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

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19 The relation between mating system and sex-biased dispersal has been debated for three

20 decades. However, the relative importance of the processes involved in this relation remains

21 poorly known. In this study, we paid special attention to kin competition. We built an

22 adaptive individual-based model fixing three mating systems (monandry, polyandry,

23 monogamy) in a metapopulation, and allowing dispersal across patches to evolve

24 independently for males and females. Our simulations showed that a difference in the number

25 of mates can determine the evolution of sex-biased dispersal. Dispersal appears strongly male

26 biased under monandry and polyandry, but balanced under monogamy. By contrast, we

27 showed that inbreeding can influence but does not promote sex-biased dispersal, and that the

28 primary sex ratio does not qualitatively affect the evolution of sex-biased dispersal under

29 monandry and polyandry. These results are driven by the interaction of two factors: the

30 variation in reproductive success between patches in the metapopulation and kin competition.

31 These two factors are influenced by the mating system, which modifies both the competition

32 for access to partners and the mean relatedness between individuals. To ascertain that kin

33 competition actually drives sex-biased dispersal, we made simulations with destruction of any

34 genetic structure in the metapopulation, and we found that in this case dispersal was not sex

35 biased.

36

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38 Keywords: dispersal, individual-based model, kin competition, mating system, sex-biased

39 dispersal, spatial heterogeneity.

40

41   Mating and dispersal are two key events in the life of an individual, which are thought

42   to be linked by several mechanisms (Greenwood, 1980; Gros, Poethke, & Hovestadt, 2009;

43   Perrin & Goudet, 2001; Perrin & Mazalov, 2000). In particular, the link between mating

44   system and dispersal has been largely invoked to explain sex-biased dispersal (Chapple &

45   Keogh, 2005; Greenwood, 1980; Mabry, Shelley, Davis, Blumstein, & van Vuren, 2013;

46   Nagy, Günther, Knörnschild, & Mayer, 2013), the most discussed feature in the dispersal

47   literature. The main hypothesis suggests that prevailing male dispersal, as observed in

48   mammals, and prevailing female dispersal, as observed in birds, are due to the predominance

49   of polygyny and monogamy in each group, respectively (Greenwood, 1980). However, more

50   than 30 years after Greenwood proposed this hypothesis, it is still debated (Dobson, 2013;

51   Johnson & Gaines, 1990; Mabry et al., 2013). Some evidence exists that links the mating

52   system and sex-biased dispersal, especially in mammals (Mabry et al., 2013), but it remains

53   challenging to conclude whether the mating system actually drives the evolution of dispersal

54   or whether these two traits only covary (Clutton-Brock & Lukas, 2012). Some modelling

55   results suggest that the mating system alone can indeed drive the evolution of dispersal

56   (Perrin & Goudet, 2001; Perrin & Mazalov, 1999, 2000). However, because dispersal is

57   influenced by many parameters (Clobert, Massot, & Le Galliard, 2012), it is often difficult to

58   determine whether its evolution depends on the mating system itself or on other life history

59   traits correlated with the mating system (Lawson Handley & Perrin, 2007).

60   Dispersal is not only widespread in life (Dobson, 1982), it is also a highly multifaceted

61   trait. Primarily, there can be natal or breeding dispersal (Dobson, 2013), as well as short- or

62   long-distance dispersal (Murrell, Travis, & Dytham, 2002). In motile animals, dispersal

63   appears as a complex process with several phases, such as departure, transfer and settlement,

64   rather than a holistic behaviour (Clobert, Le Galliard, Cote, Meylan, & Massot, 2009;

65   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

90 resources (Massot, Clobert, Lecomte, & Barbault, 1994), higher dispersal should be selected

91 for females in monogamous systems and males in polygynous systems (Greenwood, 1980).

92   The genetic environment has been shown to play a key role in the evolution of

93 dispersal. In particular, inbreeding avoidance has often been put forward to explain sex-biased

94 dispersal. In contrast, kin competition avoidance has been somewhat neglected (Dobson,

95 2013), despite some theoretical (Hamilton & May, 1977; Poethke, Pfenning, & Hovestadt,

96 2007) and empirical evidence (Clobert et al., 2012; Lambin, Aars, & Piertney, 2001). First,

97 Hamilton and May (1977) showed, using a game-theoretical approach, that dispersal can

98 evolve in response to kin competition, even if the intensity of competition is constant in space.

99 Then, Frank (1986) showed that dispersal equilibrium can be directly linked to relatedness,

100 and thus kin competition. Taylor (1988) extended this work, showing in particular that

101 haplodiploidy promotes sex-biased dispersal. In a highly cited paper, Perrin & Mazalov

102 (2000) investigated sex-biased dispersal following Greenwood's (1980) mating system

103 hypothesis and showed that sex-biased dispersal evolution is possible when males and

104 females do not compete in the same way for resources. However, this kind of deterministic

105 model can miss stochastic effects as pointed out by Gros et al. (2009). Using an individual-

106 based model (stochastic by construction), these authors put forward another mechanism to

107 explain sex-biased dispersal. They showed that sex-specific spatiotemporal variance of fitness

108 between patches in the metapopulation can promote sex-biased dispersal. However, they did

109 not unravel the role of kin competition, and they contrasted a random mating with a harem

110 system, which would magnify the expected effect.

111   In this study, we investigated the interplay of kin competition and spatiotemporal

112 variance of fitness on the evolution of sex-biased dispersal. We considered the influence of

113 genetic mating system on the coevolution of male and female dispersal behaviour in a

114 metapopulation. We modelled three genetic mating systems, monogamy, monandry and

115   polyandry, which differed only in the number of partners that females and males can have.

116   We focused on how these three mating systems, having different impacts on the genetic

117   structure of the metapopulation, and different levels of competition for mates, can affect

118   dispersal in each sex. We assessed quantitatively the effect of mating system on the dispersal

119   rate in relation to important parameters such as the sex ratio and the intensity of inbreeding

120   depression. We used an individual-based model, where dispersal was adaptive, to take into

121   account kin selection and stochasticity. We estimated the relative importance of kin selection

122   versus individual selection by breaking the genetic structure of the metapopulation using the

123   method of Poethke et al. (2007).

124

125   **\<H1\>The model**

126   In our adaptive individual-based model (Bach, Thomsen, Pertoldi, & Loeschcke,

127   2006) of dispersal evolution, mainly inspired by the work of Poethke et al. (2007), dispersal is

128   the only adaptive trait. We did not compute individual or inclusive fitness; these, as well as

129   kin interactions, were emergent properties of the simulations. The evolutionarily stable

130   dispersal rate was also an outcome of the simulations.

131   *\<H2\>Demography*

132   The model considers populations of sexually reproducing diploidic organisms occupying a

133   number n_{patch} of patches and constituting a metapopulation. The model follows a simple life

134   cycle with, in order, dispersal, mating, reproduction, birth, survival. Adults die after

135   reproduction so that generations do not overlap.

136   All patches have the same carrying capacity K, but the reproductive quality of patches

137   varies along time and across space. Patch quality is drawn from a log-normal distribution with

138   mean λ and standard deviation σ. Therefore σ describes the heterogeneity in patch quality.

139 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

140 time t is drawn from a Poisson distribution with mean $\Lambda(t,j)$. The sex of newborns is

141 determined by inheritance of the sexual chromosomes of their parents (XY model). The sex

142 ratio at birth, sr_{b}, is balanced in most simulations, but can be biased for exploratory purposes

143 by changing the probability of the inheritance of sexual chromosomes. The realized sex ratio

144 at birth is $n_{\mathrm{males}}/(n_{\mathrm{females}} + n_{\mathrm{males}})$, with n_{males} and n_{females} the counted number of

145 newborns in each sex. Its average value is equal to the probability sr_{b} of inheriting the

146 father's Y chromosome and becoming a male.

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

148 probability

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

149 where $\alpha = (\lambda^{1/\beta} - 1)/K$, N_j is population size in patch j and β parameterizes the intensity

150 of density dependence (Poethke *et al.*, 2007). The survival probability decreases with

151 increasing N_j, and decreases faster for small β. Note that N_j includes only newborns because

152 adults die after reproduction.

153 *<H2>Mating*

154 The success of a female depends on patch quality, the survival of its offspring and its mating

155 with at least one male. The mating success of a male depends on the female(s) it mates with.

156 We investigated three mating systems; in each, pairs were formed from males and females

157 drawn randomly within their patch. (1) In monandry each female mates with only one male

158 and males have no reproduction limit. (2) In polyandry each female mates with many males,

159 males have no reproduction limit and each newborn has a father chosen randomly in the

160 patch. (3) In monogamy each female mates with only one male and males are no longer

161   available after a single mating. Thus, males and females have a single partner, and some

162   individuals do not reproduce when the breeding sex ratio is unbalanced in a patch.

163   *<H2>Dispersal*

164   To allow for sex-specific dispersal, males and females are endowed with two independent loci

165   (d_m and d_f) that drive dispersal independently in each sex. Each newborn inherits two

166   dispersal alleles, one randomly chosen from its mother and one randomly chosen from its

167   father. Mutations occur with frequency f_s, the new value of a mutated allele being drawn from

168   a normal distribution with mean equal to the value of the ancestor allele and standard

169   deviation sd_s. The dispersal strategy ds_i of an individual i is identified with the mean values

170   of the two alleles expressed by its sex. The dispersal probability of the individual dp_i depends

171   on density as follows:

172
$$dp_i = \begin{cases} 0 \ if \ N_j/K \ \leq ds_i \\ 1 - \frac{ds_i}{\mathrm{N}_j/K} \ if \ N_j/K \ > ds_i \end{cases}.$$

173   Following this equation, we can see that the dispersal strategy ds_i acts as a threshold: if the

174   patch density N_j/K is under the threshold, the individual never disperses; if the patch density

175   is above the threshold, the higher the density, the higher the probability of dispersing.

176   Therefore, whenever the patch density is near the dispersal threshold, the dispersal probability

177   will be very low. Dispersal is global, toward a randomly selected patch. The cost of dispersal

178   is modelled by a probability μ of dying during dispersal. In most simulations this cost is

179   identical for males and females, but we also tested the effect of a sex-biased cost.

180   *<H2>Relatedness, inbreeding and heterozygosity*

181   Each individual is given 32 diploid neutral (not under natural selection) loci, with each locus

182   having two different alleles, A and B. For each allele of a neutral locus, the process of

183   inheritance is the same as for dispersal alleles, and mutations occur with frequency f_n.

184   Mutation performs a switch between the two alleles. This set of loci allows us to measure the

185   relatedness between two individuals at the population and metapopulation levels, taking into

186   account relatedness and possible changes in population size. The heterozygosity of an

187   individual is calculated by assessing the heterozygosity at each locus and counting the

188   heterozygous loci relative to the total number of loci. A fully homozygous individual i has a

189   heterozygosity level H_i of 0. A fully heterozygous individual has a heterozygosity level of 1.

190   On average, the heterozygosity level of an individual decreases with increasing relatedness

191   between its parents. Therefore, we use the heterozygosity level to model inbreeding

192   depression. Homozygous females can suffer a fecundity loss reducing the initial fecundity:

$$F_i = \left\{ \begin{array}{c} F_i \ if \ H_i \ \geq 0.5 \\ F_i \times (2H_i)^\rho \ if \ H_i \ < 0.5 \end{array} \right\}$$

193   where H_i is the heterozygosity level of female i and ρ is the strength of the inbreeding

194   penalty. When ρ is equal to 0, there is no homozygosity depression. When $\rho > 0$, females

195   suffer a loss in fecundity that increases with ρ.

196   *<H2>Test on kin competition*

197   As said before, kin interactions are emergent properties in an individual-based model.

198   However, as in Poethke et al. (2007), we performed simulations in a shuffled version of the

199   model to cancel kin competition. In this shuffled model, before dispersal occurs, individuals

200   are randomly redistributed in the whole metapopulation, but preserving the initial patch-

201   specific densities and sex ratios. Therefore, the genetic structure is broken, but the

202   demographic structure remains unchanged. In the unshuffled simulations, a dispersing

203   individual has less chance of competing with kin in its patch of arrival than in its patch of

204   departure. In the shuffled simulation, because individuals are randomly redistributed before

205   dispersal, the chance of competing with kin is the same across all patches. Thus, the

206   comparison between the shuffled and the unshuffled simulations allows to test specifically the

207   effect of kin competition on the evolution of male and female dispersal.

208   *<H2>Simulation parameters and outcomes*

209 The simulation parameters used are reported in Table 1. Our results were based on the final

210 outcome of many runs for each parameter set (Monte Carlo simulation). We made sure that

211 equilibrium was reached by letting the simulations run a large number of generations (15 000

212 at least) and verified that the mean dispersal rate was stable for each sex. We did not use

213 statistical significance tests that are inappropriate to compare simulation model results (White,

214 Rassweiler, Samhouri, Stier, & White, 2014). We followed the two arguments of White et al.

215 (2014): first, the potentially infinite number of replications can artificially increase the power

216 of statistical tests. Second, two sets of simulations with different parameters lead to different

217 outcomes. Thus, we focused our analysis on the magnitude of the difference between

218 simulations. Our results are shown with 95% confidence intervals to ensure that a difference

219 between two sets of simulations is not the result of stochasticity.

220 **<H1>Results**

221 *<H2>Mating system and local relatedness*

222 Our simulations show that the mating system influences the evolution of sex-biased

223 dispersal. Males and females evolve the same dispersal rate in monogamy, while the dispersal

224 rate is higher in males in the monandrous and polyandrous mating systems (Fig. 1). Moreover,

225 males disperse more in monandry than in polyandry. In the shuffled simulations, where the

226 effect of kin competition is removed, a lower dispersal rate evolves in both sexes and the male

227 bias in dispersal disappears (Figs 1 and 2).

228 The difference in dispersal between males and females in monandry and polyandry is

229 the result of the interplay of two processes. First, there is a strong kin competition effect, as

230 revealed by the lower dispersal in both sexes in the shuffled simulations (Figs 1 and 2). This

231 effect is expected to be stronger in monandry than in polyandry because a smaller proportion

232 of males reproduce in monandry, so that local relatedness is higher (illustrated in Fig. A1).

233 Second, the mating system creates an asymmetry between the sexes in the spatiotemporal

234 variability of reproductive success between patches. The variability of reproductive success

235 between patches is the same for males and females in monogamy, whereas this variation is

236 higher for males in monandry and polyandry (Fig. A2). This sex bias in the variability of

237 reproductive success persists in the shuffled simulations, i.e. when there is no kin competition

238 (Fig. A2).

239   Inbreeding also affects dispersal. Increasing the penalty of homozygosity (i.e. the cost

240 of inbreeding) increases the dispersal rate, but this average effect also depends on the mating

241 system (Fig. 3). Under monogamy, both sexes evolve higher dispersal rates with increasing

242 homozygosity penalty. Under polyandry and monandry, the increase in dispersal with higher

243 homozygosity penalty occurs mainly in males.

244

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

246   Dispersal increases with increasing heterogeneity in patch quality, and sex-biased

247 dispersal is reduced for high heterogeneity in patch quality (Fig. 2). At the same time,

248 dispersal rate decreases with increasing dispersal cost in both sexes, and sex-biased dispersal

249 only appears when the mortality of dispersers is lower than 25% (Fig. A3). We also tested the

250 effect of sex-biased dispersal cost (Fig. 4). We changed the male dispersal cost keeping the

251 female dispersal cost unchanged. As expected, a sex-biased dispersal cost modifies the

252 evolution of sex-biased dispersal. Whatever the mating system, an increased male dispersal

253 cost decreases male dispersal rate. Consequently female dispersal increases as male dispersal

254 decreases. In monogamy, the sex with the higher dispersal cost has the lower dispersal rate at

255 equilibrium. In monandry and polyandry, dispersal is female biased for high values of male

256 dispersal cost (e.g. in Fig. 4, female-biased dispersal evolves when male dispersal cost is

257 about 30% higher than female dispersal cost).

258   A bias in the primary sex ratio has different effects depending on the mating system

259   (Fig. 5). In monogamy, a bias in sex ratio induces sex-biased dispersal: the more numerous

260   sex disperses more. Although male dispersal still increases under monandry and polyandry

261   when the sex ratio is male biased, a bias in sex ratio does not qualitatively change the sex bias

262   in dispersal. In other words, the primary sex ratio does not appear to affect the evolution of

263   sex-biased dispersal in the monandrous and polyandrous mating systems.

264

265   **<H1>Discussion**

266   The importance of kin competition in the evolution of dispersal has been well

267   established by several theoretical works (Comins, Hamilton, & May, 1980; Hamilton & May,

268   1977; Poethke et al., 2007; Taylor, 1988). The situation is more contrasted with regard to the

269   evolution of sex-biased dispersal. For instance, Perrin and Mazalov (2000) have shown that

270   male-biased dispersal can evolve in polygynous/promiscuous mating systems in response to

271   kin competition. However, they did not take into account stochastic effects and used an

272   unrealistic exponential growth assumption (Gros et al., 2009). More recently, Lehmann &

273   Balloux (2007) developed an analytical model taking into account both kin competition and

274   spatiotemporal variance in fecundity, but they did not address the question of mating process

275   nor the coevolution of male and female dispersal behaviour.

276   In the present study, we have built an individual-based model to investigate the effect

277   of different mating systems, defined in our study by the number of mates, on the evolution of

278   sex-biased dispersal through their influence on kin competition. We revealed the role of kin

279   competition by contrasting models with or without genetic structure, i.e. with or without

280   indirect fitness benefits of kin competition avoidance by dispersal. Our model is focused only

281   on intragenerational kin competition and does not include parent-offspring conflict or kin

282   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

308 Mazalov (2000), our results show that mating system and kin competition influence sex-

309 biased dispersal. However, the mechanisms at stake in our simulations differ from those

310 proposed by Perrin and Mazalov. Our results show the evolution of male-biased dispersal

311 without relaxing kin competition in females, and the influence of the variance in reproduction

312 between patches. In addition, we did not limit our modelling to the assumption of exponential

313 growth.

314　　　　Both kin competition and the variance in reproductive success can be affected by other

315 factors and by the feedback of dispersal. For example, high heterogeneity in patch quality has

316 two effects: first, as widely found, it induces the evolution of a high dispersal rate (Bach et al.,

317 2006; Gros, Hovestadt, & Poethke, 2008; Poethke et al., 2007; Travis & Dytham, 1998) that

318 reduces kin competition; second, it reduces sex bias in the variance of reproductive success.

319 These two effects lower the difference between male and female benefits of dispersal and

320 ultimately lower the sex bias in dispersal. Dispersal cost also has an influence on sex-biased

321 dispersal. A very low or very high dispersal cost reduces the sex bias in dispersal (Fig. A3). A

322 potentially important element of the interaction between individual benefit, kin benefit and

323 dispersal cost is the dispersal decision rule. In our model, we used density-dependent

324 dispersal, and, therefore, individuals have information on their potential dispersal benefits

325 (Clobert et al., 2009). However, density-independent dispersal simulations led to the same

326 evolution of sex-biased dispersal in the three mating systems studied, with the same evidence

327 of the key role of kin competition (Fig. A4).

328　　　　The effect of kin competition on the evolution of sex-biased dispersal can be affected

329 by the biological and ecological characteristics of organisms. Most of the hypotheses on sex-

330 biased dispersal were proposed to explain dispersal patterns in birds and mammals, which

331 show mainly female-biased and male-biased dispersal, respectively (Dobson, 2013;

332 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).

382   We tested the effect of a change in the primary sex ratio. Many organisms within

383   different groups can modify the primary sex ratio of their offspring (Alonso-Alvarez, 2006;

384   Cockburn, 1989; Ode, Antolin, & Strand, 1998; West, Shuker, & Sheldon, 2005). It is

385   interesting to draw a parallel between sex-biased dispersal and sex-biased sex ratio because

386   both processes can evolve in response to the same factors (Leturque & Rousset, 2004; West et

387   al., 2005). We did not model the coevolution of sex ratio adjustment and dispersal (see Wild

388   & Taylor, 2004), but we tested the effect of a change in the sex ratio on sex-biased dispersal

389   under different mating systems (Fig. 5). Our results showed, as expected, a strong influence of

390   the sex ratio under monogamy because the number of available partners is crucial in this

391   mating system. By contrast, there was only a quantitative effect of the sex ratio on sex-biased

392   dispersal under monandry and polyandry: even a strongly female-biased sex ratio did not lead

393   to the evolution of a high female dispersal nor reduce the bias towards male dispersal. If we

394   had built our model with a limited number of reproductive places by patch, as in some other

395   models (Gros et al., 2008, 2009; Perrin & Mazalov, 2000; Wild & Taylor, 2004), the sex ratio

396   would have had a higher effect because of the competition between females for these places.

397   To conclude, using a model where we defined mating systems by the number of mates,

398   we found that the mating system influences the evolution of sex-biased dispersal through both

399   the pair bond pattern and the genetic structure of the population, giving a key role to kin

400   competition. However, the genetic or social emphasis on mating system can affect

401   conclusions of studies (Coltman et al., 1999; Griffith, Owens, & Thuman, 2002), especially

402   for sex-biased dispersal (Mabry et al., 2013). In particular, the social view of mating system

403   gives a greater importance to resources and it can also consider other factors of dispersal such

404   as tenure duration (Clutton-Brock & Lukas, 2012; Graw, Lindholm, & Manser, 2016) or

405   cooperation (Graw et al., 2016; Ridley, 2012). Despite our poor knowledge of the interplay of

406   social and genetic factors involved in the link between mating system and dispersal, we can

407 safely say that kin competition is universal as advocated by Lambin et al. (2001). Thus, our

408 current study strengthens Dobson's (2013) message that there is a need for studies exploring

409 the relationship between kin competition and sex-biased dispersal.

410

413

414 **References**

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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.

641   **Fig. A3.** Dispersal rate at equilibrium for males (grey) and females (black) in (a, d) monandry

642   and (e, h) polyandry with increasing heterogeneity in patch quality from (a) to (d) and from

643   (e) to (h): (a),(e): $\sigma = 0$; (b),(f): $\sigma = 0.5$; (c),(g): $\sigma = 1$; (d),(h): $\sigma = 2$. Other parameters

644   were fixed to their base value as in Table 1. Line width indicates 95% confidence interval

645   built by bootstraping the results of 100 replicate simulation runs.

646

647   **Fig. A4.** Density-independent dispersal rate at equilibrium for females (circles) and males

648   (squares) in the standard (black) and the shuffled (blank) models for the three mating systems

649   studied. (a) Monogamy, (b) monandry and (c) polyandry. Parameters were fixed to their base

650   value as in Table 1. The 95% confidence intervals built by bootstrapping the results of 1000

651   replicate simulation runs are smaller than the symbols' height (which was set to 0.05 dispersal

652   rate units to ensure visibility). We tested density-independent dispersal simply by setting

653     $dp_i = ds_i$: the probability of dispersal of an individual is equal to the value of its adaptive

654   trait, the dispersal strategy.

655

656 **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

657

658