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

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18
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

37

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

66 populations and metapopulations (Kokko & López-Sepulcre, 2006; Travis & Dytham, 1998),
67 dispersal is often defined as ‘any movement of individuals or propagules with potential
68 consequences for gene flow across space’ (Ronce, 2007, p.232). Beyond genes, dispersal can
69 also impact social interactions (Boudjemadi, Lecomte, & Clobert, 1999) and demography
70 (Massot, Clobert, Pilorge, Lecomte, & Barbault, 1992). For these reasons, dispersal is a key
71 determinant of population persistence in the context of habitat fragmentation (Parvinen,
72 Dieckmann, Gyllenberg, & Metz, 2003), climate warming (Clobert et al., 2009; Walther et al.,
73 2002) and the success of invasive species (Kubisch, Fronhofer, Poethke, & Hovestadt, 2013).

74 It is generally assumed that dispersal is costly, which includes the predispersal cost of
75 development of dispersal-related traits, as well as the cost in time, energy and exposure to
76 various risks during dispersal (Bonte et al., 2012). These costs can negatively affect survival
77 or reproductive success of dispersers. Thus, individuals should disperse only if sufficient
78 benefits of dispersal outweigh its costs. The fitness benefits of dispersal often result from the
79 avoidance of local costs related to habitat quality, inbreeding or competition (Clobert,
80 Danchin, Dhondt, & Nichols, 2001; Clobert et al., 2012). Particular attention has been paid to
81 the relative importance of the costs and benefits of dispersal for males and females, which can
82 be affected by the corresponding costs and benefits related to the mating system. For instance,
83 dispersal can depend on the relationship between the mating system and competition for
84 mates or for resources to attract mates. Investment in mating, and in obtaining associated
85 resources, varies between males and females depending on the mating system. In monogamy,
86 males compete for resources needed to feed offspring, whereas in polygyny, males compete
87 more directly for mating opportunities but less for resources. Therefore, competition for
88 resources is more challenging for males in monogamous species and for females in
89 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 $n_{\text{males}}/(n_{\text{females}} + n_{\text{males}})$, 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

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

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:

$$172 \quad dp_i = \begin{cases} 0 & \text{if } N_j/K \leq ds_i \\ 1 - \frac{ds_i}{N_j/K} & \text{if } N_j/K > ds_i \end{cases}.$$

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:

$$F_i = \begin{cases} F_i & \text{if } H_i \geq 0.5 \\ F_i \times (2H_i)^\rho & \text{if } H_i < 0.5 \end{cases}$$

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

283 often cited as being involved in dispersal evolution (Lambin et al., 2001). We showed that
284 intragenerational kin competition can play a central role in the evolution of sex-biased
285 dispersal, and that it can be, under a large range of conditions, a better candidate than
286 inbreeding risk. Therefore, our results confirm the role of kin competition in dispersal
287 evolution and bring new insights to its role in the evolution of sex-biased dispersal. Mainly,
288 we showed that, when the primary sex ratio and dispersal costs are balanced, sex-biased
289 dispersal does not evolve in the absence of genetic structure, i.e. in the absence of kin-related
290 benefit to disperse. We thus pointed out the importance of kin competition avoidance in the
291 evolution of sex-biased dispersal (Figs 1 and 2). We observed a higher male bias in dispersal
292 under monandry than polyandry (Fig. 1). Furthermore, we found that heterogeneity in patch
293 quality, dispersal cost, inbreeding and primary sex ratio also affected the evolution of sex-
294 biased dispersal. These factors can modulate the influence of the mating system.

295 In our model, the influence of the mating system can be explained by the interaction
296 between two phenomena. First, kin competition affects both sexes, but its effect is stronger in
297 monandry than in polyandry due to a higher local relatedness (Fig. A1), a consequence of a
298 smaller proportion of males that reproduce in monandry. Second, in monandry and polyandry,
299 males obtain higher benefits of dispersal because they experience a higher variance in their
300 reproductive success between patches than females (Fig. A2) as described in Gros et al.
301 (2009). In monogamy, males and females are subjected to the same competition processes;
302 thus they experience the same variance in reproductive success and disperse equally. In
303 polyandry and monandry, fewer males reproduce than females, and this difference between
304 the sexes is even more pronounced in monandry. Therefore, the variance in reproduction
305 between patches is higher for males than females, and higher in monandry than polyandry.
306 This difference between males and females, in interaction with strong enough kin
307 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

333 preponderant mating system in each of these two groups, remains under debate (Mabry et al.,
334 2013). Our model can adapt to different organisms, but our parameterization fitted better with
335 the biology of invertebrates. Invertebrates include organisms with very variable biological and
336 ecological traits, but most of them suffer a high dispersal cost and also have a high fecundity
337 (Benton & Bowler, 2012). We can expect a high fecundity (with a large variance) to induce a
338 high heterogeneity across patches that should often cancel sex bias in dispersal (Fig. 2). An
339 interesting case, according to our results, is provided by Markow and Castrezana (2000) who
340 found no sex-biased dispersal in two *Drosophila* species and a male-biased dispersal in a
341 third. The latter species showed a stronger population genetic structure and a lower dispersal
342 rate than the other two. This result is in accordance with our predictions. Sex-biased dispersal
343 was also found in other species, such as a male-biased dispersal in a butterfly (Bennett, Pack,
344 Smith, & Betts, 2013), a ground beetle (Lagisz, Wolff, Sanderson, & Laskowski, 2010), a
345 neotropical orchid bee (López-Uribe, Zamudio, Cardoso, & Danforth, 2014) and a female-
346 biased dispersal in damselflies (Beirinckx, Van Gossum, Lajeunesse, & Forbes, 2006). As
347 mentioned by Benton and Bowler (2012), invertebrates often lay many eggs in a small area
348 and should then suffer strong kin competition, which could explain the evolution of sex-
349 biased dispersal. In addition, as illustrated by our results, a better understanding of sex-biased
350 dispersal and of the effect of the mating system requires us to pay attention to other
351 parameters such as kin interactions, inbreeding, dispersal cost, intensity of local competition
352 (for resources, mates), genetic structure and sex ratio. This broader approach is also justified
353 by the accumulating evidence of the multideterminism of dispersal (Clobert et al., 2012) and
354 seems useful to explain sex-biased dispersal (Lambin et al., 2001).

355 As already mentioned, the mating system is central to explain sex-biased dispersal in
356 many species. Usually, mating systems are characterized by the number of mates of each
357 individual and the defence of mating resources (Reynolds, 1996). In our simulations, we

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

370 Local relatedness affects not only kin competition but also inbreeding. Inbreeding is a
371 key factor historically proposed to explain the evolution of sex-biased dispersal (Dobson,
372 2013). Previous deterministic models have shown that inbreeding is a good candidate to
373 explain sex-biased dispersal in the absence of kin competition, but it has weaker effects when
374 kin competition is taken into account (Perrin & Goudet, 2001). In the same way, our results
375 indicate that inbreeding is more able to reinforce an existing sex bias in dispersal than to
376 create such a bias. Whereas our model predicts a strong influence of kin competition,
377 inbreeding does not qualitatively change the results and does not promote sex-biased
378 dispersal. This is in agreement with Guillaume and Perrin (2006), although these authors
379 modelled the genetic load in a different way. Interactions between kin competition and
380 inbreeding are complex, and in many theoretical cases adding inbreeding does not affect
381 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

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413

414 **References**

415

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591

592 **Figures captions:**

593

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

599

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

607

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

613

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

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

620

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

626

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

633

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

640

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 bootstrapping 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