Chapter 1
Sexual Conflict and Evolutionary Psychology: Towards a Unified Framework

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Sexual Conflict: What Is It, Why Does It Occur, How Do We Measure It, and Why Does It Matter?

It was realized, particularly in the 1970s, that rather than being cooperative ventures, the interactions between the sexes over reproduction are often characterized by conflict rather than cooperation (Parker 1979; Trivers 1972). Therefore, as well as the exquisitely coordinated and spectacular courtship displays of birds (Krebs and Davies 1987), reproductive contests can result in mortal injury to females, the evolution of female-damaging penile spines, and female lifespan-shortening seminal fluids (Chapman et al. 2003a). A gene-centered perspective (Dawkins 1976; Hamilton 1964; Parker 1979; Trivers 1972) explains these seemingly paradoxical phenomena, which are central features of sexual conflict.

The underlying reason for sexual conflict is that males and females often "disagree" about how much energy and resources to invest in each reproductive bout and how often to make that investment. For example, males of many species often gain more fitness from mating frequently than do females (Bateman 1948). This is partly because the costs of each mating are often higher for females than males (Bell and Koufopanou 1986; Chapman et al. 2003a; Partridge and Harvey 1988; Partridge and Hurst 1998). Because mating frequency is an emergent property of the interaction of both sexes, it can only take one value—therefore the different interests of males and females cannot simultaneously be realized (Holland and Rice 1998; Parker 1979, 2006; Partridge and Hurst 1998). In any situation in which this kind of evolutionary tension exists, there is the potential for sexual conflict (Fig. 1.1). Therefore, although reproduction often requires some cooperation to succeed, there are many situations in which one sex can gain fitness (i.e., increased transmission of genes) if they can cause their partner to increase reproductive investment (Krebs and Davies 1987). The strategy by which one sex manipulates the other to increase

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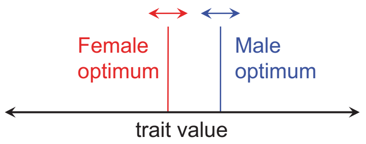

Fig. 1.1 A summary of the basis of sexual conflict. The optimum value of a reproductive trait (trait value) that maximizes male or female lifetime fitness (the number of offspring they produce over their lifetimes) is often different. The sexual conflict that arises from such differences is predicted to be particularly strong when unrelated individuals reproduce and when the mating system is nonmonogamous. These factors reduce the shared interest of each sex in what happens to the other in the future. Therefore, selection to maximize the investment of the other sex in the current reproductive bout at the expense of future costs to the other sex can be selected for. In the example shown here the optimum value of the trait for females is lower than for males. Therefore, a female's lifetime fitness would be higher if the value of the trait were lower. For males, the situation is the opposite. Since the reproductive traits in question are "shared", that is they arise because of an interaction between the sexes (e.g., mating frequency, mating duration, number of eggs laid), the trait can only take one value. Hence, when the trait is expressed at least one sex will not be at its optimum

reproductive investment can be strongly selected even if it results in significant lifetime costs to the manipulated partner. This in turn will select for the manipulated sex to evolve resistance to the manipulation. This creates the evolutionary back and forth that constitutes sexually antagonistic coevolution (Arnqvist and Rowe 2005; Holland and Rice 1998).

Over the last few decades, it has become clear that under any apparent reproductive *status quo*, there is sometimes fast and furious dynamic evolutionary change, driven by adaptation in males followed by counter-adaptation in females (Arnqvist and Rowe 2005). Unless perturbed, this sexually antagonistic coevolution can be difficult to observe at the level of the phenotype, but can productively be investigated via experimentation (Chapman et al. 2003a). Sexually antagonistic coevolution can occur between the same or different loci in males and females (intra- and interlocus sexual conflict, respectively (e.g., Chapman et al. 2003a, and see below) and can generate considerable evolutionary change. Importantly, this coevolution has the potential to lead to reproductive isolation and even speciation (Hayashi et al. 2007; Parker and Partridge 1998; Rice 1998) and is, therefore, of central importance in evolutionary biology.

A huge variety of reproductive traits can be subject to sexually antagonistic selection, from who to mate with, how often to mate, how long to mate, and how much to invest in reproduction (Chapman et al. 2003a). The potential for sexual conflict is universal across all species that engage in sexual reproduction. For instance, it does not even require the existence of separate sexes and can occur over the optimal investment allocated to either male or female sex allocation in hermaphrodites (Charnov 1979). However, whether sexual conflict is realized (Bourke and Franks 1995; Chapman 2006; Ratnieks and Reeve 1992), and the intensity with which it proceeds, depends upon several different factors, as summarized in Table 1.1.

Table 1.1 Factors affecting the expression and intensity of sexual conflict

Factor	Effect on the intensity of sexual conflict
Relatedness	Sexual conflict is exacerbated by low relatedness between reproducing partners (Bourke 2009; Dawkins 1976; Parker 1979, 2006; Rankin 2011). Low relatedness makes it much less likely that currently paired males and females will have a shared evolutionary interest in each other's future
Mating system	Sexual conflict is also exacerbated by nonmonogamous mating systems, as these also promote divergence in the genetic interests of males and females in current versus future offspring. If there is a significant chance of additional reproduction with other partners, then sexual conflict will be increased (Bourke 2009; Dawkins 1976; Parker 1979, 2006; Rankin 2011)
Biologically relevant context	Sexual conflict must be studied in a biologically relevant context. For example, it is difficult to detect patterns of elevated reproduction in populations reproducing at either a low level or at their upper limit (VanderLaan et al. 2012). Nutritional environment can also completely change the direction of sexually antagonistic interactions (Fricke et al. 2009a), so must be considered
Condition	Condition refers to the extent to which individuals can express their genotype, even under poor environmental conditions. It can therefore magnify the differences in quality between individuals (Rowe and Houle 1996) and affect the extent to which they can respond to stimuli. Therefore, condition is likely to alter the intensity of sexual conflict. Variation in condition caused by environmental variation in food availability can alter the extent to which males can express potential sexual conflict adaptations (Amitin and Pitnick 2007; Fricke et al. 2008; McGraw et al. 2007), and also the degree of female responses to them (Fricke et al. 2009a)
Sexual conflict load	Load is the magnitude of the decrease in fitness resulting from each sex not being at its optimum. The larger this difference, the more "distance" required in order to reach the optimum and therefore the stronger the selection arising from sexual conflict
Value of winning	This is the magnitude of the benefit of a sexually antagonistic adaptation in one sex versus the benefits of resisting it in the other, and will determine the strength of sexual conflict
Power	Power refers to the relative costs involved in the value of winning and will thus also determine the strength of sexual conflict
Mechanism	Even if there is the potential for conflict, it may not be manifested if there is no mechanism for each sex to alter the balance of power and winning. This could arise if one sex has effectively "won" the conflict and shut down the opportunities for the other to influence sexual conflict phenotypes (Chapman 2006)
Negative intersexual genetic fitness correlations	Several researchers have found genetic correlations for fitness across generations that vary in direction across sexes. For example, high fitness females may have high fitness sons but average fitness daughters, and vice versa (Chippindale et al. 2001; Foerster et al. 2007). These correlations intensify sexual conflict, because they can constrain the ability of each sex to reach their sex-specific optimum

Concepts and Currency of Sexual Conflict

Costs, Benefits and Fitness

Central to the understanding of sexual conflict is to clarify what is meant by costs and benefits. Though not often explicitly stated, a Hamiltonian (Hamilton 1964) definition is used, such that the outcome of sexual conflict is measured in terms of positive or negative direct fitness consequences for males and females. Direct fitness is defined as that gained through the production of an individual's own offspring. Within a kin-selected context (i.e., within related social groups), sexual conflict is expected to be low (because there are higher shared interests between partners in each other's futures), though it is still possible (Bourke 2009; Parker 1979; Rankin 2011). Some portion of the costs and benefits of sexual conflict can also be measured in terms of indirect fitness (i.e., the portion of fitness gained by helping related individuals to reproduce).

Fitness is a property of a gene, but is often also used with reference to a genotype or individual. This is legitimate in situations where the interests of genes and the individuals in which they reside concur. The currency of sexual conflict is therefore changes in gene frequency, i.e., the basic units of evolutionary change. Conflicts ultimately occur because of differences in how genes maximize their transmission to future generations through males or females. As the interests of genes and the individuals in which they reside are usually (but not inevitably) aligned, it is often convenient to think about sexual conflict in terms of conflicts between individual males and females. We usually use as a proxy for an individual's direct fitness, the number of offspring produced by an individual in their lifetime. This measure may usefully be combined with estimates of survival to give greater weight to offspring produced early in life, when natural selection is strongest (Charlesworth 1980). Fitness is not a property of a group or of a population, as these are seldom units of selection. At a population level, the mean fitness of males and females is equal (Fisher 1930; Arnqvist 2004); instead, it is the relative fitness of individual male and female genotypes that vary.

Measurements of fitness should ideally include a competitive element and a component that can capture the expression of any delayed costs of reproduction (Edward et al. 2011). If the quality of offspring, in addition to the quantity of offspring, is an important component of fitness, then fitness measures necessarily resolve into tests of the effects of the reproductive strategies of parents across generations. In some such studies, the costs experienced by female parents as a result of sexual conflict may be partially compensated for by an increase in offspring quality/fitness (Priest et al. 2008). This has led some researchers to question the sexual conflict paradigm, suggesting that if the costs of sexual conflict are compensated for by genetic benefits to future generations, then there is no conflict. However, it is clear from several studies that the magnitude of direct current costs to parents often exceeds any future indirect genetic benefits to offspring (e.g., Brommer et al. 2012; Lew et al. 2006), hence sexual conflict is the dominant source of selection. The key point is that, through careful measurements of costs and benefits and consideration of the factors summarized in Table 1.1, it is possible to predict the extent and importance of sexual conflict (Fricke et al. 2009b).

Intra- Versus Interlocus Sexual Conflict

The theory and mechanisms of sexual conflict are often cast in terms of whether the conflict is mediated by the same or different loci in males and females (Holland and Rice 1998). This is not purely a semantic categorization—differences in these underlying modes can determine the evolutionary outcome of conflict. Apart from the presence of the Y (or equivalent) sex chromosome in individuals of the heterogametic sex, each cell of an individual carries a full set of all genes in the genome. However, genes can exhibit complex patterns of tissue-, life history stage-, and sex-specific expression. For example, seminal fluid protein-encoding genes are switched on in the reproductive system of sexually mature adult males, but not in females. Genes can also exhibit sex-biased expression, particularly for reproductive genes, i.e., they are expressed at a significantly higher level in one sex in comparison to the other (Civetta and Singh 1999; Ellegren and Parsch 2007; Parisi et al. 2004). Different alleles of the same gene can have different expression levels, or expression levels of the same allele can be regulated differently in males and females. The nature and outcomes of the two major modes of sexual conflict are described below.

Intralocus Sexual Conflict A well-supported example from invertebrates is that of adult locomotory activity in the fruitfly *Drosophila melanogaster*. The positive genetic correlation between movement levels in males and females suggests that the same genes influence adult locomotion in both sexes. However, there is sexual conflict—a high level of activity is beneficial to males as it increases female encounters, leading to increased reproductive success. In contrast, females who are less active have higher fitness, because they have more time available for feeding and egg laying (Long and Rice 2007). Further evidence for intralocus sexual conflict has been gleaned from experiments conducted in fruitflies using ingenious cytogenetic techniques (Chippindale et al. 2001). In these experiments, the same genome can be expressed in males or females and the fitness consequences then measured. These experiments show that there is little fitness difference during larval development (where sexual conflict in minimal), but that at the adult stage, genomes that confer high fitness for males result in low fitness when expressed in females, and vice versa. In addition, experimental evolution experiments have, by various techniques, allowed the genomes of either males or females to evolve free of the constraint of passage through the other sex (Holland and Rice 1999; Rice 1992, 1996). This invariably results in the evolution of a genome that is "better suited" to either male or female interests. The outcome of these intralocus sexual conflicts is predicted to be an evolutionary to and fro depending on whether specific alleles currently reside in males or females (Hayashi et al. 2007; Parker 1979). Resolution of this sexual conflict is also predicted to occur via the evolution of sex limitation, i.e., the silencing of expression of the gene subject to conflict in one sex but not the other. However, this is not necessarily the end of sexual conflict (Chapman et al. 2003a; Chapman 2006).

Interlocus sexual conflict can occur when reproductive traits are influenced by different genes in each sex (e.g., mating frequency; Arnqvist and Rowe 2005).

There is a huge volume of evidence for sexual conflict under this mode (Arnqvist and Rowe 2005), provided by the economic studies of costs and benefits for males and females of manipulating the trait values up and down. A revealing example comes from studies in pondskaters, where the grasping adaptations of males that aid in attachment during mating can be made less effective at achieving matings by experimental manipulation of a specific antigrasping adaptation in females (Arnqvist and Rowe 1995). The predicted evolutionary outcomes of this type of conflict are varied and include evolutionary chases, equilibrium, divergence (Hayashi et al. 2007), or dampening down of the conflict (Arnqvist and Rowe 2005), reflecting a kind of conflict resolution.

Sexual Conflict in Action

The detailed experimental study of sexual conflict has been dominated by studies of just a few species and particularly of invertebrates, notably dungflies (*Scathophaga stercoraria* and *Sepsis cynpisea,* e.g., Martin and Hosken 2003; Parker 1970), fruitflies (*Drosophila melanogaster,* e.g., Chapman et al. 1995; Rice 1996), abalone (*Haliotis* spp, e.g., Clark et al. 2009), and various pondskater species (*Aquarius*, *Gerris* spp, e.g., Arnqvist and Rowe 2002a, b). Within the vertebrates, important work has been done on Dunnocks (*Prunella modularis,* e.g., Davies 1992) and Red Deer (*Cervus elaphus,* e.g., Foerster et al. 2007). Authors such as Haig (e.g., Haig and Wilczek 2006) have also elegantly outlined the potential for sexual conflict over embryo provisioning in plants, emphasizing the key role of relatedness among the interacting parties in driving conflict not only between the sexes, but also between parents and offspring. These examples of sexual conflict in action have usefully been synthesized in several reviews (e.g., Arnqvist and Rowe 2005; Chapman et al. 2003a). In this section, I use just a few selected examples, some with specific relevance to humans, to illustrate the evolutionary potential of sexual conflict over different reproductive traits in widely different species.

Sexual Conflict over the Effects of Seminal Fluid Proteins in Fruitflies

A valuable model for empirical studies has been the fruitfly *D. melanogaster*, and experimental evolution has been conducted to reveal the covert arms races and evolutionary constraints that accompany sexual conflict (e.g., Rice 1992, 1996). A particular focus of interest has been the actions of the seminal fluid proteins, the nonsperm components of the male ejaculate (Chapman 2001; Ram and Wolfner 2007; Sirot et al. 2014; Wolfner 2002). There are over 100 such proteins and peptides in the *D. melanogaster* male, and they are an extraordinarily diverse group of compounds in terms of structure and function (Mueller et al. 2004, 2005). They can alter female sexual receptivity, ovulation, egg laying, reproductive tract morphology, immunity, feeding behavior, nutrient balancing, sleep patterns, water retention, and lifespan (e.g., Adams and Wolfner 2007; Carvahlo et al 2006; Chapman et al. 2003b; Cognigni et al. 2011; Isaac et al. 2009; Kubli 2003; Liu and Kubli 2003; Peng et al. 2005; Ram and Wolfner 2007; Ribeiro and Dickson 2010; Sirot et al. 2014). Sexual conflict over each of these traits is possible (Sirot et al. 2014).

The genes that encode seminal fluid proteins are among the fastest-evolving (Swanson et al. 2001b). Due to their rapid evolutionary change, there are seminal fluid protein genes that are not found even among close relatives (Wagstaff and Begun 2005a, b; Wong et al. 2008). Though less is known about the seminal fluid proteins of other invertebrates and vertebrates, they appear to be similarly complex (Sirot et al. 2014). Several core seminal fluid functions are maintained across widely different species, even though the genes that encode individual components can be very divergent. These core functional types include: proteases, protease inhibitors, lipases, lectins, cross-linking transaminases, and cysteine rich secretory proteins (CRISPs; e.g., Mueller et al. 2004, 2005; Ram and Wolfner 2007). This finding shows that there can be conservation at the functional, but not genomic, level. The implication is that the lack of genomic conservation might be due, in part, to sexual conflict (Chapman 2001; Clark et al. 2009; Swanson et al. 2001b).

It was discovered some years ago that the transfer of seminal fluid proteins from male to female *D. melanogaster* during mating can decrease female lifespan and reproductive success (Chapman et al. 1995) without any demonstrable benefits for females (e.g., Brommer et al. 2012). Later work identified some of the seminal fluid protein candidates apparently responsible. One example is the 36 amino acid "sex peptide," whose transfer can increase the fitness of males, but decrease that of females that receive it (Fricke et al. 2009c; Wigby and Chapman 2005). The phenotypic effects of sex peptide include decreased female receptivity, increased egg production (Chapman et al. 2003b; Chen et al. 1988; Liu and Kubli 2003), altered female immunity (Domanitskaya et al. 2007; Peng et al. 2005), decreased sleep (Isaac et al. 2009), increased feeding (Carvahlo et al. 2006), and altered nutrient balancing (Ribeiro and Dickson 2010). These findings suggest that the transfer of elevated levels of sex peptide shifts the value of remating and investment into the current batch of eggs towards the male optimum and away from that of the female, with attendant lifespan costs for females. This is consistent with the operation of interlocus sexual conflict. Genome-wide studies of gene expression show that receipt of sex peptide by females causes a change in the expression of many different functional categories of genes, with tissue- and time-specific signatures (Gioti et al. 2012). This suggests that females have many obstacles to overcome to evolve resistance to sex peptide. Other studies indicating toxicity of seminal fluid proteins employed a technique in which seminal fluid proteins were ectopically expressed in females. Four seminal fluid proteins, including sex peptide, were found to decrease female lifespan when expressed in this way (Mueller et al. 2007).

This sexual conflict should select for counter-adaptations in females. However, as yet, we have little understanding of how females respond to the sexually antagonistic effects of male seminal fluid proteins (Wigby and Chapman 2004). Only one receptor to a seminal fluid protein in insects has been identified (Yapici et al. 2008). Hence, the study of the coevolution of interacting molecules in males and females is only just beginning (Clark et al. 2009). That said, there is good evidence for selectable genetic variation in females for the evolution of resistance to the costly effects of male seminal fluid proteins. For instance, females subjected to elevated levels of sexual conflict over evolutionary time evolved to live longer in the presence of males than did controls (Wigby and Chapman 2004). The fact that the longevity differences were not an intrinsic property of the lines and were not observed in the absence of exposure to males suggests that this was a specific response to the manipulation of sexual conflict levels.

Sexual Conflict over Sperm Egg Interactions in Marine Invertebrates

Abalone are a group of marine invertebrates that broadcast their gametes into the water column. In these species, there is good evidence for antagonistic coevolution between male sperm lysin and its female receptor, vitelline envelope receptor for lysin (VERL) (e.g., Clark et al. 2009; Lee et al. 1995; Metz and Palumbi 1996; Swanson et al. 2001a). Lysin is involved in breaking down the vitelline envelope surrounding the egg and permitting further transit of the sperm to effect fertilization. There is evidence for sexual conflict between the male's efforts to have the sperm enter the egg quickly and the female's efforts to avoid costly polyspermy (Frank 2000). The latter refers to the situation in which too many sperm enter the egg, with lethal results. The dynamic pattern of coevolution between VERL and lysin appears to have resulted in divergence in the VERL receptors in females (Clark et al. 2009; Swanson et al. 2001a). This pattern of evolutionary change is a specific prediction of sexual conflict theory (Hayashi et al. 2007) and is therefore strong evidence for sexual conflict in action.

Sexual Conflict over Mating Frequency in Pondskaters and Beetles

A powerful system for demonstrating the existence of sexual conflict is found in the pondskaters (Arnqvist and Rowe 1995, 2002a, b). Experiments show that lengthening of the female's antigrasping spines reduce the length and success of mating attempts, which is consistent with the evolution of antigrasping spines as defenses against male grasping adaptations (Arnqvist and Rowe 1995). A set of species comparisons was also conducted (Arnqvist and Rowe 2002a, b) in which the relative levels of male grasping and female antigrasping armaments were measured. Interestingly, these adaptations were well "matched" across different species in terms of the absolute size of the male graspers versus the female antigraspers.

However, when there were changes in the relative levels of armament and defense between males and females, there were predictable effects on mating rate. For example, when females had relatively lower levels of defense, mating rate was higher, and vice versa. These studies demonstrate the underlying evolutionary tensions in sexual conflict.

Coevolution driven by sexual conflict is also found in a comparative study of *Callosobruchus* seed beetles (Rönn et al. 2007). In these species, there is a predicted sexual conflict over male mating frequency. Penile spines are proposed to anchor the male during mating, but they also damage the female reproductive tract. Counter-adaptation in females is represented by the evolution of a thicker lining in the reproductive tract. The number of spines and amount of damage was found to vary across the different seed beetle species tested, and a combined measure of the degree of harmfulness of male genitalia (based on number, morphology, and distribution of spines) was correlated with the thickness of the female reproductive tract wall. As in pondskaters, the absolute armament level was independent of the degree of damage. It varied instead with the relative armament level, i.e. harm was more evident in species in which the male genitalia were relatively more spiny and where the female tract was relatively less robust. These findings fit the sexual conflict framework well.

Sexual Conflict over Ovulation in Invertebrates and in Humans

Conflicts between the evolutionary interests of males and females can also diverge with respect to different facets of ovulation, some of which have particular relevance to humans. Some evidence consistent with the sexual conflict over ovulation and the efficiency of egg fertilization has been revealed in *D. melanogaster* fruitflies. For example, there can be a break down in the efficiency of egg fertilization in matings between normal females and mutant males that lack a seminal fluid protein (Acp26Aa) that stimulates ovulation (Chapman et al. 2001). In invertebrates, ovulation can occur in response to mating or can be enhanced by signals in the ejaculate transferred during mating (Sirot et al. 2014). However, in mammals, ovulation can often be divorced from mating and the receipt of an ejaculate, and influenced instead by seasonal or cyclical factors. A different aspect of ovulation over which there can be sexual conflict is therefore whether it is concealed or unpredictable. This is of particular interest in humans, in which ovulation is thought to be concealed, it is suggested, in order to reinforce pair bonds, increase male parental care, or to reduce the intensity of male–male competition (e.g., Alexander and Noonan 1979; Benshoof and Thornhill 1979; Hrdy 1979; Strassmann 1981). Whether ovulation is concealed in humans is still a topic of debate (e.g., Kuukasjärvi et al. 2004; Thornhill and Gangestad 1999). Whatever the answer, it is possible that the evolution of even partial concealment may have been selected partly to reduce the intensity of sexual conflict generated as a side effect of competition between males.

Sexual Conflict over Immune Function in Invertebrates and Humans

In invertebrates, there are significant changes to the immune status in females following mating (Lawniczak et al. 2007). Some of these changes are caused by the actions of seminal fluid proteins (e.g., Domanitskaya et al. 2007; Peng et al. 2005; Short et al. 2012). The effect of these changes is to reduce immunity to systemic infection following mating (Fedorka et al. 2011; Short et al. 2012, but see Zhong et al. 2013). Overall, however, the functional significance and fitness effect of these changes is not yet clear. Similar findings are now reported in humans (Sharkey et al. 2012), i.e. changes in the expression of immune genes in the cells of the female cervix following receipt of a male ejaculate. The hypotheses are that post-mating immune changes in females may produce a permissive environment for implantation, may counter sexually transmitted diseases, or may provide a hostile environment to select sperm (e.g., Robertson 2005). There are, therefore, opportunities for sexual conflict over postmating immune function changes in humans and these possibilities would be of great interest for further study.

Sexual Conflict and Homosexuality

The sexual conflict framework has also recently been applied to the understanding of the persistence of male homosexuality in humans. The phenomenon to explain is that the frequency of homosexuality is significant and stable through time and has some genetic basis, yet homosexual individuals have few offspring (Vasey et al. 2007). Recent studies by Vasey and colleagues provide evidence for significant benefits consistent with the operation of kin selection (Vasey et al. 2007; Vasey and VanderLaan 2010). That is, the kin of homosexual individuals have higher than average fecundity and exhibit elevated altruistic behavior towards relatives. However, the elevated fecundity of female relatives has also been interpreted in terms of the sexually antagonistic gene hypothesis (VanderLaan et al. 2012). Because of gene-sharing among kins (e.g., on average, individuals share half of their genes with their full sib brothers), males with female relatives that possess “high female fitness” genotypes will share a portion of that genotype. This might be associated with decreased direct reproduction by such males. One way to distinguish the kin-selected and sexually antagonistic gene hypotheses is to examine their unique predictions. For example, a male with a “high female fitness” genotype might express a variety of traits closer to the female rather than male optimum. These males might, in comparison to controls, show altered patterns of attraction to the opposite sex (PL Vasey, pers. comm.), altered mate searching or mate selection, or altered degrees of investment in parental care.

Sexual Conflict as Social Behavior

It has been noted by Bourke (2009), and also considered by others (e.g., Rankin 2011), that the interactions between males and females that are subject to sexual conflict can be viewed in the wider context of social behaviors. This is because the actions of one sex (i.e., the "actor") can affect the fitness of itself and the other (the "recipient"). Hamilton (1964) classified four types of social behaviors, whereby the social behavior of the actor can:

(i) increase direct fitness of both actor and recipient (mutual benefit)
(ii) increase direct fitness of the actor but decrease that of the recipient (selfishness)
(iii) decrease direct fitness of the actor but increase that of the recipient (altruism)
(iv) decrease direct fitness in both actor and the recipient (spite).

The outcomes of sexual conflict are cast in terms of costs and benefits, which are synonymous with fitness increases or decreases in the sense used in the study of social behaviors (i.e., increases or decreases in individual lifetime offspring). Hence, we can usefully integrate sexual conflict into this wider context (see Table 1.2). Reclassifying the outcome of interactions between males and females in this way, we see that there is the potential for evolutionary disagreements between the sexes, and therefore sexual conflict, in all four types of social behavior classification. However, this is particularly so for selfish behavior, which is generally the outcome assumed to occur most frequently in this field of study.

Sexual Conflict and Selection for "Harm"

An important debate in the study of sexual conflict, and which has relevance for evolutionary psychology, is the nature of the costs inflicted on one sex by the other. In this sense, we can consider whether there is evidence that the costs inflicted by one sex upon the other represent "harm" (Johnstone and Keller 2000; Lessells 2005; Morrow et al. 2003). This is synonymous with the selection for selfishness as an adaptive strategy, unless one is suggesting that harm is different from cost. What is ultimately important whether the recipient suffers a cost in lifetime fitness, or whatever the source of that cost. Therefore, my view is that cost and harm are equivalent in evolutionary terms.

Nevertheless, in the study of sexual conflict, harm is often implied to represent a distinct type of cost. The term harm also has broad usage across different fields of study, but in the context of the social behaviors summarized in Table 1.2, it can be a selfish or spiteful behavior. In sexual conflict, it refers to various kinds of damage, such as lesions, to the female reproductive tract caused by male mating adaptations (e.g., Rönn et al. 2007). Even if, as I suggest, the conceptual basis of harm is unclear, plenty of types of evidence have been advanced as harm. For example, in bedbugs, the costs to females that arise as a side effect of male reproductive strategies can be significant. Some species of male bedbugs inseminate females through their body wall into the free body cavity, and often cause damage to the female as a result (Reinhardt et al. 2003).

Is Sexual Conflict in Humans Qualitatively or Quantitatively Different?

Building on the discussion of harm, here, I consider sexual conflict in reproductive interactions in humans and whether there is anything distinct about the type or intensity of sexual conflict in humans. The potential for sexual conflict is pervasive in humans as in many other plant and animal species. We are diploid outbreeders and individuals coming together for sexual interactions generally exhibit low relatedness. Human mating systems are varied, but importantly there is usually some degree, even if quite low, of mating outside a pair bond. Hence, the stage is set for sexual conflict for all the reasons outlined above, though whether the conflict is realized will depend on the costs and benefits involved, and the opportunity or mechanism to enact selfish behavior (Table 1.2). Costs and benefits of reproduction have been quantified to some extent from the studies of historical human societies for which demographic data records exist. These studies tend to show that women that reproduce at high rates have shorter lifespans (Helle et al. 2002; Westendorp and Kirkwood 1998). The cost of reproduction appears to be particularly high for the production of male children, due to higher gestation costs (Helle et al. 2002). Thus, there is the potential for evolutionary disagreements between male and female parents over the frequency of reproductive bouts and how much to invest in each (Dawkins 1976).

We expect sexual conflict and parent–offspring conflict over nutrient supply to the developing fetus in humans because of relatedness asymmetries. In outbreeding humans, a mother and father will be, on average, 50 % related to all their offspring. A developing offspring is 100 % related to itself, 50 % to full sibs and 25 % to half sibs. However, although there is an equality in the relatedness of male and female parents to their offspring, the residual reproductive value (or propensity to show future discounting) of male and female parents may differ, because of the costs of each reproductive bout. Therefore, a sexual conflict between parents is predicted over nutrient provisioning to the offspring because mothers may gain more than fathers by conserving investment for the future. This conflict is in addition to the parent–offspring conflict derived from relatedness asymmetries between both parents and the developing offspring. The offspring is more related to itself than to either of its parents or any future full or half sibs and will, therefore, be selected to obtain a higher level of nutrients than is optimal for the mother to give.

Sexual conflict and parent–offspring conflict over fetal provisioning is evident when something goes wrong, as in the case of various imprinting diseases. Imprinting in this context refers to a gene that shows a uniparental inheritance of

Table 1.2 Reclassification of interactions between the sexes in terms of social behavior

Effect of actor’s social behavior on itself (i.e., effect of one sex on its own fitness)	Effect of actor’s social behavior on the recipient (i.e., effect of one sex on the fitness of the other sex)	Consequence of the social behavior	Equivalent consequence in terms of sexual interactions	Potential for the outcome to result in sexual conflict	Examples
Increases fitness	Increases fitness	Mutual benefit (narrow sense cooperation)	Mutual mate choice, obligate monogamy, or lifetime pair bond commitment	No potential for sexual conflict if both sexes gain fitness from the sexual interaction. When there is obligate monogamy or lifetime commitment both sexes share their future interests (Boomsma 2007, 2013)	The outcome of sexual selection can be viewed as mutually beneficial. Here, the outcome of the sexual interactions benefits both sexes through the increased production of numerous, high quality offspring. When there is a shared future interest between males and females reproductive costs may be absent and sexual interactions can have a positive effect on the fitness of both sexes (e.g., Schrempf et al. 2005)
Increases fitness	Decreases fitness	Selfishness	Sexual conflict where the reproductive strategy of one sex benefits themselves but exacts a cost in the other	Strong potential for sexual conflict when the reproductive strategy adopted by one sex benefits themselves but decreases their current mate’s fitness (Arnqvist and Rowe 2005; Parker 1979)	Much of the data for sexual conflict can be seen as equivalent to selfish behavior. For example, female fruitflies that mate at high frequency suffer lifetime fitness costs whereas males do not (e.g., Chapman et al. 1995; Cordts and Partridge 1996; Fowler and Partridge 1989; Partridge and Andrews 1985), suggesting selfish behavior on the part of the male

Table 1.2 (continued)

Effect of actor's social behavior on itself (i.e., effect of one sex on its own fitness)	Effect of actor's social behavior on the recipient (i.e., effect of one sex on the fitness of the other sex)	Consequence of the social behavior	Equivalent consequence in terms of sexual interactions	Potential for the outcome to result in sexual conflict	Examples
Decreases fitness	Increases fitness	Altruism	Sexual cannibalism, where, e.g., males suffer the cost of being eaten by their mate, and females gain fitness through the acquisition of resources to boost fecundity	If there is altruism due to sexual cannibalism (e.g., males donate their bodies as a nuptual gift to females), there may nevertheless be sexual conflict over the optimal timing of a male's sacrifice, with perhaps the female benefiting more from earlier sacrifice than the male (e.g., Fromhage and Schneider 2005)	Sexual conflict over the timing of copulation duration is reported in sexually cannibalistic spiders (e.g., Schneider et al. 2006). In addition, males that take opportunistic matings with feeding females significantly reduce their risk of injury and of being eaten (Fromhage and Schneider 2005). Lifetime fitness consequences would be useful, to ascertain whether this represents a case of altruism on the part of the male
Decreases fitness	Decreases fitness	Spite	A reproductive strategy adopted by one sex that is costly to both. Predicted under conditions under which there is negative relatedness, where individuals are less genetically similar at a given locus than are partners on average	Ultimately, to reduce costs of spite then both sexes should become subject to directional selection to minimize the costs involved, under normal patterns of relatedness. The conditions under which spite can evolve are fairly restricted and the potential for sexual conflict is theoretically possible, but likely limited (e.g., West et al. 2007b)	No known examples

expression. In this, it is usually only the maternally inherited or only the paternally inherited copy of an allele that is expressed in the offspring. Many placental genes that influence the flow of nutrients to the developing fetus in humans are imprinted in a way that suggests they are subject to sexual conflict over nutrient provisioning (Haig 1993, 1996, 1997). This perspective predicts that paternally expressed (maternal imprint) alleles will be "greedy" and, conversely, that maternally expressed (paternal imprint) alleles will be less so (e.g., Haig and Graham 1991; Úbeda and Wilkins 2008). Exactly this situation pertains in a condition known as Beckwith Weidemann (BW) syndrome. Here, there is a change to the normal inheritance pattern (i.e., expression of the maternally inherited allele) of IGF-2/H19 genes on chromosome 11. In BW, this gene region is instead expressed solely from the paternally inherited allele. The result is fetal overgrowth disorder due to the misexpression of a "greedier" version of the IGF-2 allele. Similarly, in Prader–Willi (P–W) syndrome, there is a change in the imprinting status of a gene in the q11–13 region of chromosome 15 from the normal expression of the paternal allele to misexpression of the "less greedy" maternally inherited allele. The result is undergrowth disorder during gestation and in the early postnatal period. Such imprinting diseases in humans (Úbeda and Wilkins 2008), and similar examples in mice (Haig and Graham 1991), reveal the underlying conflicts involved (but see Hurst and McVean 1997).

Conflicts over reproductive investment could be especially fierce if there are divergences in residual reproductive value (Stearns 1992; Williams 1966a, b), i.e., the proportion of an individual's reproductive output still to come in the future. I have already invoked this type of conflict, above, when describing a strategy in which females might gain from investment over the longer term (because of their higher residual reproductive value), whereas males might not. If the guarantee of future reproductive success is lower for males than for females, this will result in strong sexual conflict over current investment patterns. The idea is that individuals that live in risky environments should not wait for the future (which they may not live to experience) and so should adopt a strategy that tries to deliver the maximum payoff now, even if the potential future cost is significant, and the payoff carries significant current risk. It seems likely that there will be differences in the optimum discount rate for males and females, with males having higher future discounting.

This topic has been explored by Wilson and Daly (1997), in terms of an especially high disposition for future discounting in males that live in risky environments. The classic work on the Ache by Hill and Hurtado (1996) on predicted age at first reproduction in humans also fits into this framework. Here, age at reproduction is earlier when mortality rates are higher. Another example in humans has been recently been described by Waynforth (2012), in which individuals with chronic health conditions likely to lead to lifespan-shortening reproduce at an earlier age. This phenomenon is also well-described in the animal kingdom. For example, Daphnia water fleas (Stibor 1992) placed in water treated with fish extract (indicating a risk of predation) reproduced earlier with larger and heavier broods than did controls.

Having outlined some evidence that sexual conflict can be predicted using reasoning grounded in evolutionary biology, it is worth considering whether human-specific features will alter the nature of conflict, or make it more or less likely. In terms of behavior within human relationships that we might think of as encompassing sexual conflict, such as punishment, what matters in an ultimate sense is the effect of these behaviors on an individual's lifetime fitness. But does the expression of these behaviors in humans represent something different from that considered in other species?

The obvious and dominant distinct features of human societies are language and cultural evolution. There has been much debate about the extent to which the transmission and evolution of culture can contribute to the evolution of cooperation or, conversely, conflict (e.g., Boyd et al. 2011; Boyd and Richerson 2005; Feldman et al. 1985; Henrich 2004; Lehmann et al. 2008). There is evidence that, in comparison to genetic evolution, cultural evolution may, rather than facilitating cooperation, instead lead to increased selfishness or harm (Lehmann et al. 2008). Future work may clarify whether the dominance of culture leads humans to have an increased frequency of conflicting interactions in comparison to our animal relatives.

There is little evidence that humans are more cooperative than other animals or plants (West et al. 2011), or that humans are atypical in having especially strong enforcement or punishment to reinforce cooperation. Such enforcement mechanisms are widespread across plants and animals (e.g., Frank 2003; Kiers et al. 2003; Mulder and Langmore 1993; Ratneiks et al. 2006; West et al. 2007a; Young et al. 2006). Instead, it is the capacity for information-gathering to assess costs and benefits of cooperation where humans may be distinct, though not qualitatively so, in comparison to our animal relatives. This ability may allow better calibration of benefits and also the likelihood of punishment (e.g., see Fehr and Gächter 2002; West et al. 2011).

Reciprocity, a form of cooperation that can occur between nonrelatives (Trivers 1971), seems to be especially important in humans. Reciprocity occurs when a benefit given by an actor to a recipient is returned in the future by the receiving individual. Unless there is some way to recognize the individual that gave the benefit, reciprocity breaks down. Hence, reciprocity depends on relatively high-level cognition, recognition/enforcement mechanisms, or constructs such as legal agreements (reviewed by West et al. 2011). If an individual receives a benefit but does not then return it, punishment may be inflicted to reinforce the reciprocity. This punishment could represent a type of selfish behavior of relevance to sexual conflict.

Exploitation

Exploitation has been well-researched in humans and may reflect sexual conflict in terms of a strategy to gain more resources by taking advantage of the other sex (Buss and Duntley 2008). The exploiters adopt selfish behavior to gain a benefit for little cost to themselves. Hence, exploitation within human reproductive encounters can be seen in the same cost and benefit terms discussed above. There can be selection for exploitation strategies in men, for example, if there are differences in optimal mating frequency (e.g., a man wanting to have sex with a woman who is not interested) or differences in investment patterns (e.g., a man wanting a brief, sexual relationship and a woman wanting a longer-term, higher-investment relationship; Buss 2003). Which of the nonmutually exclusive types of exploitative behaviors, such as seduction, pressure, deception, or assault, are employed may depend on a woman's exploitability (Goetz et al. 2012) and, thus, the costs and benefits involved. The operation of exploitation strategies therefore depends on the integration of many different and complex signals. It is not necessary that individuals know how and why they might be responding to such cues; it is the ultimate end result that matters in evolutionary terms (Buss and Duntley 2011). The adoption of exploitation should, of course, select for the evolution of mechanisms to avoid exploitation or to reduce the costs of exploitation. Exploitation is therefore of relevance to sexual conflict as it could lead to sexually antagonistic coevolution between exploitation and resistance mechanisms.

Exploitation could be particularly difficult to evolve resistance to, however, if it taps into pathways to which females "need" to respond. This has been explored by West-Eberhard (1979), and others (e.g., Arnqvist 2006), in the context of the "sensory trap" that can be exploited to influence female mate choice. The idea is that males might manipulate a female's investment through a pathway that females necessarily use to gain reproductive fitness. Imagine that the trait in question is the number of fertile eggs laid. A female should start to lay eggs only once a mating has occurred and there are sperm available for fertilization. An efficient way to coordinate this is therefore to respond to a male signal passed during mating that stimulates egg production. If such a male signal evolves to manipulate the investment of the female upwards in terms of the number of eggs to produce then he gains fitness, but the female may suffer costs. However, it may be dangerous for females to evolve complete insensitivity to those signals, because they might easily "overshoot" and reduce their fitness. Hence, the idea of the "trap" from which females may not easily escape. To counter this scenario, females could evolve divergent responses to the same male cues, with the response determined by the context in which the male cues are expressed.

Exploitation is possible in species in which multiple mating occurs, as a side effect of male–male (sperm) competition. If female remating is rapid, then any costs incurred by a later mating male from engaging in sperm competition are lowered. This is because the female reproductive tract is already "primed" for reproduction following earlier matings (e.g., Hodgson and Hosken 2006). The potential for male–male exploitation within females has been supported empirically. For example, male *D. melanogaster* fruitflies are able to tailor their ejaculates to take advantage of the fact that previous mates of a female have already boosted her fecundity. Therefore, subsequent mates can invest less in that specific ejaculate component, while maintaining the levels of others (Sirot et al. 2011). These studies suggest that there is considerable potential for adaptive adjustments to ejaculate composition, and this deserves study across many more species.

I discussed earlier whether sexual conflict can result in "harm" in the animal world, and I stressed the importance of ultimate outcomes, rather than the different mechanisms of inflicting costs, for determining root causes of these phenomena.

The distressingly common examples of violence and aggression within human sexual relationships can also be viewed in this context (Buss and Duntley 2011), that is, as direct or indirect outcomes of adaptive responses to specific scenarios. In terms of the mechanistic underpinning of these ultimate outcomes, our research shows that, even in model systems such as fruitflies, males are capable of astonishingly flexible and precise calibrations in response to the social and sexual environment. These assessments are made to match male reproductive investment in any reproductive bout, to the perceived threat levels from rivals (Bretman et al. 2009) or to the mating status of females (Friberg 2006). I expect the mechanisms employed in human sexual interactions to be especially finely tuned, and hence, it is important to understand those and where possible to measure the fitness consequences of those actions. For example, it would be of interest to better define the costs of aggression (e.g., Bleske and Buss 2001) and the responses of recipients to aggression, which may include a response akin to "convenience polyandry", i.e., matings to avoid or to reduce the costs of aggression (Thornhill and Alcock 1983). This may help to understand better not only the ultimate reasons for aggression, but also how to minimize it. An important point is that here, just as in nonhuman examples, context is crucial to the likelihood and intensity of sexual conflict. For example, conflict may be less prevalent in human relationships when economic resources are abundant (Buss and Duntley 2011) and within specific personality types (Tanha et al. 2010).

Sexual Conflict, Male–Male Competition and Male Mate Choice

Up until now, I have discussed sexual conflict mostly in terms of an interaction between a male and a female. However, across the animal kingdom there is frequent multiple mating by males and multiple mating by females with different males. Females may store the sperm of different males for hours through to months or even years (Neubaum and Wolfner 1999). Wild caught females of many insect species can carry the sperm of more than one male (e.g., Imhof et al. 1998 for *D. melanogaster*). This means that a more realistic biological scenario is for premating contests to occur between multiple males and females, and postmating contests to occur between multiple males within a single female in species that store sperm.

The existence of "lovers triangles" in human social interactions greatly intensifies conflict and competition (Shackelford et al. 2003). This is also true in insects. For example, male *D. melanogaster* fruitflies exposed to rivals prior to encountering females show significantly extended mating durations (Bretman et al. 2009). This gives the focal male a fitness advantage in competition with other males. The longer matings following exposure of males to rivals results in higher fecundity and fertility, decreased female sexual receptivity, and a higher share of paternity. The mechanism by which this is achieved is via the increased transfer of seminal fluid components such as sex peptide (Wigby et al. 2009). Given that the receipt of the sex peptide seminal fluid protein can exact costs on females (Wigby and Chapman

2005), it is evident that the heightened competition between males, as indicated by the increased length of exposure to rivals (which causes more sex peptide to be delivered to females), intensifies the conflict with females (Bretman et al. 2013a).

To detect cues that males use to indicate that they are in the presence of a male of the same species, we tested the effect of removing cues (sight, sound, touch, and smell) by multiple genetic and phenotypic methods (Bretman et al. 2011). For example, we manipulated a male's ability to hear song by exposing focal males to rivals that could not sing (either following wing removal, or by using a *vestigial* wing mutation) or by using focal deaf males. We then investigated the cues that, when removed, rendered males unable to respond to rivals. No single cue on its own was important, but any two cues from the three sensory modes, of (i) smell, (ii) hearing (specifically hearing male courtship song), and (iii) touch, were necessary to allow males to respond adaptively to rivals (Bretman et al. 2011). The finding that there is flexibility but also robustness to the cues used by males to detect rivals suggests that it is important for a male not to make a mistake by responding to a female as if it were a male conspecific, or to a male of a closely related species. This would imply that, as well as significant benefits, there are costs of responding to rivals, which ideally should be avoided unless it is relatively "certain" that rivals are present. The investigations of the lifetime fitness consequences for males of continually responding to rivals confirm the existence of costs in terms of reduced male survival and reduced later-life mating capacity (Bretman et al. 2013b). Whether different strands of information conveyed by each separate cue are weighted differently in this context is not yet known.

We know that contingent responses by males to their rivals are highly individually flexible (Bretman et al. 2012). Individual males can respond to rivals, then not respond, and then respond again across at least three different mating episodes in series. The ways that males can respond to their social and sexual environment, as illustrated by the fruitfly example, are highly sophisticated. Such evolved responses to the social and sexual environment are well known from studies in humans, as for example, in the case of speech accommodation (Giles and Powesland 1975). The outcome of such responses in fitness terms would be interesting to investigate, but presumably the benefits reside in a desire to fit in and/or to become more competitive.

The growing realization that males are sometimes making a substantial investment in mating even in promiscuous mating systems that lack parental care (Dewsbury 1982) has recently been evaluated in the context of a renewed interest in male mate choice (Clutton-Brock 2007; Edward and Chapman 2011). The idea is that if males have substantial investments to make in mating, then they may allocate that investment to specific females. This renewed interest has arisen from the realization that the investment made by males is not necessarily minimal, even in species that appear to contribute little apart from sperm to a reproductive episode.

The key factors that help to determine whether the conditions exist for male mate choice are the degree of reproductive investment a male has available to make, the availability of mates, and his capacity to mate with available mates (Edward and Chapman 2011). If more females are available for mating than a male can mate with, if there is variation in female quality, and if the benefits of choice outweigh the costs of assessment, then male mate choice can evolve. The interesting case is when there is male mate choice but little obvious investment by males other than in ejaculate transfer. However, if that investment is considerable, such as when ejaculate production and courtship costs are high, then male mate choice can still occur. The intensity of sexual conflict is expected to vary according to the magnitude of the investment made by males. This is highly likely in the case of the transfer of ejaculate molecules.

If males exhibit choice and have a substantial investment to make, this may select for intrasexual competition among females for males, or contribute to mutual mate choice. Hence, there is considerably more variation and flexibility in the sex roles adopted by males and females in the animal world than has been assumed to date. The importance of sexual conflict in these scenarios has not yet been fully addressed.

Future Prospects

There is a large literature on behavioral conflict within human and primate relationships and it would be useful to integrate this body of work further into the framework of sexual conflict described above. This might enable the identification of parallels between humans and nonhumans, and also might facilitate investigations into whether there is anything evolutionarily distinct about sexual conflict in humans. There seem to be some candidate features arising from the importance of language and culture in human relationships. For example, traits such as personality, disposition, and humor that contribute to mate choice in humans (Buss 1989) may represent distinct facets of sexual interactions that can intensify competitions or give them greater phenotypic “space” in which to occur. Furthermore, that the intensity of male–male competition can exacerbate the sexual conflict with females is now established from studies on invertebrates (Arnqvist and Rowe 2005; Civetta and Clark 2000). Therefore, the psychological adaptations to sperm competition in humans would also be interesting to investigate in this context. Further work is warranted on whether these features represent qualitative or quantitative differences in sexual conflict. Finally, it is important during any study of sexual conflict to realize that most studies consider only a snapshot in time (Rowe and Day 2006), unless working with a system in which it is possible to follow the development of sexual conflict from initiation, through establishment to eventual outcome (Paterson et al. 2010). Measurements of the current context do not necessarily indicate past selection pressures, and inferences about the ancestral importance and function of traits subject to sexual conflict should be considered with caution. It is therefore important to understand what might be the diagnostic footprint of sexual conflict within the set of observable, currently expressed adaptations (Rice 1998; Rowe and Day 2006).

The involvement of sexual conflict in human health outside the immediacy of sexual relationships would also be worth further study. For example, sexually antagonistic coevolution arising from sexual conflict has been proposed to contribute to maladapted bodily processes that can predispose to increased cancer risk (Summers and Crespi 2008). Imprinted genes, of the type that play such a central role in directing nutrient flow across the placenta to the developing fetus and whose imprinting status is thought to be influenced by sexual conflict, are also often expressed in the brain. The expression patterns of imprinted brain genes are, controversially, proposed to underlie the balance between mental health on an autistic to schizophrenic spectrum (Badcock and Crespi 2008).

In animal systems, we are just beginning to develop a predictive framework for the expected signature of sexual conflict at the genomic level (Sirot et al. 2014). For example, across different species of mammals there are correlations between the pattern of seminal fluid evolution and mating systems (Wong 2010, 2011; Wyckoff and Wu 1997). Given the wealth of genomic data from humans, there are opportunities to make significant advances in this area, once the traits and molecular mechanisms underlying sexual conflict in human sexual interactions are better known.

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