Interactions in the evolution of dispersal distance and emigration probability

Dissertation zur Erlangung des

naturwissenschaftlichen Doktorgrades

der Bayerischen Julius-Maximilians-Universität Würzburg

vorgelegt von

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Würzburg, Mai 2008

Eingereicht am: ....

Mitglieder der Promotionskommission:

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Tag des Promotionskolloquiums: ....

Doktorurkunde ausgehändigt am: ....

Ich versichere hiermit ehrenwörtlich, dass die Dissertation von mir selbständig, ohne unerlaubte Beihilfe und nur mit Hilfe der angegebenen Quellen und Hilfsmittel angefertigt ist.

Hiermit erkläre ich, dass ich mich anderweitig einer Doktorprüfung ohne Erfolg nicht unterzogen habe.

Contents

Chapter 0

General introduction

In this thesis I use mathematical and computer simulation methods to investigate certain aspects of the evolution of dispersal strategies of plants and animals. In very general terms, dispersal is a process by which species spread over a given landscape. The ability to colonize new habitats or to escape from unfavourable conditions is a key element in species survival. The loss of species as a consequence of changes in environmental conditions and its effects on biodiversity emphasize the importance of research on the evolution of dispersal strategies.

Following the definition of Howard (1960), I assume dispersal to be *"the permanent movement an individual makes from its birth site to the place where it reproduces or would have reproduced had it survived and found a mate."* This is one of the most commonly used definitions of natal dispersal. It was extended by Johnson and Gaines (1990), who state that an *"additional type of movement is breeding dispersal, or the movement from one homerange to another between attempts at reproduction, disregarding whether reproduction is successful."* (see also Greenwood and Harvey, 1982). Like in Johnson and Gaines (1990), I consider no minimum distance requirement for dispersal, because this would just be an arbitrary limitation.

I therefore consider two types of dispersal: natal dispersal, the emigration from the natal habitat, and breeding dispersal. In this thesis, breeding dispersal happens after natal dispersal. In principle breeding dispersal could also happen after a breeding attempt in the natal habitat, but this case is not considered in this thesis.

While natal dispersal is always only the first step of leaving the natal habitat, breeding dispersal can consist of multiple dispersal moves between habitats that individuals perform in order to find a suitable habitat for reproduction. In this

thesis, mating and breeding in animals happens always in the (final) habitat they occupy after optional dispersal. For philopatric (non-dispersing) individuals the natal habitat is also the breeding habitat.

The investigation of the spatial distribution of species by Charles Darwin and Alfred Russel Wallace in the 19th century (see Darwin, 1859; Wallace, 1877, 1887) was the starting point of scientific research on the spread of species. Kew (1893) investigated the dispersal of fresh-water and land Mollusca and was one of the first to report on various dispersal vectors, e.g. insects, batrachians, birds and humans (for a review see Packard, 1896). In the early 20th century Pearson and Blakeman (1906) and Brownlee (1911) started to work on mathematical models about random migration, which were later taken up by geneticists (e.g. Fisher, 1937; Haldane, 1948). The first to deliver a broad mathematical discussion of the spread and growth of species was Skellam (1951), acknowledging the developing field of evolutionary genetics.

However, it was Hamilton (1964) who first formalized the notion of genetic selection on traits that were not necessarily beneficial to the individual itself, but to its kin, making it possible to mathematically study the evolution of social behaviour and dispersal strategies that were impossible to describe with the previously established models. This concept of kin-selection (see below) was applied to investigate the evolution of dispersal strategies by Hamilton and May (1977).

After theoretical works that either considered dispersal probability (Hamilton and May, 1977; Comins et al., 1980; Comins, 1982; Motro, 1983; Travis and Dytham, 1998; Gandon and Michalakis, 1999; Cadet et al., 2003) or dispersal distance (Skellam, 1951; Kitching, 1971; Hovestadt et al., 2001; Murrell et al., 2002; Rousset and Gandon, 2002; Levin et al., 2003), the processes driving the evolution of both characters are well understood. However, these studies did not consider possible interactions in the evolution of both, dispersal probability and dispersal distance.

In this thesis I investigate interactions in the concurrent evolution of dispersal probability and dispersal distance.
Such interactions can be of various kind and they can be determined by various factors.

For example, if environmental changes lower local habitat quality, it can become necessary to emigrate from the natal patch to search for a better habitat for reproduction. Yet, depending on the spatial extent of the habitat deterioration it can take longer time and farther distances to reach a better habitat. Therefore, as long as the distances the individuals are capable of dispersing are too short to reach better patches, the slightest dispersal mortality will select against emigration,

so that dispersal probability will most likely remain low. Only when mutation and selection result in the evolution of dispersers capable of moving sufficiently long distances to reach good quality habitat, selection will favor higher dispersal probabilities. Hence, in this example there is an interaction between dispersal distance and emigration propensity.

I investigate the nature of such interactions and the effect of different factors which can influence either emigration probability, dispersal distance, or both.

The evolution of dispersal strategies is shaped by costs and benefits of dispersal, which in turn can be determined by various factors. Costs of dispersal comprise dispersal mortality, which may be affected by factors like time and distance spent on dispersal, but also metabolic investment into the ability to disperse (e.g. bigger muscles, longer wings, higher fat storage) (Jenkins et al., 2007). This metabolic investment often happens at the expense of fertility (Mole and Zera, 1993; Langellotto et al., 2000; Zera and Harshman, 2001). Another cost factor is the time spent on dispersal that an individual cannot spend on reproduction (Hanski et al., 2006). Hence, dispersal costs reduce the reproductive output of a disperser, either completely, if it dies before reproduction, or gradually, because the investment into dispersal decreases its fertility.

Benefits of dispersal include avoiding competition for resources (either inter- or intraspecific) (Lambin et al., 2001), minimizing competition with siblings (kin-competition) (e.g. Hamilton and May, 1977; Comins, 1982; Frank, 1986; Kisdi, 2004), avoiding inbreeding (Perrin and Goudet, 2001), or coping with the temporal variability of resource availabilities (Levin et al., 1984; Travis and Dytham, 1999; Gandon and Michalakis, 2001).

Generally, dispersal is favoured if the benefits are higher than the costs. Benefits and costs may act not only directly, but also indirectly, e.g. the decision of an individual to disperse may not only influence its own reproductive success directly, but may indirectly also increase the chances of its siblings to win a breeding territory or a mate and might enable them to produce adult offspring that carries parts of the genes of the disperser. This concept was introduced by Hamilton (1964) who coined the term "inclusive fitness". The notion of inclusive fitness combines the reproductive output of adult offspring not only of the individual in focus, but also the beneficial and harmful effects the individual has on the fitness of its relatives. The effects on its relatives are weighted by the coefficient of relatedness the individual has to them.

The questions I address in the following four chapters are:

- Under which conditions are local adaptations of propensity for natal dispersal and dispersal distance in a heterogenous environment possible?

- How does the capability to estimate habitat quality affect the concurrent evolution of the propensity for natal dispersal and dispersal distance, when individuals have to cope with spatial heterogeneity of habitat quality?

- How strongly does a difference between the dispersal mortality of males and females influence the evolving dispersal strategies under different dispersal mortalities? What is the effect of simultaneously acting inbreeding depression?

- How strong is the effect of a difference in the competition for reproductive resources for males and females on the evolving sex-specific dispersal probabilities? How does inbreeding depression influence the evolutionary process?

0.1   Chapter 1 - "Evolution of local adaptations in dispersal strategies"

In the first chapter of my thesis I investigate the evolution of dispersal strategies of annual plants on a small scale: within one single habitat (Gros et al., 2006). In our model this habitat island consists of a large number of small cells, each just big enough to support one single adult plant. These plants reproduce non-sexually by releasing seeds into the surrounding. I consider only a single habitat island which is surrounded by a lethal environment, called "matrix". In the matrix no seed can survive. After spreading its seeds, the adult plant dies and is replaced by an individual which developed from a randomly chosen seed that fell into its habitat cell.

On such a habitat island, the optimal, genetically determined, emigration propensity (away from the mother plant) and subsequent dispersal distance (to – optimally – another place on the island) depends mainly on the size of the habitat island and the position of an organism in this habitat. For example, if a plant grows close to the boundary between habitat and lethal matrix, optimal dispersal distance for its seeds will be short.

Yet, adaptation to local conditions, e.g. to one's location on a habitat island and to the corresponding probability of loosing offspring over the edge of the habitat, is constantly challenged by immigrating seeds that contribute their own – better

or worse adapted – genes to the gene-pool of the cell and its surrounding. I therefore expect that there is a minimum size of this habitat island below which local adaptation becomes impossible. If the habitat is too small, no differentiation will develop because all plants experience very similar conditions. Only as the habitat island becomes bigger, different areas of similar conditions emerge, to which local adaptation of dispersal strategies is possible. Such dispersal strategies consist of the probability to leave the natal cell and the subsequent distance of dispersal. I investigate how the evolution of these strategies depends on habitat size and the location on the island.

To test the influence of habitat size, I use single, circular habitat patches of various sizes that are placed in an environment of hostile matrix where no seed can survive. The habitat patches comprise cells just big enough to support one single plant, and seeds that fall into a habitat cell compete for taking over the cell to mature after the death of the adult plants. I consider plants that reproduce by parthenogenesis, i.e. all plants are females and produce daughters whose genes depend on the mother's genes only. A plant's genes determine the dispersal strategy of its seeds, e.g. how many seeds are dispersed into and out of the maternal cell, and how far they disperse. Thus, the spatial distribution of seeds around a plant is determined by its genes. When inheriting a mother's genes, mutations occur with a small probability so that genetic variation is maintained.

In our simple model, the selective forces on the genes that determine a dispersal strategy are the benefits of avoiding kin-competition by dispersal and the costs of loosing offspring which disperse outside the habitat into the lethal matrix. While dispersal in this system is driven by kin-competition, the urge for a mother to distribute its seeds as far apart from each other as possible is counterbalanced by the certain death of seeds falling into the matrix by dispersing too far.

As expected, I find that mean dispersal distances as well as mean dispersal probability increase with increasing habitat size. Furthermore, I find that there is indeed a mininum size of the habitat island, above which adaptation of individuals to their distance from the border of the habitat patch is possible. In a model with smaller sized patches, the population will be monomorphic for disperal probabilities and distances. In larger patches I find that plants that settle close to the rim of the patch evolve to disperse their offspring less frequently out of the maternal cell and over shorter distances, whereas plants in the center evolve the highest propensities to emigrate from their natal cell, as well as the highest dispersal distances. However, the evolving dispersal distances in the center in a large patch are still much shorter as they could be without loosing offspring over the edge. Hence, the selective pressure not to loose offspring over the rim of the habitat is present even in the very center of the patch.

0.2   Chapter 2 - "The effect of kin-competition and population density on the evolution of dispersal under distance dependent costs"

In the second chapter I enlarge the perspective by moving on from localized dispersal of plants within one patch, to investigating the evolution of dispersal of animals that move between multiple patches placed in a hostile environment (matrix).

Dispersal in theoretical studies has mostly been modelled as a process where, in plants and animals alike, offspring is spread randomly according to spatial probability distributions. However, dispersal in most animals is probably more a step-by-step process of subsequent decisions about whether to stay or to continue to disperse in search of a better patch of habitat for reproduction. In the model that I analyse in this chapter, I look at the influence of such a stepwise dispersal on the evolution of dispersal probability and the number of dispersal steps. The model comprises equally spaced habitat patches inside a hostile environment (called matrix) and contains individuals that disperse from one patch to the next according to a genetically determined transition probability. The hostility of the matrix affects the probability to die during every transition from patch to patch and this mortality is equal for transitions between all neighbouring patches. To judge whether a habitat patch is good enough to stay for reproduction, animals need a means to sense whatever they use as a quality criterion. In my model I assume that an animal's dispersal strategy depends on its ability to gather information about the quality of its habitat. To test the effect of this factor on the evolution of dispersal behaviour, I use three model-species that differ in sensory capacity for habitat quality.

A second factor that determines optimal dispersal distance is the landscape: the quality of the habitat patches can be correlated in space, so that both, bad quality patches, as well as good quality habitats, are grouped together. If this is the case, it is the spatial extent of such groups of patches that determines how far a disperser has to go to reach a good quality habitat, or how far it can go to remain in a cluster of good quality habitat in its quest to avoid competition with its kin.

A further impact factor is the dispersal mortality that dispersers suffer from. This mortality takes effect during every transition from one patch to the next, such that before every dispersal move a migrant has to weigh the benefits against the costs. The chance of reaching a better quality habitat, and getting more offspring there, has to be weighted against the probability to die during transition and get no offspring at all. In evolutionary terms this means that individuals with a better strategy get on average more offspring than their competitors. Therefore, the

better strategies will be carried on over generations until a stable state is reached where no other strategy can outcompete the prevailing one.

I translate the three factors: ability to gather information about habitat quality, spatial correlation in habitat quality, and dispersal mortality into a model and arrive in a setting described in the following.

I model sexually reproducing species of animals which have two genes that determine their dispersal behaviour. One gene encodes the propensity to emigrate from natal habitat, and the second – independent – gene encodes the propensity for every further dispersal step. Habitat quality in this model is determined by a parameter that controls the number of offspring a female can produce in a habitat patch. However, how many of a female's offspring survives in our model depends mainly on the total amount of offspring produced in the patch and its resulting population density. Population density not only determines offspring survival, it is known to influence dispersal behaviour in many species (Matthysen, 2005) in nature. In our model population density correlates negatively with offspring survival. I therefore use population density as an individual's measure of habitat quality. To test the influence of the ability to estimate population density on the evolution of dispersal strategies, I use three scenarios with model-species that differ in their ability to gather information about their natal habitat, and differ also in their ability to sense habitat quality during further dispersal steps.

The first of three model-species can not sense population density at all and performs all steps according to the probabilities that are directly given by its genes. The second species perceives population density after birth and performs natal dispersal only if the density exceeds its genetically determined threshold. After natal dispersal this species cannot sense population density any more and continues dispersal like the first species, that is with a probability that is directly given by its second gene – the one responsible for controlling dispersal behavior for every dispersal move after natal dispersal. The third model-species can sense population density at all times and can react to it in all dispersal steps. This species has a genetically determined threshold for the population density in its natal patch and one genetically determined threshold for population density in every other patch it enters. Only if these thresholds are exceeded, dispersal is likely to be triggered.

I find that the amount of steps a species performs indeed depends on their ability to measure population density, the spatial extent of correlation in habitat quality, and most importantly, dispersal mortality. Especially when dispersal mortality becomes high, the ability to measure quality and thus evaluate risks and benefits better, makes a difference. The biggest difference in the evolved number of dispersal steps is between the completely uninformed species and the two species

that perform at least natal dispersal only if the population density is too high. In general, the species with complete density-dependent dispersal performs the highest number of steps, followed by the species with the mixed strategy and the species that cannot perceive density at all. However, the highest percentage of natal dispersal evolves in the completely uninformed strategy if dispersal mortality is not too high, but those individuals mostly perform only this one step of natal dispersal. With high dispersal mortality, all three model-species emigrate with about the same probability from their natal habitat.

0.3 Chapter 3 - "Evolution of sex-biased dispersal: the role of sex-specific dispersal costs, demographic stochasticity, and inbreeding"

Sex-biased dispersal, where one gender becomes more dispersive than the other, is a phenomenon that attracts scientists since the first cases had been reported in mammals and birds (see Lidicker, 1975; Clutton-Brock and Harvey, 1976; Greenwood and Harvey, 1976; Greenwood, 1980). Various reasons for sex-biased dispersal, like inbreeding depression (e.g. Gandon, 1999), or differences in the gender-specific competition about resources (e.g. Perrin and Mazalov, 2000) have been proposed. However, a difference in dispersal costs is an obvious reason to expect gender-biased dispersal, because the gender with the higher costs will most likely tend to disperse less. Asymmetry in dispersal costs has also been shortly noted by Taylor (1988), and has been accounted for in the models developed by Leturque and Rousset (2003) and Wild and Taylor (2004). The latter two models, however, focus on the effect of such an asymmetry on the simultaneous evolution of sex-biased dispersal and offspring sex-ratio, and provide only qualitative statements about the correlation between sex-specific dispersal costs and the direction of the bias in dispersal. In addition, Leturque and Rousset (2003) analyzed a system with habitats that differ in female fecundity, which makes it difficult to isolate the effect of cost asymmetries on model predictions. Furthermore, the analytical models of Taylor (1988); Leturque and Rousset (2003), and Wild and Taylor (2004) ignore the effect of demographic stochasticity, which is known to influence the evolution of dispersal strategies (Ronce, 2007), and none of these models investigates the joined influence of inbreeding and cost-asymmetries.

As mentioned above, there is a multitude of dispersal related costs, yet most of them can be subsumed as dispersal mortality. A difference in dispersal mortality between genders can occur for example, if one gender is less accomplished in

dispersing and spends more time on dispersal, so that it is longer exposed to predation. Futhermore, if it needs more time for dispersal, it has also less time to find a mate or a suitable breeding place after arrival, which can prove detrimental to a disperser's fitness if it has only a short lifespan.

I therefore extend a numerical model for sex-specific dispersal proposed by Gandon (1999), to include gender-specific costs of dispersal. With this deterministic approach I can show that even slight differences in the costs of dispersal can indeed induce sex-biased dispersal. Yet, this numerical model disregards demographic stochasticity completely. Hence, to validate the numerical results against demographic stochasticity, I use individual-based simulations (IBS), with a model fitted to the numerical model. In contrast to the previous chapter, dispersal now follows the island-model of Hamilton and May (1977), so that dispersers are distributed randomly over all existing patches instead of moving only into the neighbouring patches. In the IBS I also find sex-biased dispersal, yet the sex-bias in the IBS is always less pronounced than in the numerical prediction. I could show that this can be attributed to the lack of demographic stochasticity in the numerical model because the IBS fit the numerical predictions best when applying a very high number of offspring; a measure that reduces demographic fluctuations in population density. One possible reason for a less pronounced bias in dispersal propensity is that with demographic fluctuations there is an additional incentive to disperse, because dispersers might reach a habitat with a more favorable population density. Therefore, dispersal propensity in the gender with higher dispersal costs might never approach zero. In turn, this non-zero dispersal contributes to the destruction of kin-structure so that the other gender can reduce their dispersal (see the first part of the Introduction).

In additional simulations I include inbreeding depression to validate our model against the one used by Gandon (1999). Like in Gandon (1999) inbreeding depression reduces the probability of winning a breeding territory for pairs where both partners did not disperse. A parameter δ determines how much inbreeding depression reduces the probability to win a breeding territory for philopatric pairs. I find that with inbreeding depression and asymmetric costs, the latter defines which sex evolves into being more dispersive. This holds as long as the effect of inbreeding depression, δ, is not higher than mean dispersal mortality. When δ is higher than average dispersal mortality, starting conditions determine which gender becomes more dispersive.

0.4 Chapter 4 - "Evolution of sex-biased dispersal under asymmetric competition and demographic stochasticity"

In chapter 4 I test the effect of differences in the intensity of competition for reproductive resources on the evolution of biased dispersal. Next to inbreeding-depression (e.g. Gandon, 1999) and differences in dispersal costs (see Chapter 3 of this thesis), differences in competition between genders are another possible reason for sex-biased dispersal (Perrin and Mazalov, 2000). Such differences in competition for reproductive resources are possible in systems where the genders compete about different resources independently. In one of those systems females compete for breeding space and males compete for mating with the successful females. The higher the intensity of competition, e.g. among males, the higher the variance in their individual fitness, because in this case fewer males win matings and father offspring, while a higher number of males get no offspring at all. Such an increased variance induced by competition about reproductive resources increases the incentive to disperse, because by dispersal they lower the risk that all siblings suffer from the same conditions, and they increase the probability that at least some of them immigrate into patches with lower competition. This risk-spreading strategy is called bet-hedging (Hopper, 1999). Hence, increased competition for one gender could therefore induce the evolution of sex-biased dispersal.

Perrin and Mazalov (2000) investigate this hypothesis with a numerical model. In a polygynous mating system, in which males can mate with multiple females, Perrin and Mazalov (2000) apply two different scenarios. In their first scenario (which I call *p1*) females compete for a fixed number of breeding spaces in a patch, and males compete for mating with these successful females, and all offspring survive. In contrast, in their second scenario (which I call *p2*) all females breed, males again compete for matings, but offspring suffer from a constant predation rate. In scenario *p1* females and males experience approximately the same intensity of competition, whereas in scenario *p2* all competition among females is eradicated, but males still experience competition for matings. Perrin and Mazalov (2000) find symmetric dispersal in scenario *p1* and discover sex-biased dispersal only in scenario *p2*, in which females do not suffer any competition, which is very unlikely to occur in nature.

In order to study the effect of differences in intensity of competition, I therefore use an altered scenario (which I call *p3* here), where I increase mate-competition among males but in which females still experience the same intensity of competition about breeding space as in *p1*. Mate-competition among males is most intense

if only one male per patch is allowed to mate with all successful females. While in scenario *p1* males are chosen randomly by females as mating partners (random mating), in the altered scenario (*p3*) one male is picked randomly to mate with all females (harem mating). In this chapter I show that such a system can be derived from the numerical model used by Perrin and Mazalov (2000) in scenario *p1*. However, this altered system (*p3*) also results in completely symmetric dispersal, even though competition among males is higher than among females. I can therefore conclude that under the assumptions made in the numerical modeling approach of Perrin and Mazalov (2000) different intensities of competition are not enough to induce biased dispersal, as long as competition for one gender is not completely eradicated.

The numerical model of Perrin and Mazalov (2000) completely neglects the effects of demographic stochasticity. However, demographic stochasticity has been shown to influence dispersal (see Chapter 3 of this thesis). I therefore test the influence of demographic stochasticity on the evolving dispersal probabilities in scenarios *p1* and *p3*, for which symmetric dispersal was predicted by the numerical model of Perrin and Mazalov (2000). I translated these two scenarios into corresponding individual-based models – one with random mating (which I will call RM) and one with harem mating (called H), and used low numbers of offspring per female to increase demographic fluctuations. In contrast to the results of the numerical models with random mating (*p1*) and harem mating (*p3*), I find biased dispersal by including demographic stochasticity in both mating systems in the individual-based models. The relatively small patch sizes – each patch can support about twenty breeding females – and the low numbers of three offspring per female result in different numbers of competitors in every patch which induces a between-patch variance in offspring number. In cases where this variance is higher for males than for females, male biased dispersal evolves. Cases where between-patch variance was higher for females than for males were not observed. If the between-patch variance in offspring number is equal for males and females, symmetric dispersal emerges. I find equal between-patch variance in offspring number in cases with low demographic stochasticity, e.g. caused by a doubling of the number of offspring per female, which reduces fluctuations in sex-ration in the patches. The same fluctuations are also reduced in simulations with big patches with population sizes of more than hundred individuals. In these cases, symmetric dispersal evolves, which fits to the results of unbiased dispersal found by Perrin and Mazalov (2000), as their numerical model excludes any between-patch variance.

However, due to the demographic fluctuations males experience between-patch variance in offspring number that is at least as high, but often higher than among females, because for males there are two sources of stochasticity: the fluctuating

number of male competitors and the fluctuating number of females winning a breeding territory, which matters most in small populations where the number of females lies more often below the number of available breeding spaces. Therefore, in my model males profit more from dispersal. This causes the bias in dispersal propensities towards males. Another possible reason for biased dispersal would be a differential in kin-competition caused by the mating system itself. However, in the models described here, higher kin-competition among males than among females can be excluded as the driving force of biased dispersal because this would result in a bias even with high numbers of offspring, as kin-competition is unaffected by the number of offspring, if – like in our case – all females get the same number of offspring.

I also find that the bias in the harem mating system (H) is always more pronounced than in the random mating system (RM) because the between-patch variance in offspring number for males and females in H is higher than in RM. Furthermore, due to the higher relatedness among individuals in H, higher mean dispersal propensities evolve as in RM. It is also noticeable in H that the emerging dispersal propensities are almost independent from local population size, because the effective population size – an indicator for relatedness – in such a mating system ranges only between zero and four (comp. Nomura, 2005).

Chapter 1

Evolution of spatial pattern in dispersal strategies[1]

Andreas Gros, Hans Joachim Poethke & Thomas Hovestadt

1.1   Introduction

The evolution of dispersal strategies has become an important topic in theoretical ecology (e.g. Hamilton and May, 1977; Comins et al., 1980; Frank and Slatkin, 1990; Hovestadt et al., 2001; Gandon and Michalakis, 2001; Barton et al., 2002; Dytham, 2003; Hanski et al., 2004). From an individual's perspective dispersal may be motivated by a number of reasons, e.g. avoiding competition for resources (either inter- or intraspecific; Lambin et al., 2001), minimizing kin competition (e.g. Hamilton and May, 1977; Comins, 1982; Frank, 1986; Kisdi, 2004), avoiding inbreeding (Perrin and Goudet, 2001) or coping with the temporal variability of resource availabilities (Levin et al., 1984; Travis and Dytham, 1999; Gandon and Michalakis, 2001). Generally, individuals should disperse as long as they expect a higher fitness away from their natal habitat (Frank, 1986; Metz and Gyllenberg, 2001; Poethke and Hovestadt, 2002; Dytham, 2003). However, dispersal is associated with costs and depending on landscape configuration dispersal may carry a substantial a risk. I.e., when habitat is abundant, dispersal is not very risky, but when suitable patches become scarce and widely spread, dispersal is likely to be disadvantageous (Hastings, 1983; Travis and Dytham, 1999). Consequently, we can predict the adaptation of dispersal strategies to general landscape characteristics (Hovestadt et al., 2001). However, in natural landscapes, the density and distribution of habitat is typically variable across space. Obviously, the optimal dispersal strategy will depend on the actual position within a heterogeneous landscape. Selection should thus favour local adaptation of dispersal strategies, at least as long as offspring are dispersed into a similar spatial context. However, dispersal is also the factor responsible for gene flow and fundamentally operating against local adaptation (Haldane, 1956; Kirkpatrick and Barton, 1997; Case and

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[1]Gros, A., Poethke, H. J. & Hovestadt, T. (2006) Evolution of local adaptations in dispersal strategies. – Oikos 114: 544–552

Taper, 2000). Thus, the question arises under which conditions spatial patterns in dispersal strategies can evolve. Evolutionary pressure is mainly exerted by the risk to disperse offspring across the edge of a habitat. This may cause a decrease of dispersal probability in small patches or near a habitat's border whereas a strong gene flow would counteract such a decline. Therefore, population size and reachability of habitat should play a crucial role in the emergence of locally adapted dispersal strategies. The topic has already been addressed by Travis and Dytham (1999), who could demonstrate that local adaptation can in fact emerge in a complex landscape. However, their study did not aim at a systematic investigation of the effect of patch respectively population size and was limited to only one type of dispersal kernel.

In this paper we use an individual-based model to investigate the evolution of dispersal distance and dispersal rate of asexual annual plants within a single circular patch located in a hostile matrix. In our model the landscape defines the costs of dispersal due to the loss of offspring dispersing into the matrix (Hovestadt et al., 2001). This contrasts with Hamilton and May (1977); Comins et al. (1980); Comins (1982); Ezoe (1998) and Rousset and Gandon (2002), who implement dipersal costs as an external factor. Our goal is to understand under which conditions the emergence of locally adapted dispersal strategies becomes possible and e especially compare the evolutionary outcome for different dispersal kernels in a very simple landscape, which separates our study from the one by Travis and Dytham (1999).

1.2 Material and Methods

We developed a individual-based model, with space modelled as a two dimensional grid (Berec, 2002) of equilateral landscape cells which can be either habitat or matrix. Each habitat cell can support only one established plant. Within an unbounded world of matrix cells we placed a single circular habitat patch of variable radius (25, 50, 75, 100, 125 and 150 cells) (Figure 1.1).

Each time step of the model represents a reproduction cycle of annual parthenogenetic plants. Three different procedures are executed during each time step within a simulation run, i.e. (i) reproduction, (ii) dispersal and (iii) post-dispersal competition.

(i) Reproduction: For simplicity, density-independent mortality of seeds or seedlings is not explicitly modelled. Thus each plant is considered to be a point source for seedlings rather than seeds. Each mother produces a constant number of
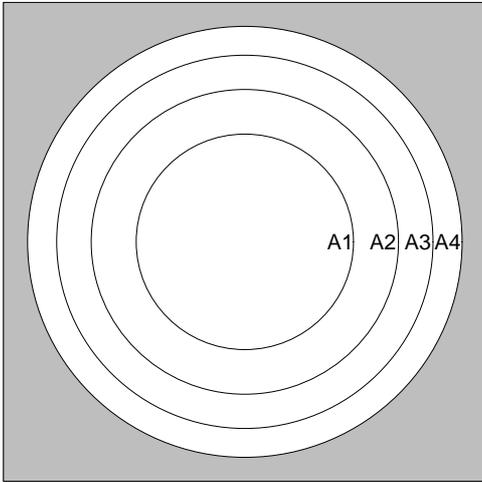
Figure 1.1: Simple patch-matrix landscape used in simulations. (white = habitat, gray = matrix). The indices mark the evaluation areas of carrying capacity each analysed for emergent dispersal strategies. The radius of patches varied from 25 - 150 in steps of 25.

five (m = 5) possible descendants. Each of these is characterized by two continuous genetic characters G_d and G_p. G_p (used with kernels Uniform, Moore and NE+) is coding for the propensity to disperse (dispersal rate) and G_d (used with kernels NE and NE+) for the mean dispersal distance. However, for simulation experiment with kernel NE G_p is without function and consequently selectively neutral. The same holds for G_d in simulation experiments with the kernels Uniform and Moore. Seedlings inherit the genes for G_d and G_p from their parents but genes mutate with a probability of 0.001 during this process. In case of a mutation G_d is altered by multiplying its value by either 0.9 or 1.1. This maintains a positive co-domain and creates mutation steps proportional to the value of the genetic character. G_p is altered by adding a random value from the uniform interval $[-0.025, 0.025]$. Its values are kept within the interval $[0, 1]$ by cutting the edges. In each simulation run the values of G_d and G_p in the start population are uniformly distributed within the interval $[0, 200]$ respectively $[0, 1]$.

(ii) Dispersal: During the dispersal process all offspring are distributed according to their inherited dispersal strategy (dispersal distance (G_d) and/or dispersal rate (G_p)). Whenever a dispersing offspring ends up in a matrix cell, it dies. There are no energetic or allocation costs associated with the decision to disperse (G_p) or a specific mean dispersal distance G_d, i.e., the cost of dispersing seeds over a long distance is similar to short distance dispersal.

In our experiments we compare the performance of four frequently used dispersal kernels:

    1. <u>Uniform (U)</u>: This kernel resembles the island model of Hamilton and

May (1977) with the modification, that our landscape is heterogeneous. Only the dispersal probability (G_p) is subject to evolution. The destination cell of a disperser is drawn randomly from all possible landscape cells. In contrast to the other kernels this kernel requires a bounded landscape. Thus, we restricted the dimension of the landscape to 400 X 400 cells in all simulation experiments implementing this kernel. The chance of a dispersing individual to arrive in a habitat cell is thus determined by the amount of habitat cells compared to the total number of cells (equals p of Hamilton and May, 1977).

2. Moore (M): A disperser draws one of the eight adjacent cells (Moore neighborhood) at random as destination (nearest neighbor dispersal; Travis and Dytham, 1999). A similar kernel is suggested by Comins (1982) for dispersal between discrete colonies of animals living on a patchy resource, and seed and pollen distributions in continuous populations of plants. Because the dispersal distance is fixed, only the propensity to disperse (G_p) evolves.

3. Negative-exponential (NE) A disperser draws a direction at random and a dispersal distance from a negative-exponential probability density function (1.1) with mean $G_d = 1/\alpha$.

$$f(x) = \alpha e^{-\alpha x} \qquad (1.1)$$

Dispersal rate is dependent on dispersal distance in this kernel and only the dispersal distance (G_d) is subject to evolution. However, a seedling remains philopatric if the dispersal distance is short enough to deposit the seedling within the maternal cell. As Levin et al. (2003) states, this dispersal kernel is probably the most commonly used one (e.g. Streiff et al., 1999; Yao et al., 1999; Bullock and Clarke, 2000; Hovestadt et al., 2000; Nathan et al., 2000; Bleher et al., 2002; Murrell et al., 2002) and does properly fit seed distributions in dense aggregations of plants like forests.

4. Negative-exponential plus dispersal rate (NE+) In this kernel the generation of dispersal distances follows the same rules as in the kernel *NE*, but a dispersal move always starts at the maternal cell's border, thus ensuring that any dispersing seedling will fall into a cell different from its origin. Hence, G_d (as a parameter of Equation 1.1) does not directly code for the mean dispersal distance in this kernel. In contrast to kernel NE, a seedling disperses only with probability G_p, respectively remains philopatric with probability $1 - G_p$. Both genetic characters, G_p and G_d, evolve.

(iii) Post-dispersal competition: After their offspring being dispersed, all adult
plants die. For each cell a single seedling is randomly drawn among all its im-
migrants to establish and reproduce in the next time-step. All other seedlings
die, i.e. we do not consider the establishment of a seed bank. To get localized
mean values for G_p and G_d, we separate the habitat into four distinct areas:
a circular area in the center (A1) and three consecutive rings (A2-A4). Each
of these areas includes an approximately equal number of cells. This implies
that the rings get "thinner" towards the edge of the habitat (Figure 1.1).

The evolutionary process in each landscape configuration was evaluated on
the base of about an equal number of habitat cells. The number of repeated
simulation runs conducted was thus inversely proportional to the patch's
area. For a radius of 150 cells we only ran 1, for patches with a radius of
25 cells, 36 replicates. The small number of replicates in large habitats was
indicated by the substantial computation time needed. Mean values of G_d
and G_p were averaged over all replicates of simulations of a landscape-kernel-
combination.

1.3   Results

We first consider the evolution of the dispersal rate, i.e. the fraction of seedlings
deposited outside the cell of origin. Dispersal rates depend on both the size of the
habitat patch and the kind of dispersal kernel. Dispersal rate is by far the lowest
with uniform dispersal (U) but also shows the strongest increase with habitat
patch size (Figure 1.2a). Both exponential kernels (NE and NE+) also exhibit
an increase in dispersal rate with increasing patch size while nearest neighbour
dispersal (M) is hardly sensitive to habitat patch area. This difference in response
to patch size results in a decreasing difference in dispersal rates between different
kernels for increasing patch area. For small patches with a radius of 25 cells only
20% of the seeds are dispersed outside the mother's cell with kernel U compared to
more than 70% with kernel NE and 90% with kernel is NE+. For patches with a
radius of 150 cells evolutionarily stable dispersal rates are 50% for global dispersers
and nearly 100% for the kernel NE+. A variance of less than 0.006 in the mean
dispersal rates across simulation runs even in the smallest patches indicates that
results are not strongly affected by genetic drift.

Mean dispersal distances is not an evolvable trait for either nearest neighbour dis-
persal (M) or global dispersal (U). For kernel M it is fixed to the mean distance
between neighbouring cells (= 1.21) and for global dispersal to approximately d
= 200, i.e. half the dimension of the simulated landscape. For the two negative-

exponential kernels (NE and NE+) evolved mean dispersal distances strongly respond to the size of the habitat patch. Even for small patches they are much smaller than the patch radius. While optimal dispersal rates are highest for the NE+ kernel, highest distances evolve with the NE kernel (Figure 1.2b).

We further checked for the emergence of systematic spatial patterns in the distribution of dispersal parameters (G_p and G_d) for each of the dispersal kernels. Evidently, there is no spatial correlation between the mother's cell and the target cell of dispersed seedlings for global dispersal (U). Consequently, no spatial structure can evolve for this dispersal kernel. In case of the other three kernels (M, NE and NE+) the development of a spatial structure critically depends on patch size . While we found no spatial structure in the experiments with small habitat patches a pronounced structure evolved in the large patches (Figures 1.3 and 1.4). Mean dispersal rate ($\overline{G_p}$) as well as mean dispersal distance ($\overline{G_d}$) of individuals was always significantly higher in the centre of the patches (area A1) than at the perimeter (area A4). This difference is strongly dependent on patch size (Figure 1.5) and may surpass 30% in large patches.
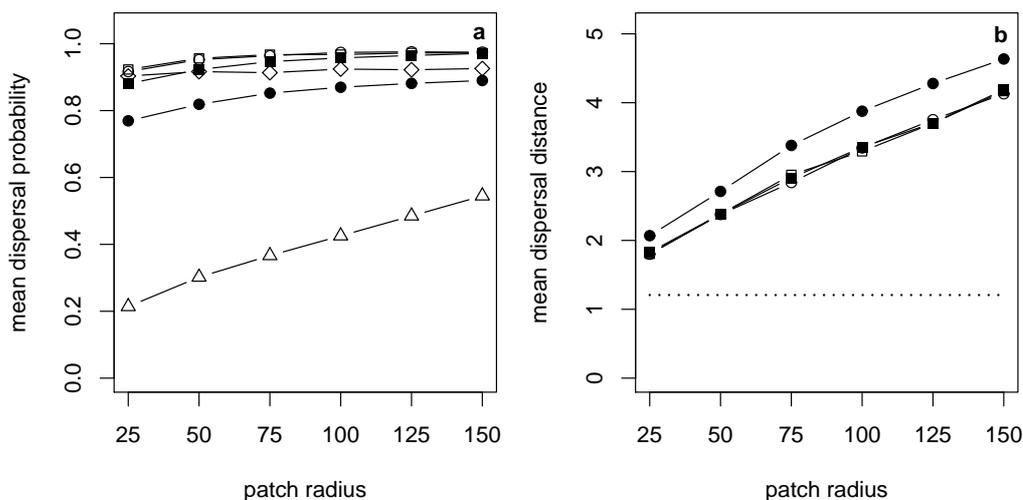

Figure 1.2: (a) Evolved mean dispersal rates (parameter G_p) with either kernel NE+ (open circles), kernel NE (filled circles), M (filled squares), or U (open triangles) in different patch sizes. (b): Evolved mean dispersal distances (parameter G_d) with either kernel NE+ (open circles), NE (filled circles), or M (filled squares) in different habitat patch sizes.
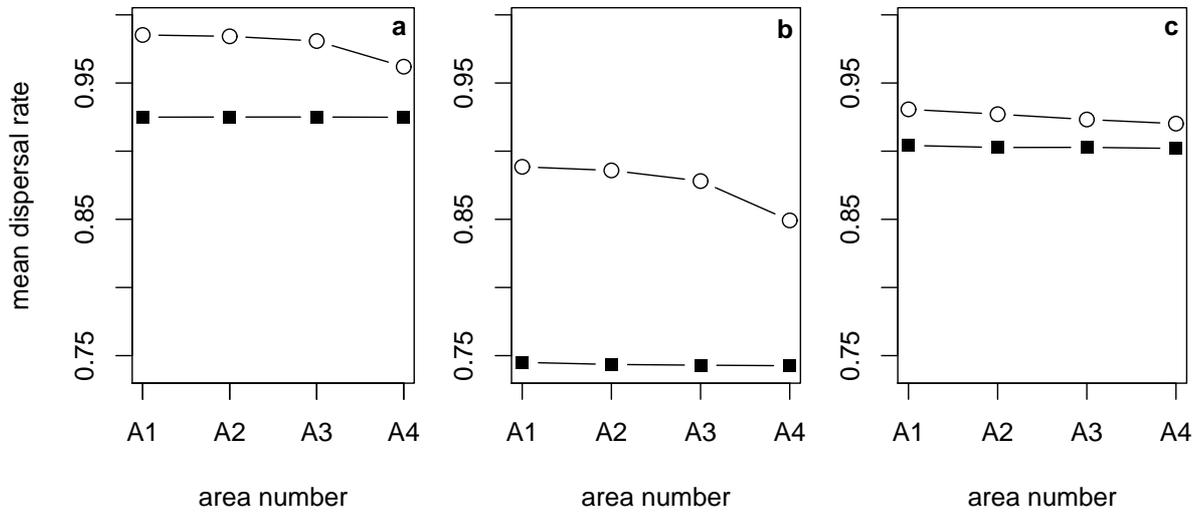
Figure 1.3: Distribution of mean dispersal rate across the different patch zones outlined in Figure 1.1 with either kernel NE+ (a), kernel NE (b), or M (c). Open circles: patch-radius 150, filled squares: 25 cells.

1.4   Discussion

Our simulations clearly demonstrate the dual effect of habitat patch size and dispersal mode on the evolution of dispersal strategies. Depending on the dispersal kernel, different adjustments are possible: either by changes in the propensity to disperse, in mean dispersal distance, or both. The evolving strategies are a result of a basic tradeoff between reducing the losses of offspring dispersing into the matrix (Comins et al., 1980) and the possibility to escape kin-competition (Hamilton and May, 1977; Ezoe, 1998; Kasuya, 2000; Kisdi, 2004). Other factors favouring dispersal are of minor importance in our model lacking any environmental stochasticity. In fact, without kin-competition dispersal would only be selected for, if there are no costs of dispersal or if habitats differ in reproductive success (Greenwood-Lee and Taylor, 2001).

For any dispersal kernel, the risk to loose offspring into the surrounding matrix will fundamentally decline as patch size increases. Consequently – and not surprising – we find a consistent increase in dispersal rates with increasing patch area in three of the four dispersal kernels implemented in our simulations. The risk of loosing offspring into the matrix also depends on the dispersal distance and will in general be largest for the kernels with the largest mean dispersal distance. This argument can explain that with uniform dispersal kernel (U) the lowest dispersal
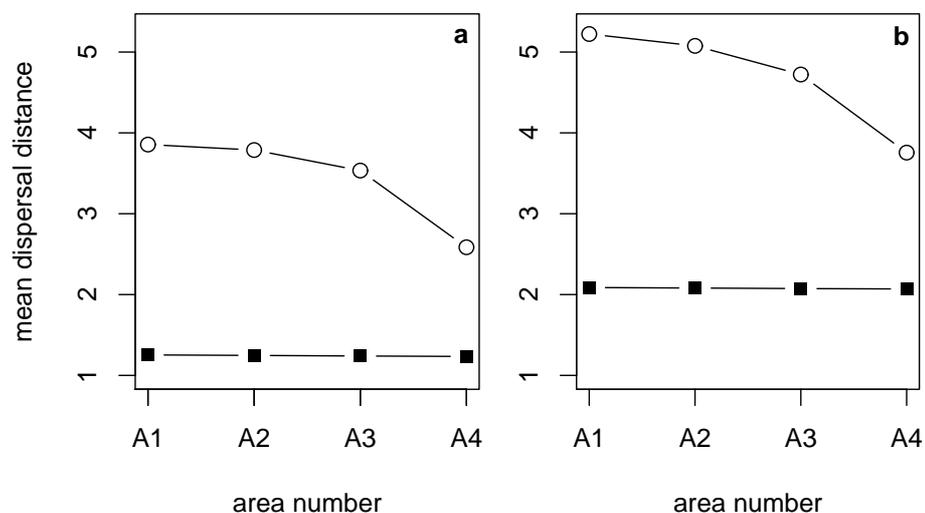
Figure 1.4: Distribution of mean dispersal distance with either kernel *NE+* (a) or *NE* (b). The panels show mean dispersal distances in evaluation areas as stated in Figures 1.1. Open circles: patch-radius 150, filled squares: 25 cells.

rates evolved, but also that this kernel is most sensitive to changes in patch size. Second with respect to dispersal distance is kernel NE and third NE+, and these kernels are inversely ranked with respect to dispersal rate and their sensitivity towards changes in patch area. It must be noted though that the dispersal rate for kernel NE is not an evolvable trait as such but the emergent result of the evolution on mean dispersal distance (G_d). It should also be noted that the highest dispersal rates evolve in the only kernel with two parameters (NE+), i.e. the most flexible one. However, the results with kernel M (nearest neighbour) do not fit into this general view. Even though mean dispersal distance is the lowest with this kernel, evolved dispersal rates are lower than with kernel NE+ and hardly sensitive to changes in patch area. We assume that this is a consequence of the restricted ability to escape strong kin-competition if dispersal is exclusively limited to the neighbouring cells (cf. Comins et al., 1980). We confirmed the influence of kin-competition by altering the number of individual offspring from m = 5 to either m = 2 or m = 10. With m = 2 the competition among relatives for free space is reduced and consequently the evolving dispersal rates respectively distances dropped in all kernels. In contrast, with m = 10 the increase in kin-competition led to an increase in the values of both genetic characters. For both exponential kernels mean dispersal distance also increases as patches become larger. It is striking that the mean values of G_d with kernel NE lie above those for kernel NE+ (Figure 1.4b). This is caused by the evolutionary "challenge" to regulate
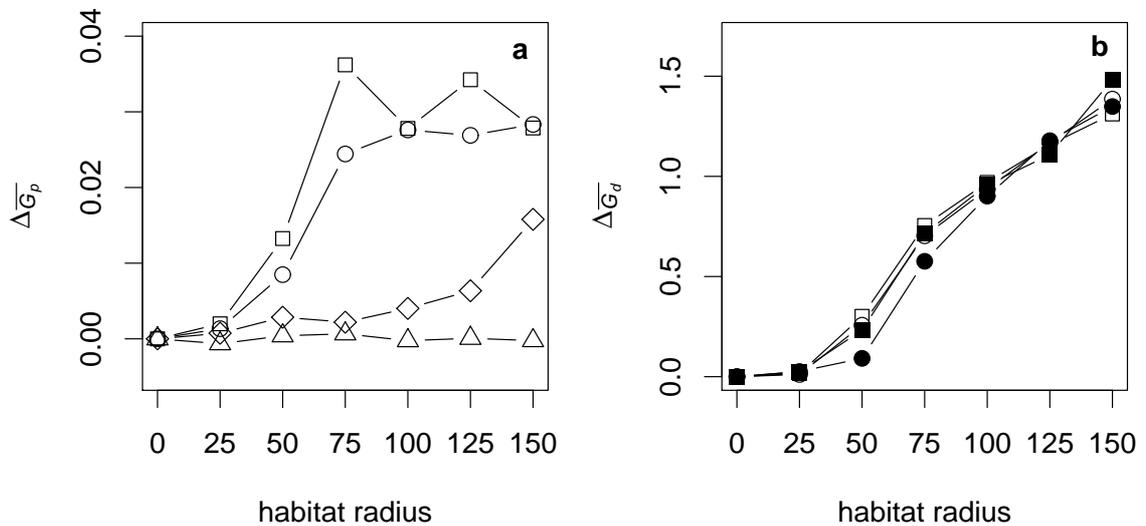
Figure 1.5: Change in the difference of evolved mean dispersal distance ($\overline{G_d}$) and mean dispersal rate $\overline{G_p}$ between area A1 and A4 ($\Delta\overline{G_d}$ and $\Delta\overline{G_p}$) with increasing habitat radius for (a) mean dispersal rate ($\overline{G_p}$) and (b) mean $1/\alpha$ ($\overline{G_p}$). Open circle: kernel *NE+*, filled circles: kernel *NE*, filled square: kernel *M*, open triangle: kernel *U*.

philopatry and dispersal distances by a single parameter in kernel NE, while NE+ allows regulating these two traits separately. To achieve a similar dispersal rate as with kernel NE+, individuals utilizing kernel NE need to increase mean dispersal distance, as otherwise too many progeny would remain within the natal cell.

The dispersal kernels differ quite remarkably in their tendency to develop spatial patterns in dispersal rate or distance. Obviously, a spatial pattern cannot and did not evolve with uniform dispersal as the starting position of a dispersing individual has no influence on the target position it will eventually reach. Surprisingly, we also found little evidence for the formation of spatial pattern under kernel M, even though we observed some decline in parameter G_p in the very outermost ring of cells. The very low dispersal distance of this kernel rather seems to promote the emergence of spatially distinct clusters of individuals of common descent (cf. Figure 1.6), a pattern frequently detected in such kinds of grid based simulations (e.g. Tilman et al., 1997; Lewis, 1997; Holmes, 1997; Levin and Pacala, 1997; Ennos, 2001). Travis and Dytham (1999) also used kernel M in their simulation study to investigate local adaptation in fractal landscapes. They found a much broader range for the dispersal rates than we and describe a clear selection for dispersal inside a patch and a distinct evolution towards non-dispersal at the habitat border.
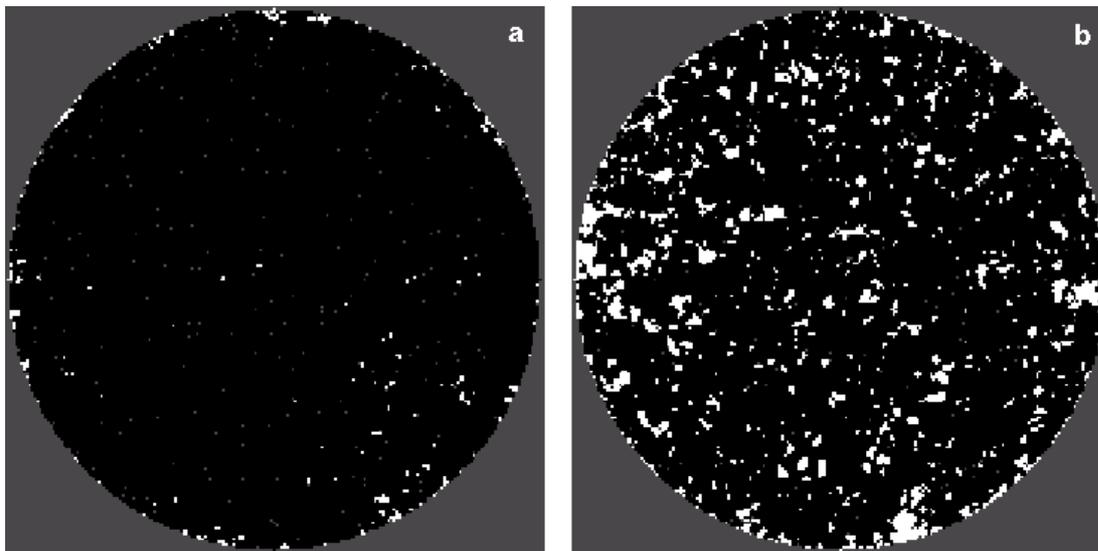
Figure 1.6: Similarity of G_p-values in patches of radius 100 with either kernel NE+ (a) or kernel M (b). A cell is colored white, if it is surrounded by seven cells with same trait values or matrix cells.

This might be caused by the broad range in the perimeter: area ratio of patches in the fractal landscapes and the difficulty of gene flow introduced by the "rugged" shape of fractal patches. For the two exponential kernels – which are probably closest to naturally occurring kernels – we observe the development of a weak spatial gradient for both, dispersal rate and especially dispersal distance in patches with a radius of 50. From then on, the difference in mean dispersal distance between the centre of the patch and the outermost ring (A4) increases rather linearly. In the largest patch mean dispersal distance is about one third larger in the centre than in the edge of the patch while the difference is less than $1/10$ in the patch with a radius of 50. However, this does not imply the evolution at the edge and in the centre are completely independent. Given the values for G_d which did evolve, the direct effect of loosing offspring is limited to cells near the border of the patch. But a reduction in dispersal distance is still noticeable in ring A2, (Figure 1.4), i.e. in a distance d ($d \in [(1-1/\sqrt{2})r, r/2]$) which is about seven times further away from the edge than the mean value for G_d in the patch centre. Obviously, gene flow "transports" the selective pressure on G_d near the patch's edge far into the interior of the patches. The simulation results clearly demonstrate the existence of a minimum patch area necessary for the evolution of locally adapted dispersal strategies. If we assume the average diameter of a tree crown to be 5 m, the minimal area of a (circular) patch in which we could expect to find a gradient in dispersal strategy would be about 0.2 km^2 (500 m diameter). In contrast for small

herbs with a average diameter of only 10 cm, a spatial structure could eventually develop in a patch of only 75 m^2. However, the evolution of dispersal distance and consequently the size of the values predicted above would certainly be different if model parameters were altered or new ones added. For example an increase in the longevity of organisms, trade-offs between dispersal distance and competitiveness (cf. Greene and Johnson, 1993; Geritz, 1995), or habitat disturbance (cf. Comins, 1982; Gandon and Michalakis, 2001) would presumably all alter the evolution of dispersal distance and the emergence of spatial patterns. A variety of plant species is able to adapt their propagation strategy to selective pressures. Michaels et al. (1988) confirmed that intraspecific adaptations of dispersal strategies are generally possible. More specifically, a plant can influence the dispersal capabilities of its offspring because seed sizes vary at individual plants (Geritz, 1995). An example for a direct adaptation to landscape structure is the change of the reproductive mode from propagation via seeds (long distance dispersal) to vegetative (nearest-neighbor dispersal) depending on local circumstances. Prati and Schmid (2000) discovered that *Ranunculus reptans* invested heavily into sexual reproduction when close to water, but more into vegetative reproduction on land. In this case the differentiation is only an indirect adjustment to landscape structure, as it results from a difference in the intensity of competition – high on land, low close to water – with a low chance of establishment from seeds away from water. Kanno and Seiwa (2004) report that the reproductive mode (sexual or vegetative) of the clonal forest understorey shrub *Hydrangea paniculata* is influenced by small scale variations in the dynamics of canopy trees. These findings, as well as our simulation results, prove an adjustment of dispersal strategies to local demographic situations are principally possible and are selected for under certain conditions.

Chapter 2
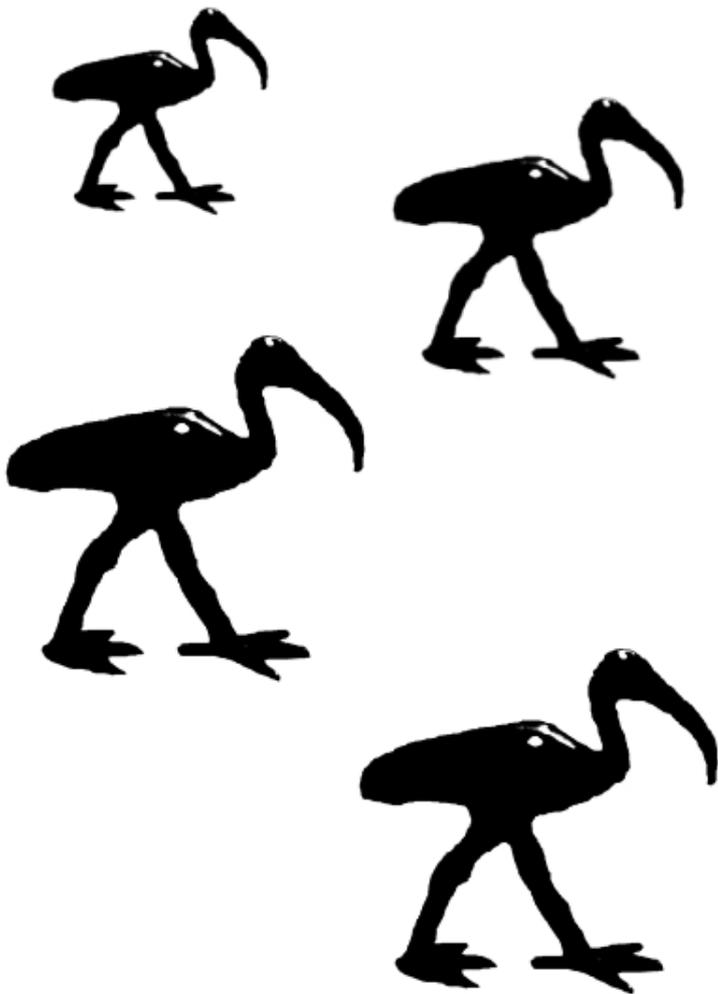
How dispersal propensity and distance depend on the capability to assess population-density

Andreas Gros, Thomas Hovestadt & Hans Joachim Poethke

2.1   Introduction

The evolution of dispersal is driven by the balance between dispersal related cost, e.g. the mortality-risk during transitions, or the energy and time spent on dispersal (Rankin and Burchsted, 1992; Zera and Denno, 1997), and numerous potential benefits. These benefits include avoidance of competition for resources (either inter- or intraspecific, Lambin et al., 2001; Poethke and Hovestadt, 2002), minimization of kin-competition (e.g. Hamilton and May, 1977; Comins, 1982; Frank, 1986; Rousset and Gandon, 2002; Kisdi, 2004; Poethke et al., 2007), avoidance of inbreeding depression (Bengtsson, 1978; Motro, 1991a; Perrin and Goudet, 2001), or coping with the temporal variability of resource availabilities (Levin et al., 1984; Travis and Dytham, 1999; Gandon and Michalakis, 2001). Another benefit of dispersal, the possibility to colonize new habitats, increases the probability of survival of a species (Alsos et al., 2007).

The growing awareness of colonization events through long-distance dispersal in plants (Nichols and Hewitt, 1994; Nathan et al., 2002; Bohrer et al., 2005; Nathan, 2006; Alsos et al., 2007) has inspired the introduction and investigation of "fat-tailed" dispersal kernels (Higgins and Richardson, 1999; Bullock and Clarke, 2000; Hovestadt et al., 2001; Austerlitz et al., 2004; Katul et al., 2005) in theoretical investigations of seed dispersal. However, as dispersal kernels describe the probability distribution of dispersal distances away from a source, the use of dispersal kernels has mostly be confined to studies of seed or pollen dispersal or that of other organisms with passive dispersal (Ezoe, 1998; Gros et al., 2006). Occasionally, kernels have also been estimated for actively moving animals (Baguette, 2003; Gilbert et al., 2004; Chapman et al., 2007) and certain kernels are implicitly assumed in metapopulation models (Hanski, 1994).

However, most actively moving animals presumably do not leave habitat patches accidentaly (van Dyck and Baguette, 2005), but because of a "decision" to do so. Furthermore, they are believed to more or less continuously monitor the status of their surroundings during movement. It is likely that they can distinguish between suitable and unsuitable habitat and can assess the expected benefit of further movement. It thus appears highly implausible that an actively moving animal will "blindly" travel a pre-set distance and settles there regardless of actual conditions and settle at an arbitrary position regardless of the actual conditions there.

Instead, when suitable habitat is patchily distributed and patches of habitat are embedded into an environment unsuitable for reproduction, animals should obviously continue their movement until they find a suitable patch. Yet, once they have reached a patch of suitable habitat, the decision whether to continue dispersal or to stay in this patch should depend on the balance between the expected costs and benefits of either decision (Frank, 1986; Metz and Gyllenberg, 2001; Poethke and Hovestadt, 2002). The expected benefits are influenced by the quality of the local habitat as well as the range of spatial correlation in habitat quality. Consequently, emigration decisions should be affected by an individual's capacity to assess the status of habitats: individuals capable to correctly evaluate the status of their habitat may make more qualified dispersal decisions than individuals not capable of such evaluation (Bengtsson et al., 1994; Johst and Brandl, 1999; Poethke and Hovestadt, 2002; Bowler and Benton, 2005).

In this paper we investigate the evolution of dispersal decisions in a patch-matrix landscape. In detail, we test a number of specific hypotheses. First, the number of successive dispersal steps should decrease with increasing dispersal costs (Murrell et al., 2002). Second, we expect the number of dispersal steps to increase with increasing spatial correlation of habitat conditions across patches because with increasing correlation animals have to disperse further to escape a cluster of bad quality patches (cf. Frank and Wissel, 1998; Ovaskainen and Hanski, 2002). Third and most importantly, we expect that species with the ability to perceive habitat quality will evolve a fundamentally different dispersal strategy – the combination of emigration propensity and the number of dispersal steps – than species lacking that ability. In which way the strategies will differ cannot easily be foreseen because dispersal has a feedback effect on prominent drivers of its evolution, e.g. population density and kin-structure (Poethke et al., 2003, 2007).

In the following we will expand a previously published simulation model (Poethke and Hovestadt, 2002) to simulate the evolution of dispersal strategies in a patch-matrix metapopulation. In this model individuals reproduce in habitat patches, can disperse to other patches and by doing so, cross inhabitable matrix, which

entails a given dispersal mortality. We extend the model aspects in three ways. First, we model dispersal as a stepwise process in which individuals decide on a step-by-step basis whether to continue dispersal or to stop. Second, we introduce spatial correlation in habitat quality. Third, we alter the ability of individuals to collect information about the status (population density) of their natal patch and any further patch they visit during dispersal.

To allow for the joint evolution of dispersal propensity (emigration probability) and dispersal distance (the number of dispersal steps), we extend the model to allow for the independent evolution of the decision to leave the natal patch and the decision to eventually continue dispersal after a new habitat patch is reached.

To account for groups of animals differing in their capacity to assess local habitat quality we compare the evolution of dispersal strategies in three different scenarios: a) all dispersal decisions are independent of local population density, b) natal dispersal depends on local population density but additional steps are density-independent, and c) dispersal is always dependent on local population density.

The first scenario (a) could apply to animals like certain butterflies that leave habitats independent of population density (e.g. Boughton, 2000). The second scenario (b) could apply to animals that acquire information about population density at the juvenile stage but disperse regardless of density as adults, such as e.g., migratory locusts (Fuchs et al., 2003), or some crickets (Fowler, 1988). In the third setting (c) we assume animals that assess local population density at all times. This most likely applies to long-lived animals like mammals, birds, and a few insect species, (e.g. some corixid species investigated by Pajunen and Pajunen, 2003).

Our work was preceded by Ruxton and Rohani (1999), who investigated the population level effects, such as mean population size and mean number of dispersal events per population, in a scenario with stepwise density-dependent dispersal, similar to our scenario c). Individuals in their model continue to disperse if the population density in the new habitat is above a given – fixed – proportion of the density of their natal habitat. Their model disregards the role of dispersal mortality, and more importantly, the authors do not investigate the evolution of dispersal strategies but only explore its consequences for population dynamics.

2.2   Methods

We use a slightly modified version of the individual-based metapopulation model of Poethke and Hovestadt (2002). The model describes population dynamics, inter-

patch dispersal and the evolution of dispersal propensity in a meta-population of a diploid, sexually reproducing species with discrete generations and density-dependent local population growth. The meta-population consists of 576 habitat patches arranged in a square lattice of 24x24 ($= 576$) cells. To avoid edge effects the metapopulation is placed on a torus. Each patch (i) supports a local population with carrying capacity $K = 40$ (total carrying capacity of the system is 23.040 individuals). Simulation experiments are initialised by placing K individuals in each of the 576 patches.

Within-patch population dynamics follow a logistic growth according to an equation suggested by Hassel (1975). Like in Murrell et al. (2002) and Poethke and Hovestadt (2002), a female gives birth to $2\Lambda_{female}$ offspring with sex allocated randomly. Λ_{female} is Poisson distributed with mean $\Lambda_{patch}(t, i)$. To account for environmental variability and generate strictly positive values only, $\Lambda_{patch}(t, i)$ (specific for patch i at timestep t) is drawn from a log-normal distribution with mean $\lambda = 2$ and a standard deviation of $\sigma = 1$. The log-normal distribution results in Λ_{patch}-values between zero and about 40. Offspring mature with a patch-specific survival probability s_i:

$$s_{t,i} = \frac{1}{(1 + aN_{t,i})} \tag{2.1}$$

with

$$a = \frac{\lambda - 1}{K} = \frac{1}{K}.$$

N_i is the local population size of patch i. Expected local population dynamic is thus described by

$$E[N_{t+1,i}] = N_{t,i} \, \Lambda_{patch}(t, i) \, s_{t,i}. \tag{2.2}$$

In all our simulations individuals are characterized by four alleles (n_1, n_2, f_1, f_2) at two diploid loci (n, f). The first of these loci (n) determines the individual's propensity for natal dispersal (P_n), and the second (f) determines its perseverance i.e. the probability (P_f) to continue dispersal once it has successfully reached a habitat patch. This locus thus determines the distance (the number of dispersal steps) covered by dispersing individuals. The alleles of these loci take continuous values and are initialised with uniformly distributed random numbers within the interval $[0.3, 0.5]$. Preliminary simulations showed that similar dispersal traits evolved independently of the starting values taken for initializing alleles.

Dispersal "decisions" can be either density-dependent (DD) or density-independent (DI), and both can apply to natal dispersal (DD_n or DI_n) and any further dispersal step (DD_f or DI_f). We translated the three scenarios of animals differing in their

μ	dispersal mortality
l	extent of spatial correlation in habitat quality
λ	growth parameter
$\mathrm{DI}_n/\mathrm{DI}_f$	phenotype of individuals that perform all dispersal steps independent of population density
$\mathrm{DD}_n/\mathrm{DI}_f$	phenotype of individuals with density-dependent natal dispersal but do all further dispersal steps independent of population density
$\mathrm{DD}_n/\mathrm{DD}_f$	phenotype of individuals that perform all dispersal steps dependent of population density
C_n	threshold density for natal dispersal (phenotypic property of DD_n-individuals)
C_f	threshold density for each further dispersal step (phenotypic property of DD_f-individual
P_n	propensity for natal dispersal and phenotypic property of DI_n-individuals
P_f	propensity for each further dispersal step and phenotypic property of DI_f-individuals

Table 2.1: Parameters and symbols used

capacity to perceive local population density (but see Introduction) into simulation settings using combinations of $\mathrm{DI}_{n,f}$ and $\mathrm{DD}_{n,f}$ dispersal. In the first scenario (a), natal dispersal propensity (P_n) as well as perseverance (P_f), i.e. dispersal propensity for all further dispersal moves, is density-independent (scenario $\mathrm{DI}_n/\mathrm{DI}_f$). In the second setting (b), natal dispersal propensity is density-dependent but perseverance is density-independent (scenario $\mathrm{DD}_n/\mathrm{DI}_f$) and in the third scenario (c) all dispersal steps are density-dependent (scenario $\mathrm{DD}_n/\mathrm{DD}_f$). These three scenarios correspond to the three types of dispersers with different sensory capacities as described in the introduction (scenario a - c).

Depending on the scenario, the alleles at the two loci code for different traits. If emigration is density-independent (uninformed), the alleles code directly for the dispersal probability $P = (\mathrm{allel}_1 + \mathrm{allel}_2)/2$, e.g. in case of density-independent natal dispersal $P_n = (n_1 + n_2)/2$. In case of density-dependent emigration, they instead code for a threshold population density which defines dispersal probability according to the following equation:

$$P = \begin{cases} 0 & if \quad C_i \leq C_{th} \\ 1 - \frac{C_{th}}{C_i} & if \quad 0 < C_{th} < C_i, \\ 1 & if \quad C_{th} \leq 0 \end{cases} \qquad (2.3)$$

with $C_i = N_i/K$, the population density in patch i, and C_{th}, the threshold density of the individual in focus below which no dispersal occurs. Previously, Poethke and Hovestadt (2002) have analytically derived that this is the appropriate functional link between population density and emigration probability in case of a time-discrete population growth and the existence of a distinct dispersal phase; the

function is analogue to the model derived by Metz and Gyllenberg (2001) for the case of continuous population growth and dispersal. Thus, in our three scenarios the dispersal strategies of an individuals are defined as given in Table 2.2.

Scenario	Dispersal strategy
DI_n/DI_f	$P_n = (n_1 + n_2)/2$
	$P_f = (f_1 + f_2)/2$
DD_n/DI_f	P_n according to Equation 2.3 with $C_{th} = C_n = (n_1 + n_2)/2$
	$P_f = (f_1 + f_2)/2$
DD_n/DD_f	P_n according to Equation 2.3 with $C_{th} = C_n = (n_1 + n_2)/2$
	P_f according to Equation 2.3 with $C_{th} = C_f = (f_1 + f_2)/2$

Table 2.2: Scenarios and corresponding dispersal strategies.

We want to stress that in any single simulation run all individuals follow the same strategy but may vary in the values of the alleles they carry. Also note that a high value of P_n respectively P_f indicates a high dispersal probability, while high values for C_n and C_f indicate a low tendencies to emigrate.
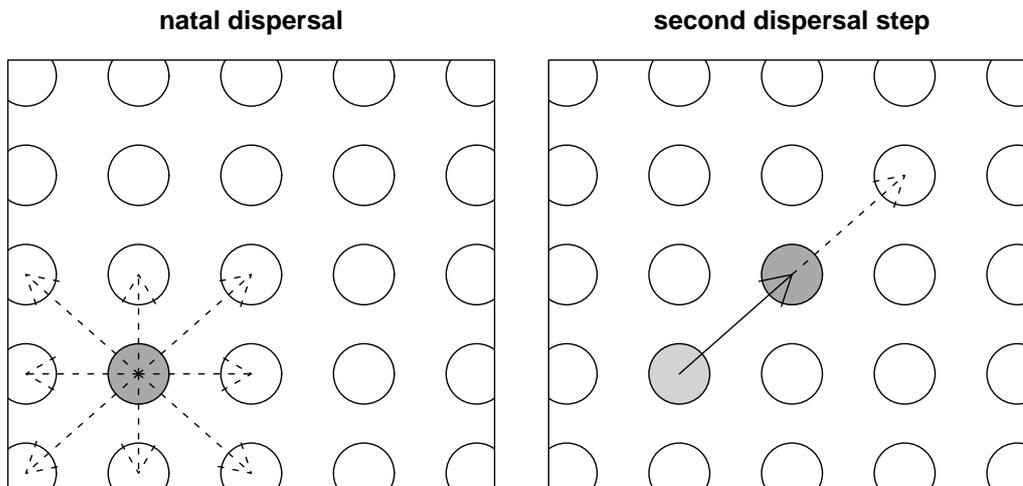
natal dispersal   **second dispersal step**

Figure 2.1: Symbolic respresentation of the landscape and two dispersal steps of a focal individual. Circles represent patches, the space in between represents the matrix. Broken arrows depict possible dispersal moves of a focal individual, continuous arrows represent successful moves. For natal dispersal an individual chooses a direction at random (left panel) and in the following steps keeps this direction (right panel).

For natal dispersal an individual randomly chooses one of eight neighbouring

patches as destination and keeps that direction in each following step (see Figure 2.1). Dispersing individuals either reach the next habitat patch in their path or die during the transition with probability μ. Exploratory simulation runs showed that individuals rarely continued their dispersal for more than 15 consecutive steps, and we therefore limited the maximum number of movement steps to 15. This simplification had only a negligible effect on simulation results but significantly reduced computation time.

When inheriting its parent's genes, mutations occur with probability 0.01 per allele. If mutations occur, the alleles of the loci n and f are altered by adding a random value drawn from a uniform distribution within the interval $[-0.1, 0.1]$. An evolutionary stable state is reached after approximately 3.000 generations, yet each simulation run included 10.000 generations. All results were recorded in the very last generation.

For each scenario we explore the effect of dispersal mortality and spatial correlation of habitat quality on the evolution of dispersal propensity and perseverance. Mortality μ per dispersal step is varied as follows: $\mu \in \{0.025, 0.05, 0.10, 0.20\}$. This cost function in combination with secenario $\mathrm{DI}_n/\mathrm{DI}_f$ resembles setting (c) in Rousset and Gandon (2002).

We modelled spatial correlation in habitat quality by overlaying the patches with a quadratic grid so that an equal number of patches fell in each grid cell. All patches in a square of the grid get the same reproductive conditions as we assign the same value of $\Lambda_{patch}(t, i_1, ..., i_k)$ to all k patches in a square. Each square's Λ_{patch}-value was drawn anew every generation (t). To account for different spatial dimensions of correlation we vary the sidelength of the squares of patches from 1 (no spatial correlation) to 4: $l \in \{1, 2, 4\}$. The spatial configuration of the grid does not change over time, so that each patch always belongs to the same square.

For each of the three scenarios ($\mathrm{DI}_n/\mathrm{DI}_f$, $\mathrm{DD}_n/\mathrm{DI}_f$, $\mathrm{DD}_n/\mathrm{DD}_f$) we run 50 simulation experiments for each combination of μ and l. In the following we use the suffixes only when neccessary, but omit them otherwise and call the scenarios just DI/DI, DD/DI, and DD/DD.

Most simulations are done with a carrying capacity $K = 40$. Yet, K influences kin competition, which is known to be a major factor driving the evolution of dispersal traits, especially when μ is high (Hamilton and May, 1977; Poethke et al., 2007). Under conditions prevailing in our model, relatedness and kin competition increase with decreasing population size – at a given rate and costs of dispersal (Taylor, 1988). Therefore, we tested the influence of different carrying capacities $K = \{20, 40, 100\}$ on the evolution of dispersal strategies in additional simulations.

For all simulations described above, we assume that dispersers stick to a straight movement path. This is the most efficient movement rule for moving away from the natal patch and the square of equal reproductive conditions the patch is located in, while the least efficient one would be a random walk. Thus, the efficiency of dispersal in destroying kin-structure (and thus avoiding kin-competition) and escaping similar reproductive conditions as one's siblings is affected by the movement rule we apply. Therefore we tested the influence of our movement rule on the evolutionary outcome by comparing the results of our standard scenario with the results we get when a disperser randomly chooses a new direction at every step.

As kin-competition is one major factor driving evolution of dispersal, we expect that individuals under both movement rules evolve dispersal strategies that result in about the same level of relatedness within the patches, yet, most likely with different dispersal probabilities and number of dispersal steps. To confirm this assumption about the effect of the movement rule on the levels of relatedness, we run additional simulations employing the random movement rule, but give all individuals the corresponding (now fixed) dispersal traits that evolved under the straight movement rule and record the resulting levels of relatedness. As a measure of relatedness we calculate G_{ST}-values (Nei, 1973) from a neutral locus whose two alleles are assigned following the "inifinite-allele" model (Kimura and Crow, 1964) and for which each mutation results in a unique allelic value. The mutation rate on these alleles is the same as for the dispersal loci in our standard scenarios. Scenarios with phenotypes that adapted their dispersal strategies to the change to random movement pattern before are expected to show higher levels of relatedness when confronted with using the dispersal strategies that evolved under the straight movement rule.

2.3   Results

In all scenarios the individuals' propensity to disperse more than one step decreases rapidly with increasing dispersal mortality μ (Figure 2.2). Even with a very benign stepwise dispersal mortality of $\mu = 0.025$ the highest average number of successful dispersal steps in any scenario is 2.68 – much less than the 15 steps limit imposed. In the following the term "mean number of dispersal steps" always refers to the mean number of successful (survived) steps of dispersing individuals.

With a still modest mortality of $\mu = 0.20$ the mean number of successful steps drops to 1.32 with strategy DD/DD ($l = 4$), whereas individuals in the other scenarios rarely perform a second step at all (Figure 2.2). The highest dispersal distances evolve in individuals with strategy DD/DD in all parameter settings,

but with a dispersal mortality of $\mu = 0.20$ and no spatial correlation ($l = 1$) in habitat quality the results differ only marginally between the strategies. In this setting ($l = 1$; $\mu = 0.20$) the propensity to perform a second step is about 0.01 with DD/DD and less than 0.005 in the other strategies (Figure 2.2).

The highest natal dispersal propensities evolves in scenario DI/DI. Figure 2.2 shows that with a low dispersal mortality of $\mu = 0.025$ in scenario DI/DI, at least a proportion of 0.8 of all individuals emigrates from their natal patch, whereas in the scenarios DD/DI and DD/DD individuals emigrate only with a probability of about 0.4. Yet, with dispersal mortality $\mu = 0.2$, the probabilities for natal dispersal in all strategies evolve to values of about 0.2 (Figures 2.2d, i, n).

Spatial correlation in habitat quality tends to increase dispersal distance, but not the propensity for natal dispersal (as shown in Figure 2.2). The precise effect of spatial correlation in habitat quality depends on dispersal mortality and the dispersal strategy (Figures 2.2 and 2.3). With a dispersal mortality of $\mu = 0.025$ an increase of correlation length l from 1 to 4 leads to an increase in the mean number of dispersal steps. As can be expected, the relative increase is highest in DD/DD. The mean number of dispersal steps increases from 1.08 to 1.56 with strategy DI/DI (a relative increase of $inc_r = (1.56 - 1.08)/1.08 = 0.44$), from 1.28 to 2.38 ($inc_r = 0.86$) with DD/DI, and from 1.41 to 2.68 ($inc_r = 0.90$) with strategy DD/DD (Figure 2.2). In contrast, with $\mu = 0.20$, only DD/DD-individuals show a noticable increase of the mean number of steps from 1.06 to 1.32 ($inc_r = 0.25$) when we increase l from 1 to 4.

Landscape correlation also affects population dynamics: mean local population density is slightly lower and more variable with $l = 4$ than with $l = 1$. Figure 2.3 shows exemplary results of mean population density and the standard deviation of population density with $\mu = 0.10$. With $l = 4$ dispersers tend to emigrate amidst clusters of high density patches and therefore dispersal does not equilibrate population densities as efficiently as in non-correlated landscapes ($l = 1$). Also, mortality during dispersal reduces population sizes.

Figure 2.4 shows the average "demographic benefit" a successful disperser receives when arriving in a new patch (with $l \in \{1, 4\}$ and $\mu \in \{0.025, 0.20\}$). Evidently, the fitness gain is highest for migrants with the complete density-dependent strategy (DD/DD), as they move, on average, into less densely populated habitats than the ones they just left, especially after natal dispersal. Dispersers with the mixed strategy (DD/DI) benefit in about the same magnitude from natal dispersal as DD/DD-individuals, while those following DI/DI gain less. However, in all following steps individuals that do not respond to local density cannot improve their situation as much as with DD/DD. In Figure 2.4 it can also be seen that the ben-
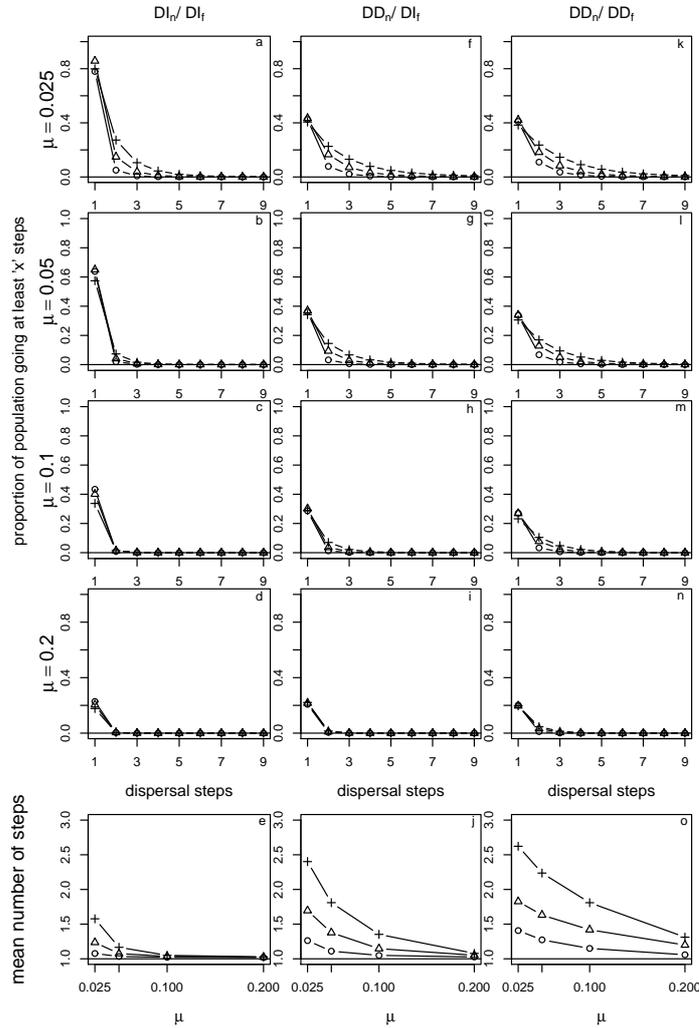
Figure 2.2: Proportion of individuals performing at least a certain number of steps and the mean number of dispersal steps of successful dispersers. Proportions of dispersers going more than 9 steps are close to zero and are not shown. Columns from left to right: strategies DI_n/DI_f, DD_n/DI_f, and DD_n/DD_f; rows from top to bottom: $\mu \in \{0.025, 0.05, 0.10, 0.20\}$, and mean number of dispersal steps for dispersing individuals. Note that for DD emigration probability is an emergent property driven by selection on threshold densities $C_{n,f}$. Symbols used: open circle: $l = 1$, open triangle: $l = 2$, cross: $l = 4$. l determines the extent of spatial correlation of reproductive conditions.

efit of the first dispersal step in simulations with $l = 1$ is higher than with $l = 4$, yet the benefits of further dispersal steps are higher with $l = 4$ than with $l = 1$.
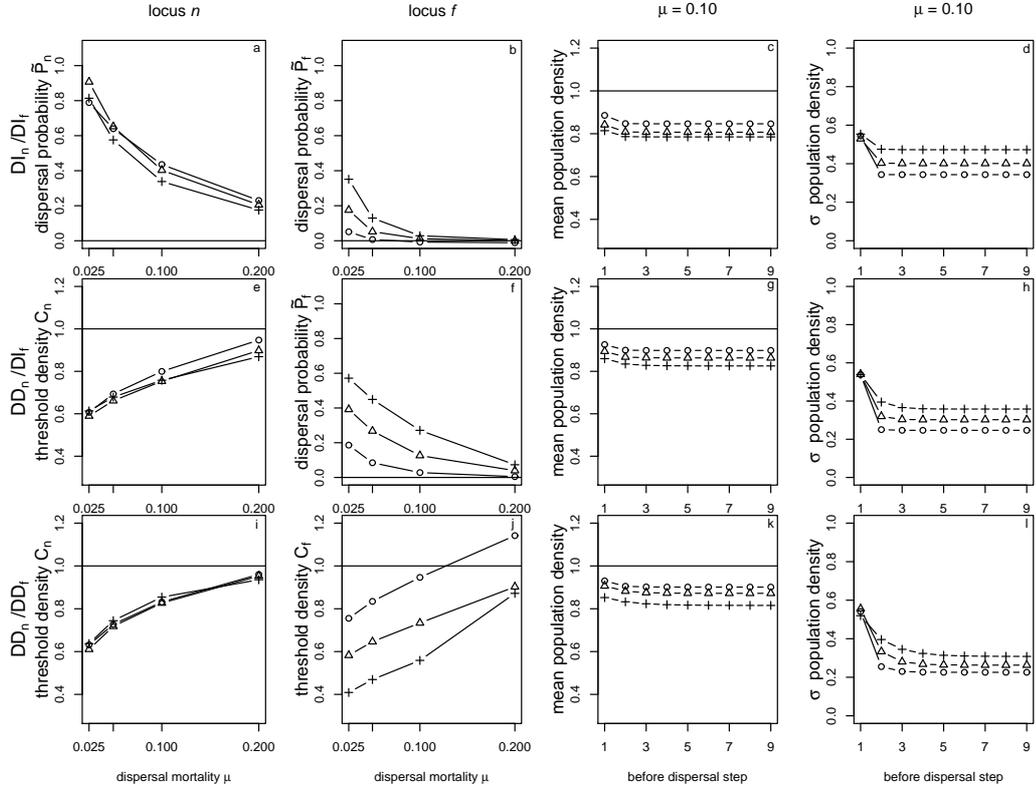
Figure 2.3: Columns from left to right: Evolved mean allele values for locus n, locus f depending on the prevailing dispersal mortality μ, mean population size, and standard deviation in population densities between patches before successive dispersal steps (the latter two columns show results from the evolved movement behaviour in simulations with $\mu = 0.10$). Locus n is associated with natal dispersal and locus f with every further dispersal move. Rows from top to bottom: strategies DI_n/DI_f, DD_n/DI_f, and DD_n/DD_f. With strategy DI_n/DI_f both loci code directly for the probability to disperse ($\tilde{P}_n = (n_1 + n_2)/2$; $\tilde{P}_f = (f_1 + f_2)/2$), whereas in strategy DD_n/DI_f the locus n describes a threshold population density $C_n = (n_1 + n_2)/2$ that has to be reached to induce possible natal dispersal (see Eqn. 2.3). In DD_n/DD_f both loci code for such a threshold density. The resulting dispersal probabilities for natal dispersal for strategies DD_n/DI_f and DD_n/DD_f can be seen in Figure 2.2. Symbols used: open circle: $l = 1$, open triangle: $l = 2$, cross: $l = 4$. l determines the extent of spatial correlation of reproductive conditions.

As mentioned before, kin-competition can be a major factor driving the evolution of dispersal traits, especially when μ is high (Hamilton and May, 1977; Rousset and Gandon, 2002; Poethke et al., 2007). For higher K, kin-competition is lower and we expect lower P_n-values to evolve. However, as K increases, so does the difference
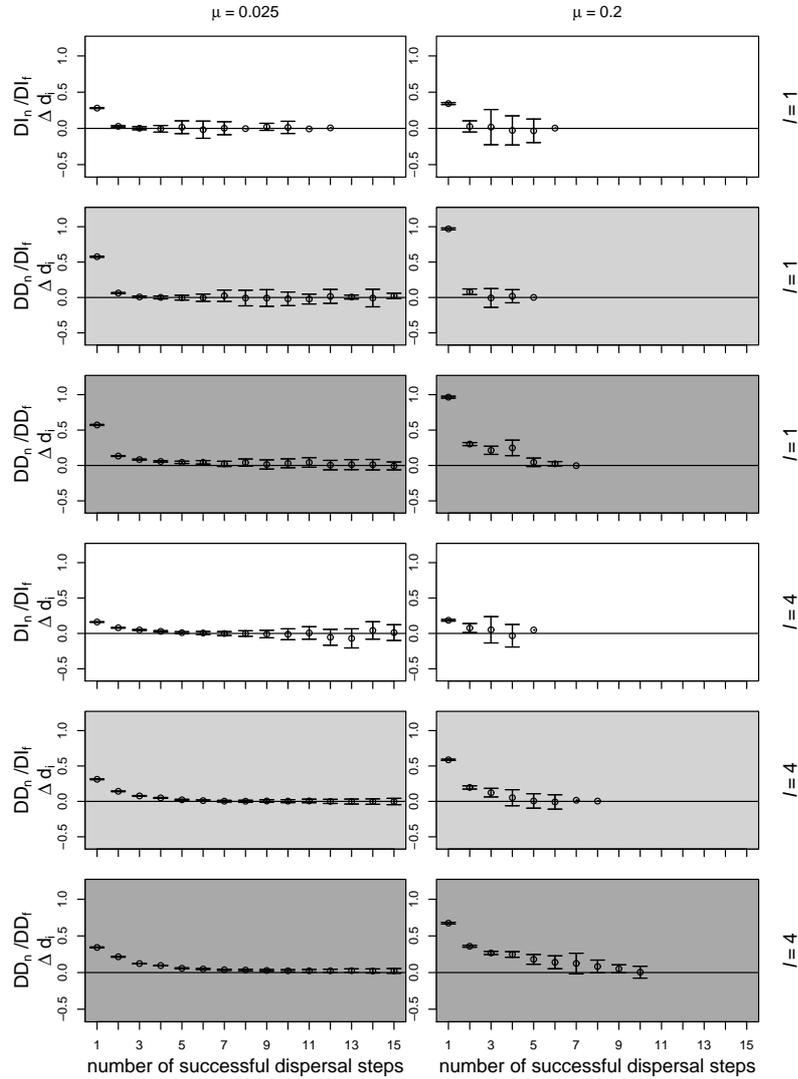
Figure 2.4: Mean stepwise difference in density between source and destination patch ($\Delta d_i = N_{i_s}/K - N_{i_d}/K$, with i_s and i_d as the indices of source and destination patches in step i) plus standard error. Points without error bars represent data from single individuals. Left column: dispersal mortality $\mu = 0.025$, right column: $\mu = 0.20$; rows 1-3: $l = 1$, rows 4-6: $l = 4$. l determines the extent of spatial correlation of reproductive conditions. A positive mean value of Δd_i indicates that migrants (on average) improved their situation by arriving in a patch with lower density than the patch they came from. Note that mean values for higher step numbers are partially based on very small sample sizes.

in total number of offspring between high and low quality patches. This might
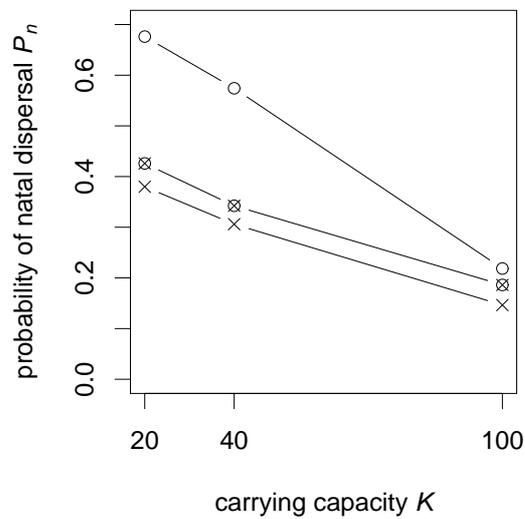
Figure 2.5: Propensity for natal dispersal (P_n), with dispersal mortality $\mu = 0.05$ and $l = 4$ (l is a parameter determining the extent of the spatial correlation of reproductive conditions). Symbols used: open circle: DI/DI; crossed circle: DD/DI; x: DD/DD.

Figure 2.6: Mean number of successful dispersal steps, with dispersal mortality $\mu = 0.05$ and $l = 4$ (l is a parameter determining the extent of the spatial correlation of reproductive conditions). Symbols used: open circle: DI/DI; crossed circle: DD/DI; x: DD/DD.
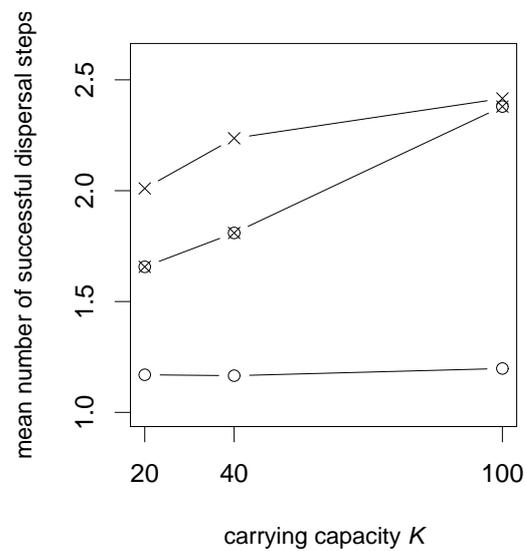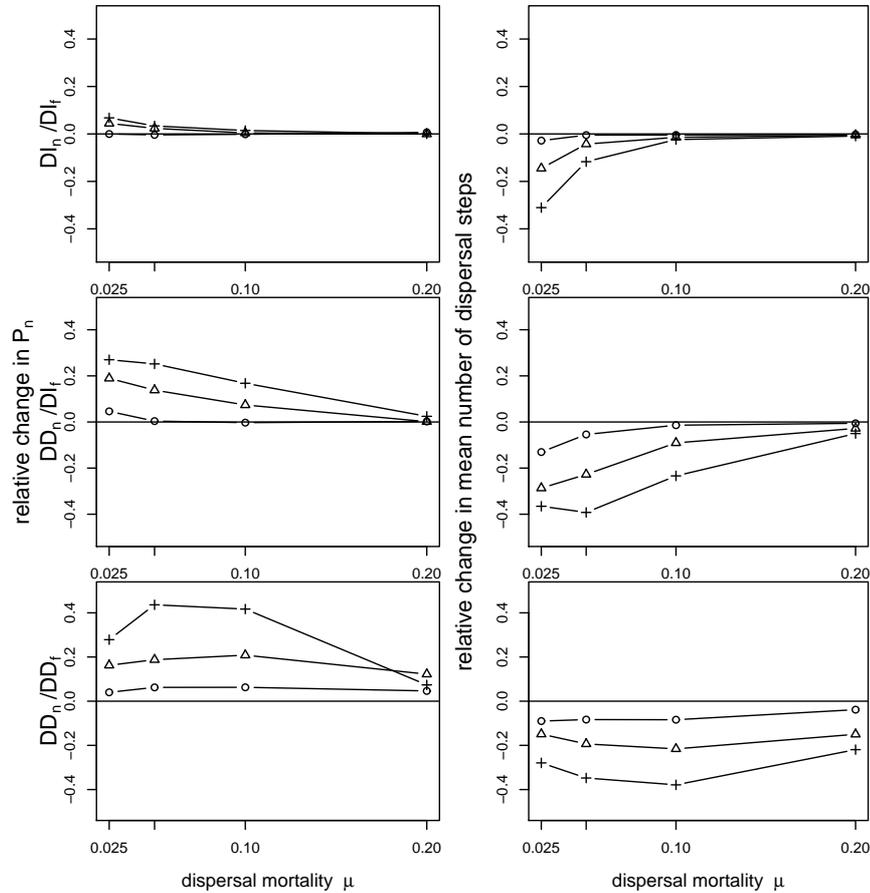
Figure 2.7: Effects of changes in movement pattern from straight to random: left
column: relative change $((x_{random} - x_{straight})/x_{straight})$ in realized propensity of natal
dispersal, P_n; right column: relative change in mean number of steps performed.
Symbols used: open circle: $l = 1$, open triangle: $l = 2$, cross: $l = 4$. l determines
the extent of spatial correlation of reproductive conditions.

lead to an increased bet-hedging incentive for dispersal and might therefore result
in an increase of P_n and/or P_f values (but see Lehmann and Balloux, 2007). We
therefore tested the influence of different carrying capacities K on the evolution
of the dispersal strategies in the different scenarios. We indeed find that with
strategy DI/DI, $\mu = 0.05$, and $l = 4$, an increase of K from 40 to 100 leads to
a reduction in the probability for natal dispersal (P_n) from 0.57 to 0.23 (relative
increase $inc_r = -0.61$), while a reduction of K to 20 leads to an increase in P_n to
0.68 ($inc_r = 0.19$). The same tendency, though less pronounced, exists also in the
density-dependent and mixed strategy (see Figure 2.5). This effect can explain

why Rousset and Gandon (2002) find even higher dispersal probabilities than we as they fixed K to a value of $K = 10$. The results in Figure 2.2 show that our results of strategy DI/DI are consistent with the results of Rousset and Gandon (2002, their Figure 2, row c).

In all results described so far we assumed that a disperser sticks to a straight movement path. To investigate how this assumption about the movement behaviour of dispersing animals affects our results we also implemented a movement rule where individuals chose a direction randomly in each dispersal step. Compared to the results with the straight movement path, with the random movement rule natal dispersal (P_n) increases, but dispersers perform fewer steps (P_f decreases) in nearly all scenarios and parameter combinations (Figure 2.7). The strength of this effect dependend on the dispersal strategy, dispersal mortality, and spatial correlation in habitat quality.

Reducing the efficiency of moving away from the natal habitat by applying the random movement rule most likely affects the degree of relatedness within the patches. We therefore recorded G_{ST}-values as a measure of relatedness and find that about the same degree of relatedness prevails under both movement rules, as individuals adapt their dispersal strategy according to kin-selection theory (Taylor, 1988). To confirm that indeed kin-competition is the major driver of the evolution of natal dispersal, we tested the effect of the increase in P_n and the decrease in P_f on the degree of relatedness. We ran additional simulations with $l = 4$ and $\mu = 0.05$, employing the random movement rule, but giving all individuals the corresponding (now fixed) allelic values that evolved under the straight movement rule. This did not affect the degree of relatedness in DI/DI where the levels of P_n were about the same under both movement rules, but in the other scenarios the G_{ST}-values doubled from 0.06 to 0.12 in DD/DI, and increased even more from 0.06 to 0.15 in DD/DD.

2.4   Discussion

Our results clearly demonstrate that once a dispersing individual has successfully reached a patch of suitable habitat the propensity to perform additional steps after natal dispersal (P_f) declines rapidly with increasing dispersal costs. Already with costs of $\mu = 0.20$ the maximum value of P_f reaches almost zero when individuals cannot assess local population density, and falls below 0.06 with completely density-dependent dispersal, even though P_n is still about 0.20. As the costs for any dispersal step remain the same in our simulations, this decline in dispersal probability must be attributed to a declining benefit of dispersal as the number of

steps increases. This decline in benefit has to do with two factors: the avoidance of kin-competition and the immigration into patches with a lower population density.

A prominent benefit of dispersal is the avoidance of kin-competition (Hamilton and May, 1977; Rousset and Gandon, 2002; Poethke et al., 2007), i.e. the "intention" to dilute kin across the landscape to avoid direct competition among them. To a great degree this is already achieved with the first dispersal step, because siblings are spread over eight neighboring patches. Yet, also further dispersal steps play a role. From Figure 2.7 it becomes clear, that the reduction of the mean number of dispersal steps induced by the change to random movement is compensated for (to a large extent) by an increase in the propensity for natal dispersal, thus maintaining the same level of relatedness (G_{ST}-value) within the patches. Therefore both factors, the propensity for natal dispersal, as well as the number of steps have an influence on the reduction of kin-structure. Yet, the change in movement mode from straight to random takes effect only from the second step on and has two consequences: first, it entails the small possibility to disperse back into the natal patch, and second, it makes escaping from similar habitat conditions harder and therefore reduces the average gain from moving into a less densely populated patch per dispersal. Therefore, the evolution of the second locus (f) – responsible for continuing dispersal – is influenced more strongly by demographic benefits, rather than by the small additional gains in inclusive fitness by further reducing kin-competition.

In other words, the relevance of kin-competition as a factor driving dispersal quickly fades away with dispersal distance (Rousset and Gandon, 2002). The intensity of kin-competition strongly depends on the carrying capacity of patches (Hamilton and May, 1977; Taylor, 1988; Poethke et al., 2007). Consequently, we find higher propensities for natal dispersal for lower carrying capacities (K) (Rousset and Gandon, 2002). In contrast to P_n, P_f, responsible for the mean number of steps performed by dispersers, increases with increasing K in DD/DI and DD/DD, yet not in DI/DI (see Figures 2.5 and 2.6). This, together with the fact, that with $l > 1$ variance in population densities between patches increases with K, shows that for phenotypes able to react to population density, demographic factors are more important for the evolution of perseverance (locus f) than the reduction of kin-competition.

The second important benefit of dispersal, moving from high to low density populations is highlighted by the observable differences between dispersal strategies (Figures 2.2 and 2.3). Individuals constantly monitoring population-density perform more dispersal steps than those with the mixed strategy or the completely density-independent strategy (Figure 2.2). This is simply because individuals with density-dependent dispersal are far more efficient in moving out of regions with

high population density (comp. Figure 2.4). This also means, that the strategies differ in the effectiveness of equalizing demographic differences between patches as can be seen in Figure 2.3. However, the degree to which demographic variance between patches is equilibrated depends not only on the dispersal strategy itself, but also on the spatial correlation of habitat quality. In a correlated environment dispersers often emigrate amidst clusters of densely populated patches and consequently immigrate more often into patches which also have a high density. Thus, dispersal in a clustered environment does not equilibrate population densities as effectively as in a uncorrelated world, even though the mean number of dispersal steps is higher in correlated worlds. This becomes also visible when comparing the mean number of steps a disperser performs, especially when spatial correlation in reproductive conditions is high. With $l = 4$, the average number of dispersal steps needed to leave the 4 by 4 square is 2.06. We find that only individuals in scenario DD/DI and DD/DD perform more than 2.06 steps, and so will – on average – be able to leave a high density square.

Another factor influencing the evolution of dispersal is inbreeding depression (Bengtsson, 1978; Wiener and Feldman, 1993). However, as inbreeding depression would affect dispersal in the same way as kin-competition and has not much additional influence when occurring in combination with it (Perrin and Goudet, 2001), we did not include it into our model.

In our simulations, the straight movement rule is more efficient for avoiding kin-competition and escaping unfavourable conditions than the random movement rule. However, note that this is only so because in our model dispersers have no need to search for new habitat because they will automatically reach the next patch, or die during transition. In more natural landscape-configurations it can depend on the movement pattern for a disperser to reach a habitat patch, thus a more random movement behaviour can be advantageous (Hein et al., 2004).

We conclude that for the evolution of "uninformed" dispersal strategies kin-competition is the dominant factor promoting dispersal, especially if dispersal costs become high ($\mu > 0.025$) and populations are small (Rousset and Gandon, 2002; Poethke et al., 2007). However, a single dispersal step is sufficient to substantially reduce competition among kin and further dispersal is not selected for as soon as dispersal cost reaches even a modest level. The demographic benefit of dispersal – arriving in a patch with lower density – is accomplished best by at least partially informed strategies. These potential benefits are much more likely to promote the evolution of multiple dispersal steps, especially, if habitat quality shows spatial correlation. Surprisingly, a comparable number of dispersal steps as in DD/DD evolves also in the mixed strategy where only natal dispersal is density-dependent (Figure 2.2). However, in a correlated environment the fact that a disperser finds

itself in a high-density patch at birth conveys the information that neighbouring patches probably have a high population density too. It thus, on average, pays to disperse at least one more time (Figure 2.4). For the completely uninformed strategy an emigrant will – on average – improve its demographic situation in the first dispersal step too, simply because more emigrants originate from high- than from low-density populations. However, this cannot be predicted for any further dispersal steps and consequently, multiple dispersal does hardly evolve under this strategy. Instead, compared to the other strategies the probability of natal dispersal evolves to higher levels, at least as long as dispersal mortality remains rather low ($\mu < 0.20$). This result is another indication of the rather complex feedback effects involved in the evolution of dispersal strategies (Poethke et al., 2003): when idividuals only disperse over short distance kin-structure is more likely to be maintained than with long-distance dispersal and consequently, higher levels of natal dispersal are selected for.

In summary, we predict that dispersal strategies with multiple dispersal steps evolve most likely in species able to assess the quality of at least their natal habitat. In uninformed species multiple dispersal steps should evolve only if dispersal costs are very low. However, as it often requires time to collect information about habitat quality we expect that secondary dispersal is more likely in long-lived species like mamals or birds.

Chapter 3
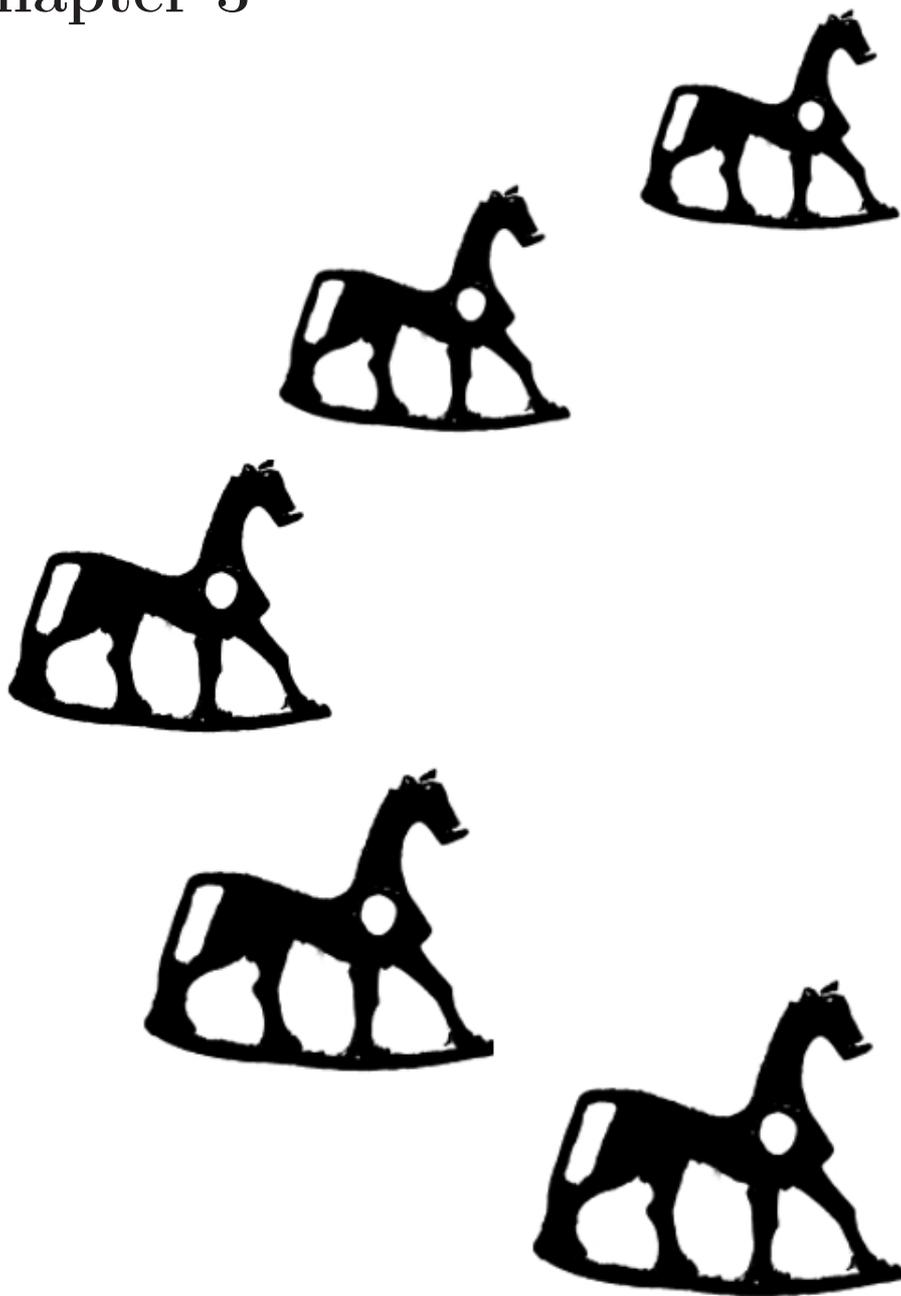
Evolution of sex-biased dispersal: the role of sex-specific dispersal costs, demographic stochasticity, and inbreeding[1]

ANDREAS GROS, THOMAS HOVESTADT & HANS JOACHIM POETHKE

3.1   Introduction

Dispersal is one of the key processes allowing for the survival of species in fragmented landscapes (Clobert et al., 2001). In the light of the dramatic and rapid changes in our landscapes and of ongoing climatic changes it is thus essential to anticipate how the dispersal abilities and propensities of species evolve in the future. This will require a proper understanding of the mechanisms driving the evolution of dispersal strategies.

At the same time, dispersal "decisions" can have far reaching consequences for the fitness of individuals: from founding of new populations to utter failure every outcome of such a decision may occur (Clobert et al., 2001). Considering the vast potential benefits as well as the substantial risks associated with dispersal it is highly plausible that dispersal decisions are context-dependent, i.e. that the decision to disperse is not taken at random but depends on actual environmental conditions, the developmental stage of an individual, and physical condition (Ims and Hjermann, 2001; Bowler and Benton, 2005; Matthysen, 2005; Hovestadt and Nieminen, in press). Investigating context-dependent dispersal strategies has thus attracted the interest of both, field biologists and theoretical ecologists.

One obvious kind of context-dependent dispersal, which has gained special interest, is sex-biased dispersal where the propensity to disperse depends on the gender of individuals. Dispersal biased towards males as well as females has both been reported (Clarke et al., 1997; Prugnolle and de Meeus, 2002; Lawson Handley and

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[1]Gros, A., Hovestadt, T. & Poethke, H. J., Manuscript submitted for publication to Ecological Modelling

Perrin, 2007), but it is not fully understood what factors are responsible for the evolution of sex-biased dispersal as such and especially what determines which of the two sexes is more dispersive (Lawson Handley and Perrin, 2007). Yet, two candidate factors favoring gender-biased dispersal have clearly been identified. The first is inbreeding avoidance: its negative consequences can readily be avoided if only one gender disperses because this prevents mating between relatives (Motro, 1991a, 1994; Gandon, 1999; Perrin and Mazalov, 1999, 2000). The second is an asymmetry in the intensity in local competition about reproductive ressources (Perrin and Mazalov, 2000; Wild and Taylor, 2004) where the gender subject to higher competition is dispersing at a higher rate. There is a third and obvious mechanism that should favor the evolution of sex-specific dispersal and that is the presence of an asymmetry in the costs associated with dispersal between the two sexes. This has already, rather parenthetically, been noted by Taylor (1988, p. 368), but he did not explore the topic in any quantitative way. Asymmetry in dispersal costs has also been accounted for in the models developed by Leturque and Rousset (2003) and Wild and Taylor (2004). Both models, however, focus on the effect of such an asymmetry on the simultaneous evolution of sex-biased dispersal and offspring sex-ratio, and provide only qualitative statements about the correlation between sex-specific dispersal costs and the bias in dispersal. In addition, Leturque and Rousset (2003) analyzed a system with habitats that differ in female fecundity, which makes it difficult to isolate the effect of cost asymmetries on model predictions. Furthermore, the analytical models of Taylor (1988), Leturque and Rousset (2003), and Wild and Taylor (2004) ignore the effects of demographic stochasticity, which is known to influence the evolution of dispersal strategies (Ronce, 2007). Finally, none of these models investigates the joined influence of inbreeding and cost-asymmetries.

To address these questions we have expanded a model of Gandon (1999) who has presented an especially thorough and broad approach to the subject. In his model he accounts for the effects of dispersal costs (but not sex-specific dispersal costs), inbreeding depression and kin-competition, but also of the ploidy-level, control over dispersal decisions (mother or offspring) and population size. Yet, whatever the model configuration, he showed that a certain level of inbreeding depression is necessary to generate sex-biased dispersal. In this paper we will introduce a simple expansion of the analytical model of Gandon (1999) to quantify how slight differences in the costs of dispersal between the two sexes contribute to the evolution of sex-biased dispersal. We will further use an individual-based simulation model (IBM) to quantitatively evaluate the validity of predictions derived from the analytical model under the more realistic condition of finite population size and demographic variability. Finally, we will exemplarily investigate how the joined effect of inbreeding depression and cost asymmetry would affect the evolution of

sex-biased dispersal.

3.2   The model

We analyze the evolution of dispersal propensity in a meta-population of an annual, sexually reproducing species with discrete generations. Each habitat patch (i) supports a local population with carrying capacity (K). In all our model variants dispersal is under offspring control. Hence, after hatching, an offspring "decides" whether to disperse or not. Dispersal is sex-specific and is controlled by the dispersers' genotype (one autosomal gene expressed only in males and another – independent one – expressed only in females). In nature dispersal usually incurs costs, such as investment in dispersal mechanism (e.g. flight muscles, longer wings), or an increased probability to die during dispersal. Like Gandon (1999) we subsume all these costs under dispersal mortality (c). Dispersal is at random with respect to which habitat patch is reached (global dispersal). After dispersal, mating and reproduction takes place whereupon the life cycle starts again. In compliance with the model of Gandon (1999), we assume monogamy, i.e. males and females first form N breeding pairs. Thus, $K/2$ is the maximum number of breeding pairs in a patch. After pair formation pairs compete for breeding territories. Successful pairs, i.e. those acquiring a territory, get an equal number of offspring (λ). Generations do not overlap. The role of the two sexes is thus completely symmetric. This is important because different intensities of competition for the two sexes may be a prominent factor promoting the evolution of sex-biased dispersal (Perrin and Mazalov, 2000, Gros et al., subm.).

Gandon (1999) bases his model on the kin-selection model of Taylor (1988) which – without inbreeding depression – makes it possible to calculate the evolutionary stable dispersal probability d^* that optimizes inclusive fitness, given certain dispersal costs (c) and a coefficient of relatedness (R):

$$d^* = \begin{cases} \frac{R-c}{R-c^2} & \text{if} \quad R > c \\ 0 & \text{if} \quad R \leq c \end{cases} \tag{3.1}$$

In the absence of inbreeding depression, this model always predicts symmetric dispersal Gandon (1999). We expand this model by introducing sex-specific costs of dispersal for females (c_f) and males (c_m) into the calculation of the coefficient of relatedness (R) and the calculation of the proportion of surviving dispersers. In this case, the modified (omitting inbreeding depression) model predicts different dispersal probabilities for the two sexes:

$$d_f^* = \begin{cases} \frac{R-c_f}{R-c_f^2} & \text{if} \quad R > c_f \\ 0 & \text{if} \quad R \leq c_f \end{cases} \qquad (3.2)$$

and to:

$$d_m^* = \begin{cases} \frac{R-c_m}{R-c_m^2} & \text{if} \quad R > c_m \\ 0 & \text{if} \quad R \leq c_m \end{cases} \qquad (3.3)$$

In the Appendix we present a more detailed derivation of these equations.

Relatedness (R) is – with offspring control of dispersal (comp. *Ro* in Gandon, 1999) – calculated as follows:

$$R \;=\; \frac{1}{2N - k_1 - (N-1)/2(2k_1 + k_2)^2} \qquad (3.4)$$

with

$$k_1 \;=\; \frac{(1-d_m)(1-d_f)}{(1-c_m d_m)(1-c_f d_f)}$$

$$k_2 \;=\; \frac{(1-d_m)(1-c_f)d_f + (1-d_f)(1-c_m)d_m}{(1-c_m d_m)(1-c_f d_f)}$$

As R recursively depends on dispersal rates, it is not possible to solve equations 3.2 and 3.3 analytically. We thus found numerical solutions for the evolutionary stable dispersal strategies using Mathematica 4.0 (Wolfram Research, Inc., 1999) by letting the system of R, d_f and d_m iterate until equilibrium.

The numerical model readily allows analyzing the factors influencing the system's behavior. Thus, the effect of the relative differences in dispersal costs $\Delta_c = (c_f - c_m)/((c_f + c_m)/2)$ and a given population size ($K = 2N$) on the evolutionary stable dispersal strategies (d_f^*, d_m^*) can be calculated directly. We exemplarily use all combinations of three values for Δ_c: $\Delta_c \in \{0.02, 0.05, 0.10\}$ and three values for population size K: ($K \in \{20, 40, 100\}$) to demonstrate the effect of K, $\bar{c} = (c_f + c_m)/2$, and Δ_c on predicted dispersal probabilities and the magnitude of sexual bias in dispersal. Without loss of generality, we always assume that dispersal is less costly for males than females. In the opposite case results would be mirror images of the ones presented here.

Monogamy makes the roles of the two sexes absolutely symmetric. Thus, as stated already by Gandon (1999) without inbreeding depression no differences in the dispersal propensity of the sexes are predicted as long as the costs of dispersal are identical for the two sexes. However, the numerical results clearly show that already with small cost differences dispersal may become strongly biased towards the sex with lower costs (Figure 3.1). The dotted lines in Figure 3.1 comply with the results of Gandon (1999) and show the symmetric ESS predicted in case of no difference in dispersal mortality ($\Delta_c = 0$). With increasing costs the bias becomes stronger and reaches a maximum exactly at the moment where the predicted dispersal probability first reaches zero for the less dispersive sex (females), i.e. where $R = c_f$. Evidently, the predicted difference in dispersal probability increases as the difference in dispersal costs (Δ_c) increases.

At a given mean cost of dispersal and a fixed level of cost-asymmetry, the sex-bias in dispersal becomes more pronounced with increasing population size (this can be deduced from the left-wards shift of the "glitch" in male and female dispersal probability as patch capacity becomes larger in Figure 3.1). This can readily be explained by the declining importance of kin-competition – a factor favoring symmetric dispersal – as population size increases (Perrin and Mazalov, 2000).

3.3   Individual-based simulations

The numerical model ignores the potential influence of demographic stochasticity which can have a strong effect on the evolution of dispersal probabilities, especially if population size is small and growth rates are low (Parvinen et al., 2003). We thus compare the numerical results (as shown in Figure 3.1) to results of simulation experiments generated with an individual-based simulation model (IBM). We use a modified version of the individual-based metapopulation model for the evolution of dispersal propensity of an annual, diploid, and sexually reproducing species with non-overlapping generations more thoroughly described in Poethke and Hovestadt (2002). Simulation experiments are initialized by placing K individuals in each patch. Note that we do not need to explicitly introduce kin-competition into our simulations as it emerges by default in any individual-based simulation (Poethke et al., 2007). As demographic effects and the role of kin-competition become less prominent with increasing population size (N), we use different carrying capacities to investigate the effects of demographic stochasticity on the evolutionary outcome. To keep the number of individuals in the whole metapopulation comparable (approximately 25000 individuals) we modified the number of local populations accordingly. Thus, the meta-population consists of 16x16, 26x26 and 36x36

habitat patches with a local carrying capacity (K) of 100, 40 and 20, respectively.

As Gandon (1999) we assume that males and females are monogamous and form pairs. Each pair that successfully acquired a breeding territory gets (λ) offspring with sex allocated randomly.

Each individual is characterized by four alleles (m_1, m_2, f_1, f_2) at two diploid loci (m, f), inherited from its parents. The first of these loci (m) determines a male's propensity for dispersal (d_m), the second (f) determines d_f in females. The alleles of these loci can take continuous values between 0 and 1. When inheriting a parent's genes, each allele transferred to the offspring mutates with probability 0.002: affected alleles are altered by adding a random value drawn from a uniform distribution within the interval [-0.02, 0.02]. To check for the influence of the initial conditions on our results we choose a broad range of initial values for m_i and f_i. Individuals are initialized as homozygote at both loci with $m_i = 0.20 - f_i$ and f_i randomly chosen from (0.00, 0.02, 0.04, 0.06 ... 0.20).

We run 50 simulation experiments for each combination of the 11 start values for f_i, m_i (as described above), the three values of K: $K \in \{20, 40, 100\}$, two values of $\overline{c}$: $\overline{c} \in \{0.05, 0.4\}$, and three values of relative differences in dispersal costs ($\Delta_c \in \{0.02, 0.05, 0.1\}$). We thus run a total of 50 x 11 x 3 x 2 x 3 = 9.900 simulations. The number of offspring was fixed to $\lambda = 10$ (but see discussion) in all simulation runs. To allow the populations to reach evolutionary equilibrium, we let simulations run for 50.000 generations. However, preliminary runs showed that equilibrium was usually reached much faster. We record the resulting values for the loci, as well as all other measures mentioned below in the gamete phase in the last generation.

Without inbreeding depression, simulation runs always converge to (approximately) the same final trait distribution independent of the values used for initializing d_m and d_f (Figure 3.1). It is always the sex with lower costs of dispersal (males) which evolves higher dispersal probability even if simulations were initialized with female biased dispersal. The results of the simulation runs fundamentally agree with the predictions derived from the numerical model. Most importantly, also in the simulations asymmetric dispersal probabilities evolve already with very slight differences in dispersal costs. Even for a relative difference in dispersal cost of $\Delta_c = 0.02$ the sex with less costs clearly dominates in dispersal and for $\Delta_c \geq 0.05$, sufficiently high mean dispersal cost ($\overline{c} \geq 0.4$) may result in an nearly complete bias with only one dispersing gender. In this respect our findings (which also emerge in the numerical model) differ from Gandon's who found that an increase in the mean cost of dispersal reduces the magnitude of the sexual bias in dispersal in the case of inbreeding depression. However, the magnitude of sex-bias consistently remains

below that predicted by the numerical model especially when the predicted mean
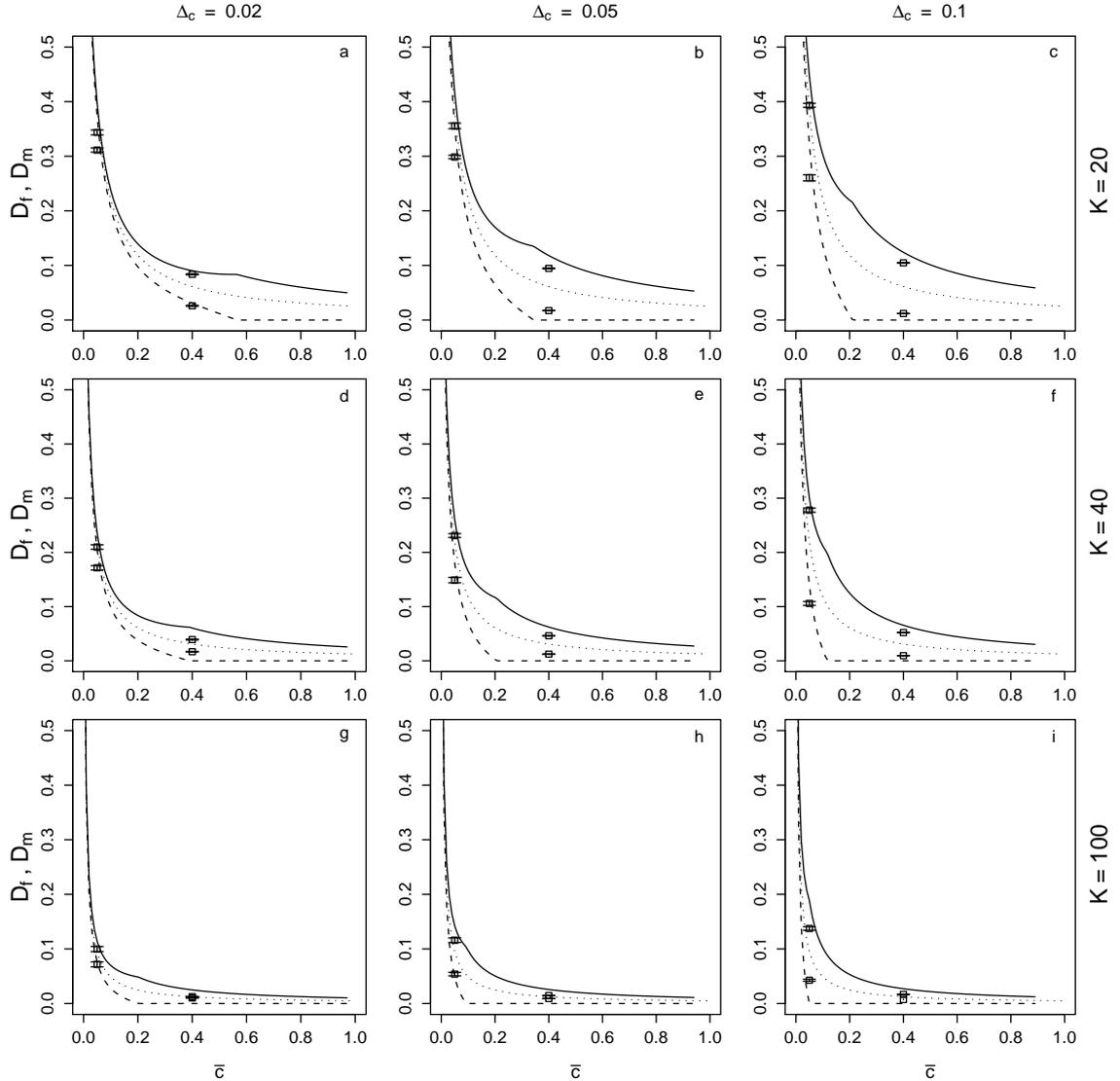dispersal probability becomes small, e.g. for $K = 100$ (Figure 3.1).

Figure 3.1: Evolutionarily stable emigration probabilities (d_f, d_m) as a function of
mean dispersal costs for different values of patch capacity ($K \in \{20, 40, 100\}$) and
for different relative differences in dispersal cost ($\Delta_c \in \{0.02, 0.05, 0.10\}$). Lines give
predictions based on numerical results, points with error bars give those emerging in
individual-based simulations. Continuous lines: female dispersal; dashed lines: male
dispersal; dotted lines: result of the numerical solution for $\Delta_c = 0$, i.e. equal costs
of dispersal for both sexes. The noticeable glitches in the curves for male dispersal
result from the bounding of female dispersal to zero (eq. 3.2)

For the case that inbreeding depression exists, Gandon (1999) already predicts completely biased dispersal (under the assumption that demographic stochasticity can be neglected). However, he predicts that there are always two evolutionary stable equilibria. Which of the two sexes will become the dispersive one should thus depend on the initial conditions, only. To investigate how the emergence of this bi-stability is affected by the presence of a cost-asymmetry we performed simulations with different combinations of initial male (d_m) and female (d_f) dispersal probabilities spanning the whole surface of the possible parameter space. The resulting evolutionary trajectories (over 1000 generations) in the d_f-d_m-space were averaged over ten replicate simulations with identical initial values for d_f and d_m. Inbreeding depression is implemented in the same way as in Gandon (1999): whenever a female and a male, which both did not disperse, form a pair, the pair's chance to gain a territory is reduced by the factor $\delta \in [0.0, 1.0]$. As the calculations of complete evolutionary vector fields is extremely time-consuming; we could do this for a number of selected cases only. We thus focus on scenarios covering a range of values of inbreeding depression ($\delta = 0, 0.4, 0.6$) for given values of habitat capacity $K = 20$, dispersal cost $\overline{c} = 0.4$, and cost asymmetry $\Delta_c = 0.1$ (comp. Fig. 3.2).
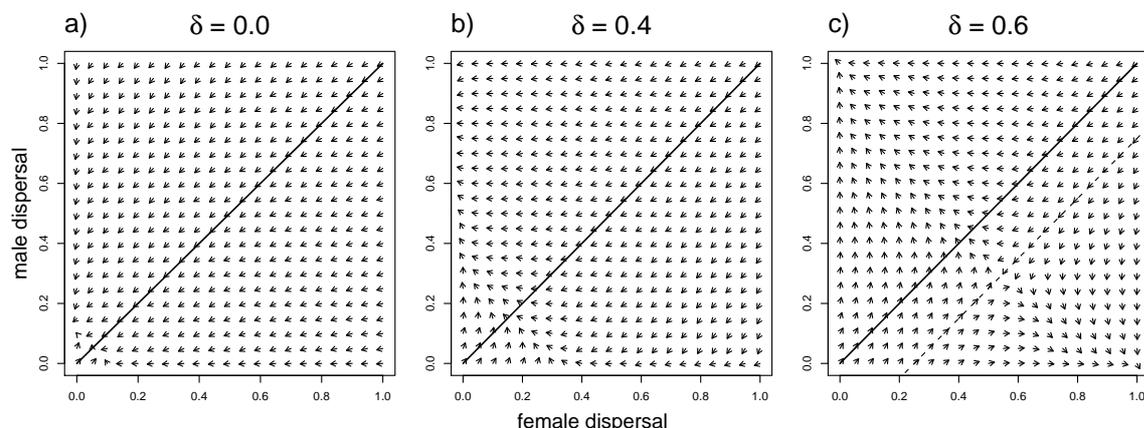

Figure 3.2: Vectorfields for different values of inbreeding depression: $\delta = 0.0$ (a), $\delta = 0.4$ (b), $\delta = 0.6$; the panels show the resulting evolutionary trajectories over 1000 generations (averaged over ten replicate simulations) in the d_f-d_m-space. Parameters used: $K = 20$, $\overline{c} = 0.4$, and $\Delta_c = 0.1$.

As long as inbreeding is less costly than dispersal, the system always settles into a state with dispersal biased in favor of males (Fig. 3.2a and b). Thus, in contradiction to the results of Gandon (1999), bi-stability vanishes completely as soon as $\delta \leq \overline{c}$. This holds already for rather small cost asymmetries (Δ_c). In accordance with Gandon (1999) we find completely biased dispersal (e.g. one sex disperses

with a probability of one) when inbreeding is more costly than dispersal ($\delta > \overline{c}$) (Fig. 3.2c). However, the range of attraction for the two equilibria is clearly affected by the cost asymmetry. The ridge separating the two fields of attraction (dotted line in Fig. 3.2c) is shifted in favor of the sex with less dispersal cost.

3.4   Discussion

Both, our numerical model and the individual-based simulations prove that differences in the cost of dispersal can lead to sex-biased dispersal. Other than with the magnitude of inbreeding depression there are no lower boundaries to the effect of cost asymmetries: even small differences are sufficient to induce sex-biased dispersal as long as the costs of dispersal do not become very small for both sexes. In contrast to Taylor (1988), Leturque and Rousset (2004), and Wild and Taylor (2004) we quantify that effect.

The results of the individual-based simulations agree well with the predictions from the numerical model as long as predicted dispersal probabilities (for both sexes) are considerably different from zero. Nonetheless, the evolved sex-bias consistently remained below the level predicted by the numerical model. This deviation should be the consequence of demographic stochasticity and of the substantial kin-structure emerging under situations, which select for low emigration rates, e.g. high costs and large carrying capacities (K) in our simulations. In the numerical model the number of offspring is considered to be high enough so that the effects of demographic stochasticity can be ignored completely. Individual-based simulation experiments, on the other hand, take demographic fluctuations into account: population sizes may fall below K, and population densities as well as sex-ratios will be variable across patches. The deviation of simulation results from those predicted by the numerical model is thus the consequence of demographic stochasticity and of the substantial kin-structure emerging under conditions, which select for low emigration rates, e.g. high costs and large carrying capacities.

In these circumstances, avoidance of the risks of demographic stochasticity by bet-hedging (Lehmann and Balloux, 2007) becomes a selective force favoring dispersal in both sexes. Additionally, with declining patch capacity, increasing variability in population size, or reduced dispersal, relatedness within patches increases, which will in turn enforce selection for dispersal in both sexes (Gandon, 1999; Rousset and Ronce, 2004). Consequently, in cases, where the numerical results predict females to be completely philopatric, we still get some female dispersal in the simulations of finite metapopulations (in agreement with Rousset and Ronce, 2004). As the inclusive fitness balance of costs and benefits (comp. Equation 3.6 in the Appendix)

also holds for the simulations, the amount of dispersal that females contribute to mean dispersal lessens selection on male dispersal and the sex-bias in dispersal is reduced. To check whether demographic stochasticity indeed contributes to selection for female dispersal, we ran additional individual-based simulations with lower λ (increased stochasticity) and higher λ (reduced stochasticity). If we set offspring number to a small value, i.e. $\lambda = 4$, the deviation from the predicted sex-bias became more pronounced and female dispersal became higher than with $\lambda = 10$ in the standard simulations. In reversal, the match between predicted sex-bias and that emerging in the simulations became closer if we raised offspring number to $\lambda = 16$.

Concerning inbreeding, Gandon (1999) showed that the evolving sex-bias will only depend on starting conditions as inbreeding avoidance itself does not define which sex should be more dispersive. However, in our simulations we could show that already a small bias in dispersal cost would favor dispersal of the sex with less costly dispersal, even in the presence of inbreeding depression. Only when the effect of inbreeding depression becomes larger than the mean costs of dispersal, initial conditions determine the evolutionary trajectory; however, the "zone of attraction" becomes larger for the sex with lower costs of dispersal. Obviously, the magnitude of sex-bias in dispersal also becomes more pronounced if inbreeding depression and cost asymmetries interact.

Direct evidence for gender-specific dispersal costs is rarely found in the literature. Ralls et al. (1980) and Holekamp (1984) report differential costs of dispersal in sperm whales respectively in ground squirrels. Also for species with non-overlapping generations, like insects, there are (to our knowledge) only few published results supporting an asymmetry in dispersal costs (Petit et al., 2001; Matter, 2006; Rabasa et al., 2007). However, we assume that the lack of corresponding evidence is more due to the fact that it has rarely been looked for in empirical research. At least there are numerous arguments suggesting that sex-biased differences in dispersal ability or costs may be common. For example, body size is very likely to affect dispersal abilities - and many species show substantial differences in body size between the sexes. Differences between genders in dispersal mortality may also arise because, at least in many insect species, females allocate resources into body mass and energy reserves for higher offspring production (del Castillo and Nunez-Farfan, 2002), and there are often trait-offs between dispersal capacity and fertility in female insects (Marden, 2000) or in some bird species (Kullberg et al., 2002). Consequently, dispersing females are often less fertile than philopatric individuals, and as dispersing females have to invest in both fecundity and dispersal ability they may pay higher costs for dispersal than males. There are also studies demonstrating higher mobility for males rather than for females,

e.g. in the Blue-Winged Grasshopper *Oedipoda caerulescens* (Maes et al., 2006). Sexual selection for agility or strength, e.g. for resource or mate defense, could also reduce mortality during dispersal.

However, it may always remain difficult to distinguish between cause and effect in cases where a sexual bias in dispersal is observed: has one sex become more dispersive because it has been more successful in doing so, or has the more dispersive sex evolved a better ability to disperse after sex-biased dispersal emerged? Presumably, it is not even reasonable to try answering this question. Instead, in an evolutionary feedback, differences in dispersal ability and sex-bias are likely to jointly increase and to stabilize an evolutionary course which was originally catalyzed by another mechanism, e.g. inbreeding depression.

3.5 Appendix

Derivation of optimal dispersal probability for the numerical simulations

Gandon (1999) bases his model on the kin-selection model of Taylor (1988) which gives a condition for evolutionary stability for an unbiased dispersal strategy:

$$c = Rk, \tag{3.5}$$

with c, the costs of dispersal, i.e. the probability to die during dispersal ($c \in [0; 1]$), R, the degree of relatedness in a population, and k, the probability to be a philopatric individual. This can be translated into a dispersal strategy by replacing k with $(1 - d)/(1 - cd)$:

$$c = R\frac{1 - d}{1 - cd}, \tag{3.6}$$

with d as dispersal probability. Equation 3.6 was also derived by Taylor (1988) and Gandon (1999). The left-hand side of Equation 3.6 represents the costs of dispersal and the right-hand side describes the gain in inclusive fitness due to dispersal. By taking the risk of dying during dispersal (c), a disperser reduces competition with $(1 - d)(1 - cd)$ philopatric individuals in its home patch which are on average related to the disperser to a degree of R. In equilibrium, dispersal is tuned so that the costs of dispersal are balancing the benefits in inclusive fitness (see below).

$(1 - d)$ is the proportion of philopatric individuals and $(1 - cd) = 1 - d + (1 - c)d$ describes the net flow of individuals in the patches and denotes the proportion of

the individuals alive after the dispersal phase. From this we get:

$$d = \frac{R - c}{R - c^2}. \tag{3.7}$$

However, with sex-specific costs of dispersal, the coefficient of relatedness R has to include these sex-specific costs as itself depends on dispersal rates:

$$R = \frac{1}{2N - k_1 - (N-1)/2(2k_1 + k_2)^2} \tag{3.8}$$

with

$$k_1 = \frac{(1 - d_m)(1 - d_f)}{(1 - c_m d_m)(1 - c_f d_f)}$$

$$k_2 = \frac{(1 - d_m)(1 - c_f)d_f + (1 - d_f)(1 - c_m)d_m}{(1 - c_m d_m)(1 - c_f d_f)}$$

Following the approach of marginal gains in fitness (MGF) an expression for the ESS dispersal strategy for the sex-specific dispersal propensities (d_m for males and d_f for females) can be obtained directly (comp. Gandon, 1999). In the following we derive an expression for the ESS dispersal propensity ($d_{m,f}^*$) under given (sex-specific) costs of dispersal (c_m for males and c_f for females).

Omitting the inbreeding depression prevailing in Gandon's model and considering only diploid individuals, the MGF of dispersal (G_d) and philopatry (G_p) yield for males (Gandon, 1999):

$$G_p = P_p(1 - kR), \tag{3.9}$$
$$G_d = P_d(1 - c_m), \tag{3.10}$$

with R as relatedness under offspring control of dispersal (see Eqn. 3.8), and

$$k = \frac{1 - d_m}{1 - c_m d_m}, \tag{3.11}$$

the probability to be a philopatric individual. P_p and P_d in Equations 3.9 and 3.10 are the probabilities of mating success of philopatric and dispersing males which (omitting inbreeding depression again) are calculated as

$$P_p = P_d \quad = \frac{1}{1-c_m d_m}. \tag{3.12}$$

The evolutionary stable dispersal probability equalizes the MGF from dispersal and philopatry, so that from $G_d = G_p$ we can derive from Equations 3.9 and 3.10 and by using Equation 3.12:

$$1 - \frac{1-d_m}{1-c_m d_m}R \quad = \quad 1 - c_m. \tag{3.13}$$

From this follows:

$$\begin{aligned}
\frac{1-d_m}{1-c_m d_m}R &= c_m, \\
\Rightarrow (1-d_m)R &= c_m - c_m^2 d_m, \\
\Rightarrow R - d_m R &= c_m - c_m^2 d_m, \\
\Rightarrow R - c_m &= d_m R - c_m^2 d_m, \\
\Rightarrow \frac{R - c_m}{R - c_m^2} &= d_m, \tag{3.14}
\end{aligned}$$

with $R > c_m$. By letting Equation 3.14 equilibrate in a numerical simulation we arrive at evolutionary stable values for d_m^*. The evolutionary stable female dispersal strategy can be obtained by changing suffix m to f and thereby we arrive at:

$$d_m^* = \frac{R^* - c_m}{R^* - c_m^2}, \tag{3.15}$$

$$d_f^* = \frac{R^* - c_f}{R^* - c_f^2}. \tag{3.16}$$

Chapter 4

Sex-specific spatio-temporal variability in reproductive success promotes the evolution of sex-biased dispersal[1]

ANDREAS GROS, HANS JOACHIM POETHKE & THOMAS HOVESTADT

4.1   Introduction

Dispersal is an ecological key mechanisms with far reaching consequences for populations and communities (e.g. Clobert et al., 2001; Chave, 2004; Hanski and Gaggiotti, 2004). Just as important, dispersal "decisions" have a profound influence on individual, respectively inclusive fitness. Empirical evidence as well as theory thus indicate that dispersal decisions should often be context-dependent (e.g. Bowler and Benton, 2005), as the fitness consequences of such decisions depend on external as well as the internal conditions of an individual (Hovestadt et al. in prep.).

Sex-biased dispersal is an especially prominent example of context dependent dispersal and has been observed in many taxa (Greenwood, 1980; Greenwood and Harvey, 1982; Liberg and von Schantz, 1985; Pusey, 1987; Baguette et al., 1998; Sundström et al., 2003; Möller and Beheregaray, 2004; Williams and Rabenold, 2005; Hammond et al., 2006; Lawson Handley and Perrin, 2007; Öckinger and Smith, 2007). The conspicuousness and relevance of this phenomenon has also attracted the attention of theoreticians who want to understand, under which conditions sex-biased dispersal is likely to evolve. The avoidance of inbreeding depression has been identified as an especially likely factor promoting the evolution of sex-biased dispersal; under many conditions inbreeding could even lead to a situation where only one sex should disperse while the other remains completely philopatric (Gandon, 1999; Perrin and Mazalov, 1999, 2000). This asymmetry should be more pronounced in polygynous mating system than under monogamy as the likelihood of mating with close relatives is higher in the former (Perrin and

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[1]Gros, A., Poethke, H. J. & Hovestadt, T., Manuscript submitted for publication to Theoretical Population Biology

Mazalov, 1999). However, if kin-competition is also taken into account asymmetries in dispersal are predicted to be smaller (Motro, 1991b, 1994; Gandon, 1999; Perrin and Mazalov, 1999).

More importantly, inbreeding avoidance as such cannot predict which of the two sexes should become the more dispersive one – this would completely depend on historical chance events (Perrin and Mazalov, 1999; Gandon, 1999, Gros et al., subm.). Thus, alternative explanations for the evolution of sex-biased dispersal have been suggested, which either on their own or in conjunction with the influence of inbreeding can explain, which of the two sexes disperses more. One obvious possibility is that dispersal is more costly for one than the other sex. In that case the gender with lower cost is likely to become the more dispersive sex, even though it is not completely impossible (if starting conditions are right) that the sex with higher costs evolves to disperses more (Perrin and Mazalov, 1999; Wild and Taylor, 2004; Leturque and Rousset, 2004, Gros et al., subm.).

Other explanations assume that the benefits of dispersal, respectively philopatry may not be identical in the two sexes. Greenwood (1980, 1983) has, for example, suggested that for male birds the benefits from taking over the natal territory are larger than they are for females; consequently females are more likely to emigrate than males in many bird species (Greenwood and Harvey, 1982). Hirota (2004, 2005) has predicted the evolution of female biased dispersal under the premise that females mate before emigration and that empty habitats are available in the landscape. In this case, females can harvest great fitness benefits from colonizing such empty habitat patches while males could not do so; and as the females are already fertilized they transport not only their own genes but also the genes of their mating partner(s). It should be noted, however, that mating before emigration is not likely to occur if avoidance of inbreeding is a strong driver of dispersal.

Perrin and Mazalov (2000) have drawn attention to the fact that the intensity of competition may be different for the two sexes as males and females potentially compete over different resources, e.g. females over food and males over mating opportunities. In an analytical model involving polygynous mating they have shown that such differences could promote the evolution of sex-biased dispersal, even in the absence of inbreeding depression. However, according to their model male-biased dispersal emerges only if resource competition among females is completely removed, i.e. if populations are allowed to grow exponentially. Otherwise, they always predict the evolution of balanced dispersal. The assumption of exponential growth is, however, rather unrealistic, especially for birds and mammals which nonetheless very often show sex-biased dispersal (Dobson, 1982; Greenwood and Harvey, 1982).

Perrin and Mazalov (2000) could – because they used a deterministic model without demographic and/or environmental stochasticity – not recognize another mechanism by which the mating system may influence the evolution of sex-biased dispersal. In this paper we will show that – even in the absence of inbreeding depression – differences in the between-patch variability in reproductive success promotes sex-biased dispersal. Both, within- and between-patch variability in reproductive success only occurs in stochastic population models; and the magnitude of this variability is, at least partly, an emergent consequence of dispersal (cf. Poethke et al., 2003; Ronce, 2007). These boundary conditions forecloses a (comprehensible) analytical approach to study the influence of variability on the evolution of evolutionary stable dispersal strategies in stochastic metapopulation models. We thus use an individual-based model to investigate the effects of kin-competition, demographic variability, and the mating system on the evolution of sex-biased dispersal. However, instead of "deactivating" resource-competition among females as Perrin and Mazalov (2000) did, we intensify mate-competition among males by introducing a harem mating system in which a single male fertilizes all females in a patch.

4.2   The model

To investigate the combined influence of mate- and resource-competition on the evolution of gender-specific dispersal, we modify an individual-based model more completely described in Poethke and Hovestadt (2002). The assumption we implement in the model are principally identical to those of Perrin and Mazalov (2000): we simulate the population dynamics, inter-patch dispersal, and the evolution of emigration probability in a metapopulation of a diploid and sexually reproducing annual species with discrete generations. Each habitat patch (p_i) supports maximally K breeding females (territories). Simulation experiments are initialised by placing $2K = N$ individuals with a sex-ratio of one in each patch. As demographic effects become less prominent with increasing population size, we use different carrying capacities (K) to investigate the influence of demographic stochasticity on the evolutionary outcome. To keep the number of individuals (and thus of mutation events) in the whole metapopulation comparable (approximately 25.000 reproducing individuals) we increase the number of local populations in correspondence with the reduction in K. Thus, the meta-population consists of 256, 676 and 1296 habitat patches with a local carrying capacity (K) of 50, 20, and 10 territories, respectively. Each mated female produces a number of offspring (λ) with a standard value of $\lambda = 3$. To explore the importance of the value of λ we also conducted tests with $\lambda = 6$. All offspring mature and can disperse. If individuals disperse, they

die during transition with probability $c \in \{0.05, 0.40\}$. Like Perrin and Mazalov (1999) we assume global dispersal, i.e. a surviving disperser arrives in any other patch with equal probability. After the dispersal phase females compete for the breeding spaces (territories) and males for mating with the successful females. Both, the females successfully occupying territories and their mating partners are selected randomly among the females, respectively males present in the patch. In all scenarios we assume that breeding success is not affected by inbreeding.

Each individual is characterised by four alleles (m_1, m_2, f_1, f_2) at two diploid loci (m, f), inherited from its parents. The first locus (m) determines the male's probability for emigration (p_m), the second (f) determines p_f in females; for both sexes the phenotype is determined as the mean of the two corresponding parental alleles. Other than in Poethke and Hovestadt (2002) we thus allow for the independent evolution of emigration probabilities in males and females but do not allow for density-dependent emigration. The alleles of these loci can take continuous values between zero and one ($m_i, f_i \in [0, 1]$). To test whether an initial bias in dispersal has an effect of the outcome of evolution, we initialize simulations for each parameter setting (λ, c, and K) with 10 different start values for male and female dispersal, always with a population mean emigration probability of 0.2: f_i is set to a value from 0.02, 0.04, 0.06 ... 0.20, and the alleles for male emigration probability correspondingly to $m_i = 0.2 - f_i$. When inheriting a parents' genes, each allele transferred to the offspring mutates with probability 0.002. If mutations occur, the alleles of the loci m and f are altered by adding a random value drawn from a uniform distribution within the interval [-0.02, 0.02].

We run 50 simulation experiments for each combination of K, λ, c, and initial emigration probabilities, i.e. 50 x 3 x 2 x 2 x 10 = 6000 simulation runs for each mating system. To allow the populations to reach evolutionary equilibrium, we let simulations run for 50.000 generations. Preliminary runs showed that equilibrium was reached after a maximum of 40.000 generations, but usually much faster. We record the resulting mean values for the loci m and f, as well as all other measures mentioned below in the gamete phase in the last generation.

We implement two different mating systems to test whether differences in the intensity of competition cause sex-biased dispersal. In our first scenario, "random mating" (RM), all females winning a breeding-space choose a single mate randomly among all males in their patch – the number of mating successes for males is thus a Poisson distributed number with an approximate mean of one. In our second scenario, "harem" (H), a single randomly chosen male mates with all successful females in the patch. Scenario RM is identical with the first scenario in Perrin and Mazalov (2000) with approximately equal competition among males and females. However, with scenario H we intensify mate competition among males instead of

removing local resource competition among females as Perrin and Mazalov (2000) did in their second scenario. We want to point out that kin-competition is, like in any individual-based simulation, implicitly accounted for in our simulations (Poethke et al., 2007).

4.3   Results

Not surprisingly, the costs of dispersal have a great influence on the evolving mean emigration probabilities (e.g. Gandon and Rousset, 1999; Gandon, 1999; Perrin and Mazalov, 1999) with much higher dispersal probabilities evolving in the harem mating system (H) compared to the random mating system (RM; Figures 4.1a, b). More importantly, an increase in patch capacity leads to a decline in emigration probability in the RM scenario, while K hardly has an effect on the emigration probability in the H scenario. The latter can be traced to the fact that K has little influence on the emergence of a kin-structure in the harem mating system where only a single male mates with all females in a patch. The effective population size $N_e = 4N_m N_f / (2N_m + N_f)$ (Wright, 1931) becomes then nearly independent of total population size, respectively habitat capacity and cannot become larger than four with a number of mating males $N_m = 1$ (N_e equals 3.33, 3.63, and 3.84 for $K = 10$, 20 and 50 respectively).

Any bias in the emigration probabilities we observe is in favour of male-biased emigration (Figures 4.1c, d). Its direction and magnitude is not affected by direction or magnitude of the sex-bias in emigration at initialization. It is especially noticeable that, in contrast to the prediction of Perrin and Mazalov (2000), male-biased dispersal also evolves in populations with mating-system RM. However, the bias evolving with RM is usually smaller than with mating system H. Furthermore, any bias decreases with an increasing number of breeding territories and completely vanishes for scenario RM at $K = 50$ (Fig. 4.1c, d).

According to the arguments put forward by Perrin and Mazalov (2000), the magnitude of the bias should correlate with the discrepancy between the intensity of local resource competition (for females) and local mate competition (for males). As competition about reproductive resources or mating opportunities increases the variance in reproductive output, variance in offspring number is a good measure for the competition a gender experiences. If we calculate the within-patch variance in reproductive performance before dispersal (Figures 4.2a, b) we actually find that the argument by Perrin and Mazalov (2000) cannot explain the outcome of our simulations. Neither the variance in reproductive success for each sex, nor the difference in this variance is affected by habitat capacity in the RM scenario.
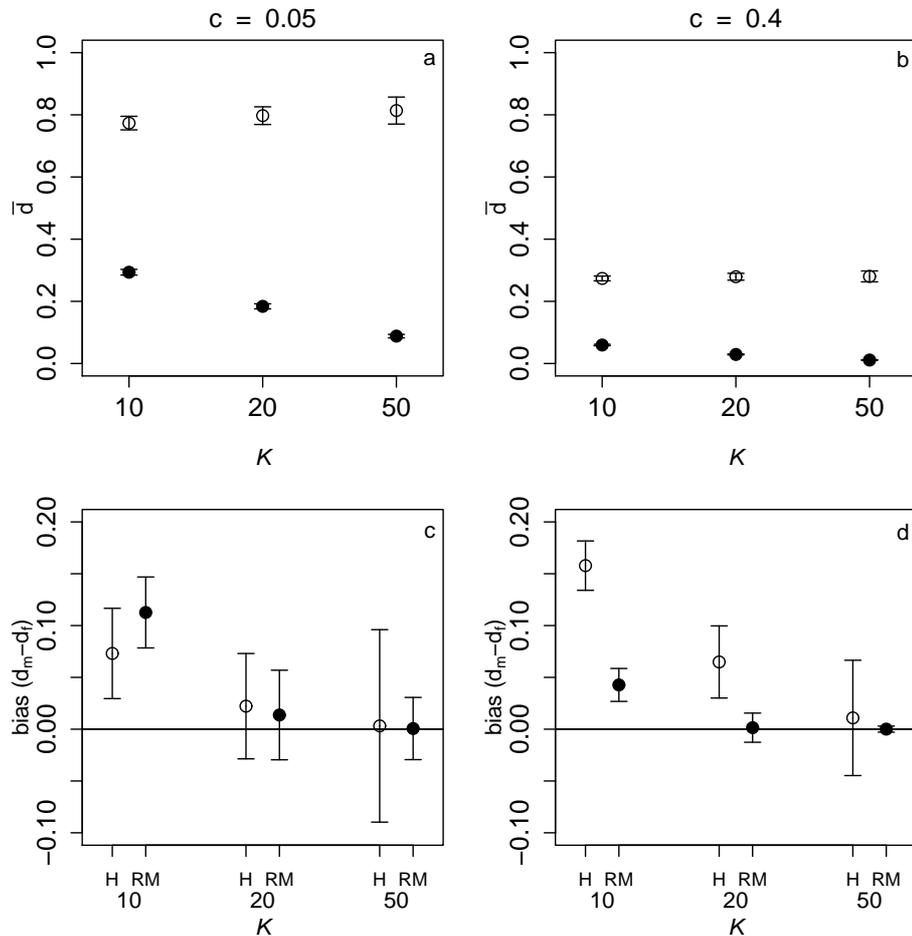
Figure 4.1: Top row: Mean emigration probability $\bar{d}$ (averaged of males and females) plotted over habitat capacity (K) for mating systems RM (filled symbols) and H (open symbols). Bottom row: Emerging difference (bias) in mean emigration probability between males and females ($d_m - d_f$) for the same scenarios. Costs of dispersal are low ($c = 0.05$) in the left column (a, c) and high ($c = 0.4$) in the right column (b, d). Error bars indicate standard errors in the mean values in the 500 replicate simulation runs.

And in the H scenario the intensity of local mate competition obviously increases with K (Figures 4.2a, b). Yet, as already stated, in both scenarios the sex-bias in emigration probability declines with increasing K.

The driving mechanism behind the selection for male-biased dispersal is, instead, the between-patch variance in reproductive success. Actually, the between-patch variance in local resource and local mate competition becomes virtually identical for large K (Figures 4.2c, d) in both, the RM and the H mating scenario. A
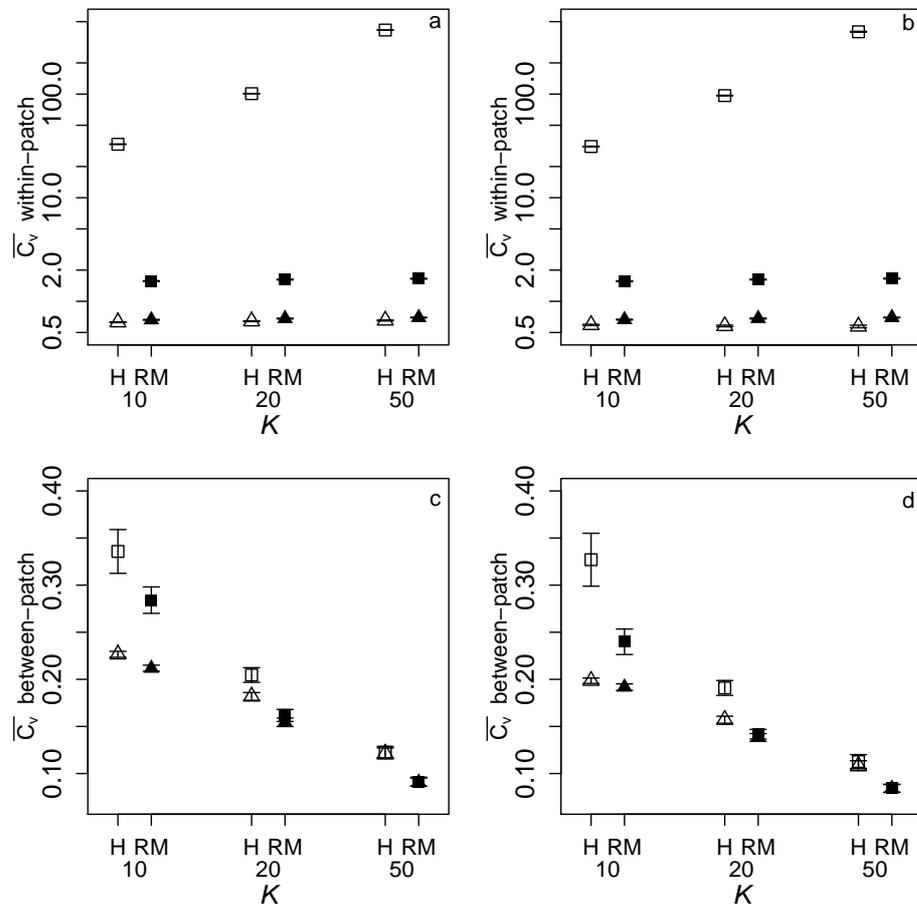
Figure 4.2: Coefficient of variation ($C_v \pm$ s.e.) in reproductive success for females (triangles) and males (squares) in dependence of the mating regime (RM: open symbols, H: filled symbols) and patch capacity K. Results are for the same scenarios as those presented in Figure 4.1. The top-row (a, b) shows the C_v for within-patch variability in per capita reproductive success. The coefficient of variation for the number of offspring was estimated separately for males and females and each patch, and then averaged across patches. In the figures (a, b), mean (across 500 simulation replicates) and standard errors of these means are given (note logarithmic scale of y-axis). The bottom row (c,d) shows the mean and standard error of the between-patch coefficient of variation in mean per capita reproductive success, separately for males and females. Data presented are mean and standard error from 500 simulations.

comparison of Figures 4.1c, d and 4.2c, d makes immediately clear that the male-bias in emigration probability vanishes as soon as there is no more difference in between-patch variance of reproductive success for females and males. This

conclusion is supported by the fact that an increase in fertility from $\lambda = 3$ to $\lambda = 6$ increases within-patch variability in reproductive success but greatly reduces between-patch variability in reproductive performance of males. Consequently, for $\lambda = 6$ we hardly see the evolution of sex-biased dispersal, even for the smallest K value (results not shown).

4.4 Discussion

The deterministic model of Perrin and Mazalov (2000) predicts that sex-biased dispersal would only evolve if females do not compete among each other at all. In such a case females obviously cannot improve their (inclusive) fitness expectations by dispersing and consequently should avoid the risks of dispersal. On the other hand, the driving mechanisms behind male dispersal is kin-competition, which obviously does not occur among females if the latter do not compete among each other at all. However, in our simulations we find that even in the scenario where both, females and males compete (RM) male-biased dispersal evolves as long as patch capacity is small. We further find a difference in sex-bias between the RM and the H scenario, while, as shown by simple algebraic operations (see Appendix), this change in mating system should not affect the magnitude of sex-bias. Our results thus contradict the predictions of Perrin and Mazalov (2000) and we have to turn to an alternative explanations for the evolution of sex-biased dispersal in this case.

It has long been stated that spatio-temporal heterogeneity in reproductive success is, apart from the influence of kin-competition and inbreeding depression, the third principal driver behind the evolution of dispersal (Hastings, 1983; Metz and Gyllenberg, 2001). Only if such variability exists can an emigrating individual expect to potentially find another patch where competition is less intense or conditions are in another way more favourable than in its natal patch; this is actually the underlying idea of the "ideal-free distribution" (Fretwell and Lucas Jr., 1970; Cressman and Krivan, 2006). Our simulations show, that sex-biased dispersal can evolve as soon as the spatio-temporal variability in competition becomes different for the two sexes. This may happen, as soon as fitness expectations for the two sexes depend on different processes. This is the case in in our simulations, just as in the model of Perrin and Mazalov (2000), as females compete over a limited number of breeding territories, while the males compete over access to females.

Between-patch variability in resource competition emerges because of demographic stochasticity which leads to variance in female population size. Male reproductive success is affected by this competition too, because it determines the number of

mating opportunities in a patch. However, for males the reproductive success also depends on the sex-ratio (in the RM scenario), respectively the number of competing males (in the H scenario). Both of these values also underlie demographic variability, especially if K is small. The overall between-patch variability is consequently larger for males than females and we thus observe male-biased emigration in the RM scenario for which the deterministic model of Perrin and Mazalov (2000) predicts symmetric emigration.

It is important to recognize that the difference in within-patch variability of reproductive success in scenarios RM and H has as such no influence on the sex-bias of dispersal. The larger within-patch variance in the H scenario only leads to the evolution of higher mean emigration probability because the effective population size is (much) smaller than in the RM scenario and kin-competition thus becomes stronger. By dispersing, however, individuals can only exploit the between-patch variance in reproductive success and increase their chances to end in a patch where they have to compete with fewer sex-mates over the relevant resources. The male-bias in the latter type of variance declines as habitat capacity increases and consequently dispersal becomes more symmetric with increasing habitat capacity. This may, however, not be the case if apart from demographic stochasticity external (environmental) stochasticity would maintain a sex-bias in between-patch variability even for large habitat patches.

Previous explanations for the evolution of sex-biased dispersal have been based on a number of fundamental principles. First, the avoidance of inbreeding depression, which as such does not, however, predict which of the two sexes should be the more dispersive (e.g. Gandon, 1999; Perrin and Mazalov, 2000). Second, there may exists fundamental asymmetries between the two sexes. These may emerge, for example, because one sex can disperse at a lower cost than the other (e.g. Taylor, 1988; Leturque and Rousset, 2003; Wild and Taylor, 2004, Gros et al., subm.), or because one sex can systematically expect higher fitness benefits when either staying at home (e.g. Greenwood, 1980) or when immigrating into another patch (Hirota, 2004). Hirota (2004) has also pointed out that male genes can "hitchhike" with dispersing females while the alternative option only rarely exists.

Our simulations suggest that there may be a third fundamental principle that can lead to the evolution of sex-biased dispersal: the existence of differences in the sex-specific spatio-temporal variance of fitness expectations in a landscape. Such differences could emerge as soon as the fitness of the two sexes are defined by different processes, which in turn are differently affected by demographic and/or environmental stochasticity. We actually believe that this is not rare and may also apply to individuals which can be classified according to other criteria than gender, e.g. males following different mating strategies than other males. In this

case we would expect that it is always the group of individuals, which experiences a larger spatio-temporal variance in fitness expectations that evolves into the more dispersive group.

4.5 Appendix

Perrin and Mazalov (2000) formulate the total fitness of a female as:

$$W_x = x_{ij}\tilde{c}\frac{Nb_0}{Nb(\tilde{x} + x\tilde{c})} + \tilde{x}_{ij}\frac{N(k_y b_t + \tilde{k}_y b_0)}{Nb(\tilde{x}_j + x\tilde{c})} \tag{4.1}$$

and, mutatis mutandis, for males total fitness is defined as:

$$W_y = y_{ij}\tilde{c}\frac{Nb_0}{Nb(\tilde{y} + y\tilde{c})} + \tilde{y}_{ij}\frac{N(k_x b_t + \tilde{k}_x b_0)}{Nb(\tilde{y}_j + y\tilde{c})} \tag{4.2}$$

x_{ij} is the individual (female) dispersal propensity of individual i in patch j, x_j denotes the average female dispersal propensity in patch j, and x describes the overall mean dispersal propensity for females. y with corresponding subscripts denote the respective male dispersal propensities. c is dispersal mortality, while the ~-sign denotes the complement (e.g. $\tilde{c} = 1 - c$). $k_y = \tilde{y}_j/(\tilde{y}_j + \tilde{c}y)$ is the probability of a male to be philopatric.

For males the first term of the right-hand side of Equation 4.2 means that if a male disperses and survives, it competes with $Nb(\tilde{y} + y\tilde{c})$ other males for access to N females and will sire b_0 offspring per successful mating. The second term on the right-hand side of Equation 4.2 means that if the male in focus remains philopatric it competes also with $Nb(\tilde{y}_j + y\tilde{c})$ other males (among which $Nb\tilde{y}_j$ have expected relatedness r) for access to N females, among which will be k_x immigrants and $\tilde{k}_x$ philopatric females. The reproductive output resulting from a mating with an immigrant is b_0 and from a mating with a philopatric female it is b_t. The difference between b_0 and b_t is the effect of inbreeding depression.

Effect of using a harem mating system

If we are to change the model of Perrin and Mazalov (2000) to allow only one male to mate with all females in a patch (H scenario), for the corresponding male fitness $\hat{W}_y$, the notion of Equation 4.2 must be adjusted accordingly. The surviving disperser competes with $Nb(\tilde{y} + y\tilde{c})$ other males for winning the harem, wins it with probability $1/(Nb(\tilde{y}+y\tilde{c}))$, and then produces Nb_0 offspring. Integrating this into a functional relation analog to Equation 4.2 directly shows that this actually does not alter the fitness-defining equation:

$$\hat{W}_y = y_{ij}\tilde{c}\frac{1}{Nb(\tilde{y} + y\tilde{c})}(Nb_0) + \tilde{y}_{ij}\frac{1}{Nb(\tilde{y}_j + y\tilde{c})}(N(k_x b_t + \tilde{k}_x b_0)) = W_y \qquad (4.3)$$

Hence, the fitness formulas for males and females are unaffected by the change towards a harem mating scheme, so that also the fitness derivatives and selection gradients remain equal. However, the expected relatedness in such a mating scheme increases greatly – but it increases as much for males as for females. Therefore, we can deduce a the evolution of a likewise unbiased – yet highly increased – mean emigration probability.

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Zusammenfassung

Kapitel 1 - Evolution lokaler Anpassungen von Ausbreitungsstrategien

Die optimale Dispersal- oder Ausbreitungsstrategie (eine Kombination aus Auswanderwahrscheinlichkeit und Ausbreitungsdistanz) hängt hauptsächlich von dem Risiko ab, in einem für Reproduktion ungeeigneten Habitat zu enden. Dieses Risiko ist am Rand eines Habitats am höchsten, und daher sollten die evolvierenden Ausbreitungsdistanzen und Auswanderwahrscheinlichkeiten zum Rand des Habitats hin abnehmen. Dieser Selektionsdruck sollte zu räumlichen Gradienten in Ausbreitungsstrategien führen.

Der Genfluss, der durch Dispersal verursacht wird, wirkt jedoch lokaler Anpassung der Ausbreitungsstrategie an die jeweilige Umgebung entgegen. Mit einem individuenbasierten Modell untersuchen wir die Evolution lokaler Anpassungen von Ausbreitungsstrategien innerhalb eines einzelnen, kreisförmigen Habitats. Ich vergleiche die evolvierenden Auswanderwahrscheinlichkeiten und -distanzen von sechs verschiedenen Ausbreitungsfunktionen (sog. Kernels, welche die Kombination aus Auswanderwahrscheinlichkeit und Ausbreitungsdistanz abbilden: zwei negativ-exponentielle Kernels, zwei schiefe Kernels, ein Kernel, der Ausbreitung nur in die unmittelbare Nachbarschaft der Mutterpflanze erlaubt (nearest-neighbor dispersal), und ein Kernel, der darin besteht, einen zufälligen Zielort auszuwählen (global dispersal)). Die Evolution der Form der Kernels untersuchen wir in Habitatinseln unterschiedlicher Größe. Ich konnte zeigen, dass eine minimale Habitatgröße nötig ist, um lokale Anpassungen der Ausbreitungsstrategien zu ermöglichen. In Habitatinseln, die diese minimale Größe überschreiten, nimmt die Differenz der Ausbreitungsdistanz zwischen Mitte und Rand des Habitats linear zu, wobei jedoch der Betrag der Differenz vom Kernel abhängt. Mit Ausnahme der Kernels "global dispersal" und "nearest-neighbor dispersal" gleichen sich die evolvierenden räumlichen Muster qualitativ für Auswanderwahrscheinlichkeit und Ausbreitungsdistanz der Kernels. Ich schließe daraus, dass trotz des Genflusses, der mit Aus-

breitung einhergeht, lokale Anpassungen der Ausbreitungsstrategien möglich sind, wenn die Habitatinsel groß genug ist. Dies gilt wahrscheinlich für jede realistische Ausbreitungsfunktion.

Kapitel 2 - Wie hängen Auswanderwahrscheinlichkeit und Ausbreitungsdistanz von der Fähigkeit ab, Populationsdichten zu bestimmen?

Ich untersuche die gleichzeitige Evolution von Auswanderwahrscheinlichkeit und Ausbreitungsdistanz für Arten, die die Populationsdichte in ihren Habitaten unterschiedlich gut wahrnehmen können. In diesem System werden die Überlebenswahrscheinlichkeiten für Nachkommen von steigender Populationsdichte negativ beeinflusst. Mit einem individuenbasierten Modell simuliere ich Dispersal als einen schrittweisen Prozess, in dem Individuen von einem Habitat zum nächsten dispergieren können, wobei sie in jedem dieser Schritte mit einer bestimmten Wahrscheinlichkeit sterben. Meine Ergebnisse zeigen, dass die Emigration aus dem Geburtshabitat stark von Verwandtenselektion beeinflusst wird, wohingegen die Tendenz, weitere Dispersalschritte zu unternehmen, zum größten Teil von der Aussicht bestimmt wird, in ein Habitat einzuwandern, das eine geringere Populationsdichte – und damit bessere Bedingungen für das Überleben der Nachkommen – aufweist, als das Geburtshabitat. Hierbei wird deutlich, dass Individuen, die sich abhängig von der lokalen Populationsdichte dazu "entscheiden", auszuwandern, im Durchschnitt größere Distanzen zurücklegen, als Individuen die unabhängig von der Populationsdichte auswandern. Dies gilt vor allem dann, wenn die Populationsdichten räumlich korreliert sind und damit dicht und weniger dicht besiedelte Habitate geklumpt vorkommen. Jedoch sorgen schon geringe Wahrscheinlichkeiten, während des Dispersal zu sterben, dafür, dass mit keiner Ausbreitungsstrategie Ausbreitungsdistanzen evolvieren, die im Schnitt mehr als zwei Schritte beinhalten.

Kapitel 3 - Evolution von geschlechterspezifischen Ausbreitungsstrategien: die Rolle von geschlechtsspezifischer Wandermortalität, demographischer Mortalität und Inzucht-Depression

Inzucht-Vermeidung und asymmetrische Ressourcen-Konkurrenz wurden schon als mögliche Auslöser der Evolution von geschlechterspezifischen Ausbreitungsstrate-

gien identifiziert. Daneben können jedoch auch unterschiedliche Wandermortalitäten die geschlechterspezifischen Ausbreitungsstrategien beeinflussen, insofern als dasjenige Geschlecht mit der höheren Wandermortalität wahrscheinlich philopatrisch wird, das andere hingegen das Dispersal übernimmt. Leider gibt es dazu wenig quantitative Daten. In diesem Kapitel untersuche ich den quantitativen Zusammenhang zwischen der Differenz in Wandermortalität und dem Ungleichgewicht in der Auswanderwahrscheinlichkeit der Geschlechter. Weiterhin untersuche ich den Einfluss von demographischer Stochastizität und wie Inzucht-Depression in Zusammenspiel mit Unterschieden in der Wandermortalität das Ungleichgewicht der Auswanderwahrscheinlichkeit beeinflusst.

Dazu habe ich ein existierendes mathematisches Modell so angepasst, dass geschlechtsspezifische Wandermortalitäten betrachtet werden können. Auf dieser numerischen Basis kann ich Unterschiede in der Auswanderwahrscheinlichkeit von Geschlechtern selbst für sehr kleine Differenzen in der Mortalität vorhersagen.

Ich bestätige diese Ergebnisse mit individuenbasierten Simulationen und zeige, dass demographische Stochastizität einen ausgleichenden Einfluss auf die Auswanderwahrscheinlichkeiten der beiden Geschlechter hat. Selbst bei gleichzeitig wirkender Inzucht-Depression bestimmen die Mortalitätsunterschiede welches Geschlecht die höhere Auswanderwahrscheinlichkeit entwickelt.

Kapitel 4 - Geschlechtsspezifische räumlich-zeitliche Variabilität des reproduktiven Erfolgs fördert die Evolution von geschlechtsspezifischen Ausbreitungsstrategien

Inzucht-Depression, asymmetrische Wandermortalität und unterschiedliche Paarungssysteme wurden als mögliche Auslöser für die Evolution von Ausbreitungsstrategien identifiziert, in denen die Auswanderwahrscheinlichkeit eines Geschlechtes die des anderen überwiegt.

Wir verwenden individuenbasierte Simulationen, um den Einfluss des Paarungssystems und demographischer Stochastizität auf die Evolution geschlechtsspezifischen Dispersals zu untersuchen. Wir betrachten dabei Meta-Populationen, in denen Weibchen um Brutplätze und Männchen um Paarungen mit erfolgreichen Weibchen konkurrieren.

Der Vergleich der Ergebnisse der Paarungssysteme "random-mating" (alle Weibchen wählen zufällig Männchen als Paarungspartner aus) und "harem" (alle Weibchen eines Habitats paaren sich mit demselben Männchen) zeigt, dass ein Unterschied in der Intensität der Konkurrenz um reproduktionsrelevante Ressourcen

alleine nicht genügt, um einen Unterschied in den Auswanderwahrscheinlichkeiten der Geschlechter hervorzurufen. Vielmehr kommt es in solchen Fällen zu besagtem Ungleichgewicht, in denen ein Geschlecht eine größere Variabilität der Nachkommenzahl zwischen Habitaten erfährt. Dann evolviert das Geschlecht mit der höheren Varianz der Nachkommenzahl zwischen Habitaten die höhere Auswanderwahrscheinlichkeit.

Summary

Chapter 1 - Evolution of local adaptations in dispersal strategies

The optimal probability and distance of dispersal largely depend on the risk to end up in unsuitable habitat. This risk is highest close to the habitat's edge and consequently, optimal dispersal probability and distance should decline towards the habitat's border. This selection should lead to the emergence of spatial gradients in dispersal strategies. However, gene flow caused by dispersal itself is counteracting local adaptation. Using an individual based model I investigate the evolution of local adaptations of dispersal probability and distance within a single, circular, habitat patch. I compare evolved dispersal probabilities and distances for six different dispersal kernels (two negative exponential kernels, two skewed kernels, nearest neighbour dispersal and global dispersal) in patches of different size. For all kernels a positive correlation between patch size and dispersal probability emerges. However, a minimum patch size is necessary to allow for local adaptation of dispersal strategies within patches. Beyond this minimum patch area the difference in mean dispersal distance between center and edge increases linearly with patch radius, but the intensity of local adaptation depends on the dispersal kernel. Except for global and nearest neighbour dispersal, the evolved spatial pattern are qualitatively similar for both, mean dispersal probability and distance. I conclude, that inspite of the gene-flow originating from dispersal local adaptation of dispersal strategies is possible if a habitat is of sufficient size. This presumably holds for any realistic type of dispersal kernel.

Chapter 2 - How dispersal propensity and distance depend on the capability to assess population density

We analyze the simultaneous evolution of emigration probability and dispersal distance for species with different abilities to assess habitat quality (population density) and which suffer from distance dependent dispersal costs. Using an individual-based model I simulate dispersal as a multistep (patch to patch) process in a world consisting of habitat patches surrounded by lethal matrix. Our simulations show that natal dispersal is strongly driven by kin-competition but that consecutive dispersal steps are mostly determined by the chance to immigrate into patches with lower population density. Consequently, individuals following an informed strategy where emigration probability depends on local population density disperse over larger distances than individuals performing density-independent emigration; this especially holds when variation in environmental conditions is spatially correlated. However, already moderate distance-dependent dispersal costs prevent the evolution of long-distance dispersal irrespectively of the chosen dispersal strategy.

Chapter 3 - Evolution of sex-biased dispersal: the role of sex-specific dispersal costs, demographic stochasticity, and inbreeding

Inbreeding avoidance and asymmetric competition over resources have both been identified as factors favouring the evolution of sex- biased dispersal. It has also been recognized that sex-specific costs of dispersal would promote selection for sex-specific dispersal, but there is little quantitative information on this aspect. In this paper I explore (i) the quantitative relationship between cost-asymmetry and a bias in dispersal, (ii) the influence of demographic stochasticity on this effect, and (iii) how inbreeding and cost-asymmetry interact in their effect on sex-specific dispersal. I adjust an existing analytical model to account for sex-specific costs of dispersal. Based on numerical calculations I predict a severe bias in dispersal already for small differences in dispersal costs. I corroborate these predictions in individual-based simulations, but show that demographic stochasticity generally leads to more balanced dispersal. In combination with inbreeding, cost asymmetries will usually determine which of the two sexes becomes the more dispersive.

Chapter 4 - Evolution of sex-biased dispersal: the role of sex-specific dispersal costs, demographic stochasticity, and inbreeding

Inbreeding depression, asymmetries in costs or benefits, and the mating system have been identified as potential factors underlying the evolution of sex-biased dispersal. We use individual-based simulations to explore how the mating system and demographic stochasticity influence the evolution of sex-specific dispersal in a metapopulation with females competing over breeding sites, and males over mating opportunities. Comparison of simulation results for random mating with those for a harem system (locally, a single male sires all offspring) reveal that even extreme variance in local male reproductive success (extreme male competition) does not induce a male bias in dispersal. The latter evolves if between-patch variance in reproductive success is larger for males than females. This can emerge due to demographic stochasticity if habitat patches are small. More generally, members of a group of individuals experiencing higher spatio-temporal variance in fitness expectations may evolve to disperse with greater probability than others.

List of publications

Gros, A., Poethke, H. J. & Hovestadt, T. 2006. Evolution of local adaptations in dispersal strategies. – Oikos 114(3): 544–552.

Gros, A., Hovestadt, T. & Poethke, H. J., Evolution of sex-biased dispersal: the role of sex-specific dispersal costs, demographic stochasticity, and inbreeding. Submitted for publication in Ecological Modelling.

Gros, A., Poethke, H. J. & Hovestadt, T., Sex-specific spatio-temporal variability in reproductive success promotes the evolution of sex-biased dispersal. Submitted for publication in Theoretical Population Biology.

Gros, A., Hovestadt, T. & Poethke, H. J., How dispersal propensity and distance depend on the capability to assess population density. Manuscript in preparation.

Wegmann, M., Gros, A., Schmitt, M. & Dech, S., Analysis of patch irreplacibility using a spatial explicit population model. Manuscript in preparation.

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Anteilsbeschreibung

An den der vorliegenden kumulativen Dissertation "Interactions in the evolution of dispersal distance and emigration probability" zugrunde liegenden Publikationen waren die Autoren zu folgenden Anteilen beteiligt:

Chapter 1: Gros, A., Poethke, H.J. & Hovestadt, T. (2006) Evolution of local adaptations in dispersal strategies. Oikos, 114: 544–552.

Die Studie wurde von den Autoren gemeinsam konzipiert. Die detaillierte Planung der Experimente, die Programmierung des Simulationsmodells, die Datenaufnahme und die Auswertung wurde von mir durchgeführt. Das Manuskript wurde von mir (70%) in Kooperation mit Dr. Hovestadt (20%) und Prof. Poethke (10%) abgefasst.

Chapter 2: Gros, A., Hovestadt, T. & Poethke, H.J. (Manuscript) How dispersal propensity and distance depend on the capability to assess population density.

Die Studie wurde von den Autoren gemeinsam konzipiert. Die Experimente wurden von mir entworfen. Die Datenaufnahme und die Auswertung wurden von mir durchgeführt. Für die Durchführung der individuenbasierten Simulationen habe ich ein Modell erweitert, das von Prof. Poethke und Dr. Mitesser erstellt wurde. Das Manuskript wurde von mir (70%) in Kooperation mit Dr. Hovestadt (20%) und Prof. Poethke (10%) abgefasst.

Chapter 3: Gros, A., Hovestadt, T. & Poethke, H.J. (submitted for publication to Ecological Modelling) Evolution of sex-biased dispersal: the role of sex-specific dispersal costs, demographic stochasticity, and inbreeding.

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Chapter 4: Gros, A., Poethke, H.J. & Hovestadt, T. (submitted for publication to Theoretical Population Biology) Sex-specific spatio-temporal variability in reproductive success promotes the evolution of sex-biased dispersal.

Die Studie wurde von den Autoren gemeinsam konzipiert. Die detaillierte Planung der Experimente, die Datenaufnahme und die Auswertung wurde von mir durchgeführt. Für die individuenbasierten Simulationen habe ich ein Modell erweitert, das von Prof. Poethke und Dr. Mitesser erstellt wurde. Das Manuskript wurde von mir (50%) in Kooperation mit Dr. Hovestadt (40%) und Prof. Poethke (10%) abgefasst.

Acknowledgements