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Kin competition drives the evolution of sex-biased dispersal under monandry and polyandry, not under monogamy

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The relation between mating system and sex-biased dispersal has been debated for three decades. However, the relative importance of the processes involved in this relation remains poorly known. In this study, we paid special attention to kin competition. We built an adaptive individual-based model fixing three mating systems (monandry, polyandry, monogamy) in a metapopulation, and allowing dispersal across patches to evolve independently for males and females. Our simulations showed that a difference in the number of mates can determine the evolution of sex-biased dispersal. Dispersal appears strongly male biased under monandry and polyandry, but balanced under monogamy. By contrast, we showed that inbreeding can influence but does not promote sex-biased dispersal, and that the primary sex ratio does not qualitatively affect the evolution of sex-biased dispersal under monandry and polyandry. These results are driven by the interaction of two factors: the variation in reproductive success between patches in the metapopulation and kin competition. These two factors are influenced by the mating system, which modifies both the competition for access to partners and the mean relatedness between individuals. To ascertain that kin competition actually drives sex-biased dispersal, we made simulations with destruction of any genetic structure in the metapopulation, and we found that in this case dispersal was not sex biased.

Keywords: dispersal, individual-based model, kin competition, mating system, sex-biased dispersal, spatial heterogeneity.

Mating and dispersal are two key events in the life of an individual, which are thought to be linked by several mechanisms (Greenwood, 1980; Gros, Poethke, & Hovestadt, 2009; Perrin & Goudet, 2001; Perrin & Mazalov, 2000). In particular, the link between mating system and dispersal has been largely invoked to explain sex-biased dispersal (Chapple & Keogh, 2005; Greenwood, 1980; Mabry, Shelley, Davis, Blumstein, & van Vuren, 2013; Nagy, Günther, Knörnschild, & Mayer, 2013), the most discussed feature in the dispersal literature. The main hypothesis suggests that prevailing male dispersal, as observed in mammals, and prevailing female dispersal, as observed in birds, are due to the predominance of polygyny and monogamy in each group, respectively (Greenwood, 1980). However, more than 30 years after Greenwood proposed this hypothesis, it is still debated (Dobson, 2013; Johnson & Gaines, 1990; Mabry et al., 2013). Some evidence exists that links the mating system and sex-biased dispersal, especially in mammals (Mabry et al., 2013), but it remains challenging to conclude whether the mating system actually drives the evolution of dispersal or whether these two traits only covary (Clutton-Brock & Lukas, 2012). Some modelling results suggest that the mating system alone can indeed drive the evolution of dispersal (Perrin & Goudet, 2001; Perrin & Mazalov, 1999, 2000). However, because dispersal is influenced by many parameters (Clobert, Massot, & Le Galliard, 2012), it is often difficult to determine whether its evolution depends on the mating system itself or on other life history traits correlated with the mating system (Lawson Handley & Perrin, 2007).

Dispersal is not only widespread in life (Dobson, 1982), it is also a highly multifaceted trait. Primarily, there can be natal or breeding dispersal (Dobson, 2013), as well as short- or long-distance dispersal (Murrell, Travis, & Dytham, 2002). In motile animals, dispersal appears as a complex process with several phases, such as departure, transfer and settlement, rather than a holistic behaviour (Clobert, Le Galliard, Cote, Meylan, & Massot, 2009; Matthysen, 2012). To investigate its fundamental effects on the genetic structure of populations and metapopulations (Kokko & López-Sepulcre, 2006; Travis & Dytham, 1998), dispersal is often defined as ‘any movement of individuals or propagules with potential consequences for gene flow across space’ (Ronce, 2007, p.232). Beyond genes, dispersal can also impact social interactions (Boudjemadi, Lecomte, & Clobert, 1999) and demography (Massot, Clobert, Pilorge, Lecomte, & Barbault, 1992). For these reasons, dispersal is a key determinant of population persistence in the context of habitat fragmentation (Parvinen, Dieckmann, Gyllenberg, & Metz, 2003), climate warming (Clobert et al., 2009; Walther et al., 2002) and the success of invasive species (Kubisch, Fronhofer, Poethke, & Hovestadt, 2013).

It is generally assumed that dispersal is costly, which includes the predispersal cost of development of dispersal-related traits, as well as the cost in time, energy and exposure to various risks during dispersal (Bonte et al., 2012). These costs can negatively affect survival or reproductive success of dispersers. Thus, individuals should disperse only if sufficient benefits of dispersal outweigh its costs. The fitness benefits of dispersal often result from the avoidance of local costs related to habitat quality, inbreeding or competition (Clobert, Danchin, Dhondt, & Nichols, 2001; Clobert et al., 2012). Particular attention has been paid to the relative importance of the costs and benefits of dispersal for males and females, which can be affected by the corresponding costs and benefits related to the mating system. For instance, dispersal can depend on the relationship between the mating system and competition for mates or for resources to attract mates. Investment in mating, and in obtaining associated resources, varies between males and females depending on the mating system. In monogamy, males compete for resources needed to feed offspring, whereas in polygyny, males compete more directly for mating opportunities but less for resources. Therefore, competition for resources is more challenging for males in monogamous species and for females in polygynous species. Because dispersal is thought to reduce the competitive ability to access resources (Massot, Clobert, Lecomte, & Barbault, 1994), higher dispersal should be selected for females in monogamous systems and males in polygynous systems (Greenwood, 1980).

The genetic environment has been shown to play a key role in the evolution of dispersal. In particular, inbreeding avoidance has often been put forward to explain sex-biased dispersal. In contrast, kin competition avoidance has been somewhat neglected (Dobson, 2013), despite some theoretical (Hamilton & May, 1977; Poethke, Pfenning, & Hovestadt, 2007) and empirical evidence (Clobert et al., 2012; Lambin, Aars, & Piertney, 2001). First, Hamilton and May (1977) showed, using a game-theoretical approach, that dispersal can evolve in response to kin competition, even if the intensity of competition is constant in space. Then, Frank (1986) showed that dispersal equilibrium can be directly linked to relatedness, and thus kin competition. Taylor (1988) extended this work, showing in particular that haplodiploidy promotes sex-biased dispersal. In a highly cited paper, Perrin & Mazalov (2000) investigated sex-biased dispersal following Greenwood's (1980) mating system hypothesis and showed that sex-biased dispersal evolution is possible when males and females do not compete in the same way for resources. However, this kind of deterministic model can miss stochastic effects as pointed out by Gros et al. (2009). Using an individual-based model (stochastic by construction), these authors put forward another mechanism to explain sex-biased dispersal. They showed that sex-specific spatiotemporal variance of fitness between patches in the metapopulation can promote sex-biased dispersal. However, they did not unravel the role of kin competition, and they contrasted a random mating with a harem system, which would magnify the expected effect.

In this study, we investigated the interplay of kin competition and spatiotemporal variance of fitness on the evolution of sex-biased dispersal. We considered the influence of genetic mating system on the coevolution of male and female dispersal behaviour in a metapopulation. We modelled three genetic mating systems, monogamy, monandry and polyandry, which differed only in the number of partners that females and males can have. We focused on how these three mating systems, having different impacts on the genetic structure of the metapopulation, and different levels of competition for mates, can affect dispersal in each sex. We assessed quantitatively the effect of mating system on the dispersal rate in relation to important parameters such as the sex ratio and the intensity of inbreeding depression. We used an individual-based model, where dispersal was adaptive, to take into account kin selection and stochasticity. We estimated the relative importance of kin selection versus individual selection by breaking the genetic structure of the metapopulation using the method of Poethke et al. (2007).

<H1>The model

In our adaptive individual-based model (Bach, Thomsen, Pertoldi, & Loeschcke, 2006) of dispersal evolution, mainly inspired by the work of Poethke et al. (2007), dispersal is the only adaptive trait. We did not compute individual or inclusive fitness; these, as well as kin interactions, were emergent properties of the simulations. The evolutionarily stable dispersal rate was also an outcome of the simulations.

<H2>Demography

The model considers populations of sexually reproducing diploidic organisms occupying a number n_{patch} of patches and constituting a metapopulation. The model follows a simple life cycle with, in order, dispersal, mating, reproduction, birth, survival. Adults die after reproduction so that generations do not overlap.

All patches have the same carrying capacity K, but the reproductive quality of patches varies along time and across space. Patch quality is drawn from a log-normal distribution with mean λ and standard deviation σ. Therefore σ describes the heterogeneity in patch quality.

The quality of a patch j at time t is $\Lambda(t,j)$. The fecundity F_i of each female i in patch j at time t is drawn from a Poisson distribution with mean $\Lambda(t,j)$. The sex of newborns is determined by inheritance of the sexual chromosomes of their parents (XY model). The sex ratio at birth, sr_{b}, is balanced in most simulations, but can be biased for exploratory purposes by changing the probability of the inheritance of sexual chromosomes. The realized sex ratio at birth is $n_{\mathrm{males}}/(n_{\mathrm{females}}+n_{\mathrm{males}})$, with n_{males} and n_{females} the counted number of newborns in each sex. Its average value is equal to the probability sr_{b} of inheriting the father's Y chromosome and becoming a male.

Newborns survive and reach the dispersal phase with the density-dependent survival probability

$$s = \frac{1}{\left(1+\alpha N_j\right)^{\beta}}$$

where $\alpha = (\lambda^{1/\beta}-1)/K$, N_j is population size in patch j and β parameterizes the intensity of density dependence (Poethke *et al.*, 2007). The survival probability decreases with increasing N_j, and decreases faster for small β. Note that N_j includes only newborns because adults die after reproduction.

<H2>Mating

The success of a female depends on patch quality, the survival of its offspring and its mating with at least one male. The mating success of a male depends on the female(s) it mates with. We investigated three mating systems; in each, pairs were formed from males and females drawn randomly within their patch. (1) In monandry each female mates with only one male and males have no reproduction limit. (2) In polyandry each female mates with many males, males have no reproduction limit and each newborn has a father chosen randomly in the patch. (3) In monogamy each female mates with only one male and males are no longer available after a single mating. Thus, males and females have a single partner, and some individuals do not reproduce when the breeding sex ratio is unbalanced in a patch.

<H2>Dispersal

To allow for sex-specific dispersal, males and females are endowed with two independent loci (d_{m} and d_{f}) that drive dispersal independently in each sex. Each newborn inherits two dispersal alleles, one randomly chosen from its mother and one randomly chosen from its father. Mutations occur with frequency f_s, the new value of a mutated allele being drawn from a normal distribution with mean equal to the value of the ancestor allele and standard deviation sd_s. The dispersal strategy ds_i of an individual i is identified with the mean values of the two alleles expressed by its sex. The dispersal probability of the individual dp_i depends on density as follows:

$$dp_i = \begin{Bmatrix} 0 \; if \;\; N_j/K \;\leq ds_i \\ 1 - \frac{ds_i}{\mathrm{N}_j/K} \; if \;\; N_j/K \; > ds_i \end{Bmatrix}.$$

Following this equation, we can see that the dispersal strategy ds_i acts as a threshold: if the patch density N_j/K is under the threshold, the individual never disperses; if the patch density is above the threshold, the higher the density, the higher the probability of dispersing. Therefore, whenever the patch density is near the dispersal threshold, the dispersal probability will be very low. Dispersal is global, toward a randomly selected patch. The cost of dispersal is modelled by a probability μ of dying during dispersal. In most simulations this cost is identical for males and females, but we also tested the effect of a sex-biased cost.

<H2>Relatedness, inbreeding and heterozygosity

Each individual is given 32 diploid neutral (not under natural selection) loci, with each locus having two different alleles, A and B. For each allele of a neutral locus, the process of inheritance is the same as for dispersal alleles, and mutations occur with frequency f_n. Mutation performs a switch between the two alleles. This set of loci allows us to measure the relatedness between two individuals at the population and metapopulation levels, taking into account relatedness and possible changes in population size. The heterozygosity of an individual is calculated by assessing the heterozygosity at each locus and counting the heterozygous loci relative to the total number of loci. A fully homozygous individual i has a heterozygosity level H_i of 0. A fully heterozygous individual has a heterozygosity level of 1. On average, the heterozygosity level of an individual decreases with increasing relatedness between its parents. Therefore, we use the heterozygosity level to model inbreeding depression. Homozygous females can suffer a fecundity loss reducing the initial fecundity:

$$F_i = \begin{Bmatrix} F_i \; if \; H_i \; \geq 0.5 \\ F_i \times (2H_i)^{\rho} \; if \; H_i \; < 0.5 \end{Bmatrix}$$

where H_i is the heterozygosity level of female i and ρ is the strength of the inbreeding penalty. When ρ is equal to 0, there is no homozygosity depression. When $\rho > 0$, females suffer a loss in fecundity that increases with ρ.

<H2>Test on kin competition

As said before, kin interactions are emergent properties in an individual-based model. However, as in Poethke et al. (2007), we performed simulations in a shuffled version of the model to cancel kin competition. In this shuffled model, before dispersal occurs, individuals are randomly redistributed in the whole metapopulation, but preserving the initial patch-specific densities and sex ratios. Therefore, the genetic structure is broken, but the demographic structure remains unchanged. In the unshuffled simulations, a dispersing individual has less chance of competing with kin in its patch of arrival than in its patch of departure. In the shuffled simulation, because individuals are randomly redistributed before dispersal, the chance of competing with kin is the same across all patches. Thus, the comparison between the shuffled and the unshuffled simulations allows to test specifically the effect of kin competition on the evolution of male and female dispersal.

<H2>Simulation parameters and outcomes

The simulation parameters used are reported in Table 1. Our results were based on the final outcome of many runs for each parameter set (Monte Carlo simulation). We made sure that equilibrium was reached by letting the simulations run a large number of generations (15 000 at least) and verified that the mean dispersal rate was stable for each sex. We did not use statistical significance tests that are inappropriate to compare simulation model results (White, Rassweiler, Samhouri, Stier, & White, 2014). We followed the two arguments of White et al. (2014): first, the potentially infinite number of replications can artificially increase the power of statistical tests. Second, two sets of simulations with different parameters lead to different outcomes. Thus, we focused our analysis on the magnitude of the difference between simulations. Our results are shown with 95% confidence intervals to ensure that a difference between two sets of simulations is not the result of stochasticity.

<H1>Results

<H2>Mating system and local relatedness

Our simulations show that the mating system influences the evolution of sex-biased dispersal. Males and females evolve the same dispersal rate in monogamy, while the dispersal rate is higher in males in the monandrous and polyandrous mating systems (Fig. 1). Moreover, males disperse more in monandry than in polyandry. In the shuffled simulations, where the effect of kin competition is removed, a lower dispersal rate evolves in both sexes and the male bias in dispersal disappears (Figs 1 and 2).

The difference in dispersal between males and females in monandry and polyandry is the result of the interplay of two processes. First, there is a strong kin competition effect, as revealed by the lower dispersal in both sexes in the shuffled simulations (Figs 1 and 2). This effect is expected to be stronger in monandry than in polyandry because a smaller proportion of males reproduce in monandry, so that local relatedness is higher (illustrated in Fig. A1). Second, the mating system creates an asymmetry between the sexes in the spatiotemporal variability of reproductive success between patches. The variability of reproductive success between patches is the same for males and females in monogamy, whereas this variation is higher for males in monandry and polyandry (Fig. A2). This sex bias in the variability of reproductive success persists in the shuffled simulations, i.e. when there is no kin competition (Fig. A2).

Inbreeding also affects dispersal. Increasing the penalty of homozygosity (i.e. the cost of inbreeding) increases the dispersal rate, but this average effect also depends on the mating system (Fig. 3). Under monogamy, both sexes evolve higher dispersal rates with increasing homozygosity penalty. Under polyandry and monandry, the increase in dispersal with higher homozygosity penalty occurs mainly in males.

<H2>*Heterogeneity in patch quality, dispersal cost and sex ratio*

Dispersal increases with increasing heterogeneity in patch quality, and sex-biased dispersal is reduced for high heterogeneity in patch quality (Fig. 2). At the same time, dispersal rate decreases with increasing dispersal cost in both sexes, and sex-biased dispersal only appears when the mortality of dispersers is lower than 25% (Fig. A3). We also tested the effect of sex-biased dispersal cost (Fig. 4). We changed the male dispersal cost keeping the female dispersal cost unchanged. As expected, a sex-biased dispersal cost modifies the evolution of sex-biased dispersal. Whatever the mating system, an increased male dispersal cost decreases male dispersal rate. Consequently female dispersal increases as male dispersal decreases. In monogamy, the sex with the higher dispersal cost has the lower dispersal rate at equilibrium. In monandry and polyandry, dispersal is female biased for high values of male dispersal cost (e.g. in Fig. 4, female-biased dispersal evolves when male dispersal cost is about 30% higher than female dispersal cost).

A bias in the primary sex ratio has different effects depending on the mating system (Fig. 5). In monogamy, a bias in sex ratio induces sex-biased dispersal: the more numerous sex disperses more. Although male dispersal still increases under monandry and polyandry when the sex ratio is male biased, a bias in sex ratio does not qualitatively change the sex bias in dispersal. In other words, the primary sex ratio does not appear to affect the evolution of sex-biased dispersal in the monandrous and polyandrous mating systems.

<H1>Discussion

The importance of kin competition in the evolution of dispersal has been well established by several theoretical works (Comins, Hamilton, & May, 1980; Hamilton & May, 1977; Poethke et al., 2007; Taylor, 1988). The situation is more contrasted with regard to the evolution of sex-biased dispersal. For instance, Perrin and Mazalov (2000) have shown that male-biased dispersal can evolve in polygynous/promiscuous mating systems in response to kin competition. However, they did not take into account stochastic effects and used an unrealistic exponential growth assumption (Gros et al., 2009). More recently, Lehmann & Balloux (2007) developed an analytical model taking into account both kin competition and spatiotemporal variance in fecundity, but they did not address the question of mating process nor the coevolution of male and female dispersal behaviour.

In the present study, we have built an individual-based model to investigate the effect of different mating systems, defined in our study by the number of mates, on the evolution of sex-biased dispersal through their influence on kin competition. We revealed the role of kin competition by contrasting models with or without genetic structure, i.e. with or without indirect fitness benefits of kin competition avoidance by dispersal. Our model is focused only on intragenerational kin competition and does not include parent-offspring conflict or kin cooperation behaviours (Perrin & Lehmann, 2001), i.e. the other two kin-related processes often cited as being involved in dispersal evolution (Lambin et al., 2001). We showed that intragenerational kin competition can play a central role in the evolution of sex-biased dispersal, and that it can be, under a large range of conditions, a better candidate than inbreeding risk. Therefore, our results confirm the role of kin competition in dispersal evolution and bring new insights to its role in the evolution of sex-biased dispersal. Mainly, we showed that, when the primary sex ratio and dispersal costs are balanced, sex-biased dispersal does not evolve in the absence of genetic structure, i.e. in the absence of kin-related benefit to disperse. We thus pointed out the importance of kin competition avoidance in the evolution of sex-biased dispersal (Figs 1 and 2). We observed a higher male bias in dispersal under monandry than polyandry (Fig. 1). Furthermore, we found that heterogeneity in patch quality, dispersal cost, inbreeding and primary sex ratio also affected the evolution of sex-biased dispersal. These factors can modulate the influence of the mating system.

In our model, the influence of the mating system can be explained by the interaction between two phenomena. First, kin competition affects both sexes, but its effect is stronger in monandry than in polyandry due to a higher local relatedness (Fig. A1), a consequence of a smaller proportion of males that reproduce in monandry. Second, in monandry and polyandry, males obtain higher benefits of dispersal because they experience a higher variance in their reproductive success between patches than females (Fig. A2) as described in Gros et al. (2009). In monogamy, males and females are subjected to the same competition processes; thus they experience the same variance in reproductive success and disperse equally. In polyandry and monandry, fewer males reproduce than females, and this difference between the sexes is even more pronounced in monandry. Therefore, the variance in reproduction between patches is higher for males than females, and higher in monandry than polyandry. This difference between males and females, in interaction with strong enough kin competition, leads to the evolution of male-biased dispersal (Figs 1, A1, A2). As in Perrin and

Mazalov (2000), our results show that mating system and kin competition influence sex-biased dispersal. However, the mechanisms at stake in our simulations differ from those proposed by Perrin and Mazalov. Our results show the evolution of male-biased dispersal without relaxing kin competition in females, and the influence of the variance in reproduction between patches. In addition, we did not limit our modelling to the assumption of exponential growth.

Both kin competition and the variance in reproductive success can be affected by other factors and by the feedback of dispersal. For example, high heterogeneity in patch quality has two effects: first, as widely found, it induces the evolution of a high dispersal rate (Bach et al., 2006; Gros, Hovestadt, & Poethke, 2008; Poethke et al., 2007; Travis & Dytham, 1998) that reduces kin competition; second, it reduces sex bias in the variance of reproductive success. These two effects lower the difference between male and female benefits of dispersal and ultimately lower the sex bias in dispersal. Dispersal cost also has an influence on sex-biased dispersal. A very low or very high dispersal cost reduces the sex bias in dispersal (Fig. A3). A potentially important element of the interaction between individual benefit, kin benefit and dispersal cost is the dispersal decision rule. In our model, we used density-dependent dispersal, and, therefore, individuals have information on their potential dispersal benefits (Clobert et al., 2009). However, density-independent dispersal simulations led to the same evolution of sex-biased dispersal in the three mating systems studied, with the same evidence of the key role of kin competition (Fig. A4).

The effect of kin competition on the evolution of sex-biased dispersal can be affected by the biological and ecological characteristics of organisms. Most of the hypotheses on sex-biased dispersal were proposed to explain dispersal patterns in birds and mammals, which show mainly female-biased and male-biased dispersal, respectively (Dobson, 2013; Greenwood, 1980). The main hypothesis, which relates sex-biased dispersal and the preponderant mating system in each of these two groups, remains under debate (Mabry et al., 2013). Our model can adapt to different organisms, but our parameterization fitted better with the biology of invertebrates. Invertebrates include organisms with very variable biological and ecological traits, but most of them suffer a high dispersal cost and also have a high fecundity (Benton & Bowler, 2012). We can expect a high fecundity (with a large variance) to induce a high heterogeneity across patches that should often cancel sex bias in dispersal (Fig. 2). An interesting case, according to our results, is provided by Markow and Castrezana (2000) who found no sex-biased dispersal in two *Drosophila* species and a male-biased dispersal in a third. The latter species showed a stronger population genetic structure and a lower dispersal rate than the other two. This result is in accordance with our predictions. Sex-biased dispersal was also found in other species, such as a male-biased dispersal in a butterfly (Bennett, Pack, Smith, & Betts, 2013), a ground beetle (Lagisz, Wolff, Sanderson, & Laskowski, 2010), a neotropical orchid bee (López-Uribe, Zamudio, Cardoso, & Danforth, 2014) and a female-biased dispersal in damselflies (Beirinckx, Van Gossum, Lajeunesse, & Forbes, 2006). As mentioned by Benton and Bowler (2012), invertebrates often lay many eggs in a small area and should then suffer strong kin competition, which could explain the evolution of sex-biased dispersal. In addition, as illustrated by our results, a better understanding of sex-biased dispersal and of the effect of the mating system requires us to pay attention to other parameters such as kin interactions, inbreeding, dispersal cost, intensity of local competition (for resources, mates), genetic structure and sex ratio. This broader approach is also justified by the accumulating evidence of the multideterminism of dispersal (Clobert et al., 2012) and seems useful to explain sex-biased dispersal (Lambin et al., 2001).

As already mentioned, the mating system is central to explain sex-biased dispersal in many species. Usually, mating systems are characterized by the number of mates of each individual and the defence of mating resources (Reynolds, 1996). In our simulations, we investigated the effect of the number of mates. In the three different mating systems (monandry, polyandry, monogamy), our results never showed a female-biased dispersal when sex ratio is balanced and cost of dispersal unbiased. We also independently tested the defence of mating resources via unequal dispersal costs between males and females, an important hypothesis to explain sex-biased dispersal (Greenwood, 1980; Gros et al., 2008). For example, males that compete for territory may pay a high cost when they disperse because they lose information on their local environment. In this case, females should have a higher dispersal rate than males because they do not pay this cost (Fig. 4). Results obtained in the Siberian jay, *Perisoreus infaustus*, by Gienapp and Merilä (2011) agree with this hypothesis. Other differences between male and female dispersal costs were identified in birds (Nevoux, Arlt, Nicoll, Jones, & Norris, 2013), mammals (Soulsbury, Baker, Iossa, & Harris, 2008) and invertebrates (Gu, Hughes, & Dorn, 2006; Nespolo, Roff, & Fairbairn, 2008).

Local relatedness affects not only kin competition but also inbreeding. Inbreeding is a key factor historically proposed to explain the evolution of sex-biased dispersal (Dobson, 2013). Previous deterministic models have shown that inbreeding is a good candidate to explain sex-biased dispersal in the absence of kin competition, but it has weaker effects when kin competition is taken into account (Perrin & Goudet, 2001). In the same way, our results indicate that inbreeding is more able to reinforce an existing sex bias in dispersal than to create such a bias. Whereas our model predicts a strong influence of kin competition, inbreeding does not qualitatively change the results and does not promote sex-biased dispersal. This is in agreement with Guillaume and Perrin (2006), although these authors modelled the genetic load in a different way. Interactions between kin competition and inbreeding are complex, and in many theoretical cases adding inbreeding does not affect dispersal evolution (Roze & Rousset, 2005).

We tested the effect of a change in the primary sex ratio. Many organisms within different groups can modify the primary sex ratio of their offspring (Alonso-Alvarez, 2006; Cockburn, 1989; Ode, Antolin, & Strand, 1998; West, Shuker, & Sheldon, 2005). It is interesting to draw a parallel between sex-biased dispersal and sex-biased sex ratio because both processes can evolve in response to the same factors (Leturque & Rousset, 2004; West et al., 2005). We did not model the coevolution of sex ratio adjustment and dispersal (see Wild & Taylor, 2004), but we tested the effect of a change in the sex ratio on sex-biased dispersal under different mating systems (Fig. 5). Our results showed, as expected, a strong influence of the sex ratio under monogamy because the number of available partners is crucial in this mating system. By contrast, there was only a quantitative effect of the sex ratio on sex-biased dispersal under monandry and polyandry: even a strongly female-biased sex ratio did not lead to the evolution of a high female dispersal nor reduce the bias towards male dispersal. If we had built our model with a limited number of reproductive places by patch, as in some other models (Gros et al., 2008, 2009; Perrin & Mazalov, 2000; Wild & Taylor, 2004), the sex ratio would have had a higher effect because of the competition between females for these places.

To conclude, using a model where we defined mating systems by the number of mates, we found that the mating system influences the evolution of sex-biased dispersal through both the pair bond pattern and the genetic structure of the population, giving a key role to kin competition. However, the genetic or social emphasis on mating system can affect conclusions of studies (Coltman et al., 1999; Griffith, Owens, & Thuman, 2002), especially for sex-biased dispersal (Mabry et al., 2013). In particular, the social view of mating system gives a greater importance to resources and it can also consider other factors of dispersal such as tenure duration (Clutton-Brock & Lukas, 2012; Graw, Lindholm, & Manser, 2016) or cooperation (Graw et al., 2016; Ridley, 2012). Despite our poor knowledge of the interplay of social and genetic factors involved in the link between mating system and dispersal, we can safely say that kin competition is universal as advocated by Lambin et al. (2001). Thus, our current study strengthens Dobson's (2013) message that there is a need for studies exploring the relationship between kin competition and sex-biased dispersal.

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Figures captions:

Fig. 1. Dispersal rate at equilibrium for females (circles) and males (squares) in the unshuffled model (filled symbols) and shuffled (i.e. without genetic structure) model (open symbols) for the three mating systems studied. (a) Monogamy, (b) monandry and (c) polyandry. Parameters were fixed to their base value as in Table 1. Error bars indicate 95% confidence interval built by bootstrapping the results of 1000 replicate simulation runs.

Fig. 2. Dispersal rate at equilibrium for females (circles) and males (squares) as a function of heterogeneity in patch quality (σ) for the three mating systems studied. (a) Monogamy, (b) monandry and (c) polyandry. Filled symbols: unshuffled model; open symbols: shuffled (i.e. without genetic structure) model. Other parameters were fixed to their base value as in Table 1. The 95% confidence intervals built by bootstrapping the results of 1000 replicate simulation runs are smaller than the symbols' height (which was set to 0.05 dispersal rate units to ensure visibility). Values shown in Fig. 1 are highlighted by vertical dotted lines.

Fig. 3. Dispersal rate at equilibrium for males (grey) and females (black) plotted against homozygosity cost on fecundity for the three mating systems studied. (a) Monogamy, (b) monandry and (c) polyandry. Heterogeneity in patch quality (σ) was fixed to 1, and other parameters were fixed to their base value as in Table 1. Line width indicates 95% confidence interval built by bootstrapping the results of 100 replicate simulation runs.

Fig. 4. Dispersal rate at equilibrium for males (grey) and females (black) for a range of male dispersal costs and for the three mating systems studied. (a) Monogamy, (b) monandry and (c) polyandry. Female dispersal cost (μ) was fixed to 0.1, and other parameters were fixed to their

base value as in Table 1. The vertical dotted line shows equality of dispersal costs between males and females. Line width indicates 95% confidence interval built by bootstrapping the results of 1000 replicate simulation runs.

Fig. 5. Dispersal rate at equilibrium for males (grey) and females (black) when the sex ratio (proportion of males) varies for the three mating systems studied. (a) Monogamy, (b) monandry and (c) polyandry. Other parameters were fixed to their base value as in Table 1. Line width indicates 95% confidence interval built by bootstrapping the results of 1000 replicate simulation runs.

Fig. A1. Mean relatedness index before dispersal between individuals of the same patches (upward triangle) and from different patches (downward triangle) in the unshuffled model (filled symbols) and the shuffled (i.e. without genetic structure) model (open symbols) for the three mating systems studied. (a) Monogamy, (b) monandry and (c) polyandry. Parameters were fixed to their base value as in Table 1. Error bars indicate 95% confidence interval built by bootstrapping the results of 1000 replicate simulation runs.

Fig. A2. Between-patch coefficient of variation in mean per capita reproductive success for females (circles) and males (squares) in the unshuffled model (filled symbols) and the shuffled (i.e. without genetic structure) model (open symbols) for the three mating systems studied. (a) Monogamy, (b) monandry and (c) polyandry. Parameters were fixed to their base value as in Table 1. Error bars indicate 95% confidence interval built by bootstrapping the results of 1000 replicate simulation runs.

Fig. A3. Dispersal rate at equilibrium for males (grey) and females (black) in (a, d) monandry and (e, h) polyandry with increasing heterogeneity in patch quality from (a) to (d) and from (e) to (h): (a),(e): $\sigma = 0$; (b),(f): $\sigma = 0.5$; (c),(g): $\sigma = 1$; (d),(h): $\sigma = 2$. Other parameters were fixed to their base value as in Table 1. Line width indicates 95% confidence interval built by bootstraping the results of 100 replicate simulation runs.

Fig. A4. Density-independent dispersal rate at equilibrium for females (circles) and males (squares) in the standard (black) and the shuffled (blank) models for the three mating systems studied. (a) Monogamy, (b) monandry and (c) polyandry. Parameters were fixed to their base value as in Table 1. The 95% confidence intervals built by bootstrapping the results of 1000 replicate simulation runs are smaller than the symbols' height (which was set to 0.05 dispersal rate units to ensure visibility). We tested density-independent dispersal simply by setting $dp_i = ds_i$: the probability of dispersal of an individual is equal to the value of its adaptive trait, the dispersal strategy.

Table 1: Simulation parameters

Name	Symbol	Base value
Patch capacity	K	100
Number of patches	n_{patch}	100
Dispersal mortality	μ	0.1
Mean patch quality	λ	2
Heterogeneity in patch quality	σ	0.5
Intensity of density dependence	β	1
Primary sex ratio	sr_{b}	0.5
Homozygosis penalty coefficient	ρ	0
Mutation frequency on dispersal alleles	f_{s}	0.001
Mutation standard deviation on dispersal alleles	sd_{s}	0.05
Mutation frequency on neutral alleles	f_{n}	0.001