



Active males, reactive females: stereotypic sex roles in sexual conflict research?

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Sexual selection research has always been a subject for debate. Much of the criticism has concerned the imposition of conventional sex roles based on an anthropomorphic view of animals imposed by the researcher. This conventional view may have hampered research, for example from acknowledging male mate choice. Sexual conflict theory is a fast-growing research field, which initially stems from sexual selection research. We investigated how the sexes are described in sexual conflict research and what characteristics they are assigned. We assessed these topics with literature studies of (1) the terminology used and (2) what parameters are incorporated in sexual conflict models. We found that males and females are consequently described with different words, which have different connotations regarding activity in the conflict. Furthermore, theoretical models mainly investigate conflict costs for females, although costs for both sexes are necessary for coevolutionary dynamics. We argue that sexual conflict research uses stereotypic characterizations of the sexes, where males are active and females reactive. Thus, previous discussions on the use of anthropomorphic terms in sexual selection seem not to have had any impact on sexual conflict research, which is why the topic of stereotyping the sexes is still of current importance. We suggest that scientific gains can be made by eliminating a sex-stereotyped perspective. © 2011 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Sexual selection research has contributed to important insights in evolutionary research, but has also been subjected to controversy and debate since Darwin (1871). Much of the debate has been devoted to the relative importance and degree of sexual selection in the two sexes (Brown Blackwell 1875 cited in Fausto-Sterling 1997; Gowaty 1997; Clutton-Brock 2007), of which much may stem from the fact that we, as researchers, have a preconceived view of how the sexes should act. In recent years, several authors have pointed at weaknesses and misinterpretations in the theory of sexual selection (Clutton-Brock 2007; Snyder & Gowaty 2007; Kokko & Jennions 2008; Roughgarden & Akçay 2010), mainly concerning the use of sex roles and how they are assigned. Well-known examples include the common extrapolation from anisogamy to sex roles stemming from Trivers (1972) (Gowaty 1997; Tang-Martinez 1997), the overreliance on Bateman's principle as an explanation of mating system differences between species (Bateman 1948; Tang-Martinez & Ryder 2005; Snyder & Gowaty 2007; Brown et al. 2009) and the use of operational sex ratio (OSR) rather than both OSR and adult sex ratio (ASR) when determining sex roles (Kokko & Jennions 2008). Other authors have

criticized sexual selection theory from other viewpoints, namely the language used, both for stereotypic description of the sexes, for example coy females (Hrdy 1986; Martin 1991; Fox Keller 2004), and for using anthropomorphic terms with provocative connotations, for example rape (Gowaty 1982).

Accumulated evidence from different taxa shows a more diverse nature of the sexes than traditionally thought, through male mate choice (reviewed in Bonduriansky 2001; Hill 1993; Amundsen et al. 1997; Gowaty et al. 2003; Bel-Venner et al. 2008; Härdling et al. 2008; Bonduriansky 2009), female competition (e.g. Kempenaers 1994; Slagsvold & Lifjeld 1994; Sandell & Smith 1996; Rosvall 2008; Rillich et al. 2009) and species with mutual mate choice (Jones & Hunter 1993; Gowaty et al. 2002; Forsgren et al. 2004; modelled in Bergstrom & Real 2000). For example, which sex is predominantly competitive does not determine whether that sex discriminates between mates, as both sexes can be simultaneously competitive and choosy (Berglund et al. 2005). The use of conventional sex roles and anthropomorphic interpretations may in fact have affected sexual selection research by delaying the realization and acceptance of female cryptic choice (Birkhead & Pizzari 2002). In international workshops it has therefore been suggested to look beyond conventional sex roles (Cunningham & Birkhead 1997; Kvarnemo et al. 2009), and proposals have been made on how to overcome the biased research tradition (e.g. Gowaty & Hubbell 2005; Kokko & Jennions 2008). However, the debate has not yet addressed sexual conflict studies, although

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sexual conflict theory emerged from sexual selection (reviewed in [Bonduriansky 2009](#)).

The novelty in sexual conflict theory lies within the sexually antagonistic selection ([Parker 1979](#)) rather than selection through mutual benefits as in classic sexual selection theory ([Darwin 1871](#); [Andersson 1994](#)). That is, in a sexual conflict the sexes' selection gradients are opposing. This means that a given trait may be selected for in one direction for males and in another for females. Previously, the focus of sexual selection research was on how variance in male reproductive success is generated ([Shuster & Wade 2003](#)), via both male competition and female choice. With the advent of sexual conflict research, the focus has shifted towards female costs of reproduction and how both sexes strive to reach their fitness interests.

In this review, we explore sexual conflict in the frame of the insights of stereotyping in sexual selection research. Ideas on what sex roles encompass may have the capacity to affect how research is carried out; thus a continued use of conventional sex roles may hamper research by limiting the potential research questions. This is the first study to address how sexual conflict theory has been conceptualized with regard to sex roles. To identify whether and to what extent sexual conflict research reflects conventional sex roles, and whether this affects research, we performed two literature searches. In the first, we focused on the terminology describing sexually antagonistic traits. This allowed us to contrast differences in how the sexes are described. If the previous discussion of stereotyped terminology in sexual selection research is acknowledged, we would expect to find neutral or nonsex-specific terms. In the second literature search, we explored which parameters are taken into account in sexual conflict models, because only the parameters that are included will be considered as important for the conflict's outcome. If sexual conflict research makes use of stereotyped sex roles we would expect to find a consistent pattern throughout both terminology and theoretical models where distinct words and characters are assigned to the sexes, and where these words and characters imply active males and passive females.

LITERATURE SEARCH

Sexual Conflict Terminology: Methods and Results

Sexual conflict researchers have utilized several terms illustrating how males and females respond to each other during a sexual conflict (e.g. 'arms race', 'battle of the sexes', 'tug of war'), and have also coined terms describing the sexually antagonistic traits. By examining the 30 most cited studies that included the keyword 'sexual conflict' in Web of Science (28 May 2009, including reviews, empirical and theoretical studies), we assessed which terms are most used (see [Appendix](#) for references). The citation range for the 30 studies was 90–390. Of the 30 studies, 23 used terms describing sexually antagonistic traits and altogether we found 17 different terms for males and 11 for females ([Fig. 1](#)). The empirical studies used fewer terms (nine in a total of 10 articles) compared to the reviews (21 in a total of 12 articles) and the model papers (16 in a total of eight articles). The terms describing sexually antagonistic traits were highly sex specific. Some examples are, for males, harassment, manipulation, coercion, persistence and adaptation, and, for females, resistance, avoidance, counteradaptation, reluctance and reduction (see [Fig. 1](#)). By categorizing each trait as active, as reactive or as neutral we could quantify the difference (see [Fig. 1](#) for categorization of terms). By 'reactive' we mean that the trait is a response to another act, and that the response trait itself does not fuel reactions by the opposite sex. We let two independent people categorize the traits, listed alphabetically, without any information on whether the terms stemmed from males or females.

The terms classified differently by the two persons were excluded from the analysis. These excluded terms were words that may be difficult to categorize because they either fall into a different part of speech or are ambiguous. For example, persistence is one of the most common terms used for describing male antagonistic traits, but it could also be understood in the sense of species persistence. We investigated whether there was a difference between how the sexes were described. We found that males were described as active and females as reactive ($\chi^2_1 = 187.39, P < 0.0001$). These terms may imply three things: (1) it is the male that has the upper hand (the male adapts while the female counteradapts; [Parker 1979](#)), (2) males seem to have more diverse and aggressive ways of safeguarding their interests while females most often 'resist' and (3) the terminology partially reflects sex-stereotypic notions.

Parameters Included in Sexual Conflict Models: Methods and Results

We surveyed all theoretical models obtained under the keyword 'sexual conflict' in BIOSIS (performed 4 March 2009, $N = 26$); both verbal and mathematical models were included but not reviews (see [Table 1](#) for references). Models for which it was impossible to assess the conflict parameters (e.g. where the main focus is outside the conflict or where costs are not incorporated at all) were excluded. By 'cost', we here mean cost arising from mating, parental investment or antagonistic interactions, but not the cost of producing antagonistic traits. Thus only costs that are inflicted by the opposite sex and not the costs that an individual bears from its own adaptations are considered. When cost for trait production is incorporated in models it is most often accounted for in both sexes and included besides the actual mating or parental investment cost, which we have here defined as conflict cost (see e.g. [Parker 1979](#); [Lankinen et al. 2006](#)). Our aim was not to question the mathematical correctness of the models, but rather to examine how extensive they are and how much variation exists between them, with regard to sex roles. From this literature study, it is evident that female cost is what has mainly been investigated in sexual conflict research ([Table 1](#)). Fourteen articles include only female conflict costs or fitness reduction in their model while none considers a cost for the male only ([Table 1](#)). The number of articles that include both a male and a female cost is very high; 12 papers consider conflict costs for both sexes ([Table 1](#)). Among the articles that include both male and female conflict costs, six model conflicts over parental care. Models over mating rate are represented only in the group with exclusively female conflict costs. Thus, there is a clear difference in what kinds of costs are incorporated, depending on the particular conflict. It is also worth noting that in some cases it is assumed that males are always much more powerful than females ([Clutton-Brock & Parker 1995](#)), that males are allowed to choose their conflict strategy before females ([Barta et al. 2002](#)), and that male fitness never decreases with mating rate ([Haygood 2004](#)). To investigate whether the trend found in the theoretical models is valid for the wider sexual conflict field, we performed an additional search on male cost and female cost found in abstracts in BIOSIS (two searches: (1) female* cost* sexual* conflict*, (2) female* cost* sexual* conflict* NOT male* cost* sexual* conflict*, 25 May 2010). Of 284 abstracts, 145 included sexual conflict and costs. This search confirmed the previous pattern: 106 abstracts considered female costs while 30 took both sexes into account and only nine considered male costs ([Fig. 2](#)).

DISCUSSION

We analysed the sex roles in sexual conflict research through literature studies and found that males are commonly described with active terms and females with reactive ones. Fitness costs

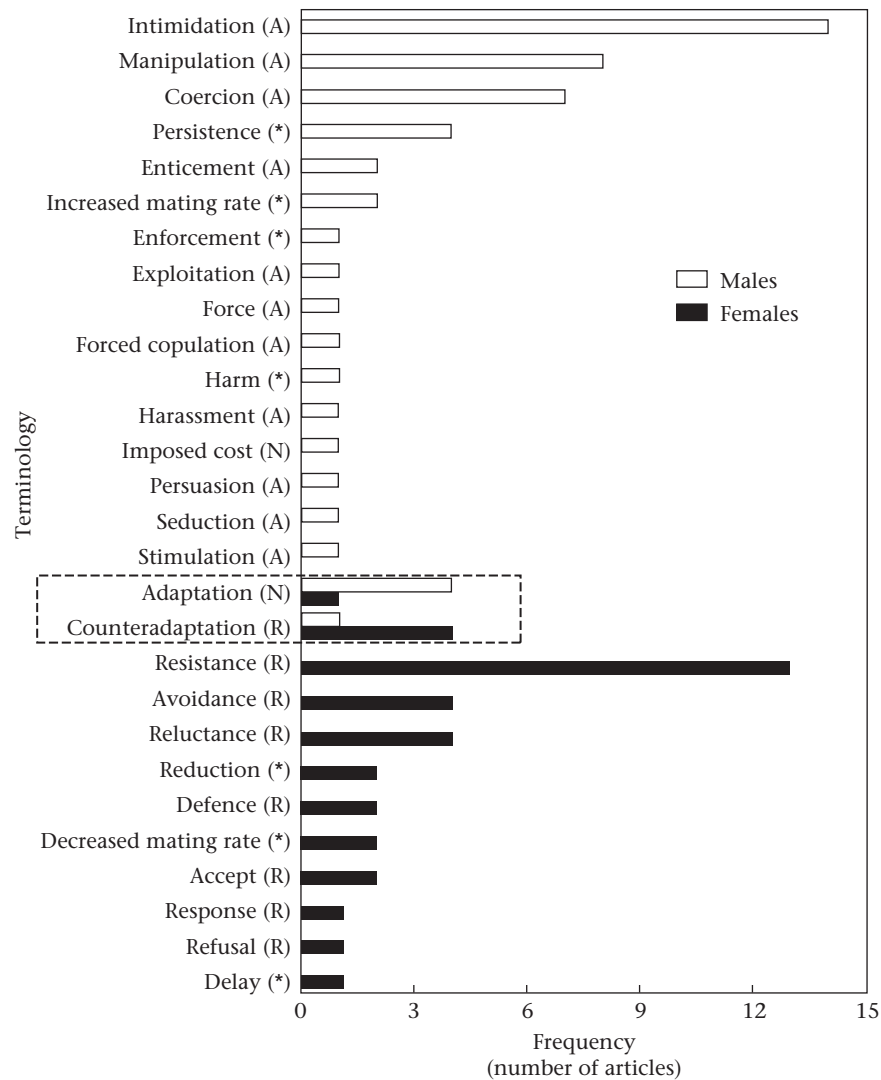


Figure 1. Terms found describing sexually antagonistic traits of the sexes in the 30 most cited sexual conflict articles (see [Appendix](#) for references). On the Y axis are the terminology used for males (white bars) and females (black bars), respectively, and on the X axis the number of articles in which the different terms are found. Within the dashed lines terms used for both sexes are highlighted. A = active; R = reactive; N = neutral (could be either active or reactive or neither). * Terms categorized differently by two independent people and thus excluded from the chi-square test.

from sexual conflicts in theoretical models are typically considered only for females. However, the bias may depend on the particular conflict being modelled. Apparently, the use of anthropomorphic and stereotyped terms in biology is commonplace, although

already intensely debated in sexual selection research ([Gowaty 1982](#); [Hrdy 1986](#); [Martin 1991](#); [Fox Keller 2004](#)). How is it that we have not learned from earlier discussions but continue stereotyping the sexes when a new research field is being established? It seems to be of major importance to consider stereotyping and its

Table 1
Number of models that incorporate conflict costs for one of the sexes or both

Parameter	Number of articles	References
Male cost only	0	
Female cost only	14	Parker 1979; Gavrillets 2000; Johnstone & Keller 2000; Gavrillets et al. 2001; Gavrillets & Waxman 2002; Andrés & Morrow 2003; Kokko & Brooks 2003; Haygood 2004; Rowe et al. 2005; Härdling & Bergsten 2006; Lankinen et al. 2006; Alonzo 2007; Hayashi et al. 2007a, b
Male and female costs	12	Leonard 1990; Clutton-Brock & Parker 1995; Smith & Härdling 2000; Hayashi & Kawata 2001; Härdling & Kaitala 2001, 2004, 2005; Barta et al. 2002; Lessells 2002; Ball & Parker 2003; Härdling & Smith 2005; Moore & Pizzari 2005

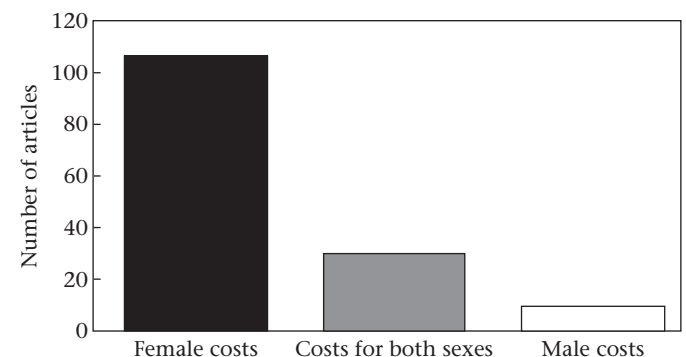


Figure 2. Number of articles taking costs of sexual conflict into account for females (black bar), both sexes (grey bar) or males (white bar).

effects continuously. Below, we discuss the implications for sexual conflict research and suggest future directions for more objective research and further progress.

On the Use of Sex-stereotyped Terminology

The terminology used in the most cited sexual conflict studies implies that males are offensive, that is, they are the ones first acquiring an antagonistic adaptation, which females then react to. In true coevolution it is not possible to disentangle who acts first; the idea that males take the first step may thus be caused by a sex-stereotypic preconception. It may of course be argued that, for purely physiological reasons, males would need to take an active step to penetrate the female. But would this mean that all (or most) female (re-)actions do not mediate further (re-)actions in males? One could also compare this situation with other situations in coevolution, such as host–parasite or predator–prey systems, where similar phrasing may be used with active terms for the parasite and predator and defensive terms for the host and prey. Still, there is one difference: in male–female coevolution both males and females need something from their partner (in contrast to the prey, which does not need anything from the predator) and it is in both sexes' interest to reproduce. They just differ in when, how often and with whom. The current characterization of sex roles in sexual conflict research can be compared to how females were described in more passive terms, for example as coy, in traditional sexual selection. Thus, males are described with active and females with reactive phrasing (Fig. 1), although both actively affect each other.

In the hermaphroditic garden snail *Helix aspersa*, sperm is digested by the recipient, and it has been suggested that sperm digestion could indeed be a direct cost to the male sexual function (see e.g. Rogers & Chase 2001; Arnqvist & Rowe 2005). In these snails the male part inserts a so-called love dart in the female genitalia, which seals the entrance and allows sperm to escape digestion. The love dart could be explained as a resistance adaptation to the (our note: manipulative) sperm digestion performed by the female sexual function. However, the love dart may be inserted to manipulate the recipient's sperm digestion (Rogers & Chase 2001). It is clearly the male that would suffer a cost, but still the response is not described with a reactive term but with an active one (manipulation). Why are different words used for describing antagonistic traits depending on whether it is a male or a female that is imposing a cost on the partner? Could it be that the antagonistic terms are based on a traditional view of conventional sex roles, that is, that in western human society males are traditionally considered as active and females as passive?

Our concern is not that the traits and behaviours are described with different words in the two sexes per se. It is rather the different connotations that are present throughout the terminology, and, in turn, how these will affect us as researchers that are our concern. The image of reactive females implied by the terminology may affect the research carried out; for example the male's response to female antagonism and the subsequent negative effects in males may not be investigated. Indeed, it should be possible to use the neutral term 'sexually antagonistic trait' for both males and females, and if necessary describe the trait further. Also, in both males and females a sexually antagonistic trait can be considered as a manipulation rather than differentiating between 'manipulation' and 'resistance'.

The anthropomorphic terminology used for describing behaviour and traits could further have affected the choice of study species. So far, only a few studies have investigated sexual conflicts in organisms beyond bisexual animal species (Bedhomme et al. 2009). Active actions, such as force, may be difficult to envisage in plants and in animals with very primitive mental resources, and the stereotypic terminology may limit research to only separate-sexed

animals. That is, sex-stereotypic terms such as 'harass' and 'resist' will certainly give a picture of a male and a female engaged in reproduction and other sexual systems may not be associated with such terms. Also, the captivating words describing the sexes' interactions ('battle', 'war' etc.) may be problematic in this respect. This may be relevant for other fields of evolutionary biology, in particular sexual selection theory, where anthropomorphic description makes it seemingly difficult to apply the theory, for example to plants.

On the Bias in Theoretical Models

Some authors have stressed the importance of defining and measuring net costs and benefits of each sex when investigating sexual conflict (Chapman et al. 2003; Fricke et al. 2009). However, we found that most sexual conflict models focus on costs only for the female (Table 1). This was particularly evident in modelled conflict over mating rate. The potential costs that males in nature may suffer from female antagonistic actions (i.e. the costs for not reaching the male optimum) in conflict over mating are not explored. Models of sexual conflict over parental care seem to have a more neutral approach to assessing the sexes' costs and benefits in the conflict, taking both males' and females' fitness interests into account. This may be a consequence of the fact that which is the care-giving sex varies between different groups of organisms, opening our eyes to the idea that care may be a maternal, paternal or biparental task. In such conflicts both sexes may have similar choices of staying or deserting, and face the same consequential costs and benefits. In conflict over mating rate, however, the sexes may have very different choices and face different consequences. Of course, no model could address all possible parameters but there may be a bias in what factors are incorporated. Although mathematically correct, the models leave out the possibility of negative effects on males from female antagonistic actions. How accurately does such a theoretical approach reflect how sexual conflict operates in nature? Parker (1979) divided the costs of mating into 'power' (relative contest costs, i.e. cost of enforcing victory, the average rates of expenditure of contest costs and the ability to inflict damage) and 'value of winning' (relative fitness difference between mating and not mating). The cost of power could be equally big for a male or a female, while the value of winning is thought to be smaller for females (Parker 1979). This idea comes from the assumption that sexual selection operates more intensely on males than on females, because the reproductive potential of males is often greater (Parker 1979). The assumption that female fitness decreases at higher mating rates is present already in Parker's (1979) paper, the first on sexual conflict theory. This view may stem from Bateman (1948) and has been criticized elsewhere (Tang-Martinez & Ryder 2005; Snyder & Gowaty 2007; Brown et al. 2009). There is support for the idea that females gain directly from polyandry in terms of increased lifetime offspring production (Arnqvist & Nilsson 2000). For both males and females, several different relationships between fecundity and mating success are possible (Arnold 1994). However, in models of sexual conflict, male fitness is mainly viewed as linearly increasing with number of matings (e.g. Gavrillets et al. 2001), while female fitness is optimal at an intermediate mating rate. If mating rate is too high, female fitness decreases and females suffer a fitness cost. Similarly, if mating rate is decreased (from female antagonistic adaptations) male fitness will be lower (than it could potentially be with a higher mating rate): will a male not suffer a fitness cost similar to females? Or are females always supposed to be harmed, which gives an additional cost besides a lower than optimal fitness?

Even if lowered male mating rates actually give the same outcome as if male costs were explicitly incorporated, there may be a problem with not acknowledging the decrease as costs. This view may imply

that it is primarily sexual selection that is operating in males (i.e. decreased fitness as lost opportunity of mating in comparison with other males) and sexual conflict, with its important feature of direct costs, is mainly operating on females (i.e. decreased fitness caused by conflict cost from male actions). An interesting parallel is what Clutton-Brock (2007) wrote concerning sexual selection in females: that despite Darwin's (1871) broad definition of sexual selection in both sexes, intrasexual competitive ability of individuals is thought to contribute to sexual selection if it occurs in males but not in females (e.g. competition for food to offspring). Maybe such narrowing of the research field is reflected in sexual conflict if female costs are attributed to the conflict, while male costs of missed opportunity of reproduction are considered as sexual selection. This is despite the possibility that it might be a female adaptation that prevents the male from reaching his optimum mating rate. Perhaps a clear division between 'harm costs' and 'lost opportunity costs' would make it easier to acknowledge costs for males.

The scientific language used could be an important factor involved in shaping the gender skew in consideration of costs. As it is, costs are imposed by active traits (of males) on an individual (female) with conflict traits or behaviours that have a more vulnerable resonance (e.g. resistance). Thus, only active terminology implies that a trait infers costs. In turn, this could strongly affect which experiments are conducted and thus which research results we will get. As a result, stereotyping may have limited the research questions and therefore not have provided an accurate picture of sexual conflicts in nature.

Male Costs and Interpretation of Behaviour in Empirical Studies

Both models and the terms describing sexually antagonistic traits imply that there are no costs inflicted on males. 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. If so, this assumption should be made explicit and preferably empirically investigated, which until now has not been done (Fig. 2). In fact, it is possible to study costs of both sexes within the same experiment. An example is Holland & Rice's (1999) study in which imposed monogamy resulted in less antagonism from both sexes and higher population fitness. Incorporating costs of both sexes could have been done in several other studies. In Rice (1996), for instance, the experimental arrest of female but not male evolution resulted in reduced female survivorship. It would be both interesting and possible to arrest male evolution to infer how male fitness components change when evolution of female antagonistic traits is allowed.

Where would one then expect to find male costs? The empirical evidence is scarce, but some examples are already present: survival during mating in isopods (Benesh et al. 2007) and cannibalism in spiders (cf. Arnqvist & Rowe 2005). The traits that male spiders possess to avoid being cannibalized (such as long legs, agility and vigilance) are said to represent sexually antagonistic adaptations, not resistance or counteradaptations! There are other cases where a male cost could be discussed, for example self-mutilation in spiders to insert a mating plug in females (in some species this self-mutilation is so extensive that the males become castrated; Kuntner et al. 2009a, b), or when females metabolize and neutralize potentially harmful substances in the sperm ejaculate (Arnqvist & Nilsson 2000). The reduction in relative mating success following neutralization of sperm toxins will be comparable to that in other males in sperm competition, but the actual cost comes from the female antagonistic trait (toxin neutralization; cf. female–female competition: Clutton-Brock 2007). Although the costs to females of toxic accessory gland proteins in the ejaculate have been much discussed, the potential costs a male incurs from female

manipulation of his ejaculates are, to our knowledge, not mentioned. Another example of a potential male cost is the sucking behaviour (digesting or removing seminal components) of recipients of the hermaphroditic marine worm *Macrostomum* sp. (Schärer et al. 2004). All these examples call for increased attention and a less constrained view of male costs in sexual conflict research (see Fricke et al. 2009).

Potential Causes of Bias and Directions for the Future

The pattern we see from our literature surveys may arise from factors other than gender bias, that is, a preconceived view of sex roles. For example, theory and research may have sprung from what is most elaborate and conspicuous in nature. Thus, arms races and the more severe 'battle of the sexes' may be what attract scientists in the first place. It may be that, since sexual conflict theory emerged from sexual selection, research has continued on the path of sexual selection where males are attributed most variation and action. It could also be that as science changes with time, we may eventually reach a state where more features of sexual conflict are studied in both sexes. However, whatever the reason is for the stereotypic pattern we discern, it may be worth asking what this bias is due to and how it will affect research.

As sexual selection research now suggests that the sex roles are less distinct than previously thought, and because important insights may be gained by looking outside the conventional sex roles (Cunningham & Birkhead 1998), it should be beneficial for sexual conflict theory to deal with the roles the sexes are assigned. Indeed, stereotyped theories may constrain rather than broaden our views and approaches. As another parallel from sexual selection theory, the importance of incorporating mutual choice in mate choice models, not using the traditional approach with only one sex that chooses, has been highlighted (Bergstrom & Real 2000). We suggest that the characterization of males and females as active and reactive (and bearing costs), respectively, may hamper the future development of sexual conflict research. For example, female adaptations and male costs may be overlooked and conflict dynamics may not be fully understood.

If there is a potential problem with the use of stereotypic sex roles in sexual conflict research, what should we do to overcome this bias? Even though we ourselves ponder these questions, we also fall into the same traps when designing experiments and when writing articles. One reason is that it is easiest to do 'what others do' and when communicating research it is convenient to use the common terminology to be best understood. However, if theory should be general it is worth being careful with terminology, striving to develop broad models (see Gowaty & Hubbell 2005, 2009) and designing empirical studies in which the same conflict features are studied in both sexes. For example, in cases with hermaphrodites, where evidence is now accumulating for the occurrence of sexual conflicts (Koene 2006; Lankinen & Kiboi 2007; Bedhomme et al. 2009; Madjidian & Lankinen 2009), conventional thinking about sex roles may be difficult or even useless.

Conclusions

Following Kuhn, objectivity in research may be an unattainable goal as scientists' perceptions are influenced by the paradigm they work within (Kuhn 1962; discussed with regard to sexual selection in Fausto-Sterling 1981; Fox Keller 1982). 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 and daring to take a step further. Good examples of how this has paved the way for new research are that male mate choice is becoming a 'hot topic' (e.g. Bonduriansky 2009) and that

female harassment of males (Bro-Jorgensen 2007) has recently been considered. Of course, we are not diminishing the importance of previous sexual conflict research, through which important insights into conflict dynamics have been obtained. However, whenever a new research field is established it may be wise to learn from the past and not fall into old traps. We hope that these reflections will encourage fruitful discussions that will help researchers consider their potential biases, gain new insights into their study systems or rediscover some overlooked aspects of the theory. Ultimately, objective research is a scientific goal, and norm-free thinking, here in terms of gender, may be a first step towards a more objective sexual conflict research field.

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APPENDIX

References from Literature Survey Addressing Terminology

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