

1 **Kin discrimination and demography modulate patterns of sexual conflict**

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3 Gonçalo S. Faria^{1,2*}, Andy Gardner¹ & Pau Carazo³

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5 1. School of Biology, University of St Andrews, Dyers Brae, St Andrews KY16 9TH, United
6 Kingdom.

7

8 2. Institute for Advanced Study in Toulouse, Université Toulouse 1 Capitole, Toulouse,
9 France.

10

11 3. Ethology lab, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of
12 Valencia, Valencia, Spain.

13

14 * corresponding author, e-mail: goncalofs@protonmail.com

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16 **Running Head:** Kin selection and sexual conflict

17

18 **Article Type:** Article

19

20 **Main text word count:** 3490

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26 **Abstract** – Recent years have seen an explosion of interest in the overlap between kin
27 selection and sexual selection, particularly concerning how kin selection can put the brakes
28 on harmful sexual conflict. However, there remains a significant disconnect between theory
29 and empirical research. Whilst empirical work has focused on kin-discriminating behaviour,
30 theoretical models have assumed indiscriminating behaviour. Additionally, theoretical work
31 makes particular demographic assumptions that constrain the relationship between genetic
32 relatedness and the scale of competition, and it is not clear that these assumptions reflect the
33 natural setting in which sexual conflict has been empirically studied. Here, we plug this gap
34 between current theoretical and empirical understanding by developing a mathematical model
35 of sexual conflict that incorporates kin discrimination and different patterns of dispersal. We
36 find that kin discrimination and group dispersal inhibit harmful male behaviours at an
37 individual level, but kin discrimination intensifies sexual conflict at the population level.

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51 *Introduction*

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53 Since their inception, the theories of kin selection and sexual selection have been subjected to
54 intense research within evolutionary biology, but traditionally they have had surprisingly
55 little interaction with one another^{1,2,3}. Recent years have seen an explosion of interest in the
56 interplay between these two processes³, both theoretically and empirically, with a particular
57 focus on how kin selection can shape the evolution of sexual conflict⁴⁻¹⁶. Specifically, one
58 widespread consequence of sexual conflict is the evolution of male traits that inflict harm
59 upon females¹⁷. Such harming behaviour not only reduces a female's fitness but can also
60 have pronounced repercussions for the population as a whole, in an outcome akin to 'the
61 tragedy of the commons'^{4,18-23}. Kin selection might curb the evolution of this harmful
62 behaviour by aligning the interests of different individuals, which implies reproductive
63 cooperation may not be limited to a few highly-social species^{14,24}, as currently surmised.

64

65 However, there is a significant disconnect between theory and empirical research on this
66 topic (Table 1). On the one hand, theory has focused on population viscosity as the driver of
67 kin selection²⁵⁻²⁶, whereby limited dispersal of individuals means that social partners tend to
68 be genetically-related and hence indiscriminate altruistic behaviour may evolve^{3-5,8-10}. On the
69 other hand, empirical research has overwhelmingly focused on kin discrimination²⁵⁻²⁶,
70 whereby individuals are capable of identifying their genealogical relatives and adjusting their
71 behaviour accordingly^{6,7,11-14,16}. This disconnect implies that current theoretical models
72 cannot make predictions as to how sexual conflict evolves when individuals are capable of
73 kin discrimination. Moreover, current theoretical work^{4,9} makes very particular assumptions
74 about dispersal patterns, such that genetic relatedness and resource competition become tied
75 together in a potentially artificial way. Specifically, this work has assumed purely-viscous

76 populations, in which reduced dispersal increases relatedness of neighbours but also
77 intensifies competition between kin, with these two factors having opposite effects on sexual
78 conflict. Consequently, it remains unclear how kin selection will act to modulate sexual
79 conflict – if at all – in ecological scenarios where relatedness and competition are not so
80 tightly intertwined.

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82 Here, we bridge the gap between theoretical and empirical understanding of the impact of kin
83 selection on sexual conflict by incorporating these key empirical aspects into a new
84 theoretical model of male harming behaviour. First, we incorporate kin-discriminating
85 behaviour and contrast its evolution with indiscriminate harming. Second, we explore how
86 kin selection modulates sexual conflict under different patterns of dispersal where relatedness
87 and competition are not intertwined. Specifically, we: (1) develop an “open model”^{27,28} that
88 describes relatedness and competition in general terms, thereby capturing the essential
89 selective forces that shape sexual conflict; (2) explore a range of “closed-model”^{27,28}
90 demographic scenarios to investigate how sexual conflict evolves in empirically-relevant
91 systems; and (3) compare the impact of harmful male behaviour at the population level under
92 different dispersal patterns and in the presence or absence of kin discrimination. Our overall
93 aim is to provide a mathematical framework that delivers concrete theoretical predictions as
94 well as improved conceptual understanding as to how sexual conflict evolves in empirically-
95 relevant scenarios.

96

97 *The role of relatedness and the scale of competition*

98

99 We consider a population divided into social groups, with each group comprising males and
100 females who are interacting with each other in fitness-modulating ways. Our focus is on male

101 harming behaviour: to the extent that a male harms a female, he increases his share of the
 102 paternity of her offspring, but reduces the overall number of offspring that she is able to
 103 produce – and, accordingly, reduces the overall fecundity of females and males within his
 104 group. Following reproduction, all adults die, and juveniles compete for reproductive
 105 resources, with a proportion a of this competition occurring locally (with social-group mates)
 106 and a proportion $1 - a$ occurring globally (with unrelated individuals). Finally, juveniles
 107 mature to adulthood, returning the population to the beginning of the lifecycle.

108

109 Mathematically, we may express a male's competitiveness for mating success as being
 110 proportional to $f_m(y)$, where y is his investment into harming, and we may express a female's
 111 fecundity as being proportional to $f_f(Y)$, where Y is the harm that she experiences. Following
 112 the standard tragedy-of-the-commons approach⁴, we assume that the harm a female
 113 experiences is equal to the average level of harming among the males in her patch (see
 114 supplementary information (SI) for the consequences of relaxing this assumption to cover
 115 cases where females are only harmed by a subset of the males in the social group).

116 Accordingly, a female's relative fitness is $W_f = f_f(Y)/(a f_f(Y) + (1 - a) f_f(\bar{Y}))$, and a male's
 117 relative fitness is $W_m = (f_m(y)/f_m(Y))(f_f(Y)/(a f_f(Y) + (1 - a) f_f(\bar{Y})))$, where \bar{Y} is the average
 118 level of harm in the population. Note that a male's fitness is modulated not only by his own
 119 competitiveness for mates but also by the fecundity of the females in his group, and the
 120 fecundity of the local females depends on the average level of harm exhibited by the males in
 121 the group – including the focal male himself. In other words, the focal male's harming
 122 phenotype y directly impacts upon the level of harming Y suffered by the females in his
 123 group. Performing a kin-selection analysis²⁹ (see SI), we find that natural selection favours an
 124 increase in male harm when $B(1 - r_{mm}) - C(1 - a)(r_{fm} + r_{mm}) > 0$, where $B :=$
 125 $(\partial f_m(y)/\partial y|_{y=\bar{y}})/f_m(\bar{Y})$ is the benefit for a male of harming females, $C := -$

126 $(\partial f_i(Y)/\partial Y|_{Y=\bar{Y}})/f_i(\bar{Y})$ is the cost for a female of being harmed, r_{fm} is the relatedness between
127 local adult females and local adult males, and r_{mm} is the relatedness between local adult males
128 (see SI).

129

130 A male who invests into harming seizes a greater share of the overall mating success of the
131 males that he competes with, yielding a direct-fitness benefit B . However, the corresponding
132 loss of mating success by local males (who are related to the actor by r_{mm}) yields an
133 inclusive-fitness loss Br_{mm} . Harming also reduces the overall number of offspring produced
134 by local females (who are related to the actor by r_{fm}) and local males by C , yielding
135 inclusive-fitness losses of Cr_{fm} and Cr_{mm} . Owing to local competition (a), this translates into
136 a loss of only $C(1 - a)$ surviving offspring for both local females and local males. Harm,
137 therefore, affects males in two different ways: directly through sexual competition between
138 males (Br_{mm}), and indirectly through reducing the overall number of offspring produced by
139 harmed females (Cr_{mm}). Consequently, relatedness between males has a greater potential to
140 shape harm in the population than relatedness between females and males, particularly under
141 localised competition (larger a ; Figure 1).

142

143 The above condition captures the selective forces modulating the evolution of harm: in
144 particular, the role of demography (a , r_{mm} and r_{fm}) and the details as to how harm translates
145 into fecundity (B and C). We now narrow our focus directly onto demography by rearranging
146 this condition into the form $C/B < A$, where $A = (1 - r_{mm})/((1 - a)(r_{fm} + r_{mm}))$ is the potential³⁰
147 for harm associated with the particular demographic context. That is, a higher A means that
148 the condition for an increase in harming to be favoured is less stringent. Accordingly, harm is
149 more likely to be favoured with lower relatedness (r_{mm} and r_{fm} closer to 0; Figure 1A&B) and
150 with more local competition (a closer to 1; Figure 1C&D).

151

152 Our result is consistent with much of the work on kin selection and sexual conflict (Table 1),
153 both theoretically and empirically. Within the theoretical literature, there has been a particular
154 focus on population viscosity as the driver of kin selection^{3,4,5,8-10}. That is, limited dispersal
155 results in individuals being genetically-related to their social partners. Łukasiewicz et al.'s¹⁵
156 experimental-evolution study of bulb-mites found that increased relatedness is associated
157 with a reduction in male harm. The coefficients of relatedness (r_{mm} and r_{fm}) appearing in the
158 above condition capture Łukasiewicz et al.'s¹⁵ result, with their increase yielding a lower
159 potential for harm (Figure 1A&B). However, theory predicts that limited dispersal does not
160 necessarily inhibit male harm: whilst limited dispersal does increase relatedness (higher r),
161 which tends to disfavour harm, it also intensifies local competition (higher a), which tends to
162 favour harm^{9,27,31-35}, and this too is captured by our condition (Figure 1C&D).

163

164 There is, therefore, entanglement between relatedness and scale of competition when harming
165 behaviour is expressed indiscriminately in the context of a purely-viscous population.

166 However, most of the empirical research on this topic has focused on the role of kin
167 discrimination in modulating sexual conflict (Table 1). Specifically, individuals identify
168 which of their social partners are kin and adjust their behaviour accordingly. Mathematically,
169 this is equivalent to varying the relatedness coefficients while holding the scale of
170 competition constant, with the potential for harm decreasing as the relatedness coefficients
171 increase (Figure 1A&B). Kin discrimination, therefore, effectively disentangles relatedness
172 and scale of competition.

173

174 Another possible way to disentangle relatedness and scale of competition involves holding
175 relatedness constant while varying scale of competition (Figure 1C&D), which is expected to

176 result in a reduction in harm as the scale of competition becomes more global (lower a). This
177 can be achieved when competition occurs between groups of individuals, such that low-
178 harming, high-fecundity groups are able to competitively displace their high-harming, low-
179 fecundity rivals. This has been explored in populations of water-striders, where male
180 aggression is disfavoured when there is between-group competition^{36,37}. Outwith sexual
181 conflict, the effect of varying the scale of competition while holding relatedness fixed has
182 been explored through dispersal of groups of relatives – budding dispersal^{35,38–41} – which is
183 one possible scenario that, mathematically, leads to the same result.

184

185 *A predictive model for empirical systems*

186

187 Our open model suggests that kin discrimination and budding dispersal can be important
188 mechanisms in defining how sexual conflict will evolve. Nevertheless, while this model
189 generalises much of the work that has been done so far in the context of sexual conflict and
190 kin selection (Table 1), it fails to offer concrete predictions on how harmful male traits will
191 evolve in biological systems, particularly given how demographic factors can affect both
192 relatedness coefficients and the scale of competition.

193

194 To gain predictive power, we explicitly define the fecundity of a focal female as $f_f = 1 - Y$
195 and the competitiveness for mating success of a focal male as $f_m = 1 + y^\beta$, where Y is the level
196 of harm present in the focal patch, y is the level of harm of a focal male, and β determines the
197 marginal benefit of harming females (see SI). Throughout this section, we consider an infinite
198 diploid population divided into patches⁴² containing three adult females and three adult males
199 (see Figure 2 for an illustration). Each female mates a large number of times, and each time
200 with a randomly and independently chosen male from her group – with the probability that

201 she mates with a particular male being proportional to his relative competitiveness for mating
 202 success. Females always disperse to new patches, while males disperse to a new patch with
 203 probability d_m . This is close to the conditions explored in empirical studies^{6,7,11-14,16} and
 204 allows us to disregard the potential effect of inbreeding which would require its own study to
 205 do it justice. Moreover, while most of those empirical studies have one adult female
 206 interacting with three adult males, their experimental populations (and most wild populations
 207 of those species) do not have male-biased sex-ratios, so here we assume a 3:3 sex ratio (but
 208 note this does not qualitatively change our results – Supplementary Figure 1).

209

210 *Absence of kin discrimination and budding dispersal* – First, let us focus on the level of harm
 211 in the absence of kin discrimination and budding dispersal. An increase in the level of harm is
 212 favoured when:

213

$$214 \frac{(1-r_{mm})(\bar{Y}^{\beta-1}\beta)}{1+\bar{Y}^{\beta}} - r_{mm}(1-a)\frac{1}{1-\bar{Y}} > 0, \quad (1)$$

215

216 where \bar{Y} is the average level of harm in the population, $a = (1 - d_m)^2/2$ is the scale of
 217 competition, and $r_{mm} = 1/3 + 2/3(1 - d_m)^2r$ is the relatedness between males in a patch (where
 218 $r = 1/(5 + d_m(2 - d_m))$ is the relatedness between individuals born in the same patch; SI for
 219 details). Note that a specifies how likely a focal male juvenile is to compete with other males
 220 in the patch for future breeding opportunities, which occurs when neither disperse to other
 221 patches⁴³.

222

223 We can use inequality (1) to calculate the optimal level of harm for indiscriminating males
 224 (Figure 3A; SI for details). We find that, as male dispersal decreases, relatedness increases
 225 (larger r_{mm}), which promotes harm. This, however, is counteracted by the scale of

226 competition (a), which becomes more local and inhibits harm. Nevertheless, the presence of
227 female-biased dispersal ($d_f = 1$) means that the two effects do not exactly cancel-out^{9,43}. That
228 is, whilst dispersal by each sex has a symmetrical impact on the scale of competition, they
229 can have asymmetrical impact on relatedness if the sexes experience different reproductive
230 skews⁴³. Accordingly, decreased male dispersal favours a higher level of harm due to
231 increased kin competition (Figure 3A).

232

233 *Presence of kin discrimination and absence of budding dispersal* – We now consider the
234 consequences of kin discrimination. Specifically, we assume that individuals who were born
235 on the same patch are able to recognise each other later in life. This has been termed
236 “familiarity”^{14,44-46}, and is thought to represent the most common cue for kin recognition in
237 nature⁴⁵⁻⁴⁷ and to be required even when direct “genetic” kin recognition is present^{14,46}. In our
238 model, for all $0 < d_m < 1$, a focal male is either interacting with: two familiar males ($r_{2mm} =$
239 $1/3 + 2/3r$); one familiar and one unfamiliar male ($r_{1mm} = 1/3 + 1/3r$), or two unfamiliar males
240 ($r_{0mm} = 1/3$; see SI). Accordingly, a male is expected to show a low level of harm when
241 interacting with two familiar males, an intermediate level of harm when interacting with one
242 familiar and one unfamiliar male, and a high level of harm when interacting with two
243 unfamiliar males (Figure 3A; for simulation results Supplementary Figure 2A).

244

245 Male dispersal continues to affect relatedness, but only through its impact on relatedness of
246 familiar males ($r = 1/(5 + d_m(2 - d_m))$; see SI). In contrast, its impact on kin competition
247 remains unchanged ($a = (1 - d_m)^2/2$) and, accordingly, increased male dispersal reduces harm
248 by making the competition more global (lower a). This suggests that, in kin-discriminating
249 species, an experimental-evolution regime that increases relatedness through reduced
250 dispersal need not necessarily lead to a reduction in harm (Figure 3A; for simulation results

251 Supplementary Figure 2A). Specifically, a male interacting with familiar males may still
252 exhibit lower harm in comparison to one interacting with unfamiliar males, but the harm
253 expressed within each treatment may actually be higher with reduced dispersal due to an
254 increase in local competition (larger a).

255

256 *Absence of kin discrimination and presence of budding dispersal* – It is also possible to
257 maintain a constant scale of competition (fixed a) while varying relatedness between social
258 partners through budding dispersal^{35,40,41}. As before, and without considering kin
259 discrimination, an increase in harm is favoured whenever the right-side of inequality (1) is
260 positive. However, now kin competition depends on budding dispersal ($a = (1 - d_B)^2$, with d_B
261 being the probability of a group dispersing to a new patch; see SI). Following budding
262 dispersal, males can still disperse between groups but without affecting the scale of
263 competition (a), only relatedness between males ($r_{mm} = 1/3 + 2/3(1 - d_m)^2r$; SI for details). If
264 we consider full budding dispersal ($d_B = 1$), then competition occurs exclusively at a global
265 scale ($a = 0$) with increased male dispersal leading to reduced relatedness and, therefore, a
266 higher level of harm (Figure 3B). Compared to a scenario where only individual dispersal is
267 present, budding dispersal generally leads to lower levels of harm (Figure 3B). The exception
268 is when there is full male dispersal ($d_m = 1$), in which case the level of harm is the same in
269 both scenarios (Figure 3B).

270

271 *Presence of kin discrimination and budding dispersal* – Adding kin discrimination into this
272 model recovers the previous result, where males interacting with familiar individuals
273 manifest a lower level of harm (Figure 3C; for simulation results Supplementary Figure 2B),
274 except that now male dispersal does not have an appreciable effect on harm (Figure 3C; for
275 simulation results Supplementary Figure 2B). This again suggests that, in species with kin

276 discrimination, increased relatedness through limited dispersal may not be relevant in
277 reducing the level of harm. Limited dispersal still affects how likely individuals are to find
278 and interact with related individuals, but its role in reducing the harm manifested by the
279 males in those encounters may be restricted.

280

281 *Discussion*

282

283 Here we develop kin-selection models to formally investigate how relatedness and the scale
284 of competition modulate sexual conflict between females and males. Using “open” models,
285 we generalise and synthesise the theoretical and empirical work done in the fields of kin
286 selection and sexual conflict (Table 2). Using “closed” models, we derive concrete
287 predictions that can be tested in future empirical studies (Table 2). Both approaches highlight
288 the role of kin discrimination and budding dispersal in modulating the extent to which males
289 harm females. Accordingly, through the disentanglement of relatedness and kin competition,
290 kin discrimination and budding dispersal increase the scope for kin selection to curb the
291 evolution of harming behaviour. These findings apply both when harm is inflicted upon a
292 female by her mates and her unsuccessful suitors (e.g. sexual harassment) and when it occurs
293 exclusively during mating (e.g. toxic ejaculates or traumatic insemination). Overall levels of
294 male harm are predicted to be lower in the latter case (Table 2; SI for details), but our main
295 qualitative conclusions hold in both scenarios.

296

297 Compared to population viscosity, kin discrimination allows for a finer-grained adjustment of
298 social behaviour in response to genetic relatedness. Through kin discrimination, individuals
299 facultatively assess their relatedness to social partners and behave accordingly^{26,29}. Kin
300 discrimination strongly contrasts with population viscosity, where an individual’s behaviour

301 is selected according to the average relatedness of the actor to her social partners²⁹.
302 Nevertheless, population viscosity has been considered an important mechanism in the kin
303 selection literature due to its simplicity. Unlike kin discrimination, it does not require
304 behavioural plasticity reliant on complex (and likely costly) cognitive processes, meaning
305 that it can occur even in simple organisms²⁶. Here, we draw attention to another possible cost
306 associated with kin discrimination.

307

308 When harming females, males gain a relative advantage concerning other males by siring
309 more offspring from those females. However, this benefit is only relative, with the total
310 number of offspring produced by these females being smaller than it would be in the absence
311 of harm. Such a cost describes what is known as a “tragedy of the commons”, whereby
312 individual competition for resources – here, offspring provided by females – reduces the
313 average productivity of the whole group^{4,9,18,19,47}. This prompts the question as to which
314 mechanism – kin discrimination or population viscosity – is worse for the population as a
315 whole.

316

317 Kin recognition makes an actor more altruistic to those that he recognises as kin but makes
318 him less altruistic to those that he does not recognise as kin. Therefore, it is not clear how kin
319 recognition should impact the overall level of altruism in the group. Faria & Gardner⁴⁷ show
320 that kin discrimination increases selfishness in the group whenever the optimal value of the
321 trait under study changes convexly with relatedness. This is the case in our model, with the
322 level of harm that males express being a convex function of relatedness (Supplementary
323 Figure 3). As a consequence, kin discrimination leads to higher average harm in the
324 population when compared to its absence, both when organisms disperse individually or in
325 groups (Figure 3D). As male dispersal approaches 0 or 1, the proportion of patches

326 comprising either only familiar or only unfamiliar males, respectively, increases. At this
327 point, presence versus absence of kin discrimination is irrelevant (Figure 3D) because males
328 only experience one type of social condition.

329

330 Therefore, kin discrimination may lead to a decrease in the overall productivity of a
331 population and consequently increase sexual conflict between males and females (Table 2). If
332 kin discrimination is also associated with cognitive costs, this suggests that kin discrimination
333 should be more prevalent in species with intermediate dispersal levels⁴⁸. Specifically, with
334 low dispersal, individuals are likely to interact with kin, making kin discrimination
335 redundant, while, with high dispersal, individuals are unlikely to encounter kin, which again
336 makes kin discrimination unnecessary. Intermediate levels of dispersal, however, are also
337 when there is a higher difference between population viscosity and kin discrimination in
338 terms of productivity. This creates an interesting trade-off – the demographic conditions that
339 make kin discrimination advantageous for the individuals are also the ones where kin
340 discrimination is more costly for the population. Far from resolving the negative
341 consequences of sexual conflict at the population level, our results suggest kin discrimination
342 actually contributes to set the scene for an evolutionary tragedy of the commons. Presence of
343 cognitive costs may erode the trade-off by making kin discrimination too costly to evolve in
344 the first place, but this is out of the scope of our model. Nevertheless, it could be an
345 interesting venue for future theoretical and empirical research.

346

347 *Acknowledgements*

348 GSF acknowledges IAST funding from the French National Research Agency (ANR) under
349 the Investments for the Future (Investissements d'Avenir) program, grant ANR-17-EURE-
350 0010, and was supported by Portuguese National Funds, through FCT – Fundação para a

351 Ciência e a Tecnologia PhD Scholarship (SFRH/BD/109726/2015), AG was supported by a
352 Natural Environment Research Council Independent Research Fellowship (NE/K009524/1)
353 and a European Research Council Consolidator Grant (771387), and PC was supported by a
354 “Ramón y Cajal” Research Fellowship (RYC-2013-12998), and by a Plan Nacional I+D+i
355 Excelencia Research Grant (CGL2017-89052-P). We thank David Shuker, Jasmeen Kanwal,
356 Mike Ritchie, Petri Rautiala, and Thomas Hitchcock for helpful comments and discussion.

357

358 *Author contributions*

359 G. S. F, A. G., and P. C. conceived the study, G. S. F. led the theoretical analysis with input
360 from A.G., and G. S. F., A. G., and P. C. wrote the paper.

361

362 *Data availability*

363 Data sharing not applicable to this article as no datasets were generated or analysed during
364 the current study.

365

366 *Code availability*

367 Code used for the simulations available at <https://github.com/GSFaria-wasp/Sexual->
368 [conflict.git](https://github.com/GSFaria-wasp/Sexual-conflict.git).

369

370 *Competing interests statement*

371 The authors declare no competing interests.

372

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523 *Figures and tables legends*

524

525 **Table 1 | Literature on the impact of kin selection on the evolution of sexual conflict**

526

527 **Table 2 | Main conclusions of our study**

528

529 **Figure 1 | Potential for harm to evolve as a function of relatedness and scale of**

530 **competition.** The harm that females are subjected to by the males is expected to increase as

531 relatedness decreases (**A & B**) and as the intensity of local competition increases (**C & D**). In

532 (**A**) and (**B**), the scale of competition is $a = 0.25$, in (**C**) the relatedness between males is r_{mm}

533 $= 0.50$, and in (**D**) the relatedness between females and males is $r_{fm} = 0.50$.

534

535 **Figure 2 | Kin-selection model of sexual conflict.** During the adult phase of the model,

536 males can harm females. In the absence of kin discrimination, all males exhibit the same level

537 of harm. In the presence of kin discrimination, males that recognize other males as being

538 related reduce the level of harm. In contrast, males that recognize other males as being

539 unrelated increase the level of harm. During the juvenile phase of the model, individuals can

540 either disperse from their patch individually – with juvenile females and juvenile males

541 competing with other juvenile females and juvenile males, respectively – or in groups – with

542 groups competing with other groups.

543

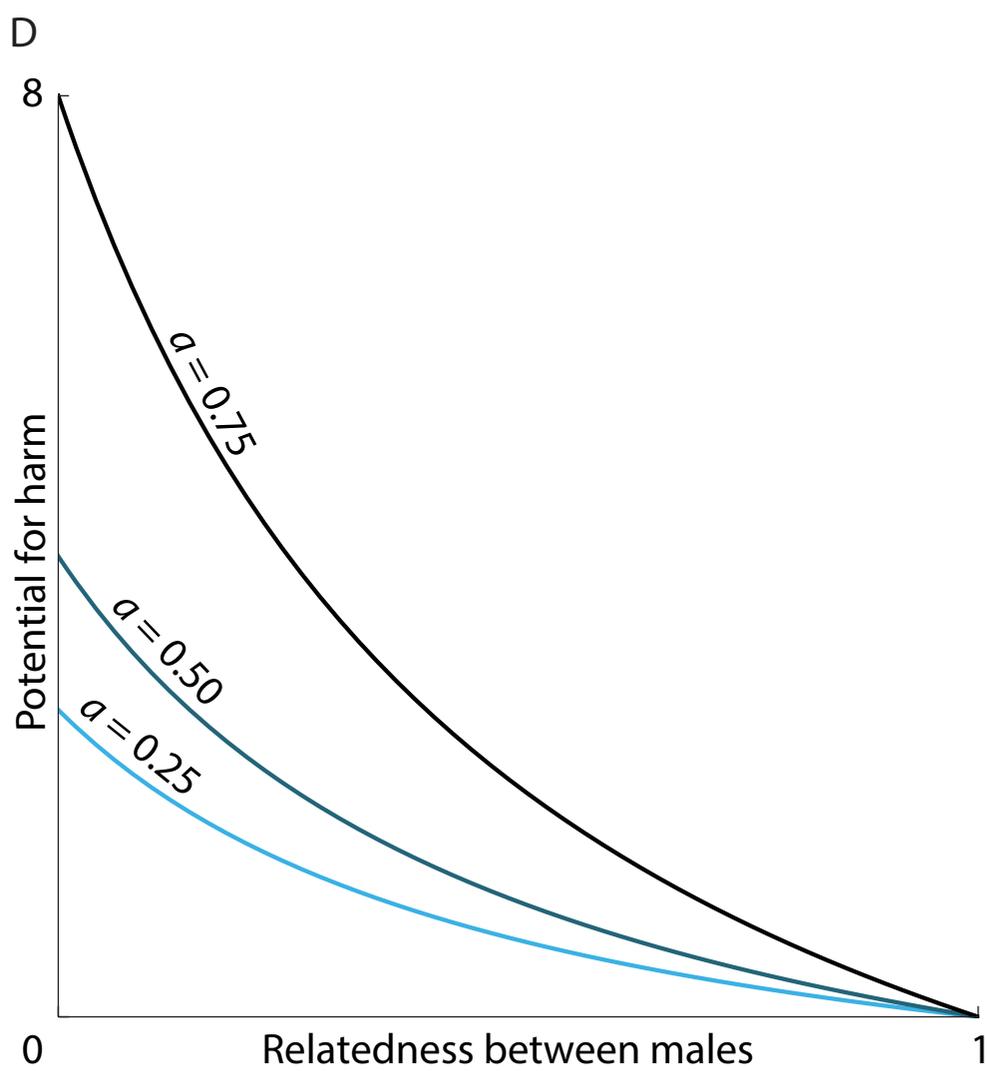
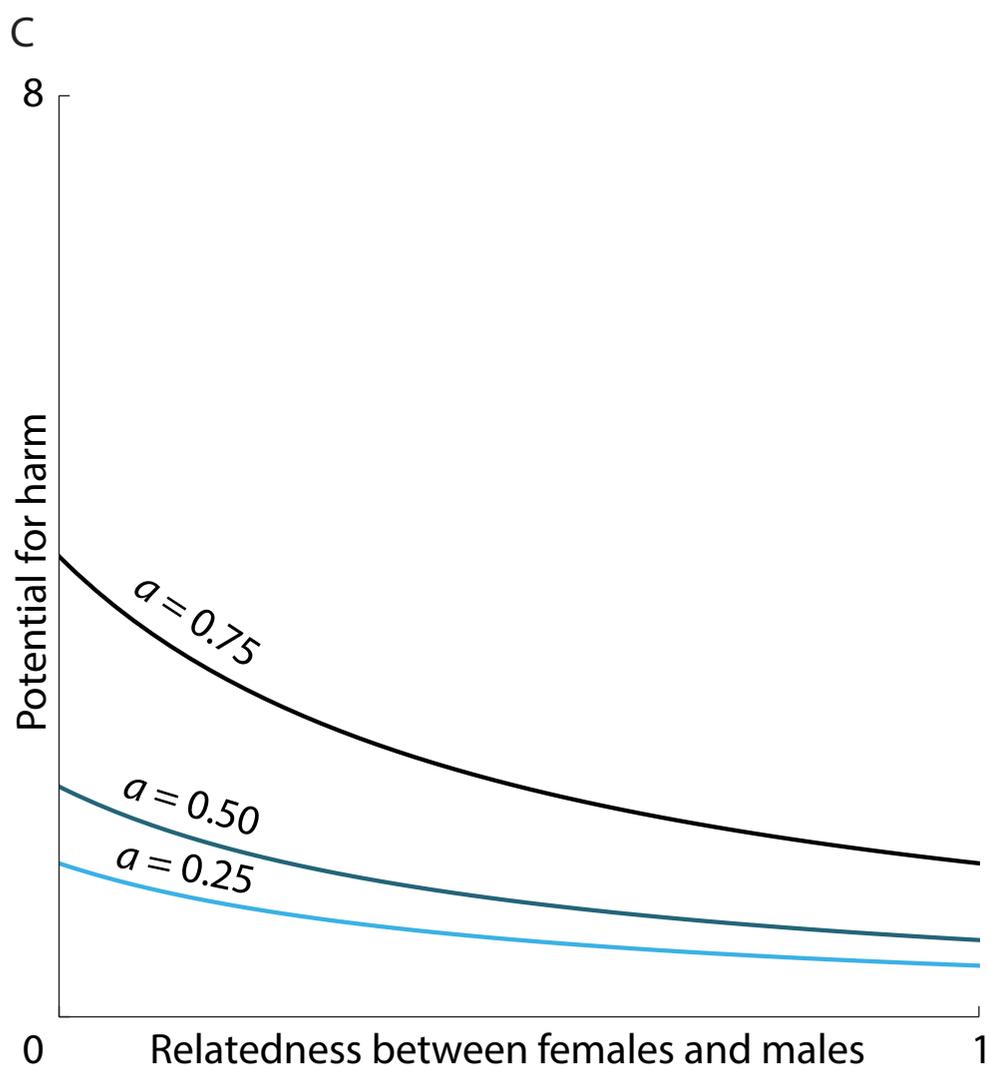
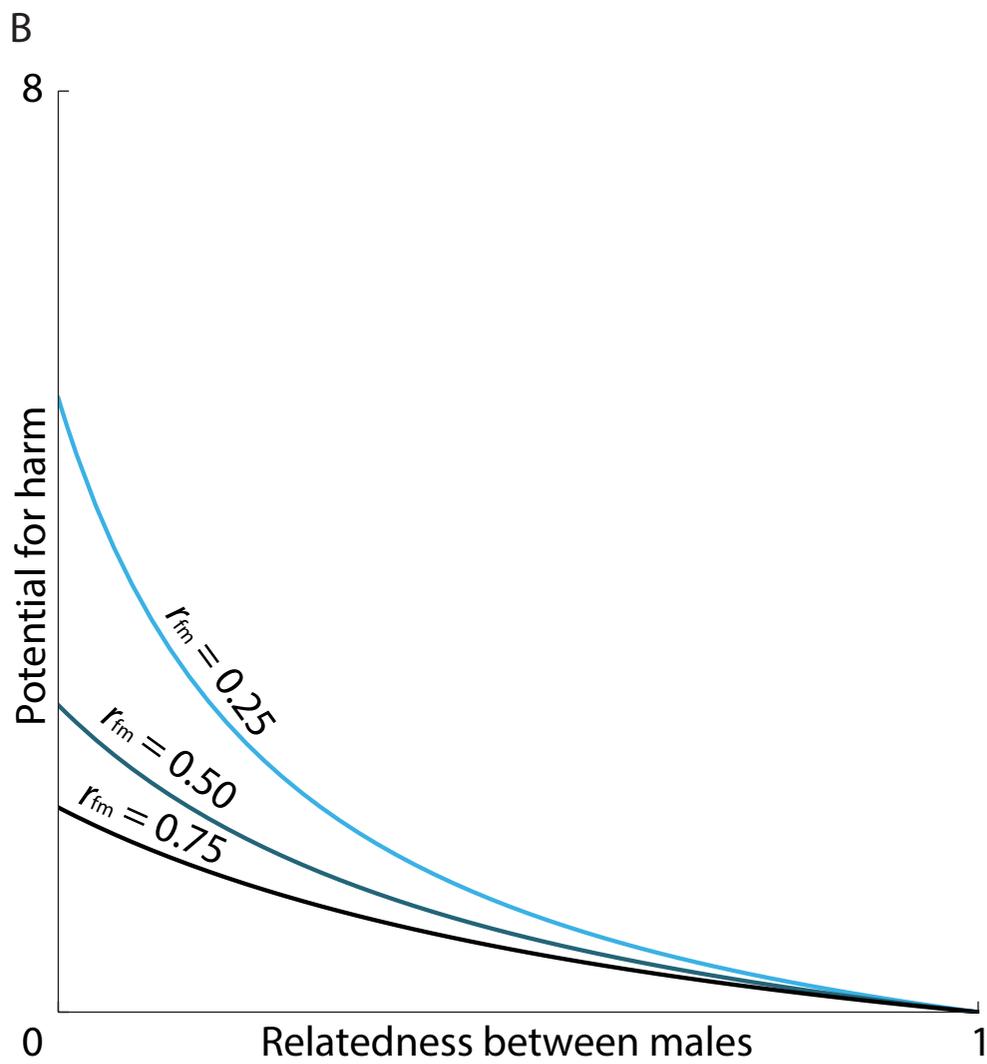
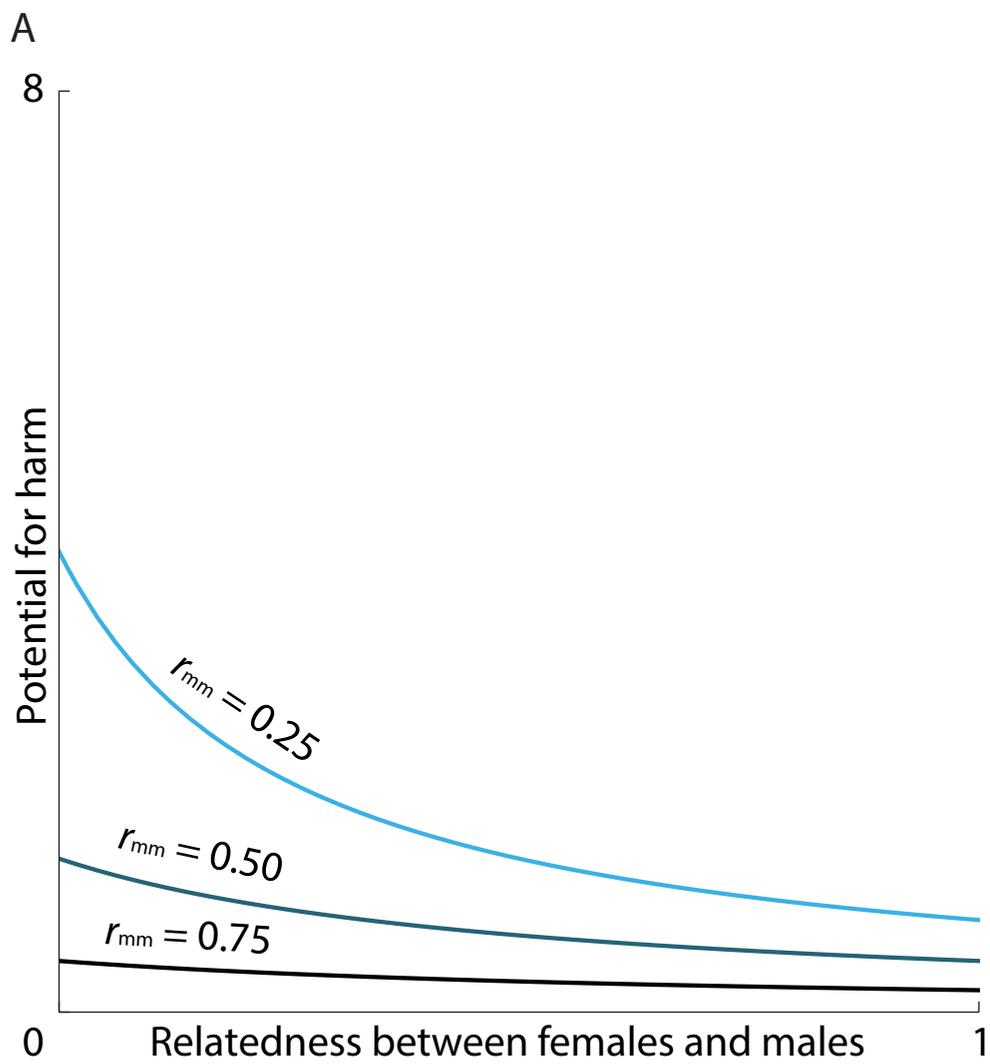
544 **Figure 3 | Optimal level of harm as a function of male dispersal (d_m) and the average of**

545 **harm in the population.** In the presence of kin discrimination and absence of budding

546 dispersal (**A**), the optimal level of harm that males express decreases as male dispersal (d_m)

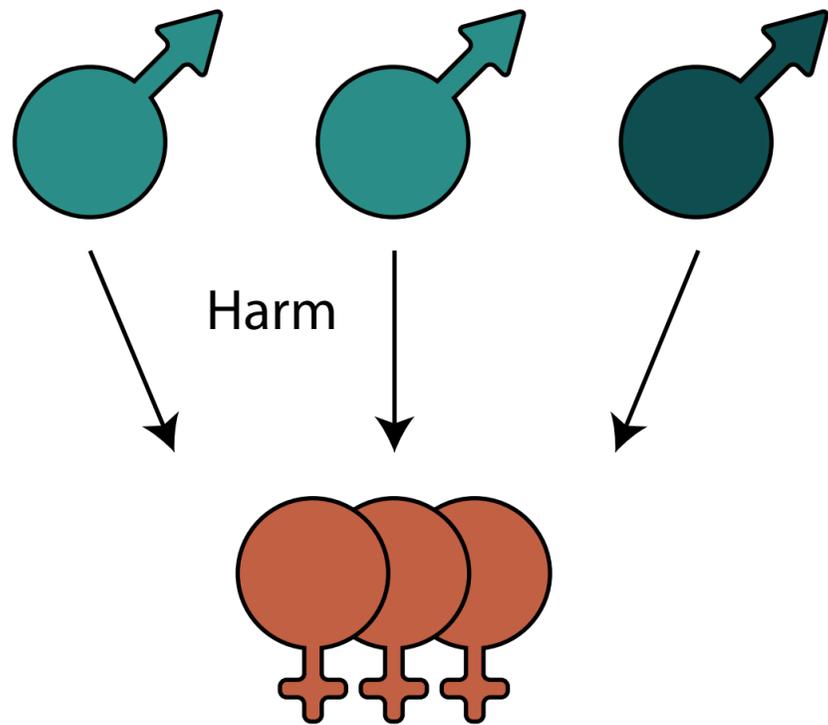
547 increases for both indiscriminating and discriminating males, but the decrease is more

548 pronounced when kin discrimination is present. In the absence of kin discrimination and
549 presence of budding dispersal (**B**), the optimal level of harm that males express increases as
550 male dispersal (d_m) increases. In the presence of kin discrimination and budding dispersal
551 (**C**), the optimal level of harm for discriminating males decreases if males are interacting only
552 with unfamiliar males and increases if males are interacting with familiar males. For
553 indiscriminating males, the optimal level of harm increases as male dispersal (d_m) increases.
554 Regardless of absence (**A**) or presence (**B**) of budding dispersal, males interacting with
555 unfamiliar males express a high level of harm, males interacting with one familiar male and
556 one unfamiliar male express an intermediate level of harm, and males interacting with two
557 familiar males express a low level of harm. The resultant average harm in the population (**D**)
558 is higher when individuals are capable of kin discrimination when compared to its absence
559 and lower in the presence of budding dispersal when compared to individual dispersal. For all
560 panels, the following parameters were used: marginal benefit of harm $\beta = 0.5$; female
561 dispersal rate $d_f = 1$; number of females $n_f = 3$; and number of males $n_m = 3$. Additionally, in
562 (**B-D**) budding dispersal rate $d_B = 1$.

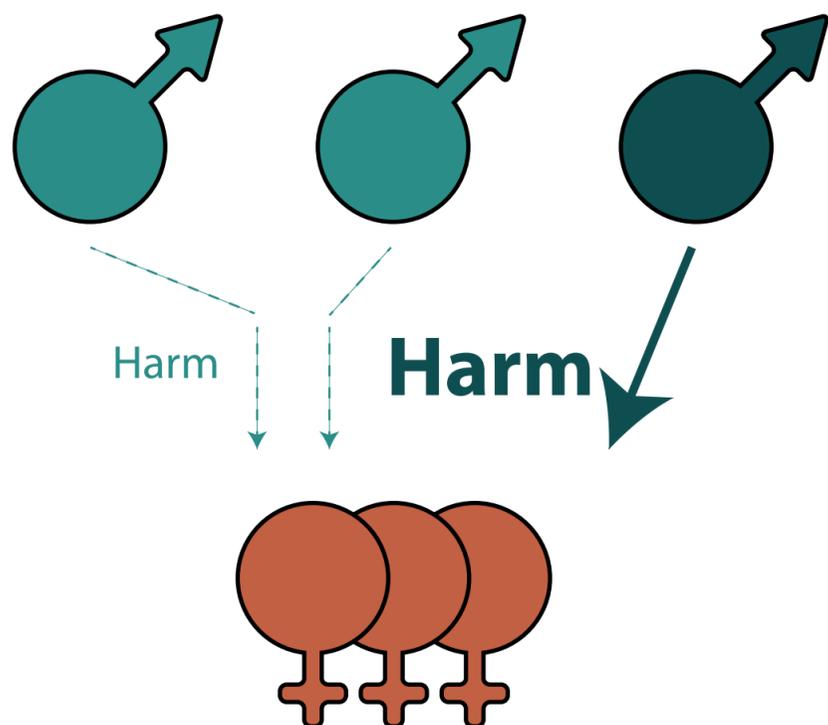


Adult phase

Absence of kin discrimination

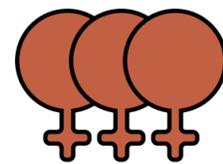


Presence of kin discrimination

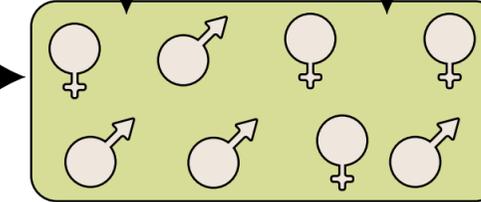
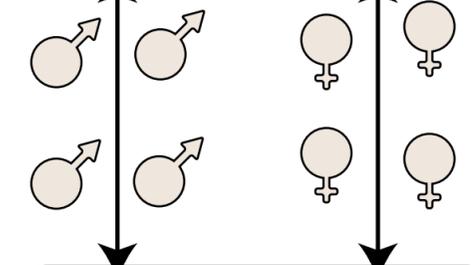
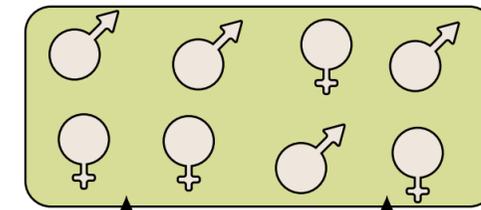


Juvenile phase

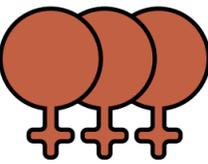
...individual dispersal



Reproduction

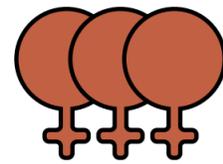


Focal patch

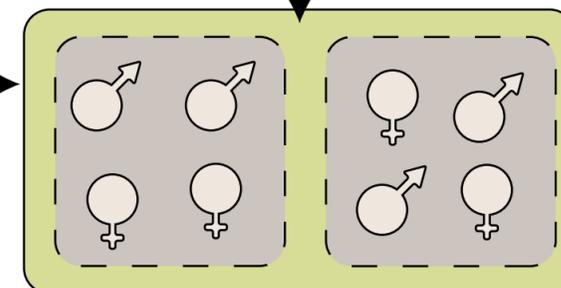
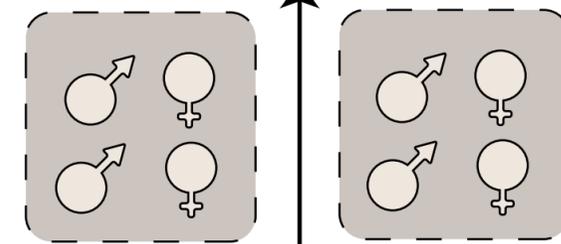
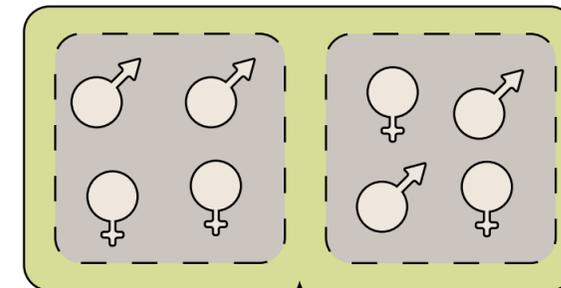


Large number of offspring are produced and individuals disperse through either...

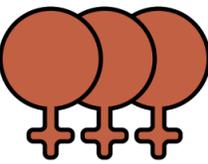
...budding dispersal

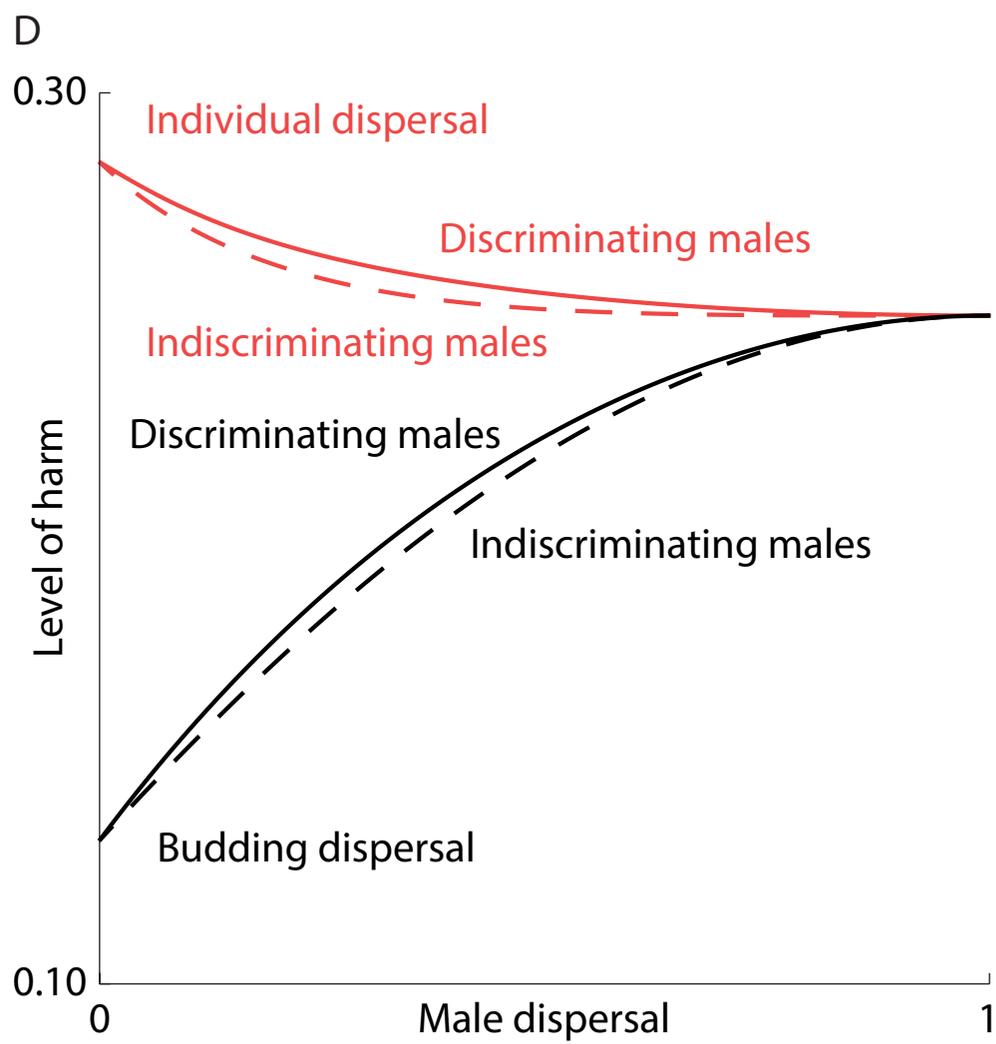
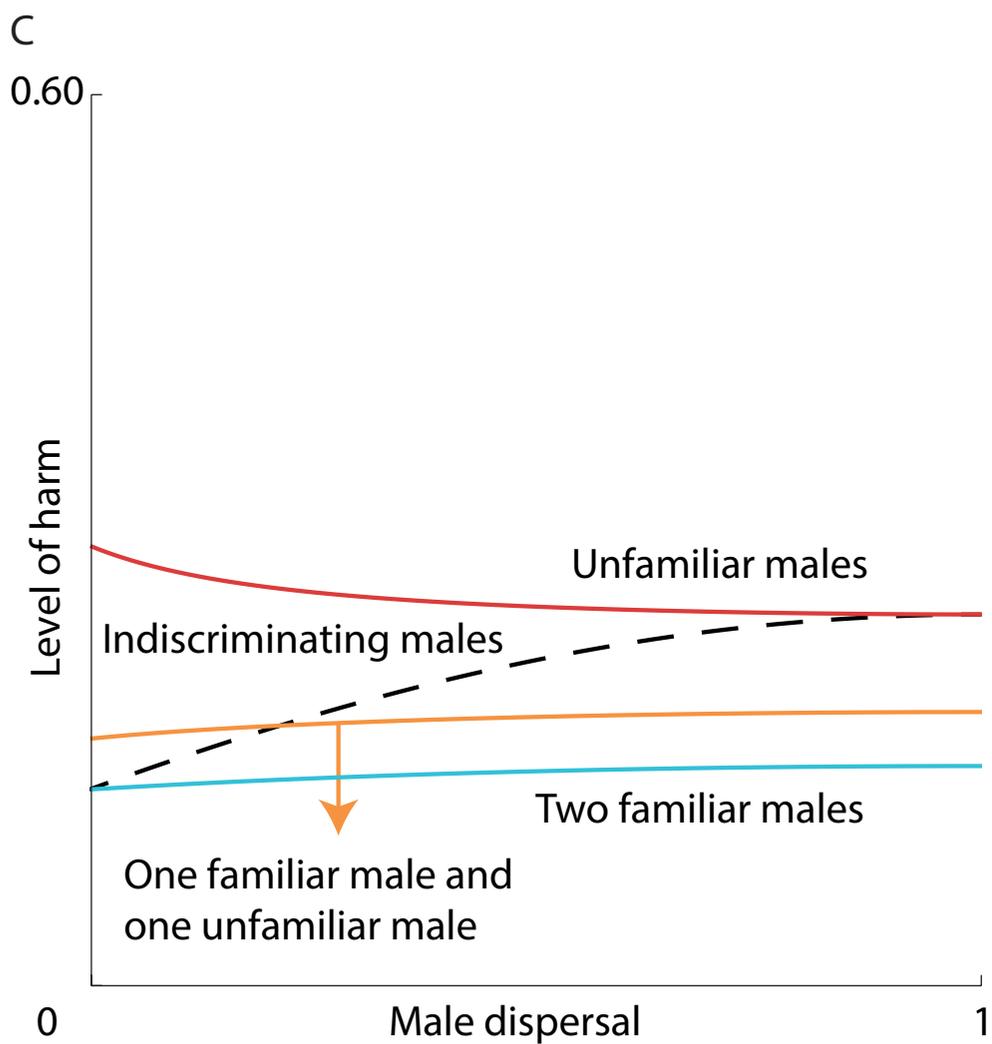
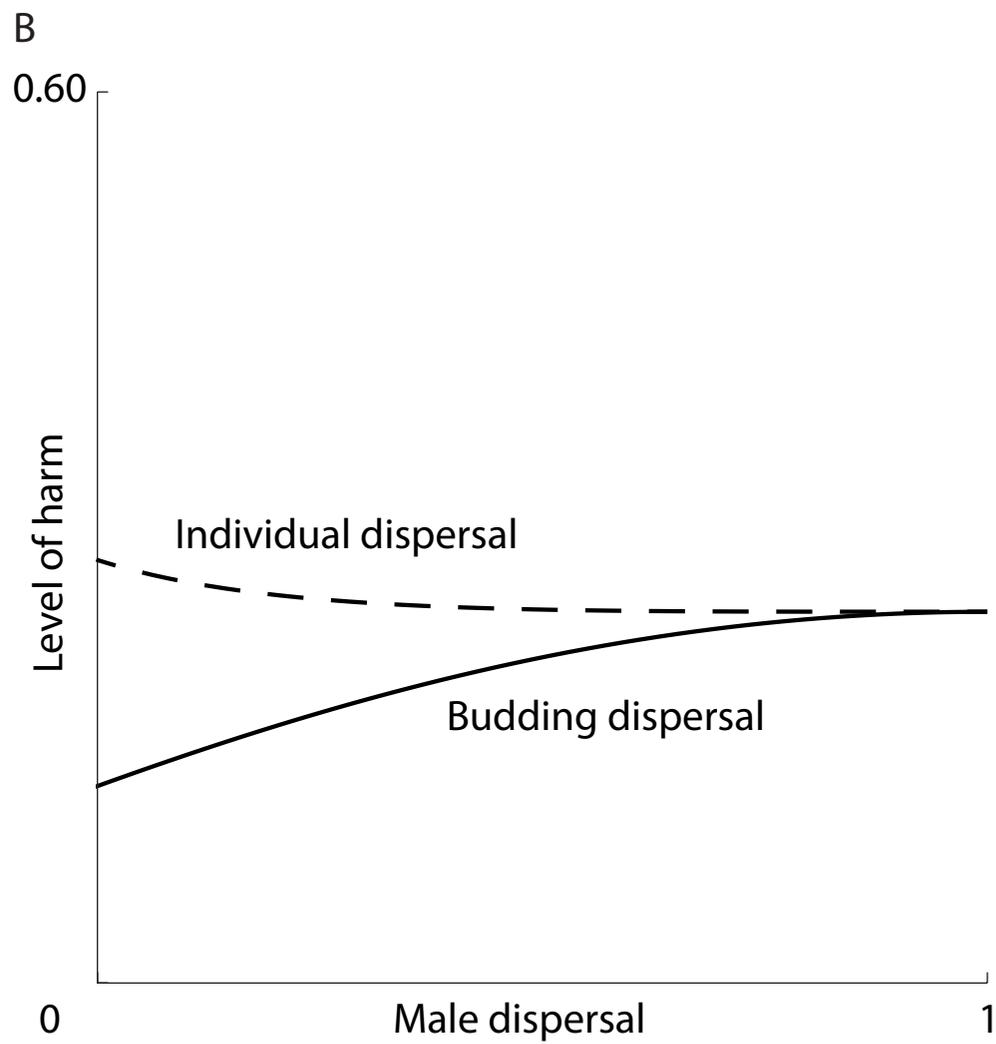
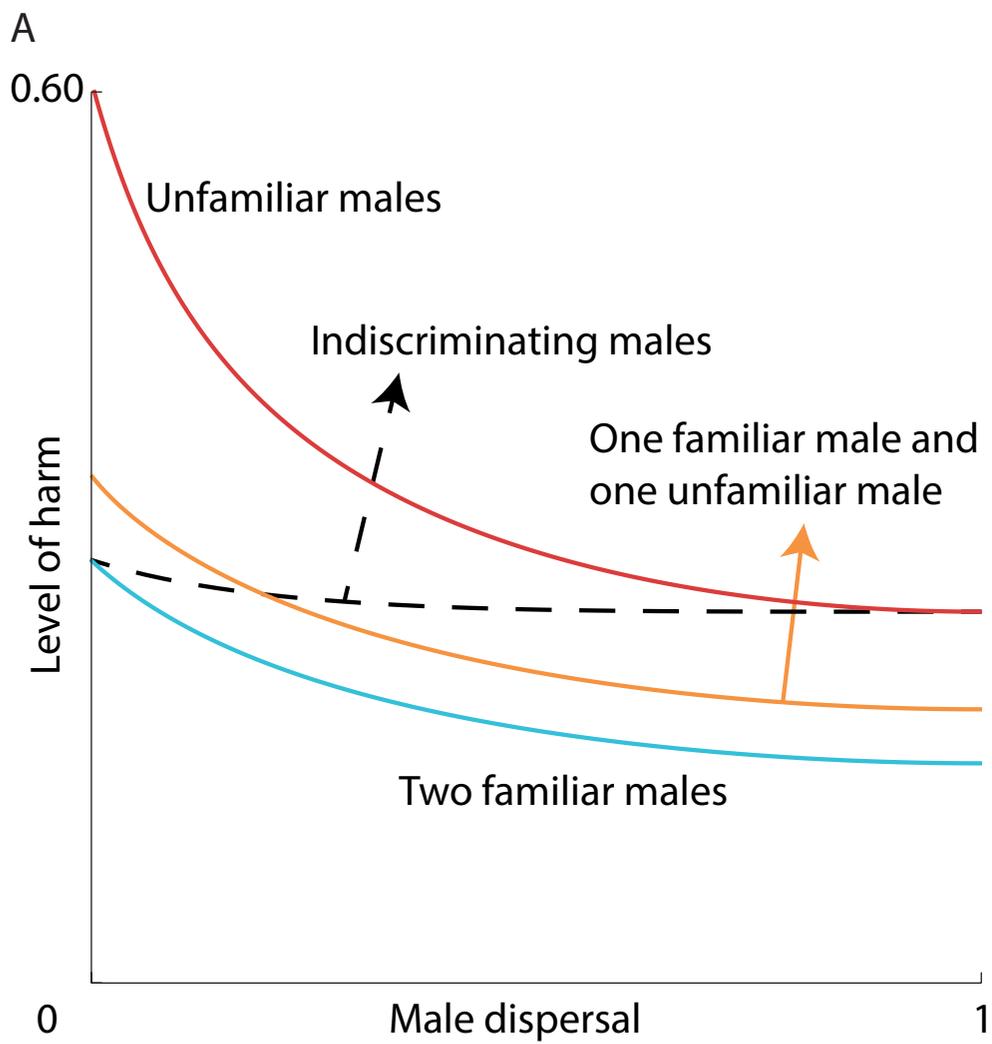


Reproduction



Focal patch





Authors	Approach	Kin selection mechanism	Notes
Rankin 2011 ⁴	Theoretical - mathematical model	Population viscosity	Rankin's model cannot be used to study sex-biased dispersal due to a mathematical error. The results can be captured by our model when dispersal is not sex-biased.
Wild et al. 2011 ⁵	Theoretical - mathematical model	Population viscosity	Insofar as there is a conflict between females and males, our model can capture their results.
Pizzari & Gardner 2012 ³	Theoretical - verbal model	Population viscosity Kin discrimination	The verbal models dedicated to the sexual conflict between females and males can be captured by our model.
Carazo et al. 2014 ⁶	Empirical - facultative adjustment of behaviour	Kin discrimination	Males of <i>Drosophila melanogaster</i> can discriminate between geneologically related and unrelated males, increasing harm to the females when interacting with unrelated males. Our model yields the same qualitative result as this experimental

			study.
Chippindale et al. 2015 ⁷	Empirical - facultative adjustment of behaviour	Kin discrimination	Replication of Carazo et al. 2014. They are unable to replicate the same patterns, therefore our model cannot yield the same qualitative results.
Pizzari et al. 2015 ⁸	Theoretical - mathematical model	Population viscosity	Insofar as there is a conflict between females and males, our model can capture their results.
Faria et al. 2015 ⁹	Theoretical - mathematical model	Population viscosity	Extends Rankin's 2011 result to sex-biased dispersal. Captured by our model.
Hollis et al. 2015 ¹¹	Empirical - facultative adjustment of behaviour	Kin discrimination	Extension of Carazo et al. 2014. They find that familiarity between the males to be important for males to reduce the harm they express. Our model yields the same qualitative result as this experimental study.
Martin & Long 2015 ¹²	Empirical - facultative adjustment of behaviour	Kin discrimination	Replication of Carazo et al. 2014 with high relatedness coefficients (i.e. inbred lines, $r > 0.5$). They are unable to

			replicate the same patterns, therefore our model cannot yield the same qualitative results.
Faria et al. 2017 ¹⁰	Theoretical - mathematical model	Population viscosity	Maternal- and paternal-origin genes are allowed to have different levels of relatedness, generating an intragenomic conflict between the two classes of genes. Their result is consistent with our model.
Tan et al. 2017 ¹³	Empirical - facultative adjustment of behaviour	Kin discrimination	Males of <i>Gallus gallus</i> can discriminate between geneologically related and unrelated males, increasing harm to the females when interacting with unrelated males. Our model yields the same qualitative result as this experimental study.
Le Page et al. 2017 ¹⁴	Empirical - facultative adjustment of behaviour	Kin discrimination	Extension of Carazo et al. 2014. They find that both familiarity and geneological relatedness between the males are necessary for males to recognize geneological

			related males and, therefore, reduce the harm that they express. Our model yields the same qualitative result as this experimental study.
Łukasiewicz et al. 2017 ¹⁵	Empirical - experimental evolution	Population viscosity	Males of <i>Rhizoglyphus robini</i> reduce harm to females when evolving in populations with higher levels of genetic relatedness. Our model yields the same qualitative result as this experimental study.
Lymbery & Simmons 2017 ¹⁶	Empirical - facultative adjustment of behaviour	Kin discrimination	Males of <i>Callosobruchus maculatus</i> can discriminate between geneologically related and unrelated males, increasing harm to the females when interacting with unrelated males. Familiarity between the males is necessary. Our model yields the same qualitative result as this experimental study.

Kin selection approach	Conclusions regarding the evolution of sexual conflict
Open & closed models	<p>Relatedness and kin competition are often entangled</p> <p>Increased relatedness, in the absence of changes in kin competition, leads to lower levels of harmful phenotypes</p> <p>Increased kin competition, in the absence of changes in relatedness, leads to higher levels of harmful phenotypes</p>
Open model	<p>Relatedness can change independently through kin discrimination</p> <p>Kin competition can change independently through group competition for reproductive patches</p>
Closed model	<p>Decreased dispersal may increase the level of harmful phenotypes through increased kin competition when individuals are capable of kin discrimination</p> <p>Dispersal may have little effect on the level of harmful phenotypes in the presence of kin discrimination and group competition for reproductive patches</p>
Populational consequences	<p>Kin discrimination can lead to increased sexual conflict at the population level and, therefore, decreased population productivity</p>