Kin discrimination and demography modulate patterns of sexual conflict

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Abstract

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

Introduction

Since their inception, the theories of kin selection and sexual selection have been subjected to intense research within evolutionary biology, but traditionally they have had surprisingly little interaction with one another[1,2,3]. Recent years have seen an explosion of interest in the interplay between these two processes[3], both theoretically and empirically, with a particular focus on how kin selection can shape the evolution of sexual conflict[4–16]. Specifically, one widespread consequence of sexual conflict is the evolution of male traits that inflict harm upon females[17]. Such harming behaviour not only reduces a female's fitness but can also

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have pronounced repercussions for the population as a whole, in an outcome akin to 'the tragedy of the commons'[4,18–23]. Kin selection might curb the evolution of this harmful behaviour by aligning the interests of different individuals, which implies reproductive cooperation may not be limited to a few highly-social species[14,24], as currently surmised.

However, there is a significant disconnect between theory and empirical research on this topic (Table 1). On the one hand, theory has focused on population viscosity as the driver of kin selection[25–26], whereby limited dispersal of individuals means that social partners tend to be genetically-related and hence indiscriminate altruistic behaviour may evolve[3–5,8–10]. On the other hand, empirical research has overwhelmingly focused on kin discrimination[25–26], whereby individuals are capable of identifying their genealogical relatives and adjusting their behaviour accordingly[6,7,11–14,16]. This disconnect implies that current theoretical models cannot make predictions as to how sexual conflict evolves when individuals are capable of kin discrimination. Moreover, current theoretical work[4,9] makes very particular assumptions about dispersal patterns, such that genetic relatedness and resource competition become tied together in a potentially artificial way. Specifically, this work has assumed purely-viscous populations, in which reduced dispersal increases relatedness of neighbours but also intensifies competition between kin, with these two factors having opposite effects on sexual conflict. Consequently, it remains unclear how kin selection will act to modulate sexual conflict – if at all – in ecological scenarios where relatedness and competition are not so tightly intertwined.

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

The role of relatedness and the scale of competition

We consider a population divided into social groups, with each group comprising males and females who are interacting with each other in fitness-modulating ways. Our focus is on male harming behaviour: to the extent that a male harms a female, he increases his share of the paternity of her offspring, but reduces the overall number of offspring that she is able to produce – and, accordingly, reduces the overall fecundity of females and males within his group. Following reproduction, all adults die, and juveniles compete for reproductive resources, with a proportion *a* of this competition occurring locally (with social-group

mates) and a proportion $1 - a$ occurring globally (with unrelated individuals). Finally, juveniles mature to adulthood, returning the population to the beginning of the lifecycle.

Mathematically, we may express a male's competitiveness for mating success as being proportional to $f_m(y)$, where y is his investment into harming, and we may express a female's fecundity as being proportional to $f_f(Y)$, where Y is the harm that she experiences. Following the standard tragedy-of-the-commons approach[4], we assume that the harm a female experiences is equal to the average level of harming among the males in her patch (see supplementary information (SI) and Extended Data Figure 4 for the consequences of relaxing this assumption to cover cases where females are only harmed by a subset of the males in the social group). Accordingly, a female's relative fitness is $W_f = f_f(Y)/(a f_f(Y) + (1 - a)f_f(\overline{Y}))$, and a male's relative fitness is $W_m = (f_m(y)/f_m(Y))(f_f(Y)/(a f_f(Y) + (1 - a)f_f(\overline{Y})))$, where $\overline{Y}$ is the average level of harm in the population. Note that a male's fitness is modulated not only by his own competitiveness for mates but also by the fecundity of the females in his group, and the fecundity of the local females depends on the average level of harm exhibited by the males in the group – including the focal male himself. In other words, the focal male's harming phenotype y directly impacts upon the level of harming Y suffered by the females in his group. Performing a kin-selection analysis[29] (see SI), we find that natural selection favours an increase in male harm when $B(1 - r_{mm}) - C(1 - a)(r_{fm} + r_{mm}) > 0$, where $B := (\partial f_m(y)/\partial y|_{y=Y=\overline{y}})/f_m(\overline{Y})$ is the benefit for a male of harming females, $C := -(\partial f_f(Y)/\partial Y|_{Y=\overline{y}})/f_f(\overline{Y})$ is the cost for a female of being harmed, r_{fm} is the relatedness between local adult females and local adult males, and r_{mm} is the relatedness between local adult males (see SI).

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

The above condition captures the selective forces modulating the evolution of harm: in particular, the role of demography (a, r_{mm} and r_{fm}) and the details as to how harm translates into fecundity (B and C). We now narrow our focus directly onto demography by rearranging this condition into the form $C/B < A$, where $A = (1 - r_{mm})/((1 - a)(r_{fm} + r_{mm}))$ is the potential[30] for harm associated with the particular demographic context. That is, a higher A means that the condition for an increase in harming to be favoured is less stringent. Accordingly, harm is more likely to be favoured with lower relatedness (r_{mm} and r_{fm} closer to 0; Figure 1A&B) and with more local competition (a closer to 1; Figure 1C&D).

Our result is consistent with much of the work on kin selection and sexual conflict (Table 1), both theoretically and empirically. Within the theoretical literature, there has been a particular focus on population viscosity as the driver of kin selection[3,4,5,8–10]. That is, limited dispersal results in individuals being genetically-related to their social partners. Łukasiewicz et al.'s[15] experimental-evolution study of bulb-mites found that increased relatedness is associated with a reduction in male harm. The coefficients of relatedness (r_{mm} and r_{fm}) appearing in the above condition capture Łukasiewicz et al.'s[15] result, with their increase yielding a lower potential for harm (Figure 1A&B). However, theory predicts that limited dispersal does not necessarily inhibit male harm: whilst limited dispersal does increase relatedness (higher r), which tends to disfavour harm, it also intensifies local competition (higher a), which tends to favour harm[9,27,31–35], and this too is captured by our condition (Figure 1C&D).

There is, therefore, entanglement between relatedness and scale of competition when harming behaviour is expressed indiscriminately in the context of a purely-viscous population. However, most of the empirical research on this topic has focused on the role of kin discrimination in modulating sexual conflict (Table 1). Specifically, individuals identify which of their social partners are kin and adjust their behaviour accordingly. Mathematically, this is equivalent to varying the relatedness coefficients while holding the scale of competition constant, with the potential for harm decreasing as the relatedness coefficients increase (Figure 1A&B). Kin discrimination, therefore, effectively disentangles relatedness and scale of competition.

Another possible way to disentangle relatedness and scale of competition involves holding relatedness constant while varying scale of competition (Figure 1C&D), which is expected to result in a reduction in harm as the scale of competition becomes more global (lower a). This can be achieved when competition occurs between groups of individuals, such that low-harming, high-fecundity groups are able to competitively displace their high-harming, low-fecundity rivals. This has been explored in populations of water-striders, where male aggression is disfavoured when there is between-group competition[36,37]. Outwith sexual conflict, the effect of varying the scale of competition while holding relatedness fixed has been explored through dispersal of groups of relatives – budding dispersal[35,38–41] – which is one possible scenario that, mathematically, leads to the same result.

A predictive model for empirical systems

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

To gain predictive power, we explicitly define the fecundity of a focal female as $f_f = 1 - Y$ and the competitiveness for mating success of a focal male as $f_m = 1 + y^\beta$, where Y is the level of harm present in the focal patch, y is the level of harm of a focal male, and β determines the marginal benefit of harming females (see SI). Throughout this section, we

consider an infinite diploid population divided into patches[42] containing three adult females and three adult males (see Figure 2 for an illustration). Each female mates a large number of times, and each time with a randomly and independently chosen male from her group – with the probability that she mates with a particular male being proportional to his relative competitiveness for mating success. Females always disperse to new patches, while males disperse to a new patch with probability d_m. This is close to the conditions explored in empirical studies[6,7,11–14,16] and allows us to disregard the potential effect of inbreeding which would require its own study to do it justice. Moreover, while most of those empirical studies have one adult female interacting with three adult males, their experimental populations (and most wild populations of those species) do not have male-biased sex-ratios, so here we assume a 3:3 sex ratio (but note this does not qualitatively change our results – Extended Data Figure 1).

Absence of kin discrimination and budding dispersal

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

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

where $\bar{Y}$ is the average level of harm in the population, $a = (1 - d_m)^2/2$ is the scale of competition, and $r_{mm} = 1/3 + 2/3(1 - d_m)^2 r$ is the relatedness between males in a patch (where $r = 1/(5 + d_m(2 - d_m))$ is the relatedness between individuals born in the same patch; SI for details). Note that a specifies how likely a focal male juvenile is to compete with other males in the patch for future breeding opportunities, which occurs when neither disperse to other patches[43].

We can use inequality (1) to calculate the optimal level of harm for indiscriminating males (Figure 3A; SI for details). We find that, as male dispersal decreases, relatedness increases (larger r_{mm}), which promotes harm. This, however, is counteracted by the scale of competition (a), which becomes more local and inhibits harm. Nevertheless, the presence of female-biased dispersal ($d_f = 1$) means that the two effects do not exactly cancel-out[9,43]. That is, whilst dispersal by each sex has a symmetrical impact on the scale of competition, they can have asymmetrical impact on relatedness if the sexes experience different reproductive skews[43]. Accordingly, decreased male dispersal favours a higher level of harm due to increased kin competition (Figure 3A).

Presence of kin discrimination and absence of budding dispersal

We now consider the consequences of kin discrimination. Specifically, we assume that individuals who were born on the same patch are able to recognise each other later in life. This has been termed "familiarity"[14,44–46], and is thought to represent the most common cue for kin recognition in nature[45–47] and to be required even when direct "genetic" kin recognition is present[14,46]. In our model, for all $0 < d_m < 1$, a focal male is either interacting with: two familiar males ($r_{2mm} = 1/3 + 2/3r$); one familiar and one unfamiliar male ($r_{1mm} = 1/3 + 1/3r$), or two unfamiliar males ($r_{0mm} = 1/3$; see SI). Accordingly, a male is expected to

show a low level of harm when interacting with two familiar males, an intermediate level of harm when interacting with one familiar and one unfamiliar male, and a high level of harm when interacting with two unfamiliar males (Figure 3A; for simulation results Extended Data Figure 2A).

Male dispersal continues to affect relatedness, but only through its impact on relatedness of familiar males ($r = 1/(5 + d_m(2 - d_m))$; see SI). In contrast, its impact on kin competition remains unchanged ($a = (1 - d_m)^2/2$) and, accordingly, increased male dispersal reduces harm by making the competition more global (lower a). This suggests that, in kin-discriminating species, an experimental-evolution regime that increases relatedness through reduced dispersal need not necessarily lead to a reduction in harm (Figure 3A; for simulation results Extended Data Figure 2A). Specifically, a male interacting with familiar males may still exhibit lower harm in comparison to one interacting with unfamiliar males, but the harm expressed within each treatment may actually be higher with reduced dispersal due to an increase in local competition (larger a).

Absence of kin discrimination and presence of budding dispersal

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

Presence of kin discrimination and budding dispersal

Adding kin discrimination into this model recovers the previous result, where males interacting with familiar individuals manifest a lower level of harm (Figure 3C; for simulation results Extended Data Figure 2B), except that now male dispersal does not have an appreciable effect on harm (Figure 3C; for simulation results Extended Data Figure 2B). This again suggests that, in species with kin discrimination, increased relatedness through limited dispersal may not be relevant in reducing the level of harm. Limited dispersal still affects how likely individuals are to find and interact with related individuals, but its role in reducing the harm manifested by the males in those encounters may be restricted.

Discussion

Here we develop kin-selection models to formally investigate how relatedness and the scale of competition modulate sexual conflict between females and males. Using "open" models,

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

Compared to population viscosity, kin discrimination allows for a finer-grained adjustment of social behaviour in response to genetic relatedness. Through kin discrimination, individuals facultatively assess their relatedness to social partners and behave accordingly[26,29]. Kin discrimination strongly contrasts with population viscosity, where an individual's behaviour is selected according to the average relatedness of the actor to her social partners[29]. Nevertheless, population viscosity has been considered an important mechanism in the kin selection literature due to its simplicity. Unlike kin discrimination, it does not require behavioural plasticity reliant on complex (and likely costly) cognitive processes, meaning that it can occur even in simple organisms[26]. Here, we draw attention to another possible cost associated with kin discrimination.

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

Kin recognition makes an actor more altruistic to those that he recognises as kin but makes him less altruistic to those that he does not recognise as kin. Therefore, it is not clear how kin recognition should impact the overall level of altruism in the group. Faria & Gardner[47] show that kin discrimination increases selfishness in the group whenever the optimal value of the trait under study changes convexly with relatedness. This is the case in our model, with the level of harm that males express being a convex function of relatedness (Extended Data Figure 3). As a consequence, kin discrimination leads to higher average harm in the population when compared to its absence, both when organisms disperse individually or in groups (Figure 3D). As male dispersal approaches 0 or 1, the proportion of patches comprising either only familiar or only unfamiliar males, respectively, increases. At this point, presence versus absence of kin discrimination is irrelevant (Figure 3D) because males only experience one type of social condition.

Therefore, kin discrimination may lead to a decrease in the overall productivity of a population and consequently increase sexual conflict between males and females (Table 2). If kin discrimination is also associated with cognitive costs, this suggests that kin discrimination should be more prevalent in species with intermediate dispersal levels[48]. Specifically, with low dispersal, individuals are likely to interact with kin, making kin discrimination redundant, while, with high dispersal, individuals are unlikely to encounter kin, which again makes kin discrimination unnecessary. Intermediate levels of dispersal, however, are also when there is a higher difference between population viscosity and kin discrimination in terms of productivity. This creates an interesting trade-off – the demographic conditions that make kin discrimination advantageous for the individuals are also the ones where kin discrimination is more costly for the population. Far from resolving the negative consequences of sexual conflict at the population level, our results suggest kin discrimination actually contributes to set the scene for an evolutionary tragedy of the commons. Presence of cognitive costs may erode the trade-off by making kin discrimination too costly to evolve in the first place, but this is out of the scope of our model. Nevertheless, it could be an interesting venue for future theoretical and empirical research.
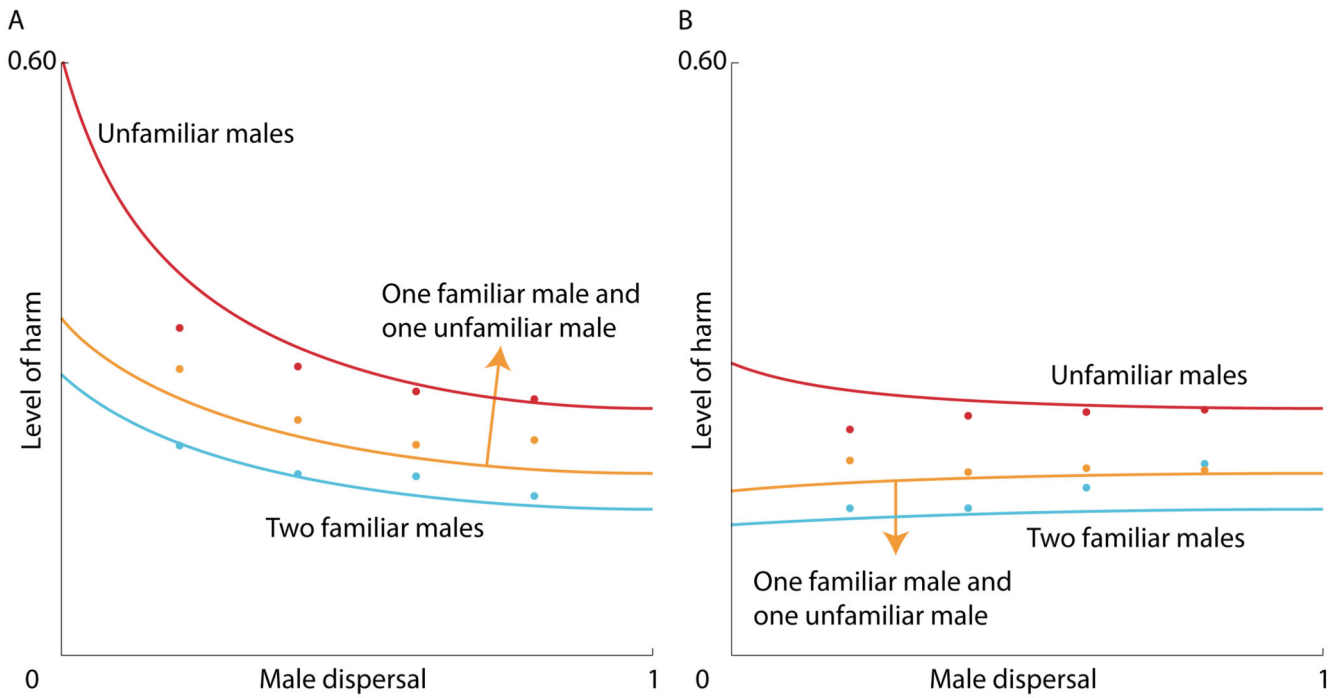
Extended Data
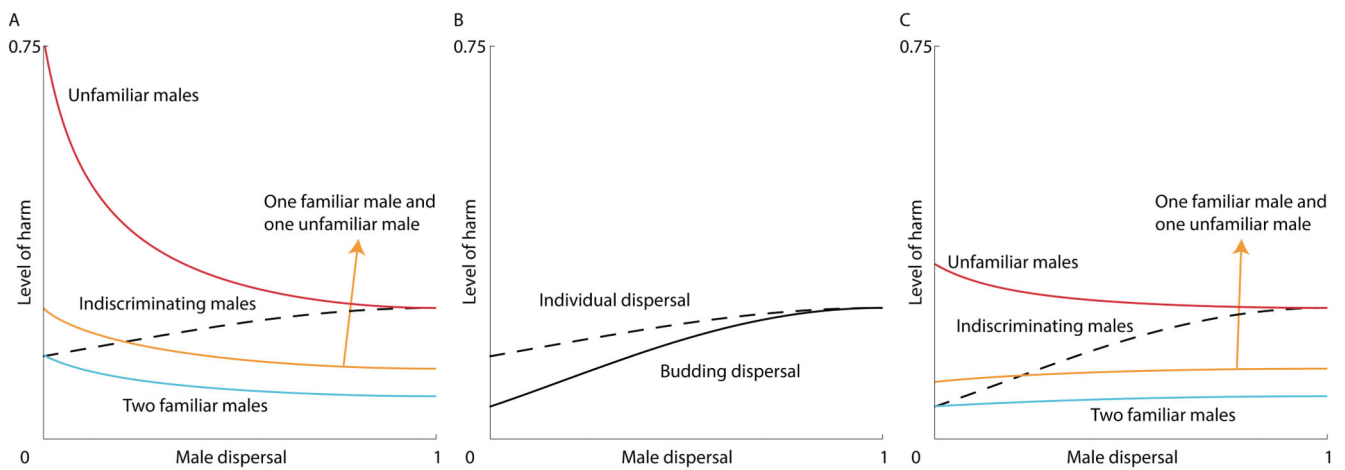
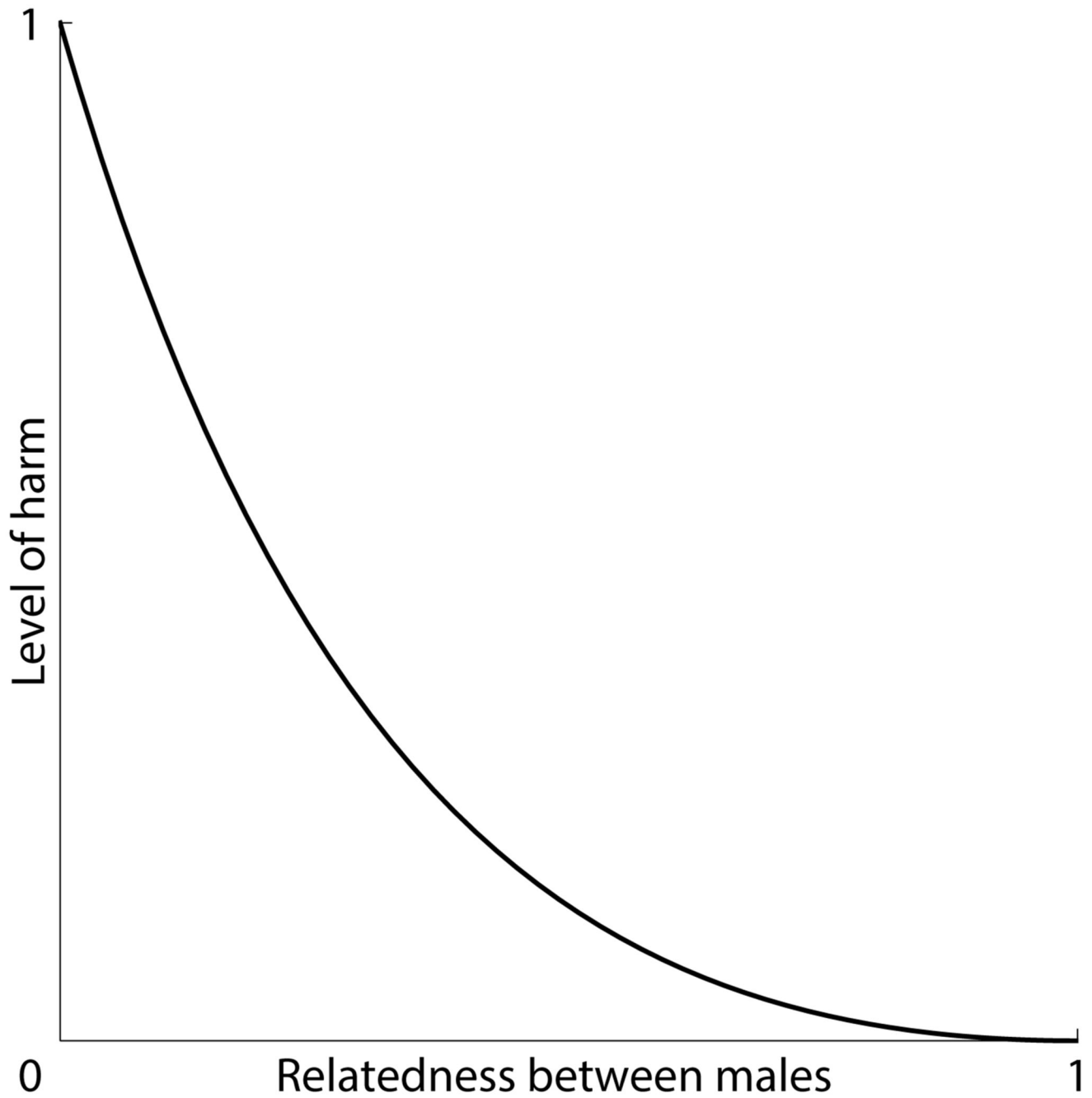**Extended Data Fig. 1. Optimal level of harm as a function of male dispersal (d_m).**
In the presence of kin discrimination and absence of budding dispersal (**A**), the optimal level of harm that males express decreases as male dispersal (d_m) increases for discriminating males and increases as male dispersal (d_m) increases for indiscriminating males. In the absence of kin discrimination and presence of budding dispersal (**B**), the optimal level of harm that males express increases as male dispersal (d_m) increases. In the presence of kin discrimination and budding dispersal (**C**), the optimal level of harm for discriminating males decreases if males are interacting only with unfamiliar males and increases if males are interacting with familiar males as male dispersal (d_m) increases. For indiscriminating males, the optimal level of harm that males express increases as male dispersal (d_m) increases. Regardless of absence (**A**) or presence of budding dispersal (**B**), males interacting with unfamiliar males express higher level of harm, males interacting with one familiar male and one unfamiliar male express intermediate level of harm, and males interacting with two

familiar males express lower level of harm. For all panels, the following parameters were used: marginal benefit of harm $\beta = 0.5$; female dispersal rate $d_f = 1$; number of females $n_f = 1$; and number of males $n_m = 3$. Additionally, in (**B-C**) budding dispersal rate $d_B = 1$.


Extended Data Fig. 2. Optimal level of harm in the absence (A) and in the presence (B) of budding dispersal as a function of male dispersal (d_m) for discriminating males.
In absence of budding dispersal (**A**), the optimal level of harm that males express decreases as male dispersal (d_m) increases. In the presence of budding dispersal (**B**), as male dispersal (d_m) increases, the optimal level of harm that males express decreases if males are interacting only with unfamiliar males and increases if males are interacting with familiar males. Regardless of absence (**A**) or presence of budding dispersal (**B**), males interacting unfamiliar males express higher level of harm, males interacting with one familiar male and one unfamiliar male express intermediate level of harm, and males interacting with two familiar males express lower level of harm. In both panels (**A-B**), the following parameters were used: marginal benefit of harm $\beta = 0.5$; female dispersal rate $d_f = 1$; number of females $n_f = 3$; and number of males $n_m = 3$. Additionally, in (**B**) budding dispersal rate $d_B = 1$. Dots represent the simulations results, with the following additional parameters used: mutation rate of 0.01; population of 4000 patches; number of generations 5×10^4. Each dot is the average of the last 1×10^4 generations.

Extended Data Fig. 3. Level of harm as a function of relatedness between males.
In the absence of kin discrimination, the level of harm that males express changes convexly with relatedness. The following parameters were used: marginal benefit of harm $\beta = 0.5$; female dispersal rate $d_f = 1$; male dispersal rate $d_m = 0.5$; and relatedness between females and males $r_{fm} = 0$.
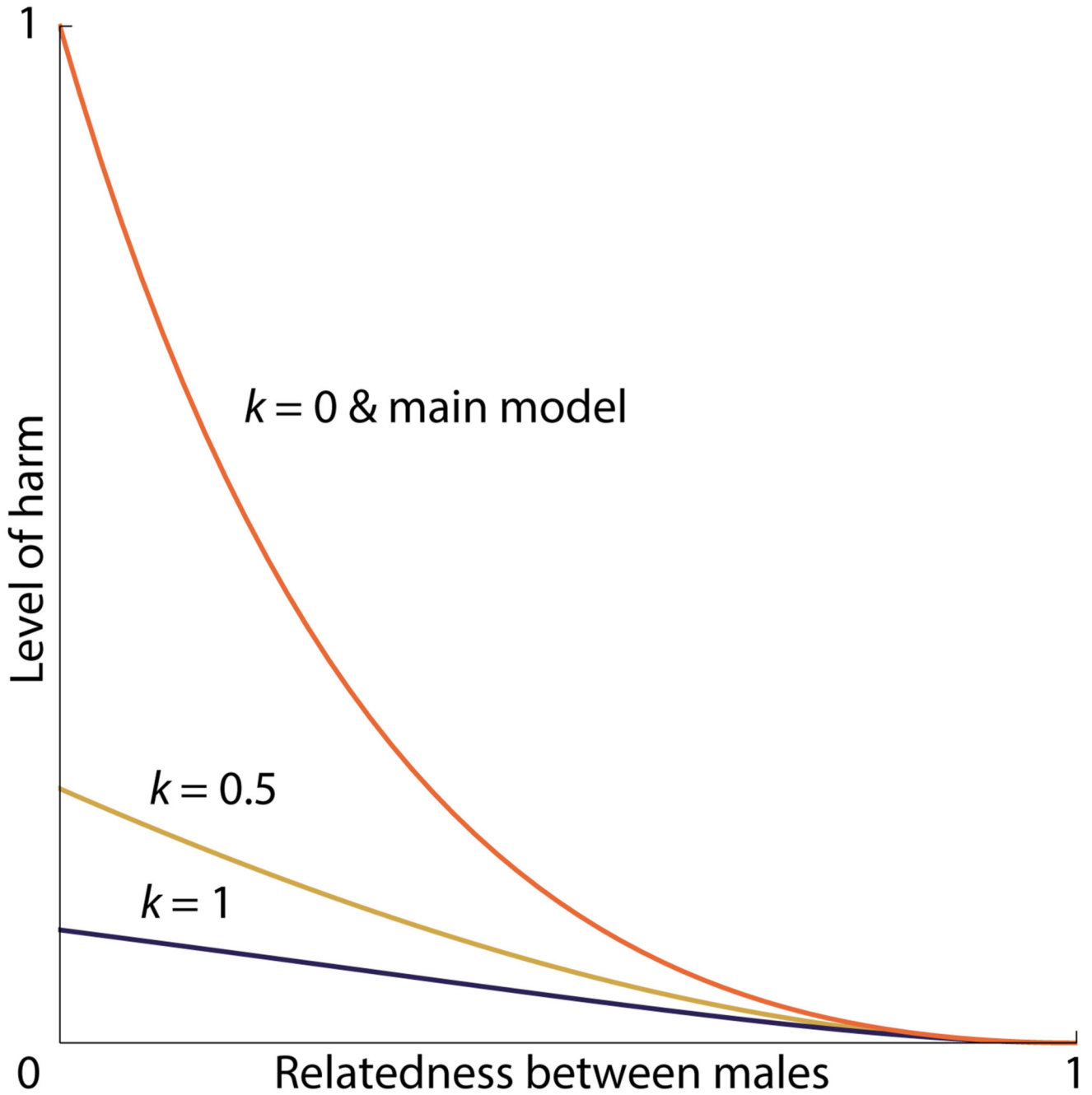
Extended Data Fig. 4. Comparison of different assumptions and how they differ from the main model.

When the level of harm that males express affect all the females in the patch ($k = 0$), the model is exactly the same as our main model. When harm that the females are subjected to comes half from the male that they mate with and half from the other males ($k = 0.5$), the model differs from our main model, with lower levels of harm. When harm that the females are subjected comes exclusively from the male that they mate with ($k = 1$), the model differs from our main model, with lower levels of harm. The following parameters were used: marginal benefit of harm $\beta = 0.5$; female dispersal rate $d_f = 1$; number of females $n_f = 3$;

number of males $n_m = 3$; male dispersal rate $d_m = 0.5$; and relatedness between females and males $r_{fm} = 0$.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgements

Data availability

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

Code availability

Code used for the simulations available at https://github.com/GSFaria-wasp/Sexual-conflict.git.

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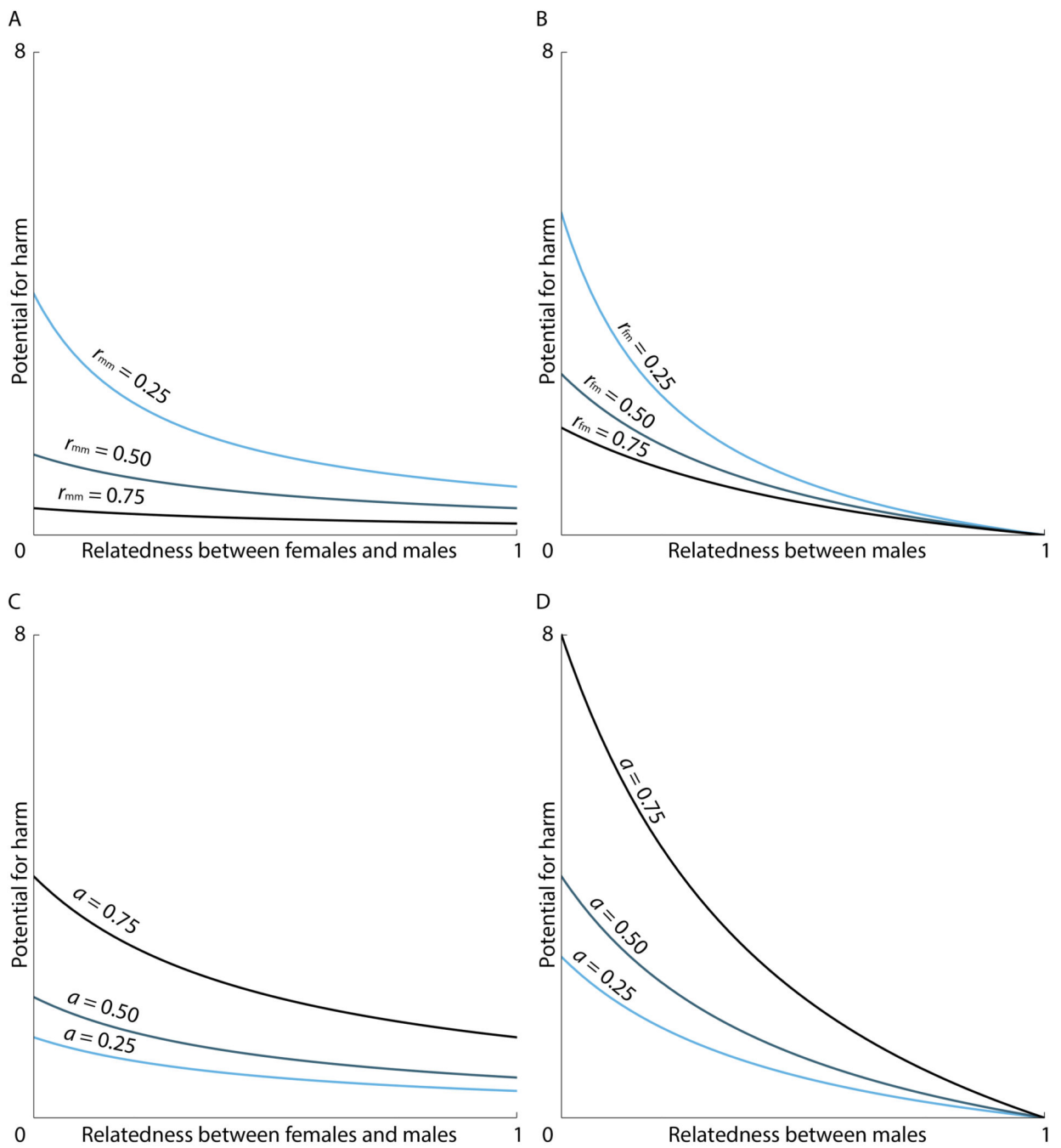
A

Potential for harm

$r_{mm} = 0.25$

$r_{mm} = 0.50$

$r_{mm} = 0.75$

0   Relatedness between females and males   1

B

Potential for harm

$r_{fm} = 0.25$

$r_{fm} = 0.50$

$r_{fm} = 0.75$

0   Relatedness between males   1

C

Potential for harm

$a = 0.75$

$a = 0.50$

$a = 0.25$

0   Relatedness between females and males   1

D

Potential for harm

$a = 0.75$

$a = 0.50$

$a = 0.25$

0   Relatedness between males   1

Figure 1. Potential for harm to evolve as a function of relatedness and scale of competition.
The harm that females are subjected to by the males is expected to increase as relatedness decreases (**A** & **B**) and as the intensity of local competition increases (**C** & **D**). In (**A**) and (**B**), the scale of competition is $a = 0.25$, in (**C**) the relatedness between males is $r_{mm} = 0.50$, and in (**D**) the relatedness between females and males is $r_{fm} = 0.50$.
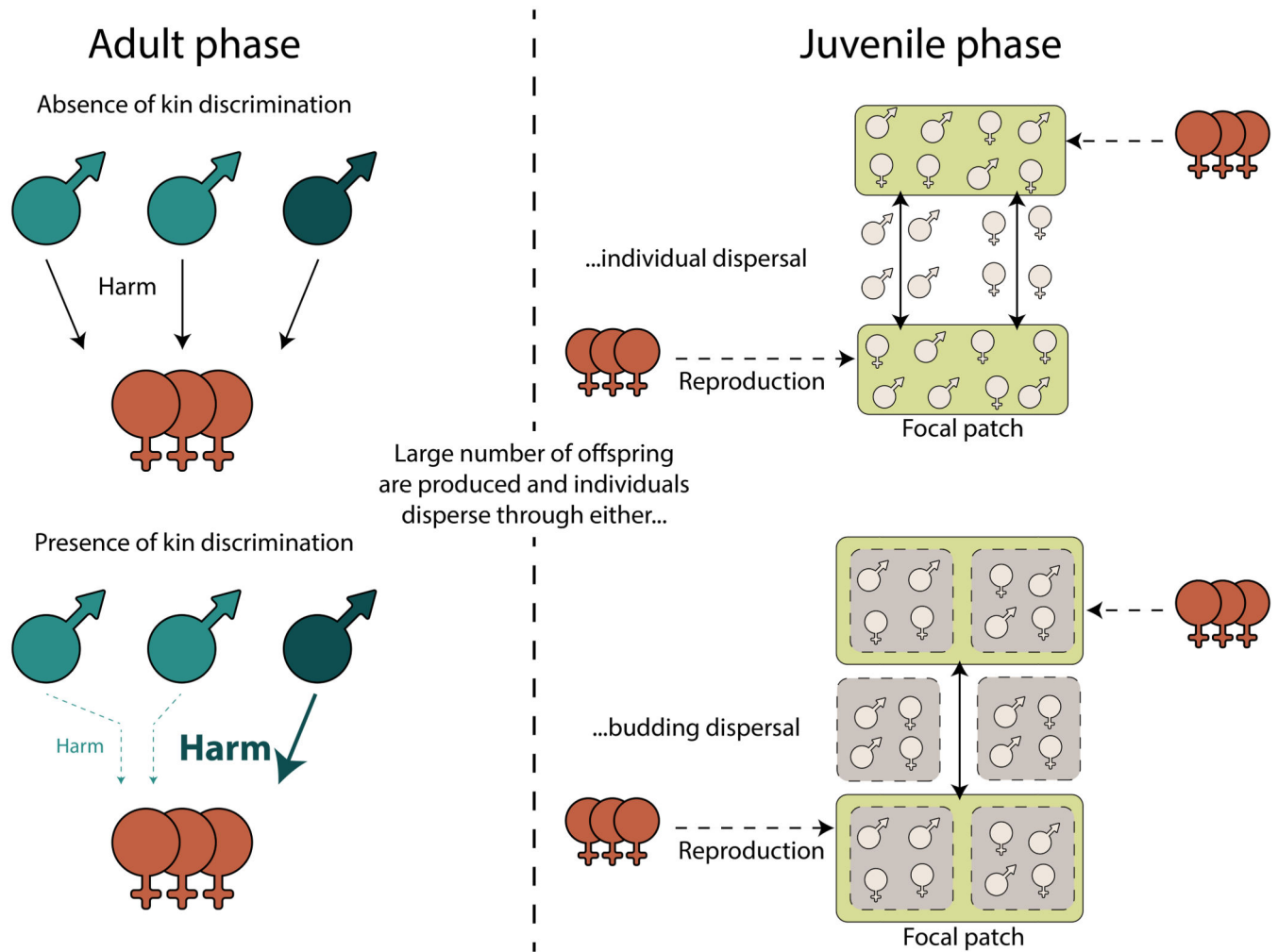
Figure 2. Kin-selection model of sexual conflict.
During the adult phase of the model, males can harm females. In the absence of kin discrimination, all males exhibit the same level of harm. In the presence of kin discrimination, males that recognize other males as being related reduce the level of harm. In contrast, males that recognize other males as being unrelated increase the level of harm. During the juvenile phase of the model, individuals can either disperse from their patch individually – with juvenile females and juvenile males competing with other juvenile females and juvenile males, respectively – or in groups – with groups competing with other groups.
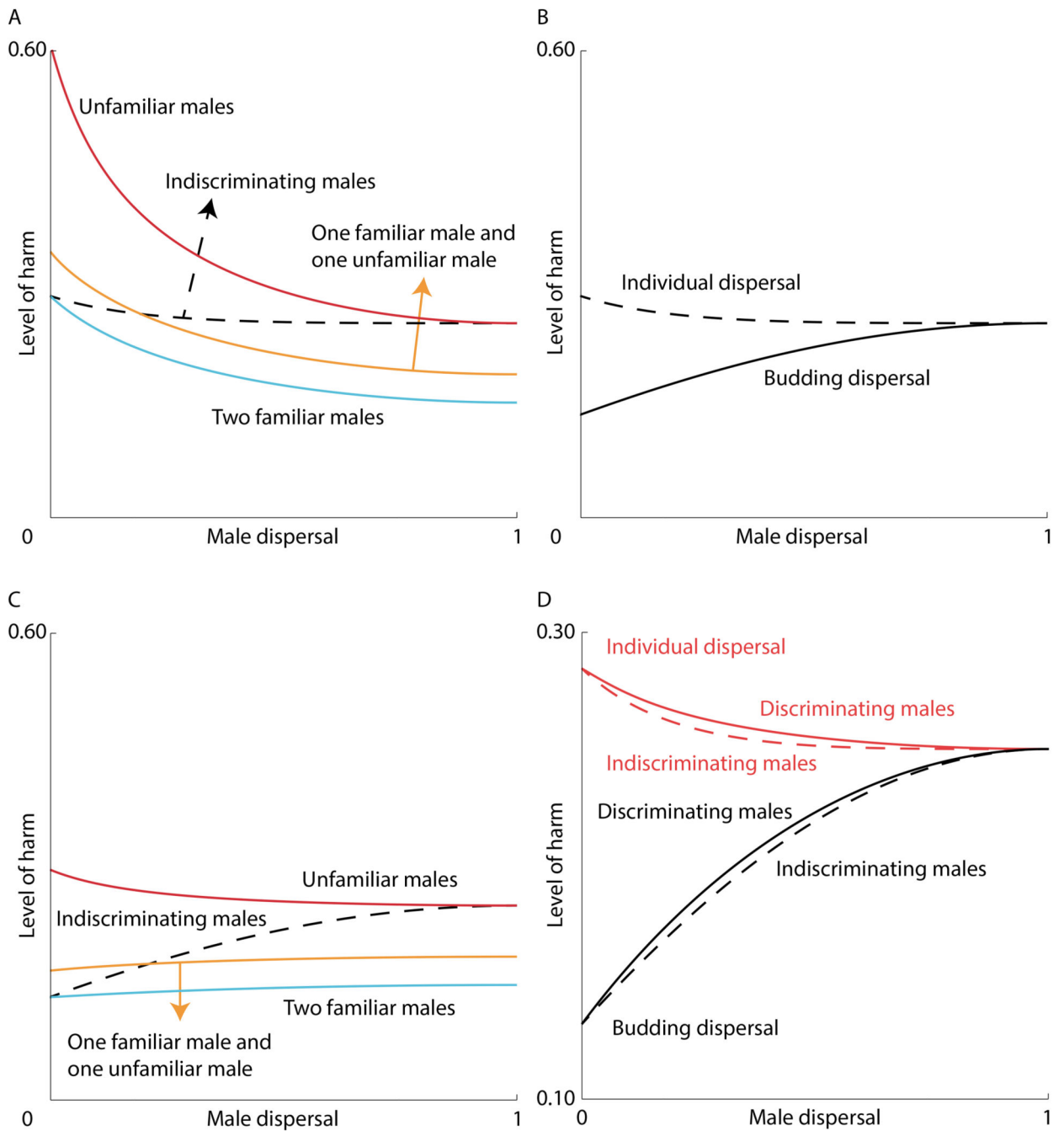
A

B

C

D

Figure 3. Optimal level of harm as a function of male dispersal (d_m) and the average of harm in the population.

In the presence of kin discrimination and absence of budding dispersal (**A**), the optimal level of harm that males express decreases as male dispersal (d_m) increases for both indiscriminating and discriminating males, but the decrease is more pronounced when kin discrimination is present. In the absence of kin discrimination and presence of budding dispersal (**B**), the optimal level of harm that males express increases as male dispersal (d_m) increases. In the presence of kin discrimination and budding dispersal (**C**), the optimal level

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

Table 1

Literature on the impact of kin selection on the evolution of sexual conflict

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 *Drosophila melanogaster* 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. inbreed 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 *Gallus gallus* 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, thefefore, 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 *Rhizoglyphus robini* 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 *Callosobruchus maculatus* 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**.

Table 2

Main conclusions of our study

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