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Parent-Offspring Conflict and the Evolution of Dispersal Distance

Jostein Starrfelt[1,*] **and Hanna Kokko**[1,2]

1. Laboratory of Ecological and Evolutionary Dynamics, Department of Biological and Environmental Sciences, University of Helsinki, P.O. Box 65, Viikinkaari 1, FIN-00014 Helsinki, Finland; 2. Research School of Biology (Botany and Zoology), Australian National University, Canberra, Australian Capital Territory 0200, Australia

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ABSTRACT: Parent-offspring conflict emerges in many different contexts, but a rarely emphasized perspective is that of space as a resource that is allocated or acquired through dispersal. Early theoretical work has shown that there are different optima in rates of dispersal between parents and offspring. Here we examine this principle when space is explicitly modeled and dispersal is achieved through a dispersal kernel. We find a consistent pattern that selection favors longer dispersal distances under maternal control of dispersal (e.g., maternal tissue surrounding a seed) compared with scenarios where offspring themselves control dispersal (as in many animals). Intriguingly, offspring control leads to better resource utilization (higher habitat occupancy) in equilibrium scenarios than does maternal control. In contrast, in species that expand their ranges, maternal control of dispersal initially leads to faster range expansion. If there is evolutionary potential for dispersal kernels to change at the leading edge of a population, this difference vanishes quickly during an invasion because offspring-controlled dispersal evolves faster and catches up with scenarios involving maternal control. There is thus less conflict in nonequilibrium scenarios. In invasive scenarios with an evolving kernel shape, disruptive selection against intermediate distances can make the kernel not only fat-tailed but also bimodal.

Keywords: dispersal evolution, dispersal distance, parent-offspring conflict, dispersal kernel, simulation model, spatially explicit.

Introduction

Dispersal of individuals from their birthplace is a ubiquitous aspect of the natural world. It has wide-reaching implications for the individual, its conspecific competitors, and the population as a whole. In understanding the evolution of dispersal, it is important to recognize that individual-level selection on dispersal and population performance may be at odds. Intriguingly, for example, there is no particular guarantee that evolved dispersal rates maximize the spread or persistence of populations (Hamilton and May 1977; Kokko and López-Sepulcre 2006). The reason for conflict between individual-level selection and population-level performance is that dispersal is perilous: the behavior of moving through unknown territories entails mortality risks, and individuals can thus be selected to avoid it, unless sufficiently counterbalanced by dispersal-favoring mechanisms such as kin competition (Hamilton and May 1977), inbreeding avoidance (Bengtsson 1978), or spatiotemporal variability in resources (Van Valen 1971). Populations, on the other hand, depend on dispersal, without which full utilization of resources in the environment would be impossible. Depending on how strongly each of the individual-level mechanisms favors dispersal, we may thus end up with species with very different potentials for expanding their ranges (e.g., Bohning-Gaese et al. 2006) or for maintaining their populations in increasingly fragmented habitats (Ozinga et al. 2009).

The evolution of dispersal strategies has received great attention, but only recently has it become clear that dispersal can evolve fast and become spatially heterogeneous in a spatially structured world (Thomas et al. 2001; Hanski et al. 2004; Haag et al. 2005; Cheptou et al. 2008; Phillips et al. 2008). In particular, the leading edge of a moving population front can be composed of individuals whose dispersal-related genotypes differ from others (Travis and Dytham 2002; Hughes et al. 2007; Darling et al. 2008; Phillips et al. 2008). Understanding the selective pressures for and against dispersal is thus particularly important when environments change, for example, when a species enters a new potentially habitable area (Hastings et al. 2005).

In this context, an old result has received little attention. Dispersal entails conflict not only between the individual-level good (fitness) and the "greater good" (population-level measures of success such as spread or persistence) but also between related individuals who interact locally (Trivers 1974; Hamilton and May 1977; Motro 1983). While several models have investigated the effects of kin interactions on dispersal evolution (e.g., Comins 1982;

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[*] Corresponding author; e-mail: jostein.starrfelt@helsinki.fi.

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Gandon and Rousset 1999; Rousset and Gandon 2002), they usually do not comment on an intriguing consequence of conflict: it matters whose genotype dictates whether and how far progeny disperse. When investigating the evolution of dispersal in higher plants, it is the genome of the parent plant that, through the development of the maternal tissue surrounding the fertilized egg, produces the phenotype involved in dispersal. However, in most mobile animals, it is more likely that dispersal strategies (assuming they are under some genetic influence) are primarily determined by the genotype of the dispersing animal. The matter is more complex than a simple plant-animal comparison, however, because behavioral interactions between animals can create plantlike scenarios too, such as parents evicting their offspring from local groups (for an example, see Sarno et al. 2003).

Motro (1982*a*, 1982*b*, 1983) developed simple models of the evolution of optimal dispersal rates of progeny, in which the optimal rate of dispersal from a natal patch was different for dispersal under parental versus offspring control. In his model, optimal dispersal rates were lower when the genotype of the dispersing individual determined the probability of leaving a patch (i.e., the individual controls its own strategy) than when the genotype of a parent determined the probability of offspring leaving. This shows that there is potential for parent-offspring conflict (i.e., a battleground; see Godfray 1999) in the evolution of dispersal rates.

Motro's (1982*a*, 1982*b*, 1983) work is rooted in the early tradition of dispersal modeling, where dispersal is modeled as a single rate, or probability, of moving. In these models, individuals have some propensity to enter a global disperser pool or to leave the natal patch for a randomly chosen different patch. All patches are connected in the same way, making the spatial dimension implicit. This global dispersal is alleviated in some models that have investigated the evolution of local dispersal (such as in stepping-stone models; Comins 1982; Gandon and Rousset 1999). In fully spatially explicit contexts, however, it is more appropriate to consider that individuals are assumed to exhibit a dispersal kernel (Travis and French 2000; Hovestadt et al. 2001; Ronce et al. 2001; Murrell et al. 2002; Rousset and Gandon 2002). This modeling approach specifies the probability distribution that the individual moves a given distance, and this distribution—the kernel—can be under selection (for a review of modeling approaches in plant ecology, see Levin et al. 2003). This is important for realism in spatially explicit contexts because long-distance dispersers can be disproportionately important as founders of new populations (e.g., Muller-Landau et al. 2003). It is also of importance in the context of range expansion and species invasions because global dispersal rates would not capture the spatial invasion of new areas.

Here our aim is to incorporate the early insight of parent-offspring conflict in models of spatially explicit dispersal evolution and investigate the population consequences of maternal versus offspring control of dispersal. The potential for parent-offspring conflict in dispersal rate is extreme in the context modeled by Motro (1983), where the offspring either stay in the same patch as the parents or disperse randomly to any other patch. We will investigate whether conflicts over dispersal also play a role when the distance dispersed varies continuously in a spatially explicit setting. We do this by first presenting a verbal model of how such a conflict might be envisioned and then constructing a spatially explicit simulation model for a more rigorous analysis.

Why Should a Parent Prefer a Different Offspring Dispersal Rule than an Offspring?

The idea of parent-offspring conflict was introduced by Trivers (1974), who showed that there can be different optima in the distribution of some investment or resource in the offspring for the parent and the offspring itself. His original example focused on the parental investment of weaning and timing of independence. Parents favor a different length of weaning and timing of independence (i.e., resource allocation) than an individual offspring would prefer. There exists a battleground for $rc < b < c$ (or $r < b/c < 1$), where r is the relatedness between (two) offspring, b is the benefit for the focal offspring in usurping a given amount of extra parental investment, and c is the cost to the sibling of being denied this (parental) investment. So if $b > c$, then it will be in both the parent's and the focal offspring's interest to divert more resources toward the focal individual, but when $rc < b < c$, it will be in the offspring's interest but not in the parent's (or the other offspring's).

How does this principle play out in dispersal evolution? Assume that a parent has produced a given number of offspring. Parent-offspring conflict can exist over allocating resources between them. In a dispersal context, the resources could be the potential breeding patches for the next generation. Assuming that only a limited number of individuals can breed in any patch (i.e., local competition), there is the incentive for the parent to increase the number of patches offspring are dispersed to as the number of offspring increases so higher clutch sizes will favor a wider dispersal kernel. The parent maximizes its inclusive fitness when its offspring compete more with less related individuals than with siblings. This is the basic kin selection argument for the evolution of dispersal in absence of (abiotic) heterogeneity and selection for avoidance of inbreeding (Hamilton and May 1977).

How does the offspring's perspective differ from this? Avoidance of kin competition applies here too, but if there is a cost to dispersal such that the mortality risk of the dispersers increases as the distance traversed increases (travel cost), then each individual offspring would prefer to be the one that encounters the least mortality risk (by dispersing less far than the average sibling). In kin selectionist words, under maternal control, the actor (mother) values all of her offspring equally, whereas under offspring control, the actor (the individual offspring) always values itself more than its siblings (Frank 1986, 1998; Taylor 1988).

Two Models of Dispersal Distance Evolution

We here develop two models to investigate the potential for parent-offspring conflict in the evolution of dispersal distance. The first, simpler model consists of individuals whose dispersal trait is governed by a one-locus diploid system, and it determines the mean of an exponential dispersal kernel. To alleviate the somewhat arbitrary assumption of an exponential dispersal kernel, we thereafter construct a more complex model in which the dispersal kernel is controlled by 10 loci, where each locus determines the probability of moving a certain distance. This allows the kernel to evolve more freely, including fat-tailed distributions (Kot et al. 1996). In both models, we use a lattice landscape, with generations following each other in discrete time. We focus here on comparing evolutionary and population dynamic consequences of two cases, when the dispersal distance of offspring is determined by (i) the mother's genotype and (ii) the offspring's genotype.

The following assumptions give the rules of the models in detail. Apart from the implementation of the dispersal kernel and time until expansion, the same model assumptions apply for both models.

Space

Dispersal evolution occurs in a lattice consisting of $n \times m$ cells. Space is not uniform; instead, each cell is a patch that is either habitable or not habitable. If a patch is unhabitable, all individuals landing there are discarded. The lattices are randomly created with differences in level of patch availability (p_A denotes the fraction of habitable patches). The height (n) of the lattices varies ($n =$ 10–20) across simulations but is fixed within each run. During an initial stationary phase, lattice width is fixed to equal its height (resulting in a square lattice where $m_{\text{stationary}} = n =$ 10–20). After a given number of generations, the lattice is extended in the eastward direction ($m_{\text{expansion}} = 400$) to simulate the evolutionary dynamics of dispersal distance during a range expansion. The boundaries are wrapped in all directions in the stationary phase to avoid edge effects (if an individual disperses off the lattice due east, it will reenter from west), whereas in the expansion phase, only the northern and southern boundaries remain wrapped. This is to be able to follow a front of a population expanding its range. During the expansion phase, individuals dispersing off the lattice in the east-west direction are reflected in the boundary just crossed, while those that disperse off the lattice in the north-south direction reenter from the opposite direction.

Reproduction

At each time step, one female within each habitable patch is randomly selected and becomes the sole breeding female in this patch. If there is no female, there is no breeding in this patch. To avoid confounding our results with mate limitation, we assume that all breeding females mate with the closest male (in Euclidean distance), whether or not this male is in the same patch. Each breeding female gives birth to a number of offspring (B), identical for all females. The sex of each offspring is randomly determined. After giving birth, all individuals of the parental generation die; thus, we simulate nonoverlapping generations. This also ensures that there is no competition directly between parents and offspring, only competition between kin within one generation.

Dispersal and the Genetic System

Model 1: The Exponential Kernel. The one-locus diploid genetic system specifies an exponentially distributed dispersal kernel. The alleles have real numerical values larger than 0, and their mean determines the kernel. Thus, if the genotypic value (i.e., the average of the two alleles) for an individual is z_i, then the probability density function of the dispersal kernel is

$$\frac{1}{z_i}\exp\left[-\left(\frac{1}{z_i}\right)d\right]. \tag{1}$$

This distribution has mean z_i, and d denotes the distance drawn from the kernel.

Model 2: The Evolving Kernel Shape. In our second model, the shape of the dispersal kernel is not set in advance. Instead, each individual possesses 10 unlinked diploid loci with allelic values constrained between 0 and 1. The dispersal kernel is implemented as a probability mass function over integer distances of 0–9 units. An individual will disperse d units with the probability

$$\Pr(d = i - 1) = \frac{z_i}{\sum_{j=1}^{j=10} z_j}, \qquad (2)$$

where z_i is the sum of the two allelic values at locus i. Equation (2) describes a normalizing procedure that ensures that the loci scale to form a proper probability mass function and that the shift $(i - 1)$ occurs because the first locus determines the probability of not dispersing at all (i.e., a distance of 0). Thus, the probability of moving d units is determined by the sum of the alleles at locus $d + 1$ divided by the sum of the allelic values at all loci. We analyze the output of this model as dispersal rate $(\Pr(d > 0))$ and mean dispersal distance, conditional on dispersing (as eq. [2] above, with sum from 2 to 10 in the denominator).

We distinguish between two cases in both models. In case i, dispersal is under maternal control; thus, offspring disperse according to the dispersal kernel specified by their mother's genotype. In case ii, dispersal is determined by the genotype of the offspring themselves, and the distances dispersed are drawn from each individual's probabilistic dispersal kernel, specified by its own trait. So in case i, all offspring of a mother draw different distances dispersed from the same distribution, and in case ii, they draw different distances drawn from different distributions. In both cases, the angle of dispersal is randomly and independently chosen (uniform distribution for any angle). The postdispersal locations of the offspring are rounded to the accuracy of the lattice cell structure, meaning that short distances drawn from the kernel lead to philopatry.

Additionally, we use two different mutation structures in both models. The first type of mutation is global (or large): each mutation leads to a new allelic value drawn from the possible ranges in the two models (see "Parameter Settings"). In the second type, mutational steps are small, so the new allelic value is within ± 0.1 allelic units of the original value. We use both of these regimes because they have differential effects on the two types of selective pressures we are interested in. As outlined below, we investigate a stable selective pressure in a population within a fixed range and a changed selective pressure in an expanding population. Large mutations will, in the stationary phase, compromise the accuracy of the resulting traits being close to their optimal values, increasing the mutational load. We therefore perform most of the analysis on the model outputs from the stationary phase only with local mutations. However, large mutations will also elevate the genetic variability in the population, allowing it to respond more easily to the ephemeral selection pressure the front will experience during an invasion. Thus, the selective pressures acting under nonequilibrial expanding conditions become more easily visible when assuming large mutations.

We also impose a mortality risk for dispersal, according to an exponential distribution denoting the probability of surviving the dispersal phase as a function of actual distance traversed. We denote risk with M_{50}, which indicates the distance for which there is a 50% survival probability. Additionally, we assume that individuals can land in unhabitable patches where they cannot produce progeny. Because we allow no new dispersal attempt for these individuals, habitat heterogeneity creates an additional risk for dispersers.

Parameter Settings

In the exponential kernel model, we limit the possible allelic values of dispersal distance to real numbers between 0 and 8. In the second model with evolving dispersal kernel shape, the allelic values are real numbers between 0 and 1, and there is no linkage between the loci. Populations are initiated by randomly placing in the habitable patches a number of individuals equal to 10 times lattice height $(10 \times n)$. The sex of each individual is randomly assigned. In the first model, their dispersal alleles are drawn from a uniform distribution over all possible allelic values. In the second model, to avoid early extinctions, individuals in the initial population were given allelic values of 1 for both alleles at the two first loci (determining the probability of not moving and moving 1 unit, respectively). Thereafter, in every generation, offspring inherit at each locus one allele from their mother and one from their father. For each of the alleles that an offspring inherits, there is a mutation probability μ.

We ran 5,000 simulations with different parameter settings, varying patch availability ($p_A = 0.23$–1), offspring number ($B = 8$–20), survival during dispersal ($M_{50} =$ 0.5–20), mutation probability ($\mu = 0.001$–0.02), and width of lattice ($n = 10$–20), as well as mutation type. We used a Latin hypercube sampling design (McKay et al. 1979) over these six parameters. All these parameter settings were applied to both maternal and offspring control over dispersal, leading to 10,000 simulations for each model. Visual inspection of the convergence of the evolutionary trajectories in unreported runs led us to choose 2,000 (10,000) generations for the stationary phase for model 1 (model 2).

Results

Who Controls Dispersal Distance Affects the Evolutionary Outcome

Our simulation results show clearly that there is potential for parent-offspring conflict in the evolution of dispersal distance in a spatially explicit setting. In the exponential kernel model, the evolved dispersal distance was almost without exception shorter if offspring rather than mother genotypes controlled the dispersal kernel (fig. 1*A*). The second model, with an evolving kernel shape, showed a similar result: when compared with maternal control, offspring control produced a higher probability for no dispersal (i.e., drawing a distance of 0) and lower probabilities for moving longer distances (fig. 1*B*).

We performed multiple linear regressions (see table 1) to investigate the effects of the different parameters on the evolved dispersal strategies and the level of conflict. Except for a small negative effect of increased size of the lattice in which the population resided, all parameters had a positive effect on the distances dispersed, with a fixed dispersal kernel shape (model 1). An increase of availability of patches, however, had a stronger effect under offspring control, which led to a lower level of conflict under high resource availability and more conflict in sparse landscapes.

Alleviating the assumption of a fixed shape of the dispersal kernel allowed us to analyze both the rate of dispersal and the distance dispersed, given that an individual disperses (see table 1, model 2). Higher patch availability, number of offspring, and survival during dispersal led to higher dispersal rates under both controls but diminished the conflict over whether to disperse. A more complex pattern occurred with dispersal distance, conditional on dispersing; higher survival during dispersal still selected for longer distances and exhibited less conflict, but larger number of offspring and higher patch availability led to shorter distances and higher level of conflict.

Conflict over Dispersal Has Population-Level Effects

The observed differences in resulting dispersal distance under maternal and offspring control also had population-level consequences (see fig. 2). Under maternal control, most individuals disperse farther than under offspring control. Therefore, the population as a whole experiences higher mortality due to dispersal under maternal control than if offspring control dispersal. A better use of spatial resources is achieved if dispersal is controlled by offspring: in the simulations for the stationary phase, patch occupancy was typically higher when offspring controlled dispersal (52% [vs. 34%] of all simulations in model 1 had higher [vs. equal] occupancy under offspring control; these numbers were 58% [vs. 28%] for model 2). This general pattern of occupancy, together with lower levels of mortality as a result of shorter dispersal distances, means that the discrepancy between individual-level fitness (which is what is maximized in our simulations) and population-level performance is larger if dispersal is under maternal control.

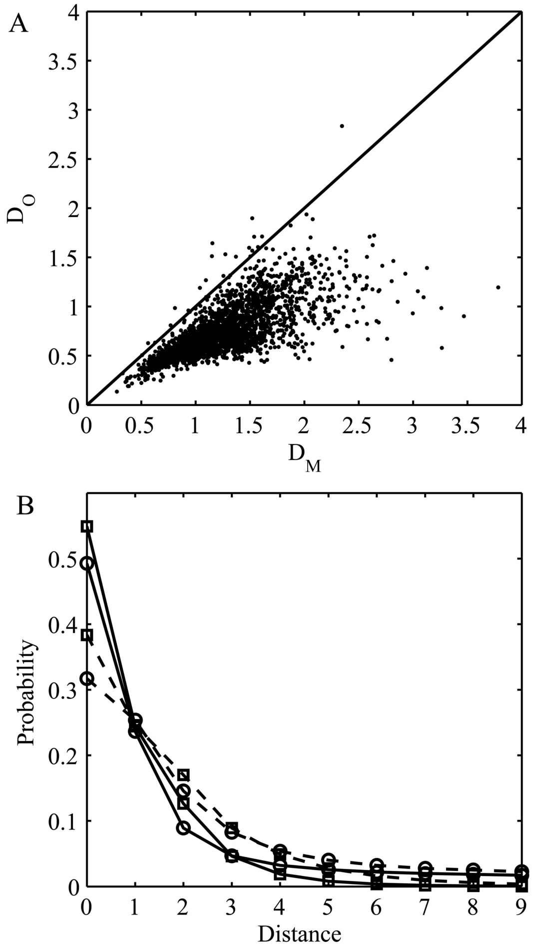

Figure 1: *A*, Model 1. The mean dispersal distance after 2,000 generations in the exponential kernel model, for all simulations where neither the maternally controlled nor the offspring-controlled case resulted in extinction (2,491 out of 2,500 parameter settings), with small mutational steps. The *X*-axis shows the mean dispersal distance under maternal control (D_M) and the *Y*-axis shows the mean dispersal distance under offspring control (D_O), with the exact same parameter settings and lattice used. Almost all points fall under the diagonal, indicating that under maternal control a longer dispersal distance is favored. *B*, Resulting dispersal kernels from both models and both controls. To aid comparison, the outcome of model 1 (*squares*) is summarized as a kernel depicting the number of individuals moving between 0 and 9 cells from their birthplace (model results based on small mutational steps). Offspring control is depicted with solid lines (*circles* = model 2) and maternal control with dashed lines. There are some differences between the models, but differences between control are consistent across models.

Conflict Is Reduced during Range Expansions

Our range expansion simulations from the exponential kernel model showed that evolution favors increased dispersal distances in the invasion front. This spatial effect occurs under both maternal and offspring control of dis-

Table 1: Effects of the model parameters on the evolved dispersal strategies and the level of conflict in both models, calculated performing a multiple linear regression

	Model 1: fixed kernel shape			Model 2: freely evolving kernel					
				Dispersal rate			Dispersal distance		
	D_M	D_O	D_M/D_O	Pr(M)	Pr(O)	Pr(M)/Pr(O)	D_M	D_O	D_M/D_O
Patch availability (P_A)	↑	↑	↓	↑	↑	↓	↓	↓	↑
Number of offspring (B)	↑	↑	↑	↑	↑	↓	↓	↓	↑
Survival during dispersal (M_{50})	↑	↑	↑	↑	↑	↓	↑	↑	↓
Mutation probability (μ)	↑	↑	↑	↑	↑	↓	↑	↑	↑
Mutation type	↑	↑	↑	↑	↑	↓	↑	↑	↓
Width of landscape	↓	—	↓	↓	↓	—	↓	—	↓

Note: The mean dispersal distances from model 2 are conditional on leaving. A dash denotes an effect not significantly different from 0. Mutation type was parameterized in the regression with local mutations as -1 and global mutations as 1; that is, a positive effect of mutation type means that the response value is higher under global mutations. The ratios have expectations higher than 1; that is, an increase of the ratio is an increase in the level of conflict. For all values of dispersal rate, $d > 0$. D_M = mean dispersal distance under maternal control; D_O = mean dispersal distance under offspring control; Pr(M) = probability of leaving natal patch under maternal control; Pr(O) = probability of leaving natal patch under offspring control.

persal (fig. 3 presents an example). This increase occurs faster and is more pronounced if dispersal distance is under offspring control (fig. 4). However, because the scenarios with offspring control typically start with shorter kernels (evolved during the stationary phase), the stronger evolutionary response under offspring control does not yield faster invasion fronts as a net effect. Invasion speeds calculated after 25, 50, and 100 generations, as well as when the front crossed columns 25, 50, 100, 200, and 300, showed no consistent differences between the controls; this indicates that the initially higher speed brought by the longer dispersal distances if a mother is deciding disappears relatively fast. The decrease in dispersal distances in figure 4 occurs when an invasion reaches the end of the lattice and the population mean dispersal distance approaches that in the preexpansion phase.

During range expansion, there is an interesting pattern emerging from the evolving kernel shape of model 2. As in model 1, there is a general increase in the probabilities for dispersing larger distances under both controls of dispersal. Contrasting with the stationary phase, where offspring avoid risky long distances, the dispersal kernels in the expansion phase under offspring control show a much more pronounced increase in the probabilities for moving the longest distances (fig. 5). Intriguingly, the distributions not only are fat tailed but also can become bimodal, such that intermediate distances are selected against.

Discussion

Our results clearly show a battleground (Godfray 1999) over dispersal distances and can be seen as an extension of Motro's (1983) and others' (see Frank 1986, 1998; Taylor 1988) more analytical approaches showing the existence of this battleground under dispersal rate evolution only. Motro's (1983) model predicted that the conflict over dispersal rate would diminish as survival during dispersal increased, similar to the predictions of our model (see table 1). These authors have focused on the decision to leave or not to leave the natal patch, with the latter putting them in direct competition with each other. Our results extend this work by showing that the conflict also exists in a more realistic case where selection acts on how far individuals disperse and whether to disperse.

Maternal control of dispersal leads to longer dispersal distances than does offspring control, and this has population-level consequences. The discrepancy between what is optimal under individual selection and what is best for the population in the context of dispersal was already pointed out by Hamilton and May (1977). Their classic (asexual) model of dispersal rates predicted that the optimal (evolving) rate was always higher than that leading to highest patch occupancy. Our results show that the discrepancy between population-level performance and individual fitness also occurs in a spatially explicit model formulation where the dispersal kernel is under evolution.

The effect of habitat availability on dispersal distance differs between the models, most likely because of the conflation of dispersal rate and dispersal distance when the kernel shape is fixed (in model 1). It is interesting to note that as both number of offspring and availability of habitable patches decrease, the dispersal rate also decreases, but the distance dispersed increases. Populations living in fragmented habitats are crucially dependent on dispersal for population viability, but these environments select for lower dispersal distances in model 1, as well as lower dispersal rates in model 2. An evolutionary rescue, where sparse habitat networks would encourage dispersal (Heino and Hanski 2001), was not found in our case; the mean dispersal distance for a whole clutch (i.e., mean of

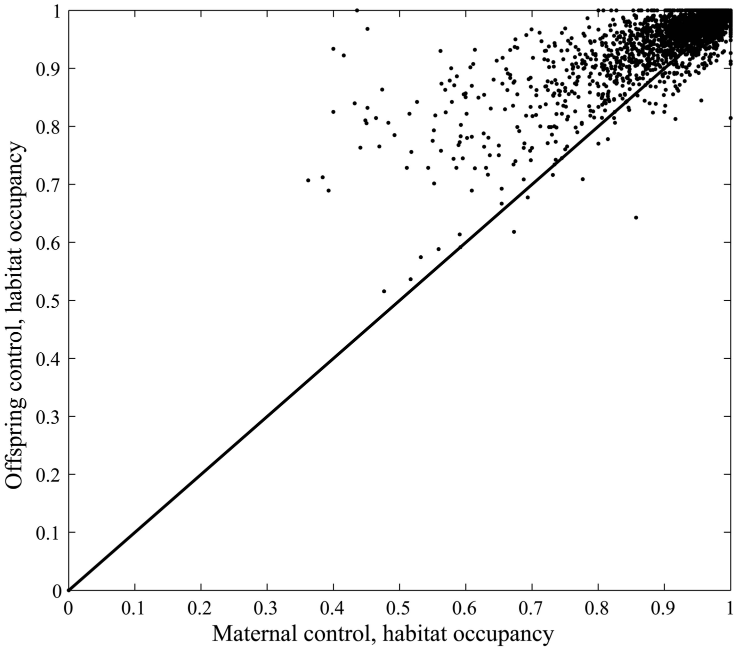

Figure 2: Model 1. The fraction of occupied patches (i.e., patches with a breeding female divided by all habitable patches) in the 2,000th generation under maternally controlled dispersal (*X*-axis) and under offspring-controlled dispersal (*Y*-axis), derived from the exponential kernel model. Although there is significant variation, a disproportionate number of simulations result in a higher proportion of the spatial resources being used when offspring control dispersal. The model with the freely evolving kernel exhibited similar results.

the unconditional dispersal kernel) decreased with lower habitat availability (results not shown).

The evolution of species ranges, a recently emerged topic of great interest (see Holt and Keitt 2005; Gaston 2009), is, almost by definition, greatly affected by dispersal strategies. One would expect that control over dispersal is important in the evolution of species ranges per se (e.g., control could affect both extent and structure of range edges), as well as in affecting the emergent trade-off between local adaptation and dispersal (Kisdi 2002; Bahn et al. 2006). Our results indicate that control over dispersal should be taken into account in trying to elucidate the evolution of species ranges.

There is already a great body of theoretical literature on the evolution of dispersal strategies. Our results illustrate a fairly general but almost forgotten point in what can determine the evolutionary dynamics and endpoints of dispersal. There are only a few recent investigations that explicitly take control over dispersal into account (Gandon 1999), but there are no particular reasons to believe that who controls dispersal does not have an effect on strategies more complex than the simplistic kernels we have used. Many dispersal models are asexual, which hides any potential effect of maternal versus offspring dispersal control. There is an interesting analogue to our results in the literature on the evolution of dormancy (dispersal in time) that can be viewed as a temporal analogue to dispersal in space in which the same conflict emerges (Ellner 1986; McNamara 1995; Hutchinson 1996). Kobayashi and Yamamura (2000) explicitly compared an asexual mode and a diploid maternal and offspring control for dormancy rate. In their model, asexuality resulted in an intermediate dormancy rate between offspring control (which yielded the lowest dormancy rate) and maternal control (leading to the highest rate). Again, offspring prefer the individually least risky option (shortest dormancy).

If we view dispersal as a mechanism for distributing offspring over a spatial resource, an interesting pattern emerges in our range expansion scenarios. As the invasion progresses, the front consists of individuals with a longer dispersal distance under both maternal and offspring control (a result well documented theoretically [Travis and Dytham 2002] and empirically [Phillips et al. 2006]). Our results from model 1 highlight an untested prediction: the difference between the front and core populations was more pronounced under offspring control. During an invasion, offspring can evolve to disperse so far that the conflict disappears; we found that offspring near the front evolved dispersal distances as high, on average, as those under maternal control. This can be understood in the

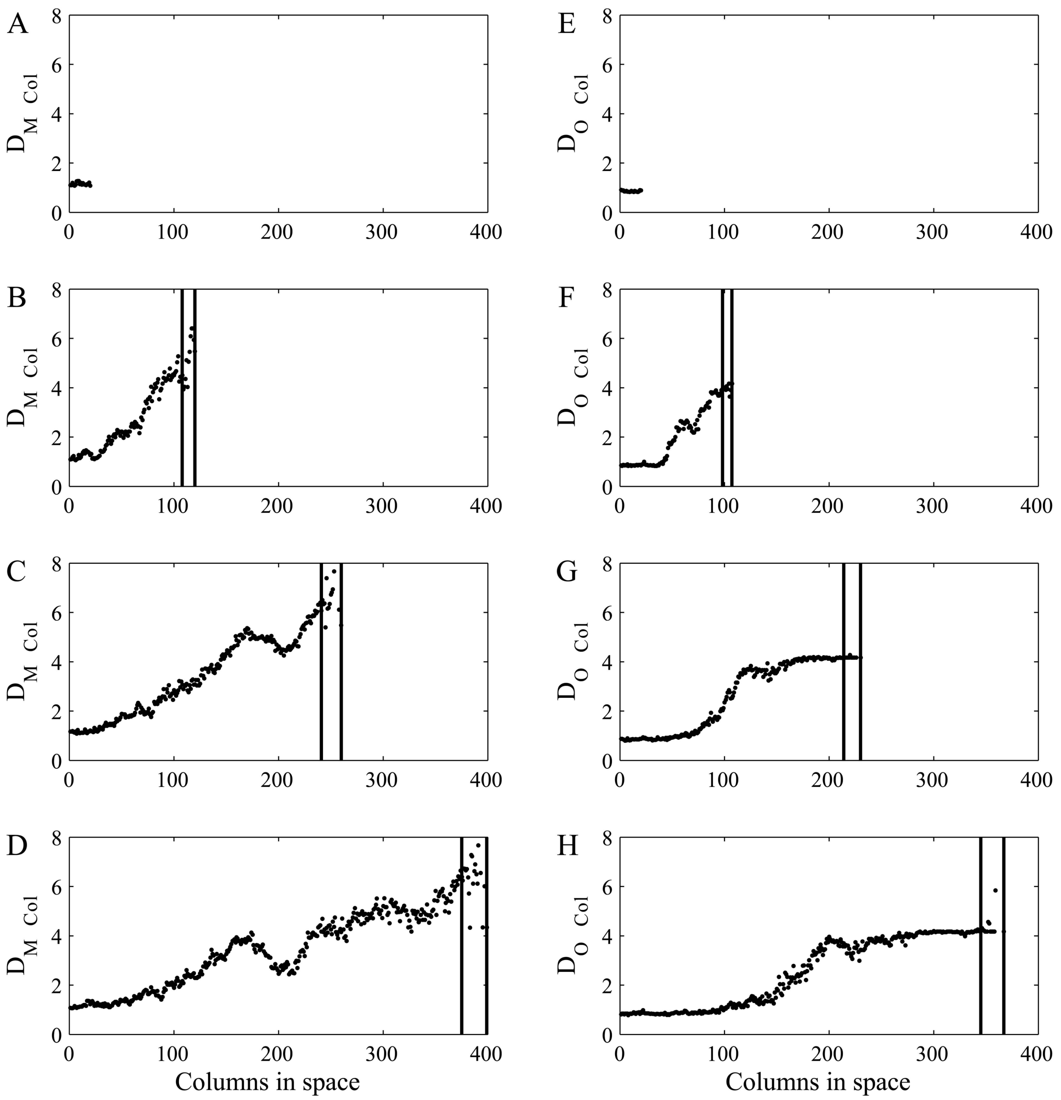

Figure 3: Model 1. The left column shows an example of the evolutionary dynamics in the expansion phase under maternally controlled dispersal. *A*–*D* show the mean dispersal distance ($D_{M\ Col}$; *Y*-axis) in each column (*X*-axis) right before the expansion starts (*A*) and after 25 (*B*), 50 (*C*), and 75 (*D*) generations under maternally controlled dispersal. *E*–*H* ($D_{O\ Col}$) show the same example under offspring-controlled dispersal. The vertical lines denote what we here define as the front, that is, the columns between the rightmost individual and the rightmost column where at least 50% of the habitable patches are occupied by a breeding female. From this example one can clearly see that individuals with a longer dispersal distance constitute a large part of the front as it moves through space. Also, note that as the front progresses, the mean dispersal distance within a given column approaches what was the mean before expansion started.

light of space as a resource. Conflict over allocating resources is less pronounced under high resource availability, which is the case when a species is expanding its range into novel territory. The conflict, however, reappears as the dispersal distances decrease after the front has passed (for an example, see fig. 3). This prediction appears to qualitatively match data on range expansion of wing-dimorphic bush crickets (Simmons and Thomas 2004), in which the proportion of long-winged individuals fell rather soon (5–10 years) after the front had passed a site.

Furthermore and perhaps even more strikingly, letting the dispersal kernel evolve any shape predicts a disproportionate increase in the probability of long-distance dispersals under offspring control, up to the point where the kernel becomes bimodal. Range fronts would thus evolve to exhibit alternative strategies (long and short dispersers),

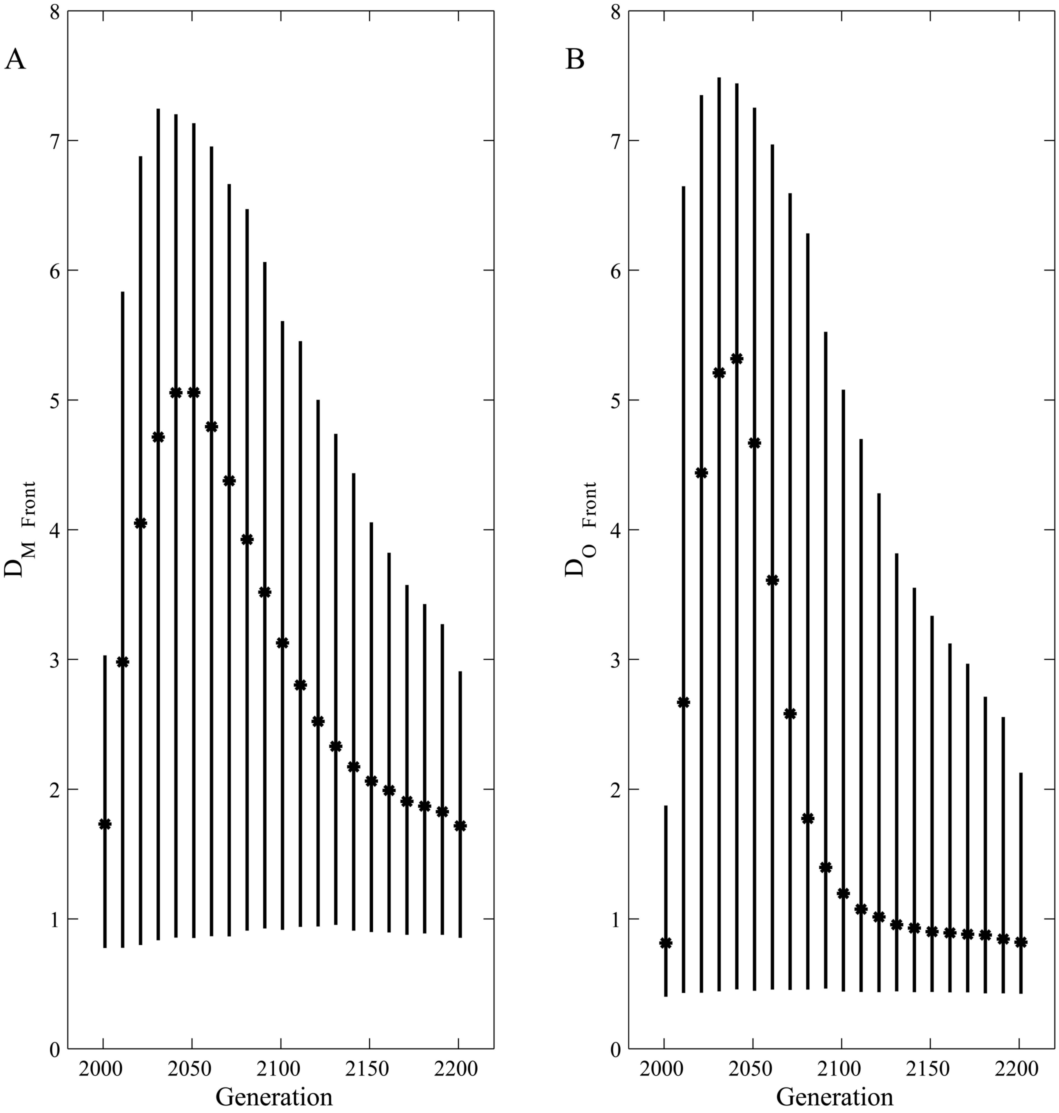

Figure 4: Model 1. Range expansion evolution in model 1 with global mutations. These summary statistics show the increase in dispersal distance over time in the invasion fronts during the range expansion. For every tenth generation, the line span from the fifth to the ninety-fifth percentile and the median is marked by a circle. *A*, Maternally controlled dispersal; *B*, offspring control. Though there is a lot of variation across simulations, most expansions result in an increased mean dispersal distance, and the pattern is more acute and quick under offspring control. After only 20 generations, the median dispersal distance across simulations is similar under both controls, whereas before expansion, the ratio is closer to 2 : 1. The decrease in dispersal distances after 50–100 generations is due to the populations reaching the end of the grid, having occupied the entire enlarged lattice.

even without the discrete dimorphism type shown by bush crickets. Previously, alternative dispersal strategies have been studied mostly either in the context of discrete dimorphism (Harrison 1980) or as plastic responses to local conditions that determine whether an offspring remains philopatric or leaves (Dickinson and McGowan 2005; Baglione et al. 2006). The finding that disruptive selection under invasion can produce a similar but genetically determined bimodality is, to our knowledge, novel (but for a related finding where maternal effects cause variation in dispersal distances of offspring, see Duckworth 2009; for bimodality in a stationary case, also see Rousset and Gandon 2002). The contrast between risk-averse offspring in the stationary phase and the "'brave explorers" that evolve in the expansion phase shows the surprising directions that dispersal evolution can take in invasive species.

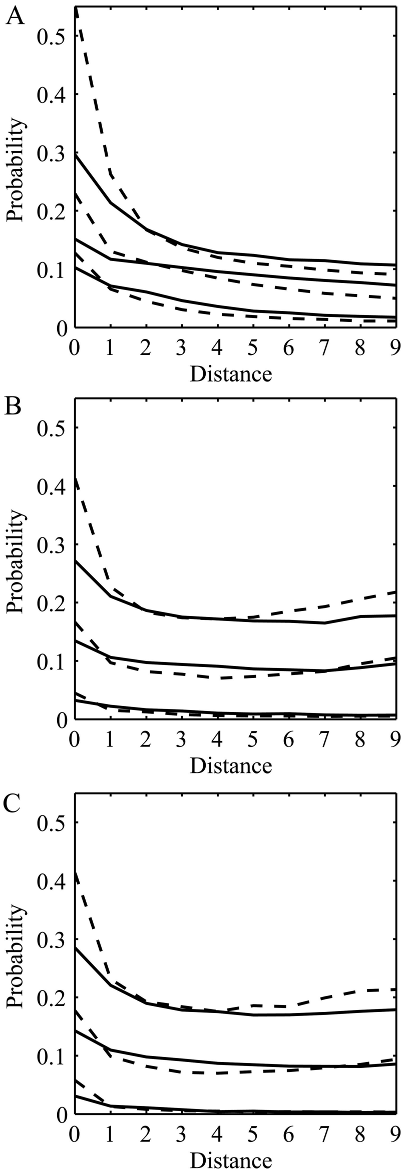

Figure 5: Model 2. Range expansion model 2 with global mutations. Resulting dispersal kernels in the front during the expansion phase when the shape is freely evolving. For each simulation, a mean kernel across all individuals in the front was recorded. This plot shows the fifth, fiftieth, and ninety-fifth percentiles of probabilities for dispersing a particular distance across all simulations. *A* shows the dispersal kernels before expansion in the whole population, *B* after 50 generations, and *C* after 100 generations. *Solid line* = offspring control; *dashed line* = maternal control. Under offspring control, the probabilities for dispersing far are noticeably higher. To check for population dimorphism (i.e., that the front consists of some highly philopatric and some long dispersers), we calculated the variance of alleles within each distance class. These variances were similar, indicating that the front consists of individuals that have a larger probability of both philopatry and long-distance dispersal (if the front consisted of some philopatric and some long dispersers, the variance of alleles would be higher for these distances classes).

Who Controls Dispersal? Resolutions to the Conflict in Different Taxa

We have shown that a battleground for control over dispersal exists, that is, that there is potential for a conflict of genetic interest between parent and offspring in dispersal. How is this conflict played out in different taxa? In many plants, this conflict will probably be resolved through a maternal force majeure (Alexander 1974) because the seed coat and fruit bodies (with possible adaptations to dispersal) surrounding the seeds are maternal tissue and therefore a product of a maternal genome.

In most animals, however, this is more complex. Parents can affect the distribution of their offspring in different ways: through behavior (indirect, e.g., through spatially distributing eggs, or direct, e.g., through territory eviction) or in more physiological ways through other maternal effects. As an example of the latter, in the side-blotched lizards (*Uta stansburiana*), Sinervo et al. (2006) showed that there is a fairly strong maternal effect on dispersal phenotype, implying that control of dispersal is somewhere between the two extremes we investigated in our model. Likewise, in the common lizard (*Lacerta vivipara*), offspring dispersal phenotypes are affected by exposure to maternal hormones (see Vercken et al. 2007 and references therein). In addition to these more physiological potential maternal influences, behavior during critical periods can greatly influence the dispersal behavior exhibited by offspring (e.g., Stephens et al. 2005). The conflict over dispersal rates and conditional dispersal distances is differentially affected by empirically measurable factors in our model; in many animals, one could easily expect parents to be able to increase the dispersal rate of their offspring, though not the distance dispersed by them to the same degree.

Thus, in many animals, though there is no seed coat surrounding them, dispersal can be greatly influenced through maternal effects and behavior, such that offspring exhibit a dispersal strategy more similar to that preferred by the mother. In our model, we considered only two extremes: completely maternally determined dispersal and completely offspring-determined dispersal.

Suggestions for Future Work

As in any modeling exercise, we have made several simplifying assumptions. While our model avoids the asexuality assumption of many earlier ones, we do not consider sex-specific dispersal kernels. Likewise, our focus on the need to find suitable habitat patches made us ignore another complication: in some organisms the patch in which an individual lands should contain both sexes before a new population can be founded (though this restriction is not true for, e.g., fertilized seeds or insects in which females disperse after mating). Future work that considers such options, by paying closer attention to details of the mating system, could address several important topics such as sex-specific dispersal when there is local variation in sex ratio (C. Meier, J. Starrfelt, W. K. Vahl, and H. Kokko, unpublished manuscript) or the effect of multiple mating. Multiple mating should prove especially intriguing in our context because it alters offspring relatedness to each other while leaving relatedness to the mother unchanged. This could escalate conflict, but the precise pattern is difficult to predict a priori, particularly if offspring sired by different males differ in their dispersal distance. In this case, average relatedness between offspring can depend on their distance from each other, opening up intriguing evolutionary avenues.

Our model 2 shows a complex relationship between factors that affect movement behavior and dispersal strategies; of particular interest is the fact that certain parameters lead to an increase in the rate of dispersal but a decrease in the distance dispersed, conditional on actually dispersing. Disentangling the complete impacts of these factors and how they affect dispersal evolution is of importance, as is clarifying how and when measured quantities of dispersal strategies (either distances or rates) are expected to be similarly or differentially affected.

Another intriguing finding from our evolving kernel shape model is that invading populations can experience disruptive selection: particularly under offspring control, the kernel exhibits relatively philopatric individuals and long-range risk-takers, with intermediates selected against. This shows that nonequilibrium conditions can yield surprisingly complex dispersal dynamics, further enhancing the message that predictions gained with too-constrained dispersal rules can mislead (Kot et al. 1996). Obviously, our model 2 includes constraints too, including the arbitrary limit of 9 units of dispersal distance; a more systematic search for bimodal or multimodal dispersal distributions could prove fruitful.

Concluding Remarks

We have extended earlier work on parent-offspring conflict in dispersal evolution and have shown that there exists a conflict in a spatially explicit setting where dispersal is modeled as a dispersal kernel; if a parent determines the dispersal strategy of its offspring, a wider kernel is selected for. In addition to this, we have shown that if individuals control their own dispersal strategies, there is less conflict between what is favored through individual-level selection and population-level performance (here measured as patch occupancy). This again highlights the importance of extending current theoretical models of dispersal distance to explicitly include control over dispersal, and it serves as a reminder of this general conflict and the need for empirical investigations into its potential resolution.

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