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Mate finding, Allee effects and selection for sex-biased dispersal

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Summary

1. Although dispersal requires context-dependent decision-making in three distinct stages (emigration, transit, immigration), these decisions are commonly ignored in simple models of dispersal. For sexually reproducing organisms, mate availability is an important factor in dispersal decisions. Difficulty finding mates can lead to an Allee effect where population growth decreases at low densities.

2. Surprisingly, theoretical studies on mate finding and on sex-biased dispersal produce opposing predictions: in the former, one sex is predicted to move less if the other sex evolves to search more, whereas in the latter, mate-finding difficulties can select for less sex bias in dispersal when mate finding occurs after dispersal.

3. Here, we develop a pair of models to examine the joint evolution of dispersal and settlement behaviour.

4. Our first model resolves the apparent contradiction from the mate search and dispersal literatures. Our second model demonstrates that the relationship between mating system and sex-biased dispersal is more complex than a simple contrast between resource defence monogamy and female defence polygyny.

5. Our results highlight that a key factor is the timing of mating relative to dispersal (before, during, or after). We also show that although movement has the potential to alleviate a mate-finding Allee effect, in some cases, it can actually exacerbate the effect.

Key-words: context-dependent dispersal, mate searching, mating system, movement, philopatry, settlement, sperm competition

Introduction

Dispersal, the movement of an individual between habitat patches, is a fundamental characteristic of organisms that links individuals and populations. Individuals disperse, influencing the spatial, genetic, social and demographic structure of populations, which can in turn change the dispersal strategies favoured by selection (Starrfelt & Kokko 2012). Understanding both the causes and consequences of dispersal is central to being able to understanding spatial population dynamics and predicting how species will respond to environmental change (Bowler & Benton 2005). For sexually reproducing species, developing proper insight also necessitates understanding sex-specific dispersal rates and distances and the consequent prospects of mate finding (Thomas, Hill & Lewis 1998; South & Kenward 2001; Miller *et al.* 2011).

There is currently a mismatch between our empirical and theoretical understanding of the complexity of dispersal (Travis *et al.* 2012). Empirical evidence suggests that during dispersal, individuals make context-dependent decisions at three stages: when to leave, where and how far to travel, and when and where to settle (Bowler & Benton 2005). Furthermore, individuals face different costs and trade-offs associated with each of these stages (Bonte *et al.* 2012). However, models of dispersal tend to be extremely simplified, often depicting it as a one-shot movement (Travis *et al.* 2012). While every model must present a simplified perspective (by definition), consistently building models with the same types of assumptions restricts our ability to understand the processes described

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by those models. A more detailed theoretical exploration of the various dispersal stages could provide a great deal of insight into the causes and consequences of dispersal.

Settlement is perhaps the least studied of the three stages (Travis *et al*. 2012), yet research that has included this stage has found settlement rules to be important. Theory predicts that selection favours settlement rules that are based on local density (Poethke, Gros & Hovestadt 2011), conspecific breeding success (Boulinier & Danchin 1997) or time spent dispersing (Baker & Rao 2004), over naive settlement rules. Density-dependent settlement rules can act to both stabilize population dynamics (Ruxton & Rohani 1998) and cause density-dependent variation in dispersal kernels (Gilroy & Lockwood 2012).

Although the causes of sex bias in dispersal have attracted extensive theoretical attention, much of these studies focus on the evolution of sex differences in emigration rates (i.e. whether individuals leave their natal area). Asymmetric costs of dispersal, either to the dispersing individuals themselves (Gros, Hovestadt & Poethke 2008) or to their parents (Liberg & von Schantz 1985), can lead to sex bias in emigration rates. Two key aspects of the cost of staying vs. emigrating are the relative strength of resource competition compared with mate competition (Perrin & Mazalov 2000) and the relative variance in reproductive success between the sexes (Gros, Poethke & Hovestadt 2009). Inbreeding avoidance also favours emigration by one sex and philopatry by the other, but inbreeding alone does not indicate which sex should leave and which should stay (Perrin & Mazalov 1999).

Intriguingly, settlement rules are not typically evaluated with respect to mate availability (for a rare exception see Gilroy & Lockwood 2012), even though the availability of potential mates should be a key determinant of fitness for sexually reproducing organisms. An individual's ability to find mates has repercussions both for the individual and for the population. Mate-finding difficulties can lead to an Allee effect (reviewed in Gascoigne *et al*. 2009; Kramer *et al*. 2009; Fauvergue 2013) where individual fitness and population growth rate decrease at low densities (Stephens, Sutherland & Freckleton 1999). Allee effects influence a number of key ecological processes, such as the spread of invasive species (Taylor & Hastings 2005; Johnson *et al*. 2006; Krkošek *et al*. 2012), control of pest species (Liebhold & Bascompte 2003; Tobin, Berec & Liebhold 2011) and the viability of endangered species (Wells *et al*. 1998; Courchamp, Berec & Gascoigne 2008).

The lack of studies on sex-specific settlement rules is not the only rationale behind our study; we have also identified a curious mismatch between two sets of literature, both containing two-sex movement models. Contradictions in the literature make it difficult to form general predictions of sex biases based on evolutionary studies of mate finding and dispersal. One movement pattern is found in theory on active mate searching. This field has long sought to understand why one sex searches more than the other (Hammerstein & Parker 1987; Kokko & Wong 2007), and why this sex is often (but not always, McCartney *et al*. 2012) the male. These studies show unambiguously that if one sex takes on a greater search effort, the other is selected to reduce risky mate-finding activities. This suggests that we should often find great sex differences in mobility as well as dispersal (if mate-searching mobility occurs at a scale that is interpretable as dispersal). A second predicted pattern arises from the literature on dispersal distances and shows the opposite: if dispersal is influenced by mate-finding prospects, then there is selection for the two sexes to have similar dispersal kernels (Meier, Starrfelt & Kokko 2011). This appears to contradict the findings from the mate search literature. Finally, taxonomic differences in dispersal sex biases have been hypothesized to reflect differences in mating systems (Greenwood 1980), but explicit considerations of the mating system in formal models of dispersal distance appear very rare (most theory uses the simplifying assumption of asexual reproduction).

Our aim is twofold. First, we aim to resolve the apparent contradiction that arises when contrasting the evolutionary predictions from the mate search literature with those of sex-specific dispersal distances, by asking whether movement of males and females is positively or negatively correlated (i.e. does mate finding lead to amplified or diminished sex biases in dispersal). For maximum clarity, this is done in a simplified setting (a toy model). Second, we relax several unrealistic assumptions of the toy model (e.g. no evolution in the settlement rules of one of the sexes). Building a more complete individual-based model allows us to relate sex biases in dispersal to varying assumptions regarding multiple mating, sperm competition and the timing of matings relative to dispersal (prior to, during or after dispersal). We also show that increased movement can act to either exacerbate or alleviate the mate-finding Allee effect present in our model.

Model 1: Linking mate searching to dispersal

RATIONALE: TWO SETS OF LITERATURE DO NOT ADD UP

In the mate search literature, Hammerstein and Parker (1987) developed a game-theoretic model to determine search strategies for males and females. They showed that there are two alternative evolutionarily stable strategies: one where only males search and another where only females search. In other words, if one sex searches, the other is favoured to not search. Empirical evidence suggests that male-search is more common than female-search across species, an asymmetry that is left unexplained by this model. A more recent study by Kokko and Wong (2007) used a time-in/time-out modelling framework to consider the evolutionarily stable search efforts for both females and males. They assume that mating rate is a function of both female and male search, and that individuals incur a mortality cost proportional to their searching effort. The results of Kokko and Wong (2007) match those of Hammerstein and Parker (1987) when similar assumptions are made, but also demonstrate that including sperm competition (females mate multiply) creates an asymmetry favouring male movement over female movement. McCartney *et al.* (2012) extend this model to include benefits to multiply mating females, which can lead to more mobile females and less mobile males. Again, the feedback between the sexes takes the form that one sex can move less if the other moves more.

In the dispersal distance literature, Meier, Starrfelt and Kokko (2011) developed a dispersal model to explore the co-evolution of male and female dispersal kernels. They showed that when individuals inhabit a landscape of patches that differ in quality (i.e. have patch-specific survival rates), emergent local variation in sex ratio can select against sex-specific dispersal rates or distances. For example, if females disperse more than do males, this creates selection on males to disperse more. This result stems from the fact that, due to environmental heterogeneity, individual-rich patches will have a surplus of the less dispersing sex after individuals of the more dispersing sex have departed (and this is not fully compensated for by immigration, as patches were assumed to vary in productivity). The results hold whether space is modelled as patches or as continuous variation in habitat quality (Meier, Starrfelt & Kokko 2011).

These two types of models generate opposite predictions about the way sex biases in dispersal emerge. Are these sex biases an almost unavoidable consequence of the mate finding process as mate search models seem to imply, or does mate finding instead diminish sex biases (which then have to have other causes) as the dispersal models by Meier, Starrfelt and Kokko (2011) suggest?

MODEL 1

Our model is based on settlement rules rather than using a predefined dispersal kernel, dispersal rate or mate search efficiency. Consequently, dispersal characteristics such as emigration rate and the number of dispersal steps are emergent properties in our model. Individuals inhabit a world of discrete patches. All individuals (both males and females) make dispersal decisions by choosing to stop dispersing and settle in a patch based on that patch's sex ratio. Note that since an individual can potentially choose to 'stop' before leaving its natal patch, the possibility of no dispersal is included as an option. Our model does not include any of the dispersal complexities of social species: we assume individuals are solitary, non-territorial, and do not form groups.

As the aim of this first model is to make a simple conceptual point, we assume that female settlement rules are given (do not evolve), and we track the evolution of male rules. Male fitness is equal to the sex ratio (mate-to-competitor ratio) in the patch where the male stops; we do not make any further assumptions about mating and reproduction; we consider these in our second model below.

During dispersal, an individual evaluates the mate-to-competitor ratio of its current patch (the ratio of males, n_{M}, to females, n_{F}, for female dispersal and the ratio of females to males for male dispersal) and either settles (with probability given below) or moves to another patch within the world, chosen at random (i.e. dispersal is global). An individual will not exceed a maximum number of dispersal steps ($s_{\max}$).

The probability that an individual settles in a patch (for steps below the maximum number) is given by

$$P_{\mathrm{F}} = \frac{1}{1 + e^{a\left(R_{\mathrm{F}} - \frac{n_{\mathrm{M}}}{n_{\mathrm{F}}}\right)}} \text{ for females,} \qquad \text{eqn 1a}$$

and

$$P_{\mathrm{M}} = \frac{1}{1 + e^{a\left(R_{\mathrm{M}} - \frac{n_{\mathrm{F}}}{n_{\mathrm{M}}}\right)}} \text{ for males,} \qquad \text{eqn 1a}$$

both being logistic functions of the mate-to-competitor ratio in a patch, which equals $n_{\mathrm{M}}/n_{\mathrm{F}}$ for females and $n_{\mathrm{F}}/n_{\mathrm{M}}$ for males (Fig. 1a). The settlement probability states that an individual is more likely to stop dispersing if it encounters a patch with a favourable mate-to-competitor ratio; the shape of the function is described by parameter a, which we assume not to vary across individuals. The potentially evolving parameter is R (R_{F} for females and R_{M} for males), which indicates the mate-to-competitor ratio that is sufficient to yield 50% settlement probability. (Negative values of R indicate that an individual is more than 50% likely to settle for any sex ratio it encounters.) R is interpretable as a measure of 'restlessness' during dispersal: small values of R lead to very little movement as almost any mate-to-competitor ratio is sufficient to prompt settlement (leftmost curve in Fig. 1a), intermediate values lead to discriminating behaviour where high mate-to-competitor ratios prompt settlement but low values do not (Fig. 1a, middle curve), and high values of R mean the individual keeps moving unless it encounters extremely favourable mate-to-competitor ratios (Fig. 1a, rightmost curve), or if a maximum number of dispersal steps have already been taken ($s_{\max} = 5$). We sum up the effect of R as the average number of dispersal steps. A value of 0 indicates that individuals generally do not leave their natal patch, a value of $s_{\max}$ indicates that individuals generally disperse blind-to-sex ratios, and a value between 0 and $s_{\max}$ indicates that individuals generally choose to stop dispersing and settle in a patch in response to its mate-to-competitor ratio.

The model is run in a world made up of 1000 patches and one of two sets of initial conditions: homogeneous (each patch starts with exactly 15 individuals) and heterogeneous (each patch starts with a random number of

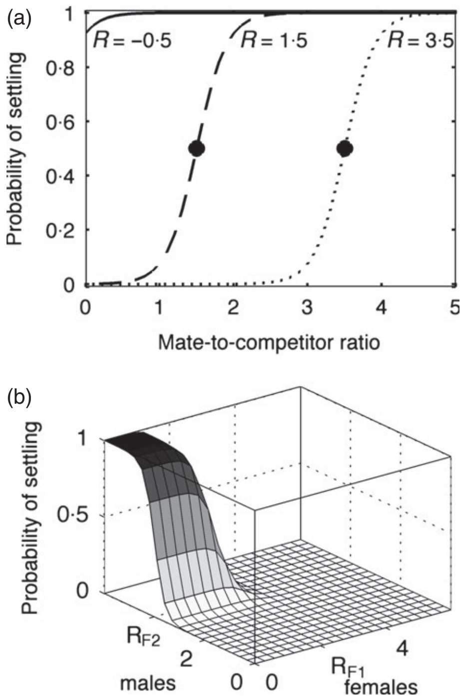

Fig. 1. The probability that an individual settles in a given patch for (a) Model 1 and (b) Model 2. In both panels, the shape parameter is $a = 5$. (a) The settlement probability is a function of the local mate-to-competitor ratio. An individual's 'restlessness', R, is defined by the location of the mid-point of this probability function (indicated by the dots); three examples are shown here ($R = -0{\cdot}5$, $1{\cdot}5$, and $3{\cdot}5$). (b). The settlement probability is a function of the local number of males and females, where females are more likely to settle for more males and fewer females (shown) and males are more likely to settle for fewer males and more females (not shown). An individual's strategy R_1 and R_2 are defined by the location of the mid-point of this probability function with respect to females and males, respectively.

individuals, drawn from a uniform distribution between 0 and 30). The sex of each individual is assigned at random, such that the overall population contains equal numbers of males and females. Individuals disperse serially, in random order, with all females in the world dispersing first, then males, one at a time.

We calculate the fitness of each male immediately after it finishes dispersing. The evolution of the male strategy was examined iteratively as follows. We initialized simulations with a population where the female strategy was fixed, and all males played the same resident strategy of $R_M = 0$. We then calculated the expected fitness of a mutant male playing either this resident strategy or a slightly different mutant strategy (for each residential R_M value, we tried five different mutant strategies: $R_M - 0{\cdot}1$, $R_M - 0{\cdot}05$, R_M, $R_M + 0{\cdot}05$, $R_M + 0{\cdot}1$). The mutant strategy with the highest average fitness (across all males in the population) was set to be the new resident strategy. This process was iterated 25 times. During the last iteration, we quantified the average number of dispersal steps taken by males and females. We ran simulations for different 'female restlessness' values: R_F ranged from -4 to 6, with 100 replicates for each value.

RESULTS

Unsurprisingly, the average number of dispersal steps taken by females increased as a function of female restlessness in both homogeneous and heterogeneous environments (Fig. 2, grey lines). Low female restlessness ($R_F \leq 0$) produced a probability of settling that was close to 1 for essentially all possible patch sex ratios (Fig. 1a), so females typically stopped in their natal patch (0 dispersal steps). Female restlessness values that exceeded 2 led to a near-zero probability of settling for most sex ratios likely to be experienced (Fig. 1a), so females typically travelled as long as possible before stopping ($s_{\max}$).

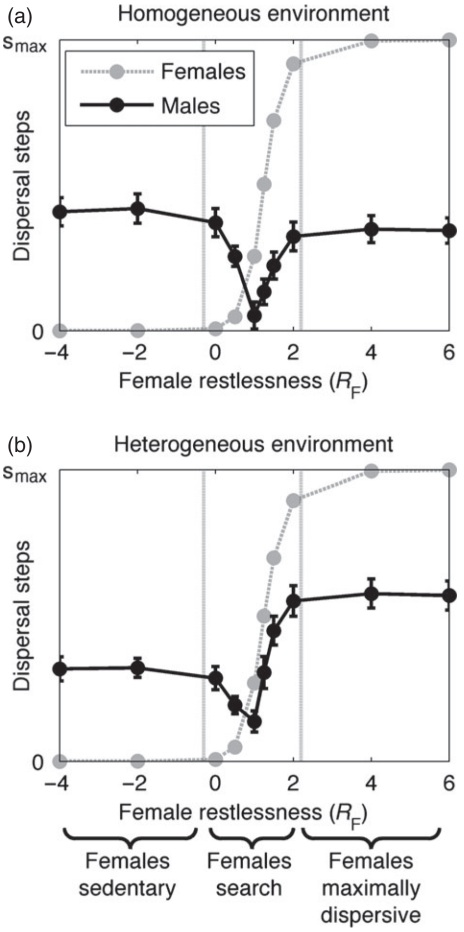

Fig. 2. The number of dispersal steps taken by females (grey lines) and males (black lines) as a function of female strategy (R_F) at the end of evolutionary simulations (25 iterations) of Model 1 with $a = 5$ and $s_{max} = 5$, in (a) homogeneous and (b) heterogeneous environments. Male strategy ('restlessness') evolves in response to different fixed female strategies (see Fig. S1, Supporting information). Points show the average number of dispersal steps across 100 replicates with bars showing standard deviation.

If female restlessness was either very low ($R_F < 0$) or very high ($R_F > 2$), the results mainly depended on whether the environment was homogeneous or heterogeneous (Fig. 2). In homogeneous environments (Fig. 2a), males evolve to use *c*. 40% of the maximum permitted number of dispersal steps (*c*. 40% of s_{max}) either when females disperse very little or when they are maximally dispersive. This pattern is different in heterogeneous environments (Fig. 2b) where males dispersed longer when females dispersed longer. This shows that our model is able to replicate a central result of Meier, Starrfelt and Kokko (2011): if the environment is spatially variable, and dispersal blind-to-local sex ratios, then dispersal by females selects for males not to be 'left behind'. If the environment is constant across space, this particular cost to staying in one patch does not arise, because departing females will be (on average) replaced by arriving females.

If the result of Meier, Starrfelt and Kokko (2011) was the only factor at play, we would predict a pattern where Fig. 2a shows no response of males to female restlessness, and Fig. 2b shows an increase. Intermediate female restlessness values, however, produced a clear dip in male restlessness: males evolved to remain relatively stationary in the only region of female behaviour where female settlement is sensitive to the number of males per female in a patch (in other regions, females are either sedentary or move always as much as the model permits them). As females are assumed to disperse first, and R values close to 1 mean that they settle in response to the local mate-to-competitor ratio, the correct interpretation of this scenario is that they move to where the males are, that is, perform the 'searching' for males. Consequently, males evolve to become sedentary (very low restlessness).

As a whole, therefore, the toy model combines a large-scale pattern where males become more dispersive when females disperse longer (but only when habitats are heterogeneous), as well as the opposite response in the part of the parameter region where female behaviour leads females close to males. Whether the scenario in Meier, Starrfelt and Kokko (2011) applies or that of mate search models, depends on whether the female movement strategy is easily interpretable as searching (in a manner that removes males' need to move to locate females). The female strategy is only sensitive to the local male-to-female ratios in the middle part of Fig. 2a,b, and here, the predictions from the mate search literature hold.

The results of this toy model indicate that there is no contradiction between the theoretical predictions of dispersal theory and mate search theory. However, this model only presents part of the picture. To gain deeper understanding, we must look at the co-evolution of male and female strategies.

Model 2: Coevolutionary simulations

Our toy model above did not inspect the possibility that models can also produce different conclusions due to differences in where, and when, matings and reproduction happen relative to dispersal. Mate-finding models assume that mating rate is an increasing function of time or effort spent searching. Meier, Starrfelt and Kokko (2011) assume individuals travel a fixed dispersal distance before settling and mate with any available individuals of the opposite sex near their final location; mating success is thus not necessarily higher if an individual has moved more. Given the general appeal of the idea that the mating system can impact sex differences in dispersal (Greenwood 1980; Dobson 1982; Clarke, Sæther & Røskaft 1997), it appears necessary to investigate several alternative temporal arrangements of dispersal and mating, and multiple mating by females and/or males.

MODEL 2

In order to fully understand the interaction between mating and movement, our second model incorporates the actual processes of mating and reproduction. To do this, we left several features of the toy model unchanged: the world consists of 1000 patches as before; we now considered them all to be homogeneous. As above, each individual has a settlement strategy that determines its probability of settling in a patch. However, this probability now depends separately on the number of females (n_F) and males (n_M) in a patch rather than just the sex ratio as in Model 1. The probability that an individual settles in a patch (for steps below the maximum number) is given by

$$P_F = \frac{1}{1 + 0{\cdot}5e^{-a(R_{F1}-n_F)} + 0{\cdot}5e^{a(R_{F2}-n_M)}} \text{ for females} \qquad \text{eqn 2a}$$

and

$$P_M = \frac{1}{1 + 0{\cdot}5e^{a(R_{M1}-n_F)} + 0{\cdot}5e^{-a(R_{M2}-n_M)}} \text{ for males} \qquad \text{eqn 2b}$$

with an example shown in Fig. 1b. Each individual's strategy now consists of two parameters (R_{F1} and R_{F2} for females and R_{M1} and R_{M2} for males). Since both sexes are free to evolve, we are now interested in evolved differences between average female and male parameters, and between female and male dispersal step number, as indicators of sex-biased dispersal.

We explored three sets of possibilities for the mating system and its interaction with dispersal, with a total of nine different mating 'scenarios':

1 SET #1, *post-dispersal mating*: Mating occurs after all individuals have settled, with two options:

#1.1 Reproduction occurs in monogamous pairs that form randomly within the settlement patch. In the case of an unequal sex ratio, some individuals of the surplus sex do not reproduce.

#1.2 Reproduction occurs polygynandrously; every offspring produced in a patch has a mother and a father randomly drawn from the individuals present. There is no reproduction in any patch that ended up with individuals of only one sex.

2 SET #2 *mate en route*: Each individual (male or female) mates during dispersal, with up to one mate per patch visited, and offspring are produced in the patch in which the mother settles. Paternity follows one of three options:

#2.1 The first male sires all the offspring of a female (first male sperm precedence).
#2.2 Each offspring produced by a female has its sire randomly drawn among all the males that the female has mated with (shared paternity).
#2.3 The last male sires all the offspring of a female (last male sperm precedence).

3 SET #3, *pre-dispersal mating*: Each female mates in her natal patch prior to dispersal and deposits eggs later, with four options:

#3.1 She mates with one male and deposits a fraction (set to $\frac{1}{1+s_{\max}}$) of her eggs in each patch she visits during dispersal and deposits the remaining eggs in the patch where she settles.
#3.2 She mates with up to 3 males (if available) and deposits eggs as in #3.1; sire of each egg is randomly drawn among the males she has mated with.
#3.3 She mates with one male and deposits all eggs in the patch where she settles.
#3.4 She mates as in #3.2 but deposits eggs as in #3.3.

Each mated female produces Poisson(b) offspring, where b is a fecundity parameter; each offspring develops randomly as a female or male. All parents die along with all but n of the offspring produced in each patch (competition occurs at the patch level). Mating and dispersal occur in the temporal order specified above. Individuals move one at a time in random order, not separated by sex (unlike in Model 1). Note for set #3 simulations, this means that immigrant males can be mates for any females who have not yet dispersed, potentially allowing males to mate in multiple patches. We assume the probability of surviving dispersal decreases with the number of steps taken, according to an exponential distribution with mean s. The parameter s then describes the expected 'safe' number of steps that an individual can disperse and still survive. Note this means that females who deposit eggs during dispersal (scenarios #3.1–3.2) are able to deposit some eggs, even if they die before settling. In our examples, we set s equal to 20 $s_{\max}$ (100) for both sexes unless otherwise indicated, which corresponds to *c*. 5% risk of dying for individuals dispersing the maximum number of dispersal steps, $s_{\max}$.

To simplify inheritance, we use haploid genetics where offspring inherit all four alleles (R_{F1}, R_{F2}, R_{M1} and R_{M2}) from the same parent (full linkage) at random with a small mutation in value (a Gaussian random number with mean 0 and standard deviation 0·05). For each simulation, we specified the starting values of R_{F1}, R_{F2}, R_{M1} and R_{M2} in the population and then evolved male and female strategies simultaneously for 500 generations (enough to typically ensure convergence). We then quantified the evolved strategies and the number of dispersal steps taken by males and females during the last simulated generation. We ran simulations under each of the nine mating scenarios above with four different sets of initial conditions for each (starting values set as: $R_{\mathrm{F1}} = R_{\mathrm{F2}} = R_{\mathrm{M1}} = R_{\mathrm{M2}} = 1$; $R_{\mathrm{F1}} = R_{\mathrm{M1}} = 1$, $R_{\mathrm{F2}} = R_{\mathrm{M2}} = 0$; $R_{\mathrm{F1}} = R_{\mathrm{M1}} = 0$, $R_{\mathrm{F2}} = R_{\mathrm{M2}} = 1$; $R_{\mathrm{F1}} = R_{\mathrm{M2}} = 2$, $R_{\mathrm{F2}} = R_{\mathrm{M1}} = 0$). These represent a range of conditions where individuals prefer to settle with at least 0–2 potential mates present (values for R_{F2}, R_{M1}) and not to settle with more than 0–2 potential competitors present (values for R_{F1}, R_{M2}). Initial conditions chosen outside of this range were generally unviable for at least one of the nine mating scenarios. (Full model code is available from Dryad, Shaw & Kokko 2014).

RESULTS

Post-dispersal mating favours unbiased dispersal

Set #1, where both mating and reproduction occurred after dispersal in each individual's settlement patch, led to unbiased dispersal. Both males and females dispersed a relatively few number of steps, indicating a settlement strategy sensitive to patch sex ratio (Fig. 3a, squares). Both males and females travelled slightly longer under polygynandry than monogamy (Fig. 3a, filled and open squares). The evolved dispersal strategies are shown in Fig. S2a,b (Supporting information).

Mating en route favours male-biased dispersal

In set #2, where mating occurred during dispersal, males travelled longer than in set #1, while females dispersal was not very different than in set #1 (Fig. 3a). Thus, mating en route clearly selects for male-biased dispersal.

Details of sperm competition matter when matings occur en route

The specific paternity pattern used to sire offspring (first or last male sperm precedence, or shared paternity) influenced male strategy and the resulting movement pattern in set #2. First male sperm precedence maximized male movement (Fig. 3a, triangles), and shared paternity led to only slightly less male movement (Fig. 3a, circles). In both of these cases, the probability of males settling in any patch was essentially zero, regardless of patch sex ratio

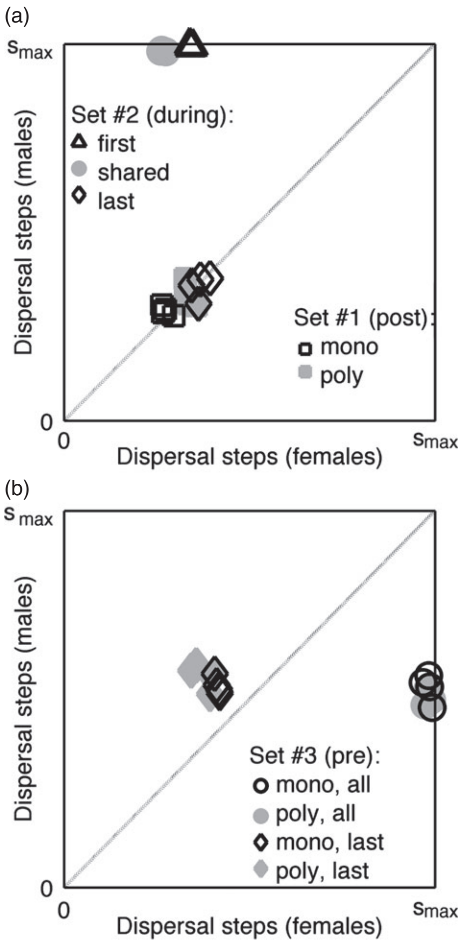

Fig. 3. The relationship between mating, reproduction and movement determines sex bias in dispersal. Each point shows the average number of dispersal steps (across the population) taken by females (*x*-axis) and males (*y*-axis) after 500 simulated generations of evolution with $n = 4$ offspring surviving per patch, $a = 5$, and $b = 10$. Scenarios where a single female's offspring are sired by single and (potentially) multiple males are indicated by open and filled symbols, respectively. Symbols in (a): Post-dispersal mating (squares), mating en route with first male sperm precedence (triangles), shared paternity (circles), and last male sperm precedence (diamonds); in (b): pre-dispersal mating with egg deposition in all patches visited (circles) or only in the last patch where the female (diamonds). The four different initial conditions per set of assumptions are each indicated by a separate symbol.

(Fig. S2c,d, Supporting information). Last male sperm precedence led to least dispersive males, and almost no sex bias in movement (Fig. 3b, diamonds; Fig. S2e, Supporting information); not too surprising as last male sperm precedence is equivalent to post-dispersal mating (set #1) whenever there is at least one male in the patch where a female settles.

Pre-dispersal mating can favour female-biased dispersal

In set #3, where mating occurred prior to moving, and females deposited eggs during dispersal, both males and females travelled longer than in set #1 (Fig. 3). The specific egg deposition pattern used (females deposit in all patches or last patch visited) influenced both the number of female dispersal steps as well as whether dispersal was male or female biased. When eggs were deposited en route, females dispersed as long as our modelling assumptions permitted them to do (Fig. 3b, circles), resulting in female-biased dispersal. Here, the probability of females settling in any patch was essentially zero, regardless of patch sex ratio (Fig. S2f,g, Supporting information). In contrast, if females could only deposit eggs once they settled, they settled sooner and the overall dispersal pattern was slightly male biased (Fig. 3b, diamonds). (Note that male dispersal is favoured since each female mates immediately prior to dispersing, allowing males who dispersed 'early' within the population order to increase mating opportunities by settling in a patch with a female-biased sex ratio.) Whether females mated with a single male or multiple prior to dispersal did not influence movement pattern (Fig. 3b, open vs. filled).

Mortality differences can amplify or diminish sex biases in dispersal

If dispersal is costlier for one sex than the other, this can potentially either amplify or diminish sex-biased dispersal, depending on the starting point (which may include a pre-existing bias due to all factors described above). For example, the 'deposit eggs en route' option of set #3.2 leads to female-biased dispersal, but increasing female dispersal mortality decreases female dispersal (while not affecting male dispersal), which diminishes this bias and

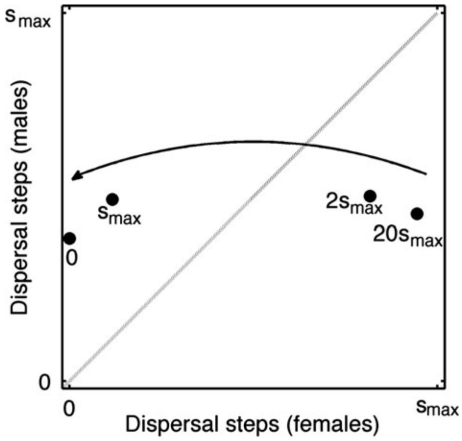

Fig. 4. Increasing asymmetry in mortality (indicated by the arrow) can either increase or decrease sex bias in dispersal. The average number of dispersal steps taken by females and males after 500 simulated generations of evolution with $a = 5$, $b = 10$, $n = 6$, using assumptions of set #3.2. The average number of 'safe' dispersal steps was held constant for males (at 20 s_{max}, where $s_{max} = 5$) and was varied for females (0, s_{max}, 2 s_{max}, and 20 s_{max}) as shown. Going from no asymmetry in mortality to a small asymmetry (from 20 s_{max} to 2 s_{max}) decreases the sex bias in dispersal, whereas increasing the asymmetry further (2 s_{max} to s_{max}) increases the sex bias.

even flips it to a male bias if the asymmetry in dispersal mortality is strong enough (Fig. 4).

Evolution can lead to movement that minimizes the Allee effect

We examined the influence of different movement strategies on the mate-finding Allee effect, by running a set of simulations where female and male strategies were held constant throughout the entire simulation, under mating scenarios #1.1 and #1.2. We ran two sets of simulations for each: one where male strategies (R_{M1} R_{M2}) were set to be the evolved values and female strategies were fixed at a range of different values ($-2{\cdot}5 \leq R_{F1}$, $R_{F2} \leq 3{\cdot}5$) and second one where female strategies were set to be the evolved values and male strategies were fixed at a range of different values ($-2{\cdot}5 \leq R_{M1}$ $R_{M2} \leq 3{\cdot}5$). At the end of 200 generations (these simulations were shorter since they did not include evolution), we quantified the fraction of mated females during the last generation, as a metric of strength of the mate-finding Allee effect (Calabrese & Fagan 2004). This reveals a pattern where too much or too little dispersal by one or both sexes renders the population unviable (Figs 5 and S3, Supporting information). Under monogamy, the proportion of unmated individuals varied more with respect to the strategy parameter corresponding to potential competitors (females in Fig. 5a, males in Fig. 5b) than with respect to the potential mates parameter (males in Fig. 5a, females in Fig. 5b). This can be understood intuitively: suboptimal decisions with respect to potential mates could result in individuals landing in a patch with no mates, leading to population collapse (white areas). In contrast, suboptimal decisions with respect to potential competitors could result in individuals landing in a patch with too many competitors, leading to a lowered mating probability, but probably not a population collapse. Under polygynandry, any female that landed in a patch with at least one male would mate, thereby removing this second effect in Fig. S3 (Supporting information). Evolution led the population towards the region of parameter space with the largest number of mated females (evolved male and female strategies from evolutionary simulations, white stars in Figs 5 and S3, Supporting information), thereby minimizing the mate-finding Allee effect.

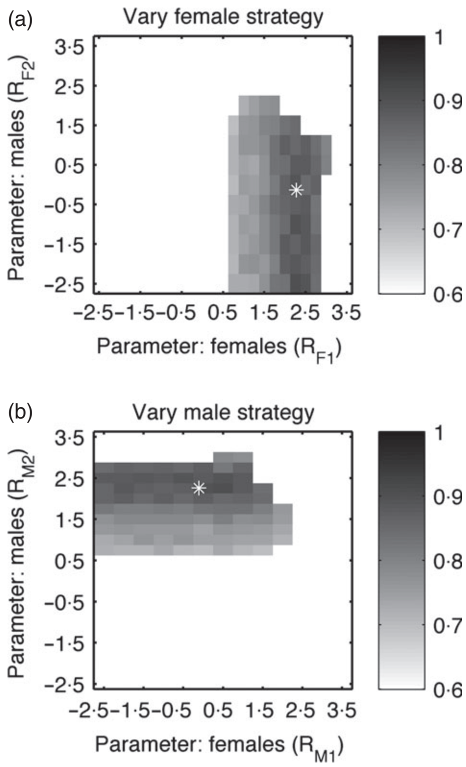

Fig. 5. The fraction of mated females in the 200th generation from simulations where female and male dispersal strategies were held constant: where (a) male strategies set as evolved values, female strategies fixed at different values and (b) female strategies set as evolved values and male strategies fixed at different values. Simulations were run with $a = 5$, $b = 10$, $n = 4$ with assumptions corresponding to set #1.1. The population was not viable in the white regions. The white star indicates the average evolved (a) female and (b) male strategy from equivalent evolutionary simulations.

Discussion

Theoretical studies of dispersal are surprisingly often developed in a one-sex context, and our understanding of sex biases in dispersal has not typically been linked to the details of mate-finding strategies. Our two-sex models link the processes of mate finding and dispersal by using dispersal settlement rules that depend on local sex ratios. We use our first model to demonstrate that a careful consideration of dispersal settlement rules resolves the apparent contradiction from the mate search and dispersal literatures: male and female dispersal can be either negatively or positively correlated, depending on whether the movement of one sex makes it easier or harder for the other to find mates. If easier, selection on the other sex to move is relaxed; if harder, the converse is true.

In our second model, we demonstrate that the relationship between mating system and sex-biased dispersal is far more complex than often considered. At the broadest scale, our results support the idea that sex bias in dispersal emerges only when there are asymmetries in the costs and benefits of dispersing between the sexes. However, we expand on the ways that costs and benefits have so far been accounted for. We find that sex bias in dispersal is more closely tied to the temporal relationship between dispersal and mating (and reproduction) than the number of males that a female mates with. This lends support for the importance of dispersal timing within the life-history cycle as a selective pressure on life-history traits (Johst & Brandl 1997; Wild & Taylor 2004).

Our results suggest that male-biased dispersal should be common in species where individuals mate while dispersing, and female-biased dispersal should be common in

Table 1. Examples of species with patterns of mating and dispersal behaviour that match our model findings

Species	Mating	Dispersal	Reference
Mating before dispersal			
Pieris rapae crucivora (cabbage white butterfly)	F mate, then disperse to oviposit	F emigrate more often than M	Ohsaki (1980)
Proclossiana eunomia (bog fritillary butterfly)	F mate once soon after emergence	F emigrate more and travel farther	Baguette & Nève (1994)
Various fig wasp species	M mate with F before dispersal	Only F disperse (M wingless)	Cook *et al.* (1997)
Paroxyna plantaginis (tephritid fly)	M territorial	F-biased dispersal to find egg-laying sites	Albrectsen & Nachman (2001)
Mating during dispersal			
Bog fritillary butterfly	At low density, M search for mates	M-biased at low density	Baguette *et al.* (1998)
Mirza coquereli (Coquerel's dwarf lemur)	F mate multiply	M roam for F	Kappeler *et al.* (2002)
Poecilia reticulata (Guppy)	Non-territorial mating system	M emigrate more and move among F	Croft *et al.* (2003)
Rhinoplocephalus nigrescens (Small-eyed snake)	M mate multiply	M move twice as far as F	Keogh, Webb & Shine (2007)
Mating after dispersal			
Oncorhynchus gorbuscha (Pink salmon)	Spawn after returning from migration	Similar tendency to stray in F and M	Thedinga *et al.* (2000)

species where females mate prior to dispersal and store sperm for later use. To our knowledge, there are no reviews of the empirical evidence for these patterns. A survey of the literature reveals a number of species with patterns matching our model predictions (Table 1). Studies with information both on the existence (or not) of sex bias in dispersal as well as details of when mating occurs with respect to the measured dispersal are surprisingly rare, perhaps due to a number of factors. First, molecular techniques are becoming commonly used to measure sex-biased dispersal (Goudet, Perrin & Waser 2002), especially in organisms that are difficult to track directly. In these cases, the actual relationship between movement and mating may not even be known. Secondly, documenting the extent to which mating occurs during dispersal can be difficult, even for species that can be tracked directly. Thirdly, most organisms move on several spatial and temporal scales and change dispersal behaviour in response to local conditions. For example, at high density, the bog fritillary butterfly has female-biased dispersal: females mate soon after emerging and disperse to lay eggs (Baguette & Nève 1994). However, at low density, the same species has male-biased dispersal: males have to actively search for females to mate with (Baguette *et al.* 1998). We recommend that future empirical studies on sex-biased dispersal explicitly consider the spatial and temporal scales at which the measured dispersal is occurring and what its relationship is to mating and reproduction.

Our point that species where females mate prior to dispersal should favour female-biased dispersal matches findings of an earlier model (Hirota 2004). It is particularly intriguing in the light of a recent suggestion (Miller & Inouye 2013) that the ability of females to mate before dispersal can increase the rate of spread of an introduced species. Recent theoretical (Miller *et al.* 2011) and experimental (Miller & Inouye 2013) work also suggests that the rate of spread is high in species with female-biased dispersal. It is therefore pertinent that our model predicts these two conditions to often co-occur: if females first mate and then move, this is likely to evolutionarily favour female-biased dispersal. These pieces taken together suggest that there are interesting eco-evolutionary dynamics between sex-biased dispersal and population rate of spread that deserve further attention.

With respect to the finding of Kokko and Wong (2007) that sperm competition selects for more mobile males than females, our results add the caveat that this is true only when individuals mate while moving (an implicit assumption of all mate search models). If individuals only mated after dispersal or if females mated and then dispersed, including sperm competition did not change the relative dispersal of males and females. The effects of sex-specific dispersal mortality on dispersal patterns can also be complex. While increasing the dispersal mortality for one sex will decrease its dispersal, this does not guarantee that this sex will disperse less than the other, if other factors promote a sex bias in the direction of the focal sex.

Our findings also have repercussions for the Allee effect, relevant to a number of conservation issues involving low-density populations (Fauvergue 2013). Given the number of models involving a mate-finding Allee effect (reviewed in Boukal & Berec 2002, 2009; plus Calabrese & Fagan 2004; Jerde, Bampfylde & Lewis 2009; Fagan *et al.* 2010; Pavlová, Berec & Boukal 2010; Gordillo 2011; Lee, Sæther & Engen 2011; Gilroy & Lockwood 2012), surprisingly few consider potential evolutionary adaptations to help mitigate this effect (Gascoigne *et al.* 2009). Although direct empirical evidence is limited, the possibility of evolving to mitigate an Allee effect has recently been demonstrated theoretically in two phenomenological models (Kanarek & Webb 2010; Cushing & Hudson 2012). Our findings add to this literature, as evolved strategies generally outperformed others with respect to the efficiency of pair formation. The best strategy for this occurred at intermediate movement; thus, although increased movement can help to alleviate a mate-finding Allee effect (see also Philip 1957; Berec & Boukal 2004), too restless individuals could in principle exacerbate it (see also Gascoigne *et al.* 2009). We did not find evidence in our models that evolution leads to such extreme movement.

Our results contribute new perspectives to the discussion on sex-biased dispersal and mating systems. Since Greenwood's seminal 1980 paper, many studies have sought to draw connections between a species' mating system and the presence and direction of sex bias in dispersal. Across birds and mammals, the predominant pattern is female-biased dispersal associated with resource defence monogamy and male-biased dispersal associated with female defence polygyny (Greenwood 1980; Dobson 1982; Clarke, Sæther & Røskaft 1997) although this is not uniformly true (Lawson Handley & Perrin 2007). Studies from other taxonomic groups have shown the pattern to be less clear (Consuegra & García de Leániz 2007). Our results take a broader look at the problem, by introducing a more diverse set of arrangements than monogamy and polygyny. Our results cast doubt on a universal link between monogamy and female-biased dispersal and between polygyny and male-biased dispersal. Instead, the existence and direction of sex bias can be strongly dependent on whether matings happen before, during or after dispersal, and whether females leave offspring along the route or only in the habitat where they settle.

We have made a number of simplifying assumptions that could be further unpacked in future studies. First, we assume that individuals are solitary and ignore any social complexities that influence the likelihood of dispersal and sex differences in dispersal behaviours (see Lawson Handley & Perrin 2007). Future studies could build on our work here to look at interactions between social systems and timing of mating with respect to dispersal. This could include a range of complexity from simple territoriality to the formation of social groups. Secondly, in our model, two separate aspects of dispersal influence the evolved dispersal strategy: the total time spent dispersing (driven by mating and breeding opportunities) and conditions of settlement patch (driven by post-dispersal mating and competition). The relative importance of these two aspects likely differs greatly among species. Studies (particularly empirical ones) that estimate the strength of these selective pressures will be quite useful in improving our understanding of dispersal and mate finding. Finally, we assume that individuals have immediate knowledge of the current sex ratio of each patch they visit. In many cases, individuals either know little about their local conditions or must invest time and/or energy to gain such information. Both of these scenarios have been shown to influence dispersal decisions in one-sex models (Bocedi, Heinonen & Travis 2012) but have not been explored in the context of sex-specific dispersal strategies.

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Data accessibility

Model code is available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.ph40n (Shaw & Kokko 2014).

References

Albrectsen, B. & Nachman, G. (2001) Female-biased density-dependent dispersal of a tephritid fly in a fragmented habitat and its implications for population regulation. *Oikos*, **94**, 263–272.

Baguette, M. & Nève, G. (1994) Adult movements between populations in the specialist butterfly *Proclossiana eunomia* (Lepidoptera, Nymphalidae). *Ecological Entomology*, **19**, 1–5.

Baguette, M., Vansteenwegen, C., Convi, I. & Nève, G. (1998) Sex-biased density-dependent migration in a metapopulation of the butterfly *Proclossiana eunomia*. *Acta Oecologica*, **19**, 17–24.

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

Berec, L.K. & Boukal, D.S. (2004) Implications of mate search, mate choice and divorce rate for population dynamics of sexually reproducing species. *Oikos*, **104**, 122–132.

Bocedi, G., Heinonen, J. & Travis, J.M.J. (2012) Uncertainty and the role of information acquisition in the evolution of context-dependent emigration. *The American Naturalist*, **179**, 606–620.

Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M.D.M., Gibbs, M. *et al.* (2012) Costs of dispersal. *Biological Reviews of the Cambridge Philosophical Society*, **87**, 290–312.

Boukal, D.S. & Berec, L.K. (2002) Single-species models of the Allee effect: extinction boundaries, sex ratios and mate encounters. *Journal of Theoretical Biology*, **218**, 375–394.

Boukal, D.S. & Berec, L.K. (2009) Modelling mate-finding Allee effects and populations dynamics, with applications in pest control. *Population Ecology*, **51**, 445–458.

Boulinier, T. & Danchin, E. (1997) The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. *Evolutionary Ecology*, **11**, 505–517.

Bowler, D.E. & Benton, T.G. (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews of the Cambridge Philosophical Society*, **80**, 205–225.

Calabrese, J.M. & Fagan, W.F. (2004) Lost in time, lonely, and single: reproductive asynchrony and the Allee effect. *The American Naturalist*, **164**, 25–37.

Clarke, A.L., Sæther, B.-E. & Røskaft, E. (1997) Sex biases in avian dispersal: a reappraisal. *Oikos*, **79**, 429–438.

Consuegra, S. & García de Leániz, C. (2007) Fluctuating sex ratios, but no sex-biased dispersal, in a promiscuous fish. *Evolutionary Ecology*, **21**, 229–245.

Cook, J.M., Compton, S.G., Herre, E.A. & West, S.A. (1997) Alternative mating tactics and extreme male dimorphism in fig wasps. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **264**, 747–754.

Courchamp, F., Berec, L.K. & Gascoigne, J. (2008) *Allee Effects in Ecology and Conservation*. Oxford University Press, Oxford, UK.

Croft, D.P., Albanese, B., Arrowsmith, B.J., Botham, M., Webster, M. & Krause, J. (2003) Sex-biased movement in the guppy (*Poecilia reticulata*). *Oecologia*, **137**, 62–68.

Cushing, J.M. & Hudson, J.T. (2012) Evolutionary dynamics and strong Allee effects. *Journal of Biological Dynamics*, **6**, 941–958.

Dobson, F.S. (1982) Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour*, **30**, 1183–1192.

Fagan, W.F., Cosner, C., Larsen, E.A. & Calabrese, J.M. (2010) Reproductive asynchrony in spatial population models: how mating behavior can modulate Allee effects arising from isolation in both space and time. *The American Naturalist*, **175**, 362–373.

Fauvergue, X. (2013) A review of mate-finding Allee effects in insects: from individual behavior to population management. *Entomologia Experimentalis et Applicata*, **146**, 79–92.

Gascoigne, J., Berec, L.K., Gregory, S. & Courchamp, F. (2009) Dangerously few liaisons: a review of mate-finding Allee effects. *Population Ecology*, **51**, 355–372.

Gilroy, J.J. & Lockwood, J.L. (2012) Mate-finding as an overlooked critical determinant of dispersal variation in sexually-reproducing animals. *PLoS ONE*, **7**, e38091.

Gordillo, L.F. (2011) The effects of reduced mating likelihood on population viability. *Natural Resource Modeling*, **24**, 207–221.

Goudet, J., Perrin, N. & Waser, P. (2002) Tests for sex-biased dispersal using bi-parentally inherited genetic markers. *Molecular Ecology*, **11**, 1103–1114.

Greenwood, P.J. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.

Gros, A., Hovestadt, T. & Poethke, H.J. (2008) Evolution of sex-biased dispersal: the role of sex-specific dispersal costs, demographic stochasticity, and inbreeding. *Ecological Modelling*, **219**, 226–233.

Gros, A., Poethke, H.J. & Hovestadt, T. (2009) Sex-specific spatio-temporal variability in reproductive success promotes the evolution of sex-biased dispersal. *Theoretical Population Biology*, **76**, 13–18.

Hammerstein, P. & Parker, G.A. (1987) Sexual selection: games between the sexes. *Sexual Selection: Testing the Alternatives* (eds J.W. Bradbury & M.B. Andersson), pp. 119–142. Wiley, Chichester, UK.

Hirota, T. (2004) The evolution of sex-biased dispersal by pre-dispersal copulation and fluctuating environment. *Journal of Animal Ecology*, **73**, 1115–1120.

Jerde, C.L., Bampfylde, C.J. & Lewis, M.A. (2009) Chance establishment for sexual, semelparous species: overcoming the Allee effect. *The American Naturalist*, **173**, 734–746.

Johnson, D.M., Liebhold, A.M., Tobin, P.C. & Bjørnstad, O.N. (2006) Allee effects and pulsed invasion by the gypsy moth. *Nature*, **444**, 361–363.

Johst, K. & Brandl, R. (1997) Evolution of dispersal: the importance of the temporal order of reproduction and dispersal. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **264**, 23–30.

Kanarek, A.R. & Webb, C.T. (2010) Allee effects, adaptive evolution, and invasion success. *Evolutionary Applications*, **3**, 122–135.

Kappeler, P.M., Wimmer, B., Zinner, D. & Tautz, D. (2002) The hidden matrilineal structure of a solitary lemur: implications for primate social evolution. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **269**, 1755–1763.

Keogh, J.S., Webb, J. & Shine, R. (2007) Spatial genetic analysis and long-term mark–recapture data demonstrate male-biased dispersal in a snake. *Biology Letters*, **3**, 33–35.

Kokko, H. & Wong, B.B.M. (2007) What determines sex roles in mate searching? *Evolution*, **61**, 1162–1175.

Kramer, A.M., Dennis, B., Liebhold, A.M. & Drake, J.M. (2009) The evidence for Allee effects. *Population Ecology*, **51**, 341–354.

Krkošek, M., Connors, B.M., Lewis, M.A. & Poulin, R. (2012) Allee effects may slow the spread of parasites in a coastal marine ecosystem. *The American Naturalist*, **179**, 401–412.

Lawson Handley, L.J. & Perrin, N. (2007) Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology*, **16**, 1559–1578.

Lee, A.M., Sæther, B.-E. & Engen, S. (2011) Demographic stochasticity, Allee effects, and extinction: the influence of mating system and sex ratio. *The American Naturalist*, **177**, 301–313.

Liberg, O. & von Schantz, T. (1985) Sex-biased philopatry and dispersal in birds and mammals: the Oedipus hypothesis. *The American Naturalist*, **126**, 129–135.

Liebhold, A. & Bascompte, J. (2003) The Allee effect, stochastic dynamics and the eradication of alien species. *Ecology Letters*, **6**, 133–140.

McCartney, J., Kokko, H., Heller, K.-G. & Gwynne, D.T. (2012) The evolution of sex differences in mate searching when females benefit: new theory and a comparative test. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **279**, 1225–1232.

Meier, C.M., Starrfelt, J. & Kokko, H. (2011) Mate limitation causes sexes to coevolve towards more similar dispersal kernels. *Oikos*, **120**, 1459–1468.

Miller, T.E.X. & Inouye, B.D. (2013) Sex and stochasticity affect range expansion of experimental invasions. *Ecology Letters*, **16**, 354–361.

Miller, T.E.X., Shaw, A.K., Inouye, B.D. & Neubert, M.G. (2011) Sex-biased dispersal and the speed of two-sex invasions. *The American Naturalist*, **177**, 549–561.

Ohsaki, N. (1980) Comparative population studies of three *Pieris* butterflies, *P. rapae*, *P. melete* and *P. napi*, living in the same area. *Researches on Population Ecology*, **22**, 163–183.

Pavlová, V., Berec, L.K. & Boukal, D.S. (2010) Caught between two Allee effects: trade-off between reproduction and predation risk. *Journal of Theoretical Biology*, **264**, 787–798.

Perrin, N. & Mazalov, V. (1999) Dispersal and inbreeding avoidance. *The American Naturalist*, **154**, 282–292.

Perrin, N. & Mazalov, V. (2000) Local competition, inbreeding, and the evolution of sex-biased dispersal. *The American Naturalist*, **155**, 116–127.

Philip, J.R. (1957) Sociality and sparse populations. *Ecology*, **38**, 107–111.

Poethke, H.J., Gros, A. & Hovestadt, T. (2011) The ability of individuaxls to assess population density influences the evolution of emigration propensity and dispersal distance. *Journal of Theoretical Biology*, **282**, 93–99.

Ruxton, G.D. & Rohani, P. (1998) Fitness-dependent dispersal in metapopulations and its consequences for persistence and synchrony. *Journal of Animal Ecology*, **68**, 530–539.

Shaw, A.K. & Kokko, H. (2014) Data from: Mate finding, Allee effects, and selection for sex-biased dispersal. *Dryad Digital Repository*, doi:10.5061/dryad.ph40n.

South, A.B. & Kenward, R.E. (2001) Mate finding, dispersal distances and population growth in invading species: a spatially explicit model. *Oikos*, **95**, 53–58.

Starrfelt, J. & Kokko, H. (2012) The theory of dispersal under multiple influences. *Dispersal Ecology and Evolution* (eds J. Clobert, M. Baguette, T.G. Benton & J.M. Bullock), pp. 19–28. Oxford University Press, Oxford, UK.

Stephens, P.A., Sutherland, W.J. & Freckleton, R.P. (1999) What is the Allee effect? *Oikos*, **87**, 185–190.

Taylor, C.M. & Hastings, A. (2005) Allee effects in biological invasions. *Ecology Letters*, **8**, 895–908.

Thedinga, J.F., Wertheimer, A.C., Heintz, R.A., Maselko, J.M. & Rice, S.D. (2000) Effects of stock, coded-wire tagging, and transplant on straying of pink salmon (*Oncorhynchus gorbuscha*) in southeastern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 2076–2085.

Thomas, C.D., Hill, J.K. & Lewis, O.T. (1998) Evolutionary consequences of habitat fragmentation in a localized butterfly. *Journal of Animal Ecology*, **67**, 485–497.

Tobin, P.C., Berec, L.K. & Liebhold, A.M. (2011) Exploiting Allee effects for managing biological invasions. *Ecology Letters*, **14**, 615–624.

Travis, J.M.J., Mustin, K., Barton, K.A., Benton, T.G., Clobert, J., Delgado, M.D.M. *et al.* (2012) Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. *Methods in Ecology and Evolution*, **3**, 628–641.

Wells, H., Strauss, E.G., Rutter, M.A. & Wells, P.H. (1998) Mate location, population growth and species extinction. *Biological Conservation*, **86**, 317–324.

Wild, G. & Taylor, P. (2004) Kin selection models for the co-evolution of the sex ratio and sex-specific dispersal. *Evolutionary Ecology Research*, **6**, 481–502.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. The male 'restlessness' strategy that evolves in Model 1 as a function of female 'restlessness' strategy for (a) homogeneous and (b) heterogeneous environments.

Fig. S2. The probability of stopping as a function of number of females and males in a patch for each females and males based on the settlement strategies in the population after 500 generations of simulated evolution.

Fig. S3. The fraction of mated females in the 200th generation from simulations where female and male dispersal strategies were held constant: where (a) male strategies set as evolved values, female strategies fixed at different values and (b) female strategies set as evolved values and male strategies fixed at different values.

Supplemental Online Material For:

Mate finding, Allee effects, and selection for sex-biased dispersal

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Figure S1. The male ‘restlessness’ strategy that evolves in Model 1 as a function of female ‘restlessness’ strategy for (a) homogeneous and (b) heterogeneous environments. The number of dispersal steps taken by males under each of these strategies is shown in the dark lines in Fig. 2.

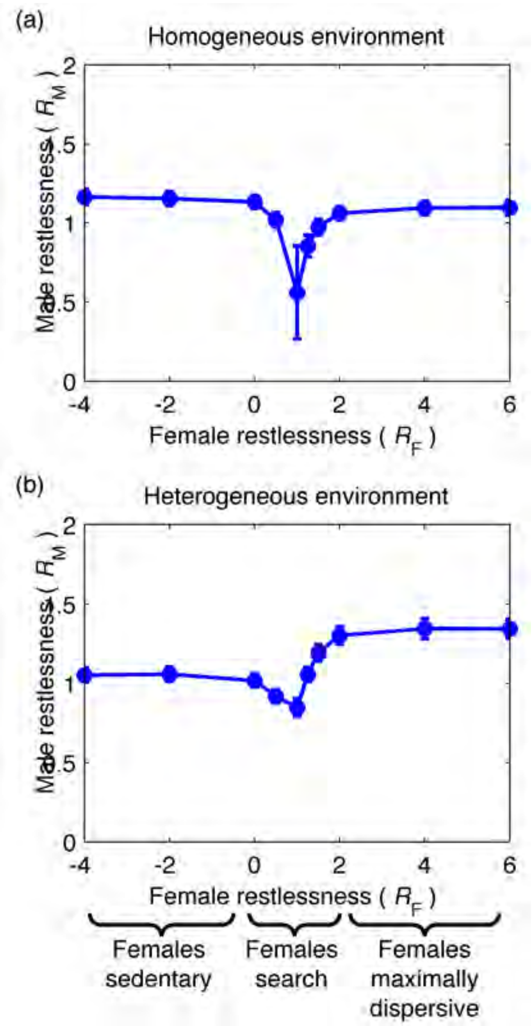
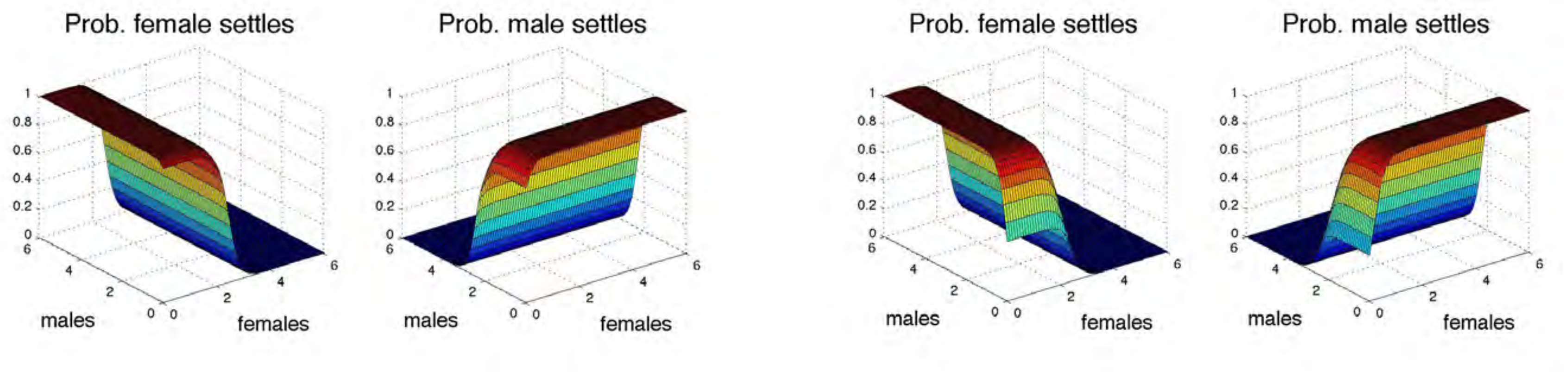


Figure S2. The probability of stopping as a function of number of females and males in a patch for each females and males based on the settlement strategies in the population after 500 generations of simulated evolution. The values of R_{F1} and R_{F2} (female strategy parameters) and R_{M1} and R_{M2} (male strategy parameters) that evolved were averaged across the 4 different replicates and used to generate these functions.



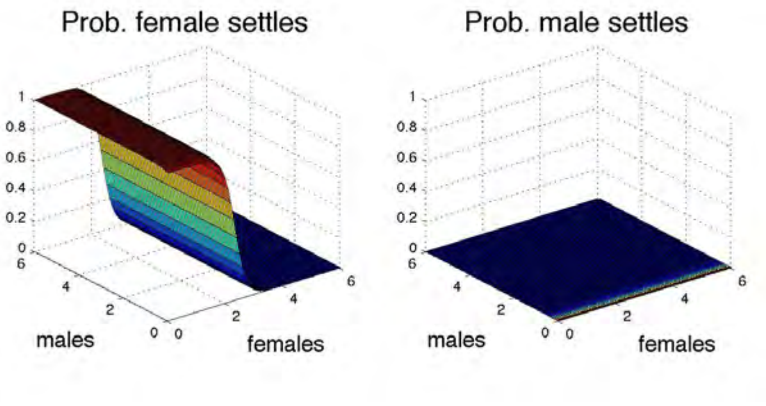
a) #1.1 Mating after dispersal, in monogamous pairs

b) #1.2 Mating after dispersal, polygynandrously

$R_{F1} = 2.28$ $R_{F2} = -0.44$ $R_{M1} = -0.15$ $R_{M2} = 2.25$

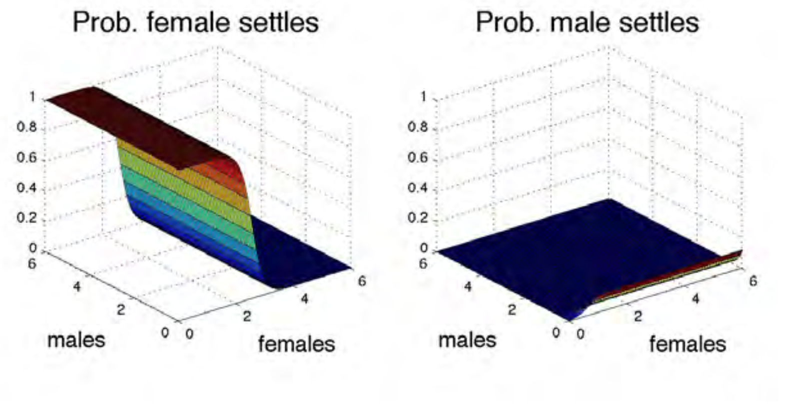
$R_{F1} = 2.15$ $R_{F2} = 0.20$ $R_{M1} = 0.28$ $R_{M2} = 2.19$

c) #2.1 Mating during dispersal, first male sperm precedence



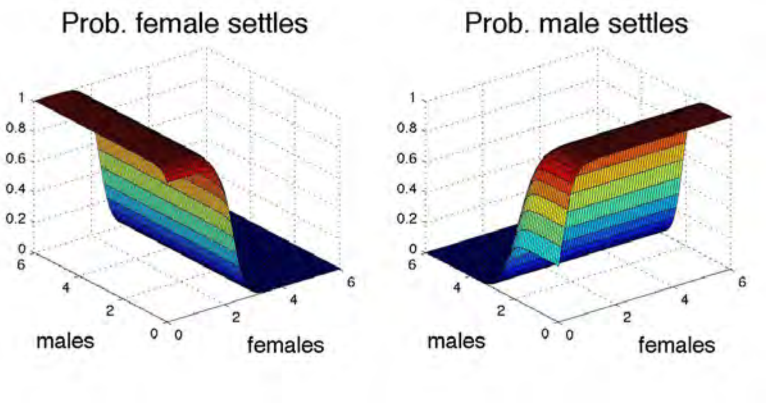
$R_{F1} = 2.19$ $R_{F2} = -0.60$ $R_{M1} = 0.43$ $R_{M2} = -1.31$

d) #2.2 Mating during dispersal, shared paternity



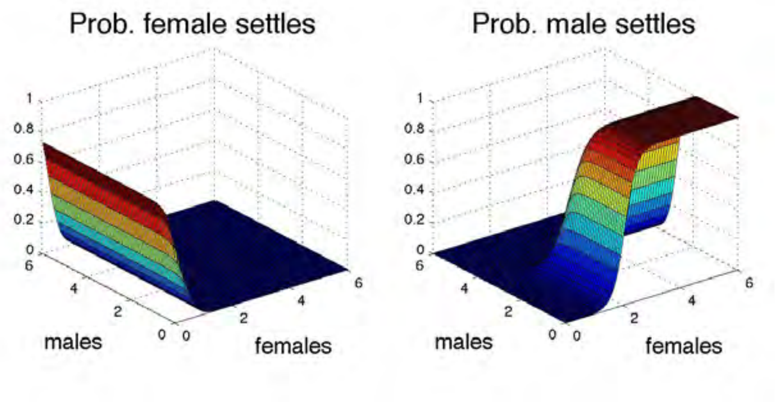
$R_{F1} = 2.40$ $R_{F2} = -0.86$ $R_{M1} = 1.21$ $R_{M2} = -0.54$

e) #2.3 Mating during dispersal, last male sperm precedence



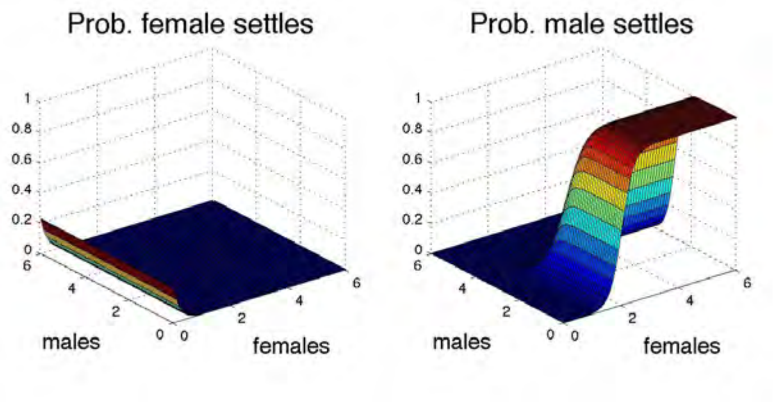
$R_{F1} = 2.11$ $R_{F2} = -0.35$ $R_{M1} = 0.25$ $R_{M2} = 2.10$

f) #3.1 Female mates once before dispersal, deposits eggs as she disperses



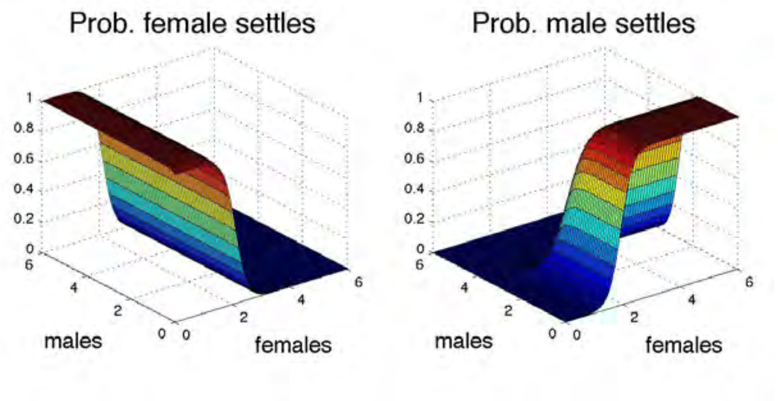
$R_{F1} = 0.06$ $R_{F2} = 0.13$ $R_{M1} = 2.18$ $R_{M2} = 2.67$

g) #3.2 Female mates with up to 3 males before dispersal, deposits eggs as she disperses



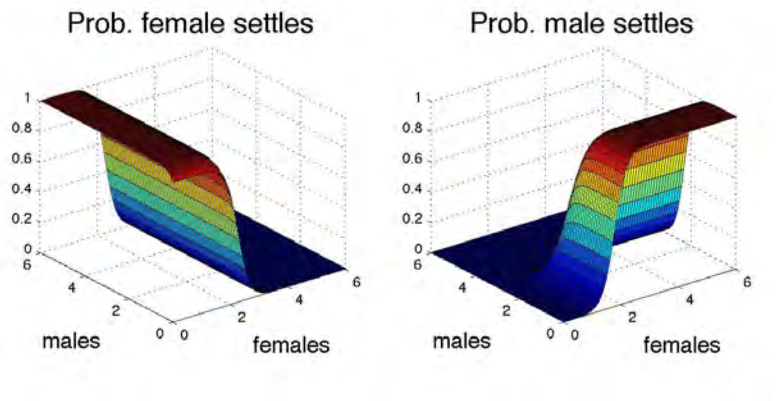
$R_{F1} = -0.38$ $R_{F2} = -0.31$ $R_{M1} = 2.15$ $R_{M2} = 2.67$

h) #3.3 As #3.1 but deposits all eggs in final patch



$R_{F1} = 1.95$ $R_{F2} = -0.58$ $R_{M1} = 2.04$ $R_{M2} = 2.58$

i) #3.4 As #3.2 but deposits all eggs in final patch



$R_{F1} = 2.09$ $R_{F2} = -0.35$ $R_{M1} = 1.89$ $R_{M2} = 2.24$

Figure S3. The fraction of mated females in the 200th generation from simulations where female and male dispersal strategies were held constant: where (a) male strategies set as evolved values, female strategies fixed at different values and (b) female strategies set as evolved values and male strategies fixed at different values. Simulations were run with $a = 5$, $b = 10$, $n = 4$ with assumptions corresponding to set #1.2. The population was not viable in the white regions. The white star indicates the average evolved (a) female and (b) male strategy from equivalent evolutionary simulations.