
Sexual Conflict

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Look at a cow pat in the summer. If you watch closely, you may see that mating male dung flies sometimes drown their mates in dung—why? The study of sexual conflict provides the answer: such dramatic effects can occur because, perhaps not surprisingly, what is best for males is not always best for females. In the example of the dung flies, the competition among males for matings can sometimes be so intense that the females caught up in it pay the ultimate price. Sexual conflict makes sense of these and other seemingly counterintuitive examples of behavior. Sexual conflict, or the “conflict between the evolutionary interests of individuals of the two sexes” (Parker 1979), arises because males and females often gain different fitness benefits for any given level of a reproductive trait (figure 23.1). As a result, males and females often cannot simultaneously both achieve their potential, maximum fitness benefits because the traits over which there is sexual conflict can take only a single value (Parker 1979). The outcome is an inevitable reduction in fitness in one or both sexes. This reduction in fitness generates a novel opportunity for *sexually antagonistic selection* to reduce the fitness cost resulting from sexual conflict (figure 23.1). Provided that there is genetic variation in the traits involved and a mechanism by which fitness costs can be reduced, sexually antagonistic selection can act to reduce for each sex the fitness costs from reproduction (Parker 2006b; Chapman 2006; Lessells 2006). However, if this in turn decreases the effectiveness or impact of the trait over which

there is sexual conflict, there may be subsequent selection for counteradaptations. If, for example, sexually antagonistic selection results in the elaboration of adaptations in males (e.g., fighting ability) followed by counteradaptations to reduce the cost of those adaptations in females (e.g., mating resistance), the result can be antagonistic coevolution between males and females (Parker 1979; box 23.1). Because this coevolution is focused on reproductive traits that could lead to differences in mating preferences and mating compatibilities within or between different populations, it has the potential to drive reproductive isolation and, ultimately, speciation (e.g., Parker & Partridge 1998; Gavrillets 2000).

The significance of sexual conflict was first realized by Trivers (1972), Dawkins (1976), and Parker (1979). Their pioneering studies, and particularly the groundbreaking work of Geoff Parker (1979), revealed the potential for conflicts of interest between males and females to generate evolutionary change (box 23.1). In a recent, large-scale synthesis of this subject, Arnqvist and Rowe (2005) expose the extraordinary diversity of traits that are potentially subject to selection arising from sexual conflict, and highlight the broad range of taxa in which such traits are found. Rather than try to capture this huge diversity in this short chapter, we refer the readers to Arnqvist and Rowe (2005) for the many excellent examples of sexual conflict in a wide range of different taxa (e.g., Parker 1979; Warner et al.

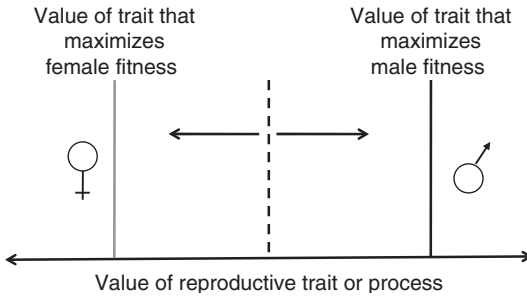


FIGURE 23.1 Schematic of fitness optima for a reproductive trait or process subject to sexual conflict. Fitness optima differ in males as compared to females (solid lines). However, the reproductive trait or process can take only one value and (unless either males or females have “won” the conflict), this is likely to lie between the male and female optima (e.g., at the dotted line). Hence there is sexual conflict because male and female optima cannot simultaneously be realized. The reduction in fitness from each sex not being at its optimum results in selection in each sex to minimize the fitness cost (in the direction of the arrows).

1995a; Rice 1996; Holland & Rice 1998, 1999; Magurran 1998; Arnqvist & Rowe 2002a; Martin & Hosken 2003; Westneat & Stewart 2003). In this chapter our aim is to focus on the concepts of sexual conflict, with a few illustrative examples. In the first section, we discuss, in turn, sexual conflict, the novel opportunity for antagonistic selection that it generates, the evolutionary potential of that selection, and finally the genetic mechanisms by which evolution resulting from sexual conflict may occur. In the second section we focus on the evolutionary potential of selection arising from sexual conflict and consider the theory and evidence that sexual conflict drives divergence both within and between species.

SEXUAL CONFLICT

Sexual conflict occurs because of differences between males and females in the optimum value of many

BOX 23.1 Key Lessons from Sexual Conflict Theory

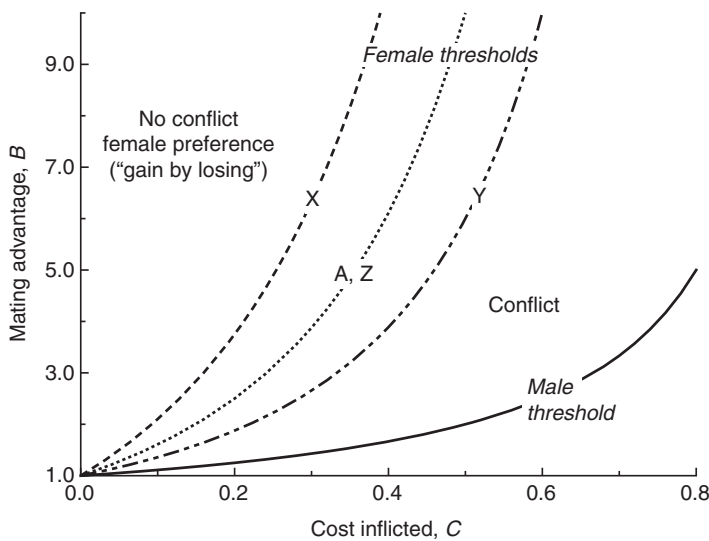


Figure 1 The spread of rare male mutants whose effects benefit males but incur costs to females (and which affects their joint progeny) under different genetic scenarios; A = dominant, autosomal (Parker 1979) or Y, X, or Z linked (Andres & Morrow 2003). A new mutation benefits males if B lies above the lower curve. The three upper curves are the thresholds for B above which it will pay the female to mate with males with the trait (at lower B, it pays the female to resist). Conflict occurs when B lies between the male and female thresholds. Reproduced with permission from Parker (2006b).

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BOX 23.1 (cont.)

Parker (1979) examined the central question of what happens when a characteristic that gives a mating advantage to males incurs a cost to the females with which they mate. Game theory models of sexual conflict were used to examine the effects of the dominance characteristic of the male trait and its frequency in the population.

The importance of the theory as illustrated by the above figure is that it identifies three zones (taken from Parker 1979, 2006b): (1) where the male trait is disadvantageous to both sexes and will not spread; (2) the sexual conflict zone—where the trait is advantageous to males but disadvantageous to females (sexually antagonistic coevolution may occur between the traits at the male locus to increase B , and those at the female locus to avoid mating with harmful males and/or to diminish harmful effects); (3) the concurrence zone—where the trait is advantageous to both sexes (selection favors both the harmful trait in males and female traits to accept or prefer males with the trait—sometimes called the “gain by losing” effect for females (Eberhard 2005).

A fundamentally important part of Parker’s (1979) theory was that it showed that sexual conflict had the potential to lead to evolutionary chases between adaptations in males and counteradaptation in females. Hence sexual conflict can act as an engine for evolutionary change.

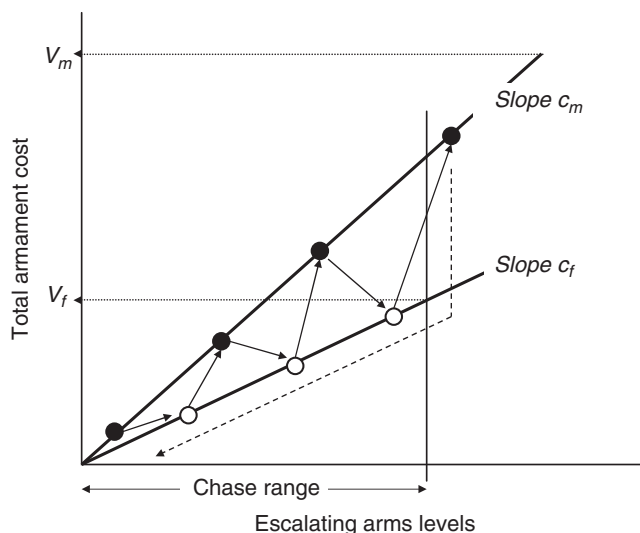


Figure II An example of an evolutionary arms race. The figure depicts an evolutionary chase in a sexual arms race model (from Parker 1979). Total arms costs are plotted against arms levels for the two sexes: at a given point on the x-axis, the total arms for each sex are exactly balanced so that the chances of winning the conflict are random; otherwise, the sex with the higher arms level wins. In this example, the value of winning for females (V_f) is lower than that for males (V_m), and the slope of the total costs with escalating arms levels is lower for females (slope c_f) than for males (slope c_m). If females start at a low arms level, males can win by a slightly greater level, which females can then outbid, and so on. As arms levels escalate, females would first reach the point where their total arms costs equal their value of winning: males can still outbid them and achieve a positive payoff. At this point females do better to reduce their arms to zero, which allows males also to reduce to a very low level. The cycle then begins again. Reproduced with permission from Parker (2006b).

aspects of reproduction (Parker 1979). Conflict occurs whenever the relationship with fitness for males and females differs for any trait (figure 23.1). Our definition is deliberately broad and includes traits having no role in interactions between the sexes as well as those that influence such interactions and result in social selection (box 23.2). Both viewpoints predict that there can be sexual conflict

over virtually any reproductive trait, and indeed sexual conflict is expected to be ubiquitous among sexually reproducing organisms. The extent of sexual conflict will be exacerbated by any factors that lead the reproductive interests of the two sexes to diverge. For example, a high degree of multiple mating with different partners coupled with low relatedness between mating partners reduces the extent

BOX 23.2 Sexual Conflict as Social Selection: Insights from Selection Theory

Sexual conflict represents a difference in the fitness optima for males and females for a given reproductive process or trait (Parker 1979). However, it may also be useful to consider sexual conflict through the related and complementary view of selection theory (Arnold & Duvall 1994; Arnold & Wade 1984; Westneat 2000). Sexual conflict can lead to social selection (Wolf et al. 1999; Westneat & Stewart 2003; table 7.1 in Arnqvist & Rowe 2005; see also box 14.1 in this volume), effectively extending into the domain of the *extended phenotype* of an individual. This is because the value of many traits subject to sexual conflict has an effect not only on the fitness of the bearer, but on the fitness of the other sex (in which that trait is not expressed). Sexual conflict is therefore created when there is a positive relationship between trait value and focal individual fitness (i.e., a selection gradient), but negative relationship between trait value in the focal sex and fitness of the other sex (an *opportunity gradient*; Arnold & Wade 1984). The extent of conflict can

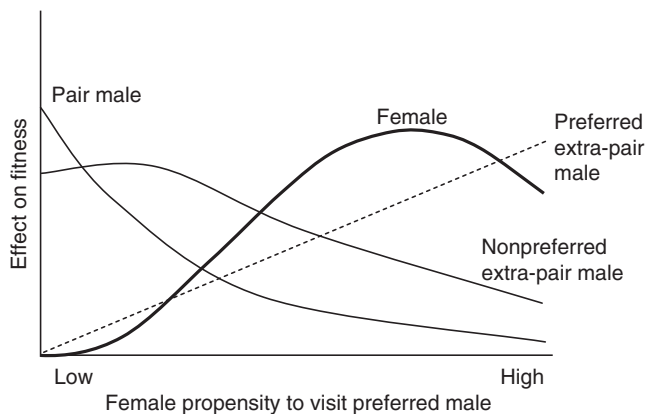


Figure 1 The relationship between the propensity of females to visit preferred males for EPCs and female fitness (thick line) that increases, except at high values, when the benefits diminish and costs increase. Preferred extra-pair males experience an increase in fitness as female visits increase (dashed line). However, the fitness of nonpreferred males or the pair male will decrease (thin lines) in different ways as females increase visits to preferred males. Both thin lines represent opportunity gradients describing sexual conflict on paired or nonpreferred extra-pair males due to the propensity of the female to pursue EPCs with preferred extra-pair males. Reproduced from Westneat and Stewart (2003) with permission.

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BOX 23.2 (*cont.*)

be described as the difference in slope of these two relationships. We illustrate this concept using an example of this theory as applied to sexual conflict over extra-pair copulations (EPCs) in birds (figure I, p. 403).

The social selection view emphasizes sexual conflict as a phenomenon that provides a novel opportunity for selection, rather than a special type or form of selection per se. The novel opportunity for selection could result in natural selection to increase viability or sexual selection to increase mating ability. Viewing sexual conflict as a type of social selection also provides the opportunity to more broadly encompass the types of processes that are subject to it (variously described as conflict traits, or shared traits; Lessells 2006; Rowe & Day 2006). Using the social selection framework, any adaptation whose relationship with fitness is opposing in males versus females is subject to sexual conflict. The social selection definition of sexual conflict predicts that any cost imposed indicates sexual conflict, regardless of any indirect genetic benefit that females may gain despite suffering costs. By extension, any female preference produces conflicts because some males are not preferred. For a further review of this topic, see Westneat (2000) and Westneat and Stewart (2003).

to which a mating pair have a stake in what happens beyond the current mating bout (Dawkins 1976). Hence traits that increase immediate investment in mating, at the expense of future investment by one of the current mating pair, can be selected.

That sexual conflict is widespread, however, does not imply that it automatically results in evolutionary change. Sexual conflict can create an opportunity for selection that is not realized if there is no trait variation in the affected sex. Moreover, for evolution to occur, there has to be (a) selection caused by sexual conflict and (b) genetic variation in a trait that covaries with the conflict-causing trait. In game theory models of sexual conflict, the likelihood of selection is described as *power* and *winning*, or the ratios of the benefits in males/females and costs in males/females, respectively (reviewed in Chapman 2006; Lessells 2006; Parker 2006b). What this boils down to is simply that, for sexually antagonistic selection to cause evolutionary change, the benefit-cost ratios have to be favorable. A related issue is that variation in the threshold or sensitivity of a trait subject to sexual conflict may also affect the potential for coevolution (Rowe et al. 2003, 2005). A general message is that the existence of sexual conflict cannot be assumed without knowledge of the costs and benefits of the adaptations involved (e.g., Parker 2006b).

Sexual Conflict Traits

The notion of traits that are subject to sexual conflict needs some qualification, because such traits

can be of diverse origin and form. For example, traits that cause sexual conflict can be expressed in one sex (e.g., male genital claspers), both sexes (hip width), or can instead be an emergent property of both sexes (e.g., mating frequency). Hence it is difficult to define general types of traits or processes that can be subject to sexual conflict. Previous authors have referred to the subjects of sexual conflict as conflict traits or shared traits (Lessells 2006; Rowe & Day 2006) to try to capture the diversity involved. What is clear, though, is that sexual conflict can fuel selection on a very diverse range of traits and processes from pre- and postmating traits through to those that control parental investment (Lessells 2006; Parker 2006b). Interestingly, sexual conflict is predicted to be more likely over mating decisions than it is over parental investment (Lessells 2006; chapter 26 of this volume). In brief, this is because the fitness returns are higher and costs lower for males that can manipulate females into mating with them as compared to the situation in which males try to coerce their mates into increasing their parental investment (reviewed in Chapman 2006; Lessells 2006).

Selection Arising from Sexual Conflict

Sexual conflict provides an opportunity for selection because of the difference in fitness optima for males and females (or the opportunity gradient represented by the effect of the trait in one sex on the fitness of the other; box 23.2). This evolutionary

tug-of-war between the sexes selects for each sex to shift the value of the trait subject to conflict to be closer to its own optimum, and hence to reduce potential costs (figure 23.1). However, this necessarily leads to increased costs in the other sex, resulting in direct selection in each sex to minimize costs and potentially to reduce the effectiveness of the original manipulative adaptation. Hence the effects of adaptations in males can select for counteradaptations in females, leading to potential cycles of adaptation followed by counteradaptation. The resulting process is sexually antagonistic coevolution, fueled by sexual conflict (Parker 1979; box 23.1).

Sexual Conflict as Fuel for Evolution

Once there is in place a cycle of sexually antagonistic coevolution, then theory shows that if the

coevolution is sufficiently strong, this can lead, under certain conditions, to diversification in the traits involved within species, as well as reproductive isolation and ultimately speciation (e.g., Arak & Enquist 1995; Parker & Partridge 1998; Gavrilets 2000; Gavrilets et al. 2001; Gavrilets & Waxman 2002; Gavrilets & Hayashi 2005; box 23.3). The evolutionary consequences of sexual conflict both within and between populations are considered in more detail below.

From Sexual Conflict to Coevolution: An Example

To illustrate the different stages of the arguments above, we consider the often-used example of sexual conflict in relation to mating frequency. Mating frequency is an emergent property of males and females, and on average, in a population with equal sex ratio, the population mating

BOX 23.3 Sexual Conflict Can Fuel Evolutionary Change Leading to Reproductive Isolation

Given that sexual conflict can drive evolutionary change leading to evolutionary chases in adaptations related to mating and reproduction, the question is, to what extent is this process expected to lead to reproductive isolation and ultimately speciation? Several authors have developed theory on this (e.g., Parker & Partridge 1998; Rice 1998, Holland & Rice 1998; Gavrilets 2000; Gavrilets et al 2001; Gavrilets & Hayashi 2005). Parker and Partridge (1998) used a game theory approach to study the mating outcomes that would occur following secondary contact of populations each having undergone sexually antagonistic coevolution in allopatry. As expected, the outcomes depend on the length of allopatry. In the short term, males can gain higher fitness by mating with females from another population, as those females have no resistance to those males. However, such matings also introduce genes for female resistance into the other population, which are advantageous to females and therefore spread. In the longer term, increased levels of divergence could lead to prezygotic isolation in such matings. The theory shows that while selection on males will usually promote gene flow and hence reduce reproductive isolation, females may usually be selected to resist hybrid matings, slowing the rate of gene flow and increasing reproductive isolation. This is because it generally pays males more to search for new mates. An important result is that sexual conflict can result in higher rates of speciation in clades in which females have relatively higher armament levels (so-called female-win clades). A corollary is that when there is reinforcement, females will promote pre-mating isolation. Lower genetic variation is expected in female-win as opposed to male-win clades. The overall conclusion is that sexual conflict can fuel reproductive isolation, but only under certain conditions.

The models developed by Sergey Gavrilets (e.g., Gavrilets & Waxman 2002) also suggest a potentially important role of sexual conflict in driving reproductive isolation. In contrast to traditional models of speciation, Gavrilets' models predict that sexual conflict can drive evolution more rapidly in large, rather than small, populations, a prediction supported by the results of a study in dung flies (Martin & Hosken 2003).

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BOX 23.3 (cont.)

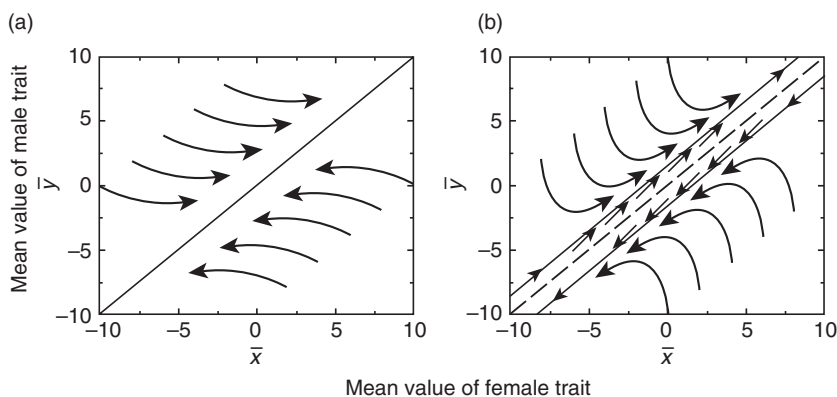


Figure 1 The figure shows the dynamics of mean trait values in Gavrilets' (2000) model. In (a), the costs of sexual conflict are low and the solid line depicts the line of equilibria. The trajectory of mean trait values is toward the line of equilibria, at which mean trait values then become static. In (b), the costs of sexual conflict are high. Points along the dotted line of equilibria are now unstable, and coevolutionary chase occurs along the continuous lines. In terms of the implications for speciation, the models show that where there are equilibria (a), points along the line of equilibrium are neutral, hence in populations that are isolated, allopatric genetic divergence could occur by drift along the line. Where there are coevolutionary chases (b), allopatric populations can diverge rapidly and simultaneously by selection in different directions. These models therefore support the idea that sexual conflict can drive speciation. Reproduced with permission from Gavrilets (2000) and adapted from Parker (2006b).

frequency of males must equal that of females. However, given that the variance in mating frequency is expected to be much higher for males than for females, we expect selection on male mating adaptations to be particularly strong. There will be sexual conflict if a high mating frequency is beneficial for male reproductive success but, in contrast, females show highest fitness at an intermediate mating frequency. This conflict sets up the opportunity for selection in males to increase mating frequency and in females to decrease it, because these outcomes would increase male or female fitness, respectively. Provided there is genetic variation in mating frequency and that both males and females have some control over mating frequency (i.e., have a mechanism with which to influence it), then there will be selection on males to mate with each available female, but for females sometimes to resist male mating attempts. Hence sexual conflict over mating decisions can lead to adaptation and counteradaptation and initiate antagonistic coevolution.

A good example is found among pond skaters (water striders, *Gerris* spp). Here, there is sexual conflict because males gain from higher mating frequencies and have a wide variance in mating success, whereas for females mating is costly in terms of reduced foraging time and higher predation risk (Rowe et al. 1994). Males are selected to attempt to mate with all available females, whereas females usually try to resist superfluous matings, with the result that violent pre-mating struggles occur in which females try to shake off courting males (Rowe et al. 1994). The mechanism by which males try to increase mating frequency is through morphological changes in claspers that aid them in gaining attachment to females during mating. Males with longer abdominal claspers are likely to have higher mating success. In contrast, abdominal spines in females serve to lower mating frequency, and, in a manipulative experiment, increased female abdominal spine length led to shorter pre-mating struggles and a lower mating rate (Arnqvist & Rowe 1995). Hence, in this example, the abdominal claspers in males

and spines in females appear to be traits subject to antagonistic selection arising from sexual conflict, with longer claspers in males leading to higher male fitness and longer spines in females to higher female fitness. Experimental and comparative evidence support the idea that the armaments in males and in females across different species of pond skaters are coevolving (Arnqvist & Rowe 2002a).

Intra- or Interlocus Sexually Antagonistic Selection

The way in which traits evolve in response to antagonistic selection may be facilitated or constrained by the underlying genetic mechanisms involved. The genetic basis of sexual antagonism can therefore, in principle, have a major impact on the speed and trajectory of coevolution. The adaptations influenced by selection arising from sexual conflict can be influenced by the same (intralocus) or different (interlocus) genes in males and females, and both have the potential to drive evolutionary change that could lead to speciation (Parker 1979; Parker & Partridge 1998; box 23.3). However, the distinctions between intra- and interlocus coevolution and their relative importance in evolutionary terms, and the outcomes they generate, have not yet been explored in detail (Chapman 2006).

For example, intralocus coevolution may constrain the evolution of, or may ultimately select for, sex limitation in genes influencing traits subject to selection from sexual conflict. This is because alleles of genes that currently reside in males are prevented from reaching their male-specific optimum by counterselection whenever those genes are expressed in females. Episodes of this type of evolutionary constraint can therefore be resolved by the evolution of sex limitation in those genes. For example, if a gene that has a male beneficial function can become expressed only in males, this may prevent counterselection against the expression of that gene in females. In interlocus coevolution, on the other hand, sex-limited genes may be the starting point of conflicts. Interlocus coevolution may instead be constrained mostly by the relative costs and benefits of the adaptations that are selected.

Evidence for Intralocus Antagonistic Selection

Adult locomotory activity in the fruit fly *Drosophila melanogaster* has been used as an example of a trait whose expression is controlled by the same

genes in males and females, but which may be subject to sexual conflict. Locomotion in adult flies appears to be controlled by the same sets of genes in both sexes, because there is a positive genetic correlation between movement levels in males and females. However, there is also sexual conflict over the optimum rate of locomotion for adults. High locomotory activity is beneficial to males because it increases their encounter rate with females, leading to higher courtship rate and higher reproductive success. In contrast, females who are less active have higher fitness than more active females, presumably as reduced locomotory activity is associated with increased feeding and oviposition (Long & Rice 2007). This sexual conflict offers the opportunity for antagonistic selection on the alleles involved, modified by whether they currently reside in males or females. This example provides a good demonstration of the diversity of types of traits and processes that can become subject to opposing selection pressure on males and females. Unlike mating rate, for example, the opposing selection in this case is not dependent on interactions between males and females (though that could also occur if males that are especially active impose larger reproductive costs on the females with which they interact), but is instead dependent on differences in the fitness effect of particular locomotion-affecting alleles when in one sex compared to the other (and remember these alleles are equally likely to occur in both sexes).

A number of experiments from the laboratory of Bill Rice have documented the presence of sexual conflicts that lead to selection on the same genes expressed in males and females in *D. melanogaster* (e.g., Rice 1992; Chippindale et al. 2001). For example, techniques have been used to allow alleles with sex-specific beneficial effects to accumulate in one sex by preventing counterselection against them in the other (Rice 1992). Another technique has involved testing the effects on fitness of the same genotypes expressed in males *versus* in females. This work demonstrated that fitness was positively correlated in larvae (when male and female interests are broadly similar), but negatively correlated in adults (when the sexes come into conflict over reproduction). Hence in adults, genotypes that resulted in high fitness for females resulted in low fitness for males and *vice versa*. The conclusion from such work is that the number of genes subject to intralocus sexually antagonistic selection is potentially high (Chippindale et al. 2001) and represents a considerable evolutionary constraint on each sex reaching its adaptive, optimum

phenotype. For other examples, see Arnqvist and Rowe (2005).

Evidence for Interlocus Antagonistic Selection

There are many traits encoded by different loci in males and females that have the potential to be shaped by selection arising from sexual conflict. We summarize here just three of the systems that have been investigated in depth and that cover premating and mating traits through to those related to parental investment (for numerous further examples, see Arnqvist & Rowe 2005).

Pond Skaters Pond skaters have provided an excellent system in which to study sexual conflict in an ecological setting (Rowe et al. 1994). Conflicts over mating decisions in pond skaters have already been discussed above in terms of the struggles over mating. Using a combination of comparative and empirical work, Arnqvist and Rowe (2002a) demonstrated ongoing sexually antagonistic coevolution in the level of armaments in males and females, in terms of male grasping and female antigrasping behaviors. The male grasping adaptations facilitate mating, and the female antigrasping adaptations act to decrease the frequency of costly, superfluous matings. Coevolution between male adaptations and female counteradaptations occurred across 15 different species of pond skaters. Interestingly, it was not the absolute level of armaments and defenses between males and females that determined the length of premating struggles and mating rates. Mating outcomes were instead determined by the relative imbalance in armaments, in other words, if males invested more in armaments than females did in resistance, males gained greater fitness, and vice versa. The conclusion is that the absolute level of armaments and defenses is not necessarily a good indicator of the level of sexual conflict.

Fruit Flies The fruit fly *Drosophila melanogaster* has been a valuable workhorse in the study of sexual conflict. Indications that mating interactions between males and females were subject to sexual conflict originally came from studies that demonstrated significant mating costs in females that mate frequently. Experiments that used genetic manipulations showed that these costs are caused by the receipt of high levels of male seminal fluid

accessory proteins (Acps) during mating (Chapman et al. 1995). Because Acps increase male reproductive success through a variety of effects on sperm competition, this suggested that a side effect of the competition among males was costly to females, leading to subsequent selection in females to reduce this cost. This is supported by the finding of a strong positive correlation between a male's ability in sperm competition and the death rate of the females with which they mated (Civetta & Clark 2000). Hence the male mating adaptations seem to be selected to increase a male's per mating share of paternity, despite the eventual cost that they may cause in females.

A number of experimental evolution studies have targeted the fruit fly mating system by altering the nature of sexually antagonistic selection. For example, Holland and Rice (1999) placed replicate lines of flies under monogamy and polyandry. In the monogamy lines, there is virtually no interlocus sexual conflict (that caused by interactions between the sexes) because the evolutionary interests of males and females become the same. After tens of generations under these selection regimes, the monogamous males became less harmful to females and monogamous females were less resistant to male-imposed mating costs. Monogamous populations also had higher net fitness. Together, these findings support the idea that when the interests of males and females become more similar, the sexes have less harmful effects on one another.

In another experimental evolution study, the adult sex ratio of males and females was altered, to investigate whether females can evolve resistance to male-imposed mating costs (Wigby & Chapman 2004). Lines of flies were set up in which the adults experienced male- or female-biased sex ratios (3 males to every female and vice versa). Females taken from male-biased populations, in which sexual conflict was predicted to be strong, were able to survive longer in the presence of males than were females from female-biased populations. These differences in survival were not found in the absence of males, which suggests that females had indeed evolved specific mechanisms to counter male mating costs. The benefits of female resistance to males have also been studied through mimicking the spread of a female resistance gene (Stewart et al. 2005). In this experiment an eye color marker was made to segregate as if it were a resistance gene that resulted in 100% reduction of mating costs in females. This trait spread rapidly through the

population after only 5 generations of selection, because these females were able to avoid incurring mating costs imposed by males.

What is striking about these evolutionary studies is that adaptations and counteradaptations selected in response to underlying sexual conflicts can arise extremely rapidly, within tens of generations. This remarkable and consistent finding suggests that sexual conflict has the ability to promote rapid evolutionary change.

Mate Desertion in Birds In species in which parents look after their young, the time spent engaged in parental investment can reduce the time that males and females can spend searching for new mates (chapters 20 and 26). For this reason there is the potential for sexual conflict to arise over which sex will provide parental care, and how much of it they will give. In the Penduline tit (*Remiz pendulinus*) both males and females can perform both biparental and uniparental care. However, both sexes benefit from starting a second nest during a breeding season and there is therefore a sexual conflict over timing of nest desertion. Thirty percent of nests end up being abandoned by both parents, resulting in complete loss of reproductive investment, which suggests that the desertion mechanism is not very highly tuned. However, if either sex manages to desert before its partner, the remaining individual may stay and provide care, whereas the deserting partner can find a new mate and start a second brood, potentially gaining higher fitness. The timing of mate desertion is a balance for males between the benefits of desertion and those of staying. For example, males aim to gain a return on their investment of time and energy in nest building and holding a high-quality territory, factors that are important in attracting females. In addition, if the male deserts before the female has laid sufficient eggs in the nest, then she will desert too. Males thus benefit from assessing a female's egg-laying status. Given that females also benefit from deserting following egg laying, they apparently try to hide the number of eggs they have laid by covering them and preventing their mate from accessing the nest. If this is successful, females may sometimes desert, leaving the male to take care of the brood (Valera et al. 1997). Hence, in this example, the underlying sexual conflict gives the opportunity for selection on a male's ability to assess a female's egg-laying status and on a female's ability to disguise her egg laying.

Contrasting Selection Opportunities Arising from Sexual Selection and Sexual Conflict

Models of sexual selection and models of sexual conflict both center on the interactions between males and females during reproduction—specifically, on the ways in which males compete with each other for matings with females and the ways in which females mate with some males instead of others. There is overlap between models of sexual selection and sexual conflict because both types focus on selection for increased reproductive success. Where the models differ, however, is in the way in which the female preference is selected and specifically whether the impact of male reproductive strategies on females is beneficial, cost neutral, or costly to females (see the excellent chapter on this topic in Arnqvist & Rowe 2005). The novel opportunity for selection provided by sexual conflict occurs when the relationship with fitness for a given trait is positive for one sex and negative for the other (figure 23.1). Whenever this is not the case, then models of sexual selection, rather than conflict, are more appropriate. However, divisions between the different types of models should not be viewed as fixed. For example, the existence, sign, and magnitude of costs of mating with specific males can be environmentally dependent, changing the opportunity for selection.

Here we briefly compare the contrasting opportunity for selection on female preference under sexual selection and under sexual conflict. In models of sexual selection based on either Fisher's *runaway* or *good genes* processes, female preference genes are selected because they become associated either with genes that increase the mating success of their sons (Fisher 1930) or increase the fitness of both sexes of offspring (Zahavi 1975). Hence, female preference genes evolve under so-called indirect selection through the effects on offspring. However, Fisherian models of sexual selection cannot explain the maintenance at equilibrium of substantial costs of mating to females (e.g., Kirkpatrick & Barton 1997) and cannot explain antagonistic coevolution when there are large mating costs in one (or both) sexes. Models of sexual selection by good genes, on the other hand, assume that female mate choice will result in increased offspring fitness, which is again counter to the expectations of models of sexual conflict. Hence models of sexual selection do not easily explain what happens to female mating biases under a sexual conflict scenario.

TABLE 23.1 Summary of single species studies comparing direct costs and indirect benefits of mating for females

Study	Species	Method	Traits Measured	Fitness Measure Calculated	Son/Daughter Fitness Measured	Generation of Offspring in Which Fitness Measured	Costs Estimated?	Are Direct Costs > Indirect Benefits?
Head et al. 2005	<i>Acheta domestica</i>	Females held with attractive or unattractive males and the number of grandchildren estimated	Sons' attractiveness, number of grandchildren produced	Rate sensitive and insensitive estimates of fitness	Sons and daughters	F1	Yes	No
Rundle et al. 2007	<i>Drosophila melanogaster</i>	Male grandchildren were bred from grandfathers that were successful or unsuccessful in gaining matings	Premating, mating success, productivity and longevity of male grandchildren	No composite fitness measure calculated	Sons and daughters	F2	No	There are indirect benefits
Orteiza et al. 2005	<i>Drosophila melanogaster</i>	To take the male offspring from the first or second mates of twice-mated females	Lifetime reproductive success of sons in a competitive environment (male postmating success)	No composite fitness measure calculated	Sons only	F1	Yes	Yes
Galliard et al. 2008	<i>Lacerta vivipara</i>	Create male and female biased sex ratio	Offspring survival and growth	Composite measure of female survival and fecundity calculated	Sons and daughters	F1	Yes	Yes
Priest et al. 2008	<i>Drosophila melanogaster</i>	Females held at three different mating frequency regimes, and fitness of mothers and daughters estimated	Female lifetime fecundity and survival and daughter fitness	Calculated fitness and inclusive fitness	Daughters only	F1	Yes	No

Note: For a gene that confers female resistance to mating costs to spread under selection arising from sexual conflict (as opposed to sexual selection) the direct costs of mating to females should be larger than the indirect benefits of mating. The table summarizes the current relevant empirical data.

The key contrast between sexual conflict and sexual selection as an explanation for female behavior is that under sexual conflict, selection on female mating decisions is direct: to avoid or reduce the costs of matings. Female mating preferences under sexual conflict are therefore best modeled by *direct benefits* theory, except that in this case the expectation is that females will exert mating biases to minimize costs rather than maximize benefits. An important issue with regard to the opportunity for selection on female preference/resistance behavior is whether indirect genetic benefits for the offspring of females that mate frequently and incur large mating costs can balance or exceed the direct cost of mating. The distinction is important because from a gene's perspective, only if direct costs to females of mating are larger than indirect genetic benefits in the offspring generation will the gene be subject to sexually antagonistic coevolution. Theory suggests that indirect genetic benefits in this situation will be small (Kirkpatrick & Barton 1997; Rowe et al. 2003, 2005), and table 23.1 provides a summary of the current empirical data from single species studies, which is mixed.

EVOLUTIONARY CONSEQUENCES OF SEXUAL CONFLICTS

In this section we consider the potential of sexual conflict to drive evolutionary change within and between species and consider the supporting theory and evidence. We focus mostly on conflicts arising from interactions between different loci (but note that conflicts arising from within loci may also have significant effects on population structure). Sexual conflict can potentially affect population fitness, the rate of adaptation, or the risk of extinction (Holland & Rice 1999; Fricke & Arnqvist 2007). However, most attention has been given to the potential of sexual conflict to generate evolutionary change resulting in population divergence. It is not yet clear, however, to what extent sexual conflict is an engine of speciation, and theory and evidence on that issue are mixed as we illustrate below.

Divergence within and between Species: Theory

The importance of sexual conflict theory lies in illuminating the evolutionary potential of sexual conflict, and showing the conditions under which it

may lead to diversification, population differentiation, and potentially speciation (e.g., Parker & Partridge 1998). The key discovery of sexual conflict theory has been that it is possible for a male adaptation to spread in a population, despite the cost that this may cause in females (Parker 1979; Gavrillets et al. 2001; Holland & Rice 1998; box 23.1). In addition, theory also shows that indirect genetic benefits of mating to females are not required for the spread of adaptations in males that are harmful to females (e.g., Cameron et al. 2003), though they may also occur.

Sexual conflict can in theory generate continual evolutionary chases between the interacting parties involved (Parker 1979; Gavrillets 2000; Holland & Rice 1998). The types of dynamics resulting from these population genetic models have the potential to lead to speciation if they promote divergent evolutionary trajectories between populations. A summary of sexual conflict speciation models (Gavrillets & Hayashi 2005) shows that some dynamics that can result from sexual conflict promote speciation (e.g., endless coevolutionary chases, diversification in both sexes) but others do not (single equilibrium or line of equilibria, cycles, diversification in one sex but not the other, etc.). The differences in dynamics (diversification versus equilibrium) that result from sexual conflict are likely to depend upon the type and strength of selection that is acting on the female trait (Rowe et al. 2003), the number of loci involved, and dominance patterns.

A game theory treatment of speciation in relation to sexual conflict, by Parker and Partridge (1998; box 23.3), adds an additional and important consideration. It examines the extent to which the differential behavior of males and females may affect the extent to which sexual conflict promotes reproductive divergence. In general, females may tend to act as a force for increasing reproductive isolation and males for decreasing it. However, if females evolve insensitivity to male traits in response to sexual conflict, then gene flow due to female behavior could increase, because females would no longer discriminate between different males (Rowe et al. 2003).

If sexual conflict is driving speciation, then individuals from different allopatric populations should be divergent in the reproductive traits that are subject to sexual conflict. This might then lead to incompatibilities or interactions in crosses between individuals from different populations. Arnqvist and Rowe (2005) suggest that sexual conflict could

thus be a particularly potent driver of speciation. This is because selection on both male and female adaptations and counteradaptations is direct and hence stronger than indirect selection resulting from sexual selection. Although both intra- and interlocus antagonistic coevolution have the potential to lead to reproductive isolation (Parker & Partridge 1998; Rice 1998), the mechanisms involved may differ. Intralocus coevolution can lead to sexual dimorphism or sex limitation. However, this could occur via different routes in different allopatric populations, and these mechanisms could be disrupted when previously separated populations mix, potentially leading to reproductive incompatibilities. Genetic correlations for traits related to mate choice that evolve separately in different populations could also alter the likelihood of interpopulation matings (box 23.3). Interlocus antagonistic coevolution is expected to be a powerful driver of change, particularly in internally fertilizing species in which genes involved in reproduction are predicted to perpetually coevolve in an arms race, and to diverge faster than the rest of the genome (Holland & Rice 1998; Rice 1998). This predicts an early signature of incipient speciation to be incompatibility of male and female reproductive tract proteins and physiology across different populations.

In the following two sections we discuss first the data supporting sexual conflict as a driver of divergence within species and then between species.

Within Species Divergence: Empirical Data

Evidence that sexual conflict is a major driver of diversification within species, with the potential to lead to speciation, would be exemplified by demonstrations of diversifying selection, of divergence in those traits between species, and of rapid coevolution in sexual conflict traits. We review this evidence below. A key and perhaps unresolved question is whether the reported evolution in reproductive traits is causal in population or species divergence or merely associated with it.

Diversifying Evolution in Reproductive Traits Subject to Sexual Conflict

There is much evidence that reproductive traits in general evolve rapidly (e.g., Eberhard 1985; Clark et al. 2006). Sexual conflict predicts the

rapid evolution of traits that are involved in antagonistic interactions between the sexes and these could include sperm-egg recognition/binding traits, reproductive proteins, mating behavior, and reproductive morphology (Rice, 1998; chapters 21 and 22).

There is evidence for positive selection (i.e., greater variance in nucleotide sequences among taxa than expected from neutral substitutions) in reproductive proteins, especially in males, from a wide range of taxa, for example, in marine invertebrates, flies, mice, plants, birds, and mammals (reviewed in Snook et al. 2009). In addition, there is considerable evidence that reproductive morphology also evolves extremely rapidly (Eberhard 1985) and is in many cases the distinguishing feature between otherwise morphologically identical species. However, whether the selection pressure in such cases results most often from sexual selection or from sexual conflict is often unclear. For instance, rapid evolution in sperm-egg recognition molecules could result from selection to avoid sexual conflict over fertilization processes, such as the need to avoid polyspermy, or from cryptic female sperm choice or sperm competition.

It is necessary to combine studies of molecular evolution with functional information, so that the selective forces acting on the traits can be identified. For this reason, we focus here on patterns of evolution in genes that are predicted to play a role in mediating sexual conflict. The best evidence comes from the study of *Drosophila* reproductive proteins, in which it has been established that the actions of proteins made in the male accessory glands result in the expression of mating costs in females (Chapman et al. 1995). Therefore, some of these proteins are examples of adaptations that are shaped by sexual conflict.

There are over 100 Acp genes, and there is evidence that some show high levels of within-species polymorphism (e.g., Begun et al. 2000). There are also now a large number of studies that have documented positive selection on Acp genes (e.g., Begun et al. 2000; Swanson et al. 2001; Haerty et al. 2007). It is also often hard to find orthologues of Acp genes even in very close relatives (Mueller et al. 2005). Early estimates put at 11% the number of Acp genes under positive selection (Swanson et al., 2001), but recent estimates are higher (Findlay et al. 2008), reflecting the increasing statistical power that comes from the higher numbers of species comparisons that are now possible.

Is there any evidence for positive selection on any of the Acp genes likely to be subject to selection from sexual conflict? The full answer is not yet known, and there are also problems that arise from limited power to detect positive selection for short genes such as those encoding Acps. However, of six genes so far implicated in causing mating costs in females (either because of toxicity to females, increased death rate following single matings or by direct tests with mutants), four have been investigated for positive selection. Of those, two or possibly three showed evidence of nonneutrality (Begun et al. 2000; Findlay et al. 2008).

There are well-studied examples of sequence evolution in reproductive genes that mediate sperm and egg recognition in marine invertebrates such as sea urchins and abalone (for review see Swanson & Vacquier 2002b). Sperm proteins in such species show extremely rapid evolutionary change, and variation in the rates of change between different taxa. However, the evidence that these proteins are selected primarily by sexual conflict remains to be confirmed, although there is evidence that sexual conflict over polyspermy (in which too many sperm attempt to enter the egg) can drive the evolution of sperm-egg interactions (Franke et al. 2002; chapter 22, this volume).

Evidence for the strength of selection acting on female reproductive proteins is generally harder to gather than for male proteins because the female targets for male reproductive proteins do not necessarily reside in the female reproductive tract. However, evidence is now accumulating that female reproductive proteins and female reproductive tract morphology (e.g., Pitnick et al. 1999) can also evolve rapidly, although the evidence that these adaptations evolve due to selection arising from sexual conflict is in most cases still lacking. Swanson et al. (2004) detected that 6% of proteins in the female reproductive tract of *D. melanogaster* were under positive selection. A later, more detailed study (Panhuis & Swanson 2006) reported positive selection on 6 out of a set of 9 female reproductive tract genes surveyed. Similarly, Kelleher et al. (2007) conducted a survey of genes from the lower reproductive tract of *D. arizonae* and found evidence for elevated rates of evolutionary change in 31 of the 241 reproductive tract proteins detected. Across vertebrates, there is evidence for elevated evolutionary change in the female reproductive proteins of birds, humans, and other mammals (reviewed by Clark et al. 2006).

Coevolution in Reproductive Traits within Species

Abalone of the genus *Haliotis* provide one of the few examples in which the patterns of evolutionary change in both male and female interacting reproductive proteins have been studied. Male sperm contain lysin, a protein that binds to the vitelline envelope receptor for lysin (VERL) and then dissolves part of the outer layer of the egg to facilitate sperm entry. Sperm lysin is highly divergent between closely related species and data from site-specific mutagenesis shows that there are specific sites at both the N- and C-terminus of lysin that control species specificity in lysine-VERL interactions (Lyon & Vacquier 1999). Concerted evolution in VERL appears to drive positive selection in lysin. The VERL is encoded by a large and repetitive sequence, only part of which shows very strong evidence for positive selection (Galindo et al. 2003). This highlights the need to identify the functionally important parts of the interacting molecules in order not to overlook evidence for coevolution.

The best evidence for rapid coevolution between male adaptations and female counteradaptations that are subject to sexual conflict comes from studies of reproductive morphology (e.g., Arnqvist & Rowe 2002a; Rönn et al. 2007). For example, in pond skaters, there is a well-documented sexual conflict over mating decisions, which drives coevolution between male abdominal clasper morphology and female abdominal spines (Arnqvist & Rowe 2002a). Relative changes in armament levels between males and females across 15 species were associated with whether the male of any particular species is relatively better at grasping females during mating contests, as described above (Arnqvist & Rowe 2002a).

Another example of coevolution driven by sexual conflict comes from a study in the seed beetle genus *Callosobruchus* (Rönn et al. 2007). In these species there is a predicted sexual conflict over male mating frequency, with male penile spines representing adaptations that anchor males during mating but cause damage to the female reproductive tract. The female counteradaptation to that damage is a thicker lining of the female reproductive tract. The amount of spininess and amount of harm caused varies across species, and furthermore the degree of male spininess is correlated with the thickness of the connective tissue in the female reproductive tract wall. As in the pond skater example, the

absolute level of armaments between males and females is independent of the degree of harm caused to females. However, the degree of harm varied instead with the relative level—in other words, harm is more evident in species in which the male genitalia was relatively more spiny and in which the female tract is relatively less robust.

A pervasive, but generally unstated, assumption underlying models of sexual conflict involving interactions between the sexes is that there will be like for like matching coevolution between male and female reproductive traits. This appears difficult to reconcile with recent findings that apparently suggest there is more genetic variation residing in male than in female reproductive or tissue specific genes. For example, Haerty et al. (2007) used data from the 12 *Drosophila* species genomes to compare rates of change in sex- or reproduction-related genes as compared to other genes. They found that genes expressed in the testis and male reproductive tract showed the most rapid patterns of gains and losses, and that genes in male reproductive tissue evolved faster than those that were female tissue specific. The fact that genes expressed only in one sex are apparently evolving faster than those expressed only in the other could mean that reproductive proteins in males are primarily subject to sexual selection among males, and that selection on females arising from sexual conflict is less strong. Alternatively, it could mean that sexual conflict is important in driving both male and female reproductive traits but there are biases that produce this result. For example, differences in expressed gene size or complexity between the sexes may make it easier to detect positive selection in male versus female reproductive genes. Alternatively, variation in the expression and function of female reproductive genes might not be encoded by nucleotide variation in the reproductive genes themselves. Finally, one sex could be more sensitive to small, subtle sequence changes, for instance, if female reproductive genes tend to be controlled at the translational level by microRNAs.

With increasing amounts of data coming from genome sequences, it would be useful to identify whether there are particular molecular signatures of sexual conflict. Although this is not yet possible, some detectable patterns are emerging; however, a fundamental problem usually remains, that functional information is needed about the selection acting on the traits involved, to distinguish the source of selection responsible. Ratios of

nonsynonymous to synonymous sequence changes of between 0.5 and 1.0 may suggest evidence for evolutionary change in the recent past (Swanson et al. 2004). Gene duplication followed by positive selection may also indicate a relic of past conflicts (Kelleher et al. 2007). Rapid evolutionary change is not by itself evidence for sexual conflict. To reach that conclusion, one needs to demonstrate the relationship between the cost to females and the rate of evolutionary change in the male manipulative trait. Hence it is not currently possible to look in the sequence data for an evolutionary signature of mating rate. To do that, one would have to examine patterns in all the relevant genes that contribute to a particular phenotype.

A fruitful experimental design, which may also avoid the problem that past conflicts can be masked by current equilibria, will be to impose differing levels of sexual conflict (e.g., monogamy versus polyandry) and then, following experimental evolution, to genotype the loci subject to sexual conflict to determine whether and how they have evolved. Only then may reliable molecular signatures of sexual conflict be detected.

Between Species Divergence: Empirical Data

If sexual conflict can lead to reproductive isolation and ultimately speciation, then allopatric populations or incipient species that have been subject to it should exhibit incompatibilities or even reproductive isolation when reexposed to one another. It was proposed that such incompatibilities, as evidenced by the pattern of outcomes when crossing allopatric populations, would themselves be footprints of sexual conflict (Andrés & Arnqvist 2001; Arnqvist & Rowe 2005). However, the results of several studies in which allopatric populations have been crossed together have yielded little consistency in results (Rowe et al. 2003).

A more profitable line of inquiry has been to impose experimental evolution of differing levels of sexual selection and sexual conflict upon replicated lines and subsequently to ask whether there is any evidence for reproductive isolation when those lines are reexposed to one another. For example, Martin and Hosken (2003) conducted an artificial selection experiment with the dung fly (*Sepsis cynipsea*), with enforced monogamous and polygamous lines held under high or low population density. Females from the monogamous line showed no discrimination

against males from either their own or one of the allopatric monogamous lines. In contrast, females from the polygamous lines did discriminate against males from allopatric lines, preferring their own males. This effect was more pronounced in the high density than the low density lines. This suggested that increased sexual conflict had selected for increased reproductive isolation, as predicted by theory (Gavrilets 2000).

A number of studies have conducted related experiments in *Drosophila melanogaster* (Wigby & Chapman 2006) and *Drosophila pseudoobscura* (Bacigalupe et al. 2007). However, none of these have subsequently provided support for the idea that sexual conflict leads to faster evolution of reproductive isolation. Lack of support could lie in the choice of traits examined or the amount of time that had elapsed, or arise because sexual conflict does not promote reproductive divergence in these species.

CONCLUSIONS

We have shown how sexual conflict arising from differences in the evolutionary interests of males and females can lead to antagonistic selection and coevolution between the sexes, in which male adaptations are selected despite the costs that they may cause the females with which they mate (Parker 1979). Sexual conflict can fuel evolutionary change within and between species and is more likely over traits and processes related to mating than over those related to parental investment. There is good evidence that sexual conflict can drive diversification within species, but there is currently mixed support for the idea that sexual conflict is a major engine of speciation. There is considerable evidence of rapid evolutionary change in male and female

reproductive proteins, but conclusive evidence that this is driven primarily by sexual conflict is so far lacking. However, recent technical and theoretical advances will allow new experimental tests of speciation by sexual conflict, in which studies will target the relevant genes and determine evolutionary signatures of sexual conflict. There is also a need for more studies from natural populations on other species and on the influence of sexual conflict on life history traits such as life span and genomic imprinting.

SUGGESTIONS FOR FURTHER READING

Sources for further reading are Parker's (1979) original treatment of sexual conflict and Trivers' (1972) chapter, both of which illuminate fundamental concepts. Arnqvist and Rowe (2005) give an in-depth treatment of the subject and conduct a deep survey into examples of reproductive traits that are potentially subject to sexual conflict. Finally, we refer readers to three special volumes on this topic in the *American Naturalist* (2005 supplement to Vol. 165) in the *Philosophical Transaction of the Royal Society of London* (2006, Vol. 361) and in *Evolutionary Ecology* (2005, Vol. 19).

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