

Kin selection and the evolution of sexual conflict

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Abstract

Males and females do not always share the same evolutionary interests. This is particularly true in the case of multiple mating, where male–male competition can often lead to adaptations that are harmful to the female, and females can evolve counter adaptations to reduce the benefits males gain from such traits. Although social evolution has made substantial progress from kin selection theory, most studies of sexual conflict have ignored the effects of genetic relatedness. Here, I use a model of male harm and female resistance to investigate how kin selection affects the evolution of sexual conflict. Building on models of social evolution, I show that relatedness inhibits sexual conflict, in terms of male harm, whereas it has no effect on the evolution female resistance. This study examines a previously neglected mechanism that can potentially help to resolve sexual conflict over mating and highlights the potential importance of considering relatedness in empirical studies of sexual conflict.

Introduction

Conflict between the sexes is a common occurrence among sexually reproducing species (Arnqvist & Rowe, 2005). Males and females do not always share the same evolutionary interests, and it is common that behaviours that are beneficial to members of one sex can result in costs to members of the opposite sex (Parker, 1979). This is particularly true in species with polygamy, where it is known that males and females frequently show different mating optima (Fowler & Partridge, 1989; Chapman *et al.*, 1995; Rice, 1996; Holland & Rice, 1999; Arnqvist & Nilsson, 2000; Arnqvist *et al.*, 2005). Whereas males that are able to mate with more females will have a higher reproductive success than other males, females that mate multiply often suffer from doing so (Arnqvist & Rowe, 2005). Competition between males often results in collateral damage to females, as females are inadvertently harmed by males trying to outcompete each other for fertilizations (e.g. Morrow *et al.*, 2003; Parker, 2006). Sexual conflict over mating can result in females having a lower fitness than they would in the absence of such conflict (Arnqvist & Rowe, 2005). This can result in

evolutionary arms races between the sexes, where adaptations in males are met with counter adaptations in females (Arnqvist & Rowe, 2002; Morrow & Arnqvist, 2003; Wigby & Chapman, 2004).

Social interactions not only affect an individual's direct fitness but also affect their indirect fitness, through helping or harming individuals that carry copies of their genes (Hamilton, 1964; Taylor & Frank, 1996; Frank, 1998; Griffin & West, 2002; Lehmann & Keller, 2006). Kin selection theory has proved a powerful tool for understanding the evolution of social behaviour, from cooperation and altruism (Hamilton, 1964; Lehmann & Keller, 2006; West *et al.*, 2007) to sex allocation and virulence (e.g. Frank, 1994; West, 2009). Kin selection has been neglected in the evolution of sexual conflict, despite its prevalence in understanding social evolution (but see Parker, 1979; Queller, 1997; Bourke, 2009). Hamilton (1964) proposed a simple classification of social behaviours based on the fitness effect (either positive/negative) of a given behaviour on both an actor and the recipient of the behaviour. In case of sexual conflict over mating, male–male competition confers a benefit to males (through extra matings) but can result in a fitness cost to females (through reduced fecundity/survivorship – e.g. Rice, 1996; Holland & Rice, 1999; Edvardsson & Tregenza, 2005; Le Galliard *et al.*, 2005). Thus, from a social-evolutionary perspective, male

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harassment of females would be defined as a purely 'selfish' behaviour as it confers a direct fitness benefit on the actor (the male) whilst inflicting an overall fitness cost on the recipient (the female). Sex can also be seen as beneficial to both sexes as males and females benefit from mating through fertilization, and females also stand to benefit from situations where males confer direct benefits to females, for example in the form of parental care (e.g. Alonzo, 2009) or nuptial gifts (e.g. Vahed, 1998; Edvardsson, 2007).

In contrast to acts of helping between individuals, it is generally thought that sexual conflict arises because male and female mating partners are typically unrelated and thus do not share any common interests (Trivers, 1972; Parker, 1979, 2006; Johnstone & Keller, 2000). Although the effects of dispersal and relatedness are well established for traits such as altruism and spite (Hamilton, 1964, 1970; Taylor, 1992; Queller, 1994a; Gardner, 2010), models of sexual conflict have tended to focus on direct costs and benefits to males and females (in terms of grand offspring production) and have generally neglected the notion of relatedness between individuals, which is known to be important in models of social evolution (but see Queller, 1997; Chapman, 2006; Bourke, 2009). In his classical paper on sexual conflict, Parker (1979) introduced a simple model of conflict between a brother and a sister and showed that a male often has more to gain from inbreeding than a female (Parker, 1979). Inbreeding avoidance is a common behaviour in many animals and can potentially create conflict between brothers and sisters over mating. Inbreeding also increases relatedness between mates and has the potential to align the interests of males and females. This could potentially act as a conflict resolving mechanism in the case of male harassment of females and female resistance of male harm.

Higher relatedness between mates will reduce the incentive to inflict harm, and higher relatedness with other members of the same sex will reduce competition for matings. This will be influenced by dispersal, the mating system and the influence of both of these factors on the relatedness of offspring in a patch (Johnstone & Cant, 2008; Gardner, 2010). Here, I examine the effects of relatedness on the evolution of male harm and female resistance. I build on models of social evolution to ask whether kin selection is a plausible mechanism to resolve sexual conflict over mating. Through their effects on relatedness, I show how sex-biased dispersal of males and females, together with local mating skew (in terms of the proportion of males and females within a patch that successfully mate), can influence the coevolution of male harm and females resistance.

Model and results

I assume that the population is divided into an infinite number of patches with a finite number of individuals

per patch (the 'infinite island' of Wright, 1931). I assume that there are n_F females and n_M males per patch. The model I use considers a population of a sexually reproducing species and is based on the neighbour-modulated fitness approach, which is an approach drawing on kin selection (Frank, 1998). Individuals are diploid and mate to produce gametes that fuse to form diploid zygotes (e.g. Johnstone & Cant, 2008; Gardner, 2010). Adults mate a sufficiently large number of times, at random, within the patch to produce a large number of offspring. Males compete within a patch for matings with females and invest y in harming females. The more males harm females, the more likely they are to gain a benefit b from extra matings with females, but this will come at a cost u to the focal male and will inflict a cost c on the female. Females invest x in resisting the effects of male harm, which comes at a cost v . Here, I am interested in simple mechanisms of male harassment of females and female resistance towards male harm, which do not necessarily involve decision-making on the part of the organism. Such a situation is representative of morphological or physical traits, such as spiked genitals or toxic seminal fluids rather than explicitly behavioural traits. The model thus assumes that there is no mate choice or inbreeding avoidance: all individuals, regardless of their genotype, therefore experience the same level of inbreeding depression.

After mating, the adults then die and offspring either stay in their natal patch or disperse to find a new patch elsewhere in the population. Males disperse with a probability m_M and females disperse with a probability m_F . I assume sex-limited expression, where both males and females carry both the harming and resistance genes, but only the respective gene is expressed in each sex (i.e. y in males and x in females) and that the genes for x and y are independent and not linked (i.e. their covariance is 0). I also assume that selection is weak, meaning that the gain from matings to males b , and the cost imposed on females c , is small relative to overall fitness (i.e. $b \ll 1$, $c \ll 1$, $u \ll 1$ and $v \ll 1$), so there is no effect on the primary sex ratio, which I assume to be 1 : 1.

From these assumptions, the expected gain from matings of male i in patch j is:

$$f_{Mij} = 1 + by_{ij}(1 - sx_j) - uy_{ij} \quad (1)$$

where s is the efficiency of female resistance to reduce the benefits a male gains from harming. The function given by eqn (1) assumes a baseline mating success of 1 (if $y = 0$ and $x = 0$, there is no harm and fertilization success is random, and therefore any male has an equal chance of fertilizing a female). The average gain to males, from matings, in patch j is:

$$f_{Mj} = 1 + by_j(1 - sx_j) - uy_j \quad (2)$$

and the average gain to males from matings across the whole population is:

$$f_M = 1 + by(1 - sx) - uy \quad (3)$$

The number of offspring produced by a focal female will depend on the level of harm she experiences and her ability to resist harm. The fecundity f_{Fij} of female i in patch j , the average fecundity f_{Fj} of all females in patch j and the average fecundity of all females f_F in the population are therefore:

$$f_{Fij} = 1 - cy_j(1 - hx_{ij}) - vx_{ij} \quad (4a)$$

$$f_{Fj} = 1 - cy_j(1 - hx_j) - vx_j \quad (4b)$$

$$f_F = 1 - cy(1 - hx) - vx \quad (4c)$$

where x_{ij} is the ability of individual i in patch j to resist males (and x_j and x are the average levels of resistance in patch j and the whole population, respectively), and h is the efficiency of a female to resist the costs of male harm. The harm to a female is given by c and v is the cost of resisting males. A full description of all parameters is given in Table 1. Following the life cycle described earlier, I write the fitness of a focal male i in patch j as:

$$w_{Mij} = \frac{f_{Mi}}{f_{Mj}} f_{Fj} \left(\frac{(1 - \bar{m})}{(1 - \bar{m})f_{Fj} + \bar{m}f_F} + \frac{\bar{m}}{f_F} \right) \quad (5)$$

The average gain from matings of a focal male is f_{Mij} , and the average gain from matings of all males within the patch is f_{Mj} . Males compete within the patch for females, and thus the mating success of a focal male will be

Table 1 Parameters used in the model.

Parameter	Description
y_{ij}	Investment in harm of individual i in patch j
y_j	Average level of harm in patch j
y	Average level of harm in whole population
x_{ij}	Investment in resistance of individual i in patch j
x_j	Average level of resistance in patch j
x	Average level of resistance across whole population
g_{ij}	Genotypic value of an individual at the locus for male harassment
a_{ij}	Genotypic value of an individual at the locus for female resistance
b	Benefit to a male from harming
u	Cost to a male from harm
c	Cost to a female from male harm
v	Cost to a female from investing in resistance
s	Efficiency of female resistance to reduce the benefit to males from harming
h	Efficiency of female resistance in reducing the costs of male harm
r	Relatedness between two individuals in a patch
m_F	Migration probability of a female
m_M	Migration probability of a male
n_F	Number of female breeders in a patch ($n_F = n_M = n$ in the case of even sex ratio)
n_M	Number of male breeders in a patch ($n_M = n_F = n$ in the case of even sex ratio)
n	Number of breeding adults of a given sex within a patch

f_{Mij}/f_{Mj} . As I assume that there are a sufficiently large number of matings, there will be f_{Fj} offspring produced from all females in the patch. This is conceptually similar to models of the tragedy of the commons (e.g. Hardin, 1968; Frank, 1995), where competition (here f_{Mij}/f_{Mj}) depletes the resources available to all members of the group (here given by f_{Fj}) and highlights the analogy between sexual conflict and the tragedy of the commons (Rankin & Kokko, 2006; Rankin *et al.*, 2007). These offspring then disperse to other patches to compete for breeding positions. As I assume an even primary sex ratio, the average dispersal of offspring is $\bar{m} = (m_F + m_M)/2$. Offspring stay in the patch with a probability $1 - \bar{m}$, in which case they will compete for breeding spots with other individuals which stay in the patch (given by $(1 - \bar{m})f_{Fj}$), and with individuals that immigrate from elsewhere (given by $\bar{m}f_F$). If a given individual disperses (with probability \bar{m}), then they will compete for breeding spots with individuals in the new patch (given by f_F).

Using similar notation as eqn (5), but using the subscript F to denote females, the fitness of a focal female is:

$$w_{Fij} = f_{Fij} \left(\frac{(1 - \bar{m})}{(1 - \bar{m})f_{Fj} + \bar{m}f_F} + \frac{\bar{m}}{f_F} \right) \quad (6)$$

The logic of eqn (6) is the same as for eqn (5), only here the number of offspring a female produces depends on the fecundity f_{Fij} of the focal female. As mating takes place within a patch, the average fitness of females within a patch w_{Fj} is equal to the average fitness of males within a patch w_{Mj} .

As the genes for both x and y are carried in both males and females, the fitness of a given gene will depend on the fitness of its male and female carriers. Because males and females contribute equally to offspring, the fitness of a focal individual is $w_{ij} = 1/2w_{Mij} + 1/2w_{Fij}$ (the 1/2 reflects the class reproductive values of males and females – Taylor & Frank, 1996; Taylor *et al.*, 2007), and the selection gradient of a focal gene z_{ij} (where z refers to the genotypic value of either y or x) is:

$$\frac{dw_{ij}}{dz_{ij}} = \frac{1}{2} \frac{\partial w_{Mij}}{\partial z_{ij}} + \frac{1}{2} \frac{\partial w_{Fij}}{\partial z_{ij}} \quad (7)$$

The change in the trait owing to selection depends on the fitness of both sexes, not just the fitness of the sex in which it is expressed, and will also be influenced by genetic correlations within a patch (Frank, 1998). Following the chain rule, the selection gradient for the male harassment trait y is:

$$\frac{dw_{ij}}{dg_{ij}} = \frac{1}{2} \frac{\partial w_{Mij}}{\partial y_{ij}} \frac{dy_{Mij}}{dg_{Mij}} + \frac{1}{2} \frac{\partial w_{Mij}}{\partial y_j} \frac{dy_{Mj}}{dg_{Mij}} + \frac{1}{2} \frac{\partial w_{Fij}}{\partial y_{ij}} \frac{dy_{Mij}}{dg_{Fij}} + \frac{1}{2} \frac{\partial w_{Fij}}{\partial y_j} \frac{dy_{Mj}}{dg_{Fij}} \quad (8)$$

where g_{ij} represents the genotypic value of the male harassment trait y in a focal individual, and the subscripts

M and F denote whether the trait is carried by males or females, respectively. The selection gradient for female resistance x is calculated in a similar way and is:

$$\frac{dw_{ij}}{da_{ij}} = \frac{1}{2} \frac{\partial w_{Fij}}{\partial x_{ij}} \frac{dx_{Fij}}{da_{Fij}} + \frac{1}{2} \frac{\partial w_{Fij}}{\partial x_j} \frac{dx_{Fj}}{da_{Fij}} + \frac{1}{2} \frac{\partial w_{Mij}}{\partial x_{ij}} \frac{dx_{Fij}}{da_{Mij}} + \frac{1}{2} \frac{\partial w_{Mij}}{\partial x_j} \frac{dx_{Fj}}{da_{Mij}} \quad (9)$$

where a_{ij} refers to the genotypic value of the female resistance trait in a focal individual. In both eqns (8) and

thus for male harm to increase from rare, in the absence of any genetic structure, there must only be direct benefits to the male. This means that the benefit b gained from an increased access to females has to be greater than the cost u of investing in harm weighted by the ability of female resistance to reduce the benefit of male harassment, $1 - sx$. In the absence of relatedness, the evolution of harm does not depend on the magnitude of harm c inflicted upon females. The condition under which male harm will invade in the absence of female resistance (i.e. when $x = 0$) is:

$$\underbrace{b - u}_{\text{Benefit to male (actor)}} > \underbrace{c}_{\text{Cost to female (recipient)}} \underbrace{\frac{(r_{mm} + r_{fm})}{2} (4 - m_F - m_M)(m_F + m_M)}_{\text{Effective relatedness}} \quad (12)$$

(9), we have a term that describes the regression of an individual's genotypic value on the respective phenotype, which we can set to unity (i.e. $dy_{Mij}/dg_{Mij} = dy_{Mij}/dx_{Fij} = dx_{Fij}/da_{Fij} = dx_{Fij}/da_{Mij} = 1$).

Eqs (8) and (9) also contain terms referring to the sex-specific regression of the neighbourhood phenotype against the phenotype of the focal individual. We can write these as $dy_{Mj}/dg_{Mij} = dx_{Mj}/da_{Mij} = r_{mm}$ (the relatedness of a male to a random male in the patch) and $dy_{Fj}/dg_{Fij} = dx_{Fj}/da_{Fij} = r_{ff}$ (the relatedness of a female to a random female on the patch, and of a female to a random male on the patch, can be written as $r_{fm} = dy_{Fj}/dg_{Mij} = dx_{Fj}/da_{Mij} = dy_{Mj}/dg_{Mij} = dx_{Mj}/da_{Fij} = r_{fm}$).

From eqns (8) and (9), it can be seen that the evolution of x and y depends on their effects both within the respective sex and between the sexes. The criterion for the trait to evolve from rare (i.e. when $z_{ij} \rightarrow 0$) is:

$$\left. \frac{dw}{dz_{ij}} \right|_{z_{ij}=z} > 0 \quad (10)$$

Evolution of harm

From the fitness functions described earlier, and looking at the selection gradient defined in eqns (8) and (9), the condition for y to increase from rare (i.e. when $y_{ij} = y_j = y = 0$) when resistance does not evolve (and thus $x_{ij} = x_j = x$) is:

$$\underbrace{b(1 - sx) - u}_{\text{Benefit to male (actor)}} > \underbrace{\frac{c(1 - hx)}{(1 - vx)}}_{\text{Cost to female (recipient)}} \underbrace{\frac{(r_{mm} + r_{fm})}{2} (4 - m_F - m_M)(m_F + m_M)}_{\text{Effective relatedness}} \quad (11)$$

If $r_{mm} = r_{fm} = 0$, or if $m_F = m_M = 0$, the right-hand side is equal to zero, and we are left with $b > u/(1 - sx)$, and

This inequality shows that increasing overall relatedness between adults will disfavour the evolution of male harm. This is attributed to the effect on harming on a male's inclusive fitness, as given by $(r_{mm} + r_{fm})/2$, both through harming females and through the impact of harming on the fitness of related mates. Although increased relatedness r_{mm} between males disfavors harm, it also increases relatedness between competitors. The term on the right-hand side of inequality (12) can be seen as the 'effective' relatedness, measured between two individuals in a patch with respect to the economic neighbourhood (Queller, 1994a). This takes into account the scale of competition between individuals in the population in a patch. Here, males compete locally with other males for mates but then produce offspring that compete either locally (if they do not disperse) or globally (if they do disperse). If migration is zero (i.e. $m_F = 0$ and $m_M = 0$), competition between offspring for breeding positions will always take place within a patch, and the 'effective relatedness' term becomes zero, meaning that there is no inclusive fitness effect on the evolution of male harassment. This highlights the need to consider the scale of competition not just between competitors (in this case the males) but with the recipients of a social behaviour (in this case the females).

Interestingly, inequality (12) shows that male altruism towards females can also evolve: if $u > b$ and $c < 0$, there is a net cost to males, whilst conferring a benefit $-c$ on

females. In such a case, males pay a cost to confer a benefit to a female, which is an altruistic act (Hamilton,

1964). This could be the case if males pay a cost to give females nuptial gifts.

Relatedness

Relatedness is calculated from the probability that two individuals on the same patch coalesce, which will depend on dispersal. Thus, limited dispersal has the joint effect of increasing relatedness between patch mates but also increasing competition among kin. Relatedness is calculated under the assumption of neutrality, meaning that a given male's investment in harm y or a female's investment in resistance x will not have a substantial influence on relatedness. With the life cycle described earlier and following Johnstone & Cant (2008) and Gardner (2010), the average relatedness between two offspring within a patch in generation $t + 1$ is:

$$r_{t+1} = \frac{1}{4} \left(\frac{1}{n_F} + \left(\frac{n_F - 1}{n_F} \right) (1 - m_F)^2 r_t \right) + \frac{1}{2} (1 - m_F)(1 - m_M) r_t + \frac{1}{4} \left(\frac{1}{n_M} + \left(\frac{n_M - 1}{n_M} \right) (1 - m_M)^2 r_t \right) \quad (13)$$

The probability that two offspring are both of a given sex is $1/4$, whereas the probability that offspring are of different sexes is $1/2$. I assume that there are n_F adult males and n_M adult females which are able to mate within a patch. Assuming random mating within the patch, the probability that two offspring share the same mother is $1/n_F$, whereas the probability that they share

tions (i.e. harming or resistance) take place between adults at mating, we must measure relatedness between adults (Johnstone & Cant, 2008). These relatedness coefficients will be based on r (the relatedness between juveniles, as given by eqn (14) but will also depend on whether the respective adults stayed on their patch (and hence be determined by m_M and m_F). The whole-group relatedness between two adult males is:

$$r_{mm} = 1/n_M + (n_M - 1)/n_M(1 - m_M)^2 r$$

where $1/n_M$ is the relatedness of a male to himself and $(n_M - 1)/n_M(1 - m_M)^2 r$ is the relatedness of a male to other males in the group. The $(1 - m_M)^2$ takes into account the probability that neither male dispersed from the patch before mating (Johnstone & Cant, 2008). The whole-group relatedness of two adult females is calculated in a similar way and is:

$$r_{ff} = 1/n_F + (n_F - 1)/n_F(1 - m_F)^2 r.$$

where $1/n_F$ is the relatedness of a female to herself and $(n_F - 1)/n_F(1 - m_F)^2 r$ is the relatedness of a female to other members of the group. The relatedness between an adult male and an adult female in the patch is given by:

$$r_{fm} = (1 - m_F)(1 - m_M)r,$$

where $(1 - m_F)$ is the probability that the respective female did not disperse and $(1 - m_M)$ is the probability that the respective male did not disperse. Putting this into inequality (12) gives us:

$b - u >$

$$c \frac{(4 - m_F - m_M)(m_F + m_M)(M_F^2(n_F - 1) - m_M(2 + n_F + m_M(n_M - 1) - 3n_M) - 2(n_F + n_M) + m_F(2 - n_F(3 - m_M) + n_M(1 - m_M)))}{4(n_M - 1)(m_F(2 - m_F) - m_M(2 - m_M) - n_F(4 - m_F - m_M)(m_F + m_M))} \quad (15)$$

the same father is $1/n_M$. Solving eqn (13), the equilibrium average relatedness between two offspring within a patch is:

$$r = \frac{n_F + n_M}{(1 - m_F)^2 n_F + (1 - m_M)^2 n_M + (4 - m_F - m_M)(m_F + m_M)n_F n_M} \quad (14)$$

As the relatedness terms given in inequalities (11) and (12) are measured between adults, we must therefore calculate r_{mm} (the relatedness between two adult males), r_{fm} (the relatedness between an adult male and an adult female) and r_{ff} (the relatedness between two adult females). These are 'whole-group' relatedness terms and consider the relatedness of an individual with another, randomly chosen, individual in the patch (which can include the focal individual). The value of relatedness given by eqn (14) is the average relatedness between two juveniles within a patch. Because interac-

This condition is plotted in Fig. 1 for an even operational sex ratio (i.e. $n_F = n_M = n$). It can be seen that increased male dispersal favours the evolution of male harassment (Fig. 1b), whereas increased female dispersal disfavors the evolution of male harassment (Fig. 1a). If the migration rate is equal (i.e. $m_F = m_M = m$), inequality (15) becomes:

$$b - u > c \frac{(1 - m)^2(n_M - n_F) + 2n_F}{2n_F(n_M - 1)} \quad (16)$$

which, under an even operational sex ratio (i.e. if we set $n_M = n_F = n$), simplifies to:

$$b - u > \frac{c}{n - 1}$$

where n is the number of individuals of a given sex. This represents the direct effect of a male on himself, through harming females within the patch: if $n = 1$ in the

aforementioned inequality, or if $n_M = 1$ in inequality (16) (i.e. there is only one male in the patch) male harassment will not evolve as the lone male will be harming himself. As the number of males increases, harassment is increasingly favoured as the direct costs, through $c/(n-1)$, decrease. This inequality is shown by the dotted line in Fig. 1. Inequality (16) shows that, under even migration of males and females, the evolution of male harm is disfavoured if adults do not disperse, whereas greater dispersal favours harm as this reduces the impact a male has on himself, and his kin, through harassing females. As dispersal takes place before mating, a male that does not disperse to a new patch will be more related to their patch mates and will therefore have an inclusive fitness advantage from abstaining from harassment.

Allowing male harm y to evolve to equilibrium, the evolutionarily stable level of harm (i.e. the ESS) is:

$$y^* = \frac{4(b-u)(1-r_{mm}) - c(r_{mm} + r_{fm})(m_F + m_M)(4 - m_F - m_M)}{(b-u)c(4(1-r_{mm}) + (r_{mm} + r_{fm})(4 - m_F - m_M))(m_F + m_M)} \quad (17)$$

It can be seen that higher values of b (and lower values of u) increase male harm, whereas, under higher relatedness, low female costs will reduce male harm. Relatedness between adults, r_{mm} and r_{mf} , is calculated as before. Figure 2a plots ESS values of male harm as a function of female migration for different values of male migration, showing that higher female dispersal decreases the level of male harm. The dotted line in Fig. 2a,b also shows the case where dispersal is equal for both sexes, meaning that dispersal does not affect the ESS. Figure 2b plots the ESS values of male harm as a function of male migration, showing that increased male dispersal increases the level of male harm. The results of Figs 1 and 2 are attributed to the fact that males compete locally within a patch for females: the more males disperse, the less related males will be to other males (and thus to their potential competitors), and so males gain a benefit from harming females and outcompeting unrelated males under higher male dispersal (Figs 1a and 2b).

Evolution of female resistance

The evolution of female resistance to male harm can be investigated using the method described earlier. Assuming that female resistance is rare (and hence $x \rightarrow 0$), the condition for a rare allele conferring resistance to invade is:

$$hcy \geq v \quad (18)$$

Here, hcy is the total harm that a given female will face from males, and v is the cost of investing in resistance. Interestingly, there are no inclusive fitness effects to a female from investing in resistance of males. Female resistance will only invade if the direct benefit hcy of resisting males is greater than the cost v of investing in resistance.

The coevolution of male harm and female resistance can result in an arms race between males and females and thus drive cycling between strategies. Figure 3 shows the coevolutionary dynamics of male harm y and female resistance x . The dynamics result in coevolutionary limit cycles between male harm and female resistance and occur independently of whether a given male and female are related (results not shown). This is an intuitive result: when $s > 0$ and $h > 0$, an increase in male harm will lead to an increase in female resistance, which in turn reduces the benefit that males gain from harm and selects for lower levels of male harm.

Discussion

The model presented here shows that the evolution male harassment of females depends not just on the direct costs and benefits from extra matings, but also from the indirect costs and benefits of sexual conflict. This puts sexual conflict over mating in the context of a wider body of work on social evolution (e.g. Hamilton, 1964; Queller, 1992; Lehmann & Keller, 2006) and highlights the role of inclusive fitness costs and benefits in the evolution of male harassment. As such, genetic relatedness between males and females can help resolve sexual conflict: relatedness prevents the evolution of male harm if the harm c that males inflict on females is less than the net benefit $b - u$ (where b is the benefit and u is the cost to males of harming) to males. This means that the cost to females, weighted by the 'effective relatedness', must be larger than the benefit gained by males for kin selection to disfavour harm. In a number of species, males inflict substantial costs on females as a by-product of competition with other males, and it is likely that the inadvertent damage inflicted upon females will, in many cases, be greater than the gain to males from extra matings (e.g. Morrow *et al.*, 2003; Edvardsson & Tregenza, 2005). In bed bugs, *Cimex lectularius*, for example, males pierce the abdomen of females to mate (Stutt & Siva-Jothy, 2001; Morrow & Arnqvist, 2003; Reinhardt *et al.*, 2003), and in the seed beetle, *Callosobruchus maculatus* spikes on the male genitalia have been shown to reduce female survival (Crudginton & Siva-Jothy, 2000; Arnqvist *et al.*, 2005; Edvardsson & Tregenza, 2005).

In the model, genetic relatedness arises through shared descent in combination with limited migration, low patch sizes and local mating skew (through the relative number of adult breeders n_F and n_M of either sex). Although increased migration of either sex will decrease relatedness among adults, sex-biased dispersal will affect the scale of competition in different ways. The results show that differential migration of the sexes influence the evolution of male harm (Figs 1 and 2). Increased female dispersal disfavors the evolution of male harm (Fig. 1a), whereas increased male dispersal favours male harm. To understand this, it is important to consider that limited dispersal tends to increase relatedness but, at the same

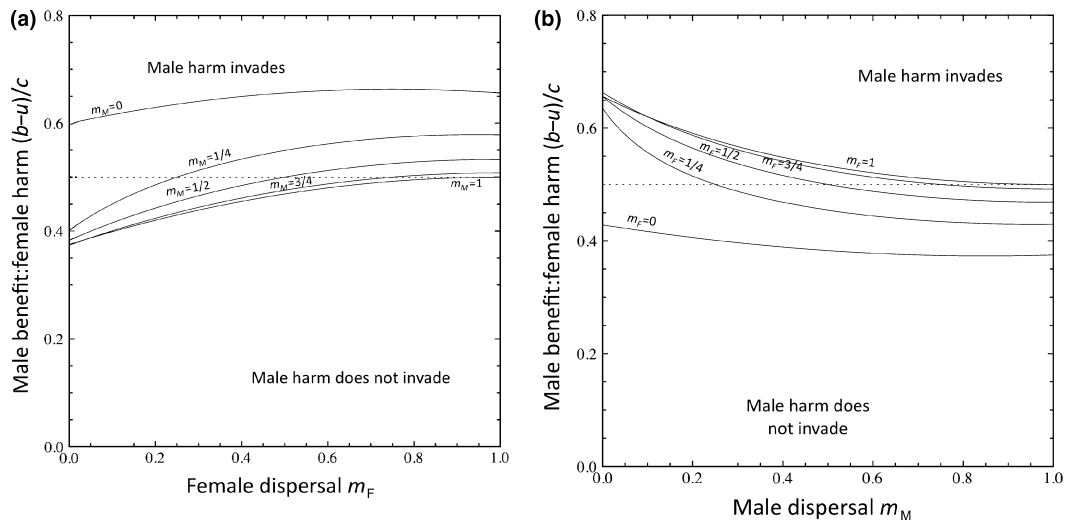


Fig. 1 Invasion threshold for male harm y in the absence of female resistance (i.e. $x = 0$) as (a) a function of female migration probability m_F and (b) as a function of male migration probability m_M . The invasion threshold is shown for an even number of adult breeders ($n_F = n_M = 3$). The y-axis represents $(b - u)/c$, the ratio of net male benefit $b - u$ to female harm c for a range of migration probabilities. Above the respective lines harm can invade. The dotted line is the invasion threshold when dispersal is even and not sex-biased (i.e. $m_F = m_M = m$). In the absence of relatedness, harm will evolve as long as $b > u$ (i.e. in the region where the y-axis is positive).

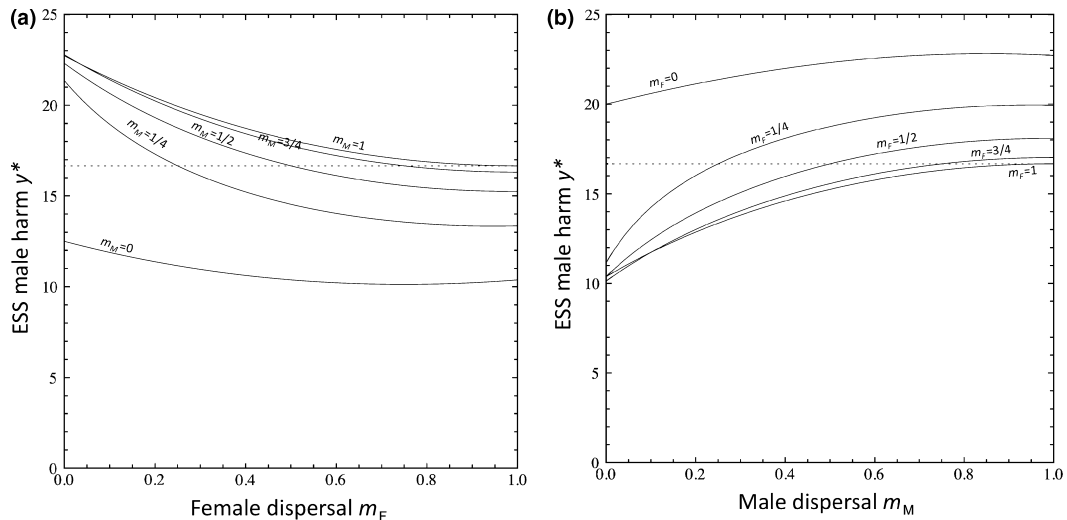


Fig. 2 ESS levels of male harm y^* as (a) a function of female migration probability m_F and (b) a function of male migration probability m_M in the absence of female resistance (i.e. $x = 0$). The ESS is shown for an even number of adult breeders ($n_F = n_M = 3$). Other parameters used are $b = 0.05$, $u = 0.03$, $c = 0.02$. Lines are plotted for a range of male migration probabilities m_M (in Fig. 2a) and m_F (in Fig. 2b). The dotted line is the invasion threshold when dispersal is even and not sex-biased (i.e. $m_F = m_M = m$).

time, also increases competition among kin by making competition more local (West *et al.*, 2001, 2002b). In the case of male harm, limited male dispersal disfavors male harm (Fig. 1b), as males that remain are now competing with kin for mates, which reduces the incentive to invest in competition. In contrast, increased male dispersal decreases competition with related males for mates and decreases relatedness between a male and his mate.

In the case of female resistance, there is no inclusive fitness effect to resisting male harm, and female resistance therefore only depends on the direct costs and benefits to a female from resisting male harm.

The results of the model highlight the importance of the mating system in determining the outcome of sexual conflict through the number of male breeders n_M and female breeders n_F . These two parameters describe the

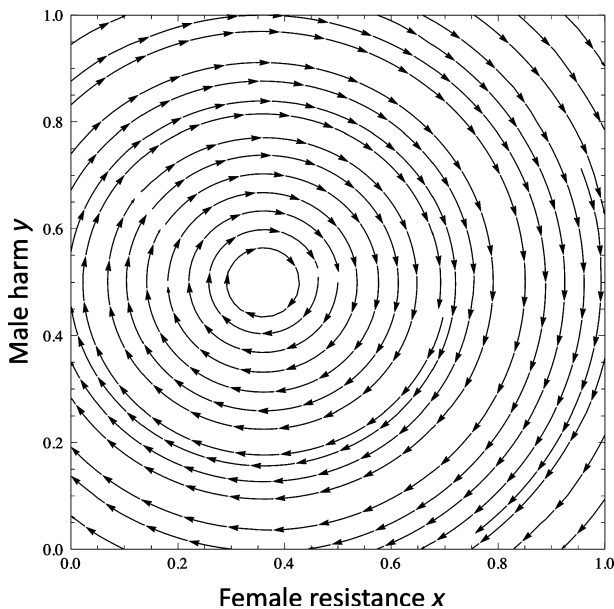


Fig. 3 Cyclical coevolutionary dynamics of male harm y and female resistance x . The dynamics are shown for an even number of adult breeders ($n_F = n_M = 3$). Other parameters used are $b = 0.05$, $u = 0.03$, $c = 0.02$, $v = 0.01$, $s = 0.75$, $h = 1$, $m_M = 0.25$, $m_F = 0.25$.

mating skew within a patch: for example if $n_M < n_F$ mating is skewed such that fewer males father offspring in the patch. It is well established that the mating system influences the intensity of sexual conflict: if males mate only with a single female, they will be selected to refrain from harm, and to increase the number of offspring their mates produce (Rice, 2000; Martin & Hosken, 2003; Wigby & Chapman, 2004; Hosken *et al.*, 2009). Similarly, it has been argued that species with a 'last-male' mating advantage (as apposed to a 'first-male' mating advantage) will evolve greater levels of toxins in the sperm, to manipulate female re-mating (Johnstone & Keller, 2000), and thus the mating system will strongly influence the outcome of sexual conflict. However, here I introduce an additional effect of the mating system on sexual conflict, namely relatedness between partners. If there is no reproductive skew and the number of adult breeders in a patch is equal (i.e. $n_M = n_F$), relatedness between partners will depend on both the migration rate (i.e. m_M and m_F) and the number reproductive males and females in the patch (i.e. n_M and n_F). However, if only a few males in the patch father most of the offspring, this can increase relatedness even if the patch size is very large and will thus inhibit the evolution of male harm.

One area where the concept of population structure has been addressed in the study of sexual selection is that of inbreeding and mate choice (Parker, 1979; Waser *et al.*, 1986; Lehmann & Perrin, 2003; Kokko & Ots, 2006). Mating with kin can increase an individual's inclusive fitness as there will be more copies of their genes in the next generation (Parker, 1979; Kokko & Ots,

2006). However, mating with one's relatives will additionally increase inbreeding depression, which will reduce fitness. This would favour mate choice for inbreeding avoidance, thus reducing the level of inbreeding depression. In the current model, all individuals, regardless of their phenotype, experience the same level of inbreeding (i.e. males that harm their mates experience the same level of inbreeding as those that do not harm their mates). In this case, inbreeding depression would not influence the evolution of male harm as there is no inbreeding avoidance between mates. The model presented here assumes no choice or conditional behaviour, and introducing inbreeding avoidance into the model, such that individuals preferentially mated with nonkin, would decrease relatedness within a patch and therefore increase the potential for sexual conflict over mating. Similarly, high inbreeding should favour the evolution of higher migration rates to avoid the deleterious effects of inbreeding depression, which could in turn reduce relatedness between mates, and favour sexual conflict.

Females have been shown to disperse as a result of harmful encounters with males (Darden & Croft, 2008). A recent study by Eldakar *et al.* (2009) demonstrated that aggressive males achieved more matings when individuals could not disperse between pools, whereas they fared worse when dispersal was allowed. This was owing to females dispersing to counter the costs of male harm, which resulted in females aggregating in patches with less aggressive males, conferring additional benefits to less aggressive males and dispersing females. It is thus likely that male harm and sex-biased dispersal will co-evolve, with females dispersing to mitigate the costs of harm from males. In guppies, for example, females disperse to un-preferred habitats to avoid harmful males (Darden & Croft, 2008). Although not specifically modelled here, such a system has the potential for interesting coevolutionary dynamics between female resistance, male harm and dispersal which could help understand the conditions under which female dispersal evolves as a form of resistance to harmful males. The importance of sex-biased dispersal in driving sexual conflict in the model here has implications with regard to which species exhibit stronger levels of male harassment: more female dispersal generally disfavors higher levels of male harm (Figs 1 and 2), whereas more male dispersal generally favours male harm (Figs 1 and 2). As mammals generally exhibit male-biased dispersal and birds generally exhibit female-biased dispersal (Greenwood, 1980), we should thus expect stronger adaptations towards male harming of females in mammals compared with birds (e.g. Úbeda & Gardner, in press).

The model here highlights the relationship between different biological conflicts. There are strong analogies between the evolution of cooperation, the evolution of virulence and sex ratio evolution (Frank, 1994; West & Buckling, 2003). All three have strong groundings in kin

selection theory (Frank, 1994). Sexual selection and conflict over mating has largely been studied separately from other areas of social evolution (e.g. Boomsma, 2007) despite the conflicts involved having many similarities (Chapman, 2006; Rankin *et al.*, 2007). Male harm of females has been argued to be analogous to a tragedy of the commons: by competing with each other over a resource (females), males inadvertently reduce the resource over which they are competing (Rankin & Kokko, 2006). An important factor influencing harm is the scale of competition (Frank, 1998; Gardner & West, 2004; West *et al.*, 2006). In the model, the scale of competition is different between males (which compete locally for mates) and offspring (which compete locally if they do not disperse), and this is dependent on sex-biased dispersal within the model. However, under even dispersal (i.e. $m_F = m_M$) and even number of breeders of each sex (i.e. $n_F = n_M$), the evolution male harm depends strongly on the number of adults n of a given sex. However, in this case, the effect is solely attributed to the direct effect of a given male on his direct fitness, from reducing the fecundity of his mates.

Many interactions occur between related individuals, and it is likely that mating may take place between related individuals. In many insects, such as wasps (Godfray & Cook, 1997; Molbo *et al.*, 2004) or bark beetles (Peer & Taborsky, 2005), for example, mating occurs on a local scale, which increases relatedness between individuals. However, this is often offset by competition with kin (West *et al.*, 2001, 2002a). In the current model, kin competition is reduced if dispersal is sex-biased: male dispersal reduces competition for mates between related males and so favours male harassment. Sex-biased dispersal can help maintain genetic relatedness, whereas at the same time can reduce kin competition. This confirms what is well known in social evolution: it is not just relatedness, but also the scale of competition with kin, that selects for more cooperative behaviours (Taylor, 1992; Queller, 1994a; Frank, 1998; West *et al.*, 2001, 2002b).

The model here highlights the potential role of population structure (through genetic relatedness) in the evolution of sexual conflict over mating. Few studies have looked at the influence of population structure on the evolution of male harm (but see Eldakar *et al.*, 2009). However, there are many systems that may lend themselves to examining the relative effects of relatedness on the evolution of sexual conflict. For example, in many species of fig wasps it is known that there are high levels of relatedness between individuals within a fig, yet there can still be high levels of male–male competition for females (Hamilton, 1979; Cook *et al.*, 1997; Bean & Cook, 2001; West *et al.*, 2001). The polyandrous spider *Stegodyphus lineatus* is a cooperative breeder, shows high levels of inbreeding and yet still shows high levels of sexual conflict over mating (Maklakov & Lubin, 2004, 2006; Bilde *et al.*, 2005; Maklakov *et al.*, 2006). This may

provide for a useful system in which to disentangle the consequences of local relatedness for cooperation whilst still allowing for high levels of sexual conflict over mating. The model here would predict that such a system would arise through sex-biased dispersal, which would allow for both cooperation within members of the same sex and conflict over mating between the sexes. Few studies have considered the influence of relatedness on the outcome of sexual conflict (Queller, 1994b; Chapman, 2006; Bourke, 2009). The model presented here highlights the role of kin selection in reducing male harassment of females. Gaining a better understanding of the way in which sexual conflict can be influenced through kin selection is important in understanding the links between different forms of social behaviour.

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