Inclusive fitness and sexual conflict: How population structure can modulate the battle of the sexes

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Competition over reproductive opportunities among members of one sex often harms the opposite sex, creating a conflict of interest between individual males and females. Recently, this battle of the sexes has become a paradigm in the study of intersexual coevolution. Here, we review recent theoretical and empirical advances suggesting that – as in any scenario of intraspecific competition – selfishness (competitiveness) can be influenced by the genetic relatedness of competitors. When competitors are positively related (e.g. siblings), an individual may refrain from harming its competitor(s) and their mate(s) because this can improve the focal individual’s inclusive fitness. These findings reveal that population genetic structure might be of paramount importance when studying the battle of the sexes. We conclude by identifying some new lines of research at the interface of sexual selection and social evolution.

Keywords:
- cooperation; kin selection; sexual conflict; sexual selection; social evolution; tragedy of the commons

‘The season of love is that of battle’

Darwin (1871) The Descent of Man and Selection in Relation to Sex (p. 48, vol. 2)

Introduction

Evolutionary tensions among members of the same sex and between the sexes are implicit in Darwin’s theory of sexual selection [1–3]. Darwin identified two episodes of sexual selection: intrasexual competition and mate choice [1, 4]. Intra-sexual conflict arises whenever the reproductive success of an individual is limited by competition with other members of the same sex over access to reproductive opportunities. Similarly, conflict between individual males and females occurs whenever their fitness cannot be simultaneously maximised by the same outcome of reproductive interactions. Mate choice represents the first such reproductive interaction, where, by definition, an individual discriminates against some prospective partners, thereby reducing their reproductive success. However, potential for conflict also lies at the heart of subsequent reproductive decisions – for example, how often to remate, and how much to care for the resulting offspring. In any mating system that offers alternative reproductive opportunities, concurrent or future, individuals are faced with the trade-off of investing in reproduction with different partners, where the optimal allocation for an individual is rarely simultaneously optimal for its reproductive partners. In the Selfish Gene, Dawkins referred to this evolutionary conflict between males and females as the battle of the sexes [5], and Geoff Parker provided the first formal discussion of this process [2, 6], laying out the foundations for the study of sexual conflict that has exploded over the last decades. This work has revealed the battle of the sexes as a fundamental and pervasive agent of evolutionary change [7].

There is an intimate link between intrasexual competition and the battle of the sexes. Sexual selection can promote traits...
that confer an advantage in intrasexual competition, even when they impose costs on members of the opposite sex. In fact, it is conceivable that some traits confer a competitive advantage precisely because they harm members of the opposite sex. This could happen if males used harm to either manipulate female reproductive behaviour [8] – for example, as a form of coercion or punishment [9], as suggested for lesser grey shrikes (Lanius excubitor) [10], or to increase female reproductive investment in the current reproductive event – for example, by accelerating their death [11], as shown in fruit flies (Drosophila melanogaster) [12]. In the majority of cases, however, harm is likely collateral damage of intrasexual competition. Here, we focus mainly on competition among males and the consequences that this may have for females under different levels of population structure. We note however, that – as Darwin himself was clearly aware – females too can compete for access to males, and population structure is also likely to influence female competition (we identify the study of female perspectives as a priority of future research; see below). Darwin envisioned intrasexual competition as driven by limited access to mating opportunities (i.e. pre-copulatory competition). We now know that because females mate with multiple males (polyandry), males may face a second round of competition after mating, when the ejaculates of multiple males compete over the share of paternity of a single set of ova (i.e. post-copulatory competition). Empirical studies have documented a staggering diversity of cases in which both pre- and post-copulatory sexual selection in males leads to harm of females. Figure 1 presents two such examples: pre-copulatory sexual harassment [13] and post-copulatory pathological polyspermy [14]. So strong is the link between sexual selection and the battle of the sexes that one has been identified with the other [7].

Population structure

A notable assumption shared implicitly or explicitly by most studies of sexually selected harm is that populations are randomly mixed (or unstructured). In this scenario, the competitors of a focal male will then be, on average, no more genetically similar to him than is a random individual in the entire population, meaning that local competitors are unrelated (Box 1). Consequently, the focal male will have no genetic interest in his competitors’ reproduction and is expected to act in his own selfish interest [15]. The assumption of an unstructured population is therefore consistent with Darwin’s view of intra-sexual interactions as a ‘battle’ among individuals over access to mates.

However, natural populations often deviate from this assumption: they are structured into genetically distinct neighbourhoods, or groups (Box 1). In pre-copulatory sexual interactions, for example, genetic structure will often arise because of limited dispersal before mating (e.g. if brothers stay in their natal group and compete for mates there). In this scenario, the competitors of a focal male will be, on average, more genetically similar to him than a random individual in the entire population, meaning that competitors are related [15]. From an evolutionary perspective, this is fundamental because the focal male will have a genetic interest in the reproduction of his competitors and may, therefore, act in the interest of others. Specifically, Hamilton [16] predicted that individuals will appear as if trying to maximise their ‘inclusive fitness’, which recognises that individuals can transmit genes into future generations through both their own reproductive success (direct fitness) and the reproductive success of their relatives (indirect fitness; Box 1). A number of recent articles have reviewed the inclusive fitness consequences of sexual interactions [23–26]. Here, we focus on two key demographic factors that are relevant to inclusive fitness: group structure and relatedness.

When will group structure and relatedness mediate intrasexual competition? On the one hand, positive (i.e. higher than average) relatedness among competing males promotes cooperation, which we define broadly as a trait that is selected for its beneficial effect on neighbours (thus including reduced competitiveness over local mates). On the other hand, modern inclusive fitness theory predicts that increased local competition among relatives can inhibit cooperation, thereby counteracting the effect of relatedness (reviewed in [27–29]). These ideas are uniquely illustrated by a
Box 1

Inclusive fitness in structured populations

We are interested here in populations with spatial genetic structure, where neighbours are more genetically similar than the average similarity in the population. Such structuring can arise as a consequence of mechanisms that limit the dispersal of individuals from the place of their birth to the place of their breeding. Under these conditions, the frequency of individual alleles fluctuates across different parts of the population (i.e. the population is subdivided), and physical proximity predicts genetic similarity [15]. Genetic structure is fundamental to understand the evolution of social traits, such as competitive behaviours, which affect the fitness of a focal ‘actor’ as well as that of its neighbours (‘recipients’). When competitors are unrelated to each other, as in a large, well-mixed population, higher competitiveness is selected when it increases the fitness of the actor despite the costs it may impose on recipients. In structured populations, however, selection on a social trait depends on its direct impact on the focal actor’s fitness as well as its indirect consequences, through an impact on the fitness of the actor’s relatives [16]. This paradigm has been critical to explain the evolution of altruistic behaviours, where the actor pays a direct fitness cost to increase the fitness of others. An altruistic behaviour – and indeed any social trait – can spread provided that its direct fitness effect (−c) is offset by its indirect effect (Rb), where b is a fitness effect on recipients, and R is a measure of genetic relatedness between actor and recipients [16]. Hence, social traits can be favoured when −c + Rb > 0, a condition known as Hamilton’s rule.

What exactly is the relatedness coefficient in Hamilton’s rule? Crucially, it is a three-parties concept involving the genetic value (i.e. allele frequency or breeding value) in a focal actor g∗; the average genetic value in the focal actor’s neighbours ḡ∗; and the average genetic value in the entire population g. Hamilton [16] assumed that the expected genetic value of the focal actor’s neighbours, given the actor’s own genetic value, can be written as:

\[
E\left( g_{\gamma} | g_{\gamma}, g_{z} \right) = R g_{\gamma} + (1-R)g_{z},
\]

which implies that neighbours will share the genetic value of the actor with probability R, in which case \( g_{\gamma} = g_{z} \), or they will not share it with probability \( 1-R \), in which case \( g_{\gamma} \neq g_{z} \).

It follows that relatedness can be viewed as a regression of \( g_{\gamma} \) on \( g_{\gamma} \), with the coefficient (slope) defined as \( R = (g_{\gamma} - g_{z}) / (g_{\gamma} - g) \) [15, 17]. This definition makes it clear that the relatedness coefficient is measured with respect to a ‘reference’ population – in this case, the global population with average genetic value \( g \).

Alternatively, it is sometimes helpful to measure relatedness with respect to the arena in which individuals compete for access to the next generation, which may be at a more local scale than the global population [18]. For example, we consider the case in which the number of juveniles produced by each group is independent of its genetic composition, owing to some local regulation of juvenile numbers before dispersal (‘soft selection’ [15, 19, 20]). In this case, a focal actor’s fitness – defined as its number of surviving offspring in the next generation – depends only on its success in competition, before dispersal, with others in the local group (i.e. the spatial scale of competition is completely local). Therefore, it can be helpful to use the local group of competitors as the reference population, in which case the ‘effective relatedness’ \( R_e \) between group mates will be zero \( (R_e = (g_{\gamma} - g_{z}) / (g_{\gamma} - g) = 0) \). This helps to explain why, in sexual contests where a group of related males compete for a share of their group’s fixed total fecundity (hence \( R > 0 \) but \( R_e = 0 \)), males can be selected to compete with each other as if they were not related at all [21, 22] (see Box 2).

A typical scenario of intrasexual competition among males for access to local females. Here, we consider an illustrative example in which a group of potentially related males compete for access to a fixed number of local females (Box 2). The question is: how will selection shape male competitiveness, and how will this depend on the relatedness among rival males driven by population structure?

Our example shows that the optimal male competitiveness can critically depend on whether male competitiveness results in harm to females (Fig. 2). When females are not harmed by male competitive traits, the predicted optimal competitiveness is completely independent of male relatedness (black line). This is because all groups in the population are equally productive, and so all competition for access to the next generation occurs within groups (‘soft selection’ [15, 19, 20]). In this case, a focal male cannot benefit from helping a random neighbour because this would necessarily lead to more competition faced by the focal male himself (i.e. the spatial scale of competition is completely local). Instead, males should be more competitive whenever this improves their direct fitness, and this is predicted to occur in groups with few competing males (small group size) (e.g. [33]). This is because small group size allows the focal actor to enjoy a significant fraction of the reduced competition that results from harming his rivals. In contrast, when females are harmed by male competitive traits, the predicted optimal male competitiveness is lower than when there is no female harm (Fig. 2, red lines), and the optimal competitiveness (hence harm to females) declines with increasing relatedness among rival males. This is because males can influence the productivity of their group, and their inclusive fitness can be improved by ‘exporting’ more offspring into the global population (i.e. the spatial scale of competition is relatively global, and selection is relatively ‘hard’). Consequently, when local males are related, a focal male can gain an indirect fitness benefit by reducing his competitiveness and thereby promoting the reproduction of his neighbours. Moreover, in contrast to the prediction that competitiveness increases as
group size declines (above), the optimal male competitiveness under female harm can decrease as group size declines. This is because, in smaller groups, a focal male makes up a significant fraction of the group, and so his competitiveness can have a larger negative effect on his own fitness (via female harm). These predictions embody the ‘sexual tragedy of the commons’, where local females represent a common resource that may be diminished by higher male competitiveness [34, 35]. In the following section, we review the evidence that genetically related males can mitigate the sexual tragedy of the commons by cooperating over local females.

**Empirical evidence**

Can we detect patterns in the empirical literature that are consistent with the ideas above? A systematic analysis of empirical studies investigating the role of population structure on sexual competition is beyond the scope of this review. Instead, we provide a sampler of the available evidence as a proof of concept that inclusive fitness arguments based on population structure are of potentially broad generality.

The prediction that male investment in pre-copulatory competition increases as group size declines (from Fig. 2) is consistent with patterns of intrasexual competition among male fig wasps: across species, average male aggression does not depend on the average relatedness of competing males [22], but it does increase as the number of males per fig declines [36]. A similar pattern is observed for the strength of selection on male armaments in beetles, which tends to be stronger when males compete in smaller groups (Biernaskie J, Foster KR, unpubl.). These observations are consistent with theory, if we assume that male harm of females is largely negligible in these clades.

Several studies have also investigated whether increased within-group male relatedness might promote pre-copulatory cooperation (as defined above) among males of a wide range of species (Table 1). Such examples include: the formation of coalitions of related males to compete against other groups, communal displays in leks (where a group of males assemble for communal display), and cooperative polyandry (where males tolerate each other and share access to mates). Cooperation among local males can arise in response to direct selection, via concessions, coercion, punishment or mutualism [3], for example, to curtail the threat of bachelor males in primate societies [84] or that of unfamiliar competitors in some territorial birds (‘the dear enemy effect’) [85]. In some cases however, cooperation appears to be conditional on high local relatedness among cooperators (Table 1), suggesting that indirect fitness benefits of helping relatives may also have at least contributed to the evolution and maintenance of cooperation, consistent with inclusive fitness arguments [86]. Distinguishing between the contribution of direct and indirect effects in sexual cooperation is not always straightforward, because the two are clearly not mutually exclusive. For example, a recent study of Guinea baboons (Papio papio) found reduced male–male aggression within local gangs. Since there was no evidence that, within gangs, males cooperated preferentially with relatives, the study concluded that this pattern was caused by direct effects [39]. However, the study also found that male relatedness was significantly higher within gangs than across the entire population [39], suggesting that indiscriminate cooperation (see below) with gang members is also associated with some indirect benefits. We would expect such benefits to be particularly relevant in populations with high reproductive skew among males and where relatives compete locally over reproductive opportunities.

Evidence consistent with the expectation that relatedness among rival males reduces post-copulatory competition [87] is more limited. Often studies focus on patterns of paternity sharing, which may result from both pre- and post-copulatory mechanisms (e.g. [61] in Table 1). In several species, however, sperm have been shown to cooperate in the formation of fast-moving ‘trains’ of sperm. In some organisms, for example, sperm cooperate to form aggregations that out-perform single sperm [88–94], even though aggregation may reduce the fertilising ability of individual sperm [89]. In polyandrous species, sperm cooperation might be expected to occur preferentially between related sperm [24, 90], and this kin discrimination has indeed been recently found in a polyandrous species of deer mice (Peromyscus maniculatus). On the other hand, a sister species that evolved under little sperm competition (P. polionotus) displays indiscriminate sperm aggregation, as one would expect if the sperm of a male do not typically compete with unrelated sperm [79]. In the honeybee (Apis mellifera), a eusocial insect where queens are polyandrous, there was a weak tendency for the seminal fluid of a male’s ejaculate to have more detrimental effects on the sperm of unrelated (vs. related) rival males [81]. However, this tendency was non-significant and absent in other...
Box 2

Sexual selection in a group-structured population

Here, we describe a simple mathematical model that illustrates how population structure can mediate intrasexual competition (results presented in Fig. 2). We consider a large (effectively infinite) population of groups, each with \( n \) adult males and a fixed number of local females. We suppose that males compete over access to the females, using traits such as weaponry or aggression (herein ‘competitiveness’), and then die after mating. Inseminated females, on the other hand, disperse into the global population and produce clutches of offspring in the vacant groups. Among the offspring in each group, \( n \) males survive to compete for mates in the next generation (where survival is independent of competitiveness over mates). Hence, positive relatedness among competing males can arise because some of those males may be brothers. This scenario is similar to the life history of many insects, including fig wasps, where the average relatedness among adult males in a group depends on how many different mothers lay clutches in each group [30].

To model selection for male competitiveness, we use a ‘neighbour-modulated’ fitness approach [31–33]. We assume a simple genetic system with two segregating alleles: a resident allele encoding competitiveness \( z \), and a mutant allele encoding a slightly different competitiveness, \( x \). Suppose that the mutant allele is globally rare, but – owing to relatedness – it may be carried by a focal mutant’s group mates, whose average competitiveness we denote \( y \). We assume that the competitive ability \( C \) of a focal mutant depends on: (i) his own competitiveness relative to the average of his group mates; and (ii) can decrease as group size declines, mediated by \( c \). Formally, the competitive ability of the focal male is \( C_x = \frac{x}{y}(1 - cx) \), and, by the same logic, the average competitive ability of one of his group mates is \( C_y = \frac{1}{(n - 1)}(y(1 - cy)) \).

We assume that the focal male’s share of his group’s fecundity will depend on his competitive ability relative to the total competitive ability in the group:

\[
F(x, y) = \frac{C_x}{C_x + (n - 1)C_y}K(1 - hy),
\]

where \( K \) is the maximum group fecundity, and – crucially – we allow this to decline with the average competitiveness of the whole group \( (y = \frac{x}{n + y(n - 1)/n}) \), reflecting the possibility of harm to females (mediated by \( h \)). Finally, we measure the focal male’s fitness as \( W = F(x, y)F(z, 2) \), where \( F(x, z) = (1/n)K(1 - hz) \) is the fecundity of individuals in the global population.

Following the standard approach of [31], the direction of selection for competitiveness can be written as:

\[
\frac{dW}{dx} = \frac{\partial W}{\partial x} \bigg|_{x-y-z} + \frac{\partial W}{\partial y} \bigg|_{x-y-z} \times R.
\]

In this equation, the first term on the right-hand side is the direct effect of the focal male’s competitiveness on his own fitness, and the second term is equivalent to the indirect fitness effect, through an effect on group mates with relatedness \( R \). The optimal level of competitiveness satisfies \( \frac{dW}{dx} \big|_{x-y-z} = 0 \). Solving this, we find that when female harm is absent \( (h = 0) \), the optimum is \( z^* = n / (c[2n - 1]) \), which predicts that male competitiveness \( z \) will not depend on relatedness; and (ii) will increase as group size declines. When female harm is present \( (h > 0) \), the optimum is more complicated (not shown) and predicts that male competitiveness \( z \) will decrease with increasing relatedness; and (ii) can decrease as group size declines, as long as the harm to females exceeds the cost of individual competitiveness \( h \) (Fig. 2).

Few studies have addressed the extent to which male relatedness can modulate sexually selected male harm of females. By exposing female least killifish (Heterandria formosa) to males that were either unrelated or highly related to each other (but always unrelated to the female), Ala-Honkola et al. found that: (i) the size of females’ offspring decreased over time when females were exposed to unrelated males but not when exposed to highly related males; and (ii) females exposed to the latter treatment survived longer [83]. These results may reflect a cost to females as a result of high competitiveness among non-related males. However, it is also possible that low within-brood relatedness exacerbates sibling conflict in this placental species, thus explaining why offspring size declined over time in the ‘low relatedness’ treatment. In a recent experimental study of the fruit fly (Drosophila melanogaster), males fought less with each other and courted females less intensely when grouped with related (vs. unrelated) males [78]. In addition, females exposed to males related to each other reproduced for a longer period of their lifetime and experienced lower reproductive senescence.

polyandrous eusocial species (while the lack of tendency found in monandrous species is expected) [81]. There are two possible explanations for the paucity of evidence for cooperation in post-copulatory interactions. First, it is notoriously difficult to study the social interactions among ejaculates and distinguish the operation of male- and female-driven episodes of post-copulatory sexual selection (i.e. sperm competition and cryptic female choice), which may target male relatedness in different ways (see below). Greater appreciation that the arena for sexual selection and sexual conflict extends well beyond mating should spur further work on the effects of relatedness on post-copulatory interactions in the future. Second, differences in the role of male relatedness in pre- versus post-copulatory sexual selection may reflect variation in group size and the scale of competition occurring before and after mating (see below). Clearly, more systematic information on patterns of sex-specific dispersal, polyandry and male group size (or ejaculate group size) is required to assess the role of population structure as a modulator of sperm competition.

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Table 1. Some examples of empirical investigations of the ideas that within-group relatedness: (a) promotes pre-copulatory male cooperation, (b) promotes post-copulatory male cooperation, and (c) reduces male harm of females

| Class         | Species                          | Form of male ‘cooperation’                                         | Evidence for kin-bias* | Reference |
|---------------|----------------------------------|--------------------------------------------------------------------|------------------------|-----------|
| **Mammalia**  | Barbary macaque (Macaca sylvanus) | Preferential cooperation among relatives                           | Yes                    | [37, 38]  |
| **Mammalia**  | Guinea baboon (Papio papio)       | Mutual tolerance in gangs of high relatedness                      | Partly                 | [39]      |
| **Mammalia**  | Red howler monkey (Aloatta seniculus) | Preferential coalitions among relatives                           | Partly                 | [40]      |
| **Mammalia**  | Geoffroy’s tamarin (Saguinus geoffroyi) | Preferential cooperation among relatives                           | Yes                    | [41]      |
| **Mammalia**  | Lion (Panthera leo)               | Preferential coalitions among relatives                           | Yes                    | [42, 43]  |
| **Mammalia**  | Cheetah (Acinonyx jubatus)        | Preferential coalitions among relatives                           | Yes                    | [44]      |
| **Mammalia**  | Kinkajou (Potos flavus)           | Mutual tolerance, mate sharing among relatives                    | Possiblyb              | [45, 46]  |
| **Mammalia**  | Slender mongoose (Herpestes sanguineus) | Mutual tolerance, mate sharing among relatives                   | Possiblyb              | [47]      |
| **Mammalia**  | Bottlenose dolphin (Tursiops truncatus/sp.) | Preferential coalitions among relatives                           | Yes                    | [48, 49]  |
| **Mammalia**  | Oribi (Ourebia ourebi)            | Mutual tolerance, mate sharing among relatives                    | Yes                    | [50]      |
| **Mammalia**  | Jamaican fruit bat (Artibeus jamaicensis) | Preferential coalitions among relatives                           | Yes                    | [51]      |
| **Aves**      | Wild turkey (Meleagris gallopavo)  | Preferential cooperation among relatives in courtship displays    | Yes                    | [52]      |
| **Aves**      | Peacock (Pavo cristatus)          | Preferential lekking with relatives                               | Yes                    | [53]      |
| **Aves**      | Red grouse (Lagopus l. scoticus)  | Mutual tolerance, courtship displays among relatives             | Yes                    | [54]      |
| **Aves**      | Black grouse (Tetrao tetrix)      | Preferential lekking with relatives                               | Yes                    | [55]      |
| **Aves**      | White-winged trumpeter (Psophia leucoptera) | No preferential mate sharing among relatives                  | No                     | [56]      |
| **Aves**      | Tasmanian native hen (Gallinula mortierii) | Mutual tolerance, mate sharing among relatives                  | Yes                    | [57, 58]  |
| **Aves**      | Pukeko (Porphyrio porphyrio)      | Larger coalitions among relatives                                 | Possiblyb              | [59]      |
| **Aves**      | Galapagos hawk (Buteo galapagoensis) | No preferential mate sharing among relatives                   | No                     | [60]      |
| **Aves**      | Acorn woodpecker (Melanerpes formicivorus) | Reduced reproductive skew in coalitions of co-breeding males   | Partly                 | [61]      |
| **Aves**      | Golden collared × White collared manakin (Manacus vitellinus × M. candei) | Preferential cooperation in courtship displays in hybrid zones | Yes                    | [62]      |
| **Aves**      | White-bearded manakin (Manacus manacus) | Clusters of relatives within leks                                | Partly                 | [63]      |
| **Aves**      | Blue manakin (Chiroxipha caudata) | No preferential lekking with relatives                           | No                     | [64]      |
| **Aves**      | Lance-tailed manakin (Chiroxipha lanceolata) | No preferential cooperation in courtship displays              | No                     | [65]      |
| **Aves**      | Long-tailed manakin (Chiroxipha linearis) | No preferential cooperation in courtship displays              | No                     | [66]      |
| **Aves**      | Blue-backed manakin (Chiroxipha pareola) | No preferential lekking with relatives                           | No                     | [67]      |
| **Aves**      | Blue-crowned manakin (Lepidothrix coronata) | No preferential lekking with relatives                           | No                     | [67]      |
| **Aves**      | Wire-tailed manakin (Pipra filicauda) | Mixed evidence for preferential lekking with relatives          | Partly                 | [67, 68]  |
| **Aves**      | White-crowned manakin (Pipra pipra) | No preferential lekking with relatives                           | No                     | [67]      |
| **Aves**      | Alpine accentor (Prunella collaris) | No preferential mate sharing among relatives                    | No                     | [69]      |
| **Aves**      | Dunnock (Prunella modularis)      | No preferential mate sharing among relatives                    | No                     | [70]      |
| **Aves**      | American crow (Corvus brachyrhynchos) | Some evidence for mate sharing among relatives                  | Partly                 | [71]      |
| **Aves**      | Carrion crow (Corvus c. corone)   | Preferential mate sharing among relatives                        | Yes                    | [72]      |
| **Osteichthyes** | Daffodil cichlid (Neolamprologus pulcher) | Preferential mutual tolerance and mate sharing among relatives restricted to young males | Partly                 | [73]      |

(Continued)
Examples were selected among studies, which included pre-zygotic reproductive interactions (i.e. not involving parent–offspring interactions and parental care) and presented explicit information about male–male relatedness at some scale. aThis does not rule out the possibility that direct benefits may also be at work. bSmall sample size, weak or indirect evidence.

as reflected by a sharper age-dependent decline in offspring viability with maternal age in females exposed to unrelated males – a pattern that echoes the killifish study [83]. Similarly, male flies in highly related groups enjoyed a longer lifespan than males in unrelated groups, perhaps because related males courted females less and fought other males less intensely. These results show that under experimental conditions, *D. melanogaster* behave in a way that is broadly consistent with the predictions of inclusive fitness models [25, 26]. The origin of this behaviour however remains unclear. Lab-adapted *D. melanogaster* populations seem unlikely to display the genetic structure required for the evolution of male

| Class       | Species                             | Form of male ‘cooperation’                                                                 | Evidence for kin-biasa | Reference  |
|-------------|-------------------------------------|-------------------------------------------------------------------------------------------|------------------------|------------|
| Osteichthyes| Tanganyikan cichlid (*Julidochromis ornatus*) | No preferential mutual tolerance and mate sharing among relatives                        | No                     | [74]       |
| Osteichthyes| Tessellated darter (*Etheostoma olmstedi*) | No preferential nest and mate sharing among relatives                                      | No                     | [75]       |
| Insecta     | Fig wasp (*Kradibia tentacularis*)   | No reduced competition among relatives (but indiscriminate male cooperation to help females out of fig) | No                     | [76]       |
| Insecta     | Fig wasp (*Pleistodontes imperialis*) | No reduced competition among relatives (but indiscriminate male cooperation to help females out of fig) | No                     | [77]       |
| Insecta     | Fruit fly (*Drosophila melanogaster*) | Reduced male aggression among relatives                                                   | Yes                    | [78]       |
| (b) Male relatedness and post-copulatory cooperation | Mammalia Deer mouse (*Peromyscus maniculatus*) | Preferential cooperation among related sperm evolved under sperm competition               | Yes                    | [79]       |
|             | Mammalia Deer mouse (*Peromyscus polionotus*) | Indiscriminate sperm cooperation without sperm competition                                   | Yes                    | [79]       |
|             | Mammalia House mouse (*Mus musculus domesticus*) | No evidence for reduced investment in sperm competition with relatives                   | No                     | [80]       |
|             | Aves Acorn woodpecker (*Melanerpes formicivorus*) | Reduced reproductive skew in coalitions of co-breeding males                            | Partly                 | [61]       |
|             | Insecta Fruit fly (*Drosophila melanogaster*) | No evidence for reduced investment in sperm competition with relatives                   | No                     | [78]       |
|             | Insecta Honeybee (*Apis mellifera*)    | No evidence for differential sperm: seminal fluid interactions among related ejaculates in polyandry | No                     | [81]       |
|             | Insecta Bumblebee (*Bombus terrestris*) | No evidence for differential sperm: seminal fluid interactions among related ejaculates in monandry | Yes                    | [81]       |
|             | Insecta Fungus growing ant (*Acromyrmex echinatior*) | No evidence for differential sperm: seminal fluid interactions among related ejaculates in polyandry | No                     | [81]       |
|             | Insecta Fungus growing ant (*Trachymyrmex cf. zeteki*) | No evidence for differential sperm: seminal fluid interactions among related ejaculates in polyandry | No                     | [81]       |
|             | Insecta Fungus growing ant (*Atta colombica*) | Reduced female harm in groups of related males                                             | Yes                    | [81]       |
|             | Insecta Australian field cricket (*Teleogryllus oceanicus*) | No evidence for reduced investment in sperm competition with relatives                   | [82]                   |
| (c) Male relatedness and female harm | Mammalia Guinea baboon (*Papio papio*) | Reduced male aggression of females in related groups                                     | Partly                 | [39]       |
|             | Osteichthyes Least killifish (*Heterandria formosa*) | Modulation of female reproductive success                                                 | Possiblyb             | [83]       |
|             | Insecta Fruit fly (*Drosophila melanogaster*) | Reduced female harm in groups of related males                                             | Yes                    | [78]       |
sexual cooperation. One possibility is that cooperation among related males has evolved in structured ancestral natural populations and then retained in captivity. A non-mutually exclusive alternative is that, because male relatives shared the same rearing environment [78], the observed cooperation may reflect a response evolved through some direct benefits of familiarity per se (although it is unclear what these benefits might be in this species). Finally, cooperative behaviours might reflect unknown transient properties of populations emerging under certain conditions. Collectively, these studies illustrate a rather eclectic picture. Table 1 tentatively categorises empirical evidence as consistent or inconsistent with theoretical predictions. However, data on population structure, local group size, mating system and female harm is often lacking to resolve the extent to which inclusive fitness mechanisms explain this variation because of their nuanced yet potentially important impact on the battle of the sexes. These studies also raise a number of outstanding questions and routes for future research, some of which we address below.

**Familiarity, shared environment and other proximate mechanisms underpinning kin-biased male competition**

There are two basic mechanisms that would lead to preferential cooperation among highly related males. First, when males tend to live in groups with high relatedness, natural selection can favour males who indiscriminately cooperate with their neighbours (i.e. no kin recognition is required, as was assumed in our model in Box 2). Second, especially when males encounter competitors of differing relatedness, selection can favour males with the ability to recognise and preferentially benefit over non-kin. Indeed, plastic responses such as those reported in some studies (Table 1) require some mechanism of kin recognition. These mechanisms are diverse and taxon-specific. Innate mechanisms rely on the direct recognition of individuals sharing the same alleles (‘genetic kin recognition’ [95]). In structured populations, however, where relatives tend to be clustered, kin can be discriminated through cues acquired from the environment.

Acquired mechanisms include cues derived by sharing the same environment or diet, social familiarity and phenotype-matching [96, 97]. For example, several insects may utilise cues in the cuticular hydrocarbons (CHC), and the possible role of gut microbiota has also received prominent attention [98]. Careful experimental work recently conducted across different *Drosophila* species indicates that kin recognition is complex and mediated by combinations of multiple innate and acquired mechanisms [99]. From a cognitive standpoint, the mechanisms involved in innate kin recognition are considerably more complex than those based on familiarity or environmentally acquired cues [100]. In addition, innate kin recognition requires the maintenance of sufficient genetic variability in a context where kin discrimination itself will work to erode such variability [95]. Hence, it seems probable that mechanisms of kin recognition that are based to some degree on familiarity or other environmentally acquired cues will be more common than purely innate mechanisms. Acquired cues might be especially relevant for male cooperation in *D. melanogaster*, where individuals can assess genetic relatedness based on familiarity cues. Recent work has shown that a male *D. melanogaster* is not only less interested in mating with his previous partners, but also less interested in novel females that recently mated with his own brothers [101]. One intriguing hypothesis therefore is that a male might recognize related males as a weaker perception of self. Reduced investment in sexual competition in the presence of kin may then reflect a generalised Coolidge effect. The Coolidge effect refers to reduced sexual interest by a male in partners with whom he has already mated, a likely strategic economisation of his reproductive resources across multiple partners, observed in a range of promiscuous species [102]. This scenario implies a combination of direct benefits (preferential sperm investment in sexually novel females) and indirect benefits (reduced sperm competition with relatives) potentially at work. Similarly, males can modulate investment in mate guarding and/or post-copulatory investment in response to varying levels of sperm competition [103]. The specific mechanisms employed in this endeavour may vary substantially across taxa, but it seems that in at least some cases males may accomplish this by assessing the variability of male odours in the environment [104], in which case a mixture of odours from related males may be perceived as reflecting a lower number of rivals (and hence decreased competition). The examples above raise the possibility that acquired kin-recognition mechanisms might be co-opted from other functional contexts, due to inclusive fitness benefits arising from population structure. The fundamental implication is that, if kin discrimination is entirely or partly determined by acquired cues, then the inclusive fitness benefits of kin-biased male cooperation require a population structure which links relatedness to spatial proximity (Box 1).

The mechanisms mediating female harm are also likely to be diverse and taxon-specific. In the case of fruit flies, female harm might be caused by male–male fighting and male sexual harassment, which may accelerate female reproductive ageing [78], although the specific physiological pathways of such mechanisms remain unclear. In other species, mating with genetically unrelated males may incur higher immunological costs to females, which must respond to a wider range of semen antigens compared to females mating with a more genetically homogeneous pool of males [105]. Such immunological costs may be particularly relevant for viviparous species, in which females mating with genetically diverse males (i.e. males genetically different from each other) may also need to accept a more genetically diverse set of embryos [106].

**How evolutionarily stable is intrasexual cooperation?**

The nature of kin recognition mechanisms outlined above is relevant here because it may have bearings on the evolution-
D. melanogaster groups, where males competed with relatives and unrelated males, the unrelated individuals were found to be disproportionately successful [78]. This study utilised recessive mutants in order to assign offspring paternity, and the ecological relevance of this pattern requires further confirmation. These results nonetheless raise the possibility that limitations in kin recognition may enable a minority of unrelated males to infiltrate groups of relatives and take advantage of the reduced competitiveness in these groups. This may occur, for example, if a male was only able to recognize his own average relatedness to members of a group, rather than perceive his relatedness with each individual group member separately (i.e. if focal male A is related by $R = 0.5$ to B and $R = 0.125$ to C, A perceives that he is related by $R = 0.3125$ to the average group member). A majority of relatives may then perceive the same group as more related than a minority of unrelated males.

Females may also play a key role in these dynamics. While groups of related males offer a more benign environment to females, they also reduce the genetic diversity of offspring, which may be detrimental, e.g. under environmental stochasticity or high risk of inbreeding within groups. Under such circumstances, females may be caught in a delicate balance between reducing male harm while also increasing the genetic diversity of their offspring. The best female strategy in these cases might then be to stick with groups of males who are related to each other but to seek out mating opportunities with unrelated males and favour fertilisation by their sperm. This is strikingly consistent with female behaviour in some social species. For example, in some natural populations of chimpanzee (Pan troglodytes), females benefit from the resources provided by males within their social group but occasionally stray to seek copulations with more genetically different males outside of their social groups [107]. The reproductive advantage achievable by mating with a series of males unrelated to each other may thus be due (at least in part) to female preference. den Boer et al. [81] indicate that cryptic female choice can over-ride the effect of interactions between related ejaculates in Atta ants. In diploid organisms, these female strategies would eventually result in the break down of local male relatedness by producing offspring with multiple males (which are half- rather than full-sibs), thus undermining the long-term potential for inclusive fitness mechanisms [23]. Finally, females are expected to co-evolve resistance to- or tolerance of male-imposed harm, which means that variation in male harm across species and populations will depend not only on population structure but also on the co-evolutionary trajectories between males and females. In the future, it will be critical to resolve these female-driven mechanisms and their potential impact on the evolutionary stability of male cooperation (see below).

**Whether males compete before or after copulation may matter**

As suggested above, within-group relatedness, group size, and the scale of competition may change drastically between pre- and post-copulatory competition, depending on the species-specific pattern of female mating and dispersal [26]. For example, in some mating systems males may compete locally to mate with a female that may then disperse to a new patch where another group of males compete to mate with her [108]. In such systems, both the group size and the relatedness of males involved in pre-copulatory competition (i.e. the males competing to mate with a female) can differ considerably from the group size and relatedness of males involved in post-copulatory competition (i.e. the males that mated with a female, whose ejaculates compete to fertilise her ova). Hence, the inclusive fitness predictions for pre- and post-copulatory traits may differ widely. In addition, if a male’s investment in post-copulatory competition is traded off against his investment in pre-copulatory competition [109], then the optimal male competitiveness may change drastically before and after copulation. Future theoretical and empirical efforts should seek to clarify these dynamics. In general, one would predict that for a given level of polyandry, males should invest less in sperm competition (i.e. lower relative testis mass) in species where female dispersal limits sperm competition to a local scale, compared to species where females remate more globally. However, the potential effect of cryptic female choice also needs consideration. For example, females might cryptically bias fertilisation in favour of the sperm of males unrelated to other male partners (see above).

**The two-way interaction between sexual cooperation and population demography**

Most of the deleterious effects of male competition are bound to be cumulative and hence increasingly important with age because any differential fitness effects will not usually impact the early life history of an individual. Because of this age-dependence, the fitness consequences of male competition will vary depending on background population dynamics. Early reproduction is particularly important in expanding populations because, in this demographic context, an organism’s fitness will not only depend on the amount of offspring it produces but also crucially on how early it reproduces. Under such circumstances, an organism will value reproduction early in life over lifetime output, and late-life fitness effects such as those described above will likely have a limited impact on its net fitness. In contrast, mid- or late-life fitness effects are likely to be more important in stable or contracting populations, where any effect on an organism’s reproductive senescence will have a negative impact on its net fitness [110]. Hence, a consistent late-life bias in the fitness effects derived from male cooperation (e.g. a reduction in the rate of female reproductive senescence) may be more important in stable or contracting populations than in growing populations. Indeed, rate-sensitive estimates of the fitness benefits of reduced male–male competition and female harm suggest that this may be the case in D. melanogaster [78].

Measuring the immediate inclusive fitness consequences of sexual cooperation only answers part of the question, however, because reduced female harm may also impact
future generations by decreasing deleterious parental trans-generational effects. Therefore, to fully understand the demographic effects of male cooperation and reduced female harm, it is critical to study potential cross-generational effects. The capacity for parents to induce non-genetic phenotypic effects in their offspring in response to environmental changes has been widely documented, and this can exert profound long-lasting effects with consequences across multiple generations [111]. For example, a recent study found that increased sexual pre-copulatory interactions alone produce negative trans-generational survival and ageing effects in D. melanogaster [112]. Given that male relatedness may relax both male–male aggression and female harm in this species (see above), it is conceivable that similar trans-generational parental effects may add to the benefits of sexual cooperation in groups of related male fruit flies. Furthermore, in the presence of trans-generational effects, reduced sexual conflict may turn out to be important irrespective of background population dynamics (i.e. in growing, stable and contracting populations) because trans-generational effects can potentially impact early reproduction in the next generation of offspring [112].

**What does this all mean for ‘real’ populations? Population structure in the wild**

In order to resolve the biological relevance of the above mechanisms, we must have much better data on the structure of natural populations. Some natural populations are exceptionally well characterised. Unfortunately, however, little is known about the intensity and mechanisms of female harm in these populations. On the other hand, the battle of the sexes has been studied in exquisite detail in some organisms; however, these are often captive or lab-adapted populations of species for which comparatively little knowledge exists about natural populations. Recent evidence of individual recognition in lab populations of fruit flies suggests that even these high-density, lab-adapted populations may have retained vestigial adaptations from an evolutionary past, when natural populations were perhaps more structured (see above). We need data on sex-biased dispersal and mating patterns, and on the network of social and sexual interactions across individuals of known genetic relatedness to measure the size and relatedness of local groups of competitors.

**Conclusions**

The last 20 years or so have seen an explosion of studies of the battle of the sexes. As a result of this vigorous effort, we now understand how sexual selection can drive the evolution of male competitive traits that harm females. Surprisingly, however, we still lack a framework to explain the staggering diversity of patterns of female harm observed across species and populations. Here, we discuss recent theoretical and empirical work suggesting that inclusive fitness mechanisms might play a fundamental role in modulating harm, and we argue that because of these mechanisms, interpreting patterns of variation in female harm requires explicit consideration of population ecology and structure, which has often been lacking in most research of the battle of the sexes [113]. Population structure ultimately determines group size and the relatedness of competing males, thus dictating patterns of direct and indirect selection on male competitiveness and female harm. We identify some key questions in the rapidly emerging field at the interface between sexual selection and social evolution. Five avenues appear particularly promising for future research: (i) the mechanisms underpinning male cooperation and reduced female harm; (ii) the evolutionary stability of cooperation amongst male relatives; (iii) conceptual differences between pre- and post-copulatory sexual competition; (iv) the role of population demography and (v) the study of natural populations.

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