus, we consider three scenarios: (1) natal dispersal, where individuals disperse as juveniles from their site of birth to that of first reproduction; (2) breeding dispersal, where individuals disperse as adults to other breeding sites; and (3) natal and breeding dispersal, where individuals disperse both as juveniles and as adults. In Scenarios 2 and 3, individuals may decide several times during their life to disperse. We determine the number of dispersers for natal dispersal $mN_g^j(t)$ from the number of surviving juveniles, and the number of dispersers for breeding dispersal $mN_g^a(t)$ from the number of surviving adults (Fig. 1).

We performed two sets of simulations: First, we selected five density-independent dispersal probabilities ($m = 0.1, 0.2, 0.3, 0.4$ and 0.5) and combined them with the above three age class scenarios resulting in 15 competing genotypes. Second, we selected two density-independent and two density-dependent dispersal modes ($m = 0.1, m = 0.5$; increasing dispersal, threshold dispersal). Combining these four dispersal modes with the above three age class scenarios resulted in 12 competing genotypes.

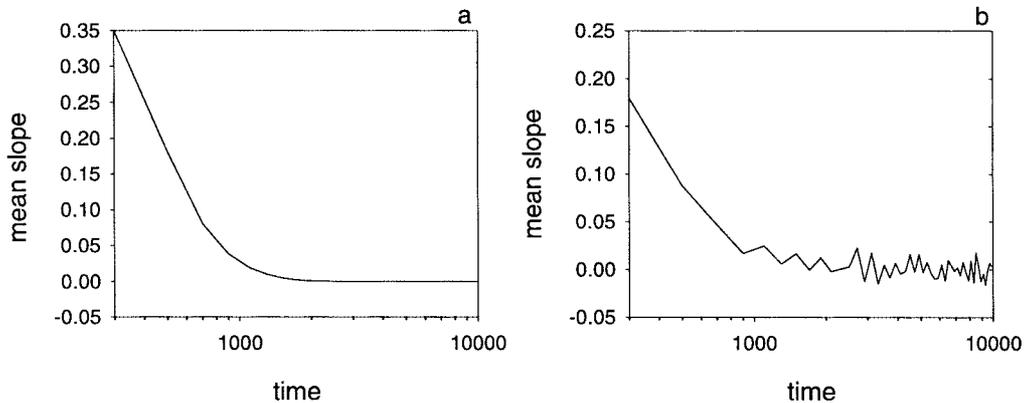


Fig. 2. Example of the mean slope of the frequency of a particular genotype versus simulation time (calculated per 100 years and averaged over 100 simulation runs; birth rate $b = 2$). (a) Genotype with low breeding dispersal in a temporally constant environment; (b) genotype with high natal and breeding dispersal in a temporally fluctuating environment.

Evolutionary outcome

We define the global evolutionary outcome as the mean percentage of individuals of genotype g , $f_g = N_g(t_f)/N(t_f)$, at a given final time t_f . $N_g(t_f) = \sum_h N_g^h(t_f)$ is the total population size of genotype g summed over all habitats, and $N(t_f) = \sum_h \sum_g N_g^h(t_f)$ is the global population size. We started our simulations with random initial population sizes of genotypes and averaged frequencies over 1000 time steps after t_f and 100 simulation runs. To test what final time t_f is sufficient for stable frequencies of genotypes, we calculated the mean slope of frequencies versus simulation time (D. Roff, personal communication). In a temporally constant environment, this slope approaches zero over time (Fig. 2a). In a temporally varying environment, there is a similar pattern but, as expected, small fluctuations around zero are possible (Fig. 2b). In a temporally constant environment, 2000 time steps proved to be sufficient for stable frequencies of genotypes, but in a temporally varying environment, stable frequencies are reached somewhat later. For certainty, we show the evolutionary outcome at a final time of 10,000 time steps. We study the influence of age structure by plotting the evolutionary outcome versus the birth rate b and thus versus an increasing number of juveniles in the population.

RESULTS

In our first set of simulations, only genotypes with density-independent dispersal compete. In a temporally constant environment, low natal dispersal is favoured at small birth rates, and low breeding dispersal is favoured at medium to high birth rates (Fig. 3). Other dispersal probabilities ($m > 0.1$) did not survive the competition. Note that the position of the switch in the evolutionary outcome from low natal to low breeding dispersal depends on details of density regulation (that is, on the strength determined by the parameter β and on the type determined by density-dependent birth rates or density-dependent birth and death rates). If β and b are large, then complex dynamics are possible. In this case, genotypes with high natal and breeding dispersal can co-exist with genotypes with low breeding dispersal

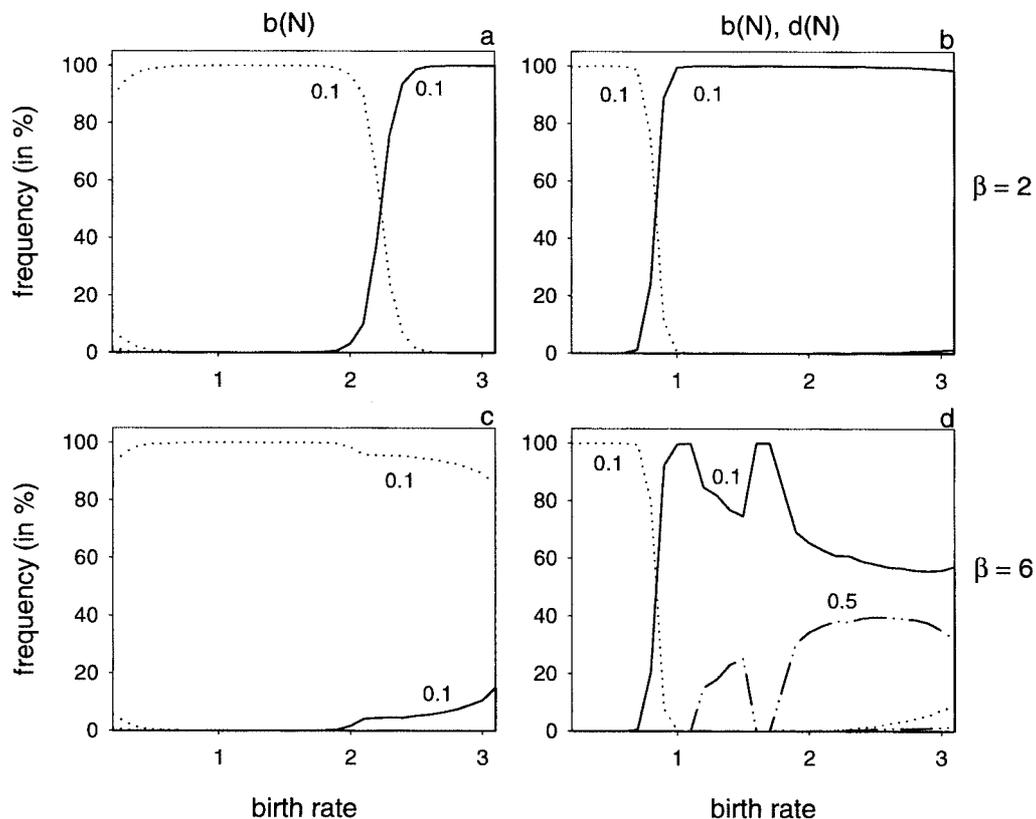


Fig. 3. Evolutionary outcome of competition between genotypes using density-independent dispersal strategies in a temporally constant environment. The left-hand panels show the results if the birth rate is density-dependent; the right-hand panels show the results if both the birth rate and the death rate are density-dependent. We give results for two strengths of density-dependence β . The numbers on the curves characterize the magnitude of dispersal (dispersal probability m). Types of line characterize the age class of dispersers (solid line = breeding dispersal, dotted line = natal dispersal, dash-and-dotted line = natal and breeding dispersal; for further explanation, see model section within the text).

(Fig. 3d). In a temporally varying environment, the composition of the evolutionary outcome depends on details of the density regulation as well. Low and high natal dispersal can co-exist over a wide range of birth rates when density affects only the birth rate (Fig. 4a,c). High natal and breeding dispersal are favoured over a wide range of birth rates when density affects both the birth rate and the death rate (Fig. 4b,d). If density-dependent dispersal is included in the competition, then genotypes with threshold dispersal in both age classes are favoured over a wide range of birth rates. This result is more or less independent of the strength and the type of density regulation (Fig. 5).

DISCUSSION

Our results suggest that: (1) dispersal may be strongly biased to juveniles even when dispersing juveniles have no special advantages over dispersing adults; (2) the evolution

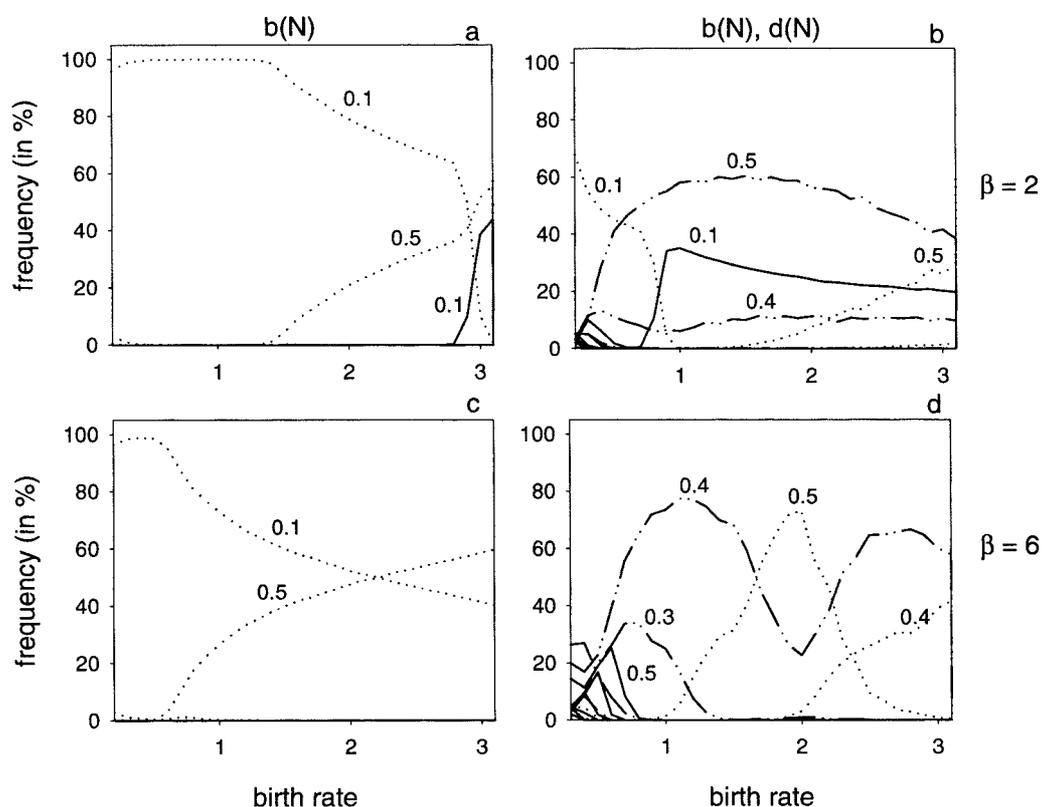


Fig. 4. Evolutionary outcome of competition between genotypes using density-independent dispersal strategies in a temporally varying environment. For details, see legend to Fig. 3.

of natal versus breeding dispersal depends on details of the density regulation and the temporal variability and spatial heterogeneity of the environment; and (3) the mode of dispersal (density-independent or density-dependent dispersal) may influence the evolution of natal versus breeding dispersal.

In a spatially heterogeneous but temporally constant environment, low dispersal is favoured because any dispersal would take on average more individuals from large (favoured) to small (unfavoured) habitats (Hastings, 1983; Holt, 1985; Johnson and Gaines, 1990; McPeck and Holt, 1992). If only a part of the population is allowed to disperse (for example, a special age class), then the dispersal strategy that produces the lowest number of dispersers is a strategy with a low dispersal probability *and* with the dispersal decision made in the age class with the lowest number of individuals. At low birth rates b , the number of juveniles is small and the lifetime of adults is long, so low natal dispersal is favoured (Fig. 3). An increase in b leads to an increase in the number of juveniles and to an increase in the death rate d of adults (shorter lifetimes of individuals). Therefore, the number of adults within the population decreases and low breeding dispersal becomes the dispersal strategy with the lowest number of dispersers (Fig. 3a,b). Thus, the observed switch from low natal to low breeding dispersal reflects the general theory of the evolution

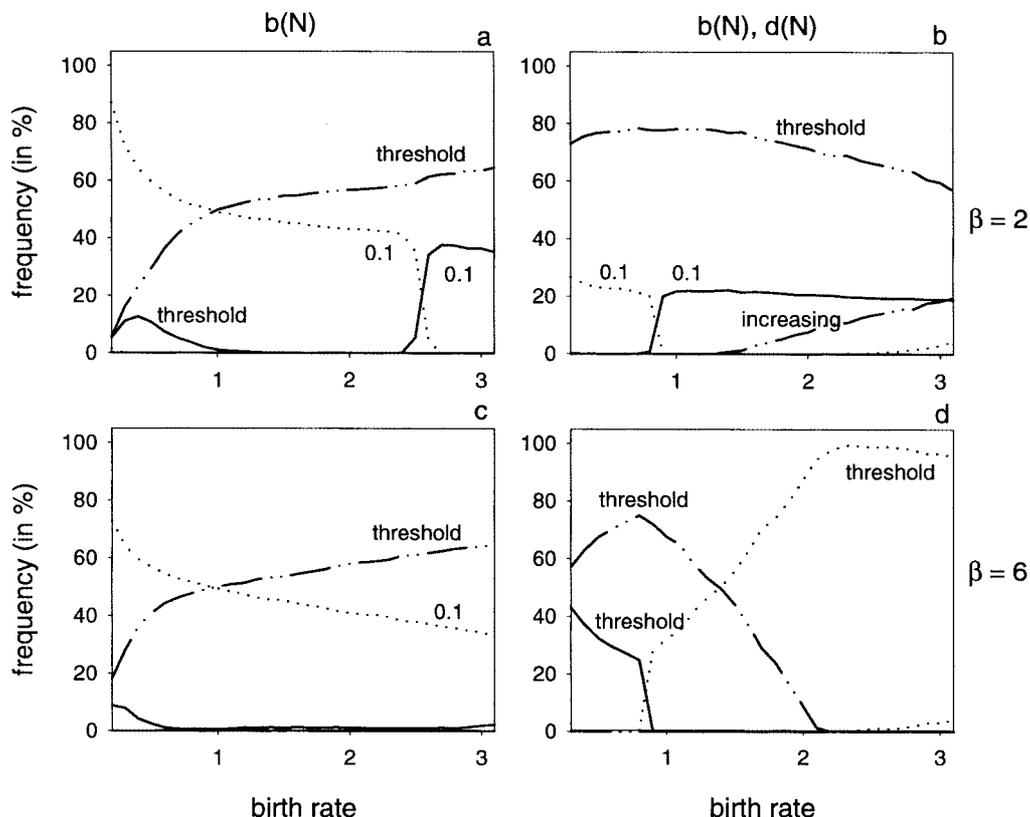


Fig. 5. Evolutionary outcome of competition between genotypes using density-dependent dispersal strategies in a temporally varying environment. The threshold-like density-dependence of dispersal probability is labelled ‘threshold’; the continuously increasing dispersal probability with density is labelled ‘increasing’ (see model section). For other details, see legend to Fig. 3.

of dispersal. It also shows that the age structure – that is, the number of juveniles compared to the number of adults within the population, given by $b/(1-d)$ – influences the evolution of natal versus breeding dispersal. Thus, if dispersal takes place during a special stage in the life history, the distribution of individuals over the stages influences the evolution of dispersal.

At large birth rates and overcompensatory density-dependence, complex population dynamics may occur. In this case, genotypes with low breeding dispersal and genotypes with high natal and breeding dispersal co-exist (Fig. 3d). This is in line with the results of Holt and McPeck (1996), who showed that a persistent polymorphism of low and high dispersal may result from chaotic population dynamics. At high birth rates, low dispersal is represented by low breeding dispersal (see above), whereas high dispersal is represented by genotypes with a large dispersal probability and with dispersal in the juvenile and the adult age class.

In contrast to the spatial heterogeneity of the environment that drives evolution to no dispersal, temporal variability of the environment favours dispersal because, on average,

bad local conditions can be compensated by dispersal (e.g. Gadgil, 1971; Levin *et al.*, 1984; McPeck and Holt, 1992; for a review, see Johnson and Gaines, 1990). In a spatially heterogeneous and temporally varying environment, these two influences interact, leading to the co-existence of low and high dispersal strategies due to frequency-dependent selection (Heino *et al.*, 1998). Our results confirm this general trend: in a temporally varying environment, genotypes with high dispersal can co-exist with genotypes with low dispersal (Fig. 4). Whether selection leads to monomorphism or polymorphism depends on the interaction between the environmental conditions (the degree of spatial heterogeneity compared to that of temporal variability) and the types of strategies which compete (Figs 4, 5).

Including the age class of dispersers, we found that yet another process is important for the evolutionary outcome: the differential influence of density on the age classes (for the general importance of density-dependence in evolution, see Holt, 1996; Johst *et al.*, 1999). On the one hand, density-dependence of the birth and death rates may influence the age structure; on the other, environmental fluctuations act via the density (i.e. the ratio of population size to the actual carrying capacity) on the age classes. If birth rate is density-dependent, environmental fluctuations affect only the juvenile age class and thus high natal dispersal is favoured (Fig. 4a,c). If both birth and death rate are density-dependent, environmental fluctuations affect both age classes. Consequently, the combined strategies of natal and breeding dispersal may survive the evolutionary competition (Fig. 4b,d). Thus, our results suggest that density-dependence in juvenile survival may foster natal dispersal, whereas density-dependence in adult survival may foster breeding dispersal. Therefore, in vertebrate populations, where density often has a main effect on fecundity or juvenile survival (Charnov, 1990), natal dispersal should be common.

If dispersal is density-dependent and serves as a tool to leave overcrowded habitats before reproduction, breeding dispersal becomes competitive to natal dispersal even if density affects only the birth rate (Fig. 5). Therefore, not only the density-dependence of the birth and death rates, but also the density-dependence of dispersal, may influence the evolution of natal versus breeding dispersal.

In conclusion, our results demonstrate that, for a full understanding of the evolution of dispersal, factors which increase dispersal probability (for example, temporal variability of the environment, complex dynamics) or decrease dispersal probability (for example, spatial heterogeneity, high mortality of dispersers) must be discussed in relation to the number of potential dispersers within the population, which may depend on age structure. Thus, in determining why natal or breeding dispersal is favoured in a particular species, field ecologists should also consider the frequency, the density-dependence and the environmental interaction of the corresponding age class.

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