

Mate limitation causes sexes to coevolve towards more similar dispersal kernels

Christoph M. Meier, Jostein Starrfelt and Hanna Kokko

C. M. Meier (christoph.meier@helsinki.fi), J. Starrfelt and H. Kokko, Lab of Ecological and Evolutionary Dynamics, Dept of Biosciences, PO Box 65, FI-00014 University of Helsinki, Finland. JS also at: Centre for Evolutionary and Ecological Synthesis (CEES), Dept of Biology, Univ. of Oslo, PO Box 1066 Blindern, NO-0316 Oslo, Norway. HK also at: Evolution, Ecology and Genetics, Research School of Biology, Australian National Univ., Canberra ACT 0200, Australia.

Sex-specific dispersal behavior has been documented in a wide range of different species. Avoidance of inbreeding and kin competition as well as different benefits of philopatry have been invoked as explanations for these patterns. All of these factors have, however, focused on explaining why dispersal behavior differs between the sexes. In this paper, we make the case that dispersal causes an increase in spatial variability in the sex ratio which can reduce the local availability of mates, and thus feed back to influence the evolution of sex-specific dispersal and lead to more, rather than less, similar dispersal behavior in the sexes. We investigate this mechanism in two different models, first in a conceptually simple case showing why the coevolutionary effect arises, second in an individual-based model where we model a population in explicit space with dispersal implemented as dispersal kernels. While our mechanism is not expected to completely remove sex-bias in dispersal, it can act alongside other selection pressures to reduce such biases. Our model thus shows that dispersal of one sex can have an effect on the selective pressures on the opposite sex, without implementing inbreeding avoidance or differential benefits or costs of dispersal.

The evolution of dispersal is driven by every organism's need to adjust their distribution in space in response to environmental fluctuations. Fluctuations of biotic or abiotic conditions which are external to the population require the ability to disperse to track favorable conditions and to assure global persistence. Factors intrinsic to populations can also create sufficient variation in space for dispersal to evolve. The seminal paper by Hamilton and May (1977) showed that relatedness structure (which amounts to spatial variation in whether an individual competes with kin) is sufficient to promote dispersal even under the absence of external environmental fluctuation. Dispersal evolution in response to the risk of inbreeding (Gandon 1999) and demographic stochasticity (i.e. variance in individual reproduction and mortality; Cadet et al. 2003) can similarly be understood as responses to these types of spatiotemporal variation.

Dispersal itself can be the cause of further spatial variation. Inevitably, each movement of individuals in space affects local densities which can potentially feed back on the evolution of dispersal. This phenomenon is well studied in examples including density-dependent dispersal, where individuals react in response to relative differences in population densities (Bowler and Benton 2005), and dispersal evolution in source–sink systems (Morris 1991, Schmidt et al. 2000).

Spatial variation in external environmental conditions, level of inbreeding, and kin competition have also been

considered in the extensive literature on evolution of sex-specific dispersal (Gandon 1999). The main focus of this literature is solely to explain the sex bias in dispersal. Thus, typically, factors that vary between the sexes have been brought forward as an explanation for the sex bias in dispersal, including sex-specific fitness consequences due to the genetic architecture of the sexes (Hedrick 2007), the differing importance of philopatry for local mating success between sexes (Greenwood 1980), and the difference in dispersal and mating success (Handley and Perrin 2007). However, most studies on evolution of sex-specific dispersal consider space only implicitly, possibly losing some of the complexities (Ronce 2007). Tacitly they all assume a constant sex ratio and density across the entire population (although they often do account for relatedness structure).

This assumption of zero variation in sex ratio and density can become problematic in situations where reproductive opportunities are not distributed uniformly in space. A spatially non-uniform distribution of the sexes will increase the variance in local sex ratio, with consequences for the reproductive success of each sex (Fisher 1930, West 2009). For example, local mate limitation is known to constrain reproduction (South and Kenward 2001, Berec and Boukal 2004, Robinet et al. 2008, Contarini et al. 2009). At the extreme, assuming a life history where the local presence of both sexes is necessary for reproduction, any local population will go extinct if one sex is completely missing.

To our knowledge only four models on the evolution of sex-specific dispersal have included variation in local sex ratio. Hirota (2007) compared the evolution of sex-specific dispersal strategies when dispersal was conditional on either local density or sex ratio, and found that sex-specific timing of dispersal evolved differently depending on which of these two cues was used by individuals as a trigger of dispersal. Thus individual sex-specific responses to the local sex ratio can alter the course of dispersal evolution from what would be predicted by responses to demographic stochasticity that do not differentiate between males and females. The other three models are individual-based models (Gros et al. 2008, 2009, Bonte et al. 2009) which account for spatial variation in kin-competition, and asymmetric (i.e. sex-specific) dispersal costs, demographic stochasticity, spatial variation in sex ratio, and except for the first model they also account for spatial variation in inbreeding. These models aim to predict the sex bias in dispersal, to then study how this bias is affected by the type of spatial variation. Bonte et al. (2009) investigated sex-specific dispersal evolution when local sex ratio becomes female biased due to a male killing endosymbiont. Kin-competition therefore increased for males relative to females and selection lead to male-biased dispersal, decreasing the extinction risk in this sex-biased population. In Gros et al. (2008), the bias in dispersal between the sexes evolved to be less pronounced with spatial variation in sex ratio, compared with analytical solutions that lacks all demographic stochasticity (including spatial sex-ratio variation). The last model (Gros et al. 2009) comments on the different resource demands of the two sexes: males require females to breed with, females compete over vacant breeding resources, and thus the variance of reproductive success differs between the sexes. The sex bias in dispersal disappears if the between-patch variance in reproductive success becomes similar for the two sexes (Gros et al. 2009).

The above three studies hint at consequences of explicit spatial variation in sex ratio for the evolution of sex-specific dispersal. However, none of these studies have explicitly pointed out that dispersal itself can cause an increase in spatial variability of the sex ratio, which can reduce the local availability of mates for a non-disperser (although Gros et al. 2009 make a brief comment about a female's male relatives being selected to avoid dispersal if this is likely to make their sister mate-less). This means that if one sex disperses much, then this can feed back to increase selection for dispersal in the other sex. This potentially introduces a new and thus far unexplored selective force influencing the evolution of sex-specific dispersal.

If one sex becomes locally scarce due to low levels of immigration, an individual of this less dispersing sex, if it reaches this location, would have more potential mates than a member of the opposite sex. The less dispersing sex could thus be expected to evolve towards longer or more frequent dispersal. Assuming (as we do throughout this paper) that the presence of a mate is required for each reproductive bout, each sex can be interpreted as a necessary resource for the opposite sex, required for achieving reproduction. Therefore we might expect the sexes to 'track' each other, by which we mean a coevolutionary process that tends to reduce sex differences in the dispersal kernel (not active tracking of, say, scent or pheromone trails). Coevolution between the sexes'

dispersal traits should lead to a better matched distribution between individuals of either sex, lowering the frequency of failing to locate a mate.

In this line of thinking, individuals of the opposite sex can be thought to be the resource that reproduction depends on, which means that the equalizing process bears similarities to the way ideal free distributions are predicted to arise through individuals seeking best resource levels (Holt and Barfield 2001). The analogy is incomplete, of course: the resource is not a static 'habitat' but it evolves, movement is typically not free, and reproduction does not always increase linearly with mate availability (it obviously requires other resources too, and mate availability beyond one mate does not always increase reproductive output, especially for females). Our aim here is to test if mate limitation due to an uneven distribution of the different sexes across space constitutes enough selection pressure to induce coevolution among the sexes towards more similar dispersal kernels when space is explicitly considered. First, we illustrate with a simple thought experiment how minimal the requirements are for such a coevolutionary mechanism to play a role in dispersal evolution. Second, we present a spatially explicit individual-based simulation model to investigate if we find coevolution in this setting.

Model 1. The potential for coevolution

In our first model, we will not provide a full description of any evolutionary or population dynamic process. Instead our aim is to provide a thought experiment by giving a snapshot of a process that can make individuals of one sex disperse more if the opposite sex (for any reason) does so. We wish to illustrate how the dispersal of one sex increases the selection for the opposite sex to co-adapt. To best illustrate this point, our 'snapshot' of a population deliberately does not consider any kin structure or any other mechanism that may promote or hinder dispersal evolution. By reducing complexity to a minimum, we intend to show how a specific factor can impact on spatially variation in sex ratio and on sex-specific fitness in isolation from all other effects.

We consider a population inhabiting a landscape of 1000 habitat patches, initially with $n = 30$ individuals per patch. On average the sex ratio is 1:1, thus with probability 0.5 an individual is female or male (i.e. a binomial distribution within each patch). We assume that patches differ in quality with respect to a patch-specific survival rate q_i . The expected population size of a patch is $n \times (1 - q_i)$ and the exact number varies among patches due to demographic stochasticity (i.e. each patch is initially assumed to contain 30 individuals, then each is assigned a sex, then each individual survives with probability q_i). In our first example, q_i is uniformly distributed between 0 and 1 (later we will relax this assumption which so far creates very strong variation in patch quality). Because of habitat quality variation, some patches contain many males as well as many females, while others contain few individuals of either sex, with some demographic variation around this expectation (thus there can be male-only or female-only patches prior to dispersal).

Next, we allow one sex, the females, to disperse. We define female dispersal rate ($0 < d_f < 1$) as the probability with

which each female disperses globally, i.e. to any other patch than her natal patch. In this simple thought experiment we ignore costs of dispersal and assume that any non-natal patch in the population is reached with equal probability.

After females have dispersed and distributed themselves across patches, for each male, the expected reproductive success at each of the two possible dispersal options (no other males actually disperse so that expected reproductive success is independent of the action the other male might take):

- (1) Stay in the natal patch
- (2) Disperse and land in any other patch than the natal patch

Male expected reproductive success in patch k is calculated as the expected number of females in patch k divided by the number of males in patch k (self + competitors). The number of females / male is a good measure of the expected payoff (reproductive output) of dispersing or non-dispersing males, as long as we ignore intergenerational complications such as autocorrelated patch quality across years (which would generate predictable differences in the reproductive success and thus value of females). The incentive for the average male to disperse depends on the difference in payoff between the strategy (2)–(1) across all males in the population. If this payoff is positive, the male can increase its reproductive success by dispersing.

When females are immobile ($d_F = 0$), males, on average, do not benefit from dispersing (Fig. 1A). Males already tend to occur on high-quality patches where there are, on average, many females as well, and moving will not increase the odds of finding a female-rich patch. Moreover, despite no explicit costs of dispersing included in the model, the overall payoff difference between the strategies (2)–(1) is negative and disfavors dispersal: dispersing males can end up in patches that had no females, while males in their natal patch experience this fate less often (because males tend to coexist with females in high-density localities). However, the situation is different if females disperse. Random dispersal tends to reduce the number of females in patches that originally had many females (emigration exceeds immigration when there are many potential emigrants), and increase the number of females in patches that had few (the above argument reversed). If males do not disperse but females do, then patches with many individuals will end up with a surplus of males – and, consequently, fewer females per male than what a male would gain, on average, by residing in any other randomly chosen patch in the population.

It follows that a male would benefit from leaving if they can assess that they are in a male-surplus patch, which is in line with the findings of Hirota (2007). But it is a more exciting finding that the male would also benefit, on average, if he leaves regardless of such information (Fig. 1B–C). The benefit becomes larger with increasing female dispersal.

Patches that had a surplus of females before females depart tend to lose the most females, whereas patches with a surplus of males most likely remain having a deficit of females. This explains why an average male is selected to move away from his natal patch to ‘follow’, probabilistically speaking, females that have departed (Fig. 1). Obviously the selection on male dispersal behavior depends on female dispersal, and gets stronger as the rate of female dispersal increases.

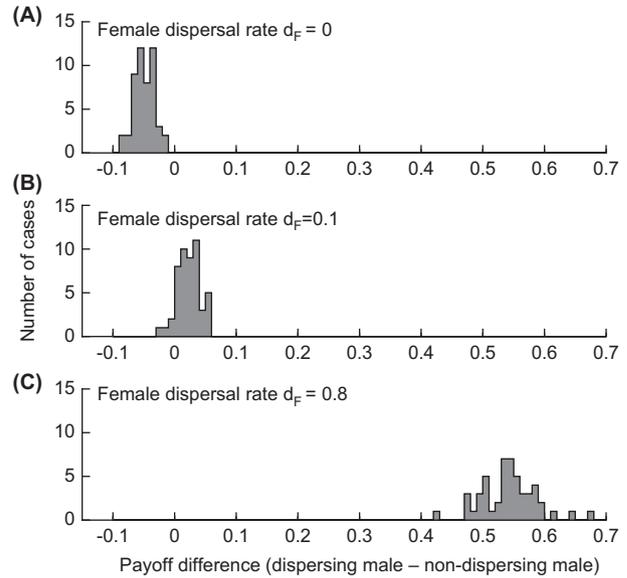


Figure 1. The expected payoff difference between the philopatric and the dispersal strategy for males in model 1 with uniformly distributed patch quality (between 0 and 1) and 30 individuals per patch to start with. When females dispersed either not at all, with probability of 0.1, or with probability of 0.8, the mean payoff for males across 50 simulations was -0.054 , 0.018 and 0.538 , respectively.

Even though our model is exceedingly simple, it already involves assumptions that could and should be relaxed: e.g. the uniform distribution of survival across habitats implies very high variance in survival, and distributions with smaller variance might make the effect milder. Indeed, repeating the above exercise with normally distributed (with $\mu = 0.5$, $\sigma = 0.2$, and truncated to fall between 0 and 1) habitat qualities q_i leads to a markedly smaller change in the difference in payoff between (1) and (2), although the process still works in the qualitatively identical direction. In Fig. 1 the means in difference in payoff shifts from -0.054 to 0.018 and 0.538 when female dispersal changes from 0 through 0.1 to 0.8, while with the normal distribution the corresponding numbers are -0.016 , 0.005 and 0.186 ; when patches vary even less ($\sigma = 0.1$), these numbers become very small, -0.005 , 0.003 and 0.009 . It thus appears that the process is not dependent on the shape of the distribution per se but it does require sufficient spatial variation in demography, without which sex ratio variation would be too small to have a discernible effect.

Our simple example gives rise to many caveats to discuss. First, to make our conceptual point as clear as possible, our model excludes many factors known to influence dispersal evolution. It firstly examines the potential for coevolution, and shows that a selection for male dispersal depends on how much females disperse – but without examining how soon this selective pressure diminishes as other males begin dispersing too as a result of a higher dispersal rate. We thus do not derive the eventual game-theoretic equilibrium of the dispersal rate (which would necessitate additional assumptions about reproduction, kin structure and possibly other sources of stochasticity, making the model immediately less general). Our model instead simply shows that too low (zero)

male dispersal is selected against even in the absence of kin competition, when females, for any conceivable reason, disperse more than males. Details of, say, kin competition will then obviously interact with the above process to determine the final outcome. It is conceivable, however, that other factors, such as kin-structure, might be more important in the long run and override the selective pressure for one sex to adapt to the dispersal behavior of the opposite sex such that coevolution never becomes important. Second, so far, we only investigated the process from a male perspective. It is unlikely to operate identically for both sexes. For females, the number of males/female is rarely a good proxy for reproductive output of a female, nonetheless avoiding complete matelessness may be a significant selective pressure for both sexes. Third, it might be that few dispersers are sufficient to reduce the spatial variation in sex ratio. We are interested in if this selective pressure can have an effect that remains visible when dispersal of an individual can feed back on the behavior all other individuals in the population.

Instead of expanding this simplistic global dispersal model further, we opted to examine whether the basic prediction that coevolution between the dispersal trait of males and females also occurs if we follow a single spatially explicit population in detail over time. We make space explicit by examining a population where the density varies from high (in a core area) to low (near the edge of the species' range) (Fig. 2). Within this population the two sexes have to be sufficiently close in space to find each other for a mating. The question is if this selects the sexes to have more similar dispersal kernels (the only way evolution in our model can influence the distribution of each sex in space), analogous to model 1 where dispersal rates were likely to become more similar.

Model 2. Coevolution in a population with spatially explicit dynamics

Overview

Our model 2 is two-sex, individual-based, in continuous space and in continuous time. The model thus accounts for demographic stochasticity and stochasticity in the spatial

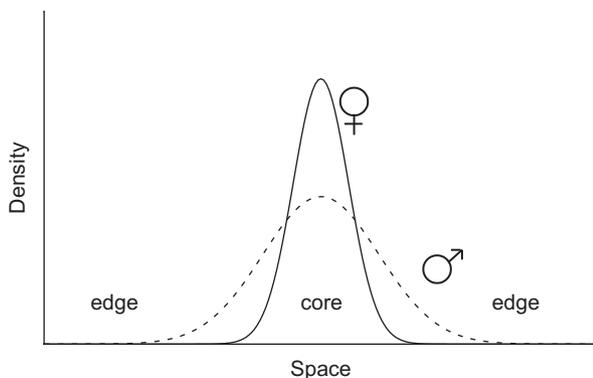


Figure 2. The distribution of individuals in a hypothetical population where the spatial distribution of males and females overlap, but males disperse on average further than females. At the center of the population there is a surplus of females. Males would benefit from a dispersal strategy that distributes them less often to the edge where they remain unmated.

distribution of individuals, which inevitably creates variation in the local sex ratio. Variation in the spatial distribution of individuals and the local sex ratio is further increased by assuming the environment to be heterogeneous due to an external factor that affects the mortality of individuals differentially depending on their location.

Individuals in this population experience all their life events stationary at a location (x, y) except for a single dispersal event immediately after birth (i.e. natal dispersal). Dispersal distance is controlled by a sex-specific alleles D_F in females and D_M in males which have the potential to evolve (below).

Space

The area inhabited by the population is in principle limitless. However, mortality increases linearly with distance from the origin $(x = y = 0)$. In practice, persistence far from the origin is, therefore, impossible. The mortality function limits population growth across space such that the population stabilizes in size at a dynamic equilibrium after a few generations. At the same time this spatial heterogeneous mortality generates individuals with different reproductive success at locations along a (two-dimensional) gradient.

Reproduction

Reproduction is initiated by females with rate of $r = 1$ (see section Time, below, for how rates are implemented). If a female is about to reproduce, the program checks if she has an available mate; if not, reproduction fails to materialize. Mating is possible on a local scale and because space is continuous, we simply define a radius within which individuals are able to find a mate. We specify that a male is 'present' if his distance from the focal female is less than d_{mate} (thus the female is at the centre of a circle of radius d_{mate}). When at least one male is present, a female can produce a brood. If the female has several possible partners within her reach she always mates with the closest. This resembles a mating system with monogamy, though a female can possibly mate again, even with other males, if she survives long enough to reproduce again.

Brood sizes ($n_{\text{offspring}}$) are drawn from a Poisson distribution which introduces demographic stochasticity (Travis and Dytham 1998, Travis et al. 1999, Kendall and Wittmann 2010). The mean of this distribution reflects the maximum available breeding resources (constant and set to 40 in our examples), decreasing with the number of competitors n_{comp} that use these resources:

$$n_{\text{offspring}} \sim \text{Poisson} \left(\frac{40}{n_{\text{comp}}} \right) \quad (1)$$

The n_{comp} is the number of all individuals independent of their sex (including the mate) that compete with the focal female. Individuals are competitors if they reside within a radius d_{comp} (here $d_{\text{comp}} = d_{\text{mate}}$) from the focal female. Note that because competitors decrease the number of offspring that a female produces, these conditions inevitably create selection for dispersal through avoidance of kin-competition.

Dispersal

Offspring are randomly assigned to be male or female (with primary sex ratio 1:1). At birth they inherit two haploid dispersal alleles D_F and D_M , each from either the mother or the father with equal probability. Of these alleles D_F is expressed in females and D_M in males, and they specify the mean dispersal distance for a dispersal kernel of negative exponential shape. Newborn individuals disperse in a random direction (angle) with the distance drawn from their individual-specific dispersal kernel. The exponentially shaped dispersal kernel produces long distance dispersal with a low frequency (Cousens et al. 2008). Note that despite dispersal being mandatory, the distances are free to evolve towards negligibly small values, thus de facto philopatry (non-dispersal) is included as a possible dispersal strategy.

Before the offspring actually disperse, there is a small probability m for each allele to mutate. We mimic a mutation process of a polygenic trait by assuming that most mutations have a small effect, with a small probability for very large mutations. We use a log-transformation to make sure that dispersal distances cannot become negative:

$$D'_F = e^{(\ln(D_F)+\epsilon)} \quad \text{and} \quad D'_M = e^{(\ln(D_M)+\epsilon)} \quad (2)$$

Here ϵ is a random number from a normal distribution with mean 0 and variance σ^2 and it is the same for both sexes.

Death

Reflecting our assumption that the environment is of highest quality near the core (origin), the mortality rate varies between individuals depending on the distance from the origin d_{Origin} :

$$\mu(x, y) = \mu_0 + \alpha d_{\text{Origin}} \quad (3)$$

This equation specifies that mortality rates reaches its lower limit, μ_0 , when an individual resides at $x = 0, y = 0$. We assume $\mu_0 > 0$ to ensure that no individual can live forever. Mortality increases concentrically from the point of origin with a linear gradient α . Implicitly, this generates a distance-dependent dispersal cost, because far-dispersing individuals are, on average, more likely to end up far away from the origin where mortality is higher.

Time

Individuals can disperse, reproduce and die. Dispersal is not treated as an independent event; instead we assume that offspring perform natal dispersal immediately after being born. Our simulation computes events of reproduction and death in a mixed order to avoid systematic prioritizing of an event of one type. We modeled all events in continuous time (denoted t) as a Gillespie process (Gillespie 1977, 1992), where the order of events is not pre-defined and any event has an instantaneous influence on local dynamics.

For every individual we specify the mean waiting times for this individual to be involved in an event (death or reproduction), according to the individual-specific rates

of mortality μ and reproduction r . The Gillespie process assumes that the rate with which events occur is constant over time until an event has actually occurred which changes the state of the population; from this it follows that all waiting times obey a negative exponential distribution around the mean waiting time. Thus, we can find the actual waiting time for all currently possible events by drawing values from the exponential distribution. These are denoted T_D , the waiting times until death (for all individuals) and T_R , all times until reproduction (for all females, because only they can initiate a reproduction event):

$$T_D \sim \text{Exp}(\mu(x, y)) \quad T_R \sim \text{Exp}(r) \quad (4)$$

Here $\text{Exp}()$ denotes the exponential distribution, $\mu(x, y)$ is the mortality rate for all individuals at their current locations and r is the reproductive rate of females, which we set at 1.

From all waiting times (death and reproduction) we pick the shortest value (Δt) and this determines when the next event, and of which type, occurs in the entire population. Timekeeping is then updated from t to $t + \Delta t$. The individual, who “produced” the shortest time Δt , is the focal individual to whom the next event happens. Thereafter we need to create a new distribution of waiting times for all events and all individuals of the entire population, as the location and number of individuals has now changed. Δt is on average shorter in large populations with a large number of events.

Three coevolutionary scenarios

We ran all simulations under three different scenarios (I–III). In scenarios I and II, we intended to find out if the dispersal distance of one sex constitutes a selective pressure that affects the dispersal distance of the opposite sex. We have to test this for each sex separately because the sexes in our model are different: only females give birth. In scenario I, we fixed the dispersal kernel of females, so that only the male dispersal kernel was allowed to evolve. If male dispersal tracks the local availability of females, they should respond to the (fixed) female kernel such that selection acts against dispersing very far when females do not distribute themselves very widely in space. We can detect such a response as a positive correlation between the fixed (female) and the freely evolving (male) trait across simulations. In scenario II the roles were reversed: the female trait could evolve, whereas male dispersal kernel was fixed.

Scenarios I and II allow us to test if a reduction (or increase) in mean dispersal distance in one sex is enough to create some selection for the other sex to evolve towards a similar dispersal kernel. In scenario III, we assumed no such artificial fixation of one sex to particular trait value for the dispersal kernel; instead both sexes evolve their dispersal kernels simultaneously.

We were not entirely certain which pattern we should expect from this third scenario. If the two sexes evolve independently of each other, we would see no correlation between the dispersal kernels of the two sexes. However, the same outcome could be result of the two sexes coevolving, but external environmental conditions selecting so strongly for specific optima of the trait values D_F and D_M , that the

correlation between these two values across all simulations would also be zero. In that case we would have to rely on the information of the first two scenarios, to decide if dispersal distances in one sex create a selection pressure on the opposite sex. However, in scenario III it is also possible that a third pattern might arise. If stochasticity is strong and coevolution of the two sexes continually keeps responding to this stochasticity at a fast timescale, we could see a correlation between the trait values D_F and D_M despite the expectation that both approach a (coevolved) single point as their respective optima. Thus, if we find a positive correlation in all three scenarios, we will have found a very strong signature of coevolution.

Initial values

We ran 500 replicates for each of the three scenarios I (males evolve), II (females evolve) or III (both evolve). Across scenarios we used the same sets of parameter values. Within scenarios, the 500 replicates used identical parameter values except that we varied the initial values for the sex specific dispersal trait D_F and D_M .

The initial values of D_F for females and D_M for males were drawn from a uniform distribution between 0 and 10 for each sex (values higher than 10 diffused the initial population so widely that the population usually went extinct). For a most effective exploration of the parameter space of D_F and D_M across replicates we used the latin hypercube (McKay et al. 1979) design of MatLab. Individuals were initially monomorphic for D_F and D_M , and variation was introduced by mutation during the simulation, if they were allowed to evolve.

Across all replicates the initial population was fixed at 1000 individuals with an even sex ratio. For the initial spatial population configuration we always used the same spatial distribution (Supplementary material Appendix 1, Fig. A1). To improve the chance that the initial distribution of individuals became a viable population, we placed the individuals at coordinates which we had stored beforehand from a 'pilot simulation', i.e. a preliminary run. To reduce the influence of this initial population configuration we let the individuals die, reproduce and disperse for 20 time units before any evolutionary change in the trait value could happen (one unit corresponds roughly to generation time because we scaled birth rate as $r = 1$). In the following we refer to this as the settlement period.

The spatially explicit equation for mortality (Eq. 3) was the main factor in our model determining the size of the simulated population. The computational resources we had at hand allowed us to simulate a population size of approximately 10 000 individuals. With this constraint in mind we chose $\mu_0 = 1.5$ and $\alpha = 0.05$. These values produced a large population with a mild spatial gradient in mortality such that extensive areas of high and low density could emerge at different locations within the same population.

We chose the simulation time (number of time units that t is allowed to increase to) based on a visual examination of the simulation for trends in population growth and change in trait values D_F and D_M . We observed no systematic trend in these values after the first 100 time units. To make sure that the simulations have sufficient time to converge, we

let the populations evolve for a total of 1000 time units (in addition to the settlement period).

To reach further confidence that our simulation had converged, we conducted a statistical test where we repeated the simulation twice for each scenario using 30 different starting values for D_F and D_M . For scenarios I and II the trait value of the fixed sex was the same as in the original run, however, the evolving sex started with a different initial value for mean dispersal distance. In scenario III both sexes started with a different trait value from the original run. In all 30 repetitions we ranked at the beginning and at the end of 1000 time units whether the evolving sex in the 2nd run evolved to a longer mean dispersal distance than in the 1st run. We used a χ^2 test to decide if the beginning ranking had any systematic influence on the rank in the end, which would indicate that the trait values are not yet independent from the initial value and thus had not reached convergence.

Reported values

At the end of each simulation run, i.e. settlement time and 1000 time units evolving time, we recorded whether the population had gone extinct. For persisting populations, we recorded the means, computed across individuals, of sex-specific dispersal traits D_F and D_M . To detect coevolution between the sexes we performed a Spearman rank correlation analysis between the D_F and D_M across all persisting populations and for each of the three scenarios. The reason for using Spearman rank correlations is that the uniform distribution of resulting values D_F and D_M inherently violates the assumption of a bivariate normal joint distribution of these two variables, which underlies all correlation analyses that are not based on rank coefficients (Quinn and Keough 2002).

For the simulation and the statistics we used MatLab version R2009a (MathWorks™ 2009), the simulation model was then compiled for the programming language C and run on the Murska computer cluster at CSC Finland.

Results

After the settlement the sexes had a characteristic distribution in space according to their initial dispersal kernel (the higher the mean dispersal distance the more they spread out), and this created the opportunity to study whether coevolution between the sexes in dispersal trait value occurs (Fig. 3; for a thorough analysis of the spatial distribution of the individuals in our simulation, see Appendix 1).

The χ^2 test confirmed that there was no correlation between the initial dispersal trait value and the evolved trait value within the evolving sex and across all scenarios, thus evolution of these traits converged in our simulations (scenario I for males $p = 0.564$, scenario II for females $p = 0.700$, scenario III for males $p = 0.702$ and females $p = 0.240$).

We initiated 500 replicates for each of the three coevolutionary scenarios and at least 2/3 of these persisted for 1000 time units (333, 391 and 386, respectively; Fig. 4). Non-persisting populations usually went extinct already during the settlement period (50.9, 77.1, and 78.1% respectively). In all three scenarios, extinctions of these populations were

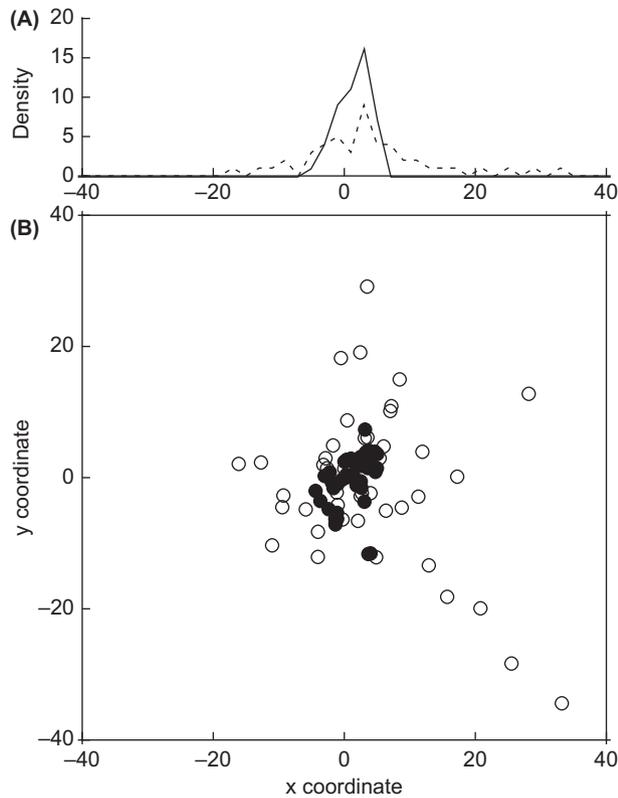


Figure 3. The spatial structure of a population with a strong bias in sex-specific dispersal distances after a settlement period of 20 generations (model 2). To produce this figure neither males (•) nor females (◦) were allowed to evolve to deviate from initial values which were set at $D_F = 9.82$, $D_M = 0.82$. The upper figure shows the distribution of females (dotted line) and males (solid line) along the x-coordinate. Other parameter values: $d_{\text{mate}} = d_{\text{comp}} = 1$, $\mu_0 = 1.5$, $\alpha = 0.05$, $m = 0.01$, $\sigma^2 = 0.3$.

associated with one of the sexes starting with a too short mean dispersal distance. There was also an asymmetry between the sexes: when males initially did not disperse far but females did, populations were more likely to go extinct than when females initially did not disperse far but males did. Populations that went extinct past the settlement period were mostly cases where females were forced to disperse too far without a possibility for them to evolve shorter distances. In these cases extinction was largely independent of the dispersal distance of males (Fig. 4A).

Signs of coevolution were found in all three scenarios. Males evolved to disperse further when females were fixed to use longer dispersal distances (Fig. 4A). Likewise, females evolved to disperse further when longer dispersal distances were imposed on males (Fig. 4B). Spearman rank correlation coefficients between means of male and female dispersal kernels in scenario I and II were positive (0.344, and 0.541, respectively, both $p < 0.001$). The positive correlation between evolved means of female and male dispersal kernels also emerged in scenario III where both sexes were free to coevolve (Fig. 4C, Spearman rank correlation 0.4796, $p < 0.001$).

Figure 4 also shows the direction of selection in sex-specific dispersal kernels in persisting populations. Compared with the white area, dots group closer around the diagonal

(which indicates no bias and $D_M = D_F$), except for the ones that had dispersal of one sex fixed at a long distance. Moving closer to the diagonal indicates a reduction of the bias in mean sex-specific dispersal distance.

The range of the trait values for sex-specific dispersal kernel is reduced after evolution in all three scenarios (Fig. 5A–C). In scenario I, where females were fixed, males adapted to dispersal distances which were more similar with dispersal distances of the females (Fig. 5A). In scenario II the same pattern occurred with reversed roles of the sexes, but it was less strong (Fig. 5B). Also we found an asymmetry between scenario I and II: when males dispersed on average further than females, females were not adapting so close to dispersal distance of males.

Discussion

Our model shows a so far overlooked force in sex-specific dispersal evolution: male and female dispersal kernels can coevolve due to mate-location failures. Our thought experiment shows why this should be the case in a population with discrete habitat patches and discrete generations, while the individual-based model shows that the effect can be visible in a very different arrangement with continuous space and time. Under all investigated scenarios, dispersal distances in one sex exerted a selection pressure on the opposite sex, the response of which is shown by the correlation between the mean of dispersal kernels. This coevolution occurs because more similar sex-specific dispersal kernels lead the sexes to match each other's distribution better when individuals spread across space. This benefits each individual in a manner analogous to ideal free distribution theory (Holt and Barfield 2001). A kernel that evens out male and female distributions reduces the variance in the local sex ratio which has positive fitness consequences for both sexes. Tracking the dispersal distance of the opposite sex lowers the risk for a dispersing individual to end up at a location of unfavorable sex ratio, or at the extreme, at a location with no potential mates at all.

Coevolution of the sexes might attenuate any extreme bias in sex-specific dispersal distances. It does not mean that sexes are predicted to have identical dispersal kernels – indeed, our models rarely produced an outcome this strong. Factors like inbreeding, kin competition avoidance or sex-specific benefits of philopatry are well acknowledged explanations for sex biases in dispersal (Motro 1991, Lehmann and Perrin 2003, Handley and Perrin 2007, Bonte et al. 2009). As we show here, coevolution between the sexes in dispersal kernel is another factor which tends to reduce sex bias in dispersal, and thus, it has the potential to mitigate such bias-promoting factors.

To show that it is important for both sexes to adapt towards more similar dispersal kernels we ran three scenarios. Within two of these we artificially imposed a fixed dispersal kernel on females or males and let the other sex evolve. In both scenarios, when males or females were forced to use a fixed dispersal kernel, it had an effect on the evolved dispersal distances in the opposite sex. Given that many authors describe a hierarchy where the spacing of females follows the spacing of breeding resources (not males) and males seek females (Emlen and Oring 1977, Shuster and Wade 2003),

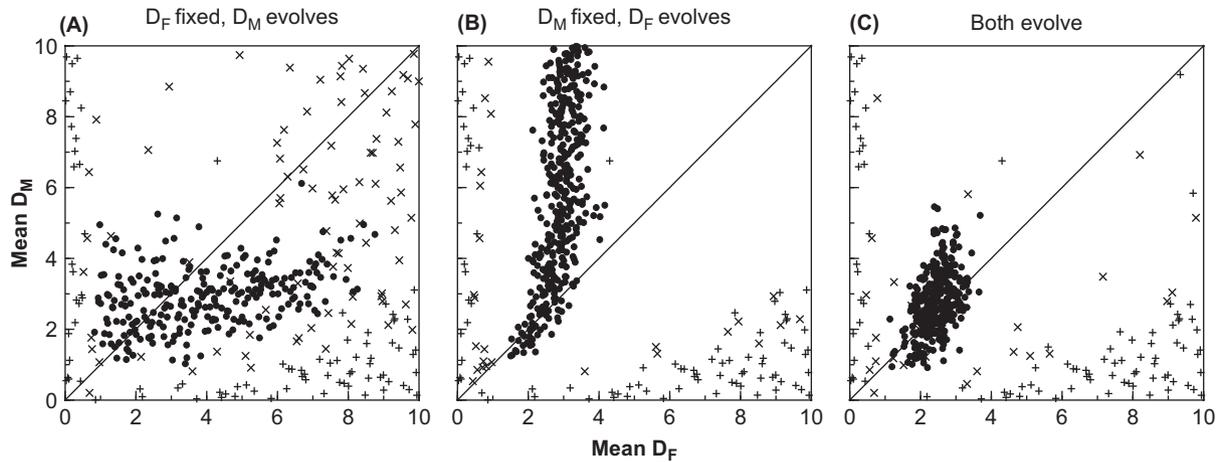


Figure 4. Results of 500 simulations for each of three scenarios: males could adapt to the fixed dispersal kernel of females (A), females could adapt to the fixed dispersal kernel of males (B), and both sexes were free to evolve (C). Simulations were run for a single set of parameters ($d_{\text{mate}} = d_{\text{comp}} = 1$, $\mu_0 = 1.5$, $\alpha = 0.05$, $m = 0.01$, $\sigma^2 = 0.3$); they differed only in the combination of initial mean of the dispersal kernels of males and females. Symbols indicate the initial mean of the dispersal kernels of populations that went extinct during the settlement period (+), during the time we simulated evolution (x), and the evolved means of the population that persisted (*). The smaller the bias in sex-specific dispersal in a population the closer the symbols are to the diagonal (solid line). The white areas (where + and x are missing) show the parameter space where populations were viable.

it may appear surprising that in our results both sexes adapt in relation to the dispersal kernel of the opposite sex. This is explicable: after most dispersal moves females may not experience much mate-finding difficulties at a new location in reality. Yet, if we consider dispersal kernels that include long distances too, we find conditions where also females run into risk of remaining mate-less: active mate searching by males will not help females if no such males exist nearby. Newer studies have indeed pointed out that spatiotemporal varia-

tion associated with dispersal can easily create conditions in which females too run the risk of remaining mateless (Calabrese et al. 2008, Fagan et al. 2010).

We incorporated minimal sex differences in our model as the life history of each sex was largely identical. However, there is an important difference in how easily mate availability guarantees reproduction in each sex. Mate availability only begins to limit female reproduction in our model when $n_{\text{mate}} = 0$, whereas for males $n_{\text{mate}} > 0$ does not yet guarantee

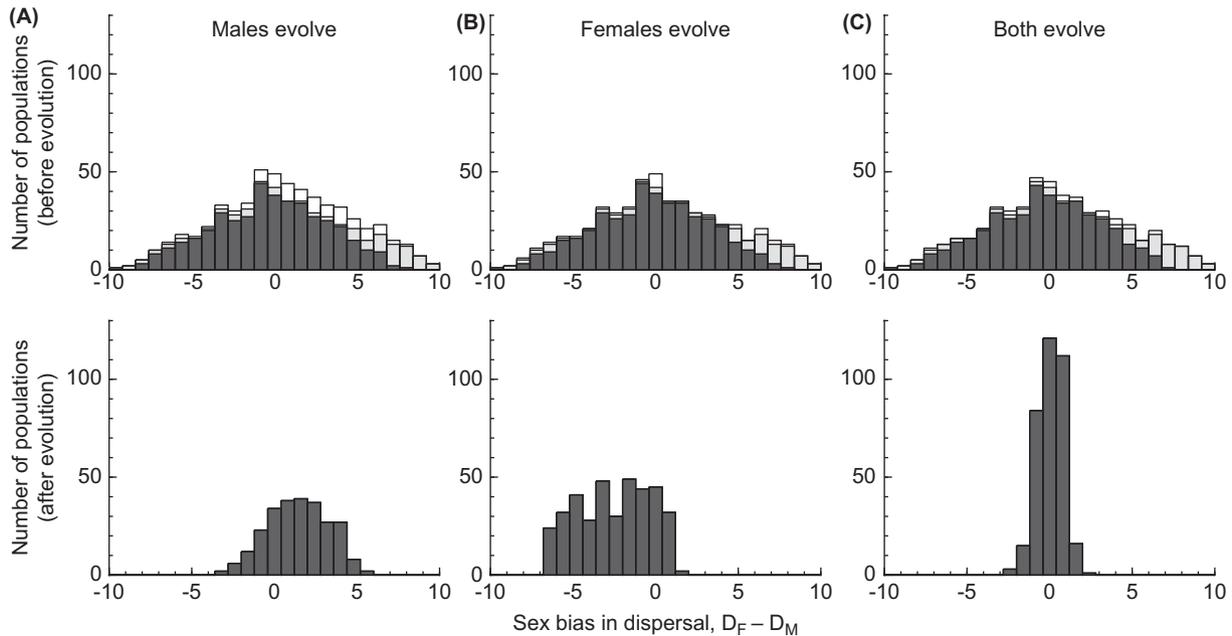


Figure 5. The number of viable (black bars) and extinct populations during settlement period (grey bars) and during the time we simulated evolution (white bars) across the bias in sex specific dispersal ($D_F - D_M$) for the three scenarios (A–C). The range of the bias in sex specific dispersal for populations that are viable after settlement period is -8.67 to 7.83 , -8.67 to 7.39 , and -8.67 to 6.76 for the three scenarios (upper plots) and it is reduced after evolution: -3.97 to 5.13 , -7.19 to 0.84 , -3.06 to 1.69 in all three scenarios (lower plots). Parameter values as in Figure 4.

a mating because another male may be located closer to the female and this male will mate with her instead. (There are also other reasons why an individual might fail to reproduce – e.g. dying before a reproductive event is scheduled to take place in the Gillespie process – but these other reasons have no built-in sexual asymmetry). This sexual asymmetry does not prevent coevolution of the sexes, however, it means that population persistence is less dependent on well adapted dispersal behavior of males than females (among persisting populations we observed long fixed mean dispersal distances in males but not in females). Obviously, we have to keep in mind that a different mating system than the one we used could lead to somewhat different predictions. However, it is not clear why variations would destroy the need to co-adapt, although mating systems where mate searching occurs before dispersal, or systems with facultative asexuality, form clear exceptions.

Why has this selective force, which pulls dispersal kernels closer together, not been discussed in studies of sex-biased dispersal so far? As Ronce (2007) pointed out, dispersal models still often, somewhat paradoxically, do not include an explicit consideration of space, and this may lead to important processes remaining hidden. Many models (starting from the classic study of Hamilton and May 1977) assume an island population model and treat dispersal as movement from a natal patch to ‘elsewhere’. These models assume patches to be identical across space in terms of density. This kind of treatment is common in models predicting sex-biased dispersal too (Perrin and Mazalov 2000, Leturque and Rousset 2003). Because the local sex ratio cannot vary in such models, it is perhaps not surprising that the interdependency of selection has not been discovered in the literature so far. Our findings indeed rest on explicitly considering the variation in local sex ratio in our model, and thus, we observed a different evolutionary outcome for the evolution of the shape of the dispersal kernel.

There are many empirical examples where a population-wide constant sex ratio does not hold. Bird populations often exhibit strongly male-biased sex ratios in small habitat fragments (Dale 2001, Ahlering and Faaborg 2006) or areas near the edge of the species range (Steiffetten and Dale 2006). This pattern arises easily (and without the need to have biased primary sex ratios) because most bird populations have female-biased mortality (Liker and Szekely 2005) leading to male-biased adult sex ratios (Donald 2007). Beside systematic life history differences between the sexes, spatial variation in sex ratio can also be increased by mere demographic stochasticity.

Our findings also call for a greater integration of studies of dispersal and mate-location. While dispersal and mate searching are not synonymous (Langellotto and Denno 2001), they share certain characteristics: at the very least both involve locomotion. Thus, while our model, in which individuals move in random directions, does not consider mate-searching explicitly, it highlights potential intriguing interactions between dispersal and mate location: if one sex mate-searches very efficiently then this reduces selection in the other sex to spend effort in searching (Kokko and Wong 2007). This tendency for the sexes to diverge rather than converge in movement traits is in stark contrast with our current findings, and highlights that the answers depend on

scale and also on whether reproduction is allowed to occur during the movement phase of an individual’s life (as in mate-searching models) or not (as in dispersal models like ours). In other words, a far moving individual in our current model was assumed not to gain reproductive success along the way, while this can happen in mate-searching models where movement rates increase mate encounter rates (Kokko and Wong 2007, Kiorboe and Hirst 2008).

Future work that combines global movement (dispersal) with local interactions that determine how mating pairs form (mate searching) could prove interesting, not only because of the interacting spatial scales, but also because the relevant traits may be genetically linked. An individual with good locomotory capacity can conceivably reduce its dispersal costs and simultaneously perform efficient mate search, and such correlations may have intriguing consequences for mobility in the opposite sex. We thus encourage more work to be conducted to combine these spatiotemporal scales, both empirically and theoretically.

Further, we suggest that our mechanism should be investigated in combination with factors that promote the evolution of biases in sex-specific dispersal. In the present work our intention was to prove the principle that coevolution between the two sexes can happen and that it has the potential to reduce dissimilarity in the dispersal behavior of the two sexes. A next step would include an analysis of how much it counteracts factors like inbreeding, kin competition avoidance or different benefits of philopatry, which are known to promote sex differences in dispersal traits.

Acknowledgements – We are greatly indebted to Wouter K. Vahl for his substantial contribution which increased the quality of this manuscript immensely. We thank CSC – IT center for science, in Espoo, Finland for the use of their computer-cluster facilities. CMM and HK were funded by the Academy of Finland, HK additionally by the Australian Research Council, and JS was funded the Finnish School in Wildlife Biology, Conservation and Management (LUOVA).

References

- Ahlering, M. A. and Faaborg, J. 2006. Avian habitat management meets conspecific attraction: if you build it, will they come? – *Auk* 123: 301–312.
- Berec, L. and Boukal, D. S. 2004. Implications of mate search, mate choice and divorce rate for population dynamics of sexually reproducing species. – *Oikos* 104: 122–132.
- Bonte, D. et al. 2009. Sex-specific dispersal and evolutionary rescue in metapopulations infected by male killing endosymbionts. – *BioMed. Central Evol. Biol.* 9: 16.
- Bowler, D. E. and Benton, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. – *Biol. Rev.* 80: 205–225.
- Cadet, C. et al. 2003. The evolution of dispersal under demographic stochasticity. – *Am. Nat.* 162: 427–441.
- Calabrese, J. M. et al. 2008. Reproductive asynchrony in natural butterfly populations and its consequences for female matelessness. – *J. Anim. Ecol.* 77: 746–756.
- Contarini, M. et al. 2009. Mate-finding failure as an important cause of Allee effects along the leading edge of an invading insect population. – *Entomol. Exp. Appl.* 133: 307–314.
- Cousens, R. et al. 2008. Dispersal in plants a population perspective. – Oxford Univ. Press.

- Dale, S. 2001. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. – *Oikos* 92: 344–356.
- Donald, P. F. 2007. Adult sex ratios in wild bird populations. – *Ibis* 149: 671–692.
- Emlen, S. T. and Oring, L. W. 1977. Ecology, sexual selection, and evolution of mating systems. – *Science* 197: 215–223.
- Fagan, W. F. et al. 2010. Reproductive asynchrony in spatial population models: how mating behavior can modulate Allee effects arising from isolation in both space and time. – *Am. Nat.* 175: 362–373.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. – Oxford Univ. Press.
- Gandon, S. 1999. Kin competition, the cost of inbreeding and the evolution of dispersal. – *J. Theor. Biol.* 200: 345–364.
- Gillespie, D. T. 1977. Exact stochastic simulation of coupled chemical reactions. – *J. Phys. Chem.* 81: 2340–2361.
- Gillespie, D. T. 1992. *Markov processes: an introduction for physical scientists*. – Academic Press.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. – *Anim. Behav.* 28: 1140–1162.
- Gros, A. et al. 2008. Evolution of sex-biased dispersal: the role of sex-specific dispersal costs, demographic stochasticity and inbreeding. – *Ecol. Model.* 219: 226–233.
- Gros, A. et al. 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 May, R. M. 1977. Dispersal in stable habitats. – *Nature* 269: 578–581.
- Handley, L. J. L. and Perrin, N. 2007. Advances in our understanding of mammalian sex-biased dispersal. – *Mol. Ecol.* 16: 1559–1578.
- Hedrick, P. W. 2007. Sex: differences in mutation, recombination, selection, gene flow and genetic drift. – *Evolution* 61: 2750–2771.
- Hirota, T. 2007. The evolution of sexual difference in dispersal strategy sensitive to population density. – *Appl. Entomol. Zool.* 42: 173–179.
- Holt, R. D. and Barfield, M. 2001. On the relationship between the ideal free distribution and the evolution of dispersal. – In: Clobert, J. et al. (eds), *Dispersal*. Oxford Univ. Press, pp. 83–96.
- Kendall, B. E. and Wittmann, M. E. 2010. A stochastic model for annual reproductive success. – *Am. Nat.* 175: 461–468.
- Kiorboe, T. and Hirst, A. G. 2008. Optimal development time in pelagic copepods. – *Mar. Ecol. Progr. Ser.* 367: 15–22.
- Kokko, H. and Wong, B. B. M. 2007. What determines sex roles in mate searching? – *Evolution* 61: 1162–1175.
- Langellotto, G. A. and Denno, R. F. 2001. Benefits of dispersal in patchy environments: mate location by males of a wing-dimorphic insect. – *Ecology* 82: 1870–1878.
- Lehmann, L. and Perrin, N. 2003. Inbreeding avoidance through kin recognition: choosy females boost male dispersal. – *Am. Nat.* 162: 638–652.
- Leturque, H. and Rousset, F. 2003. Joint evolution of sex ratio and dispersal: conditions for higher dispersal rates from good habitats. – *Evol. Ecol.* 17: 67–84.
- Liker, A. and Szekely, T. 2005. Mortality costs of sexual selection and parental care in natural populations of birds. – *Evolution* 59: 890–897.
- McKay, M. D. et al. 1979. Comparison of 3 methods for selecting values of input variables in the analysis of output from a computer code. – *Technometrics* 21: 239–245.
- Morris, D. W. 1991. On the evolutionary stability of dispersal to sink habitats. – *Am. Nat.* 137: 907–911.
- Motro, U. 1991. Avoiding inbreeding and sibling competition – the evolution of sexual dimorphism for dispersal. – *Am. Nat.* 137: 108–115.
- Perrin, N. and Mazalov, V. 2000. Local competition, inbreeding and the evolution of sex-biased dispersal. – *Am. Nat.* 155: 116–127.
- Quinn, G. and Keough, M. 2002. *Experimental design and data analysis for biologists*. – Cambridge Univ. Press.
- Robinet, C. et al. 2008. Dispersion in time and space affect mating success and Allee effects in invading gypsy moth populations. – *J. Anim. Ecol.* 77: 966–973.
- Ronce, O. 2007. How does it feel to be a rolling stone? Ten questions about dispersal evolution. – *Annu. Rev. Ecol. Evol. Syst.* 38: 231–253.
- Schmidt, K. A. et al. 2000. Habitat selection under temporal heterogeneity: exorcizing the ghost of competition past. – *Ecology* 81: 2622–2630.
- Shuster, S. M. and Wade, M. J. 2003. *Mating systems and strategies*. – Princeton Univ. Press.
- South, A. B. and Kenward, R. E. 2001. Mate finding, dispersal distances and population growth in invading species: a spatially explicit model. – *Oikos* 95: 53–58.
- Steiffetten, O. and Dale, S. 2006. Viability of an endangered population of ortolan buntings: the effect of a skewed operational sex ratio. – *Biol. Conserv.* 132: 88–97.
- Travis, J. M. J. and Dytham, C. 1998. The evolution of dispersal in a metapopulation: a spatially explicit, individual-based model. – *Proc. R. Soc. B* 265: 17–23.
- Travis, J. M. J. et al. 1999. The evolution of density-dependent dispersal. – *Proc. R. Soc. B* 266: 1837–1842.
- West, S. A. 2009. *Sex allocation*. – Princeton Univ. Press.

Supplementary material (available online as Appendix O19487 at www.oikos.oikosoffice.lu.se). Appendix 1.