



The evolution of dispersal – the importance of information about population density and habitat characteristics

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The evolution of mobility patterns and dispersal strategies depend on different population, habitat and life history characteristics. The ability to perceive and make use of information about the surrounding environment for dispersal decisions will also differ between organisms. To investigate the evolutionary consequences of such differences, we have used a simulation model with nearest-neighbour dispersal in a metapopulation to study how variation in the ability to obtain and make use of information about habitat quality and conspecific density affects the evolution of dispersal strategies. We found a rather strong influence of variation in information on the overall rate of dispersal in a metapopulation. The highest emigration rate evolved in organisms with no information about either density or habitat quality and the lowest rate was found in organisms with information about both the natal and the neighbouring patches. For organisms that can make use of information about conspecific density, positively density-dependent dispersal evolved in the majority of cases, with the strongest density dependence occurring when an individual only has information about density in the natal patch. However, we also identified situations, involving strong local population fluctuations and frequent local extinctions, where negatively density-dependent dispersal evolved.

Dispersal is essential for the persistence of many species, as it allows populations to track changes in the location of suitable habitat. Dispersal strategies can depend on many different factors, including species-specific traits such as morphology (Srygley and Chai 1990, Hughes et al. 2007), social structure (Yaber and Rabenold 2002, Le Galliard et al. 2005) and life-history (Levin 1984), as well as environmental factors such as climate (Best et al. 2007, Hughes et al. 2007), landscape structure (Kuch and Idelberger 2005), habitat quality (Lin et al. 2006) and the local abundance of conspecifics (Fletcher 2006, 2007). The ability to perceive and acquire information about different characteristics of the environment varies greatly among organisms and this is likely to affect the evolution of dispersal. Even so, the consequences of variation in information about the environment for the nature of dispersal strategies and for the overall amount of dispersal occurring in a population have been rather little studied. To investigate how dispersal strategies depend on whether organisms make use of information about habitat quality and population density in the natal and neighbouring patches we use individual-based simulation modelling.

For an organism, an important type of information is whether it is positioned in suitable or unsuitable habitat. In unsuitable habitat the most beneficial behaviour would be to emigrate, assuming suitable habitat is available. There will usually be variation in quality among habitat patches and individuals will generally benefit from reaching high habitat quality, but to do so they need information. In

addition to habitat quality, the number of conspecifics within a local patch can affect several aspects of the life of an individual. A scarcity of conspecifics can result in reproduction failure (Kuussaari et al. 1998). In group living animals, low population density can result in poor predator defence (Kenward 1978) as well as low foraging success (Baird and Dill 1996). There are also examples where the presence of conspecifics is a means to identify suitable habitat (Stamps 1988). On the other hand, high conspecific abundance can cause competition over resources, overcrowding and population crashes (Dethier and MacArthur 1964, Belovsky et al. 1999, French and Travis 2001, Metcalf et al. 2007). For females, high population densities can also be costly in terms of male harassment (McLain and Pratt 1999, Sirov and Brockmann 2001, Chilvers et al. 2005) and forced copulations (Cordero 1999). In a theoretical model based on grasshopper behaviour (Bauer et al. 2005), male harassment in high male density was found to induce positively density-dependent female dispersal, regardless of habitat quality in high-density patches. Thus, conspecific density can have many different effects on the suitability of a habitat patch, apart from habitat quality per se.

Information about habitat suitability can be obtained directly from environmental cues such as resource abundance (Baker 1984, Oro et al. 2004, Lin et al. 2006) or from the presence of conspecifics, as in the case of conspecific attraction (Gilbert and Singer 1973, Stamps 1988, Muller 1998). Some animals also assess their surroundings using public information, i.e. information

about how conspecifics perform or behave (Danchin et al. 2001). Intraspecific social interactions, such as when males court or pursue females, could be a source of information about population density (Enfjäll and Leimar 2005).

Although many organisms have the ability to evaluate habitat quality at the location where they are situated, there is great variation in information about the suitability of neighbouring or more remote surroundings. Information about neighbouring patches is available if these are situated within the perceptual range of the organism, for example visually or by olfactory cues (Zollner and Lima 1997, Schooley and Wiens 2003, Hein et al. 2005, Merckx and Van Dyck 2007). Information can also be obtained by exploring surrounding areas before settlement (Norberg et al. 2002, Haugland and Larsen 2004). Organisms with information only about habitat characteristics in their natal patch are likely to make different dispersal decisions than organisms with information about habitat characteristics in both natal and neighbouring patches, because the latter can compare the natal patch with the surroundings. Thus, the information situation ought to be important for the evolution of dispersal.

Empirical studies on various species have shown that conspecific density can have a significant effect on dispersal (insects; Shapiro 1970, Odendaal et al. 1989, Baguette et al. 1996, 1998, Fonseca and Hart 1996, Enfjäll and Leimar 2005, birds; Forero et al. 2002, mammals; Aars and Ims 2000, Ims and Andreassen 2005, Stoen et al. 2006). There are also a number of recent models on the evolution of density-dependent dispersal (Jánosi and Scheuring 1997, Travis et al. 1999, Metz and Gyllenberg 2001, Poethke and Hovestadt 2002, Kun and Scheuring 2006) in which individuals are assumed to have information about the population density in their natal patch or in both natal and surrounding patches (Bach et al. 2007). A general conclusion from this work is that positively density-dependent dispersal (more per capita emigration from high densities) is to be expected under a relatively broad set of circumstances.

In our analyses here, we extend this work by also examining situations where individuals can make dispersal decisions based on independent sources of information about population density (local population size) and habitat quality, in the natal and possibly also in neighbouring patches. We pursue the question of how the information situation should influence the nature of evolved dispersal strategies, for instance the tendency to base emigration decisions on the population density in the natal patch, and the overall rate of dispersal in a metapopulation. We also identify circumstances that could promote negatively density-dependent dispersal. To investigate how information about habitat quality and conspecific density affect the evolution of dispersal we model the evolution of dispersal in a metapopulation. We use different assumptions about the type of information that an individual makes use of (the information situation), ranging from no information at all up to information about habitat quality and population density in both the natal and destination patches. Using individual-based simulation, we then analyse how the information situation influences the evolution of dispersal strategies.

Model description

We study a metapopulation residing on a 20×20 grid of patches, with nearest neighbour dispersal and opposite edges of the grid connected to form a torus. There is random variation in the habitat quality (carrying capacity) of the patches, such that the quality of the patch at position (i, j) at time t is

$$K(i, j, t) = \max[K_0 + \phi, K_{\min}] \quad (1)$$

where ϕ is an independent normal deviate with mean zero and standard deviation σ and K_{\min} is the lowest possible habitat quality. This means that habitat quality variation is spatially and temporally uncorrelated. Generations are non-overlapping with a local population dynamics of the Ricker type, adapted from Ranta et al. (1995) and Heino (1998). Given that there are N_f females present at the time of reproduction in a patch with habitat quality K , the expected number of offspring emerging as adults in the patch the following generation is

$$\bar{N}_0 = \min[2N_f \exp(r(1 - 2N_f/K)), N_{\max}] \quad (2)$$

where r is a population growth-rate parameter and N_{\max} is an upper limit to the local population size (the upper limit N_{\max} is introduced to ease the numerical implementation; this ceiling is chosen high enough not to be reached except for exceptional fluctuations in habitat quality). The actual number N_0 of offspring emerging in the patch is randomly chosen as the nearest integer below or above \bar{N}_0 , in such a way that the expected number is \bar{N}_0 . Patches can go extinct ($N_0 = 0$) if $\bar{N}_0 < 1$, which can happen when $2N_f$ is considerably larger than K and r is large. For each of the N_0 offspring emerging in the patch, its mother is randomly chosen among the N_f females in the previous generation and its sex is randomly determined, giving an even sex ratio on average. Each of the newly emerged females can gain some information (below) about the habitat quality and local population density in her home patch and in a randomly selected neighbouring patch (on the torus, there are four neighbouring patches), and this information can be used by the female as a basis for the decision to disperse. For a female that estimates the habitat qualities in the home and neighbouring patch as Q_1 and Q_2 , respectively, and estimates (below) the population densities in the home and neighbouring patch as N_1 and N_2 , respectively, the probability of dispersing to the neighbouring patch is a logistic function of these estimates:

$$P = \frac{1}{1 + \exp(-a_1 Q_1 - a_2 Q_2 - b_1 N_1 - b_2 N_2 - d_0)} \quad (3)$$

where a_1 , a_2 , b_1 , b_2 , and d_0 are five parameters that define the dispersal strategy of the female. Each of the five parameters is determined by the genotype at an autosomal diploid locus with additive allelic effects, and there is no linkage between loci. The parameters determine how sensitive a female will be to variation in the estimates of habitat quality and population density. Females mate only once, with a randomly selected male in the patch of emergence and at a time before the dispersal decision. If, by chance, there are no males in the patch of emergence, females are assumed to stay unmated, and thus do not produce any offspring. For simplicity, only females disperse,

so the dispersal genotype is only expressed in females. A dispersing female dies with probability μ and arrives to reproduce in the (randomly chosen) neighbouring patch with probability $1-\mu$.

Different situations of habitat and population information

A female could estimate the habitat quality of a patch, and we assume that the estimate (i.e. Q_1 or Q_2 in Eq. 3) is equal to the true quality K of the patch. A female may also estimate population density (i.e. N_1 or N_2 in Eq. 3), based on the number, X , of males that she encounters in a given time period. We assume that X is Poisson distributed with mean λN_m , where N_m is the number of males in the patch, and that the female estimates the population in a patch as $2X/\lambda$. The factor 2 is based on the assumption of an even sex ratio on average in the patch. In simulations, we use pseudorandom numbers to construct this estimate for a female.

In our analyses, we make different assumptions about whether females take information about habitat quality and population density into account when making dispersal decisions. We distinguish six different information situations (Table 1). For instance, a female could be completely uninformed (u) about both habitat quality and population density. The way we implement this in a simulation is to require that the parameters a_1 , a_2 , b_1 and b_2 in Eq. 3 are equal to zero, and only the parameter d_0 is free to evolve. The interpretation could either be that the information is not available to the female, or that the female does not make use of the information for dispersal decisions. Further information situations are that females make use only of information about habitat quality in the natal patch (h) or of population density in the natal patch (d), and we implement this by letting the corresponding parameter in Eq. 3 evolve (a_1 or b_1), in addition to d_0 . A female might make use of information about both habitat quality and population density in the natal patch (hd), in which case we allow both parameters a_1 and b_1 to evolve. It is also conceivable that the female, by temporarily visiting a neighbouring patch, or by observing it at a distance, can be informed about habitat quality and population density in a neighbouring patch. In principle, one can imagine information situations in addition to the ones listed in Table 1, up to a hypothetical situation where a female is informed about habitat quality and population density in all patches in the metapopulation, but these situations seem increasingly unlikely. In any case, a study of the situations

in Table 1 will provide some understanding of the influence of information about habitat quality and population density on the evolution of dispersal.

Simulation details

The allelic effects at the loci coding for the parameters a_1 , a_2 , b_1 and b_2 were constrained to stay between -0.1 and 0.1 (i.e. genotypic values between -0.2 and 0.2), whereas the allelic effects at the locus coding for d_0 were between -200 and 200 (genotypic value between -400 and 400). As explained above, depending of the information situation studied (Table 1), only some of the loci were free to mutate and evolve, with the remaining parameters being put equal to zero. Mutational increments to the allelic effects were drawn from a reflected exponential (Laplacian) distribution with mean zero and standard deviation 0.01 for the alleles coding for the parameters a_1 , a_2 , b_1 and b_2 and standard deviation 20 for d_0 , except that allelic effects were constrained to stay within their limits. To start off simulations for a given set of parameter values, a population was run with a high mutation probability (0.01 per allele and generation) for 10 000 generations. This was to allow accumulation of a considerable amount of genetic variation. Replicate simulations (typically 10 replicates) were then started from this base population, with the mutation probability set much lower (0.00005), and each replicate simulation was run for 20 000 additional generations. All random events in the simulations, such as dispersal decisions, mortality and mutation, were implemented using pseudorandom numbers. The sequence of events in a simulated generation was (1) reproduction in each local patch according to Eq. 2, (2) random determination of patch quality for the patches in the next generation, (3) local random mating in each patch, (4) females gain information and make dispersal decisions, (5) random migration mortality. The procedure was implemented as a C++ program. Unless stated otherwise, we used the following standard parameter values: $K_0 = 100$, $\sigma = 50$, $K_{\min} = 5$, $r = 1$, $N_{\max} = 500$, $\mu = 0.1$, $\lambda = 0.3$.

Results

As seen in Eq. 3, we assume that dispersal strategies can be expressed as a logistic dependence of the dispersal probability on the habitat quality and population density estimates of a female. Fig. 1 shows examples of these strategies for a situation where females only use information about population density in the natal patch. In such a case, the probability of dispersing to a neighbouring patch can be written as

$$p = \frac{1}{1 + \exp(-b_1 N_1 - d_0)} \quad (4)$$

which is a special case of Eq. 3 for which a_1 , a_2 and b_2 are zero. Each female in a metapopulation has her own dispersal strategy, given by the values of b_1 and d_0 that are set by her genotype. The strategies shown in Fig. 1 were obtained by computing the average b_1 and d_0 in the entire metapopulation, and then averaging this over ten replicate

Table 1. The six different information situations with regard to dispersal decisions in the model.

Label	Basis for dispersal decisions
u	No information
h	Habitat quality in natal patch
d	Population density in natal patch
dd	Population density in both natal and neighbouring patches
hd	Both habitat quality and population density in natal patch
hhdd	Habitat quality and population density in both natal and neighbouring patches

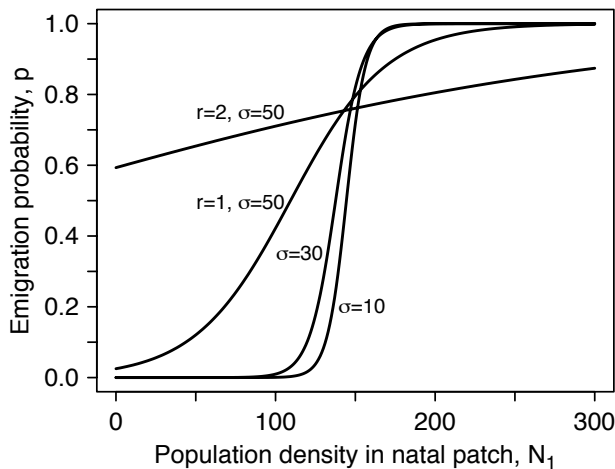


Figure 1. The probability of female emigration away from different estimated population densities. The information situation is that only conspecific density in the natal patch is taken into account (d), in which case the emigration probability p as a function of the estimated population density N_1 is given by Eq. 4. The curves show the sigmoid dependence of p on N_1 for the average strategy at evolutionary equilibrium for different values of the growth rate r and the standard deviation σ of the variation in patch quality: $r = 2, \sigma = 50$; $r = 1, \sigma = 50, 30, 10$.

simulations (mean \pm SD: $r = 2, \sigma = 50$: $b_1 = 0.005 \pm 0.001$, $d_0 = 0.38 \pm 0.17$; $r = 1, \sigma = 50$: $b_1 = 0.033 \pm 0.013$, $d_0 = -3.66 \pm 1.21$; $r = 1, \sigma = 30$: $b_1 = 0.123 \pm 0.010$, $d_0 = -16.87 \pm 1.24$; $r = 1, \sigma = 10$: $b_1 = 0.167 \pm 0.017$, $d_0 = -24.04 \pm 2.43$). In these simulations, the genetically determined parameters kept varying over the generations and the metapopulation did not reach complete genetic uniformity. Instead, a certain amount of genetic variation was maintained as a result of mutation–selection–drift balance in a fluctuating environment. For the situations illustrated in Fig. 1, patch habitat quality

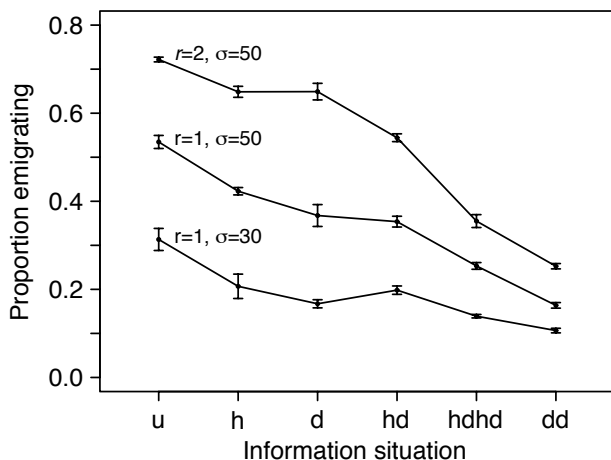


Figure 2. The proportion of emigrating females for different information situations. The mean (\pm SD) proportions are based on 10 replicate simulations. A female's knowledge about conditions in the natal and neighbouring patches varies among the information situations (Table 1). Three curves are shown, with different values of the growth rate r and the standard deviation σ of the variation in patch quality: $r = 2, \sigma = 50$; $r = 1, \sigma = 50$; $r = 1, \sigma = 30$,

fluctuates around a mean of $K_0 = 100$, and patch population densities will then fluctuate around approximately this value. With our assumed parameter values of $\lambda = 0.3$, a female will on average base her estimate of population density on encountering around 15 males ($0.3 \times 100/2$), which means that her estimate will be relatively accurate.

The effect of information on the overall rate of dispersal

To study the evolution of emigration for different situations of information about habitat quality and population density, we compared the six information situations in Table 1. We first allowed an evolutionary equilibrium to be established in the simulated metapopulation, and then computed the average proportion of emigrating females over a period of 100 generations. The results for the different information situations are shown in Fig. 2. For all cases that we investigated, the highest average proportion of females emigrating was found in the u situation, i.e., when females do not use information about either habitat quality or population density (Fig. 2). The general tendency was that there is less dispersal when females use more information, although the ranking of the information situations in Fig. 2 shows that more information does not always lead to a reduction in dispersal, since the situation $hhdd$ leads to more dispersal than dd .

One reason for females to disperse is to improve their reproductive success by reaching higher quality habitat or less crowded patches. Variation in reproductive success between patches can thus be regarded as a cause of dispersal, which is consistent with the high rates of dispersal in the $r = 2, \sigma = 50$ case in Fig. 2, but dispersal also has the effect of reducing such variation, by evening out differences between patches. We investigated if there was any systematic difference between the information situations in Fig. 2 in the amount of variation in per capita reproductive success between patches, but we found no clear pattern. The reason could be that in those situations where females have more information about habitat quality and local population density, and thus might be more efficient at evening out differences, they tend to disperse less (Fig. 2), so there is less reduction of the variation in reproductive success.

Dispersal mortality and local temporal habitat quality variation

Dispersal mortality and habitat quality variation are among the most commonly studied factors with a presumed effect on the evolution of dispersal. More dispersal is expected for lower dispersal mortality and for greater variability in habitat quality. Our simulations support this general idea, both in situations where no information is used and when individuals base their dispersal decisions on information about natal habitat quality and population density (Fig. 3). The difference between the information situations (u and hd) in the overall rate of dispersal is greatest for low dispersal mortality and high habitat quality variation, i.e. those situations where the overall rate of dispersal is high. Without any variation in habitat quality ($\sigma = 0$ in Fig. 3b),

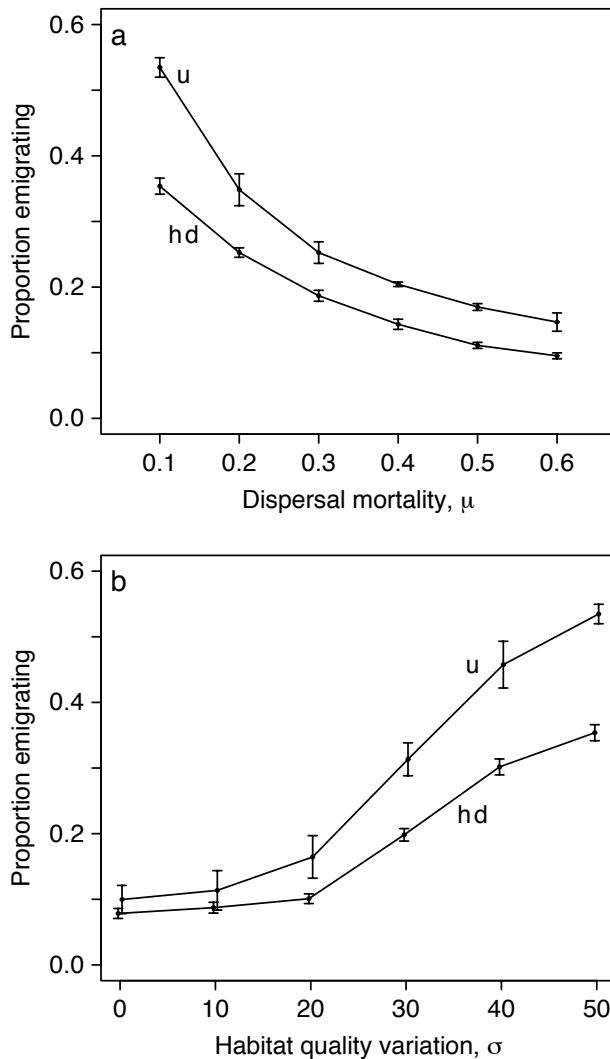


Figure 3. The influence of dispersal mortality and habitat quality fluctuations on the proportion of emigrating females, for two different information situations (u and hd). The mean (\pm SD) proportions are based on 10 replicate simulations. (a) the proportion of emigrating females for different levels of dispersal mortality, μ . (b) the proportion of emigrating females for different levels of habitat quality variation. The points have been shifted slightly left and right, for clarity.

the information situation has little effect on the overall rate of dispersal.

Density-dependent dispersal

In the information situations we have analysed (Table 1), individuals in the four situations d, dd, hd and hdd can take information about population density into account when making dispersal decisions, whereas in the u and the h situations no information about population density is used. In the four cases where population density information could be used, our simulations showed that density-dependent dispersal evolved, in the sense of a correlation between the population density in a natal patch and the proportion of females emigrating from that patch (Fig. 4). Using the standard parameter values, positively density-

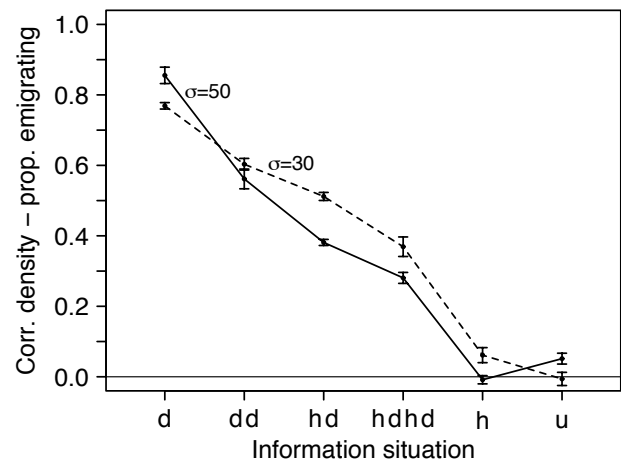


Figure 4. The correlation between population density in the natal patch and the proportion of emigrating females for the different information situations in Table 1. The solid curve corresponds to standard parameter values and for the dashed curve $\sigma=30$. The mean (\pm SD) correlations are based on 10 replicate simulations. For each simulation, when an evolutionary equilibrium had been reached, the correlation over patches between the actual population size in a patch and the proportion of females emigrating from that patch was computed.

dependent dispersal evolved, with the strongest density dependence (the highest correlation) in the d situation, where only information about population density in the natal patch is taken into account (Fig. 4). There was no density dependence in the h situation and only a very weak correlation between density and emigration in the u situation (Fig. 4; this weak correlation seems to be the result of the distribution of genetic variation in the parameter d_0). The results were similar when there was somewhat less habitat quality variation ($\sigma=30$; although the weak correlations for the h and u situations differed from the $\sigma=50$ case).

Negatively density-dependent dispersal

We also searched for circumstances that could lead to negatively density-dependent dispersal. Changing the parameter values to a combination of a low average carrying capacity (low K_0), limited variation in the carrying capacity (low σ), and very high growth rate parameter (very high r) we found that negatively density-dependent dispersal can evolve (Fig. 5a). For $r>4$, the correlation between population density in the natal patch and the proportion of emigrating females changes from positive to negative. This coincides with a decrease in patch occupancy (Fig. 5b). Using the Ricker equation in Eq. 2, high values of r will cause frequent local population crashes and accordingly high numbers of empty patches. Under these conditions, the within-patch relatedness among females increases. We used two neutral loci to estimate this relatedness among individuals within a local patch (Fig. 5b). The explanation for negatively density-dependent dispersal might be that females avoid harming their relatives by crowding neighbouring patches, which would happen if a high proportion of females emigrated from a high-density patch.

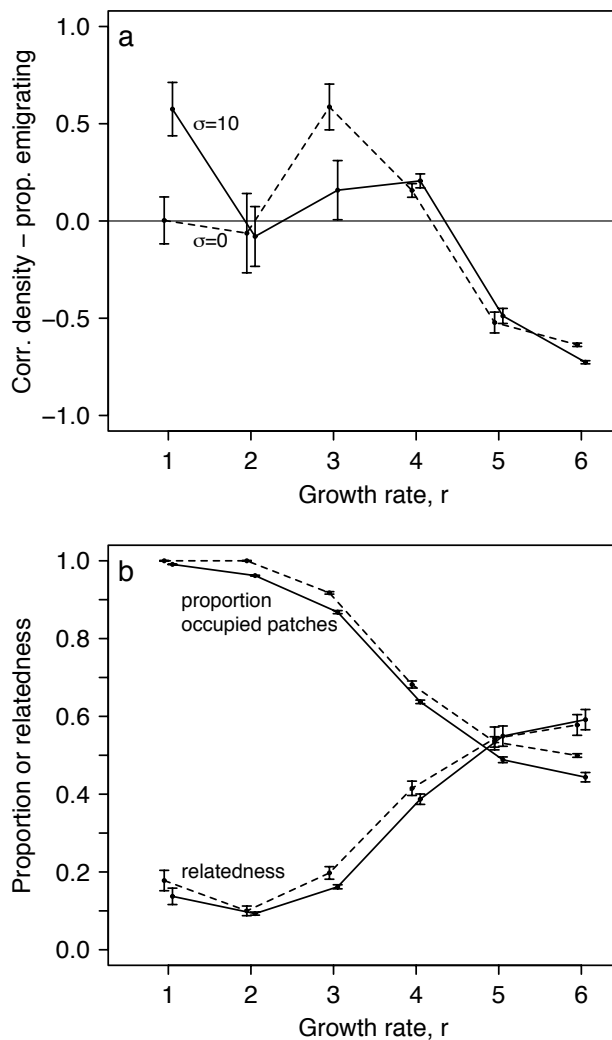


Figure 5. The influence of the growth rate parameter r in Eq. 2 on density-dependent dispersal, the proportion of occupied patches and the within-patch relatedness for the information situation d. The mean (\pm SD) values are based on 10 replicate simulations. (a) the correlation between population density in the natal patch and the proportion of emigrating females for different values of r . The zero-line indicates where dispersal changes from positively density dependent to negatively density dependent. (b) for the same simulations the proportion of patches that have positive population density and the average within-patch relatedness (immediately prior to dispersal) for different values of r . Within-patch relatedness is determined as the intraclass correlation over patches of a neutral quantitative genetic trait (based on two additional unlinked loci in the genotype). The points have been shifted slightly left and right, for clarity. Parameter values: $K_0 = 30$, $\sigma = 10$ (solid curves) and $\sigma = 0$ (dashed curves); $N_{\max} = 500$ except $N_{\max} = 1000$ for $r = 6$, $\sigma = 0$ and $r = 5$, $\sigma = 10$, and $N_{\max} = 2000$ for $r = 6$, $\sigma = 10$.

Discussion

Using an evolutionary model where the qualitative nature of the information about environmental circumstances can be varied, we found that such variation is important for the evolution of dispersal in spatially and temporally variable environments. For simplicity, we assumed that females could directly observe habitat quality and that they estimated population density from their encounters with

males. Our results are however likely to be robust to changes in the details of how individuals obtain information, as long as the information is relatively accurate.

Information situation and the rate of patch emigration

When comparing emigration rates among the different information situations, the highest emigration rates evolved when individuals had no information about either habitat quality or population density (situation u, Fig. 2). This might be explained by the costs associated with overcrowding. In metapopulations like the ones we have modelled, with spatially varying subpopulation sizes, most individuals will be born in high-density patches. Those born in high density will face greater competition over resources, and will therefore on average benefit from emigration. However, when information about habitat quality is not used for dispersal, individuals that are more prone to emigrate will on average do better, because of the higher probability of being born in high local population density. Thus, one ought to expect that unconditional dispersal entails greater dispersal proneness, and this is what we find in our simulations.

The simulations of the different information situations shows that the overall emigration rate declines noticeably as information about habitat quality and population density in the natal patch is used (h, d and hd in Fig. 2). Also in these cases, most individuals are born in high-density patches and gain from emigrating, but by using information about the natal patch, dispersal becomes conditional and will only be triggered by unfavourable local conditions, and therefore individuals will be less prone to emigrate from high habitat quality and/or low conspecific density. Experimentally, resource scarcity as well as high conspecific density has been found to trigger emigration (Shapiro 1970, McMahon and Tash 1988, Fonseca and Hart 1996, Rowe and Richardson 2001, Enfjäll and Leimar 2005). In the information situations in our model where also information about the suitability of neighbouring patches could be used (hhdd and dd, Table 1), emigration probabilities were even lower (Fig. 2). Since emigration can be costly (due to dispersal mortality), individuals can benefit from limiting emigration to only occur when they know that better habitat is available in neighbouring patches. Instead of responding directly to local conditions (as in the h, d and hd situations, Table 1), hhdd and dd individuals have the opportunity of responding to suitability gradients and thereby emigrate towards more suitable patches.

Previous studies on dispersal biology show that many species appear to use information about their surroundings for dispersal decisions. It has been suggested that even plants have means by which to tell the intensity of competition from neighbouring conspecifics, and thereby adjust the rate of seed germination (Dyer et al. 2000). Further, observations of density-dependent dispersal in various species (insects; Shapiro 1970, Odendaal et al. 1989, Baguette et al. 1996, 1998, Fonseca and Hart 1996, Enfjäll and Leimar 2005, birds; Forero et al. 2002, mammals; Aars and Ims 2000, Ims and Andreassen 2005, Stoen et al. 2006) suggest that many animals perceive

information about conspecific density, at least in their natal patch, and incorporate this information in dispersal decisions. This suggests that there are some general conclusions to be drawn from our simulations on variation in the information situation. Information about both conspecific density and habitat quality will shape the evolution of dispersal: because the ability to perceive such information has large evolutionary benefits it ought to be found in many species.

Positively density-dependent dispersal

Positively density-dependent dispersal has been found in several species. In our model, we find that when organisms have information about conspecific density, either only in the natal patch (*d* and *hd*, Table 1) or in both the natal and surrounding patches, (*dd* and *hhdd*, Table 1), emigration rates increase with population density. This agrees with recent theoretical modelling on dispersal (János and Scheuring 1997, Travis et al. 1999, Metz and Gyllenberg 2001, Poethke and Hovestadt 2002, Kun and Scheuring 2006, Bach et al. 2007). However, whereas conspecific density is commonly regarded as causing emigrations due to overcrowding and competition over resources and therefore is only considered in relation to patch carrying capacity, (Travis et al. 1999, Poethke and Hovestadt 2002, Bach et al. 2007), our approach allows density-dependent dispersal to evolve independently of variation in habitat quality. In the two information situations *d* and *dd* the only information used concerns population density, whereas variation in habitat quality or patch carrying capacity is not used for dispersal decisions (Eq. 3). Still, positively density-dependent dispersal evolves. Thus our model shows that high conspecific density per se can inflict costs and induce emigration, supporting the results by Bauer et al. (2005).

In our model, the most strongly positively density-dependent dispersal was found in the *d* situation where only conspecific density in the natal patch is used. Adding the information about habitat quality (information situation *hd*) lowers the density–emigration correlation (Fig. 4), because individuals also take the habitat quality into consideration in dispersal decisions. In the *hd* situation, individuals will thus not leave high-density patches as long as the habitat quality is high enough, but might instead leave low-density patches if habitat quality is very poor. Adding information also about population density and patch quality in neighbouring patches resulted in further decrease in the natal patch density–emigration correlation (Fig. 4).

Negatively density-dependent dispersal and kin competition

Even though the majority of species studied in terms of density-dependent dispersal have displayed positively density-dependent dispersal, there are exceptions where instead individuals have been found to leave low-density patches at higher per capita rates (Gilbert and Singer 1973, Kuussaari et al. 1996, Ims and Andraessen 2005). Many evolutionary models of density-dependent dispersal only consider positively density-dependent dispersal (Travis et al. 1999, Metz

and Gyllenberg 2001, Poethke and Hovestadt 2002, Kun and Scheuring 2006), while negative density-dispersal relationships have been little studied. To explore under which circumstances negatively density-dependent dispersal can evolve, we investigated a range of parameter combinations for our model and found situations where negatively density-dependent dispersal evolved (Fig. 5). Two properties of our model are likely to contribute to the phenomenon. First, for Ricker population dynamics (Eq. 2) with very high values of the parameter *r*, local populations can increase far above carrying capacity in a single generation, which is then followed by a population crash and possibly local extinction in the next generation, potentially producing many empty patches in the metapopulation (Fig. 5b). At the same time, within-patch relatedness can be rather high (Fig. 5b). Second, dispersal in our model is only between nearest-neighbour patches, which means that immigrants into a patch can be related. If a large number of relatives arrive in a previously empty patch, causing overcrowding and perhaps a subsequent local extinction, they will be harming each other's reproductive success. Greater restraint in emigration from very high density patches can thus be a means for females of assisting their dispersing sisters, avoiding overcrowding the patch of arrival. This effect will be more pronounced when variability in the suitability of patches is mostly driven by variation in population density, rather than by variation in habitat quality. A low carrying capacity ($K_0 = 30$ in Fig. 5) has the effect of increasing the within-patch relatedness. For high values of the parameter *r*, we found an average relatedness among females within a local patch of around 0.5, corresponding to the relatedness among full sisters. It is worth noting that the effect of lower per capita emigration from high-density local populations is likely to disappear if individuals could disperse randomly over the entire metapopulation, because this would sharply reduce kin competition in the patch of arrival. It is thus only under rather special circumstances that one would expect negatively density-dependent dispersal to evolve. Traditionally kin-competition is regarded as a major driving force of dispersal and as a result of kin competition in the natal patch emigrating individuals are assumed to gain inclusive fitness from kin left in the natal patch (Hamilton and May 1977, Comins et al. 1980, Poethke et al. 2007). However, our results suggest that kin-selection at least sometimes could reduce dispersal at high densities. Gandon and Michalakis (1999) have previously made the same point in a theoretical work where they found that kin-competition among immigrants reduced emigration rates at high densities.

Dispersal mortality and local temporal variation in habitat quality

Dispersal costs are generally assumed to have strong effects on emigration rates. As the costs of dispersal increase, the potential benefits of dispersal will decrease and emigration probabilities will therefore be expected to decline. In agreement with other theoretical work (Travis et al. 1999, Poethke and Hovestadt 2002, Kun and Scheuring 2006), we found a strong effect of dispersal mortality on emigration rates. For both information situations we studied

(u and hd), there was a rapid decline in emigration probabilities as dispersal mortality increased (Fig. 3a).

The habitat quality of a local patch will often vary among years. We found that these temporal fluctuations in habitat quality can have strong effects on emigration rates. With stable local population dynamics, individuals will be born in suitable patches and will not gain from emigrating. Our results illustrate that this is true regardless of the information situation (Fig. 3b). With increasing variation in local habitat quality, we found that emigration rates increase, in agreement with previous results (McPeck and Holt 1992, Kun and Scheuring 2006).

Conclusions

To optimise its dispersal decisions an organism can benefit from obtaining and making use of information about habitat quality and conspecific density. Lack of information selects for high and unconditioned emigration. However, with unconditional dispersal, many individuals will move towards poorer environments and high emigration rates can be costly in terms of dispersal mortality. Information about habitat quality and/or conspecific density in the natal patch will help an individual to reduce the risk of performing emigration towards poorer habitat. Information about conditions also in neighbouring patches will enable individuals to emigrate almost exclusively towards better habitat. Reducing emigration rates will additionally reduce the per capita dispersal mortality. Information about conspecific density will mainly result in positively density-dependent dispersal. However, in metapopulations with temporally constant habitat quality and a combination of very high reproductive rate and a relatively low carrying capacity, we found negatively density-dependent dispersal to evolve. Using Ricker dynamics, such metapopulations suffer rapid turnovers, resulting in low patch occupancy and high within-patch relatedness, allowing negatively density-dependent dispersal to evolve as a result of kin competition.

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