ORIGINAL ARTICLE

ASSORTATIVE MATING COUNTERACTS THE EVOLUTION OF DISPERSAL POLYMORPHISMS

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Polymorphic dispersal strategies are found in many plant and animal species. An important question is how the genetic variation underlying such polymorphisms is maintained. Numerous mechanisms have been discussed, including kin competition or frequency-dependent selection. In the context of sympatric speciation events, genetic and phenotypic variation is often assumed to be preserved by assortative mating. Thus, recently, this has been advocated as a possible mechanism leading to the evolution of dispersal polymorphisms. Here, we examine the role of assortative mating for the evolution of trade-off-driven dispersal polymorphisms by modeling univoltine insect species in a metapopulation. We show that assortative mating does not favor the evolution of polymorphisms. On the contrary, assortative mating favors the evolution of an intermediate dispersal type and a uni-modal distribution of traits within populations. As an alternative, mechanism dominance may explain the occurrence of two discrete morphs.

KEY WORDS: Costs, dominance, metapopulation, polymorphism, trade-off.

Besides birth and death events, emigration and immigration are the major processes that govern the dynamics of spatially structured populations. Therefore, dispersal behavior is a key life-history attribute and its evolution is of central importance for ecology. Major advances in this field have been summarized recently by for example, Bowler and Benton (2005) or Ronce (2007). In short, there are a number of selective forces that favor dispersal as for example kin competition (Hamilton and May 1977; Poethke et al. 2007), the avoidance of inbreeding (e.g., Bengtsson, 1978; Ravigné et al. 2006), or habitat variability—either spatio-temporal (McPeek and Holt 1992) or demographic (Travis and Dytham 1998; Cadet et al. 2003). In the extreme case of local population extinctions, dispersers may recolonize empty habitat patches (Comins et al. 1980; Roff 1994). Yet, dispersal may bear important physiological costs (e.g., Zera and Mole 1994). Furthermore, increased predation pressure during the migratory phase or the risk of not finding suitable habitat (e.g., Cody and Overton 1996) are some of the costs associated with dispersal. These forces lead to a reduction of dispersal.

A large number of theoretical studies are concerned with the prediction of one evolutionary stable dispersal rate (Gandon and Michalakis 1999; Poethke et al. 2003). Some models highlight the conditions necessary for a coexistence of more than one dispersal strategy (Roff 1994; Holt and McPeek 1996; Doebeli and Ruxton 1997; Leimar and Norberg 1997; Mathias et al. 2001; Parvinen 2002; Bonte et al. 2010). Such polymorphisms may be behavioral, phenotypic, or genotypic. Behavioral polymorphisms can be found in any model and in many animal and plant species: only a fraction of individuals disperse, whereas the others stay in their patch of origin. Polymorphisms may be phenotypic as in social insects or aphids (Itô 1989), for example. Finally, polymorphisms may be found at the genetic level (e.g., Bonte et al. 2010). Of course, any combination is possible. Here, we will focus on polymorphisms that arise at the genetic level and are expressed in the phenotype (by adaptations to the specific behavior). Evidently, a behavioral response is the final result. In general, such dispersal polymorphisms can evolve when dispersal is costly, that is selection favors residents at the local population scale, while

empty habitat patches guarantee a high fitness gain to individuals establishing new populations. Spatially and temporally varying environments may similarly lead to the evolution of polymorphisms (e.g., McPeek and Holt 1992; Parvinen 2002; Poethke et al. 2011).

Dispersal polymorphisms are known from a large variety of plant (Levin and Muller-Landau 2000) and insect taxa—for example, the sand field cricket *Gryllus firmus* (Roff 1994; King and Roff 2010), the soapberry bug *Jadera haematoloma* (Winchell et al. 2000) or the silver-spotted skipper *Hesperia comma* (Hill et al. 1999). Individuals of such species differ in their dispersal abilities due to differences in, for example, wing size or load, flight muscles or fat reserves (Harrison 1980)—in most cases individuals of the macropterous morph also show a higher tendency to disperse (e.g., Roff and Fairbairn 1991).

A question of central importance is how variation can be maintained within a species or population and finally lead to the evolution of clearly distinct strategies. Some possible mechanisms have been summarized, for example, by Roff (1994) and comprise for example frequency-dependent selection (Cockerham et al. 1972; Clarke 1979). Furthermore, it has been shown theoretically (Roff 1994) and empirically for many species (Reznick 1985) that the evolution of such polymorphisms is often shaped by trade-offs between life-history parameters.

Trade-offs imply that although a specific investment of resources increases one component of fitness another component of fitness is reduced at the same time (Roff and Fairbairn 2007). In the above-cited examples an increase in dispersal ability is correlated with a decrease in fertility (Zera and Denno 1997; Tanaka and Suzuki 1998; Roff 2002; Roff et al. 2002). It is widely accepted that trade-offs play an important role in shaping evolutionary trajectories. Yet, at least theoretically, it is less clear how life-history trade-offs and the evolution of polymorphisms are exactly connected (Roff and Fairbairn 2001, 2007).

In a laboratory study on the dimorphic planthopper *Prokelisia dolus* Langellotto et al. (2000) found evidence for assortative mating based on wing form. This mating pattern is seen as a requirement for evolutionary branching in sexually reproducing species (e.g., Doebeli 1996; Dieckmann and Doebeli 1999) and is commonly found in many insects (Crespi 1989). In general, assortative mating is a mechanism that underlines and stabilizes differences especially in the context of sympatric speciation (Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2003; Gavrilets 2003) because it preserves genetic and phenotypic variation (Wright 1921).

Here, we are interested in the effects of assortative mating on the evolution of dispersal polymorphisms. In contrast to a majority of theoretical studies on dispersal evolution (for a discussion see Ronce 2007) we use a diploid system. We additionally construct an analogous haploid model to analyze the influence of the genetic system assumed (see also Parvinen and Metz 2008). As outlined above, investment in dispersal ability reduces the amount of resources available for reproduction. As a logical consequence, we incorporate a trade-off between dispersal ability and fertility into our model (for recent examples of the few studies that do account for such trade-offs see Burton et al. 2010; Travis et al. 2010). Using an individual-based simulation model, we will first screen the parameter space for regions with polymorphic dispersal strategies. Secondly, we hypothesize that assortative mating underlines and stabilizes trade-off-driven dispersal polymorphisms and eventually expands regions with polymorphic strategies in parameter space. To our knowledge, the connection between dispersal polymorphisms evolving due to fitness trade-offs and assortative mating has never been investigated theoretically in a diploid model before.

The Model

We use an individual-based simulation approach (see e.g., Travis and Dytham 1999; Poethke and Hovestadt 2002; Kubisch et al. 2010) which can be thought to reasonably describe any annual univoltine insect living in a metapopulation. The focal organisms are diploid. An individual has two evolving loci, one coding for emigration probability ($0 \leq \bar{d} \leq 1$) and a second one for the relative investment in dispersal ability ($0 \leq \bar{\rho} \leq 1$). This investment involves a reduction in fertility that will be described in more detail below. Since both loci influence dispersal, we assume genetic linkage between them, that is no recombination. Intuitively this is clear, because it makes no sense to trade (large) amounts of fertility for dispersal ability while being a nondispersive individual and vice versa (for a formal analysis of the joint evolutionary dynamics of dispersal tendency and ability see Yukilevich 2005). We nevertheless tested this in preliminary simulations and could confirm our assumption: without linkage intermediate values for $\bar{d}$ and $\bar{\rho}$ evolved; polymorphisms were never found.

GENETICS

As the modeled organisms are diploid, we implemented maternally and paternally inherited alleles at both loci (d_1, d_2 and ρ_1, ρ_2). These can mutate with a fixed probability of $m_1 = 0.001$. If a mutation occurs, the allele values inherited from the parents are changed by adding a random value drawn from a uniform distribution ($0 \pm \Delta_m$, with $\Delta_m = 0.1$). Reflecting conditions are assumed at the lower and upper limits. This implementation was chosen to avoid an artificial fixation to extreme values (0 or 1). We tested our model with other mutation procedures (i.e., resetting values smaller than 0 and larger than 1, respectively, to 0 and 1) and found no qualitative effect.

To check whether the mode of inheritance has any influence on our results, we implemented (1) a linear relationship between

genotype and phenotype, that is the individual emigration probability ($\bar{d}$) as well as the relative investment in dispersal ability ($\bar{\rho}$) are calculated as mean values from the two respective alleles and (2) dominant/ recessive inheritance. In the latter case, dominance (implemented as an extra locus x_1^d, x_2^d and x_1^ρ, $x_2^\rho \in \{0; 1\}$) is allowed to evolve for both alleles at all loci. If an allele is dominant ($x = 1$) and the other not ($x = 0$), the phenotype is determined uniquely by the value of the dominant allele. If both alleles were either dominant or recessive, we calculated the phenotype as the arithmetic mean (see eq. 1).

$$\bar{d} = \begin{cases} \frac{1}{2}(d_1 + d_2) & \text{if} \quad x_1^d = x_2^d \\ x_1^d d_1 + x_2^d d_2 & \text{if} \quad x_1^d \neq x_2^d \end{cases}$$

$$\bar{\rho} = \begin{cases} \frac{1}{2}(\rho_1 + \rho_2) & \text{if} \quad x_1^\rho = x_2^\rho \\ x_1^\rho \rho_1 + x_2^\rho \rho_2 & \text{if} \quad x_1^\rho \neq x_2^\rho \end{cases} \tag{1}$$

Mutation between the dominant and the recessive state was possible with a rate of $m_2 = 0.0001$. We assume this lower mutation rate, because the switch between dominance and recessivity has an important qualitative impact on the observed phenotypes, whereas the evolving life-history parameters (d and ρ) only change quantitatively in a restricted interval (Δ_m). In addition to these two diploid models, we ran simulations with an analogous haploid (clonal) model.

POPULATION STRUCTURE AND DYNAMICS

We assumed a metapopulation with a total of 1000 habitat patches. We implemented global natal dispersal and random external patch extinctions that occurred with a probability ϵ. Locally, a Beverton–Holt model for logistic population growth was assumed (Beverton and Holt 1957). The patch-specific mean number of offspring $R_{t,p}$ can then be calculated for every time step (t) as

$$R_{t,p} = \lambda_{t,p} \cdot \frac{1}{1 + aN_t} \tag{2}$$

with the susceptibility to crowding $a = \frac{\lambda_0 - 1}{K}$. The carrying capacity was set to $K = 100$ individuals for all patches.

Mean individual fecundity at the global scale is given by λ_0. Every patch is characterized by temporally variable environmental conditions. This has been incorporated into our model by drawing a patch-specific mean fecundity $\lambda_{t,p}$ from a log-normal distribution with mean λ_0 and standard deviation σ. σ thus determines the magnitude of (annual) environmental fluctuations in growth conditions. Such habitat variability is known to have important effects on dispersal strategies, as increasing σ favors more dispersive individuals (reviewed for example in Bowler and Benton 2005). Heterogeneous landscapes are also assumed to favor evolutionary branching (e.g., McPeek and Holt 1992; Parvinen 2002).

THE TRADE-OFF: FERTILITY VERSUS DISPERSAL ABILITY

After mating with a randomly chosen male in its patch, every female produces a certain number of offspring drawn from a Poisson distribution with mean $R_{t,p}^I$, the mean individual number of offspring. $R_{t,p}^I$ is determined by the patch-specific mean number of offspring ($R_{t,p}$) and the individual relative investment into dispersal ability ($\bar{\rho}$) of the female:

$$R_{t,p}^I = R_{t,p} \cdot (1 - \bar{\rho}). \tag{3}$$

Similar approaches have been taken by Burton et al. (2010) in their study of a three-trait trade-off between dispersal, reproduction and competitive ability during range expansion or by Travis et al. (2010) who model a trade-off between seed production and investment in inflorescence height that of course influences dispersal distance.

During dispersal emigrants die with the probability μ^I. The individual mortality risk depends on the landscape-specific dispersal mortality (μ_0) and on the genetically determined amount of resources allocated to dispersal ability ($\bar{\rho}$): the more an individual invests into dispersal ability, the lower its mortality risk becomes; yet, at the same time its fertility is reduced (see eq. 3). An increase in dispersal ability, for example by accumulating more fat reserves, growing larger wings, or developing better flight muscles, is equivalent to reducing dispersal mortality (μ_I). We assume that the resulting individual mortality risk (μ^I) follows a negative exponential function

$$\mu^I = \mu_0 \cdot e^{-\gamma\bar{\rho}} \tag{4}$$

governed by γ, which determines the steepness of this function. Consequently, γ represents the payoff, that is the efficiency of investment into dispersal ability: if the payoff (γ) is small, large amounts of fertility would have to be traded for a comparatively small reduction in dispersal mortality and vice versa. To test the generality of our model, we ran additional simulations with linear and sigmoid trade-off functions. However, the results presented below hold for all three types of trade-off functions tested.

ASSORTATIVE MATING

Assortative mating is implemented as follows: instead of choosing a random male from the local population for mating, the females choose—with a certain probability (α)—a mate according to their Euclidean distance in phenotype space. This was implemented as a weighted lottery. The parameter α is the proportion of females mating nonrandomly and can be seen as the strength of assortative mating (O'Donald 1960). For female f in patch p the distance in phenotype space to male m is calculated as

$$distance_{f,m} = \sqrt{(\bar{d}_f - \bar{d}_m)^2 + (\bar{\rho}_f - \bar{\rho}_m)^2} \tag{5}$$

Table 1. Model parameters and meanings with tested values.

parameter	values	significance
K	100	habitat capacity
σ	0, 0.5, 1, 1.5	environmental stochasticity
ϵ	0, 0.02, 0.04, . . . , 0.2	random patch extinction probability
λ_0	2, 3, 4	fecundity
μ_0	0, 0.1, 0.2, . . . , 1.0	landscape-specific dispersal mortality
γ	0, 1, 2, . . . , 20	payoff, that is efficiency of investment into dispersal ability
α	0, 0.05, 0.1, 0.25, 0.3, 1.0	strength of assortative mating
d	*evolving* $\in [0, 1]$	emigration probability
ρ	*evolving* $\in [0, 1]$	relative investment in dispersal ability
x	*evolving* $\in \{0; 1\}$	dominance ($x{=}1$), recessivity ($x{=}0$)
m_1	0.001	mutation rate for life-history traits
Δ_m	0.1	mutation width for m_1
m_2	0.0001	mutation rate for dominance

with $\bar{d}$ and $\bar{\rho}$ being the phenotype of the individuals, that is incorporating dominance if evolved (see eq. 1).

SIMULATIONS

The allele values of the two evolving loci (d_1, d_2 and ρ_1, ρ_1) were initialized with random values drawn from a uniform distribution between zero and one. To allow the system to reach an equilibrium state, simulations were run for 10,000 generations. Typically, equilibrium was reached after a much shorter time span, that is within 2000 to 5000 time steps. For each parameter combination simulations were replicated 25 times. For an overview of the parameter space tested refer to Table 1.

For the systematic analysis of large ranges of parameter space, we used an index indicating the presence of dispersal polymorphisms: we computed Hartigan's Dip Test Statistic for Unimodality for the distribution of the emigration probability alleles (d). This statistic increases with increasing departure from unimodality (package "Diptest"; R Development Core Team 2010). Since the focal behavior here is the reduction of dispersal mortality, that is investment in increased dispersal ability, the figures do not show the trait $\bar{\rho}$ but the relative reduction of dispersal mortality calculated as $1 - e^{-\gamma\bar{\rho}}$ (see eq. 4).

Results

THE EVOLUTION OF DISPERSAL POLYMORPHISMS

A clear dispersal polymorphism evolved for a wide variety of parameter combinations. Figure 1A shows a typical example: while the alleles for dispersal propensity (d) and ability (ρ) showed a bimodal distribution, a trimorphism evolved in phenotype space due to heterozygous individuals. Of central influence for the evolution of polymorphisms is the payoff (γ, eq. 4), that is the

efficiency of investing into dispersal ability. Depending on the other parameters, deviations from the monomorphic state could evolve for intermediate values of the payoff parameter (Fig. 2A). Below $\gamma \leq 5$ (unprofitable and low payoff) a single dispersal phenotype evolved with low emigration probability ($\bar{d} < 0.4$ depending on the other parameters) and an accordingly small investment in dispersal ability ($\bar{\rho} \ll 0.05$). For the other extreme (ca. $\gamma > 18$; advantageous payoff) one single highly dispersive phenotype ($\bar{d} > 0.8$) evolved which invested heavily in dispersal ability ($\bar{\rho} > 0.15$).

Another factor of considerable influence is the external extinction probability (ϵ). Stable polymorphisms emerged for intermediate values (Fig. 2B).

Increasing dispersal mortality (μ_0) selected for polymorphic strategies (Fig. 2A,B). A similar effect was found for environmental stochasticity (σ): more interpatch variability led to polymorphisms even when the payoff was low (small values of γ). In general, fecundity (λ_0) had little influence on the evolution of dispersal dimorphisms.

These findings are robust regardless of the mode of inheritance implemented: if we assumed a linear relationship between genotype and phenotype, a phenotypic trimorphism evolved, while a clear bimodal distribution was found for both traits at the allele level (Fig. 1A). A dominant recessive mode of inheritance did not alter the results fundamentally: dominance always evolved for emigration probability (d) and led to a clear dimorphism at the phenotype level (Fig. 1B), while the underlying allele distribution did not change qualitatively. Nevertheless, note that the dispersal morph alleles became rarer. More exactly, dominance only evolved for alleles coding for high emigration probability, whereas nondispersive alleles evolved to be recessive. No dominance evolved for the relative investment in dispersal ability (ρ).
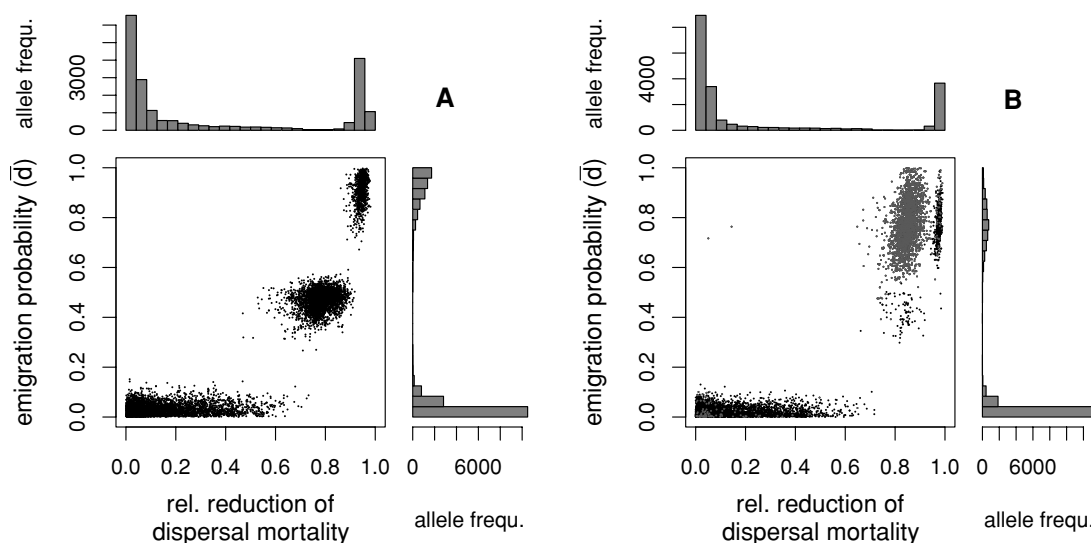
Figure 1. Evolution of dispersal polymorphisms under random mating ($\alpha = 0$). The scatter plots show phenotype space. Every point represents a diploid organism. The histograms show the allele distribution for both traits. Panel A shows results when we assumed intermediate inheritance (i.e., a linear relationship between genotype and phenotype): a clear polymorphism with homozygous dispersers and nondispersers as well as an intermediate type (heterozygous individuals) evolved. For panel B, dominance was allowed to evolve, which led to a dimorphism in phenotype space. The gray points indicate heterozygous individuals for emigration probability with a dominant allele. Due to mutations at the dominance locus, some heterozygous individuals still have an intermediate phenotype. Dominance only evolved for the emigration probability (*d*) and not for the locus determining the relative investment in dispersal ability (ρ). Scatter plots and histograms are based on 10,000 individuals randomly chosen from the last generation of 25 simulation repeats. Simulation parameters were : $\gamma = 12$, $\lambda_0 = 3$, $\sigma = 1.0$, $\mu_0 = 0.5$, $\epsilon = 0.05$.

THE ROLE OF ASSORTATIVE MATING AND PLOIDY

In contrast to our hypothesis and to existing suggestions (see introduction), assortative mating did not enhance the evolution of dispersal polymorphisms. On the contrary, with assortative mating only intermediate dispersal strategies evolved (Fig. 3A). This result was obtained regardless of the mode of inheritance. In addition to this, we could show that if assortative mating was introduced to the system after a stable polymorphism had been allowed to evolve ($t > 5000$), the polymorphism vanished (not shown). Note that already a small tendency for assortative mating (α) leads to a complete homogenization of the metapopulation: if more than one-fourth of all females mated assortatively ($\alpha > 0.25$), no dispersal polymorphism evolved in our simulations.

Qualitatively, we found the same result for the haploid (clonal) model (Fig. 3B). Although we scanned the parameter space as for the diploid model (results not shown), we did not find polymorphic dispersal strategies (the parameter values tested are listed in Table 1).

Discussion

It is intuitively clear that investment into dispersal ability should only evolve when environmental conditions favor the evolution of a sufficiently high level of dispersal. Basically, three evolutionary relevant forces influence dispersal propensity: dispersal mortal-ity (μ_0) selects against high emigration probabilities ($\bar{d}$) whereas random patch extinctions (ϵ) and environmental stochasticity (σ) have the opposite effect (Comins et al. 1980; Ronce et al. 2000; Poethke and Hovestadt 2002; Poethke et al. 2003). It is trivial that individuals will not invest into dispersal ability (low values for traits $\bar{d}$ and $\bar{\rho}$) when dispersal is not favored (low values for ϵ and high values for μ_0), especially because the two loci governing these features are genetically linked. An equally monomorphic evolutionary stable strategy evolves when dispersal is highly advantageous (high values for ϵ and low values for μ_0). Individuals under such conditions will heavily invest into dispersal ability (high values for traits $\bar{d}$ and $\bar{\rho}$).

Of course, a prerequisite for substantial investments into dispersal ability is a sufficiently high efficiency of the investment, that is, an advantageous payoff (γ). The steeper the trade-off function (eq. 4), the smaller the costs—in terms of fertility—become to achieve a certain reduction in dispersal risk. This explains why low efficiency, that is, a small payoff γ, favors monomorphic populations following a resident (or low-dispersal) strategy with no investment into dispersal ability. High efficiency (high values of γ) leads to monomorphic populations in which all individuals show relatively high emigration probabilities and large investment into dispersal ability.

For intermediate efficiencies (Fig. 2A) the dispersive phenotype still profits from the advantages of dispersal for example,
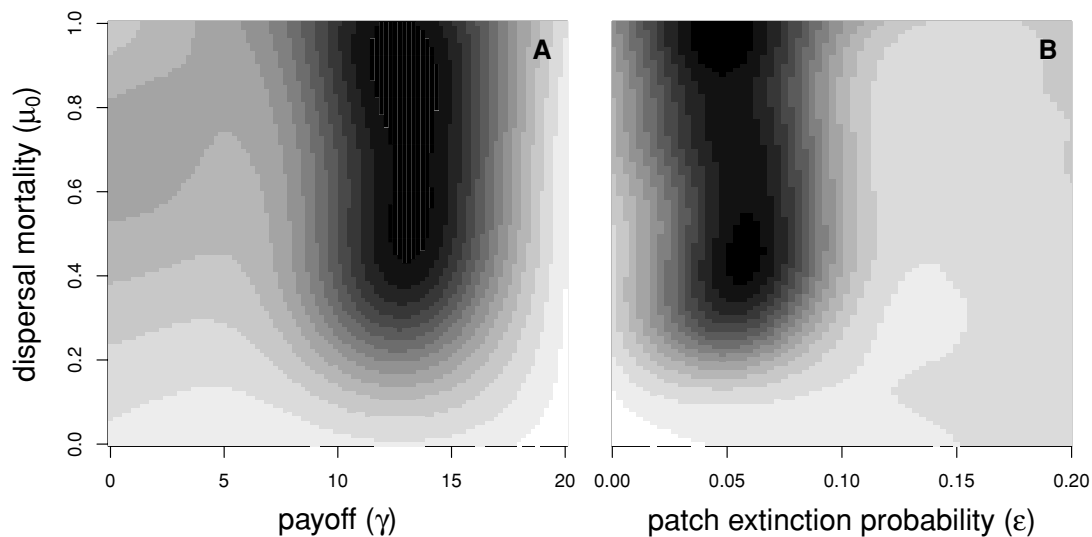
Figure 2. Evolution of dispersal polymorphisms under random mating ($\alpha = 0$) as a function of landscape-specific dispersal mortality (μ_0) and (A) the payoff, that is, the efficiency of investing in dispersal ability (γ) and (B) patch extinction probability (ϵ). As an index for the evolution of dispersal polymorphisms we used Hartigan's Dip Test Statistic for Unimodality. Darker colors indicate a stronger departure from unimodality (indication of polymorphism) in the distribution of the emigration probability (*d*). Note that the results are identical for the distribution of the relative investment in dispersal ability ρ. Each panel shows a thin-plate spline regression of 650 simulation results each with three repeats. Fixed model parameters were: $\sigma = 1.0$ (A, B); $\lambda_0 = 3.0$ (A, B); $\epsilon = 0.05$ (A); and $\gamma = 12$ (B).

reduced kin competition (Hamilton and May 1977; Poethke et al. 2007) or colonizing empty habitat patches (for reviews see Bowler and Benton 2005; Ronce 2007), while mitigating the associated costs of dispersal. By contrast, a nondispersive phenotype benefits from higher fertility, that is such individuals have a growth advantage in direct competition with the dispersive morphs. This allows

nondispersers to invade locally any population of dispersers. Yet, because the persistence of local populations is limited by patch extinctions, a purely resident strategy cannot persist. Thus, in a haploid system neither strategy is evolutionarily stable (Fig. 3B). However, in a diploid system with random mating heterozygotes with intermediate phenotypes are produced. This allows the
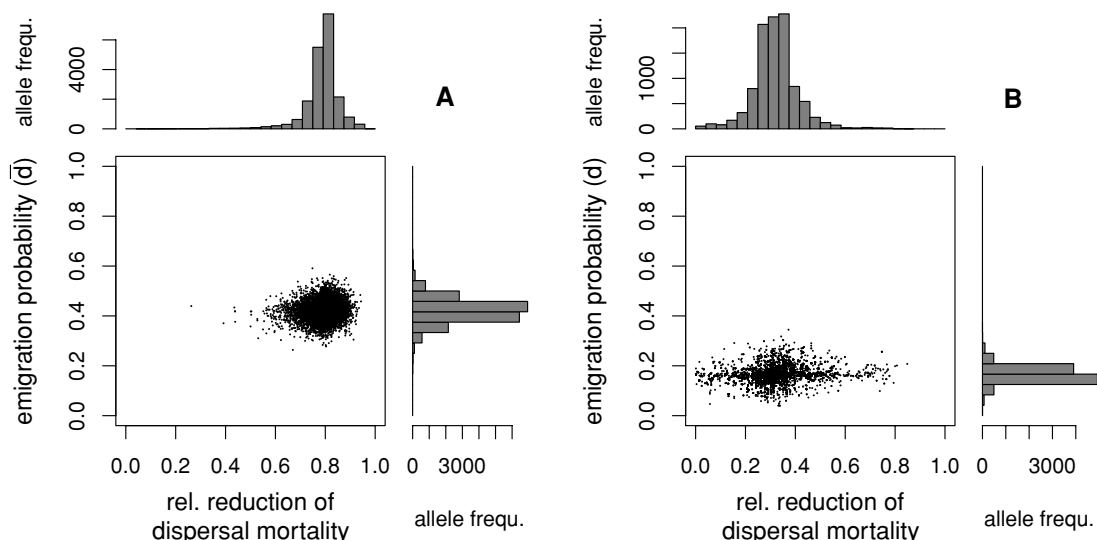

Figure 3. Evolution of dispersal strategies with assortative mating (panel A; $\alpha = 0.3$) and clonal reproduction (haploid individuals; panel B). No polymorphisms evolved under these assumptions. The scatter plot shows phenotype space. Every point represents a diploid organism after 10,000 generations of evolution. Here, 10,000 randomly chosen individuals from 25 simulation repeats are shown. The histograms visualize the allele distribution of both traits. For panel A, we assumed a linear relationship between genotype and phenotype. Note that the results are identical if dominance was assumed. Simulation parameters were : $\gamma = 12$, $\lambda_0 = 3$, $\sigma = 1.0$, $\mu_0 = 0.5$, $\epsilon = 0.05$.

resident haplotype (low values for d and ρ) to "hitch-hike" in heterozygous individuals together with the dispersive haplotype. Thus, it can persist even in unstable environments as long as there is a sufficiently high frequency of haplotypes for dispersive behavior. It is immediately clear that here selection is frequency dependent (Roff 1994), because a rising frequency of haplotypes for dispersiveness in the population increases the mobility as well as the advantage of the undispersive type in local competition.

At the same time, this example of genetic "hitch-hiking" explains why our results indicate that assortative mating does not favour the evolution of polymorphic strategies but destabilizes polymorphisms once evolved (Fig. 3A). Assortative mating in a population leads to a lack of heterozygotes and thus prevents nondispersive haplotypes from hitch-hiking on heterozygous individuals together with dispersive ones. Consequently, an intermediate phenotype that in itself represents the optimal compromise between fertility and investment into dispersal ability will evolve under such circumstances.

Note that some models of speciation come to similar conclusions (for a review see e.g., Ritchie 2007). However, the underlying mechanisms are distinctly different: Kirkpatrick and Nuismer (2004) argue that a widely accepted key assumption of speciation models is that all individuals have equal reproductive success. Yet, obviously in nature rare phenotypes are penalized by assortative mating, because they are less likely to find a mate than very common phenotypes. Thus, assortative mating may counteract the evolution of polymorphic strategies. By contrast, in our model assortative mating penalizes the more frequent, nondispersive haplotype.

As Parvinen and Metz (2008) note, the evolutionary stable dispersal rate in haploid and diploid models may be considerably different in quantitative and qualitative terms. For our model, this is in part explained above. Note that the evolutionary stable emigration probability for the haploid model (Fig. 3B) is considerably smaller than in the other simulations. This is due to the fact that the effective population size in the diploid model is considerably smaller than in the haploid case, because we used the same values for carrying capacity ($K = 100$) while omitting the males. In the diploid model, especially with nonrandom mating, an important number of males will not be able to reproduce. Such an effect and its influence on the evolutionary stable dispersal rate has been quantified by Gros et al. (2009) for a different system of nonrandom mating (harem formation). Furthermore, the effective population size in the sexual system may be further diminished due to skewed sex-ratios after recolonization events. In general, such smaller population sizes select for higher dispersal rates (Travis and Dytham 1998).

The evolution of dominance in our simulations (Fig. 1B) indicates that the intermediate (heterozygote) strategy is less fit than both extreme morphs (Pimm 1979; Udovic 1980).

Dominance prevents the expression of the intermediate phenotype (Van Dooren 1999) without destroying the polymorphism. Now the population consists of two distinct phenotypes. Obviously, dominance is an effective mechanism allowing the maintenance of alternative strategies. Note that it is always the allele for dispersiveness that becomes dominant. This is due to the fact that the undispersive genes need the dispersive type to reach new patches. As dominant alleles for the dispersive type are more "effective" in realizing dispersal, the dispersal morph alleles become rarer with dominance (Fig. 1B). The same is true for the investment into dispersal ability. Since the relation between investment and dispersal mortality reduction is nonlinear (eq. 4), the heterozygotes achieve nearly the same relative reduction in dispersal mortality compared to homozygous dispersers (Fig. 1B).

In their study on the wing dimorphic planthopper *P. dolus* Langellotto et al. (2000) demonstrate that a trade-off between flight capability and reproduction exists in this species. Furthermore, the authors show that this trade-off can not only be found in females but also in males. In addition to these findings, the authors present some evidence for nonrandom mating: assortment seems to be based on wing form. Yet, the results obtained from single-choice preference experiments overall only suggest a trend. The authors nevertheless do conclude that individuals of *P. dolus* mate assortatively.

Our model does not support the hypothesis that assortative mating plays a role in the establishment or stabilization of trade-off-driven dispersal polymorphisms. Therefore, either Langellotto et al. (2000) overrated the significance of their results or the proportion of assortatively mating individuals in the examined population was very small. Our model would support the latter interpretation because it predicts the evolution of dispersal polymorphisms as long as less than ca. 25% of the individuals mate assortatively ($\alpha < 0.25$).

In summary, our results suggest that, in contrast to dominance, assortative mating is not a mechanism relevant for the maintenance of dispersal polymorphisms. Furthermore, we were able to underline the importance of frequency-dependent selection for the evolution of dispersal polymorphisms due to fitness trade-offs. In our model, the local patch extinction rate is a key component favoring dispersal polymorphisms. We thus confirm the significance of turnover due to local extinctions (Roff 1994; King and Roff 2010).

Our findings underline the importance of carefully choosing an appropriate relationship between genotype and phenotype when modeling dispersal evolution. A majority of theoretical studies assume a simple clonal form of reproduction (e.g., Doebeli and Ruxton 1997; Mathias et al. 2001; Bonte et al. 2010). Exceptions can be found when sex-specific strategies are investigated (e.g., Perrin and Mazalov 2000; Bonte and de la Peña 2009). Here, we demonstrate that such assumptions may strongly alter model

predictions, quantitatively as well as qualitatively (see also Parvinen and Metz 2008).

Finally, our work leads to testable hypotheses. (1) The evolution of trade-off-driven dispersal polymorphisms is limited to spatiotemporally variable metapopulations (Hanski 1999) or to expanding ranges (Phillips et al. 2010). In the latter case spatial selection has the same consequences as spatio-temporal variation, that is patch turnover, in equilibrium metapopulations (Duckworth 2008). (2) Trade-off-driven dispersal polymorphisms should only be found in species without (strong) assortative mating. In general, dimorphisms at the phenotype level can be favored by the evolution of dominance.

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LITERATURE CITED

Bengtsson, B. O. 1978. Avoiding inbreeding–at what cost. J. Theor. Biol. 73:439–444.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Chapman & Hall, London.

Bonte, D., and E. de la Peña. 2009. Evolution of body condition-dependent dispersal in metapopulations. J. Evol. Biol. 22:1242–1251.

Bonte, D., T. Hovestadt, and H. J. Poethke. 2010. Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. Oikos 119:560–566.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol. Rev. 80:205–225.

Burton, O. J., B. L. Pillips, and J. M. J. Travis. 2010. Trade offs and the evolution of life-histories during range expansion. Ecol. Lett. 13:1210–1220.

Cadet, C., R. Ferrière, J. A. J. Metz, and M. van Baalen. 2003. The evolution of dispersal under demographic stochasticity. Am. Nat. 162:427–441.

Clarke, B. C. 1979. Evolution of genetic diversity. Proc. R. Soc. Lond. B 205:453–474.

Cockerham, C. C., T. Prout, S. S. Young, and P. M. Burrows. 1972. Frequency-dependent selection in randomly mating populations. Am. Nat. 106:493–515.

Cody, M. L., and J. M. Overton. 1996. Short-term evolution of reduced dispersal in island plant populations. J. Ecol. 84:53–61.

Comins, H. N., W. D. Hamilton, and R. M. May. 1980. Evolutionarily stable dispersal strategies. J. Theor. Biol. 82:205–230.

Crespi, B. J. 1989. Causes of assortative mating in arthropods. Anim. Behav. 38:980–1000.

Dieckmann, U., and M. Doebeli. 1999. On the origin of species by sympatric speciation. Nature 400:354–357.

Doebeli, M. 1996. A quantitative genetic competition model for sympatric speciation. J. Evol. Biol. 9:893–909.

Doebeli, M., and U. Dieckmann. 2003. Speciation along environmental gradients. Nature 421:259–264.

Doebeli, M., and G. D. Ruxton. 1997. Evolution of dispersal rates in metapopulation models: branching and cyclic dynamics in phenotype space. Evolution 51:1730–1741.

Duckworth, R. A. 2008. Adaptive dispersal strategies and the dynamics of a range expansion. Am. Nat. 172:S4–S17.

Gandon, S., and Y. Michalakis. 1999. Evolutionarily stable dispersal rate in a metapopulation with extinctions and kin competition. J. Theor. Biol. 199:275–290.

Gavrilets, S. 2003. Models of speciation: what have we learned in 40 years? Evolution 57:2197–2215.

Gros, A., H. J. Poethke, and T. Hovestadt. 2009. Sex-specific spatio-temporal variability in reproductive success promotes the evolution of sex-biased dispersal. Theor. Popul. Biol. 76:13–18.

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

Hanski, I. 1999. Metapopulation ecology. Oxford Univ. Press Inc., Oxford, UK.

Harrison, R. G. 1980. Dispersal polymorphisms in insects. Annu. Rev. Ecol. Syst. 11:95–118.

Hill, J. K., C. D. Thomas, and D. S. Blakeley. 1999. Evolution of flight morphology in a butterfly that has recently expanded its geographic range. Oecologia 121:165–170.

Holt, R. D., and M. A. McPeek. 1996. Chaotic population dynamics favors the evolution of dispersal. Am. Nat. 148:709–718.

Itô, Y. 1989. The evolutionary biology of sterile soldiers in aphids. Trends Ecol. Evol. 4:69–73.

King, E. G., and D. A. Roff. 2010. Modeling the evolution of phenotypic plasticity in resource allocation in wing-dimorphic insects. Am. Nat. 175:702–716.

Kirkpatrick, M., and S. L. Nuismer. 2004. Sexual selection can constrain sympatric speciation. Proc. R. Soc. Lond. B 271:687–693.

Kubisch, A., T. Hovestadt, and H. J. Poethke. 2010. On the elasticity of range limits during periods of expansion. Ecology 91:3094–3099.

Langellotto, G. A., R. F. Denno, and J. R. Ott. 2000. A trade off between flight capability and reproduction in males of a wing-dimorphic insect. Ecology 81:865–875.

Leimar, O., and U. Norberg. 1997. Metapopulation extinction and genetic variation in dispersal-related traits. Oikos 80:448–458.

Levin, S. A., and H. C. Muller-Landau. 2000. The evolution of dispersal and seed size in plant communities. Evol. Ecol. Res. 2:409–435.

Mathias, A., E. Kisdi, and I. Olivieri. 2001. Divergent evolution of dispersal in a heterogeneous landscape. Evolution 55:246–259.

McPeek, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. Am. Nat. 140:1010–1027.

O'Donald, P. 1960. Assortive mating in a population in which two alleles are segregating. Heredity 15:389–396.

Parvinen, K. 2002. Evolutionary branching of dispersal strategies in structured metapopulations. J. Math. Biol. 45:106–124.

Parvinen, K., and J. A. J. Metz. 2008. A novel fitness proxy in structured locally finite metapopulations with diploid genetics, with an application to dispersal evolution. Theor. Popul. Biol. 73:517–528.

Perrin, N., and V. Mazalov. 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. Am. Nat. 155:116–127.

Phillips, B. L., G. P. Brown, and R. Shine. 2010. Life-history evolution in range-shifting populations. Ecology 91:1617–1627.

Pimm, S. L. 1979. Sympatric speciation—simulation-model. Biol. J. Linn. Soc. 11:131–139.

Poethke, H. J., C. Dytham, and T. Hovestadt, 2011. A metapopulation paradox: partial improvement of habitat may reduce metapopulation persistence. Am. Nat. *In press*.

Poethke, H. J., and T. Hovestadt. 2002. Evolution of density-and patch-size-dependent dispersal rates. Proc. R. Soc. Lond. B 269:637–645.

Poethke, H. J., T. Hovestadt, and O. Mitesser. 2003. Local extinction and the evolution of dispersal rates: causes and correlations. Am. Nat. 161:631–640.

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

R Development Core Team. 2010. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at http://www.R-project.org. ISBN 3-900051-07-0.

Ravigné, V., I. Olivieri, S. C. Gonzalez-Martinez, and F. Rousset. 2006. Selective interactions between short-distance pollen and seed dispersal in self-compatible species. Evolution 60:2257–2271.

Reznick, D. 1985. Costs of reproduction—an evaluation of the empirical evidence. Oikos 44:257–267.

Ritchie, M. G. 2007. Sexual selection and speciation. Annu. Rev. Ecol. Evol. Syst. 38:79–102.

Roff, D. A. 1994. Habitat persistence and the evolution of wing dimorphism in insects. Am. Nat. 144:772–798.

———. 2002. Life history evolution. Sinauer Associates, Sunderland, MA.

Roff, D. A., and D. J. Fairbairn. 1991. Wing dimorphisms and the evolution of migratory polymorphisms among the insecta. Am. Zool. 31:243–251.

———. 2001. The genetic basis of dispersal and migration, and its consequences for the evolution of correlated traits. Pp. 191–202 in J. Clobert, E. Danchin, A. A. Dhondt and J. D. Nichols, eds. Dispersal. Oxford Univ. Press, Oxford, UK.

———. 2007. The evolution of trade offs: where are we? J. Evol. Biol. 20:433–447.

Roff, D. A., S. Mostowy, and D. J. Fairbairn. 2002. The evolution of trade offs: testing predictions on response to selection and environmental variation. Evolution 56:84–95.

Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. Annu. Rev. Ecol. Evol. Syst. 38:231–253.

Ronce, O., F. Perret, and I. Olivieri. 2000. Evolutionarily stable dispersal rates do not always increase with local extinction rates. Am. Nat. 155:485–496.

Tanaka, S., and Y. Suzuki. 1998. Physiological trade offs between reproduction, flight capability and longevity in a wing-dimorphic cricket, *Modicogryllus confirmatus*. J. Insect Physiol. 44:121–129.

Travis, J. M. J., and C. Dytham. 1998. The evolution of dispersal in a metapopulation: a spatially explicit, individual-based model. Proc. R. Soc. Lond. B 265:17–23.

———. 1999. Habitat persistence, habitat availability and the evolution of dispersal. Proc. R. Soc. Lond. B 266:723–728.

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

Udovic, D. 1980. Frequency-dependent selection, disruptive selection, and the evolution of reproductive isolation. Am. Nat. 116:621–641.

Van Dooren, T. J. M. 1999. The evolutionary ecology of dominance-recessivity. J. Theor. Biol. 198:519–532.

Winchell, R., H. Dingle, and C. D. Moyes. 2000. Enzyme profiles in two wing polymorphic soapberry bug populations (*Jadera haematoloma*: Rhopalidae). J. Insect Physiol. 46:1365–1373.

Wright, S. 1921. Systems of mating. iii. assortative mating based on somatic resemblance. Genetics 6:144–161.

Yukilevich, R. 2005. Dispersal evolution in fragmented habitats: the interplay between the tendency and the ability to disperse. Evol. Ecol. Res. 7:973–992.

Zera, A. J., and R. F. Denno. 1997. Physiology and ecology of dispersal polymorphism in insects. Annu. Rev. Entomol. 42:207–230.

Zera, A. J., and S. Mole. 1994. The physiological costs of flight capability in wing-dimorphic crickets. Res. Popul. Ecol. 36:151–156.

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