Monogamy and the Battle of the Sexes

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Abstract

Sexual conflict has been suggested to be important in the evolution of reproductive traits, with much recent theoretical and empirical evidence emphasizing its role in generating sexually antagonistic coevolution in the context of promiscuous mating. Here we shift attention to the role of sexual conflict in a monogamous mating context. Conflicts can arise, for example, when males are successful in imposing monandry at a cost to female fitness, or when females impose monogyny on males. Conflict over remating can also generate monogamy. For example, when males invest heavily in attempting to impose female monandry, the cost of their investment may prevent them from securing additional mates. We emphasize that sexual conflicts need not always generate sexually antagonistic coevolution, and that it is important to consider whether mating decisions are controlled primarily by males or females. Finally, we briefly discuss approaches to distinguish between conflict and classical modes of sexual selection, as this highlights difficulties associated with deciding whether monogamy is enforced by one sex or the other. We suggest that documenting the current fitness consequences of mate choice and mating patterns provides insight into the relative importance of classic and conflict modes of selection.

INTRODUCTION

Sexual conflict: differences in the evolutionary interests of the sexes originating from relatedness asymmetries

Monogamy: a mating system in which males and females typically mate with only one partner

Sexual conflict, the evolutionary divergence in the interests of males and females (85), is an area of rapidly increasing research. Evolutionary conflict between the sexes has its roots in sexual reproduction, and the evolution of the sexes (anisogamy) may be a direct result of a fundamental conflict between mates over reproductive investment (67, 85). Sexual conflict occurs because sexual partners are not genetically identical and so their reproductive interests almost never exactly coincide (**Figure 1**). This means that individuals of either sex could generally achieve higher reproductive success if a mating partner were to invest greater reproductive effort in their current, shared reproductive event at the expense of future reproductive opportunities (86). This fundamental conflict of interest leads to potential conflicts over all the shared activities that make up sexual reproduction. Mating is one example of a shared activity, and conflict over whether to mate or not is expected to occur when male fitness increases with the number of females inseminated, but female fitness is maximized with one or few copulations.

Sexual conflict is often characterized as most intense or costly when there is multiple mating by both sexes (96). However, although this is true when comparing polyandry with hypothetical or experimentally evolved cases of lifelong monogamy, in which individuals of either sex have no options for reproduction other than with their allocated mating partner, such conditions probably never apply in natural systems. More typically, individuals of either sex may have alternative reproductive options available to them, even in apparently monogamous mating systems, and optimal strategies are unlikely to coincide exactly from each mating partner's point of view. For example, in species with biparental care, a male may have opportunities to maximize his reproductive success by seeking additional copulations, but such a strategy results in conflict with his partner if it reduces the male's investment in their shared brood (65). Similarly, a singly mated female might have the potential to increase the number of offspring she produces by mating with more than one male, although this results in conflict with any previous mate owing to likely dilution of his paternity success. In both cases, the resulting conflicts may lead to selection on one sex to restrict the mating behavior of the other, with the result that monogamous mating patterns can arise against the interests of one sex or the other. Hence, rather than being a state of harmonious agreement of interests between the sexes,

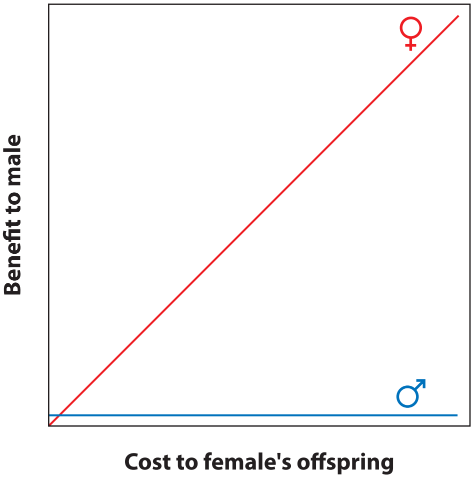

Figure 1

Sexual conflict can be understood in terms of Hamilton's inclusive fitness argument (92). An individual that can influence the allocation of a resource between competing demands (present and future offspring) favors one over the other when $b/c > rc/rb$, where b is the benefit to the receiver of the resource (current offspring), c is the cost to the individual who does not get the resource (future offspring), and r is the relatedness of the two (receiver and nonreceiver) to the individual influencing the allocation. The ratio rc/rb differs for different individuals that influence the resource allocation, as shown by this plot. The colored lines represent the relatedness cost-to-benefit ratios of males and females. Because females are equally related to current and future offspring, [the female rc/rb ratio is 1 (*red line*)], they make decisions purely on the basis of the benefit-to-cost ratio. However, with polyandry and complete sperm replacement with each mating, a male's relatedness to individuals affected in the future is 0, so the relatedness ratio for a male is 0 (*blue line*). The area between the two lines is the area of sexual conflict. Redrawn from Reference 92.

monogamy in natural systems may often result from and/or promote intense sexual conflicts.

There have been several reviews of sexual conflict (11, 65, 86, 129) and of the benefits of polyandry to females (8, 49). Here, we focus our review primarily on sexual conflict in systems in which either one or both sexes mate only once. Such situations are of particular interest because the fundamental basis of sexual conflict is the potential for one or both members of a mating pair to benefit by withholding some of their resources for use in future reproductive opportunities. If future opportunities do not exist, then the optimal strategy is fundamentally altered. When there are strictly no opportunities to mate more than once, there may be conflicts of interest prior to mating (over finding the best partner), but once mating has occurred conflict disappears. In contrast, if the potential for future matings still exists, then conflict can still exist after mating if monogamy is imposed by one sex on the other. For this reason we stress the importance of considering which sex is likely to most influence mating patterns. For example, in the yellow dung fly, *Scathophaga* (*Scatophaga*) *stercoraria*, there is evidence that multiple matings can be costly to females (51, 120) and that they need only one copulation for full fertility over several clutches of eggs (83). However, because males are much bigger than females and can physically force them to mate, copulation typically occurs each time a female lays a clutch of eggs. In this case, although it appears likely to be in the female's interest to mate less frequently, males have greater control over mating rates and can override female interests.

MATING CONFLICTS IN INSECTS

Insects provide some of the best examples of conflicts over mating and resulting adaptations and have become model systems for studies of the costs and benefits of mating. The bush cricket *Kawanaphila nartee* is an excellent example of sexual conflict over mating, with environmental conditions flipping the optima for each sex. As with many bush crickets, the males provides a female with a nuptial gift (the spermatophylax) that the female consumes while sperm are transferred from the spermatophore to her reproductive tract. In this system females are choosy and reluctant to mate when environmental food is abundant, but when food becomes scarce, females become far less choosy as they attempt to forage on the male-provided gift. The reverse is true of males who become choosy when food is scarce (41, 110).

Conflict over mating is especially obvious when mating struggles occur. Water striders (9, 10) and the dung fly, *Sepsis cynipsea*, are well-studied examples. Female *S. cynipsea* deposit their eggs in cow dung. Males aggregate at droppings and wait for incoming females. Any female encountered by a male is leapt upon and a dramatic and violent struggle typically follows (84). Struggles can last for up to 20 min, and in the field approximately 40% of pairs copulate (124). Female reluctance may be due partly to harm caused by males during copulation (17), the reasons for which are obscure (48, 117). This system highlights a number of questions relating to the influence of sexual conflict on mating rate:

- Are struggles an attempt by females to prevent costly matings or are they a form of mate-quality assessment?
- Are struggles costly, or could indirect (genetic) benefits outweigh direct costs?
- Does level of female resistance depend on the state of the female (e.g., virgin/mated)?

Although larger male *S. cynipsea* tend to be paired, the size of males in copula does not differ from those that are paired (1, 123), which tentatively suggests that struggles are not acting as a filter. The precise costs of struggles have not been calculated, but there do appear to be direct fitness costs to females in this system. If net direct costs are relatively small, then indirect benefits could compensate for them. However, if they are relatively large [say greater than about 5% of fitness, which is greater than the average variance in offspring viability explained by sire effects (74)], then indirect benefits are unlikely to offset them, although net costs could be reduced (20, 50, 58).

Monogyny: a mating system in which males typically mate with only one female

Monandry: a mating system in which females typically mate with only one male

MATING CONFLICTS AND SEXUAL COEVOLUTION

Evidence of coevolution between the sexes resulting from mating conflict has been suggested on the basis of comparative reproductive anatomy. Bed bugs provide one of the starkest examples of the evolutionary consequences of conflict over mating and how mating costs can be ameliorated over evolutionary time. Males have evolved hypodermic genitalia that pierce the female body wall and ejaculate into the female's hemocoel, rather than intromission and insemination via the female reproductive tract proper. However, females have evolved several structures that reduce the costs of traumatic insemination (80, 111, 113). Similarly, as a result of the intense mating struggles of water striders, in which males attempt to grab and mount females, females have evolved antigrasping structures that help them to thwart male mating attempts, and there is correlated evolution of male and female structures across species (9, 10).

Experimental evolution has also been used to investigate the potential for sexually antagonistic coevolution. Typically, such studies are designed to impose monogamy (thereby reducing sexual conflict) in one treatment while allowing polyandry in another, so that measures of fitness can be compared for populations exposed to contrasting levels of sexual conflict after periods of experimental evolution. Although results are mixed, several of these studies provide evidence of fitness costs associated with sexually antagonistic coevolution (22, 46, 69, 70, 95). That is, when compared with strict monogamy, polyandry is often associated with evolution driven by sexual conflict. Although this has led to an emphasis on polyandry as a generator of sexual conflict, we emphasize here that conflict is also apparent in other mating systems. In the following sections, we consider the role of sexual conflict in mating systems that involve single mating by one or both sexes.

MATING CONFLICTS AND SINGLE MATING IN INSECTS

There are many instances of single mating by one or both sexes, which can be for or against the interests of one or both sexes (**Table 1**). Although males are invariably under selection to mate more than once, this selection may be balanced by the benefits of devoting all their effort to a single female, such that net selection on males may favor monogyny. The sex that benefits from mating only once can determine the potential for subsequent selection, and expected outcomes are as predicted by Parker's (85) models: They depend on the relative power of either sex, the benefits of winning a conflict, and the relative costs of escalation. Within this general framework, we now discuss instances where patterns of single mating appear to be differentially influenced by males or females, and possibly have different fitness consequences for them.

Male-Enforced Monandry

Monandry, when females mate with only one male, could be caused by female resistance to remating (female control) or to males switching off female receptivity after mating, even if this compromises female fitness (male control). This can generate differences in the direction of selection acting on each sex, as in the former case there may be no cost to females' fitness, while in the latter there potentially is a cost to female fitness. In addition, the availability of alternative mating opportunities also influences fitness costs of manipulation. However, it may not always be possible to decide if, for example, male-induced monogamy is costly to females or to differentiate between female- or male-induced monogamy.

There are a number of cases in which female monandry does appear to be a simple case of direct male induction. In *Aedes aegypti* mosquitoes, male accessory gland substances permanently terminate female receptivity, and individual males can do this in up to 64 females (26). A similar pattern is found

Table 1 Selection driving mating rate towards monogamy or away from monogamy[a]

Mating system	Source of selection[b]	Adaptation	Coevolutionary dynamic: feedback
Monogamy			
↓	Selection on male because matings increase his reproductive success (the potential for this selection is ubiquitous and constantly opposes monogamy)	Conflict: Male coerces or seduces female into mating Cooperation: Male provides direct benefit to female in return for mating	Negative: Females evolve to prevent manipulation Negative: Cost of mating to male reduces capacity to remate Positive: Direct benefit to female of matings
↓	Selection on female as matings provide genetic benefits to her offspring	Conflict: Female solicits rematings and exercises post-copulatory choice Cooperation: Female accepts matings and exercises post-copulatory choice	Positive: Polyandrous female have sons adapted to sperm competition Negative: Male attempts to reduce female remating Negative: Reduced benefits of choice as variance in mate quality declines
↓	Selection on female because male provides her with direct benefits	Conflict: Female sequesters resources from male (e.g., eats him) Cooperation: Male invests in offspring	Negative: Male attempts to reduce investment Positive: Female solicits matings Negative: Cost of mating to male reduces capacity to remate
Promiscuity			
↓	Selection on male since reduced female mating rate increases his paternity share	Conflict: Male reduces female remating via seminal plugs and seminal proteins	Negative: Females evolve to prevent manipulation Positive: Benefits to male of decreasing costs imposed on mates increases, reducing conflict
↓		Cooperation: Male provides benefit to female in return for reduced remating (e.g., no mating during consumption of nuptial gift)	Positive: Increased paternity assurance leads to increased male investment Negative: Benefits of matings to female may exceed costs
↓	Selection on female due to her costs of mating	Conflict: Female avoids or rejects matings Cooperation: Female reduces imposed mating costs without affecting mating rate	Negative: Males evolve new coercive strategies Positive: Male remains with any female he encounters Negative: If benefits of matings to female exceed costs
Monogamy			

[a] Illustrates how monogamous systems can be driven toward higher mating rates (top half of table) and how systems currently characterized by high mating rates (promiscuity) can be driven toward monogamy (lower half of table). Particular selection pressures due to costs or benefits of matings to either males or females can drive adaptations in either or both sexes that are either beneficial to one member of a potential mating pair but not the other (conflict) or beneficial to both mating partners (cooperation). These adaptations in turn create new selection pressures which may act to continue the change in mating rate in the same direction (positive feedback) or may act to drive the mating rate in the opposite direction (negative feedback). Conflict adaptations create selection on one sex that favors monogamy while the other opposes it, whereas cooperative adaptations create selection for or against monogamy in the same direction in both sexes.

[b] This is a potential for selection, not the only source of it.

in 12 other mosquito species, and there is even evidence of partial cross-specificity of these compounds between species, extending to *Drosophila melanogaster* (26). This finding resembles the impact of the sex peptide (SP) Acp70a in *D. melanogaster*, which suppresses female receptivity (59) and reduces female fitness (131). Experimental manipulations reveal that SP can also induce nonreceptivity in female *Helicoverpa* moths (32), and that injection of the moth sex peptide HezSP into female *D. melanogaster* reduces their receptivity to males (32). These findings suggest there may be a physiological pathway shared by female insects, which is targeted by these male seminal peptides (126). Further corroboration of the shared similarity among insect accessory gland proteins (Acps) comes from a recent genome-wide analysis in *Anopheles gambiae* mosquitoes revealing homologies with 40% of the known *D. melanogaster* Acps, including SP (28). However, although male mosquitoes can stop females from remating, it is not known if this is costly for females. Females may have merely shifted the cost of producing substances that shut down their receptivity onto males (29).

Another probable example of male-induced monogamy occurs in the house fly, *Musca domestica*, in which males transfer compounds in the ejaculate that in most cases permanently switch off female receptivity (5, 62, 63, 98, 99). However, if mating is stopped after sperm transfer but before seminal fluid transfer, females will mate again (5), and females mating more than once have higher lifetime reproductive success, at least in the laboratory (68). Similarly, male bumble bees (*Bombus terrestris*) transfer a mating plug to females that apparently switches off female receptivity permanently, despite apparent female benefits of polyandry (13, 14). This plug is formed by the male accessory glands and is composed of four fatty acids, with linoleic acid the suppressive substance (13). Many male butterflies also produce elaborate mating plugs formed by specialized accessory glands, and these plugs are attached to the female's genital opening (81). In at least some cases, females cannot remove the plugs, which remain attached to them for the duration of their lives. One example is the large plug that covers the genital opening of female *Cressida cressida*, providing a life-long chastity belt that results in monandry (82).

Apart from potential costs to females associated with reduced copulation rate, mating plugs can also be costly to females because they interfere with egg laying. Such costs can lead to selection on females to remove plugs and counter-selection on males to make plugs larger and/or more difficult to remove. Evidence that mating plugs are a costly investment for males comes from attine fungus-growing ants. In this group, mating plugs are reported only from monogynous species (75). Furthermore, males of monandrous species have large accessory glands that produce the mating plug, whereas males of polyandrous species have smaller accessory glands (12, 72). Such observations are consistent with male control over female mating frequency in species with large accessory glands (12), although comparative associations do not necessarily indicate causation (64). Another extreme example of males attempting to stop female remating occurs in honey bees (*Apis mellifera*). Drones that successfully copulate with a queen sever their genitalia and leave them inside the queen as copulation ends. The drone then dies, but unfortunately for them, the queen can expel the aedeagal plug and remate (118).

Control over remating diverges still further from male control towards an interaction between the sexes in butterflies. In the green-veined white butterfly, *Pieris napi*, males transfer ejaculatory nutrients that increase female fecundity and life span (128), such that females benefit from polyandry (132). In an attempt to reduce female remating frequency, males also transfer ejaculatory antiaphrodisiacs, which repel subsequent males after a mating (2). However, antiaphrodisiacs only have a transient effect and males also transfer a large number of nonfertile (apyrene) sperm, which fill the female's sperm storage organ and delay female receptivity (24). There is genetic variation among females in the number of nonfertile sperm stored, and this covaries with female remating tendency (125). Many females remate, but some 10%–15% never do, despite ample opportunity and negative impacts of monandry on their reproductive output (130). In *P. napi* there is clear sexual conflict over many aspects of reproduction. In addition, although female mating patterns have a genetic basis, it is not yet clear whether monandry can be explained by some genotypes having a lower threshold to male manipulation. These observations are consistent with theoretical expectations that males should evolve multiple ways of trying to influence female mating behavior. This example also illustrates that female mating behavior can be highly variable within a population, which is consistent with Buridan's ass–type diversification (38).

Male prevention of further mating can be costly to females for reasons other than mating plugs interfering with oviposition. In the cockroach *Nauphoeta cinerea* monandry is enforced during a female's first reproductive cycle, when males use their spermatophore to switch off female receptivity (76). This is costly to females in several ways. This cockroach has a well-defined dominance hierarchy, and females prefer subdominant males over dominant ones when given the choice. Nonetheless, because females mate only once, they are frequently constrained to mate with the nonpreferred dominant male (77). Furthermore, singly mated females may experience sperm limitation (79), particularly when mated with nonvirgin males, which are often severely sperm depleted (44, 76). A similar situation exists in the monandrous sandfly *Lutzomyia longipalpis*, in which females frequently suffer reduced fertility due to mating with recently mated, sperm-depleted males (54). In general, females mating to preferred males may frequently run the risk of receiving insufficient sperm, which can result in reduced offspring production (90, 129). In addition to the conflict this generates over mating rate, reduced fertility may promote female-female competition over access to attractive males.

Costs to Males from Manipulation Attempts Can Result in Monogamy

Male attempts to manipulate females can also be costly for males (127) and, if costly enough, may eventually lead to monogamy, even though the mating conflict may not be resolved (**Table 1**). For example, in butterflies there is an inverse relationship between mating plug production and sperm production. This may be explained in part by the lower risk of sperm competition in species with large plugs, as they have lower female mating frequency (109), but the association may also reflect the cost of producing the plug itself (71). It is possible that the cost of producing a spermatophore in *N. cinerea* has also come at the cost of reduced sperm production (79).

In some cases, male costs are so great that they simply cannot mate again, as discussed for honey bees. Excessive investment in costly mating plugs by male attine ants may also have resulted in males losing their ability to mate multiply, leading to the evolution of suicidal copulations (18), although this also depends on the likelihood that males could remate anyway. Similarly, in many spiders, parts of the male intromittent organ are broken off during copulation, and males are unable to mate again, even though amputation does not result in male death (36). As with honey bees, however, these attempts to prevent female remating are not always successful. In other species, there may be additional benefits to males that sacrifice further use of their intromittent organs during copulation. Male *Euborellia plebeja* earwigs possess paired genitals, which often break off inside the female's genital tract during copulation (56). However, this does not prevent female promiscuity and also does not appear to hinder egg laying. Rather than act as a chastity belt, the long intromittent organ instead appears to function in removing rival males' sperm from the female's sperm storage organ (55). The fitness costs of losing the aedeagus has presumably led to the evolution of the paired earwig intromittent organ.

Monogyny and Female Enforcement

Females may also prevent males from remating. This is often associated with females controlling a resource critical to overall reproductive success. For example, in *Nicrophorus defodiens* burying beetles, mated pairs defend a carcass in which females lay their eggs and either one or both parents care for the young. On large carcasses more than one brood can be supported, and males increase their fitness by attracting additional females. This is not in the interests of the resident female, as an additional female means increased resource competition from unrelated larvae on the carcass and reduced paternal care. Females therefore prevent males from releasing mate-attracting pheromones by physical punishment. This results in female-coerced monogyny on large carcasses (30).

Other examples of female-enforced monogyny are found in species of cannibalistic spiders and insects. In the red-back spider, *Latrodectus hasseltii*, for example, males must insert both pedipalps to ensure successful sperm transfer and high paternity. Longer-duration copulations are associated with increased sperm transfer and paternity (4), and cannibalized males have increased paternity because they achieve longer copulations (112). The suicidal nature of a successful copulation precludes males from mating multiply, but it is unclear if male survival leads to additional matings and higher male fitness. Another example of death during copulation is found in the spider *Argiope aurantia*. Here the male dies during copulation and his entire body forms a mating plug (33). Other less-dramatic examples of male sacrificial copulations come from spiders in which males break off part of their copulatory organs to form a permanent plug, preventing females and themselves from remating and thus enforcing monogamy (73). This in turn probably selects for male sacrifice, because with no intromittent organ subsequent reproductive chances are lost.

In the preceding examples, males appear to be complicit and actively sacrifice all or part of themselves to achieve high paternity, and there may be no sexual conflict over suicide if males have no alternative reproductive options. However, there could be sexual conflict if males prevent females from achieving their mating optima by plugging. In any case, in other sexually cannibalistic species there is probably sexual conflict over cannibalism, as males appear less complicit in their deaths and the link between cannibalism and male fitness is lacking. For example, the male praying mantid *Tenodera aridifolia sinensis* adopts risk-averse behaviors when approaching females to minimize the risk of getting eaten (61). Eating the male is advantageous for females because they are frequently food limited and a male represents a valuable nutrient resource that increases female fecundity (16, 52). Furthermore, and unlike the situation in which many male spiders may have no alternative mates even if they survived intact (35), male mantids inseminate multiple females in the field (52), so cannibalistic death is probably not in the male's interest.

There is scope for sexual conflict over male investment in preventing further mating by females. However, this does not mean high male mating investment always results in sexual conflict, as this critically depends on other male mating opportunities and the fitness consequences of male investment for females. If there is limited scope for additional copulations, then there may be reduced sexual conflict over male investment because there is no need for males to save resources for future copulations. This hypothesis assumes females are in compliance with the additional investment. However, limited male mating opportunities can be associated with sexual conflict. In the white widow spider, *Latrodectus pallidus*, approximately 20% of searching males encounter a female, whereas females frequently mate with several males. Coupled with intense male-male competition, the low female encounter rate favors a high-investment male mating strategy (107). Here there is sexual conflict over female mating, and males lucky enough to find a female invest in prolonged cohabitation and courtship and are occasionally eaten by females. In polyandrous situations like this sexual conflict is obvious, but as the preceding discussion shows, mating systems in which one or both sexes mate only once can also include substantial conflict.

MATING CONFLICT: CONTROL AND CONSEQUENCES?

Either sex can predominantly control mating patterns. This is exemplified by yellow dung flies, honey bees, and house flies. Whichever sex controls mating rates at the border between single and multiple mating will determine fitness alignment and subsequent selection (**Table 1**). For example, if males benefit from a higher female mating rate, this could select for nuptial gifts to entice more mating (**Table 1**). This could then select for females to mate at an even higher rate to accrue ever-greater benefits and eventually select for such substantial contributions that males now become limited in their ability to mate multiply (**Table 1**). This reflects the findings in *Kawanaphila nartee* (110). Alternatively, if females benefit from monogamy and have more control, this could select for males that remain with any female they encounter and result in single matings for males too (**Table 1**). This second scenario probably represents the conventional view of monogamy (29, 85), but as emphasized here, there are many potential benefits of polyandry (49). Some benefits to females of matings may even approach comparable magnitude to male benefits of multiple mating, especially when sperm depletion or genetic incompatibility is involved.

Females are often thought have more control in the context of preventing unwanted copulations (29, 85), but what about their ability to resist male attempts to enforce monogamy against their interests? This may be more difficult in some instances as males may simply mate-guard, but other male adaptations to prevent female remating may be less effective. Females often seem capable of removing obstructions to their genital tract (honey bees), although this is not always true (butterflies). Some male adaptations may be harder for females to overcome than others, particularly those adaptations that rely on mimicking normal physiological responses of females (seminal fluid proteins) or filling sperm storage organs (apyrene sperm). If females do respond, this may create selection on males for multiple manipulative traits. The examples of apparent manipulation associated with effects of seminal fluid might actually be explained by females shifting costs of producing their own hormonal substances to males, although to demonstrate this unequivocally would be difficult.

Similar arguments also apply to cases in which females may be restricting male mating rates, although this appears to be less common, probably because in many cases there is no reason to expect that females would benefit from preventing males from remating. In most cases, examples of females restricting male remating appear to result as an indirect side effect of female attempts to increase resources and/or parental investment available to their young (e.g., burying beetles and cannibalism).

Sexual selection: the advantage certain individuals have over other individuals of the same sex and species in exclusive relation to sex

INTERLOCUS CONFLICT THEORY

The concept of sexual conflict has a long history, and the recent increase in interest is due in part to reviews by Holland and Rice (45, 97). They suggested that many aspects of sexual selection previously attributed to female preference for phenotypically or genetically superior males could instead be explained by male manipulation of females, and that sexual selection has its foundation in females' attempts to minimize naturally selected (direct) costs of reproduction rather than efforts to maximize direct or indirect benefits (45). A similar conceptual framework could be applied to understanding the selection that results in monogamy. As for mate choice, monogamy might be beneficial to female fitness, perhaps by reducing costs of engaging in superfluous copulations. Alternatively, monogamy may result from males manipulating female mating rates, with the cost involved in the manipulation prohibiting further mating by males themselves. Hence, from a female perspective, monogamy might be beneficial or costly.

Holland and Rice's chase-away hypothesis was controversial from its inception and generated considerable debate (39, 101). Deciding between sexual selection models was difficult prior to the chase-away hypothesis (19), and the addition of another potential explanation for sexual selection did little to improve the situation (11). However, it is conceptually easy to decide if there is likely to be sexual conflict over a trait or some shared activity. What would happen to trait expression in one sex (or the outcome of an interaction) if complete control of expression was given to the other sex? Would the values of the trait change? For example, if females had complete control over male parental investment (if we consider that to be a trait), would males invest more? In many if not most instances the answer to this question would be yes, and as a result there is likely to be sexual conflict over many sexual interactions and traits. The more difficult question to answer is has this generated selection and this in turn evolution? Much argument has occurred over this point, and over how to address this question (7, 9, 25, 89).

Sexual conflict is not selection, and therefore sexual conflicts may not generate sexually antagonistic evolution, or any evolution. Sexual conflict is potential for selection (86) in the same way that variance in reproductive success is potential for selection (122). In the case of monogamy, it is therefore possible that conflicts exist but are unresolvable by further adaptation in one sex or the other. An additional point noted many times in the evolutionary literature (60, 108) but occasionally overlooked in recent sexual conflict literature is that selection is not evolution. However, when sexual conflicts are translated into selection they may generate an evolutionary arms race between the sexes (27). In addition, sexual conflict may generate sexual selection and vice versa, but this is not invariably true for the reasons outlined above and because not all sexual selection results in sexual conflicts; for example, male-male competition does not necessarily generate sexual conflict (86).

A number of theoretical investigations have examined interlocus conflicts using simulations, game theory, and population and quantitative genetic modeling approaches (6, 37, 43, 66, 78, 102). We discuss only a few of these here. Dawkins (27) introduced one of the earliest models of a general sexual arms race, with female strategies of being coy or fast and male strategies of being faithful or philandering. Coy females need lots of courtship before they mate and they pay a time cost for this, whereas fast females mate with any male they encounter. Faithful males are prepared to court for a long time and help the female with reproduction, whereas philanderers do not persist with courtship, preferring to search for less-demanding females, and do not help with any offspring rearing. Dawkins argues that when fast females predominate, philanderers are favored, which select for coy females, which in turn select for faithful males, which in turn select for fast females, and so on. Although he suggested the system has an Evolutionarily Stable State (ESS), subsequent work indicates that the cycles described above do occur (106).

Parker (85) used a range of approaches to investigate the invasion condition for dominant and recessive sexually antagonistic alleles, sexual conflict and mate choice, and the evolutionary outcomes of conflicts over mating. He found that the dominance or recessivity of a mutant allele influences the likelihood of conflict remaining at fixation, and that the greater the disparity in gamete replenishment time, the greater the sexual conflict over mating. Parker's findings concerning the evolutionary outcome of sexual conflicts over mating (i.e., who wins) are especially revealing. In these games, there are no indirect effects. Males can either persist or give up, and females can either mate or not mate and are assumed to have mated previously, so they do not necessarily need to mate again. Outcomes depend on the type of game investigated. Using a war-of-attrition approach, in which winning a conflict is determined by the persistence of the interactors, with the most persistent winning—the main conclusion is that either sex can win depending on the starting conditions, on the strength of selection (benefits of winning), and on relative costs of escalation. The winner is the sex that spends more than the value of the resource, although as subsequently shown (42), an ESS for this type of game depends on players making mistakes. In this instance, mistakes are over payoff asymmetries. Using an opponent-independent cost approach, in which investment levels and costs are not dependent on what the opponent does but are fixed prior to the encounter (e.g., body size), cycles of coevolution [unresolvable evolutionary chases (lack of an ESS)] are a frequent outcome. This type of game assumes contest costs are trivial and the best strategy depends on what the opponents are doing. A genetic model that investigates conflicts over mating rate—males had a higher rate than females—also frequently generated cycles of coevolution (37), consistent with Parker's opponent-independent cost game (85) and with the verbal model of Holland & Rice (45). As in Holland and Rice's model, the shape of female responses were fixed but could move (i.e., the threshold response could evolve, but not the sensitivity) (**Figure 2**), and no selection for increased fitness of offspring due to genetic quality was included. In addition, and as Parker showed, outcomes depend upon starting conditions with both stable equilibria and cycles reported.

More recent work only serves to reinforce the contingent nature of the end points. In a series of models that explored outcomes of sexual conflict when females could respond in different ways to direct costs imposed by males (costs were independent of male phenotype), the channel of female response greatly altered evolutionary outcomes (102). When females could only alter the threshold response (**Figure 2**), cycles of coevolution were found. However, when females could only alter the sensitivity of their response (**Figure 2**), there were no cycles of coevolution when selection on sensitivity was weaker than selection on the male trait. Females simply became insensitive to manipulation (102). When both sensitivity and thresholds were allowed to evolve, responses depended on which female trait was subjected to weaker selection. This work addresses one of the original critiques of the chase-away hypothesis—only threshold responses were considered (101)—and appears to justify the concerns raised.

Figure 2

Hypothetical preference functions for some male traits showing two thresholds (T.1 and T.2) and three sensitivity curves (1, 2, and 3). Threshold T.1 is smaller than T.2, and the shape of sensitivity curves 1 and 2 are identical, whereas curve 3 is less steep, and once a threshold has been crossed the response of females is greater in curves 1 and 2 than in curve 3. Males that do not make the appropriate threshold cannot stimulate females into mating (and are not acceptable as mates). The original chase-away hypothesis seems to only include changes in threshold (101), and by allowing sensitivity to evolve, chase-away (cycles of antagonistic coevolution) may frequently not occur (102).

Female preference functions are critical to evolutionary responses to reproductive conflicts. Specifically, what are preference threshold and sensitivity-independent traits, can they evolve, and what selection acts on them? How the female sensory system operates is critical, a point made in other sexual selection contexts (19, 47, 57, 103). Rowe et al. (102) also suggest that under more natural situations males may carry many manipulative traits, especially if females are quick to quash advantages of any particular trait. This conclusion is supported by verbal theory (45) and by other models (78). Finally, models of direct fitness benefits to females suggest such systems are open to invasion by cheats (i.e., individuals who shift resources from providing the benefit to the revealing trait) (105), which should generate substantial sexual conflict and potential for selection.

An emerging theme from the theory discussed above is that cycles of antagonistic coevolution may not be as frequent as verbal models suggest, and that outcomes are typically contingent on initial conditions. Furthermore, as with sexual selection more generally, female preference functions appear to be a crucial parameter in determining evolutionary outcomes. These models primarily make predictions about the evolutionary equilibria expected under certain conditions. However, it is not clear whether real populations exist at or near equilibrium, and if they do not, then the models also show that initial conditions and all forms of selection (direct and indirect) strongly influence evolutionary trajectories. It might even be fair to say that if more efficient traits can be envisaged, the system is not at equilibrium. Nevertheless, there are many examples of obvious sexual conflicts, especially over mating decisions.

SEXUAL SELECTION AND SEXUAL CONFLICT

Deciding whether monogamy, monandry, or monogyny is in the interests of either sex is difficult, and this problem parallels that of choosing between classical and conflictual models of sexual selection. Classical models assume that females make decisions that are beneficial, or at least generate no net fitness cost. At some level, females have control of mating decisions and are making rational choices, whether in multiple- or single-mating systems. The realization that males can entice, force, or otherwise coerce females into making suboptimal or irrational decisions expands this classical view and suggests that male interests can at times subvert female interests. Because female preference (classical models) and resistance (conflict models) generate sexual selection on males, they have essentially the same outcome, and it is only the nature of selection acting on the female that differs. For example, more-attractive males could reduce female fitness by preventing females from remating, or they could enhance female fitness via genetic benefits to their offspring. However, it is difficult to decide precisely which mode of sexual selection is predominant, and the current level of debate reflects this, although similar discord has occurred in the recent past (3). Nevertheless, equilibrium predictions potentially allow researchers to differentiate between modes of selection (11). If selection is driven by sexual conflict, we expect direct, negative selection to operate on female preference. This does not mean that mating with an attractive male necessarily lowers female fitness, because mating costs can be independent of male phenotype, but direct costs to female preference may accrue because attractive males can entice females to mate too often (119). This distinction is exemplified by recent work with *Drosophila*. For *D. melanogaster*, females suffer a direct fitness cost through mating with preferred males (34, 87, 88), and mating multiply reduces fitness components (21, 22, 131). In contrast, in *D. simulans*, mating once with an attractive male has no effect on direct measures of female fitness (number or rate of offspring produced) (115), and furthermore, multiple mating enhances female lifetime reproductive success, suggesting that direct costs of mating too frequently are also nonexistent (116). In addition, the lack of an association between male attractiveness and female fitness in *D. simulans* does not appear to be the result of female expression of the male attractiveness trait (60), because females do not express courtship behavior. However, although male attractiveness is heritable (114), it is currently unclear exactly which traits female *D. simulans* favor. So with conflict-driven sexual selection there is direct, negative selection on females, and if there is positive direct or indirect selection on female preference, then classical models apply (11). Unfortunately, if male-female coevolution is ongoing, equilibrium conditions may not apply (31), and there is evidence for mismatches between female preferences and male traits (100). An additional problem arises with measuring net selection. This is a general issue that is not easily resolved, especially outside of the laboratory, and concern about this and, more importantly, the utility of measuring selection more generally, prompted

Grafen to ask why we should bother to measure selection at all (40; for a response see Reference 108). We are not so pessimistic but suggest that perhaps the best we can do is attempt to document the current female fitness consequences of mating preferences and establish if attractive males do entice females to mate suboptimally. Or, in the case of monogamy, would mating more frequently be beneficial to females? At least then we could determine which selection probably operated on female preference and mating patterns in the recent past and what it is likely to be in the near future (122), regardless of how dynamic the system is.

SUMMARY POINTS

1. Sexual conflict is inevitable, and examples of insects that have evolved in response to selection driven by conflict are numerous. However, conflict may not always result in cycles of antagonistic coevolution.
2. Conflicts between the sexes are likely to be common under monogamy and include examples in which males impose monogamy on females and vice versa.
3. Documenting current selection on the traits of interest provides insights into selection that probably operated in the recent past and could allow us to infer the likely mechanisms involved—classical or antagonistic—or at least their relative importance.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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