

Opinion piece

The conditional economics of sexual conflict

Sexual conflict is a fundamentally important aspect of male–female interactions. In this opinion piece, we emphasize two approaches that warrant significantly greater attention. First, we review the importance of understanding the ‘economics’ (costs and benefits) of sexual interactions and note surprisingly large, unrecognized gaps in our knowledge. Second, we highlight the novel obstacles and opportunities afforded by the dependence of sexually antagonistic (SA) selection on both the local environment and condition of the interacting individuals. We conclude that more research in these two areas is essential to fully understand the evolution of SA interactions and will provide significant new insights into the extent to which coevolution of the sexes is shaped by conflict. We argue that these approaches, although not new to the field, are undervalued and under-represented.

Keywords: accessory gland proteins; nuptial gifts; sexually antagonistic coevolution

1. INTRODUCTION

Sexual conflict is now widely recognized as an important component of male–female interactions. It creates a novel opportunity for selection, not captured by models of sexual selection, which can drive the coevolution of sexually antagonistic (SA) traits that can potentially result in opposing fitness effects in the two sexes (Arnqvist & Rowe 2005). In this opinion piece, we make two points about well known but under used approaches.

First, we emphasize that economic studies have an essential role in assessing the extent of SA interactions and thus their potential to drive coevolution. Theory shows that the extent to which SA traits coevolve, and the extent to which population fitness declines as a result, depend crucially on the mating ‘economy’, i.e. the fitness costs and benefits of traits that mediate male–female interactions (Parker 1979; Rowe & Day 2006). There are now many examples in which sexual conflict is thought to drive the evolution of mating behaviour and morphology. However, there are surprisingly few systems in which the full economy of sexual traits has been assessed, including costs of producing and bearing traits, benefits of trait expression and costs and benefits of processing or resisting traits for the other sex. The lack of such data is notable because economic studies are needed (i) to infer the extent to which SA coevolution influences overall population

fitness and (ii) to substantiate broad-scale patterns suggested by comparative and experimental evolution studies, which otherwise are indistinguishable from patterns predicted by other models of sexual selection (Arnqvist & Rowe 2005; Rowe & Day 2006).

Our second point is that, although the role of density and environmental factors in studies of sexual selection is well recognized (e.g. Kokko & Rankin 2006; Candolin & Heuschele 2008), such effects have been largely overlooked in studies of sexual conflict. New empirical data demonstrate that the economics of antagonistic traits and interactions can depend on both the local environment and condition of the interacting individuals, which together greatly reduce the precision with which the outcome of SA coevolution can be predicted. This concern may be especially important for economic studies conducted in uniform laboratory environments.

2. THE ECONOMY OF CONFLICT

Two critical questions in determining whether sexual conflict underlies the evolution of male and female traits are: (i) is there SA selection on the traits shared by the two sexes that arise from sexual interactions (e.g. mating rate and offspring provisioning)? and (ii) are there sex-specific traits that function to shift the shared trait in the direction favoured by the bearer?

As an example, consider the mating interactions of *Callosobruchus* beetles. The optimal mating duration is predicted to be higher for males than for females, and females reduce mating duration and increase their fitness, by kicking at males using their enlarged hind legs (Crudgington & Siva-Jothy 2000). These data establish that mating duration is under SA selection and that enlarged female rear legs are an SA trait. A manipulation of mating duration, followed by measurements of fitness in the two sexes, is an economic study that would identify mating duration as a shared trait under SA selection. A manipulation of leg size in females, followed by measurements of mating duration, is a functional study that could identify leg size as an SA trait.

There are many systems for which answers to questions (i) and (ii) above are partially known. Several studies have shown divergent sex-specific optima for traits shared between the sexes, hence predicting SA selection. For example, in contrast to males, females tend to experience costs from elevated mating rates, e.g. in invertebrates (*Drosophila melanogaster*, *Cimex lectularius* and *Gerris* spp.), birds (*Prunella modularis*) and fishes (*Poecilia reticulata*). Sexual conflict also occurs over the shared trait of brood care in penduline tits (*Remiz pendulinus*), burying beetles (*Nicrophorus* spp.), dung beetles (*Onthophagus taurus*) and in Galilee St Peter’s fish (*Sarotherodon galilaeus*) (Arnqvist & Rowe 2005). In other systems, potential SA traits have been identified, including ejaculate proteins in *Drosophila*, the needle-like aedagus in *C. lectularius*, the notal organ in *Panorpa* scorpion flies and the ‘gin trap’ in *Cyphoderris strepitans* (Arnqvist & Rowe 2005). In studies of sexual conflict, there are remarkably few examples of SA traits in females. Two examples of female morphological SA traits include the spermatheca in female *C. lectularius* (Reinhardt *et al.* 2003) and the abdominal spines in female

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Gerris incognitus (Arnqvist & Rowe 1995). There are also examples of female behaviours that function to reduce the costs or effectiveness of harassment by males, e.g. avoidance of male mate guarding (Bussiere *et al.* 2006) and shoaling behaviour in fish (Pilastro *et al.* 2003). Surprisingly, the number of studies providing evidence for coevolution between male and female SA traits in natural populations is currently limited to just two: one in *Gerris* water striders (Arnqvist & Rowe 2002) and one in *Callosobruchus* beetles (Rönn *et al.* 2007). In summary, fully realized cases of the full economy of mating interactions subject to SA selection are scarce indeed.

To highlight how functional and economic studies can offer new and significant insights, we explore two examples. *Drosophila* has been extensively studied as a model for sexual conflict. Yet even here there remains much to learn. Male harassment and mating are costly to *D. melanogaster* females, and both male harmfulness to females and female resistance to mating costs can evolve (e.g. Rice 1996). Male-imposed mating costs for females are caused by the transfer of ejaculatory proteins such as the 'sex peptide' (Wigby & Chapman 2005), which increases male paternity (Fricke *et al.* 2009). Thus, sex peptide is a potential mediator of sexual conflict. However, our understanding is incomplete because we also need to know (i) whether females can resist, and evolve resistance to, the effects of sex peptide; (ii) the extent of female resistance costs; (iii) the costs of sex peptide production and transfer; and (iv) the extent to which antagonistic selection is environmentally determined and condition dependent. Hence, a considerable depth of information is required.

In our second example, we point out that recent economic studies suggest the potential for conflict over nuptial gift giving, a system long considered a model for cooperation. In some species, nuptial gifts have a demonstrated nutritional benefit (Gwynne 2008); however, in others, such benefits are small or absent, with the main function of gifts instead being the transfer of male seminal products that can manipulate female behaviour (Vahed 2007a). There is no shortage of data on the phenotypic effects of gifts to answer question (ii) above (reviewed in Vahed 2007a; Gwynne 2008). However, there are as-yet surprisingly limited data on sex-specific selection on those shared traits influenced by gifts (question (i)). Testing the hypothesis that nuptial gifts are subject to SA selection requires economic studies that measure the long-term effects of gifts on female lifespan and lifetime fecundity. Studies that have adopted this approach have cast doubt on the generality of the cooperative benefits of gifts (e.g. Perry & Rowe 2008). Instead, for some species, gift ingestion influences shared traits in ways that are likely to benefit males (e.g. increasing female resistance to remating, Perry & Rowe 2008) but for which benefits or costs to females are unknown. Data on the costs of trait production are also rare. One of the few examples of male production costs for a potential SA trait comes from a comparative study in bushcrickets, in which the production of large nuptial gifts that reduce female remating rate was shown to be costly to males (Vahed 2007b).

3. ENVIRONMENTAL SENSITIVITY AND CONDITION DEPENDENCE

It has long been recognized that ecological factors such as resources, density, mate availability and the condition of the players involved all affect the strength of sexual selection and interactions between the sexes (e.g. Emlen & Oring 1977; Candolin & Heuschele 2008). However, apart from an examination of sexual conflict and mate availability (Kokko & Rankin 2006), almost no consideration has been given to the effects of local environment and condition in economic studies of sexual conflict. Instead, coevolution between males and females driven by SA selection has essentially been viewed as an invariant process. In terms of sexual selection, Candolin & Heuschele (2008, p. 447) highlight that 'surprisingly little attention has been given to how plasticity influences the costs and benefits of sexually selected traits and their adaptive value under changing conditions'. We stress that this is even more marked in studies of SA traits.

Expanding the study of the economics of sexual conflict to span a realistic range of environmental and individual conditions is likely to create both obstacles and opportunities. Obstacles will arise because environmental and condition dependence means that more work is necessary: it will generally not be sufficient to conduct functional and economic studies under one set of conditions. For example, the ecological setting can significantly change the economics of sexual conflict. Male seaweed flies (*Coelopa frigida*) harass females more intensely (leading to a higher mating rate) when held on the preferred oviposition site of brown algae compared with the naturally sympatric brown algae (Edward & Gilburn 2007). Population-level characteristics are also part of the local environment and can influence selection on SA traits. For example, females in populations with male-biased sex ratios or under higher population densities can experience increased male harassment, which may lead to reduced female resistance, as in the water strider *Gerris buenoi* (Rowe 1992). Hence, measures of conflict and exaggeration of SA traits could be intensified under high harassment (Arnqvist 1992).

In addition, the local environment is also likely to determine the effectiveness of each sex in moving the value of a shared trait towards its own optimum, through effects on individual condition. For example, female nutritional condition alters the strength and even the sign of the effect of nuptial gift giving on traits such as fecundity and remating interval (Bonduriansky *et al.* 2005). Furthermore, the size/quality of nuptial gifts can depend on male condition (e.g. Vahed 2007a). Such condition dependence may lead to variable selection pressures on each sex depending on whether the gift is beneficial, or costly and manipulative. Thus, attention to condition dependence is required to design effective studies of sexual conflict and SA traits.

New opportunities may include the possibility of direct tests of how mating economics influence the outcome of SA interactions, by using experimental manipulations of condition to alter trait costs and benefits. There are also potentially exciting new

insights into how SA dynamics switch from mutualistic to antagonistic (Fricke *et al.* 2008). In order to assess the likely importance of such phenomena, we need more investigations of the relative environmental sensitivity and plasticity of male and female traits. This could differ, given that interacting SA traits can be morphological in one sex and behavioural in the other (e.g. male claspers versus struggling or fleeing in females). Studies are required that test the effect of environmental variation on (i) female resistance and (ii) male traits that are suspected to function in overcoming female resistance. Such female behavioural plasticity could itself evolve and contribute to variability in responses to SA selection between different populations.

4. CONCLUSIONS

We have highlighted that economic studies of the traits involved in sexual conflict are incomplete and that the value of such studies is underappreciated. There are surprising gaps in our knowledge of the economics of sexual conflict and especially of SA traits in females, just as there are in similar studies of sexual selection. Such studies are important because they allow us to identify the traits subject to selection arising from sexual conflict and to correctly interpret comparative and experimental evolution studies.

Our second aim was to underscore the importance of the local environment and of individual condition on sexual conflict. Such effects can make the design and interpretation of large-scale pattern studies of sexual conflict challenging. However, exploring the effects of local environment and of individual condition on antagonistic interactions will also lead to new insights and a richer understanding of SA coevolution.

In some ways, the current state of affairs mimics an earlier debate in life-history research, in which the most appropriate way in which to measure life-history trade-offs was discussed (e.g. Partridge & Harvey 1985; Reznick 1992). There, the general outcome was that strongest inferences came from manipulative rather than correlational studies and that conclusions were stronger when supported by both phenotypic and genetic approaches. To borrow from that earlier debate, we now need studies that are trait-centred, manipulative rather than correlational and that use multiple approaches.

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