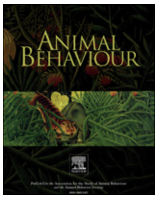
Animal Behaviour 83 (2012) e10–e13

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Sex role stereotyping and sexual conflict theory

J. C. Perry [a,*], L. Rowe [b]

[a] The Edward Grey Institute, Department of Zoology, University of Oxford, Oxford, U.K.
[b] Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Canada

ARTICLE INFO

Article history:
Received 2 August 2011
Initial acceptance 9 September 2011
Final acceptance 6 October 2011
Available online 2 March 2012
MS. number: 11-00610

Keywords:
male cost
sex role
sexual conflict
sexual selection

The field of sexual selection has been subject to criticism for the potential biases researchers bring to their work (e.g. Gowaty 1997, 2003, 2004; Zuk 2002; Dewsbury 2005; Ah-King 2007). Recently, Karlsson Green & Madjidian (2011; hereafter KGM) argued that sexual conflict studies have not been subject to the same scrutiny regarding sex role stereotyping as the broader field of sexual selection. To redress this, they survey the sexual conflict literature with respect to (1) the terminology used to describe male and female interactions, and (2) how these interactions are modelled in theoretical work. KGM conclude that sex role stereotyping is abundant in this literature, with males and females described using ‘active’ and ‘reactive’ terms, respectively. Furthermore, they find that sex stereotypes appear to have had a negative impact on sexual conflict theory.

KGM examined whether 26 verbal and mathematical models citing the keyword ‘sexual conflict’ incorporated costs to females, males or both sexes, where costs are defined as ‘arising from mating, parental investment or antagonistic interactions, but not the cost of producing antagonistic traits’ (page 902). They conclude that 14 models include costs to females only, while 12 include costs to both sexes and none considered male costs only. KGM then asked whether this trend reflected the wider literature, and found that of 145 studies with the keywords ‘sexual conflict’ and ‘costs’, well over half included female costs only while 30 included costs to both sexes and nine included male costs only. From these results, KGM conclude that ‘both models and the terms describing sexually antagonistic traits imply that there are no costs inflicted on males’ (page 905).

In our view, a discussion of the sex role stereotyping in sexual conflict research is well worth having, and we expect that KGM’s article will stimulate important conversations. However, it is not the case that sexual conflict models ignore male costs, and we believe there is often a theoretical or biological reason for a focus on females. In this forum article, we make three points that contrast with the claims in KGM or give context to their observations. First, the focus on females in sexual conflict research arises from sexual conflict’s position in the broader theory of sexual selection. Second, all models of sexually antagonistic coevolution, by definition, include costs to both males and females. Finally, we conclude by suggesting that if terminology is misleading researchers about the underlying theory, the best antidotes are to go back to the original theories and to avoid drawing inference from terminology alone.

A FOCUS ON FEMALES

The focus on females in sexual conflict research has its roots in sexual selection theory, and has its utility in distinguishing between the competing models. Moreover, it is worth noting that there has been earlier criticism that sexual selection research did

---

[*] Correspondence: J. C. Perry, The Edward Grey Institute, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.
E-mail address: jennifer.perry@zoo.ox.ac.uk (J. C. Perry).

0003-3472/$38.00 © 2012 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2012.01.030

not focus enough on females (Kirkpatrick & Ryan 1991; Ahnesjö et al. 1993), which appears to be the mirror image of KGM's criticism. The essential differences between the major models of sexual selection, including sexual conflict, are in the forces of selection acting on traits that lead to biases in mating success described by sexual selection (reviewed in Kirkpatrick & Ryan 1991; Arnqvist & Rowe 2005). These models typically focus on sexual selection on males, and therefore on the traits in females that bias mating success in males, largely because elaborate male traits that do not confer any obvious survival advantage were the initial puzzle that gave rise to sexual selection theory. It is easy to understand why males have this or that elaboration, if females bias mating success towards males possessing the elaboration, but it is not easy to understand why females have evolved to bias mating success in this way. Sexual selection models explore the various reasons why this might be so, and these key differences in the models of sexual selection account for the focus on the forces of selection acting on females.

The features that distinguish sexual conflict models from other sexual selection models are that selection is direct and sexually antagonistic. In the most commonly modelled case, there is direct selection favouring increased mating frequency in males (similar to almost all sexual selection models), and decreased mating frequency in females towards an intermediate optimum. Traits that increase their bearers' mating rate are favoured in males, whereas traits that decrease mating rates towards the female optimum are favoured in females. Thus, selection on mating rate is sexually antagonistic; there is sexual conflict over mating rate. The same reasoning applies to such shared traits as offspring provisioning and reproductive rate (Rowe & Day 2006). When traits in females reduce their mating rate and at the same time bias mating success towards certain traits in males, then there is sexual selection on males resulting from sexual conflict, and both male and female traits are sexually antagonistic traits.

The focus on costs to females in the sexual conflict literature thus arises from the central assumption of sexual conflict models: a discrepancy between the sexes' fitness optima for a given trait. When females have a lower fitness optimum than males, this discrepancy is a result of female costs (e.g. direct costs of mating or reproductive investment imposed by the environment or by interactions with males). Biologists interested in evaluating sexual conflict have therefore frequently attempted to identify these costs to females.

ALL MODELS OF SEXUALLY ANTAGONISTIC COEVOLUTION INCLUDE COSTS FOR BOTH SEXES

While research aimed at distinguishing sexual conflict from other models of sexual selection has focused on how selection acts on female biasing traits (for good reason, we argue above), it simply is not the case that the underlying models of sexual antagonistic coevolution largely ignore male costs.

> 'An individual with a mutant trait that increases its direct fitness in an interaction involving sexual conflict will, by definition, decrease the fitness of an individual of the opposite sex with which it interacts.' **Parker (2006, page 235)**

Following their review of sexual conflict models, KGM conclude that 'the models leave out the possibility of negative effects on males from female antagonistic actions' (page 904), and that 'theoretical models mainly investigate conflict costs for females, although costs for both sexes are necessary for coevolutionary dynamics' (page 901). In fact, all models of sexually antagonistic coevolution must and do employ costs to both sexes.

Broadly, sexual conflict describes 'a conflict between the evolutionary interests of individuals of the two sexes' (Parker 1979, page 124), or in terms of selection, 'sexually antagonistic selection on shared traits' (Rowe & Day 2006, page 278). Sexually antagonistic coevolution describes the coevolutionary outcome owing to sexual conflict. From this definition alone, it is easy to see that any model of sexually antagonistic coevolution must include costs to both sexes. In the case of mating rate, traits affecting mating rate that are favoured in one sex will impose a cost on the other sex, and vice versa.

In fact, KGM acknowledge that 'it is possible that the costs inflicted on males are implicitly there, for example through lost opportunity costs of mating if females develop higher resistance towards males' (page 905). They ask, when males are held below their optimal mating rate, 'Will a male not suffer a fitness cost similar to females?' (page 904). The answer is emphatically yes; this must be so if the model explores sexually antagonistic coevolution, and these male costs are explicit rather than implicit in sexual conflict theory.

In addition to the costs to males and females of being held off their optima, a second form of cost arises from natural selection. The specific (sexually antagonistic) traits in each sex that are favoured through their effect on mating rate can have natural selection acting on them, as when they are costly to produce, maintain or employ. These costs may include producing a sexually antagonistic morphological trait (e.g. as reflected in impaired development, Arnqvist 1994; Westlake & Rowe 1999), or engaging in a sexually antagonistic behaviour (e.g. energetic costs, Stevenson & Bancroft 1995; predation costs during precopulatory struggles, Rowe 1994). KGM exclude 'production costs' in their definition of costs, yet these costs do not differ from the others in this set, as they represent natural selection on antagonistic traits. Moreover, these male costs are analogous to the natural selection on female antagonistic traits on which KGM focus.

Examples of Male Costs in Sexual Conflict Theory

In contrast to KGM's conclusions, models of sexually antagonistic coevolution include costs to both sexes of being held from their optima (i.e. sexually antagonistic selection is assumed). Furthermore, the models often include costs of sexually antagonistic traits to the bearer. We illustrate this by considering how costs are treated in three models, two classified by KGM as incorporating female costs only (Parker 1979; Andrés & Morrow 2003) and one classified as including both male and female costs (Moore & Pizzari 2005). We then discuss an empirical example of male costs proposed by KGM to show how such costs are included in existing theory.

First, Parker's (1979) models provide the first formal theory for sexually antagonistic coevolution. In Parker's model of sexual conflict over whether to mate, both forms of male costs described above occur. First, both sexes experience direct costs from antagonistic interactions: females incur costs from both mating and resisting mating, while males pay a cost of attempting to mate (Parker 1979, page 150). These costs form a major focus of the model, with two cases considered: when the magnitude of costs for both sexes depends on traits expressed by the opposite sex, or when the magnitude of costs is fixed (e.g. as when the sexes invest in and pay costs of sexually antagonistic traits before sexual interactions occur). In both cases, male costs influenced the outcome of sexually antagonistic coevolution. Indeed, the relative costs to each sex of expressing sexually antagonistic traits were explicitly explored by setting costs to be equal in both sexes or higher in either males or females: 'Cost functions will also be asymmetrical; i.e., it may cost a female far less to prevent a male mating than it would cost the male to ensure that he could manage to mate' (page 162). In addition to these male costs of engaging in antagonistic sexual interactions or expressing sexual traits, the model also includes costs to males from being held from their fitness optimum for mating rate by resistant females.

Second, KGM report that Andrés & Morrow's (2003) model considers costs to females only. However, there is a key difference between this model and most of the other models considered: it is not coevolutionary, and therefore costs to males imposed by antagonistic female traits are outside its scope. Instead, the model investigates the spread of a sexually antagonistic allele in one sex only. The allele confers a mating advantage but harms the opposite sex. Let us refer to the sex bearing the antagonistic allele as male. Here, the evolution of female traits is not investigated because the goal is to study how genetic factors influence the spread of the harming allele. Thus, the two kinds of costs seen in our previous two examples do not occur: males are not held from their fitness optimum by antagonistic female traits, and males do not pay a direct cost through natural selection on the harming allele. However, it is difficult to see where costs to males might be incorporated in this model. Should natural selection act on the harming allele, such that it confers a mating advantage benefit but also a direct cost to males? We have noted above that KGM do not appear to consider such direct male costs to be a cost of sexual conflict. Beyond this, such a cost would not change the predictions of this model; it would act as a constant to depress male fitness, but the prediction remains that the harming allele spreads as long as the mating advantage benefit outweighs the cost of lost offspring production through the harmed mate. The forms of male cost that KGM discuss in their review, arising from sexually antagonistic female traits, have no place in this model because it is not a coevolutionary model or question.

Third, KGM classify a model by Moore & Pizzari (2005) as containing costs to both sexes. We agree, and we emphasize that the kinds of male costs incorporated are present in all of the coevolutionary models that KGM classify as female cost only. Moore & Pizzari used a quantitative genetic approach to model a sexual conflict over mating rate, in which there is coevolution between a male trait that acts to increase mating rate and a female trait that decreases it. The optimal male mating rate is higher than that of females and natural selection acts on both male and female mating rate (i.e. both sexes have an optimum above which mating is costly). It may be on this basis that KGM have concluded that the model contains costs for both sexes. However, the relevant part of the model is the area between two sexes' optima (where sexual conflict occurs). The model predicts two possible outcomes: sexually antagonistic coevolution between male and female traits, or reduced female trait expression because the costs of mating for females are outweighed by indirect genetic benefits. We note that in the outcome involving sexually antagonistic coevolution, males experience costs from being held from their fitness optimum by antagonistic female traits, just as in the models that KGM classify as considering female costs only.

Finally, we take up a challenge laid out in KGM's critique. KGM describe a potential example of male costs from sexually antagonistic interactions: when males transfer harmful ejaculate substances to females during mating and females neutralize these substances. This neutralization represents an antagonistic female trait that imposes costs on males. We suggest that this example fits neatly into the very models of sexual conflict that KGM claim do not account for male costs. For example, consider Parker's (1979) model (discussed above) and imagine that the shared trait over which the sexes are in conflict is the transfer and receipt of ejaculate along with the harmful effects induced (reviewed by Chapman 2001; Gillott 2003). Here, the antagonistic male trait is the transfer of such substances, which imposes a cost on females analogous to the cost of mating in Parker's (1979) model. It is reasonable to refer to the antagonistic female trait of neutralizing ejaculate substances as a resistance trait because it functions to resist male-imposed harm. In Parker's (1979) formulation, males pay a cost of expressing sexually antagonistic traits and from being held from their optimal mating rate by female antagonistic traits. In the example of harmful male ejaculate and female neutralization, we can imagine exactly analogous costs to males. It is reasonable to expect that males will experience direct costs from producing and perhaps from transferring harmful ejaculate substances (i.e. natural selection on the antagonistic male trait), and likewise, males are prevented from transferring their optimum amount of the active form of such substances because females express the antagonistic trait of neutralizing the substances. Understanding male costs in this example does not require a new theoretical approach. Rather, existing sexual conflict theory captures male costs.

In summary, in our review of the 14 models that KGM classify as including female costs only, we find that only 10 consider sexually antagonistic coevolution. Of the four that do not (including Andrés & Morrow 2003, discussed above), one models a game among males (Johnstone & Keller 2000), one models intralocus conflict rather than the interlocus conflict considered by the rest of the models (Kokko & Brooks 2003), and another does not model antagonistic trait evolution in either sex (Alonzo 2007). All 10 of the models that claim to be about sexually antagonistic coevolution do in fact include male costs, which is not surprising, as by definition they must. We further identify seven models of sexually antagonistic coevolution not considered by KGM (Parker & Partridge 1998; Härdling et al. 2001; Rowe et al. 2003; Kokko 2005; Gavrilets & Hayashi 2006; Rice et al. 2006; Rowe & Day 2006); all of these also incorporate costs to both sexes. In each case, the costs to males are incorporated in the same ways as identified in the models above.

FORMAL THEORY IS BOTH PRECISE AND EXPLICIT, WHEREAS TERMINOLOGY OFTEN IS NOT

We agree with KGM (and others, e.g. Ahnesjö et al. 1993; Eberhard 1996; Gowaty 2004; Dewsbury 2005) that much of the terminology used in the sexual conflict literature (e.g. males 'winning the battle of the sexes') might lead to misinterpretation of the assumptions underlying the models themselves, or the phenomena the models are meant to capture, and consequently drive research in unintended directions. This risk is increased when models and their terminologies extend widely in influence, when their origins may be forgotten as the new idea gains traction and sweeps through a field. When this occurs, both supportive and contrary points of view may have little to do with the models themselves and more to do with the imagery they inspire. As an example of this phenomenon, it is clear that the way terms are used in the theoretical literature for sexual conflict does not reflect KGM's (and perhaps popular) interpretation of their meaning. KGM take 'reactive' terms to imply traits that 'do not fuel reactions by the opposite sex' (page 902). However, in the models of sexual conflict reviewed, female traits that are termed 'reactive' (e.g. resistance to male mating attempts) indeed drive evolution in male traits, thus driving sexually antagonistic coevolution. KGM state that only 'active' terminology implies that a sex or trait imposes costs on the opposite sex, but this is not reflected in the theory where both sexes impose costs on each other.

The risk of misinterpretation is particularly strong when terms have apparently analogous usage in human interactions or endeavours. Unlike mathematical models, terminology is often neither precise nor explicit in conveying the thinking underlying its use; in fact, it seems unlikely that any terms describing sexual interactions will be completely free of this risk. This is a fact that we should be aware of and guard against. One way we can do this is to steer clear of making inferences from terminology. In the case of the sexual conflict theory discussed here, reviewing the models' assumptions would reveal that they all include costs to both males and females. It is also clear that there is a need for a constant dialogue within the field so that we can reach a consensus on terminology that is, as much as possible, both descriptive and free from value-laden connotation. Indeed, such dialogue will doubtless result in replacing terms that distract readers from the science behind sexual conflict.

CONCLUSIONS

We disagree with KGM's assessment of the models underlying sexual conflict, and note that the focus on female costs in sexual conflict research has a biological and theoretical basis. However, we agree with KGM that descriptive terminology can both arise from biases and lead to more biases. Although we do not believe it would be helpful to throw out sex-specific terminology, we share common ground with KGM in stressing the importance of giving consideration to terminology choices.

KGM conclude their review by stating: 'We believe that researchers in sexual selection can develop a more accurate picture of the sexual conflict process by becoming aware of and acknowledging their biases' (page 905). Here we are in full agreement, but would add that there is real value in understanding the models underlying the theories of sexual conflict and their assumptions.

We thank T. Day, C. Hinde, K. Karlsson Green, J. Madjidian, D. McLennan, J. Ward and two anonymous referees for comments that improved the manuscript. We are supported by the Natural Sciences and Engineering Research Council of Canada through grants to L.R. and a postdoctoral fellowship to J.P. L.R. is also supported by the Canada Research Chairs program.

References

Ah-King, M. 2007. Sexual selection revisited: towards a gender-neutral theory and practice. A response to Vandermassen's 'Sexual selection: a tale of male bias and feminist denial'. *European Journal of Women's Studies*, **14**, 341–348.

Ahnesjö, I., Vincent, A., Alatalo, R. V., Halliday, T. & Sutherland, W. J. 1993. The role of females in influencing mating patterns. *Behavioral Ecology*, **4**, 187–189.

Alonzo, S. H. 2007. Conflict between the sexes and cooperation within a sex can alter classic predictions of mating systems theory. *Evolutionary Ecology Research*, **9**, 145–156.

Andrés, J. A. & Morrow, E. H. 2003. The origin of interlocus sexual conflict: is sex-linkage important? *Journal of Evolutionary Biology*, **16**, 219–223.

Arnqvist, G. 1994. The cost of male secondary sexual traits: developmental constraints during ontogeny in a sexually dimorphic water strider. *American Naturalist*, **144**, 119–132.

Arnqvist, G. & Rowe, L. 2005. *Sexual Conflict*. Princeton, New Jersey: Princeton University Press.

Chapman, T. 2001. Seminal fluid-mediated fitness traits in *Drosophila*. *Heredity*, **87**, 511–521.

Dewsbury, D. A. 2005. The Darwin–Bateman Paradigm in historical context. *Integrative and Comparative Biology*, **45**, 831–837.

Eberhard, W. G. 1996. *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton, New Jersey: Princeton University Press.

Gavrilets, S. & Hayashi, T. I. 2006. The dynamics of two- and three-way sexual conflicts over mating. *Philosophical Transactions of the Royal Society B*, **361**, 345–354.

Gillott, C. 2003. Male accessory gland secretions: modulators of female reproductive physiology and behaviour. *Annual Review of Entomology*, **48**, 163–184.

Gowaty, P. A. 1997. Sexual dialectics, sexual selection and variation in reproductive behavior. In: *Feminism in Evolutionary Biology: Boundaries, Intersections, and Frontiers* (Ed. by P. A. Gowaty), pp. 351–384. New York: Chapman & Hall.

Gowaty, P. A. 2003. Sexual natures: how feminism changed evolutionary biology. *Signs*, **28**, 901–921.

Gowaty, P. A. 2004. Sex roles, contests for the control of reproduction, and sexual selection. In: *Sexual Selection in Primates: New and Comparative Perspectives* (Ed. by P. Kappeler & C. van Schaik), pp. 37–54. Cambridge: Cambridge University Press.

Härdling, R., Smith, H. G., Jormalainen, V. & Tuomi, J. 2001. Resolution of evolutionary conflicts: costly behaviours enforce the evolution of cost-free competition. *Evolutionary Ecology Research*, **3**, 829–844.

Johnstone, R. A. & Keller, L. 2000. How males can gain by harming their mates: sexual conflict, seminal toxins, and the cost of mating. *American Naturalist*, **156**, 368–377.

Karlsson Green, K. & Madjidian, J. A. 2011. Active males, reactive females: stereotypic sex roles in sexual conflict research? *Animal Behaviour*, **81**, 901–907.

Kirkpatrick, M. & Ryan, M. J. 1991. The evolution of mating preferences and the paradox of the lek. *Nature*, **350**, 33–38.

Kokko, H. 2005. Treat 'em mean, keep 'em (sometimes) keen: evolution of female preferences for dominant and coercive males. *Evolutionary Ecology*, **19**, 123–135.

Kokko, H. & Brooks, R. 2003. Sexy to die for? Sexual selection and the risk of extinction. *Annales Zoologici Fennici*, **40**, 207–219.

Moore, A. J. & Pizzari, T. 2005. Quantitative genetic models of sexual conflict based on interacting phenotypes. *American Naturalist*, **165**, S88–S97.

Parker, G. A. 1979. Sexual selection and sexual conflict. In: *Sexual Selection and Reproductive Competition in Insects* (Ed. by M. S. Blum & N. A. Blum), pp. 123–166. New York: Academic Press.

Parker, G. A. 2006. Sexual conflict over mating and fertilization: an overview. *Philosophical Transactions of the Royal Society B*, **361**, 235–259.

Parker, G. A. & Partridge, L. 1998. Sexual conflict and speciation. *Philosophical Transactions of the Royal Society B*, **353**, 261–274.

Rice, W. R., Stewart, A. D., Morrow, E. H., Linder, J. E., Orteiza, N. & Byrne, P. G. 2006. Assessing sexual conflict in the *Drosophila melanogaster* laboratory model system. *Philosophical Transactions of the Royal Society B*, **361**, 287–299.

Rowe, L. 1994. The cost of mating and mate choice in water striders. *Animal Behaviour*, **48**, 1049–1056.

Rowe, L. & Day, T. 2006. Detecting sexual conflict and sexually antagonistic coevolution. *Philosophical Transactions of the Royal Society B*, **361**, 277–285.

Rowe, L., Cameron, E. & Day, T. 2003. Detecting sexually antagonistic coevolution with population crosses. *Proceedings of the Royal Society B*, **270**, 2009–2016.

Stevenson, I. R. & Bancroft, D. R. 1995. Fluctuating trade-offs favour precocial maturity in male Soay sheep. *Proceedings of the Royal Society B*, **262**, 267–275.

Westlake, K. P. & Rowe, L. 1999. Developmental costs of male sexual traits in the water strider *Rheumatobates rileyi*. *Canadian Journal of Zoology*, **77**, 917–922.

Zuk, M. 2002. *Sexual Selections: What We Can and Can't Learn About Sex From Animals*. Berkeley, California: University of California Press.