Female plasticity tends to reduce sexual conflict

David V. McLeod* and Troy Day

Sexual conflict is the divergence of evolutionary interests between the sexes. A neglected aspect of sexual conflict theory is that the conflict often occurs within the female's body, which can lead to a power asymmetry between the sexes. In particular, the female may often be able to respond flexibly to the actions of the male, and so exhibits plasticity. Here, we consider the implications of female plasticity, and find that it tends to result in lower levels of sexual conflict. We then relate our results to a comparison of pre- versus post-copulatory sexual conflict, and we also show that this asymmetry between males and females reduces the likelihood of runaway selection, preventing co-evolutionary arms races. Finally, we discuss our results in the context of the evolution of adaptive harm and sexual conflict when there are direct benefits.

That the evolutionary interests of males and females sometimes differ has long been of interest to biologists[1-4]. This divergence of interests is referred to as sexual conflict, and usually arises either from between-sex differences in optimal mating rate (pre-copulatory conflict) or from between-sex differences in optimal output per mating (post-copulatory conflict)[4]. Pre-copulatory conflict has resulted in the evolution of traits such as the grasping and anti-grasping morphology in water striders[5] and traumatic insemination in bed bugs[4], whereas post-copulatory conflict may underlie the evolution of traits such as seminal fluid proteins (SFPs), which induce physiological and behavioural changes in females[6] at the expense of female fitness[7,8] (but see ref. [9]), and the co-evolution of counteracting female-expressed traits[10,11] (but see ref. [12]).

Sexual conflict theory generally assumes that neither sex has an information advantage over their opponent[2,13-17]. Yet the arena of sexual conflict is often the female body, thereby potentially generating an informational power asymmetry[18,19]. In terms of evolutionary game theory, this asymmetry can be best understood as the difference between a simultaneous and a sequential game. When both sexes play their strategies simultaneously (for example, the grasping and anti-grasping morphology of water striders), co-evolution proceeds according to a simultaneous game. However, often the male has to commit to a particular strategy (for example, some composition of SFPs), whereas because the ensuing interaction takes place in her body, the female can potentially respond to the male's attempt at manipulation by plastically altering her counter-strategy in a way that depends on what the male has done. When this occurs, co-evolution proceeds according to a sequential game.

Here, we show that the informational asymmetry of the sequential game tends to result in lower levels of sexual conflict compared with the simultaneous game. We then relate our results to a comparison of pre- versus post-copulatory sexual conflict, as pre-copulatory conflict may often be akin to a simultaneous game, whereas post-copulatory conflict often matches the sequential game. We also show that when the assumptions of the chase-away hypothesis[20] are satisfied, the informational asymmetry often prevents runaway selection and co-evolutionary arms races otherwise predicted by the simultaneous game. Finally, we discuss how our results provide new insights into the evolution of adaptive harm and sexual conflict when the female receives direct benefits.

Results

Consider a large, well-mixed sexual population and two heritable traits, a male trait, ρ, and a female counter-strategy, κ. Trait expression is sex-specific and trait inheritance occurs by fair meiosis. Sexual conflict is frequently generated by male intrasexual competition, and therefore the evolution of ρ maximizes relative male fitness, $W_{\male}(\rho,\kappa)$, which is the product of the expected number of matings, $M_{\male}(\rho,\kappa)$, and output per mating, $F(\rho,\kappa)$. The term 'relative' is used because typically a male's absolute reproductive success is determined by his ability to procure paternity relative to that of other males. On the other hand, in the absence of female intrasexual competition, the evolution of κ maximizes female lifetime production of offspring, $W_{\female}(\rho,\kappa) \equiv M_{\female}(\rho,\kappa)F(\rho,\kappa)$, at a demographic steady state (see Supplementary Information).

Our focus is on sexually antagonistic selection[4,20], and so the action of the traits has a negative effect on the (relative) fitness of the opposite sex; that is, $\partial W_{\female}/\partial \rho < 0$ and $\partial W_{\male}/\partial \kappa < 0$. For example, in a pre-copulatory setting, mate competition might select for a higher male mating rate than that which is optimal for females, whereas in a post-copulatory setting, the male might attempt to increase the number of offspring produced per mating, and by doing so decrease the lifetime reproductive success of the female (for example, because SFPs increase female mortality[7,8]). We will suppose that the female trait controls the allocation of resources into the female's physiological/behavioural processes, and so without loss of generality, we suppose that increasing κ increases her number of matings, $\partial M_{\female}/\partial \kappa > 0$, while decreasing her output per mating, $\partial F/\partial \kappa < 0$.

We denote the co-evolutionary outcome for the simultaneous game as $(\rho^{\star},\kappa^{\star})$ and the outcome for the sequential game as $(\hat{\rho},\kappa_{\female}(\hat{\rho}))$, where $\kappa_{\female}(\rho)$ is the female's best-response function. We will let $\rho_{\male}(\kappa)$ denote the male best-response function, and assume that both the male and female best-response functions are evolutionarily stable, that is, $\partial^2 W_{\male}/\partial \rho^2|_{\rho=\rho_{\male}(\kappa)}<0$ and $\partial^2 W_{\female}/\partial \kappa^2|_{\kappa=\kappa_{\female}(\rho)}<0$. The change in female fitness due to plasticity is then $\Delta W_{\female} = W_{\female}(\hat{\rho},\kappa_{\female}(\hat{\rho})) - W_{\female}(\rho^{\star},\kappa^{\star})$, whereas the change in relative male fitness is $\Delta W_{\male} = W_{\male}(\hat{\rho},\kappa_{\female}(\hat{\rho})) - W_{\male}(\rho^{\star},\kappa^{\star})$.

Although sexual conflict is typically defined as a difference in the fitness optima between sexes[2,4,19,21], this definition cannot be used to compare populations differing in their trait composition in our model, such as two different co-evolutionary equilibria. This is because any difference in fitness optimum is a property of the fitness landscape, rather than a property of a particular population.

Department of Mathematics and Statistics, Queen's University, 99 University Ave, Kingston, Ontario K7L 3N6, Canada. *e-mail: 13dm38@queensu.ca

Thus the difference in fitness optima is a metric for potential rather than actual sexual conflict (this is related to one sex 'winning' a conflict[19]). Hence, when comparing co-evolutionary equilibria, what we are interested in is how close (in terms of fitness) a particular population is to either the male or female fitness optima. Consequently, we consider male and female sexual conflict separately, and will say plasticity reduces female sexual conflict if it increases relative female fitness, $\Delta W_{\female} > 0$, and similarly for male sexual conflict (if $\Delta W_{\male} > 0$).

As plasticity can only select for $\rho \neq \rho^\star$ if relative male fitness increases (see Supplementary Information), it follows that plasticity always reduces sexual conflict from the male's perspective. However, the effect on sexual conflict from the female's perspective is more subtle. The reason for this is that, although a female who is able to respond plastically to the actions of a male will always be individually fitter than one who can not (as we are not attaching explicit costs to plasticity; see also ref. [22]), female plasticity also alters the selective pressures on the (co)-evolving male subpopulation. In doing so, the female inadvertently selects for male variants that may either increase or reduce female fitness in comparison with the male variants that are selected in the simultaneous game. Thus female plasticity, despite always increasing individual female fitness (and so being selectively advantageous[22]), induces selective pressure on the male, and this alters the phenotypic composition of the male subpopulation in a way that can be beneficial or detrimental to the female subpopulation.

To determine which long-term effect of plasticity is expected, suppose that plasticity results in a small change in the optimal male trait. Then we can approximate $\Delta W_{\female}$ as

$$\Delta W_{\female} \approx \left[\frac{\partial W_{\female}}{\partial \rho} + \kappa'_{\female}(\rho) \frac{\partial W_{\female}}{\partial \kappa} \right] (\hat{\rho} - \rho^\star) \tag{1}$$

By definition of $(\rho^\star, \kappa^\star)$, $\partial W_{\female}(\rho^\star, \kappa^\star)/\partial \kappa = 0$, whereas since ρ is sexually antagonistic, $\partial W_{\female}/\partial \rho < 0$. Therefore, if $\hat{\rho} < \rho^\star$, then $\Delta W_{\female} > 0$ and so plasticity decreases female sexual conflict. Conversely, if $\hat{\rho} > \rho^\star$, then plasticity increases female sexual conflict. Which of these cases occurs will depend on the female fitness function $W_{\female}$.

To determine whether $\hat{\rho} < \rho^\star$ or $\hat{\rho} > \rho^\star$ we first write

$$\Delta W_{\male} \approx \left[\frac{\partial W_{\male}}{\partial \rho} + \kappa'_{\female}(\rho) \frac{\partial W_{\male}}{\partial \kappa} \right] (\hat{\rho} - \rho^\star) \tag{2}$$

where the term in square brackets is the selection gradient of the male trait in the sequential game (see Supplementary Information). As before, we know that $\partial W_{\male}(\rho^\star, \kappa^\star)/\partial \rho = 0$, whereas $\partial W_{\male}/\partial \kappa < 0$ by assumption. Therefore, the direction of change in ρ as a result of plasticity will be opposite to the sign of $\kappa'_{\female}(\rho)$: if $\kappa'_{\female}(\rho)$ is positive then plasticity selects for reduced ρ (that is, $\hat{\rho} < \rho^\star$) and vice versa. This condition can be expressed in terms of the female fitness function by noting that $\kappa'_{\female}(\rho)$ has the same sign as $\partial^2 W_{\female}/(\partial \rho \partial \kappa)$ (see Supplementary Information). This latter quantity represents the change in the selection gradient on the female trait with a change in ρ. Thus if larger values of ρ result in stronger selection for female resistance (that is, greater investment in number of matings at the expense of output per mating), then $\partial^2 W_{\female}/(\partial \rho \partial \kappa) > 0$ and thus $\kappa'_{\female}(\rho) > 0$. This means that $\hat{\rho} < \rho^\star$ and so the net result is that plasticity reduces sexual conflict from the female's perspective. Conversely, if larger values of ρ result in weaker selection for female resistance (that is, greater investment in output per mating at the expense of number of matings) then $\partial^2 W_{\female}/(\partial \rho \partial \kappa) < 0$ and thus $\kappa'_{\female}(\rho) < 0$. This means that $\hat{\rho} > \rho^\star$ and thus plasticity will increase sexual conflict from the female's perspective.

Discussion

Pre- versus post-copulatory conflict. Consider how these predictions relate to pre- versus post-copulatory conflict. Pre-copulatory conflict typically arises from male intrasexual competition selecting for a higher mating rate than that which is optimal for females. Although some pre-copulatory behavioural adaptations may involve both sexes dynamically adjusting their behaviour during the course of each encounter (for example, through a negotiation process[23]), many pre-copulatory adaptations are fixed strategies or investments, such as the grasping and anti-grasping morphology in water striders[5], or the traumatic insemination seen in bed bugs[4]. Thus the predicted co-evolutionary outcome is that of the simultaneous game. Although some post-copulatory conflict should also be viewed as a simultaneous game, such as when the female counter-strategy is a morphological (and thus fixed) investment, as in the co-evolution of seminal receptacle length and giant sperm seen in *Drosophila*[24], many post-copulatory processes involve females responding to actions by the male (such as when the male transfers SFPs in the ejaculate). For example, in many species SFPs form a mating plug to prevent females from remating[25], and females may either physically remove[26] or up-regulate proteases to degrade the mating plug[27,28]. Importantly, the female response to the mating plug depends on its size and complexity[25]; for example, in one study protease activity was negatively correlated with plug mass[29]. As the female response varies based on the mating plug, and by extension the male phenotype[29], this is a sequential game. Another example is sex peptide (SP), an SFP that increases ovulation[30] and reduces the receptivity of females to remating[31], while imposing costs on females[8]. Evidence suggests that females have evolved resistance to elevated levels of SP by up-regulating proteases to regulate and degrade SP[32], as well as down-regulating SP receptors required for SP functioning[33]. Although studies have not yet examined whether the level of up- or down-regulation on the part of the female is correlated with the amount of SP transferred, it seems likely that females will not, for example, produce the same quantity of proteases for a small versus large amount of SP present. Thus the female response (amount of protease produced or level of down-regulation of SP receptors) will be dependent on the male phenotype (quantity of SP transferred), and so we have a sequential game. Indeed, whenever the proteolytic processing or degradation/inactivation of SFPs is dependent on either the type or quantity of SFPs present, the female response will therefore depend on the male phenotype, and so the co-evolutionary outcome is that predicted by the sequential game. When this holds, our model predicts that female plasticity lowers male sexual conflict while, provided the female resists males by increasing her investment in her number of matings at the expense of her output per mating, sexual conflict will be reduced from the female's perspective as well. Indeed, consideration of the male selection gradient in equation (2) (term in square brackets) reveals that if the female resists the male, then selection on the male trait in the sequential game will always be reduced compared with the simultaneous game (see Supplementary Information). The biological implication is that the complex and costly adaptations seen in pre-copulatory conflict[4] should be less likely to evolve from post-copulatory interactions in which the female can respond flexibly to males.

Chase-away hypothesis. The role played by female plasticity also has important implications for the chase-away hypothesis[20], which supposes that males have some persistence trait increasing male fitness at a cost to females. This, in turn, selects for female resistance, leading to increased male persistence[20]. Models based on this hypothesis have used the framework of a simultaneous game to show that various evolutionary outcomes are possible, including speciation, runaway evolution and evolution to fixed equilibria[13–16]. Our model predicts that female plasticity will not only reduce selection for exaggeration of the male trait, but it can lead to qualitatively

different co-evolutionary outcomes. For example, suppose the male strategy is to transfer some quantity of SP or form a mating plug of some desired size and complexity. Such a strategy increases the male's expected output per mating (for example, SP elevates female ovulation rate and reduces the likelihood of female remating[30]); however, increasing the amount of SFPs transferred comes at some energetic cost to the male[4], potentially increasing his mortality and thereby reducing his ability to procure future matings. Thus $\partial F/\partial \rho > 0$ and $\partial M_{\male}/\partial \rho < 0$. The male trait is sexually antagonistic and so the costs to the female outweigh any short-term reproductive benefits that the female may obtain from the male manipulation (as in the case of SP[8]). Now suppose the female counter-strategy to manipulation is to reduce her investment in the current mating, such as by degrading SFPs or removing mating plugs, so as to increase her likelihood of remating. Thus the female trait is sexually antagonistic. In Fig. 1, we have constructed such an example using these general assumptions (see Supplementary Information for specific details). In this example, in the simultaneous game the male is selected to 'manipulate' the female, which leads to the evolution of the male trait in the direction given by the red arrows, in turn selecting for the female to resist the actions of the male, leading to evolution of the female trait in the direction given by the blue arrows. As the female resistance does not depend on the value of the male trait in the simultaneous game, female resistance selects for increased male antagonism, leading to runaway selection on the male trait and a co-evolutionary chase between the sexes (Fig. 1). Conversely, in the sequential game the female resistance depends on the value of the male trait and so predicts evolution to a fixed co-evolutionary equilibrium, as there is a clear maximum of male fitness restricted to the female best-response function (Fig. 1). Thus female plasticity provides an additional mechanism preventing the exaggeration of male traits, and can lead to dramatically different co-evolutionary outcomes.

Adaptive harm. Until now we have focused on conflict in which the action of the male increases output per mating, $\partial F/\partial \rho > 0$, and damage to the female is attributable to pleiotropy. It has been argued, however, that it may sometimes be selectively advantageous for males to intentionally harm females[34,35], a phenomenon called adaptive harm. Adaptive harm assumes that the harm potentially reduces the female's overall reproductive output, and so relative male fitness is a non-increasing function of harm as well (that is, $\partial W_{\male}/\partial \rho \le 0$). Thus if the female response is fixed, harm will never be adaptive. However equation (2) indicates that this may not be true under female plasticity (note that plasticity is also assumed by refs [34,35]). Closer inspection of equation (2) reveals that in addition to plasticity, adaptive harm requires a minimum of two preconditions: (1) that the female does not resist harm (for example, divert resources to survival/remating) and (2) that effectively synergistic interactions between the harm and female response occur (see Supplementary Information). This is likely to be satisfied in a very limited number of situations and so harm will rarely be adaptive, contrary to what previous models have suggested[35,34]. Indeed, an experimental test showed that the female resists harm (by remating[36]), which our model predicts would preclude the possibility of harm being adaptive. These difficulties are likely to explain the paucity of empirical evidence for adaptive harm[6]. Notably, when the stringent conditions are satisfied, adaptive harm represents a case in which plasticity backfires and female sexual conflict increases.

Direct benefits. Although we have assumed the male trait is sexually antagonistic ($\partial W_{\female}/\partial \rho < 0$), sexual conflict can also be generated if, for example, SFPs are beneficial to females ($\partial W_{\female}/\partial \rho > 0$). Now the conflict arises because the female wants the male to 'manipulate' at a level greater then he wants; this is the difference between models of sexually antagonistic selection and those of direct benefits[4].
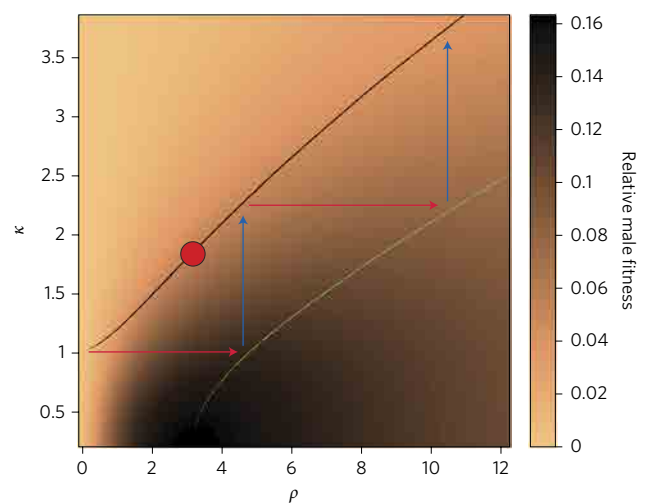

Figure 1 | Existence of a co-evolutionary outcome for the sequential game despite the simultaneous game predicting runaway selection. Plotted surface is relative male fitness, $W_{\male}(\rho,\kappa)$, the black curve is the female best-response function, $\kappa_{\female}(\rho)$ and the green curve is the male best-response function, $\rho_{\male}(\kappa)$. The red circle on the female best-response function is the maximum of male fitness restricted to the female best-response function; this is the co-evolutionary outcome predicted by the sequential game. The arrows indicate the direction of evolution (blue for female trait and red for male trait) for the simultaneous game, demonstrating runaway selection on the male trait. Details on this example can be found in the Supplementary Information.

For example, nuptial gifts are protein-rich substances in the ejaculate providing direct benefits to females (e.g. increased nutritional uptake[37,38]), while representing a significant investment by the male, as the ejaculate can be up to 15–30% of male body weight (reviewed in ref. [4]).

Our predictions about how plasticity alters the optimal level of 'manipulation' still hold; however, our expectation for the effect on female sexual conflict is reversed (this is a consequence of taking $\partial W_{\female}/\partial \rho > 0$ in equation (1)). In a direct benefits scenario, plasticity reduces female sexual conflict if manipulation causes females to invest more in output per mating and less in the number of matings. The logic here is simple: females wish males to provide costly benefits, and so to entice them to do so, the female must 'reward' the male's investment by increasing her short-term reproductive output. If she instead 'punishes' the male by increasing her remating effort, plasticity will select for males to provide fewer benefits to females.

For example, comparative studies of butterflies indicate that female remating increases with the size of nuptial gift[4,39]. As female remating rates in these species are often low, it has been suggested that perhaps the ejaculate contains compounds inhibiting remating and, rather than nuptial gifts, the male ejaculate should be viewed as a 'Medea' gift[38,4]. Our model indicates that because the female responds to increasing nuptial gift size by increasing her investment in remating, the female is actually selecting for the male to reduce his investment in nuptial gifts, increasing sexual conflict. Therefore, the largest nuptial gifts should be expected for species whose remating rate decreases with the size of the gift.

That plasticity can sometimes worsen the conflict outcome for females, such as when nuptial gifts prompt females to invest in remating or as in the case of adaptive harm, is counter-intuitive because plasticity provides the female with more information. Although it is true that having additional information improves individual fitness[22,40], it has selective consequences at the population-level. In particular, female plasticity changes the selective environment for

the male subpopulation, which can lead to the evolutionary success of male phenotypes that are more detrimental to female lifetime reproductive success than the male phenotype that was optimal in the simultaneous game. Thus in certain circumstances, plasticity, despite being adaptive for the individual female, can exacerbate male intrasexual competition to the detriment of the population as a whole, increasing female sexual conflict.

Here, we have considered the implications that female plasticity has for sexual conflict. We have shown that plasticity tends to result in lower levels of sexual conflict, and have argued that often plasticity represents a key difference between pre- and post-copulatory conflict. We have demonstrated that when plasticity is included in the chase-away hypothesis, the likelihood of runaway selection and co-evolutionary chases is reduced. Finally, we related our findings to a number of biological scenarios, providing new insight into adaptive harm and direct benefit models.

Data availability. Data sharing is not applicable to this Article as no data sets were generated or analysed.

References

1. Trivers, R. L. in *Sexual Selection and the Descent of Man* (ed. Campbell, B.) 136–179 (Aladine, 1972).
2. Parker, G. in *Sexual Selection and Reproductive Competition in Insects* (eds Blum, M. & Blum, N. A.) 123–166 (Academic, 1979).
3. Chapman, T., Arnqvist, G., Bangham, J. & Rowe, L. Sexual conflict. *Trends Ecol. Evol.* **18,** 41–47 (2003).
4. Arnqvist, G. & Rowe, L. *Sexual Conflict* (Princeton Univ. Press, 2005).
5. Arnqvist, G. & Rowe, L. Antagonistic coevolution between the sexes in a group of insects. *Nature* **415,** 787–789 (2002).
6. Sirot, L. K., Wong, A., Chapman, T. & Wolfner, M. F. Sexual conflict and seminal fluid proteins: a dynamic landscape of sexual interactions. *Cold Spring Harb. Perspect. Biol.* **7,** 1–24 (2014).
7. Civetta, A. & Clark, A. G. Correlated effects of sperm competition and postmating female mortality. *Proc. Natl Acad. Sci. USA* **97,** 13162–13165 (2000).
8. Wigby, S. & Chapman, T. Sex peptide causes mating costs in female *Drosophila melanogaster*. *Curr. Biol.* **15,** 316–321 (2005).
9. Fricke, C., Bretman, A. & Chapman, T. Female nutritional status determines the magnitude and sign of responses to a male ejaculate signal in *Drosophila melanogaster*. *J. Evol. Biol.* **23,** 157–165 (2010).
10. Chapman, T., Liddle, L. F., Kalb, J. M., Wolfner, M. F. & Partridge, L. Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. *Nature* **373,** 241–244 (1995).
11. Rice, W. Sexually antagonistic male adaptation triggered by experimental arrest of female evolution. *Nature* **381,** 232–234 (1996).
12. Abbott, J. K., Innocenti, P., Chippindale, A. K. & Morrow, E. H. Epigenetics and sex-specific fitness: an experimental test using male-limited evolution in *Drosophila melanogaster*. *PLoS ONE* **8,** e70493 (2013).
13. Gavrilets, S. Rapid evolution of reproductive barriers driven by sexual conflict. *Nature* **403,** 886–889 (2000).
14. Gavrilets, S., Arnqvist, G. & Friberg, U. The evolution of female mate choice by sexual conflict. *Proc. R. Soc. Lond. B* **268,** 531–539 (2001).
15. Gavrilets, S. & Waxman, D. Sympatric speciation by sexual conflict. *Proc. Natl Acad. Sci. USA* **99,** 10533–10538 (2002).
16. Rowe, L., Cameron, E. & Day, T. Escalation, retreat, and female indifference as alternative outcomes of sexually antagonistic coevolution. *Am. Nat.* **165,** S5–S18 (2005).
17. Clutton-Brock, T. H. & Parker, G. A. Sexual coercion in animal societies. *Anim. Behav.* **49,** 1345–1365 (1995).
18. Eberhard, W. G. *Female Control: Sexual Selection by Cryptic Female Choice* (Princeton Univ. Press, 1996).
19. Parker, G. A. Sexual conflict over mating and fertilization: an overview. *Phil. Trans. R. Soc. B* **361,** 235–259 (2006).
20. Holland, B. & Rice, W. R. Chase-away sexual selection: antagonistic seduction versus resistance. *Evolution* **52,** 1–7 (1998).
21. Chapman, T. Evolutionary conflicts of interest between males and females. *Curr. Biol.* **16,** R744–R754 (2006).
22. McNamara, J. M. & Dall, S. R. X. Information is a fitness enhancing resource. *Oikos* **119,** 231–236 (2010).
23. McNamara, J. M., Gasson, C. E. & Houston, A. I. Incorporating rules for responding into evolutionary games. *Nature* **401,** 368–371 (1999).
24. Lupold, S. *et al.* How sexual selection can drive the evolution of costly sperm ornamentation. *Nature* **533,** 535–538 (2016).
25. Schneider, M. R., Mangels, R. & Dean, M. D. The molecular basis and reproductive function(s) of copulatory plugs. *Mol. Reprod. Dev.* **83,** 755–767 (2016).
26. Koprowski, J. L. Removal of copulatory plugs by female tree squirrels. *J. Mammal.* **73,** 572–576 (1992).
27. Kelleher, E. S. & Pennington, J. E. Protease gene duplication and proteolytic activity in *Drosophila* female reproductive tracts. *Mol. Biol. Evol.* **26,** 2125–2134 (2009).
28. Dean, M. D. *et al.* Identification of ejaculated proteins in the house mouse (*Mus domesticus*) via isotopic labeling. *BMC Genomics* **12,** 306 (2011).
29. Mangels, R. *et al.* Genetic and phenotypic influences on copulatory plug survival in mice. *Heredity* **115,** 496–502 (2015).
30. Chapman, T. *et al.* The sex peptide of *Drosophila melanogaster*: female post-mating responses analyzed by using RNA interference. *Proc. Natl Acad. Sci. USA* **100,** 9923–9928 (2003).
31. Ravi Ram, K. & Wolfner, M. F. Seminal influences: *Drosophila* Acps and the molecular interplay between males and females during reproduction. *Integr. Comp. Biol.* **47,** 427–445 (2007).
32. Pilpel, N., Nezer, I., Applebaum, S. W. & Heifetz, Y. Mating-increases trypsin in female *Drosophila* hemolymph. *Insect Biochem. Mol. Biol.* **38,** 320–330 (2008).
33. Prokupek, A. M., Kachman, S. D., Ladunga, I. & Harshman, L. G. Transcriptional profiling of the sperm storage organs of *Drosophila melanogaster*. *Insect Mol. Biol.* **18,** 465–475 (2009).
34. Johnstone, R. A. & Keller, L. How males can gain by harming their mates: sexual conflict, seminal toxins, and the cost of mating. *Am. Nat.* **156,** 368–377 (2000).
35. Lessells, C. M. Why are males bad for females? Models for the evolution of damaging male mating behavior. *Am. Nat.* **165,** S46–S63 (2005).
36. Morrow, E., Arnqvist, G. & Pitnick, S. Adaptation versus pleiotropy: why do males harm their mates? *Behav. Ecol.* **14,** 802–806 (2003).
37. Vahed, K. The function of nuptial feeding in insects: a review of empirical studies. *Biol. Rev.* **73,** 43–78 (1998).
38. Arnqvist, G. & Nilsson, T. The evolution of polyandry: multiple mating and female fitness in insects. *Anim. Behav.* **60,** 145–164 (2000).
39. Karlsson, B. Resource allocation and mating systems in butterflies. *Evolution* **49,** 955–961 (1995).
40. Pike, R. K., McNamara, J. M. & Houston, A. I. A general expression for the reproductive value of information. *Behav. Ecol.* (in the press).

Author contributions

D.V.M. and T.D. formulated the research question, designed and analysed the model, and wrote the manuscript.

Competing interests

The authors declare no competing financial interests.