Sexual Conflict and Sperm Competition

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Traits that increase a male's fertilization success during sperm competition can be harmful to females and therefore represent a source of sexual conflict. In this review, we consider the variety of male adaptations to sperm competition (MASC) that may give rise to sexual conflict—including mate guarding, prolonged copulations, the transfer of large numbers of sperm, and the manipulation of females through nonsperm components of the ejaculate. We then reflect on the fitness economics influencing the escalation of these sexual conflicts, considering the likelihood of females evolving traits to offset the negative effects of MASC when compared with the strong selection on males that lead to MASC. We conclude by discussing the potential evolutionary outcomes of sexual conflict arising from MASC, including the opportunities for females to mitigate conflict costs and the prospects for conflict resolution.

Male mate competition can lead to sexual conflict because male traits that increase the chances of securing a mate can reduce female fitness. For example, intense male–male competition for females in yellow dungflies can lead to females drowning in dung (Parker 1970a), or the large mandibles used to win male–male competition in *Gnathocerus* flour beetles reduce female fitness. This occurs via a chain of intra- and intersexual genetic correlations that results in female body morphology deviating from a fitness-optimizing feminine shape (Harano et al. 2010). Male–male competition can also continue after mating in the form of sperm competition, which arises whenever the ejaculates of two or more males are in direct competition to fertilize the same set of ova (Par-

ker 1970b, 1998). Sperm competition will select for male traits that increase a male's fertilization success, yet these traits can also be harmful to females and therefore represent a source of sexual conflict, even in situations in which females initiate polyandry (Stockley 1997).

In this article, we begin by briefly reviewing some of the many male adaptations to sperm competition (MASC) and how these can give rise to sexual conflict. We then go on to discuss factors that may govern the extent of sexual conflict arising from MASC. In particular, we reflect on the importance of the relative costs and benefits of these traits to males and females, as understanding the fitness economics of sexual conflict is central to determining the potential evolutionary trajectories of MASC. We con-

D.A. Edward et al.

clude by discussing avenues through which females could mitigate costs and the prospects for conflict resolution.

CAUSES OF SEXUAL CONFLICT

If the expression of a trait increases the fitness of one sex while reducing fitness of the other, sexual conflict occurs. In principle, it is straightforward to decide whether there is sexual conflict over a trait by simply asking, would trait values change if expression levels were completely controlled by only one sex. For example, if female influence on copulation duration or sperm storage is removed, does copulation duration increase/decrease or do sperm storage patterns differ (e.g., Hellriegel and Bernasconi 2000)?

Within this general framework there exists a wide variety of MASC that can lead to sexual conflict. Male adaptations include mating behaviors, such as mate guarding and extended or repeated copulation; alterations to ejaculate size or composition, including sperm number; and the use of copulatory plugs and strategic allocation of mating effort, including male mate choice (Parker 1970b, 1998; Edward and Chapman 2011). Some MASC may reduce either the risk or intensity of sperm competition (Parker 1998). For example, mate guarding or mating plugs made from ejaculate components (e.g., Fenton 1984) or detached male genitals (e.g., Nessler et al. 2007; Kuntner et al. 2009) can prevent or delay female remating, and a similar function has been suggested for copulatory stimulation (Stockley 2002). Indeed, any male trait that reduces female remating rates may have evolved, in part at least, through selection arising from the risk of sperm competition. Other MASC, rather than reducing competition, can increase male fitness when sperm directly compete. For example, adaptations that function in physically removing or debilitating rival sperm (e.g., Cordoba-Aguilar et al. 2003). MASC can also be classified as benefiting either the earlier mating male over subsequent competitors (i.e., defensive traits), or benefiting later mating males when a female has previously mated (i.e., offensive traits). Such adaptations

can each increase male fertilization success when sperm competition does arise and can result in sexual conflict.

The majority of examples of sexual conflict arising from MASC reviewed here relate to interlocus conflict (i.e., conflicting alleles are present at different loci in males and females). For example, a sexual conflict over mating duration may be determined by male persistence traits that are expressed at one locus and female resistance traits expressed at a different locus. However, MASC can potentially also give rise to intralocus sexual conflict (i.e., when an allele at a single locus has contrasting fitness effects when expressed in either males or females). Although there is currently limited direct evidence of this (Lewis et al. 2008), in *Callosobruchus maculatus*, males that are more harmful to their mates, which may increase male fitness, sire daughters that are more susceptible to harm (Gay et al. 2011).

Male Mating Behavior

Mate Guarding

Males can prevent or reduce the risk of sperm competition by guarding their mates. Mate guarding is found in many taxa and is manifest as either extended physical contact (including extended copulation—see below) or remaining close to recent partners so that copulations with other males can be delayed or prevented.

The prolonged association between males and females that occurs with mate guarding must generate opportunity costs for both sexes, as the time involved might otherwise be spent on other fitness-related activities such as foraging (e.g., Westneat 1994; Komdeur 2001). Mate guarding may be particularly costly for females if guarding males have low fertility, as reported for cockroaches, *Nauphoeta cinerea*, in which males that have become sperm depleted will continue to enforce female monogamy (Montrose et al. 2004). In some cases, mate guarding can also limit a female's ability to exercise cryptic mate choice, for example by delaying sperm ejection (Helfenstein et al. 2003), or may limit other aspects of behavior such as choice of oviposition sites (Smith et al. 2002). However,

mate guarding can also be beneficial for females if it reduces sexual harassment. Indeed, female blackbirds, *Turdus merula*, appear to actively prolong sexual activity to induce mate guarding, as they benefit from reduced harassment by other males and also receive greater paternal care of offspring from their guarders as a result (Wysocki and Halupka 2004).

Nonetheless, if mate guarding is costly for females, selection will favor female traits that reduce guarding duration. For example, females may struggle to escape from males, as in sepsid flies (Parker 1972; Hosken et al. 2003). However, this can generate additional costs for females (e.g., physical injury) and the extent of female resistance will depend on the relative costs of guarding and resistance. Where mate guarding is important to male reproductive success, as it is in sepsids (guarding males only mate after egg laying) (Parker 1972; Hosken et al. 2003), then males should respond to female resistance, potentially leading to coevolutionary arms races between male guarding and female resistance strategies. An excellent example of this is the correlated evolution of male grasping and female antigrasping structures found across 15 species of gerrid water striders (Arnqvist and Rowe 2002).

Extended or Repeated Copulations

Another MASC is to prolong mating, either by extending copula duration, pre- or postejaculation (e.g., Cordoba-Aguilar et al. 2009), or copulating repeatedly with the same female (e.g., Laird et al. 2004; Stockley and Preston 2004; Preston and Stockley 2006). There are many examples of males strategically altering copulation to benefit either from the guarding effect of this behavior (see above) or from transferring larger ejaculates to potentially achieve greater fertilization success (e.g., Wedell 1998; Martin and Hosken 2002).

Extended or repeated copulations typically allow males to pass more sperm or other non-sperm ejaculate components to their mates (see the section Ejaculate Variation below) and can also allow males to displace the ejaculates of previous rivals (Parker and Simmons 2000).

This is clearly beneficial in situations in which sperm number is the primary determinant of fertilization success during sperm competition (Parker 1984, 1998). Extended or repeated copulations may also give males greater opportunity to assess female mating status and to strategically adjust mating effort accordingly (see the section Strategic Allocation of Male Mating Effort below). Additionally, it has been suggested that males may repeatedly attempt to mate with the same female to assess receptivity to further copulations (Sato and Kohama 2007).

Prolonged copulations are likely to generate costs of mate guarding for females because the time might otherwise be spent on other activities. In addition, prolonged and repeated copulations may increase the risk of physical injury or disease transmission associated with mating (Hosken et al. 2003). If increased copulation duration or frequency is costly for females, then selection will favor traits that reduce these costs. For example, females may struggle to terminate copulation sooner, although males extend copulation beyond the female optima (Mazzi et al. 2009) and may even control kicking duration (Wilson and Tomkins 2014). Where males have evolved to physically prevent females escaping, struggles such as these may lead to physical injury of females (e.g., Hotzy and Arnqvist 2009; Johns et al. 2009). Nevertheless, an assessment of the level of sexual conflict arising from prolonged copulations should also consider potential benefits to females. Costs may be mitigated if females benefit from, for example, an increased ability to assess male quality or reduced costs of harassment from other males (e.g., Eberhard 1996). Females may also directly benefit from the receipt of more sperm or nuptial gifts (Arnqvist and Nilsson 2000).

Ejaculate Variation

Sperm Number, Quality, and Morphology

When sperm compete numerically, a male may increase his fertilization success simply by ejaculating more sperm (Parker 1998). This response to sperm competition risk has been shown repeatedly (e.g., Gage 1991; Simmons

D.A. Edward et al.

et al. 1993; Wedell 1998; Martin and Hosken 2002). Males can increase sperm number by increasing copulation duration, ejaculating repeatedly with the same female (see section above) or by increasing sperm transfer rates. This male strategy has many potential costs to females, including reducing female control of paternity and increasing the risk of polyspermy. This could explain why the female reproductive tract is typically hostile to sperm (Birkhead et al. 1993) and females may eject unwanted sperm (e.g., Manier et al. 2010; Dean et al. 2011b). Alternatively, when the intensity of sperm competition is high, or anticipated payoffs of mating are relatively low, males may benefit from transferring fewer sperm (Parker et al. 1996), or searching for alternative mating opportunities (Schwagmeyer and Parker 1990). In rainbow darters, *Etheostoma caeruleum*, larger males often forego mating opportunities in which there is a high intensity of sperm competition, instead conserving resources in anticipation of less competitive future matings (Fuller 1998). This may be costly for females if they benefit from polyandry or from mating with larger males.

In addition to varying sperm numbers, adjusting sperm quality may also be a MASC (Ball and Parker 1996). For example, sperm competition risk can influence sperm morphology and performance (Gage and Morrow 2003). However, selection for increased sperm swimming speed/fertilization efficiency is thought to be a key factor in the incidence and impact of polyspermy (Snook et al. 2011). So although highly competitive sperm may be advantageous for males, they may result in ova loss for females. If so, increased sperm competition, and associated MASC, may select for tolerance to polyspermy, which could explain why in some taxa, such as birds, polyspermy does not result in fertilization failure (Snook et al. 2011).

Greater investment in sperm number or sperm quality will ultimately trade off against other traits (Parker 1998). Sperm number and quality may also trade off against each other, in which case selection to increase either trait will depend on the mechanism of sperm competition (Immler et al. 2011). Alternatively, both sperm number and sperm quality may in-

crease in response to sperm competition (Locatello et al. 2007) potentially forcing a trade-off with nonejaculate traits. For example, ejaculate quality may trade off with attractiveness (Evans 2010; Rowe et al. 2010) or immune function (Simmons 2012), and testes size has been shown to trade off with traits such as flight capability (Saglam et al. 2008) and weaponry (Simmons and Emlen 2006). It is therefore possible that increased investment in ejaculates could trade off with traits that directly enhance female fitness, such as nuptial gift size or provision of parental care (e.g., Simmons et al. 1993). For example, male secondary sexual traits can trade off with paternal care provision (Smith 1995) and such trade-offs could be mediated by testosterone production (Wingfield et al. 1990; Mascaro et al. 2013).

Greater investment in each ejaculate, without a concomitant increase in sperm production, could contribute to female sperm limitation (Wedell et al. 2002). For example, in two heteropterans with different mating systems, male investment in spermatogenesis differs and this has profound effects on female fitness (Franco et al. 2011). In the monoandrous *Macrolophus pygmaeus*, females receive enough sperm to fertilize the majority of their ova. In contrast, in the polyandrous *Nesidiocoris tenuis*, females run out of sperm soon after mating, and so must readily accept copulations and spend longer in copula to maintain fertility. Ultimately, if the cost of producing a competitive ejaculate is sufficiently high, male mating rates may be reduced. This could influence the direction of sexual selection as female–female competition for mates increases (Lorch 2002; Wedell et al. 2002).

In many taxa males produce more than one sperm type, but usually only one sperm class are fertilizing sperm (eusperm) (Pitnick et al. 2009). Nonetheless, the nonfertilizing (apyrene or para-) sperm can affect the outcome of sperm competition and their receipt can be costly for females. In *Drosophila pseudoobscura*, for example, the survival of eusperm within the female reproductive tract is highest when greater numbers of apyrene sperm are also inseminated (Holman and Snook 2008). Additionally, in the green-veined white butterfly, *Pieris napi*,

nonfertile sperm fill the female sperm storage organ, reducing female receptivity to further copulations, which is clearly in male interests (Wedell 2001). The receipt of nonfertile sperm is costly for females as it reduces fertility, which will be compounded if remating is delayed. The precise function of most apyrene sperm is unclear, but larger apyrene sperm may fill female sperm storage organs or block female genital tracts, excluding sperm from other males (see the section Copulatory Plugs below). Again, this is likely to be beneficial to males but costly to females if polyandry is in female interests.

Nonsperm Ejaculate Substances

In addition to sperm, ejaculates can contain a wide variety of substances that influence sperm competitiveness. These have been particularly well studied in *Drosophila melanogaster* (e.g., Wolfner 2002; Chapman 2008), although they are taxonomically widespread (Perry et al. 2013). Seminal peptides found in the ejaculate of male *D. melanogaster* influence many aspects of female physiology and behavior, including female remating rate, egg production rate, and sperm storage. By manipulating these female traits, males increase their fertilization success. Furthermore, it has been shown that male *D. melanogaster* strategically adjust allocation of seminal peptides in accordance with female mating status and the perceived risk of sperm competition (Wigby et al. 2009; Fedorka et al. 2011; Sirot et al. 2011) as predicted by theory (Hodgson and Hosken 2006). However, male manipulation comes at a cost to females, as seminal fluid proteins reduce female longevity (Chapman et al. 1995) and alter egg production schedules to reduce female lifetime reproductive success (Wigby and Chapman 2005). Furthermore, if female evolutionary responses to male manipulation are halted, males evolve to be even more manipulative and females pay even greater costs (Rice 1996).

There is evidence that females evolve to mitigate the costs of nonsperm ejaculate components. For example, resistance to seminal fluid proteins evolves when female *D. melanogaster* are subjected to higher mating rates (Wigby

and Chapman 2004). Studies have also begun to identify candidate genes expressed in the female that interact with male seminal proteins (Swanson et al. 2004; Chow et al. 2010). Male adzuki bean beetles (*Callosobruchus chinensis*), for example, transfer substances to females during mating that reduce female receptivity. Female beetles from strains in which the potency of these substances is greater were found to have evolved greater resilience to their effects, suggestive of coevolution between male manipulation and female resistance (Yamane and Miyatake 2012).

Nonsperm ejaculate substances can also interfere with the female immune response (Morrow and Innocenti 2012). These traits may have evolved because sperm are foreign bodies and females often show an immune response after insemination that may indirectly, or directly, target sperm. In the cricket, *Allonemobius socius*, seminal components interrupt phenoloxidase activity, a key pathway in insect immunity, thus compromising female immune function (Fedorka and Zuk 2005). Although this may benefit males by ensuring that a greater number of their sperm survive to compete, it may also leave females more vulnerable to disease.

Copulatory Plugs

Another MASC is to block the female genital tract with a copulatory plug. Copulatory plugs are found in many taxa (e.g., Lung and Wolfner 2001; Dixson and Anderson 2002; Moreira and Birkhead 2004; Ramm et al. 2005) and can prevent or delay female remating (e.g., Takami et al. 2008) or facilitate sperm transport within the female reproductive tract (e.g., Dean 2013). Copulatory plugs are often derived from the nonsperm portion of the ejaculate, although the male genitalia themselves can also act as plugs (e.g., Herberstein et al. 2012). Plugs can be costly to females if they prevent remating but they can also prevent females from using or storing sperm efficiently. There is indirect evidence that females find copulatory plugs costly to some extent as they are often removed shortly after copulation (e.g., Takami et al. 2008) and females can produce proteases that degrade the

D.A. Edward et al.

structure of the plug (Dean et al. 2011a). This has the potential to generate antagonistic coevolution between males and females, with males selected to improve plug efficacy and females to remove or degrade them. There is evidence for this in rodents, in which a number of different ejaculatory proteins form the plug along with a variety of protease inhibitors that disrupt the action of female degradation enzymes (Dean et al. 2011a). A further female-borne cost of plugs can arise if males attempt to mate with “plugged” females (e.g., Moreira and Birkhead 2004). Females could incur physical harm, particularly if males have evolved traits such as penile spines to assist in plug removal.

Again, however, an assessment of the level of sexual conflict arising from copulatory plugs should also consider potential benefits to females. Plugs can be large enough to ensure that some of the plugging cost can be offset if the female is able to consume the plug on removal or absorb nutrients from the plug as it is degraded. A plug may also be beneficial if this increases fertility (Timmermeyer et al. 2010; Dean 2013) or protects the female from male harassment (e.g., Kuntner et al. 2012).

Strategic Allocation of Male Mating Effort

Another way for males to maximize fitness returns when faced with the risk of sperm competition is to either not mate with, or allocate fewer resources to, already mated females (e.g., Simmons et al. 2003; Friberg 2006). Saved resources might then be allocated elsewhere. It is now increasingly accepted that males can be choosy, particularly if, in the face of intense sperm competition, males are under strong selection to produce larger or more complex ejaculates that may limit mating rates (Lorch 2002; Wedell et al. 2002; Edward and Chapman 2011). If the energy required to mate is high, the prospects of securing paternity are low and if other females are likely to be available, then males might be better off searching for alternative mates (Schwagmeyer and Parker 1990). However, it should be remembered that strategic allocation of mating effort will only benefit males if alternative, more economical mating opportunities are available

to which saved resources can be reallocated (e.g., Fuller 1998; Barry and Kokko 2010).

If males allocate fewer resources (i.e., fewer sperm or smaller ejaculates), or are less willing to mate with nonvirgin females, this could reduce female fertility. Females could also incur costs of reduced mate choice, for example by not being able to “trade up” to a better mate, or be unable to secure additional fitness-enhancing nuptial gifts. Female adaptations to avoid costs of strategic allocation of male mating effort might include disguising mating status or perhaps even signaling competitively to attract males (e.g., Clutton-Brock 2009; Stockley et al. 2013). Female signals that indicate greater fecundity might convince a male that the potential rewards of mating outweigh potential costs of sperm competition (e.g., LeBas et al. 2003).

THE EXTENT OF SEXUAL CONFLICT

Costs and Benefits to Males

MASC are often costly for males and thus may limit other reproductive investment. For example, increasing ejaculate production or producing larger copulatory plugs may require significant energetic investment and trade-off against other fitness components (Hosken 2001). Similarly, prolonged guarding or copulatory behaviors can be costly in terms of both time and energy. This can potentially result in trade-offs such as that between mate guarding and territory size in male stitchbirds, *Notiomystis cincta* (Low 2005). The costs of MASC are further evidenced by examples of strategic ejaculate allocation and variation in male mating behavior and mate guarding behavior according to perceived levels of sperm competition (Komdeur 2001; Wedell et al. 2002; Bretman et al. 2009). If MASC were not costly there would be little or no selection for plasticity in their expression. Costs may also be more obvious than this. As an extreme example, the ability of males to remate is limited when genitals are broken off during mating to form a copulatory plug (e.g., Nessler et al. 2009).

The costs of expressing MASC will ultimately impose a limit on the evolution of these traits and hence the potential to inflict harm on fe-

males could be self-limiting. However, the harm inflicted on females may still be significant as male costs are often outweighed by very strong selection for these characters. If the risk or intensity of sperm competition is high, selection can thus still favor the expression of MASC that are very costly to males. For example, in the orb-web spider, *Argiope lobata*, males break off part of their genitalia to form a copulatory plug that increases their share of paternity if the female should remate. This occurs despite the very significant cost of a reduction in the male's ability to remate, and an increased risk of sexual cannibalism (Nessler et al. 2009). Nevertheless, the fitness benefits of depositing the plug are sufficient to outweigh even these extreme costs, which is in part owing to the paucity of future mating opportunities (Nessler et al. 2009). This shows that the strength of selection on males through sperm competition can be sufficient to select for costly characters, which in turn can generate sexual conflict.

Costs and Benefits to Females

Although MASC can be under strong selection, corresponding selection in females to resist them may be weaker as MASC are unlikely to cause a complete loss of female fitness. Basically, the variance in male reproductive success is typically higher than that in females. Thus in general we might predict, at least initially, greater selection for males to express MASC than for females to evolve resistance to them. The balance of selection may therefore tend to favor the evolution of MASC, with weaker selection for female resistance to them. Consequently, females probably suffer a greater conflict load (i.e., females may be further from their fitness optima as a result of sexual conflict). However, this prediction is complicated by the costs of female resistance (see the section Mitigation and Resolution of Sexual Conflict below).

Finally, there are potential female benefits from MASC. An assessment of these benefits is important not only for accurately determining the conflict load, but also the precise trait, or aspect of a trait, over which there may be a sexual conflict. For example, a copulatory plug

can improve fertilization success and thus benefit both sexes (e.g., Timmermeyer et al. 2010; Dean 2013). Consideration should then be given to whether there is conflict over plug formation per se, or only over the optimal size or consistency of the plug.

It may also be important to consider how fitness costs of MASC are measured. Male manipulation of female egg production may function as a MASC as it will benefit males if more fertilized eggs are produced before females remate. This manipulation can have a detrimental effect on female lifespan and/or lifetime reproductive success (Chapman et al. 1995; Wigby and Chapman 2005). However, the production of more offspring at a young age will also contribute to an individual's intrinsic rate of offspring production. This can enhance female fitness, particularly if other females in a population are also being stimulated to produce more offspring so that population size is increasing (Edward et al. 2011). Thus, female fitness may, under certain conditions, be increased despite a reduction in overall lifetime reproductive success. This highlights the importance of not only considering the potential fitness benefits of MASC to females but also greater consideration of the way that fitness is measured.

In summary, to understand the precise nature and extent of sexual conflict arising from MASC it is important to understand the costs and benefits of conflict in both sexes. The effects of MASC can be complex, and although there is often an obvious cost to females, potential benefits of these traits can easily be overlooked. A key challenge for future research is a more complete consideration of the fitness economics of sexual conflict and improved measurement of the costs involved.

MITIGATION AND RESOLUTION OF SEXUAL CONFLICT

Although it is clear that MASC can give rise to sexual conflict, the evolutionary trajectories of such conflicts are less clear. Although there is potential for selection arising from MASC to favor female traits that directly counter them, conflict need not lead to selection. Outcomes

D.A. Edward et al.

depend in part on how costly it is to resist MASC and the strength of selection imposed on females. An important factor here is that despite strong selection acting on males, female resistance traits could be relatively cheap to produce and express (Parker 1979, 1984). For example, although a copulatory plug may be very costly to produce, it could be relatively easy for a female to remove. This kind of asymmetry could tilt evolutionary outcomes of these conflicts in favor of females, despite stronger selection acting on males. However, although female cost-avoiding responses to one MASC could potentially resolve a specific conflict, this could have the potential to select for an alternative MASC, thus kick-starting new rounds of sexually antagonistic coevolution.

Sperm competition is intimately related to polyandry, and because of this, the causes and patterns of polyandry may also be particularly important in determining the nature of sexual conflict that results. It is clear that females can benefit from polyandry (Arnqvist and Nilsson 2000; Fedorka and Mousseau 2002; Slatyer et al. 2012), yet mating too often can be costly (Arnqvist and Nilsson 2000). Hence, the net benefits or costs of polyandry should influence specific sexual conflicts arising from MASC.

If actual rates of polyandry are greater than the female optima, selection will favor female traits that reduce mating rates. Selection for reduced rates of polyandry should in turn be expected to reduce levels of sperm competition and thus potentially also reduce the costs arising from MASC—although it could spark other sexual conflicts if males are moved below their optimal mating rates. Alternatively, if rates of polyandry are below the female optima, females will be selected to increase multiple mating. In this case females can generate a conflict load from MASC via selection for polyandry. As long as fitness benefits of polyandry exceed subsequent fitness costs of MASC we would expect selection for rates of polyandry to be maintained. However, it is not easy to disentangle cause and effect. Females may be seen to have higher fitness with increased mating because they have evolved to reduce costs by storing fewer sperm. That is, because sperm are so easy to

acquire females do not need to store them. Thus, it is not always clear whether female multiple mating is because males transfer few sperm or females simply do not want to store them.

Additionally, as rates of polyandry are often only indirectly associated with sexual conflict arising from MASC it is not inevitable that an individual reduction in mating rates will reduce costs of this conflict. If a majority of females in a population are polyandrous and/or if MASC are relatively cheap to produce, it is likely that they will be expressed even at low risk of sperm competition. Consequently, a female trait that reduces mating rates is unlikely to confer an immediate benefit to its bearer through reduced costs of MASC. However, if males assess female mating status to determine the risk of sperm competition and adjust the expression of MASC accordingly, then an individual female with a lower rate of polyandry could benefit from a reduction in costs associated with MASC.

In summary, a resolution of sexual conflict over MASC may be reached directly or indirectly via reduced rates of polyandry. However, this will be dependent on the benefits of polyandry to females, including whether rates of polyandry are above or below optima, and whether MASC are tailored according to the immediate risk of sperm competition. Unfortunately at this point in time it is not even clear how sexual conflict generates selection generally, and not just how often MASC actually reduce female fitness. These are areas that need empirical work on a broad range of taxa to allow us to have some feel for general patterns.

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Sexual Conflict and Sperm Competition

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D.A. Edward et al.

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