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Original Article

Condition-transfer maternal effects modulate inter-locus sexual conflict

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Strong sexual selection frequently favors males that increase their reproductive success by harming females, with potentially negative consequences for natural populations. Understanding what factors modulate conflict between the sexes is hence critical to understand both the evolution of male and female phenotypes and the viability of populations in the wild. Here, we model the evolution of male harm while incorporating male-induced maternal effects on offspring quality. We show that because male harm can induce condition-transfer maternal effects that reduce the quality of a harming male's own offspring, maternal effects can partially align male and female evolutionary interests and significantly curb the evolution of male harm. These effects are independent of relatedness, the scale of competition, mating system, and whether male harm comes before (i.e., harassment) and/or during/after (i.e., traumatic inseminations or toxic ejaculates) mating and are particularly salient when maternal effects influence offspring ability to inflict (sons) or resist (daughters) harm. Our results underscore the potential importance of considering maternal effects to unravel the evolution of sexual conflict.

Key words: **evolution, maternal effects, population growth, population viability, sexual conflict, sexual selection, sexually antagonistic coevolution.**

INTRODUCTION

Strong sexual selection frequently leads to scenarios where male and female evolutionary interests misalign—known in the literature as sexual conflict (Andersson 1994). This, in turn, can trigger sexually antagonistic coevolution (Parker 1979; Holland and Rice 1998), where sexual strategies in one sex evolve to counteract those of the opposite sex. Sexually antagonistic coevolution leads to inter-locus sexual conflict (i.e., when traits under sexually antagonistic selection depend on different genetic loci in males and females, leading to conflicting evolutionary interest between the sexes) or intra-locus sexual conflict (i.e., when these traits share the same underlying loci in both sexes); both currently recognized as key evolutionary processes shaping male and female adaptations and life-history traits (Arnqvist and Rowe 2005). At a population level, inter-locus sexual conflict frequently leads to adaptations in males that harm females (Chapman et al. 1995; Rice 1996) and reduce population growth, in a process akin to "the tragedy of the commons" (i.e., where selection for selfish competition among males reduces a common finite resource that decreases population growth; Rankin et al. 2011). From male harassment and coercion (Han and Jablonski 2010; Perry and Rowe 2015) to toxic ejaculates (Wigby and Chapman 2005) and traumatic insemination (Crudgington and Siva-Jothy 2000; Reinhardt et al. 2015), harmful male adaptations are both widespread across the tree of life and extraordinarily diverse in the level of harm they inflict on females, and thus in their potential consequences for population viability. A current priority in evolutionary biology is hence to identify factors that modulate sexual conflict and explain the diversity of male harm adaptations observed in nature. For example, recent research shows that, by aligning the interests of males and females, kin selection has the potential to modulate the evolution of male harm to females (Rankin 2011; Carazo et al. 2014; Faria et al. 2015, 2020; Lukasiewicz et al. 2017).

Studies seeking to explain the evolution of antagonistic or harmful male adaptations have focused on direct costs (to females) and benefits (to males), as well as the potential indirect genetic benefits to females through their male offspring (Cameron et al. 2003; Pizzari and Snook 2003; Maklakov et al. 2005; Parker 2006;

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Garcia-Gonzalez and Simmons 2010; Brennan and Prum 2012). On the one hand, manipulative or harmful traits allow males to sire a greater proportion of a female's offspring (e.g., by decreasing female re-mating) at the expense of that female's overall fecundity. On the other hand, females may obtain indirect genetic benefits by mating with particularly harmful or manipulative males because their own male offspring will inherit these genes, albeit theoretical and empirical evidence shows indirect genetic benefits are generally weaker than direct benefits (Cameron et al. 2003; Pizzari and Snook 2003; Parker 2006).

Maternal effects can drastically modulate offspring quality (Mousseau and Fox 1998) and are largely mediated by maternal condition (i.e., condition-transfer maternal effects; Rossiter 1996; Qvarnström and Price 2001; Saino et al. 2005; Bonduriansky and Crean 2018). Male harm can severely impact female condition (Arnqvist and Rowe 2005) and, although its transgenerational effects have only been studied in a handful of species, it can induce maternal effects that reduce the quality of a male's own offspring (Tregenza et al. 2003; Brommer et al. 2012; Gasparini et al. 2012; Dowling et al. 2014; Carazo et al. 2015; Zajitschek et al. 2018). For example, female guppies (*Poecilia reticulata*) exposed to greater harassment produce smaller daughters and sons with shorter gonopodia (Gasparini et al. 2012), whereby female size is related to fecundity and large gonopodia are favored in both inter- and intra-sexual selection in this species (Brooks and Caithness 1995; Evans and Pilastro 2011; Gasparini et al. 2012). Furthermore, previous studies have already suggested that maternal effects may have the potential to modulate sexual conflict effects on female offspring (Foerster et al. 2007; Lund-Hansen et al. 2021).

In this study, we develop a mathematical model to formally examine whether male harm can induce maternal effects that reduce the quality of a harming male's own offspring and, in doing so, bring together male and female interests and abate sexual conflict. In particular, we use a personal-fitness (i.e., neighbor-modulated fitness) kin-selection approach (Hamilton 1964a,b; Taylor and Frank 1996) that incorporates the effects of kin selection, an important factor in the evolution of male harm to females (Faria et al. 2020). Given the potential for maternal effects to bring together the evolutionary interests of females and males, we aim to analyze if such effect happens in conjunction or independently of kin selection. We analyze three scenarios: 1) the absence of maternal effects on offspring quality, 2) the presence of maternal effects on offspring fecundity (females) and competitiveness (males), and 3) the presence of maternal effects on offspring's ability to inflict (males) and resist (females) harm (i.e., sexual selection quality).

METHODS

Model without maternal effects

We use a neighbor-modulated fitness approach—an optimization function to calculate the optimal level of harm (see Hamilton 1964a,b; Taylor and Frank 1996). We consider an infinite population divided into social groups (Wright 1931) containing n_f females and n_m males. We follow the approach developed by Faria et al. (2020). Specifically, males invest in a harming trait that increases their personal reproductive success relative to other males but reduces the overall fecundity (number of offspring) of the females in the social group. Each male's reproductive success is directly proportional to his competitiveness for mating success and inversely proportional to the average competitiveness for mating success of the males in his social group (see below and Supplementary Material for mathematical formulation). Male harm happens within "social groups" because this simulates what typically happens in nature, whereby males compete for female access within mating patches. This includes both proper social groups and, more commonly, temporal aggregations (e.g., leks, local mating aggregations around resources, etc.). In addition, this approach allows us to control for kin and demographic effects, which have been shown to be important modulators of male harm (Faria et al. 2020). We consider two different types of populations differing in their mating system: 1) monogamic females, where females mate with only one male while males compete to gain access to the females (Figure 1), and 2) polygamic females, where all males mate with all females in the social group (Figure 1). We acknowledge this is a simplification, but our focus was to examine the two extreme contexts in which the two types of harm modeled (i.e., prior or during/after mating) seem to be highly beneficial to males (i.e., harassing females when mating success is most important and inflicting mating harm when sperm competition is most important).

Accordingly, a focal female's fecundity $f_f(x',y) = 1 - k\,x' - (1-k)y$ is a function of the level of harm that the male she mates with inflicts (x') and of the average level of male harm males present in the social group (y), with k determining the degree to which harm comes during mating ($k = 1$) or before mating as a result of male competition to access females ($k = 0$). At one extreme ($k = 1$), harm comes exclusively from the male that mates with the female, as harm is linked to mating (as in traumatic insemination), and mating harm makes the female unavailable for further mating events. In other words, harm happens exclusively during mating, and such extreme traumatic insemination effectively makes females monogamous, such as is the case with genital ablation in some spiders (Mouginot et al. 2015). At the other extreme ($k = 0$), harm comes from all males in the social group, which aims to simulate male harm happening exclusively via the harassment of females during pre-copulatory male-male competition (i.e., irrespective of which male mates with the female). Importantly, in our model, we consider a continuum, such that a population may lie at any point between those two extremes. Our aim is to understand when one type of harm may be favored over the other, but we stress that harassment and traumatic insemination need not be traded-off between each other in nature. Note that, when considering a polygamic population, the variable k disappears because all males are mating with all females, and thus, all males harm females irrespective of whether this happens during or after mating (therefore, $f_f(y) = 1 - y$).

A focal male's competitiveness for mating success $f_m(x) = 1 + x$ is a function of the level of harm expressed by that focal male (x). His actual mating success depends on how much the other males in the social group invest into harm $f_m(y) = 1 + y$ and, therefore, the relative mating success of the focal male over the other males in the social group is $f_m(x)/\,f_m(y)$. After mating, each female produces a number of offspring proportional to her fecundity $f_f(x',y)$, with an even sex ratio. Adults then die, and juvenile females and males compete for reproductive resources, with a proportion a of this competition occurring locally with social group mates and a proportion $1 - a$ occurring globally with unrelated individuals (Figure 1). Thus, a takes into account all elements that contribute to determine the scale of competition, from local to global. In other words, a specifies the likelihood of a focal male juvenile competing with other local males in the patch for future breeding opportunities, which occurs when neither disperse to other patches (Faria et al. 2020). Finally, n_f females and n_m males survive at random within each social group to adulthood, returning the population to the

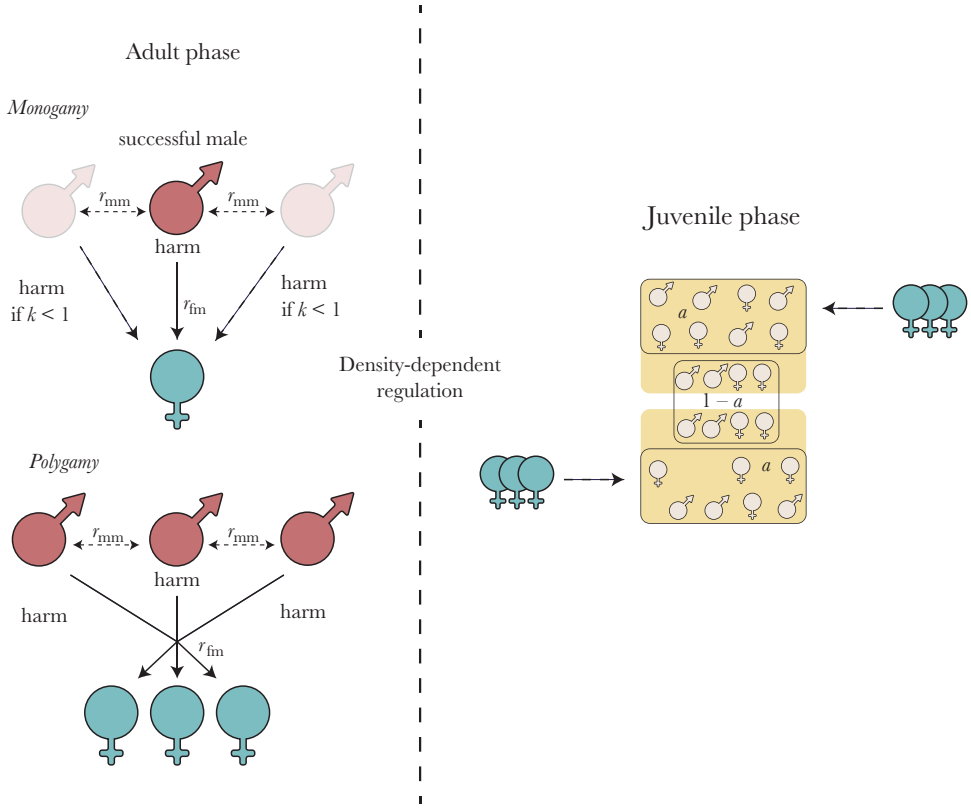

Figure 1

Graphical representation of the theoretical model. During the adult phase, and assuming monogamy, only one adult male is successful in mating with one adult female (that r_{mm} and r_{fm} represent male-male and female-male relatedness, respectively; k reflects the extent to which harm is inflicted during mating ($k = 1$) or before mating ($k = 0$) as a result of male-male competition for females). In this case, male harm to females depends on the value of k, with harm only coming from the male that mates if $k = 1$ and with non-mating males in the social group also harming females if $k < 1$. Assuming polygamy, all adult males mate with all adult females, with all males harming all females in the process. During the juvenile phase, females and males compete for reproductive opportunities. Competition occurs between local individuals in proportion to a, with competition occurring between local and non-local individuals in proportion to $1 - a$.

beginning of the lifecycle. Our model thus assumes competition for n_f and n_m reproductive spots (i.e., the number of females and males that compete successfully and reproduce; see Faria et al. 2015).

Model with maternal effects

As given in the section "Model without maternal effects" (Figure 1), we consider an infinite diploid population divided into social groups (Wright 1931) containing n_f females and n_m males following a similar life cycle. We now also assume that there are two types of individuals: low-quality individuals and high-quality individuals. High-quality individuals are assumed to be no different than the individuals present in the model without maternal effects. We consider two possible scenarios: 1) quality affects an individual's fecundity (females) and competitiveness (males) or 2) quality affects an individual's ability to inflict (males) and resist (females) harm. Thus, in our model, maternal effects affect F1 female and male quality differently, with low-quality individuals being produced in proportion to the harm that their mother received, which altogether impacts parental female and male fitness (see Supplementary Material for details).

Focusing on the first scenario: a focal low-quality female's fecundity is a function of the level of harm of the male that she mates with and of the average level of male harm present in the social group minus a cost s due to her low quality $f^{l}_{f}(x',y) = 1 - k\,x' - (1 - k)y - s$ (for a monogamic female) and $f^{l}_{f}(y) = 1 - y - s$ (for a polygamic female); a focal low-quality male's competitiveness for mating success is a function of the level of harm expressed by that focal male minus a cost s due to his low quality $f^{l}_{m}(x) = 1 + x - s$; a focal high-quality female's fecundity is a function of the level of harm of the male that she mates with and of the average level of male harm present in the social group $f^{h}_{f}(x',y) = 1 - k\,x' - (1 - k)y$ (for a monogamic female) and $f^{h}_{f}(y) = 1 - y$ (for a polygamic female); and a focal high-quality male's competitiveness for mating success is a function of the level of harm expressed by that focal male $f^{h}_{m}(x) = 1 + x$.

Focusing on the second scenario, a focal low-quality female's fecundity is a function of the level of harm of the male that she mates with and of the average level of male harm present in the social group multiplied by $1 + h$ due to her low quality $f^{l}_{f}(x',y) = 1 - (k\,x' + (1 - k)y)(1 + h)$ (for a monogamic female) and $f^{l}_{f}(y) = 1 - y(1 + h)$ (for a polygamic female); where h denotes the extra harm caused by reduced female resistance due to her low quality. A focal low-quality male's competitiveness for mating success is a function of the level of harm expressed by that focal male multiplied by $1 - t$ due to his low quality $f^{l}_{m}(x) = 1 + x(1 - t)$, where t denotes the reduction in harm caused by the male's low quality. A focal high-quality female's fecundity is a function of the level of harm of the male that she mates with and of the average level of

male harm present in the social group $f^{h}_{f}(x',y) = 1 - k\,x' - (1-k)y$ (for a monogamic female) and $f^{h}_{f}(y) = 1 - y$ (for a polygamic female). Lastly, a focal high-quality male's competitiveness for mating success is a function of the level of harm expressed by that focal male $f^{h}_{m}(x) = 1 + x$. Competition in the social group then follows the same logic described above in the section "Model without maternal effects" (Figure 1).

RESULTS

Model—Following Taylor-Frank approach (see Supplementary Material for details) and assuming that $n_f = n_m$ (i.e., the number of females and males are the same in each social group), the optimal fitness equations (optimum level of harm; see Supplementary Material for details) in a population where females are monogamic are:

$$\left(\frac{1}{1+z^*} - k\frac{1}{1-z^*}\right)(1-r_{mm}) - \frac{1}{1-z^*}(r_{fm}+r_{mm})(1-a) = 0, \quad (1)$$

for the model without maternal effects;

$$\left(\frac{1}{1+z^*-sz^*} - k\frac{1}{1-z^*-sz^*}\right)(1-r_{mm}) - \frac{1}{1-z^*-sz^*}(r_{fm}+r_{mm})(1-a) = 0, \quad (2)$$

for the model with maternal effects on fecundity (females) and competitiveness (males); and

$$\left(\frac{1-tz^*}{1+z^*(1-tz^*)} - k\frac{1+hz^*}{1-z^*(1+hz^*)}\right)(1-r_{mm}) - \frac{1+hz^*}{1-z^*(1+hz^*)}(r_{fm}+r_{mm})(1-a) = 0, \quad (3)$$

for the model with maternal effects on the ability to inflict (males) and resist harm (females), where: z^* is the optimal level of harm favored by natural selection; r_{mm} is the relatedness between males in a social group; and r_{fm} is the relatedness between females and males in a social group. Regardless of the model considered, the inclusive fitness interpretation is the same. Specifically, a male increases his mating success by investing into harming (first term). As k increases, harming is increasingly done during mating and this imposes a further cost on the focal male's mating success as it reduces the potential number of offspring that he has with a female (first term). Both are weighted by the relatedness between the focal male and local males, given that an increase in focal male's mating success leads to a corresponding loss of mating success by the other males. This translates into an inclusive fitness loss if the focal male is related to them $(1 - r_{mm})$. Harming also reduces the overall fecundity of local females, which also decreases the number of offspring produced by local females and males (second term). Such reduction in fecundity can lead to an inclusive fitness loss if the focal individual is related to both local females and males $(r_{fm} + r_{mm})$. Finally, such inclusive fitness loss is weighted by the scale of competition $(1 - a)$, that is, how much individuals compete with local social group mates for reproductive resources (Taylor 1992).

The conditions for harm to be favored in a polygamic population are essentially the same, with the exception that the term being multiplied by k disappears. Accordingly, the inclusive fitness interpretation is the same as above, except that the males do not pay a direct cost for harming the females. The optimal level of harm can now be obtained by solving equations (1–3) to z^*.

While the results are similar across the different models, there are relevant quantitative differences (Figures 2 and 3). Importantly, the harm benefits are smaller, and costs are higher, when maternal effects are present, and more so when maternal effects influence the ability of offspring to inflict (males) or resist (females) harm (Figures 2 and 3). This happens regardless of harm coming before (i.e., male harassment) and/or during (i.e., traumatic insemination) mating (Figure 2a), relatedness levels (Figures 2b,c and 3a,b), or polygamy (Figures 2 and 3). The exception is when local competition is high (Figures 2d and 3c). When local competition is high, maternal effects on fecundity reduce the level of harm more than maternal effects on sexual quality. Note that these results extrapolate generally to any processes that, like maternal effects, affect male/female offspring quality.

DISCUSSION

We found that maternal effects reduce the optimal level of male harm, especially when harm curtails offspring quality during sexual selection (Figures 2 and 3). The latter, however, can change with the scale of competition (i.e., as a approaches 1 and competition becomes increasingly local; Figures 2D and 3D), leading to maternal effects on fecundity reducing the level of harm more than maternal effects on sexual quality. The reason for such a difference between maternal effects on fecundity versus sexual quality is due to the former only reducing daughter fecundity, but not sons' chances of reproduction. In contrast, maternal effects on the sexual quality of sons seem particularly disruptive to a male's long-term fitness. As local competition increases, competition occurs between males of similar quality, thus reducing the importance of such effects and increasing harm to levels above those for maternal effects on fecundity. Regardless, maternal effects consistently reduce harm for different types of male harm (i.e., male harassment and traumatic insemination), mating systems, across different levels of relatedness, and levels of local competition (Figures 2 and 3). It is worth noting that, for simplicity, we focused on monogamous versus completely polygamous scenarios (i.e., we did not explore intermediate levels of polygamy), but our results were very robust across these two extreme scenarios, strongly suggesting that they can be generally extrapolated across mating systems. As previously shown, relatedness can shape the level of harm under each one of the different models (Figures 2B and 3A for male–male relatedness and Figure 2C and B for female–male relatedness), but our results also show that relatedness (and particularly so female–male relatedness; Figures 2C and 3B) modulates the degree to which maternal effects curtail harm as well as the relative importance of maternal effects on offspring fecundity versus sexual quality.

Differences in the optimal level of male harm across different populations are therefore not only predicted to reflect differences in relatedness and the scale of competition, leading to the kin selection effects previously described in the literature (Faria et al. 2020) but also in the biology of male harm and its impact on offspring quality. For example, differences in harm may arise due to intraspecific differences in local ecological conditions that may compromise female condition, making it more vulnerable to male harm (e.g., food availability), or due to inter-specific differences in the importance of maternal effects across taxa. Generally, our model predicts that sexual conflict via male harm will be lower whenever harm induces condition-transfer maternal effects on offspring quality, in a manner that is proportional to these effects. Previous studies had already suggested that maternal effects may have the

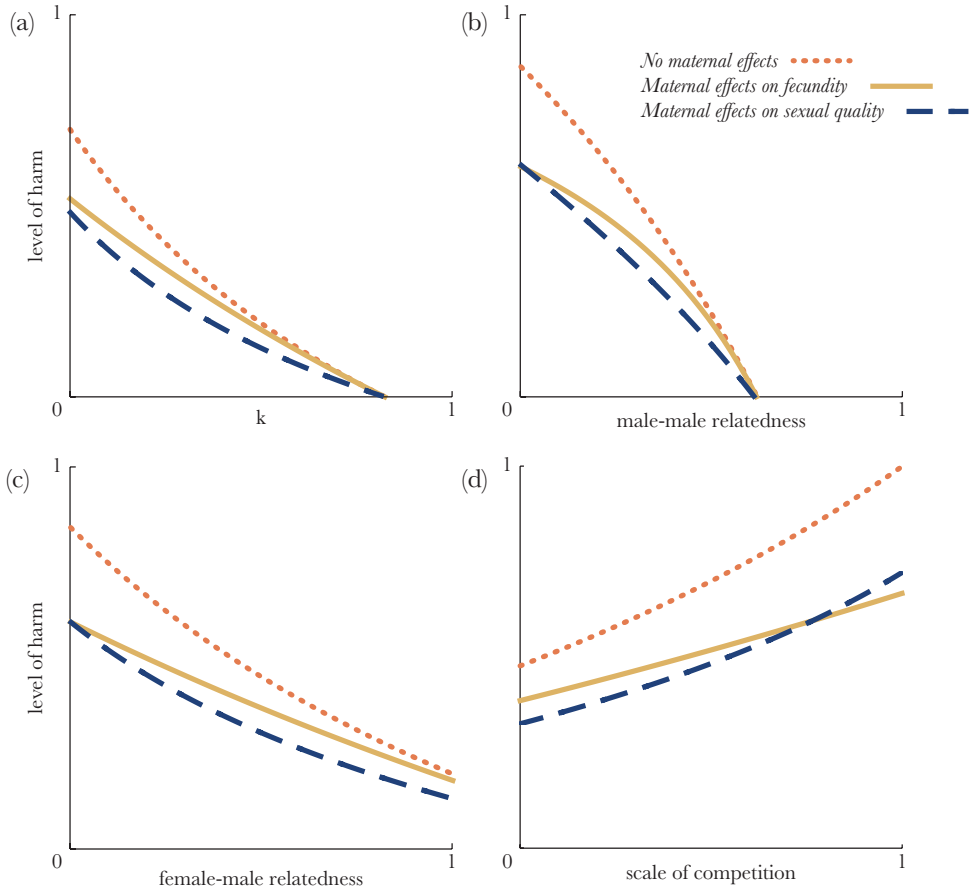

Figure 2

Optimal level of harm favored in monogamic females. The level of harm that is favored by natural selection depends on the absence or presence of maternal effects in monogamic females. Accordingly, the absence of maternal effects leads to higher levels of harm than in the presence of maternal effects, more so when they affect the individuals' sexual quality. Such effect is present regardless of k (i.e.. the degree to which harm occurs before and/or during mating) (A) of the levels of relatedness between individuals in the social group of a population of monogamic females (B and C). When local competition is high, maternal effects still lead to lower levels of harm, but maternal effects on fecundity can lead to lower levels of harm when compared with maternal effects on sexual quality (D). For all panels, the following parameters were used: number of males $n_m = 3$; number of females $n_f = 3$; fecundity and competitiveness cost $s = 0.5$; sexual cost for females $h = 0.5$; and sexual cost for males $t = 0.5$. In A and D: relatedness between males $r_{mm} = 0.15$; and relatedness between females and males $r_{fm} = 0.15$. In B, C, and D: harm exclusive from sexual partners $k = 0$. In A, B, and C: level of local competition $a = 0.5$. In B: relatedness between females and males $r_{fm} = 0.15$. In C: relatedness between males $r_{mm} = 0.15$.

potential to partially compensate for sexual conflict effects on female offspring (Foerster et al. 2007; Lund-Hansen et al. 2021). Here, we show that male harm-mediated maternal effects indeed have the potential to shape sexual conflict evolution.

The overarching prediction that stems from our results is that, all else being equal, we might expect lower levels of male harm to females in taxa where maternal effects on offspring quality are higher, more amenable to changes in maternal condition, and/or in which offspring quality (relative to quantity) loads heavily on parental fitness. Specifically, we would predict generally lower levels of male harm in species with prolonged gestation (e.g., viviparous/ovoviviparous vs. oviparous), in species with extended maternal provisioning (e.g., matrotrophic vs. lecithotrophic), in species with (vs. without) parental care, and at large in species that are under strong K- (vs. r-) selection (i.e., in species that favor investment in offspring survival vs. quantity). Identifying maternal effects as a potential modulator of sexual conflict thus gives rise to specific predictions about where male harm might have evolved and how intense we might expect it to be. To assess these theoretical predictions, we conducted a systematic search in the literature to identify studies reporting solid quantitative or qualitative evidence of male harm to females and, for these species, collected data on three proxies of maternal effects: parental care, extended gestation, and extended maternal provision (see Supplementary Material for details). Our aim was to perform a meta-analysis of this association across the tree of life but, unfortunately, the resulting dataset did not encompass enough variation in the key variables of interest related to maternal effects (e.g., maternal provisioning, gestation period, parental care, level of male harm, etc.) to address a formal analysis. Namely, we found very little scope for maternal effects in the relatively few species for which male harm has been well studied (see Supplementary Material and accompanying data for details), and thus not enough co-variation between both variables. However, there are some general qualitative trends in the data that are worth discussing.

Overall, we found evidence of male harm for 87 species across the tree of life (see Supplementary Figure 1 and accompanying Supplementary Material). Male harm seems particularly

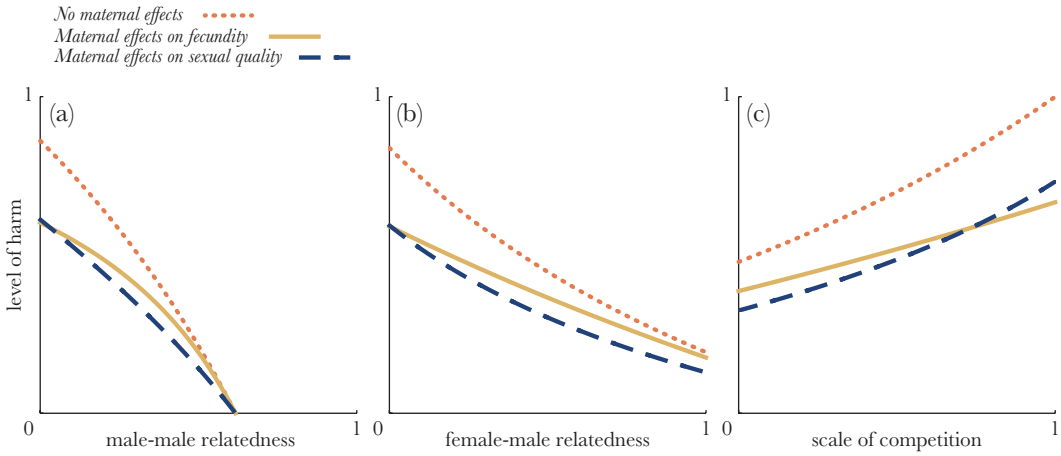

Figure 3

Optimal level of harm favored in polygamic females. The level of male harm that is favored by natural selection depends on the absence or presence of maternal effects in polygamic females. Accordingly, the absence of maternal effects leads to higher levels of harm than in the presence of maternal effects, more so when male harm affects the individuals' sexual quality. Such an effect is present regardless of the levels of relatedness between individuals in the social group (A and B). When local competition is high, maternal effects still lead to lower levels of harm, but maternal effects on fecundity can lead to lower levels of harm when compared with maternal effects on sexual quality (C). For all panels, the following parameters were used: number of males $n_m = 3$; number of females $n_f = 3$; fecundity and competitiveness cost $s = 0.5$; sexual cost for females $h = 0.5$; and sexual cost for males $t = 0.5$. In A and B: level of local competition $a = 0.5$. In A: relatedness between females and males $r_{fm} = 0.15$. In B: relatedness between males $r_{mm} = 0.15$. In C: relatedness between males $r_{mm} = 0.15$; and relatedness between females and males $r_{fm} = 0.15$.

widespread, intense and sophisticated in insects, which include the best-known cases of sexually antagonistic coevolution driven by male harm (Perry and Rowe 2015) along with many instances of traumatic insemination (Crudgington and Siva-Jothy 2000; Arnqvist et al. 2005; Siva-Jothy 2006; Tatarnic et al. 2014; Reinhardt et al. 2015), including toxic ejaculates (Wigby and Chapman 2005) and extreme coercion (Han and Jablonski 2010). Furthermore, indirect evidence based on the description of male genitalia (and the fitness consequences of similar structures in other species) suggests adaptations for traumatic insemination may occur in as many as ca.1400 species more (see Supplementary Material for details). Albeit there are many obvious exceptions (e.g., eusocial insects), insects are very frequently under strong r-selection, oviparous and normally lack extended maternal provision and parental care. Gastropods, where traumatic insemination also seems common, seem to follow a similar pattern (see Supplementary Figures 1 and 2 and Supplementary Material). In contrast, male harm appears to be relatively rare or weak in vertebrates, especially so in taxa with widespread parental care and prolonged gestation such as birds and mammals (see Supplementary Figures 1 and 2 and Supplementary Material). As a matter of fact, well-studied cases of male harm reported so far in vertebrates consist exclusively of collateral damage to females (i.e., harassment and/or coercive mating), as opposed to traumatic insemination adaptations, where male fitness benefits derive from harming females per se (i.e., direct damage; Aloise King et al. 2013).

The absence of adaptations for direct harm in mammals is particularly salient given the strength of male–male competition in many species within this group (Andersson 1994). Furthermore, although harassment is widely interpreted as an inherently costly male phenotype for females, it does not necessarily translate into a reduction in female fitness. For example, female resistance to male harassment has been suggested to function as a form of mate choice as a way of screening high-quality males (Cordero and Eberhard 2003). Thus, the mere existence of male harassment and/or coercion does not necessarily imply fitness costs to females. Different forms of sexual harassment and/or coercion to females have been reported for a number of vertebrates (and are probably common; Clutton-Brock and Parker 1995), such that in these cases, intense courtship is assumed to be harmful for females. However, direct evidence that such harassment reduces female fitness is limited (Magurran and Ojanguren 2007; Makowicz and Schlupp 2013; Iglesias-Carrasco et al. 2019). For example, forced copulations are common in waterfowls (reported for at least 55 species; McKinney et al. 1983; McKinney and Evarts 1998), where they are frequently accompanied by male harassment behavior that can occasionally result in injuries and even the death of the female (McKinney et al. 1983). Nonetheless, evidence that such behavior has net harmful effects on females is more restricted (see Adler 2010; Supplementary Figure 1). In short, available data may seem to be generally aligned with the prediction of a relationship between the importance of maternal effects within broad taxonomic groups and evidence of costly male harm, particularly in the case of direct harm to females. However, it is important to stress that this cannot be taken as preliminary evidence in support of this hypothesis because existing studies do not span enough co-variation in the scope of maternal effects and male harm to perform a formal analysis.

To conclude, in this study, we aim to bring attention to male-induced maternal effects as a potentially important factor in the evolution of sexual conflict. Similarly to relatedness (Rankin 2011; Carazo et al. 2014; Faria et al. 2015, 2020; Lukasiewicz et al. 2017), we show that maternal effects can align the evolutionary interests of males and females and abate conflict over sexual strategies. Such effects could be important to understand sexual conflict evolution in nature for two main reasons. The first is the existence of variation in condition-transfer maternal effects that can impinge on offspring quality, both across and within taxa (Royle et al. 2012; Bonduriansky and Crean 2018). The second is the well-established fact that male harm can have a dramatic impact on female condition (Arnqvist and Rowe 2005). We thus suggest that future

empirical studies should aim to test the general ideas we lay out here (see above) arising from the interplay between maternal effects and male harm, which could further our understanding of sexual conflict.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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AUTHOR CONTRIBUTIONS

Roberto García-Roa (Conceptualization [Equal], Data curation [Equal], Investigation [Equal], Methodology [Equal], Writing – original draft [Supporting], Writing – review & editing [Equal]), Gonçalo Faria (Formal analysis [Lead], Investigation [Equal], Methodology [Lead], Validation [Equal], Visualization [Equal], Writing – original draft [Supporting], Writing – review & editing [Equal]), Daniel Noble (Conceptualization [Supporting], Data curation [Supporting], Formal analysis [Supporting], Methodology [Supporting], Supervision [Supporting], Writing – review & editing [Supporting]), and Pau Carazo (Conceptualization [Lead], Data curation [Equal], Formal analysis [Supporting], Funding acquisition [Lead], Methodology [Supporting], Supervision [Lead], Writing – original draft [Lead], Writing – review & editing [Lead])

CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by Carazo (2023)

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