The ability of individuals to assess population density influences the evolution of emigration propensity and dispersal distance

Hans Joachim Poethke [a,*], Andreas Gros [a,b], Thomas Hovestadt [a,c]

[a] *University of Würzburg, Field Station Fabrikschleichach, Glashüttenstrasse 5, 96181 Rauhenebrach, Germany*
[b] *New England Complex Systems Institute, 238 Main Street, Suite 319, Cambridge, MA 02142, USA*
[c] *Muséum National d'Histoire Naturelle, CNRS UMR 7179, 1 Avenue du Petit Château, 91800 Brunoy, France*

ARTICLE INFO

ABSTRACT

We analyze the simultaneous evolution of emigration and settlement decisions for actively dispersing species differing in their ability to assess population density. Using an individual-based model we simulate dispersal as a multi-step (patch to patch) movement in a world consisting of habitat patches surrounded by a hostile matrix. Each such step is associated with the same mortality risk. Our simulations show that individuals following an informed strategy, where emigration (and settlement) probability depends on local population density, evolve a lower (natal) emigration propensity but disperse over significantly larger distances – i.e. postpone settlement longer – than individuals performing density-independent emigration. This holds especially when variation in environmental conditions is spatially correlated. Both effects can be traced to the informed individuals' ability to better exploit existing heterogeneity in reproductive chances. Yet, already moderate distance-dependent dispersal costs prevent the evolution of multi-step (long-distance) dispersal, irrespective of the dispersal strategy.

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 inter- or intraspecific competition for resources (Lambin et al., 2001; Poethke and Hovestadt, 2002), minimization of kin-competition (e.g. Hamilton and May, 1977; Comins, 1982; Frank, 1986; Comins and Hassell, 1987; Rousset and Gandon, 2002; Kisdi, 2004; Poethke et al., 2007) avoidance of inbreeding depression (Bengtsson, 1978; Motro, 1991; Perrin and Goudet, 2001) or coping with the temporal variability of resource availability (Levin et al., 1984; Travis and Dytham, 1999; Gandon and Michalakis, 2001). The possibility to colonize new habitats, another benefit of dispersal, is critical for the persistence of a species (Alsos et al., 2007).

So far theoretical studies on dispersal of actively moving organisms have mainly focused on the emigration of individuals, while the dispersal process itself and the question how far to disperse has been mostly ignored. Instead, the dispersal distance

has been tackled with rather arbitrary assumptions like nearest neighbor (e.g. Travis et al., 1999; Gros et al., 2006) or global (e.g. Poethke and Hovestadt, 2002) dispersal. 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 studies on seed dispersal. However, dispersal kernels describe the probability distribution of dispersal distances away from a source. The use of dispersal kernels has thus mostly been confined to studies of seed or pollen dispersal, or that of other organisms with passive dispersal (Ezoe, 1998; Gros et al., 2006) in continuous landscapes.

Although kernels have occasionally 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), they appear inappropriate to capture the behavior of actively moving individuals. Such animals presumably do not leave habitat patches accidentally (Van Dyck and Baguette, 2005), but because of a decision to do so. Moreover, they are believed to more or less continuously monitor the status of their surroundings during movement (Nathan et al., 2008). It is likely that they can distinguish between suitable and unsuitable habitat and can assess the expected benefit of further

* Corresponding author.
E-mail addresses: poethke@biozentrum.uni-wuerzburg.de (H.J. Poethke), andreas@necsi.edu (A. Gros), hovestadt@biozentrum.uni-wuerzburg.de (T. Hovestadt).

movement (Baker and Rao, 2004). Habitat selection of actively moving animals has been object to several theoretical and empirical studies (for a review see Morris, 2003). Numerous examples show that animals react not only to habitat quality but also on local population density (Morris and MacEachern, 2010). For this reason it is rational to consider dispersal of actively moving organisms as a three phase process with different factors influencing decisions concerning (i) emigration, (ii) movement and (iii) settlement (Clobert et al., 2009).

When suitable habitat is patchily distributed and patches of habitat are embedded into an environment unsuitable for reproduction, animals should continue their movement until they find a suitable patch (Baker and Rao, 2004; Stamps et al., 2005). In this case the realized dispersal distance of individuals will crucially depend on the mean distance between patches of suitable habitat (e.g. Hein et al., 2004). Yet, once dispersing individuals have discovered a patch of suitable habitat, they may either settle or decide to continue their search for a new breeding site. In this case, the final dispersal distance of actively moving animals will strongly depend on their perseverance i.e. the probability to continue dispersal after having reached a patch of suitable habitat. It is conceivable that an individual able to estimate the quality of its natal site is also able to assess the quality of a site it has arrived in, and may consequently continue to disperse if the quality of that site is perceived as too low.

We thus propose that dispersal distances should strongly depend on the capability of individuals to use information on habitat quality in their dispersal decision whereas uninformed dispersers should typically not continue dispersal once they have reached a new potential breeding habitat. In the following we expand a previously published simulation model (Poethke and Hovestadt, 2002) to test this hypothesis. We compare the evolution of dispersal distances for different degrees of spatial correlation in environmental conditions. Local population density is a critical determinant of intraspecific competition and dispersal is strongly motivated by the search for less populated habitats (Ruxton and Rohani, 1999; Travis et al., 1999; Poethke and Hovestadt, 2002). To account for organisms differing in their capacity to assess local population density, we thus implement informed (in this case density dependent) as well as uninformed (density independent) dispersal into the model and compare the effect of either strategy on the evolution of dispersal.

More specifically, we test a number of hypotheses: (1) The number of successive dispersal steps decreases with increasing dispersal costs (cf. Murrell et al., 2002). (2) The number of dispersal steps increases with increasing spatial correlation in environmental conditions. With increasing spatial correlation, animals have to disperse further to escape poor conditions (cf. Frank and Wissel, 1998; Murrell et al., 2002; Kallimanis et al., 2006). (3) Most importantly, we test the hypothesis that short distance (that from the natal site to the first suitable site encountered) dispersal prevails for uninformed dispersers, while dispersal events that cover more than one step will only be found – in significant proportion – for the case of informed (density dependent) dispersal.

2. The model

We use a modified version of the individual-based metapopulation model of Poethke and Hovestadt (2002). The model simulates the population dynamics, inter-patch dispersal, and the evolution of dispersal propensity in a metapopulation of a diploid, sexually reproducing species with discrete generations and density-dependent local population growth. The metapopulation consists of habitat patches arranged in a square lattice of

$24 \times 24 = 576$ cells. To avoid edge effects the metapopulation is closed into a torus (edges are wrapped). Each patch (i) supports a local population with carrying capacity $K = 40$; total carrying capacity of the system is thus ca. 23,000 individuals. Simulation experiments are initialized by placing K individuals in each of the 576 patches.

Within each patch populations grow according to a logistic growth model suggested by Hassell et al. (1976). Similar to Murrell et al. (2002) and Poethke and Hovestadt (2002), a female gives birth to a Poisson distributed number of offspring with mean $\lambda_{mean}(t, i)$. To account for environmental variability, $\lambda_{mean}(t, i)$ (specific for patch i at timestep t) is drawn from a log-normal distribution with mean $\bar{\lambda} = 2$ and a standard deviation of $\sigma = 1$. Offspring are randomly allocated to either sex. Offspring survival during maturation is dependent on the total number of offspring hatched in a patch (N_i). Thus, offspring mature with a density dependent survival probability s where $s = K_i/[K_i + (\bar{\lambda} - 1)N_i]$.

In all of 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), the second (f) determines its perseverance, that is the probability (P_f) of continuing to disperse once it has successfully reached a suitable habitat patch. These alleles take continuous values and are initialized 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 (see Fig. A2). Dispersal "decisions" can be either density-dependent (DD) or density-independent (DI). We performed simulation experiments for three different scenarios differing in the assumptions concerning the animals' capacity to perceive local population density and to adjust their dispersal behavior accordingly. In the first scenario (scenario DI_n/DI_f) natal dispersal propensity as well as perseverance, i.e. dispersal propensity for all further dispersal moves, is density-independent. In the second scenario (DD_n/DI_f) we assume that individuals can assess the population density in their natal patch, but do not have ability to assess the density of any patch they reach thereafter. Thus, natal dispersal propensity is density-dependent (DD_n) but perseverance is density-independent (DI_f). In the third scenario (DD_n/DD_f) all dispersal steps are density-dependent.

In the case of density independent dispersal, dispersal probability (the phenotype) is calculated according to the mean value of both alleles at the respective loci. This holds for density independent natal dispersal probability ($P_{DI,n} = (n_1 + n_2)/2$) as well as for the probability to continue dispersal ($P_{DI,f} = (f_1 + f_2)/2$) in the two scenarios with density independent perseverance (DI_n, DI_f and DD_n, DI_f).

In the case of density dependent natal dispersal, individual alleles do not determine the dispersal probability but a threshold density $C_n = (n_1 + n_2)/2$ for dispersal. The actual dispersal probability $P_{DD,n}$ is then calculated according to the model derived by Poethke and Hovestadt (2002) as

$$P_{DD,n} = \begin{cases} 0 & \text{if } C_i < C_n \\ 1 - \frac{C_n}{C_i} & \text{if } C_i \geq C_n \end{cases} \tag{1a}$$

Accordingly, the probability to continue dispersal in the case of density dependent perseverance (DD_n, DD_f) is calculated as

$$P_{DD,f} = \begin{cases} 0 & \text{if } C_i < C_f \\ 1 - \frac{C_f}{C_i} & \text{if } C_i \geq C_f \end{cases} \tag{1b}$$
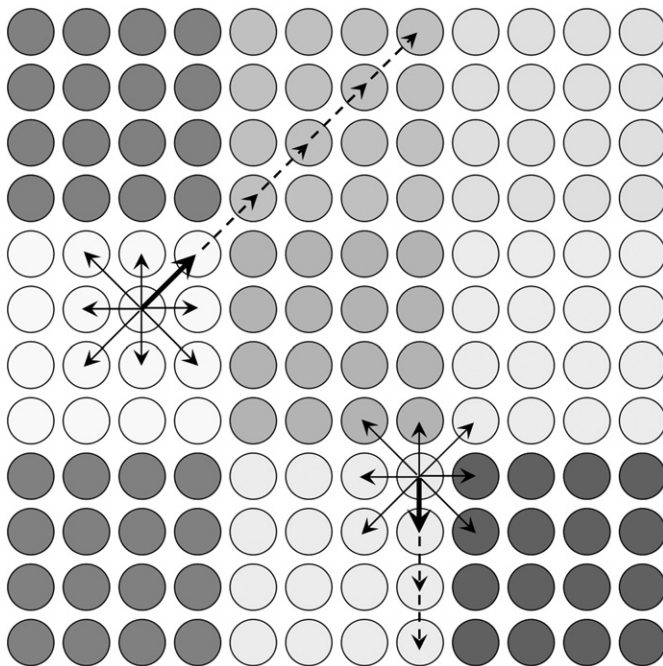
with $C_f = (f_1 + f_2)/2$.

For a full discussion concerning the adequacy of this model structure for density dependent dispersal see Poethke and

Hovestadt (2002) and Hovestadt et al. (2010). It should be noted that Ruxton and Rohani (1999) already utilized a model very similar to our DD_n/DD_f model version to address questions concerning the stabilizing effects of dispersal on population dynamics.

The three scenarios may correspond to three types of dispersers with different sensory capacities. The first scenario (DI_n/DI_f) could apply to animals such as certain butterflies that leave habitats independent of population density (e.g. Boughton, 2000). The second scenario (DD_n/DI_f) may apply to animals that acquire important information about population density during their larval 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 (DD_n/DD_f) we assume animals that have the ability to assess local population density at any time. 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).

For natal dispersal an individual randomly chooses one of eight neighboring patches as destination and then assesses successive patches along this trajectory thus keeping its direction in each following step (see Fig. 1). Dispersing individuals either reach the next habitat patch or die during the transition with probability μ. Exploratory simulation runs showed that individuals very rarely continued their dispersal for more than 10 consecutive steps (see also Section 3), and we therefore limited the maximum number of movement steps to 15. This had a negligible effect on simulation results but significantly reduced computation time.

We modeled spatial correlation in habitat quality by aggregating patches into clusters and assigning an identical value of $\lambda_{mean}(t, i)$ to all k patches within such a cluster. To account for different spatial dimensions of correlation we vary the side-length of clusters from

$l=1$ (cluster-size $k=1$; no spatial correlation) to $l=4$ (cluster-size $k=16$; see Fig. 1). Reproductive conditions ($\lambda_{mean}(t,i)$) for each cluster were drawn anew every generation (t). The spatial configuration of clusters does not change over time, so that each patch always belongs to the same cluster.

When inheriting its parent's genes, mutations occur with a small probability ($m=0.01$) per allele. If mutations occur, the affected alleles are altered by adding a random value drawn from a uniform distribution within the interval $[-0.1, 0.1]$. Preliminary simulation experiments showed that an evolutionary equilibrium is usually reached after approximately 3000 generations (see Fig. A2), yet each simulation run included 10,000 generations. All results were recorded in the last generation. We varied stepwise dispersal mortality μ as follows: $\mu=\{0.025, 0.05, 0.10$ and $0.20\}$.

3. Results

In all scenarios we find that uninformed dispersers (DI_n) evolve higher probabilities of natal dispersal than informed dispersers (DD_n; Fig. 2a), while consecutive dispersal steps occur with higher probability for informed dispersers (DD_f) than for uninformed dispersers (DI_f; Fig. 2b). Not surprisingly, natal dispersal probability (Fig. 2a) as well as the mean number of additional steps moved (Fig. 2b) decreases rapidly with increasing dispersal mortality (μ). In general, individuals are thus inclined to settle in the first patch they arrive in as soon as dispersal mortality rises beyond even moderate levels ($\mu \geq 0.1$). The effect of dispersal mortality on natal dispersal is more pronounced for the case of density independent natal dispersal than for informed dispersal (Fig. 2a).

Evolution of elevated natal dispersal probabilities for uninformed (DI_n, density independent) compared to informed natal dispersal (DD_n) has already been described by Enfjäll and Leimar (2009) and Hovestadt et al. (2010): density dependent dispersal more efficiently exploits inter-patch differences in population density, but also more efficiently homogenizes population density across patches. To demonstrate this Fig. 3 compares the demographic benefits, that is, the mean difference in population size between the source and destination patch for the first five dispersal steps of emigrants. Evidently, the very first dispersal

Fig. 1. Symbolic representation of the landscape and dispersal behavior of two representative individuals. Circles represent patches of suitable habitat, the space in between the hostile matrix. Clusters of circles of similar shading represent clusters of patches with similar environmental conditions (for this case $4 \times 4 = 16$ patches per cluster). Thin arrows depict possible dispersal moves during natal dispersal of a focal individual (nearest neighbor dispersal). For natal dispersal an individual chooses a direction at random (fat arrow) and in the following steps it keeps this direction (broken arrows).
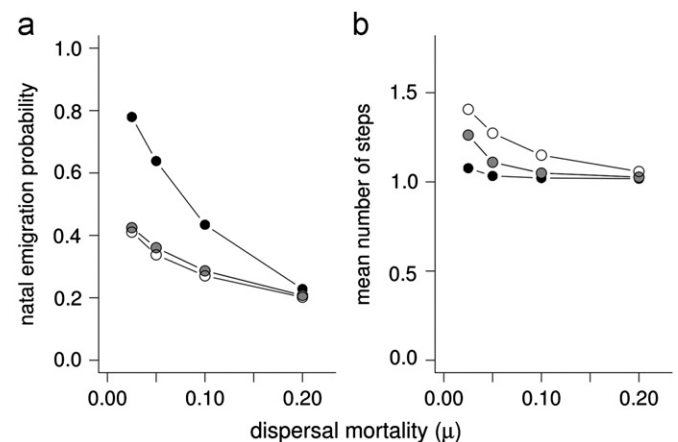

Fig. 2. Influence of dispersal mortality (μ) on natal emigration probability (a) and the mean number of steps an emigrant takes (b), for uninformed dispersal (DI_n/DI_f; filled circles), density dependent natal dispersal but density independent dispersal for any subsequent dispersal steps (DD_n/DI_f; gray circles), and completely density dependent dispersal (DD_n/DD_f; open circles). Result of simulation experiments in worlds of 576 patches of capacity $K=40$ with uncorrelated environmental fluctuations (cluster-size $k=1$).
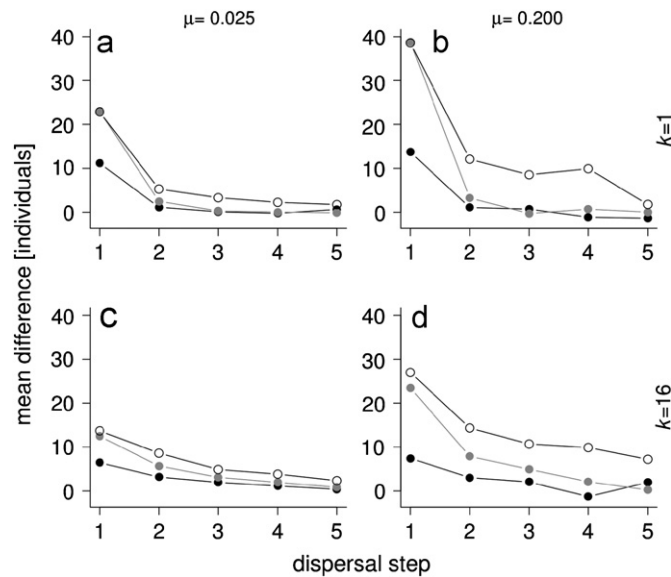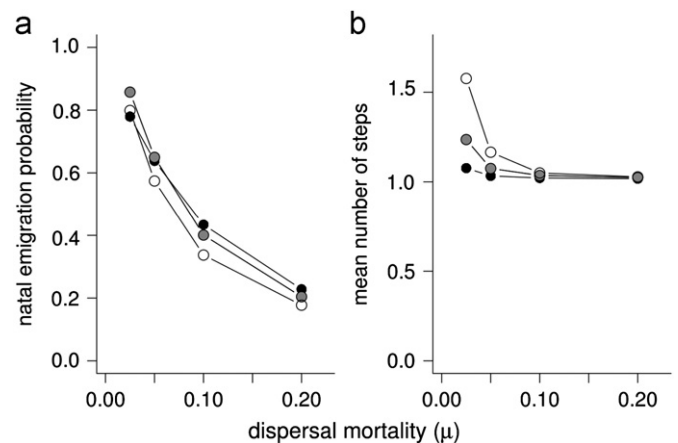
Fig. 3. Mean stepwise difference in population density between start- and target-patch for the first five consecutive dispersal steps of dispersing individuals following different dispersal strategies (DI_n/DI_f=filled circles; DD_n/DI_f=gray circles; DD_n/DD_f=open circles). Left column (a, c) gives results for low dispersal mortality (μ=0.025), and right column (b, d) for high dispersal mortality (μ=0.200). Upper row (a, b) gives results for uncorrelated (cluster-size k=1) lower column (c, d) those for correlated (cluster-size k=16) environmental conditions. Result of simulation experiments in worlds of 576 patches of capacity K=40. In any generation, patches within same cluster are exposed to identical environmental conditions (λ_t).

Fig. 4. Influence of dispersal mortality (μ) on natal emigration probability (a) and the mean number of steps an emigrant covers (b) for completely uncorrelated worlds (k=1; filled circles), spatial correlation distance l=2 (k=4; gray circles) and spatial correlation distance l=4 (k=16; open circles). Result of simulation experiments with density independent dispersal (DI_n/DI_f) in worlds of 576 patches of capacity K=40. In any generation, patches within same cluster are exposed to identical environmental conditions (λ_t).

step is the most profitable one, i.e. is associated with the largest decline in pre- (natal patch) compared to post-dispersal (target patch) density. This holds for density dependent as well as for density independent dispersal. For example, with low dispersal cost (μ=0.025) and an accordingly high emigration probability, uninformed natal dispersers (DI_n/DI_f) arrive after their first dispersal step in a patch with on average 10.8 fewer competitors than in their natal patch (full dots, Fig. 3a). If these individuals continue to disperse their second step will bring them to a patch with on average only 1.1 fewer individuals then their first target. With higher dispersal cost (μ=0.200) emigration probabilities become generally lower but, correspondingly, the demographic benefits of natal dispersal increases (Fig. 3b). Thus, with higher dispersal mortality (μ=0.200) uninformed natal dispersers (DI_n/DI_f) arrive after their first dispersal step in a patch with on average 13.7 fewer individuals than in their natal patch (full dots, Fig. 3b).

Informed dispersal allows a more efficient exploitation of inter-patch differences in population density. Even for the case of low dispersal cost (and relatively high emigration probability), density dependent natal dispersers (DD_n/DI_f and DD_n/DD_f) arrive in patches with on average 22.8 fewer individuals than in their natal patch (gray dots and open dots in Fig. 3a). For the case of high dispersal cost (μ=0.200) the mean reduction in local population size achieved increases to 38.6 individuals (gray dots and open dots in Fig. 3b).

The difference in the potential demographic benefit gained by dispersal between informed and uninformed strategies is not restricted to the first dispersal step: it is even more pronounced for the steps following natal dispersal. While the mean demographic benefit of a second dispersal step (i.e. the mean difference in population density between the target of their first (natal) dispersal step and the target of their second step) for completely uninformed dispersers (DI_n/DI_f) is only 1.1 individuals (largely independent of dispersal cost, see filled circles in Fig. 3a and b),

completely informed dispersers (DD_n/DD_f) will realize a mean demographic benefit of 5.2 individuals in the case of low dispersal cost (μ=0.025; open circles in Fig. 3a) and of 12.1 individuals for high dispersal cost (μ=0.200; open circles in Fig. 3b) with a second dispersal step. Even those individuals that show informed dispersal in their first step but density independent dispersal in all other steps (DD_n/DI_f, gray circles) do profit slightly more from steps following natal dispersal than completely uninformed dispersers.

Natal dispersal equalizes population density to a considerable degree, thus reducing the potential benefits of further steps, while the costs for any such step remain the same. Consequently, even in scenarios with a rather benign cost of dispersal (e.g. μ=0.1), only 2–5% of the emigrants take more than one dispersal step. With spatially correlated environmental fluctuations (Fig. 3c and d) however, the demographic benefit for natal dispersal decreases while the benefit for all further dispersal steps increases. An increase in the demographic benefits gained by moving additional steps particularly emerges for individuals following uninformed secondary dispersal (for DI_n/DI_f compare filled dots in Fig. 3a and b with c and d; for DD_n/DI_f compare gray dots in Fig. 3a and b with c and d) and it is largest for individuals that show density dependent natal dispersal but density independent dispersal in all other dispersal steps (DD_n/DI_f).

Spatial correlation has only a negligible effect on the probability of natal dispersal (Fig. 4a) but the number of additional dispersal steps taken is strongly influenced by the spatial correlation in environmental conditions (Fig. 4b); here we only show results for scenario DI_n/DI_f but results for the two other strategies are analogous (see Appendix A). At low dispersal mortality (μ=0.025) the mean number of dispersal steps increases from 1.08 to 1.58 as cluster dimension increases from k=1 to k=16. Nonetheless, only 34% of all emigrants will continue dispersal after the first dispersal step (see black dots in Fig. A1). However, at a dispersal mortality of μ=0.1, the mean number of dispersal steps increases only from 1.02 to 1.05.

4. Discussion

The results of our evolutionary simulation experiments show that organisms with active dispersal should typically settle into

the first patch of suitable habitat they encounter, i.e. disperse over short distances. Even for rather low levels of dispersal mortality individuals hardly ever continue dispersal once they have reached a suitable patch. This supports the findings by Barton et al. (2009), who modeled the (evolution of) movement rules of organisms during transition. They found that organisms should target their movement to the first (nearest) patch when patches become rare and movement in the matrix thus becomes more costly. Selection for settlement in the first patch encountered particularly evolves for uninformed dispersers and for spatially uncorrelated environmental conditions. Yet even in spatially correlated environments density independent dispersers mostly settle in the neighboring patch as soon as stepwise dispersal mortality becomes moderate (e.g. $\mu \geq 0.1$). Thus, most of these dispersers did not even leave the range of environmental correlation in the scenarios with extended spatial clusters.

Under density dependent natal dispersal, the general tendency of individuals to leave the natal patch decreases. However, at the same time, the average dispersal distance (number of consecutive dispersal steps) is increased. Thus, the largest mean number of dispersal steps recorded emerges for completely informed dispersal (DD_n/DD_f) in spatially correlated landscapes. However, even in these scenarios, individuals typically move less than two steps as soon as stepwise mortality risk becomes moderately large ($\mu \geq 0.1$).

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 additional dispersal steps as the number of steps increases. This declining benefit has two main causes: (1) kin competition, a major driver of dispersal (Hamilton and May, 1977; Rousset and Gandon, 2002; Poethke et al., 2007), is already largely reduced with the first dispersal step, because siblings are spread over eight neighboring patches. Note that individual based simulation models of the evolutionary process account for kin competition by default (Poethke et al., 2007). (2) The chance to reach a habitat with fewer competitors decreases with every dispersal step simply because any round of dispersal homogenizes population density ever further. The fact that spatial correlation has little effect on natal emigration probabilities (see Fig. 4a) despite the fact that demographic benefits decline, supports the notion that this step is to a large degree driven by avoidance of kin-competition. Only selection on taking further steps seems to be sensitive to demographic benefits. The ability to control these latter benefits – moving from high- to low-density populations – is responsible for the significant differences between informed and uninformed dispersal strategies.

The evolution of elevated dispersal probabilities for uninformed (DI_n, density independent) compared to informed natal dispersal (DD_n) can be traced to the fact that density dependent dispersal more efficiently exploits inter-patch differences in population density, but also more efficiently homogenizes population density across patches (Enfjall and Leimar, 2009; Hovestadt et al., 2010). This is the flip side of the larger demographic benefit achieved by dispersing individuals following a density-dependent emigration strategy (Fig. 3). Clearly, homogenizing occurs most rapidly when the overall number of emigrants is large, i.e. when dispersal mortality is low.

Only the DD strategy is adjustable in a way that allows "compensating" increased dispersal costs by also increasing the benefits as individuals emigrate only from especially densely populated populations and thus collect especially large demographic fitness benefits *given* they survive dispersal (Poethke et al., 2007). This explains the fact that under density-dependent emigration natal dispersal is rarer, but consecutive dispersal steps occur with higher probability.

Even when individuals disperse with a fixed probability (DI_n), more natal emigrants come, for simple statistical reasons, from high density patches. Apart from the effect of kin-competition (Hamilton and May, 1977; Poethke et al., 2007), it is this simple truism that makes even density independent natal dispersal a beneficial strategy in landscapes that exhibit spatio-temporal variability in population density. For dispersal steps following natal dispersal this argument does not hold however. Only immigrants, i.e. individuals that previously dispersed already, are allowed to decide whether they want to continue dispersal or not, but a correlation between population density and the number of immigrants no longer exists.

On the other hand, with completely density dependent dispersal (DD_n/DD_f) immigrants can "recognize" that they have arrived in a high-density patch and decide to move on. The probability that this is indeed the case is supported by another mechanism already described by Hovestadt and Poethke (2006): under density dependent dispersal the distribution of the number of emigrants becomes much more leptokurtic with occasional "mass emigration" from patches that have particularly good years. Such events also imply that large numbers of individuals immigrate into the neighboring patches. Consequently, dispersal itself creates a spatial correlation in population density and makes it more profitable to continue dispersal over several steps to leave the zone of correlation in population density. It is indeed this later effect that explains why, rather surprisingly, the mixed strategy (DD_n/DI_f) also evolves higher probabilities for consecutive dispersal steps. Due to the aforementioned effect, the recognition of high density in the natal patch allows already predicting that, after the first 'round' of dispersal, population density in neighboring patches will be large too, even if individuals do not have the ability to perceive the actual density there.

In our model we assume that individuals either have information on local population density or not and that information acquisition is not costly. In real systems information acquisition may come with a cost, e.g. as investment into sensual capabilities or into time needed for information acquisition. Animals often use environmental cues (e.g. Stamps and Krishnan, 2005; Ichiki et al., 2011) or information derived from the presence of heteropecifics (e.g. Monkkonen et al., 1999) to assess local habitat quality. Such indirect information will necessarily be less precise. Thus, situations of intermediate information status will exist, too. It requires further investigation to understand how information precision and investment into its acquisition would affect the evolution of conditional dispersal strategies.

Despite the enormous interest of theoretical ecologists in the evolution of dispersal and its ecological consequences, the great majority of studies on dispersal evolution have so far focused on the evolution of dispersal propensity (e.g. Hamilton and May, 1977; Janosi and Scheuring, 1997; Travis and Dytham, 1999; Travis et al., 1999; Poethke and Hovestadt, 2002; Parvinen et al., 2003), while a smaller number of papers investigate the evolution of dispersal distance (e.g. Ezoe, 1998; Savill and Hogeweg, 1998, 1999; Hovestadt et al., 2001; Murrell et al., 2002; Rousset and Gandon, 2002; Higgins et al., 2003; Muller-Landau et al., 2003; Starrfelt and Kokko, 2010; Travis et al., 2010).

Usually the evolution of dispersal distances and the prediction of evolutionarily stable dispersal kernels are analyzed under the assumption of "passive" and uncontrollable movement as it occurs in seed dispersal, while investigating dispersal propensity has been a focus of animal ecologists. At least in part this dichotomy is explained by the different mechanisms that govern dispersal in plants and animals. In active as well as in passive dispersers, dispersal incurs different types of cost. First, species that belong to either dispersal group must invest in equipment that allows dispersal. This may be the flight apparatus of wind

dispersed seeds (Tackenberg et al., 2003), the elaiosoma of ant dispersed seeds (Pfeiffer et al., 2010), the wings and flight muscles of Orthoptera (e.g. Zera and Harshman, 2001), or the silk thread of spiders (e.g. Bonte et al., 2003). Such investment costs are paid once and are more or less independent of the distance an individual will ultimately travel. However there are further costs that are related to dispersal distance. With passive dispersal (especially in plants) the number of propagules produced is typically large and dispersal is under maternal control. From the perspective of a tree, it is the overall distribution of offspring that counts and it may pay in evolutionary terms to allocate at least some offspring to risky long-distance dispersal. This promotes the evolution of "fat tailed" dispersal kernels (Hovestadt et al., 2001; see also Roy et al., 2001; Rousset and Gandon, 2002; Starrfelt and Kokko, 2010).

However, as explained in the introduction these approaches appear ill suited for the case of actively moving organisms where the dispersal distances observed should be traced to the interaction between landscape attributes and the rules governing the movement and especially the settlement of organisms. Actively moving animals may continuously monitor their surroundings (Getz and Saltz, 2008; Nathan et al., 2008) and decide whether they continue to move or stay once they have found a patch of habitat. At this moment the dispersing individual may decide to either settle or move on. According to our results the tendency to move on will clearly depend on the risk associated with searching for other suitable habitats (cost of dispersal). In addition we would predict that species with well developed sensory (and cognitive) abilities that are readily able to assess population density or habitat quality are more likely to move on than species that do not have such abilities. On the other hand, individuals that need much time (in relation to life-expectancy) or energy to collect such information would typically settle in the first habitat they find.

Dispersal distance is an emergent property depending on behavioral rules on the one hand and landscape attributes on the other (Baguette and Van Dyck, 2007). As "smart" animals are unlikely to settle just somewhere in the "matrix" the distribution of dispersal distances will strongly be defined by the typical distances between patches of suitable habitat. We believe that our, certainly simplifying approach, is a useful step to better understand the evolution of dispersal distances in actively moving organisms as an emergent property defined by landscape attributes on the one hand and settlement rules on the other.

In summary we predict that with uninformed dispersal multiple dispersal steps should evolve only if stepwise dispersal costs are rather low. Multiple dispersal steps are most likely to evolve in species able to assess the quality of at least their natal habitat and in landscapes that show strong spatial correlation of environmental conditions. However, as it presumably requires time to collect information about habitat quality we expect that secondary dispersal will most likely occur among long-lived species with considerable sensory and cognitive abilities like mammals or birds.

Acknowledgments

Appendix A

See Figs. A1 and A2.
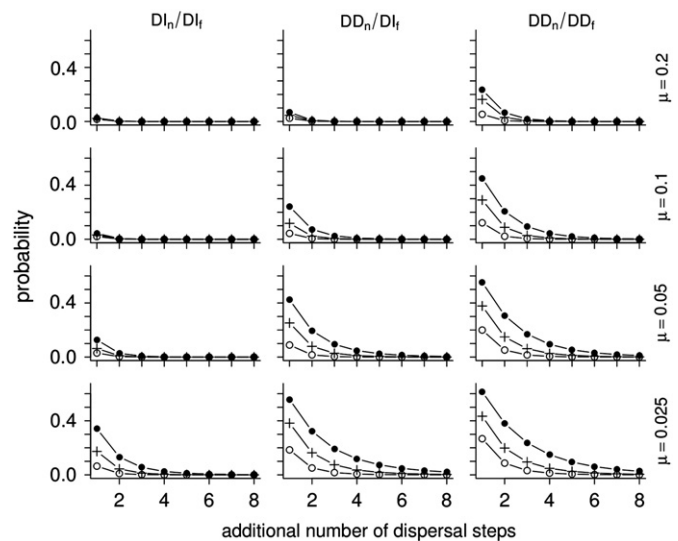
Fig. A1. Probability to perform at least n additional dispersal steps following initial natal dispersal, with n plotted on the x-axis, as a function of dispersal cost (μ; rows) and the mode of dispersal (columns). DI_n/DI_f: completely uninformed dispersal, DD_n/DI_f: density dependent natal dispersal but uninformed dispersal in all subsequent dispersal steps. DD_n/DD_f: completely density dependent dispersal. Different symbols reflect results for different scales of spatial correlation. Open circles: results for completely uncorrelated environmental conditions (cluster-size $k=1$), crosses for clusters of $k=4$ patches, and filled circles for clusters of $k=16$ patches. In any generation, patches within same cluster are exposed to identical environmental conditions (λ_t).
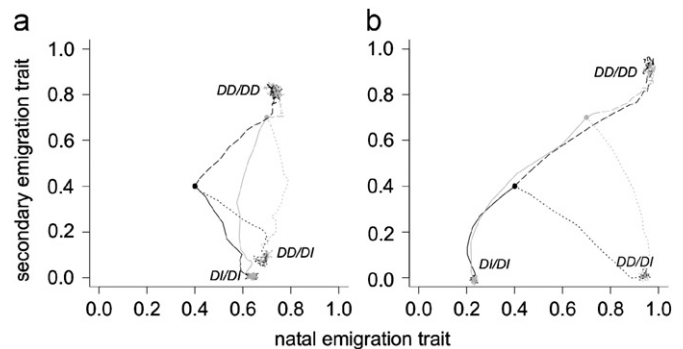
Fig. A2. Exemplary plots of evolutionary trajectories for different dispersal mortalities (a: $\mu=0.05$ and b: $\mu=0.20$) and for each of the three different dispersal strategies investigated: DI_n/DI_f (continuous lines), DD_n/DI_f (dotted lines), and DD_n/DD_f (hatched lines). For each strategy we initialized simulations at two different trait values for the two evolving traits (black and gray dot). Note that the trait evolving is emigration probability for density-independent emigration (DI) but the density threshold (C_n and C_f of Eq. (1)) for density-dependent emigration (DD). Emigration probabilities for the latter are shown in Figs. 2 and 4.

References

Alsos, I.G., Eidesen, P.B., Ehrich, D., Skrede, I., Westergaard, K., Jacobsen, G.H., Landvik, J.Y., Taberlet, P., Brochmann, C., 2007. Frequent long-distance plant colonization in the changing Arctic. Science 316, 1606–1609.

Austerlitz, F., Dick, C.W., Dutech, C., Klein, E.K., Oddou-Muratorio, S., Smouse, P.E., Sork, V.L., 2004. Using genetic markers to estimate the pollen dispersal curve. Molecular Ecology 13, 937–954.

Baguette, M., 2003. Long distance dispersal and landscape occupancy in a metapopulation of the cranberry fritillary butterfly. Ecography 26, 153–160.

Baguette, M., Van Dyck, H., 2007. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. Landscape Ecology 22, 1117–1129.

Baker, M.B., Rao, S., 2004. Incremental costs and benefits shape natal dispersal: theory and example with Hemilepistus reaumuri. Ecology 85, 1039–1051.

Barton, K.A., Phillips, B.L., Morales, J.M., Travis, J.M.J., 2009. The evolution of an 'intelligent' dispersal strategy: biased, correlated random walks in patchy landscapes. Oikos 118, 309–319.

Bengtsson, B.O., 1978. Avoiding inbreeding—at what cost? Journal of Theoretical Biology 73, 439–444.

Bohrer, G., Nathan, R., Volis, S., 2005. Effects of long-distance dispersal for metapopulation survival and genetic structure at ecological time and spatial scales. Journal of Ecology 93, 1029–1040.

Bonte, D., Deblauwe, I., Maelfait, J.P., 2003. Environmental and genetic background of tiptoe-initiating behaviour in the dwarf spider Erigone atra. Animal Behaviour 66, 169–174.

Boughton, D.A., 2000. The dispersal system of a butterfly: a test of source-sink theory suggests the intermediate-scale hypothesis. American Naturalist 156, 131–144.

Bullock, J.M., Clarke, R.T., 2000. Long distance seed dispersal by wind: measuring and modelling the tail of the curve. Oecologia 124, 506–521.

Chapman, D.S., Dytham, C., Oxford, G.S., 2007. Modelling population redistribution in a leaf beetle: an evaluation of alternative dispersal functions. Journal of Animal Ecology 76, 36–44.

Clobert, J., Le Galliard, J.F., Cote, J., Meylan, S., Massot, M., 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12, 197–209.

Comins, H.N., 1982. Evolutionarily stable strategies for localized dispersal in 2 dimensions. Journal of Theoretical Biology 94, 579–606.

Comins, H.N., Hassell, M.P., 1987. The dynamics of predation and competition in patchy environments. Theoretical Population Biology 31, 393–421.

Enfjall, K., Leimar, O., 2009. The evolution of dispersal—the importance of information about population density and habitat characteristics. Oikos 118, 291–299.

Ezoe, H., 1998. Optimal dispersal range and seed size in a stable environment. Journal of Theoretical Biology 190, 287–293.

Fowler, H.G., 1988. Dispersal of early instars of the mole cricket, Scapteriscus tenuis, as a function of density, food, and pathogens (Orthoptera, Gryllotalpidae). Entomologia Generalis 13, 15–20.

Frank, K., Wissel, C., 1998. Spatial aspects of metapopulation survival—from model results to rules of thumb for landscape management. Landscape Ecology 13, 363–379.

Frank, S.A., 1986. Dispersal polymorphisms in subdivided populations. Journal of Theoretical Biology 122, 303–309.

Fuchs, E., Kutsch, W., Ayali, A., 2003. Neural correlates to flight-related density-dependent phase characteristics in locusts. Journal of Neurobiology 57, 152–162.

Gandon, S., Michalakis, Y., 2001. Multiple causes of the evolution of dispersal. In: Clobert, J., Danchin, E., Dhondt, A.A., Nichols, J.D. (Eds.), Dispersal. Oxford University Press, New York, pp. 155–167.

Getz, W.M., Saltz, D., 2008. A framework for generating and analyzing movement paths on ecological landscapes. Proceedings of the National Academy of Sciences of the United States of America 105, 19066–19071.

Gilbert, M., Gregoire, J.C., Freise, J.F., Heitland, W., 2004. Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer Cameraria ohridella. Journal of Animal Ecology 73, 459–468.

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

Hamilton, W.D., May, R.M., 1977. Dispersal in stable habitats. Nature 269, 578–581.

Hanski, I., 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63, 151–162.

Hassell, M.P., Lawton, J.H., May, R.M., 1976. Patterns of dynamical behavior in single-species populations. Journal of Animal Ecology 45, 471–486.

Hein, S., Pfenning, B., Hovestadt, T., Poethke, H.J., 2004. Patch density, movement pattern, and realised dispersal distances in a patch-matrix landscape—a simulation study. Ecological Modelling 174, 411–420.

Higgins, S.I., Nathan, R., Cain, M.L., 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? Ecology 84, 1945–1956.

Higgins, S.I., Richardson, D.M., 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. American Naturalist 153, 464–475.

Hovestadt, T., Kubisch, A., Poethke, H.J., 2010. Information processing in models for density-dependent emigration: a comparison. Ecological Modelling 221, 405–410.

Hovestadt, T., Messner, S., Poethke, H.J., 2001. Evolution of reduced dispersal mortality and 'fat-tailed' dispersal kernels in autocorrelated landscapes. Proceedings of the Royal Society of London Series B—Biological Sciences 268, 385–391.

Hovestadt, T., Poethke, H.J., 2006. The control of emigration and its consequences for the survival of populations. Ecological Modelling 190, 443–453.

Ichiki, R.T., Kainoh, Y., Yamawaki, Y., Nakamura, S., 2011. The parasitoid fly Exorista japonica uses visual and olfactory cues to locate herbivore-infested plants. Entomologia Experimentalis et Applicata 138, 175–183.

Janosi, I.M., Scheuring, I., 1997. On the evolution of density dependent dispersal in a spatially structured population model. Journal of Theoretical Biology 187, 397–408.

Kallimanis, A.S., Kunin, W.E., Halley, J.M., Sgardelis, S.P., 2006. Patchy disturbance favours longer dispersal distance. Evolutionary Ecology Research 8, 529–541.

Katul, G.G., Porporato, A., Nathan, R., Siqueira, M., Soons, M.B., Poggi, D., Horn, H.S., Levin, S.A., 2005. Mechanistic analytical models for long-distance seed dispersal by wind. American Naturalist 166, 368–381.

Kisdi, E., 2004. Conditional dispersal under kin competition: extension of the Hamilton—may model to brood size-dependent dispersal. Theoretical Population Biology 66, 369–380.

Lambin, X., Aars, J., Pierney, S.B., 2001. Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the empirical evidence. In: Clobert, J., Danchin, E., Dhondt, A.A., Nichols, J.D. (Eds.), Dispersal. Oxford University Press, New York, pp. 110–122.

Levin, S.A., Cohen, D., Hastings, A., 1984. Dispersal strategies in patchy environments. Theoretical Population Biology 26, 165–191.

Monkkonen, M., Hardling, R., Forsman, J.T., Tuomi, J., 1999. Evolution of heterospecific attraction: using other species as cues in habitat selection. Evolutionary Ecology 13, 91–104.

Morris, D.W., 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136, 1–13.

Morris, D.W., MacEachern, J.T., 2010. Active density-dependent habitat selection in a controlled population of small mammals. Ecology 91, 3131–3137.

Motro, U., 1991. Avoiding inbreeding and sibling competition—the evolution of sexual dimorphism for dispersal. American Naturalist 137, 108–115.

Muller-Landau, H.C., Levin, S.A., Keymer, J.E., 2003. Theoretical perspectives on evolution of long-distance dispersal and the example of specialized pests. Ecology 84, 1957–1967.

Murrell, D.J., Travis, J.M.J., Dytham, C., 2002. The evolution of dispersal distance in spatially-structured populations. Oikos 97, 229–236.

Nathan, R., 2006. Long-distance dispersal of plants. Science 313, 786–788.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences of the United States of America 105, 19052–19059.

Nathan, R., Katul, G.G., Horn, H.S., Thomas, S.M., Oren, R., Avissar, R., Pacala, S.W., Levin, S.A., 2002. Mechanisms of long-distance dispersal of seeds by wind. Nature 418, 409–413.

Nichols, R.A., Hewitt, G.M., 1994. The genetic consequences of long-distance dispersal during colonization. Heredity 72, 312–317.

Pajunen, V.I., Pajunen, I., 2003. Habitat selection in rock pool corixids: the effect of local density on dispersal. Hydrobiologia 495, 73–78.

Parvinen, K., Dieckmann, U., Gyllenberg, M., Metz, J.A.J., 2003. Evolution of dispersal in metapopulations with local density dependence and demographic stochasticity. Journal of Evolutionary Biology 16, 143–153.

Perrin, N., Goudet, J., 2001. Inbreeding, kinship, and the evolution of natal dispersal. In: Clobert, J., Danchin, E., Dhondt, A.A., Nichols, J.D. (Eds.), Dispersal. Oxford University Press, New York, pp. 123–142.

Pfeiffer, M., Huttenlocher, H., Ayasse, M., 2010. Myrmecochorous plants use chemical mimicry to cheat seed-dispersing ants. Functional Ecology 24, 545–555.

Poethke, H.J., Hovestadt, T., 2002. Evolution of density-and patch-size-dependent dispersal rates. Proceedings of the Royal Society of London Series B—Biological Sciences 269, 637–645.

Poethke, H.J., Pfenning, B., Hovestadt, T., 2007. The relative contribution of individual and kin selection to the evolution of density-dependent dispersal rates. Evolutionary Ecology Research 9, 41–50.

Rankin, M.A., Burchsted, J.C.A., 1992. The cost of migration in insects. Annual Review of Entomology 37, 533–559.

Rousset, F., Gandon, S., 2002. Evolution of the distribution of dispersal distance under distance-dependent cost of dispersal. Journal of Evolutionary Biology 15, 515–523.

Ruxton, G.D., Rohani, P., 1999. Fitness-dependent dispersal in metapopulations and its consequences for persistence and synchrony. Journal of Animal Ecology 68, 530–539.

Roy, D.B., Rothery, P., Moss, D., Pollard, E., Thomas, J.A., 2001. Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. Journal of Animal Ecology 70, 201–217.

Savill, N.J., Hogeweg, P., 1998. Spatially induced speciation prevents extinction: the evolution of dispersal distance in oscillatory predator–prey models. Proceedings of the Royal Society of London Series B—Biological Sciences 265, 25–32.

Savill, N.J., Hogeweg, P., 1999. Competition and dispersal in predator–prey waves. Theoretical Population Biology 56, 243–263.

Stamps, J.A., Krishnan, V.V., Reid, M.L., 2005. Search costs and habitat selection by dispersers. Ecology 86, 510–518.

Stamps, J., Krishnan, V.V., 2005. Nonintuitive cue use in habitat selection. Ecology 86, 2860–2867.

Starrfelt, J., Kokko, H., 2010. Parent–offspring conflict and the evolution of dispersal distance. American Naturalist 175, 38–49.

Tackenberg, O., Poschlod, P., Bonn, S., 2003. Assessment of wind dispersal potential in plant species. Ecological Monographs 73 (2), 191–205.

Travis, J.M.J., Dytham, C., 1999. Habitat persistence, habitat availability and the evolution of dispersal. Proceedings of the Royal Society of London Series B—Biological Sciences 266, 723–728.

Travis, J.M.J., Murrell, D.J., Dytham, C., 1999. The evolution of density-dependent dispersal. Proceedings of the Royal Society of London Series B—Biological Sciences 266, 1837–1842.

Travis, J.M.J., Smith, H.S., Ranwala, S.M.W., 2010. Towards a mechanistic understanding of dispersal evolution in plants: conservation implications. Diversity and Distributions 16, 690–702.

Van Dyck, H., Baguette, M., 2005. Dispersal behaviour in fragmented landscapes: routine or special movements? Basic and Applied Ecology 6, 535–545.

Zera, A.J., Denno, R.F., 1997. Physiology and ecology of dispersal polymorphism in insects. Annual Review of Entomology 42, 207–230.

Zera, A.J., Harshman, L.G., 2001. The physiology of life history trade-offs in animals. Annual Review of Ecology and Systematics 32, 95–126.