

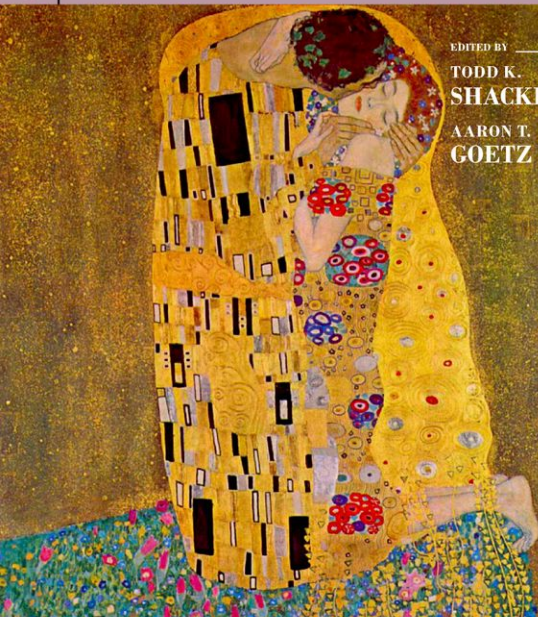
EDITED BY

TODD K.

SHACKELFORD &

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GOETZ



≡ The Oxford Handbook of  
SEXUAL CONFLICT  
*in* HUMANS

# The Oxford Handbook of Sexual Conflict in Humans

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# The Oxford Handbook of Sexual Conflict in Humans

*Edited by*

Todd K. Shackelford

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PART

1

# Introduction to Sexual Conflict

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## Sexual Conflict in Humans

Todd K. Shackelford, Aaron T. Goetz, James R. Liddle, *and* Lance S. Bush

### Abstract

This chapter provides an introduction to and brief overview of empirical and theoretical work on sexual conflict in humans, some of which is showcased in the current volume. We begin the chapter with a brief review of evolution by natural selection. We then discuss the application of evolutionary principles to psychology, with a focus on human psychology. With this background established, we present an overview of theory and research on sexual conflict in humans. Sexual conflict was a recurrent feature of human evolutionary history, just as it has been in every sexually reproducing species that does not practice lifelong genetic monogamy. One source of much of the conflict between men and women can be reduced to an asymmetry in reproductive biology: Fertilization and gestation occur within women, not men. This asymmetry produces (1) sex differences in minimum obligatory parental investment and (2) paternity uncertainty, but maternity certainty. These consequences of internal fertilization and gestation help to account for many phenomena in humans, including sexual coercion, commitment skepticism, sexual overperception, and a host of adaptations associated with sperm competition.

**Key Words:** sexual conflict in humans, infidelity, paternity uncertainty, sperm competition

An understanding of sexual conflict, in general, and human psychological and physiological adaptation to sexual conflict, in particular, requires familiarity with the basics of evolutionary theory. Many excellent introductions to evolution exist to which we refer readers (see Coyne, 2009; Dawkins, 2009; Dennett, 1995; Mayr, 2001). We nevertheless begin with a brief overview of evolution that will lead us into the subject of this chapter.

### A Primer on Evolution

Three conditions must be met for evolution to produce the complexity and variety of organisms we see today. In a population of reproducing organisms, so long as there is variation of traits, heritability of these variations, and a nonrandom impact of these variations on survival and reproduction,

evolution by natural selection will occur (Darwin, 1859/2006).

The first component of evolution by natural selection is variation. If we consider a population of sexually reproducing organisms, we will note that individual members of that species differ. Differences in coloration, size, and a plethora of other traits that may or may not be easily perceived are always present. These differences result from the recombination of parent genes in offspring, and from the occasional mutation of genes. The key point is that without variation, there is nothing available for natural selection to “select.”

The second component of evolution by natural selection is heritability. Even with variation in a population, if these variations are not passed down from parents to offspring with relatively high fidelity,

natural selection cannot operate. Fortunately, the “recipe” for most of an organism’s characteristics is supplied by the genes inherited from its parents, and the replication of genes during meiosis is a process marked by exceptionally high fidelity.

The third component of evolution by natural selection is differential reproduction. There is a struggle for existence, and not every organism is successful at surviving and reproducing. Heritable variation acts as a nonrandom determinant of which organisms will survive and reproduce. Over hundreds, thousands, or millions of generations, inherited traits that promote greater survival and reproductive success accumulate, whereas alternative traits vanish from the gene pool. This is natural selection, the primary mechanism by which evolution occurs.

A key product of natural selection is adaptation—a characteristic that is reliably inherited from parents and that aids an organism in survival and reproduction. But organisms are not comprised entirely of adaptations. In addition to adaptations, organisms may have many features best characterized as by-products or noise (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998). A by-product is a characteristic that exists as an incidental consequence of an adaptation. Researchers have noted many examples of by-products. The whiteness of bones, for instance, is not an adaptation but a by-product of the build-up of calcium, an adaptation designed to produce bones that are not easily broken (Buss et al., 1998; Symons, 1992). Noise, on the other hand, is not an adaptation or a by-product of an adaptation but refers instead to random changes in gene frequency that have no survival or reproductive impact on an organism.

These three products of natural selection are important to keep in mind when considering human psychology from an evolutionary perspective. Before discussing the application of evolutionary psychology to sexual conflict in humans, it is important for readers to have a clear understanding of what evolutionary psychology is, and what it is not.

## Defining Evolutionary Psychology

Most readers will be familiar with an overview similar to the preceding account, but the full implications of natural selection are often overlooked. It is not simply the case that arms and legs and eyes and ears were shaped by natural selection as tools for survival. Behavior is no less important to an organism’s reproductive success, and its behavior must be suited to its environment. It is no coincidence that

a tiger has a mind built for hunting prey and a deer has the mind of an herbivore. But behavior is not like eyes or ears. The question arises as to how natural selection selects for variations in behavior when, after all, genes are recipes for building a body, and a behavior is not a physical structure you can build with the right combination of proteins.

The answer to this question lies in the evolution of the brain, the organ that produces behavior. It is readily apparent how natural selection can favor genetic variants that have a direct impact on the structure of an organism’s bones or the color of its skin, but some adaptations are indirect. For instance, Gaulin and McBurney (2001, p. 26) note that, “selection can improve the efficiency of blood circulation only by improving the design of the circulatory organs such as the heart, arteries, and veins.” Natural selection likewise selects for behavior indirectly, by selecting for variation in the information-processing mechanisms of the brain.

Evolutionary psychology represents this application of evolutionary principles to the study of the human mind. Evolutionary psychology is not a particular subdiscipline or field of study within psychology, but an approach that can be applied to all areas of psychological research (Gaulin & McBurney, 2008; Tooby & Cosmides, 1992). For example, an evolutionary psychological approach has been used to investigate adaptations related to social behavior (Cosmides, 1989), learning (MacDonald, 2007; Weber & Depew, 2003), memory (McBurney, Gaulin, Devineni, & Adams, 1997), and perception (Rhodes, 2006). Thus, the application of evolutionary principles to the study of the mind is not limited to a specific subject. All aspects of human cognition are ultimately explained by the structure and function of the evolved mechanisms of the mind.

Two key concepts that guide an evolutionary approach to psychology are the environment of evolutionary adaptedness and evolved psychological mechanisms. The implications of these key concepts—which are discussed below—grate against what has been termed the “standard social science model” (Tooby & Cosmides, 1992). It is instructive to briefly highlight this shift in approach to the mind inspired by evolutionary science before tackling the key concepts that distinguish an evolutionary psychological approach from other psychological perspectives.

## A New Paradigm

Pinker (2002) notes that the mind has long been regarded as a sort of blank slate, void of content

prior to its first experiences. According to this view, it is experience that molds and shapes the mind to suit its environment. With the advent of computer technology, this blank slate model evolved into a conception of the mind as a sort of general-purpose computer (Tooby & Cosmides, 1992). The mind was regarded as a device with a few basic processing principles that guided it in sorting out the content of experience. According to this perspective, the way we process information about the world, whether it is language or morals, customs or relationships, draws on the same content-independent, domain-general cognitive mechanisms.

Evolutionary psychologists have abandoned the standard social science model. Over the past few decades, the confluence of data streaming in from cognitive science, biology, and neuroscience has given way to a new paradigm in psychology (Pinker, 2002; Tooby & Cosmides, 1992). Evolutionary psychologists have adopted a modular view of the mind, seeing the mind as possessing distinct modules, or information-processing mechanisms, selected for processing particular types of input and generating particular types of output (Fodor, 1983). Rather than view the mind as a single, general-purpose organ, we can more accurately describe it as a set of organs, each with its own evolutionary history and its own specialized function. Different selection pressures caused the evolution of distinct cognitive solutions to adaptive problems, a principle known as functional specialization.

*Evolved psychological mechanisms.* Evolutionary psychologists maintain that the mind is comprised primarily of domain-specific mechanisms, although a few scholars have argued that one or a few relatively more domain-general mechanisms also might exist (see MacDonald, 1991). Whatever the extent to which modularity applies to the human mind, we can note several characteristics to describe most evolved mechanisms that comprise human nature. Buss (2004) sums up the features of an evolved psychological mechanism:

1. It exists in the form that it does because it solved a specific problem of survival or reproduction recurrently over evolutionary history.
2. It is designed to take in only a narrow slice of information.
3. The input tells an organism the particular adaptive problem it is facing.
4. The input is transformed through decision rules into output.

5. The output can be physiological activity, information to other psychological mechanisms, or manifest behaviors.

6. The output is directed toward the solution to a specific adaptive problem (pp. 50–52).

For example, consider how a specific module for inducing fear of snakes would fit the above criteria. First, such an adaptation would clearly solve a specific problem of survival: avoiding dangerous animals. Second, a module for detecting dangerous animals may indeed take in only a limited type of information—it may induce the individual to pay special attention to serpentine forms and to motivate fear only in response a specific type of phenomena: perception of snakes. The third and fourth criteria are also met, in that the input—sensory processing of a snake or something snakelike—provides the individual with the information to produce a response appropriate to that particular input based on the adaptive problem that mechanism evolved to solve, which in turn activates a particular decision rule: fear and increased attention to the stimuli. The outcome of detecting a snake meets the final criteria, as the evolved mechanism for fear of snakes induces the individual to take action to evade the danger, a physiological response evolved to prevent bodily harm.

It turns out that we do appear to possess an innate predisposition for noticing and fearing snakes, but we do not seem to possess a similar aversion to other dangerous stimuli, such as cars or guns (Hagen, 2005; Öhman & Mineka, 2001). The apparent incongruity that arises from this fact is that modern hazards pose a more serious threat to many of us than do snakes. The solution to this dilemma is that snakes were a part of our ancestral environment for a long enough time to exert sufficient selection pressures to produce such a fear module, whereas relatively novel aspects of our environment, such as cars, have not had sufficient time or selective impact to drive natural selection to build a module for fearing and avoiding them. This solution is clarified by describing a second key concept of evolutionary psychology, the environment of evolutionary adaptiveness.

*Environment of evolutionary adaptiveness.* The importance of identifying the relevant features of the environment of evolutionary adaptiveness for humans cannot be overstated. To generate testable hypotheses about the mental tools we should expect humans to have, we must know something about

the conditions under which our ancestors evolved. However, environment of evolutionary adaptedness does not refer to one specific habitat or time period. Rather, it represents, “a statistical composite of the adaptation-relevant properties of the ancestral environments encountered by members of ancestral populations, weighted by their frequency and their fitness-consequences” (Tooby & Cosmides, 1990, pp. 386–387; see also Cosmides & Tooby, 1994; Daly & Wilson, 1999). For any given adaptation, there was a particular set of selection pressures to which that adaptation arose as a solution. The conditions that gave rise to one adaptation will differ from those that gave rise to another, and thus the environment of evolutionary adaptedness of each adaptation will differ. For instance, an organism with both a shell and an acute sense of smell would likely have evolved these adaptations under different circumstances and for different reasons. Its ancestors may have evolved a keen sense of smell to locate food but evolved a shell to protect them from predators. Mental modules arose in the same way. A mental module for preferring specific foods would evolve under different circumstances and solve a different adaptive problem than a mental module for detecting whether someone is cheating in a social context.

Hagen (2005) points out that, “[E]nvironments change, so the causal structure of the environment an adaptation finds itself in may not correspond to the causal structure the adaptation evolved in, and therefore the adaptation may not work as designed” (p. 8). This leads us to an important observation: Given the plodding pace of evolution by natural selection, the mechanisms our minds possess took a crushingly long time to evolve, and for the vast majority of this time we lived in small tribes of nomadic hunter-gatherers (Pinker, 2002; Tooby & Cosmides, 1992). Several evolutionary psychologists (e.g., Pinker, 2002) have described modern humans as being stuck with a Stone Age mind, which underwent much of its evolution in hunter-gatherer tribes under conditions that persisted over hundreds of thousands of years, but which in many respects differs from our modern environment (Hagen, 2008). Despite the slow pace of natural selection, however, we should not jump to the conclusion that the environment of evolutionary adaptedness for most human adaptations differs dramatically from the contemporary environment (Hagen, 2005). Although some features of our modern environments differ from features of our ancestral environments, most of the adaptations we possess are likely to be operating as they were designed to operate. If

they did not, and were our environments to have changed dramatically and rapidly from our ancestors, Hagen (2005) points out that we would probably be headed toward extinction:

The human species is clearly not going extinct; hence the common belief that [evolutionary psychology] claims humans currently live in an entirely novel environment is incorrect. Most aspects of the modern environment closely resemble [aspects of our ancestral environments]. Hearts, lungs, eyes, language, pain, locomotion, memory, the immune system, pregnancy, and the psychologies underlying mating, parenting, friendship, and status all work as advertised – excellent evidence that the modern environment does not radically diverge from [our ancestral environments]. (p. 154)

Evolutionary psychologists do not argue that current environments are “entirely novel,” and Hagen (2005) notes the many functional similarities between the ancestral past and the present. However, it does appear that until a few thousand years ago, our ancestors lived similarly to modern-day hunter-gatherer tribes. Modern life in developed countries may be similar to the environments of our ancestors in many fundamental ways, but we cannot ignore the differences that exist. Modern technology, for example, now provides many humans with environmental input that did not exist for the majority of our history as a species. Because the information-processing mechanisms of the brain function by responding to environmental input, it is important to consider contemporary environments and the novel ways in which they may interact with evolved psychological mechanisms.

The concepts of evolved psychological mechanism and environment of evolutionary adaptedness, although fundamental to evolutionary psychology, represent only a portion of the major tenets related to this approach to human behavior. But rather than simply continue to describe what evolutionary psychology *is*, we believe it is useful to round out our description of evolutionary psychology by describing what it *is not*, particularly by highlighting and correcting some of the major misconceptions associated with an evolutionary psychological approach to human behavior.

### **Myths, Misconceptions, and Misrepresentations of Evolutionary Psychology**

Despite phenomenal growth in evolutionary psychology, this perspective has continued to be plagued

by misconceptions and misrepresentations. An exhaustive response to these criticisms is beyond the scope of the present chapter, and there are already numerous responses that address the majority of these criticisms (see Buss, 2004; Geher, 2006; Hagen, 2005; Kurzban, 2002; Liddle & Shackelford, 2009; Sell, Hagen, Cosmides, & Tooby, 2003; Workman & Reader, 2008). An audience new to an evolutionary approach to psychology might be put off by many of these common misunderstandings, and a brief overview will serve to put such misunderstandings aside.

*Misconception #1: Evolutionary psychology is pan-adaptationist.* One charge leveled against evolutionary psychologists is that they regard every aspect of behavior as an adaptation, and they have failed to acknowledge the importance of other sources of genetic change (Gould, 2000). This claim is false. Evolutionary psychologists have made a point of explicitly noting that evolution does not only lead to the production of adaptations, but it also results in the accumulation of by-products and noise (Kurzban, 2002, provides a copious list of evolutionary psychologists stating as such).

But what makes this claim so obviously mistaken is that there are so many examples of evolutionary psychologists explicitly proposing and testing by-product hypotheses. Symons (1979) hypothesized over 30 years ago that the human female orgasm is a by-product of an adaptation (namely, male orgasm). Other examples include Thornhill and Palmer (2000) hypothesizing that rape is a by-product of the male sex drive, Pinker (1994) hypothesizing that music is a by-product of language and that art is a by-product of habitat selection, and Dawkins (2006) hypothesizing that religion is a by-product of evolved mechanisms that arose to solve adaptive problems unrelated to a religious predilection. Not only do evolutionary psychologists acknowledge the presence of by-products, their published works are saturated with references to them (see Buss, 2005).

*Misconception #2: Evolutionary psychology is unscientific.* Another pair of criticisms frequently aimed at evolutionary psychology is that it consists of little more than ad hoc storytelling, and that it is based on untestable, unfalsifiable speculation over unknown details of our evolutionary past. Both of these criticisms are based on the argument that we know too little about the relevant features of “the” environment of evolutionary adaptedness to make verifiable claims about the evolved architecture of the mind. For instance, Gould (2000) has asked, “...how can we possibly obtain the key information that would be required to show the validity of adaptive tales about

the [environment of evolutionary adaptedness] ... we do not even know the original environment of our ancestors...,” and goes on to insist that, “...the key strategy proposed by evolutionary psychologists for identifying adaptation is untestable and therefore unscientific” (p. 120; originally quoted in Kurzban, 2002; Kurzban also cites other examples of similar charges, such as Benton, 2000, p. 262).

There are several problems with these criticisms. First, Sell and colleagues (2003) note that the charge of generating ad hoc hypotheses is inconsistent with how evolutionary psychologists have actually conducted research. Rather than attempt to find suitable explanations for previously acknowledged facts, evolutionary psychologists have tended to generate hypotheses for the purpose of discovering new facts. For instance, evolutionary psychologists hypothesized that men would experience greater distress over a romantic partner’s sexual infidelity than emotional infidelity, whereas women would experience greater distress over a partner’s emotional infidelity than sexual infidelity (Daly, Wilson, & Weghorst, 1982; Symons, 1979). Rather than conjure an explanation for an already recognized fact of human psychology, this research discovered the existence of a previously unknown sex difference in human psychology.

Second, the charge that we know too little about “the” environment of evolutionary adaptedness (as noted above, there are as many environments of evolutionary adaptedness as there are adaptations) to generate anything more than armchair theories seems to be based on the misconception that an environment of evolutionary adaptedness is substantially different from today’s environment and that it is more mysterious than the crucial historical assumptions that permeate other fields, such as physics, geology, and biology (Sell et al., 2003). We may not know much about the specific details of the evolutionary history of humans, but the notion that we know too little to generate hypotheses is not defensible in light of the rather modest assumptions evolutionary psychologists actually make to generate and test hypotheses. Hagen (2005) notes that the physical and chemical laws that govern the universe were the same, and the ecological and geographical features of the world were the same insofar as the landscape was dotted with trees, caves, hills, lakes, and populated with similar types of plants, animals, and pathogens. Likewise, important sociological phenomena were similar insofar as there were men and women who lived in family groups that consisted of parents, siblings, offspring, and people of varying ages and relatedness.



If these details seem insufficient to allow for the generation of defensible evolutionary hypotheses, Hagen (2005) comments: “We know that in ancestral environments women got pregnant and men did not. This single fact is the basis for perhaps three-quarters or more of all [evolutionary psychology] research” (p. 156). In other words, women but not men must heavily invest in individual offspring—they must carry a child to term and nurse it afterwards, and this disparity alone has generated numerous hypotheses about how men and women interact with one another that have been tested and confirmed (Buss, Larsen, Westen, & Semmelroth, 1992; Buss et al., 1999; Camilleri & Quinsey, 2009; Goetz & Causey, 2009; Hughes, Harrison, & Gallup, 2004; Miller & Maner, 2008; Stieger, Eichinger, & Honeder, 2009; Stone, Goetz, & Shackelford, 2005; Wiederman & Kendall, 1999). The bottom line is that evolutionary psychology is no less capable of generating testable hypotheses than any other scientific approach, and contrary to the claims of critics, we, in fact, know a great deal about the *relevant* aspects of our evolutionary past.

*Misconception #3: Evolutionary psychology implies determinism.* One of the most frequent criticisms of evolutionary psychology is that it implies genetic determinism (Nelkin, 2000; Rose, 2000; Shakespeare & Erikson, 2000). Genetic determinism is the view that all behavior is determined by our genes, and that free will or the environment plays little if any role (Buss, 2004). Evolutionary psychology implies no such thing. This misunderstanding is particularly worrisome because it continues to resurface in unexpected places, such as in Jerry Coyne’s book *Why Evolution is True* (2009). Coyne’s otherwise masterful marshaling of evidence for evolution is diminished by his critique of evolutionary psychology, which he opens by asking, “So if our evolution as social apes has left its imprint on our brains, what sorts of human behavior might be ‘hardwired?’” (p. 226).

The misunderstanding Coyne displays is a simple but important one. Evolutionary psychologists do not claim that behavior is hardwired. Rather, they contend that natural selection has shaped numerous information-processing mechanisms that interact with input (e.g., the environment) to produce behavior (Liddle & Shackelford, 2009). Hagen (2005) notes that even if the structure of these mechanisms were genetically determined, this would not imply that *behavior* is genetically determined. Evolutionary psychology takes an interactionist approach, which requires that two criteria be met to produce a

particular behavioral output: (1) a module for processing particular kinds of input, and (2) appropriate environmental stimuli to activate that module (Buss, 2004).

Thus, contrary to the claim that evolution has shaped brains that produce fixed, rigid behaviors “hardwired” by our genes, evolutionary psychologists maintain that we possess a set of richly context-dependent modules that produce behavior contingent on environmental variables. Indeed, not only does evolutionary psychology not imply genetic determinism, but its most prominent proponents also have repeatedly and explicitly rejected genetic determinism, insisting that by ignoring the necessary interaction between genes and the environment, genetic determinism is not only false but also nonsensical (Kurzban, 2002).

With these misconceptions of evolutionary psychology set aside, we can turn our attention to putting an evolutionary approach into practice and examining sexual conflict, with a special focus on humans.

## **Evolutionary Perspectives on Human Sexual Conflict**

The modern application of evolutionary principles to the study of human psychology and behavior has paved the way for new avenues of research not present just 20 years ago. One of these research avenues is sexual conflict. Sexual conflict occurs when the evolutionary interests of males and females diverge (Parker, 1979; Trivers, 1972). Although human mating is often viewed as a cooperative venture between two individuals of the opposite sex with a common reproductive goal (see Leo, Miller, & Maner, this volume), the evolutionary interests of human males and females are certainly asymmetrical (Buss, 1989; Li, Sng, & Jonason, this volume). A review of the literature examining lifetime infidelity and paternal discrepancy rates indicates that humans are not a monogamous species. Infidelity rates vary depending on when, how, and to whom the question is asked, but dozens of studies document that infidelity is common, and infidelity rates in some samples exceed 50% (see Table 1 in Koehler & Chisholm, 2007). Paternal discrepancy rates (also known as cuckoldry rates or nonpaternity rates) reflect a key reproductive consequence of female infidelity (when men unwittingly raise children to whom they are not genetically related), and these rates—even with the advent of modern contraception—are consistently above 0% and are as high as 30% in some samples (Anderson, 2006; Bellis, Hughes,

Hughes, & Ashton, 2005; Cerda-Flores, Barton, Marty-Gonzales, Rivas, & Chakraborty, 1999; Sasse, Muller, Chakraborty, & Ott, 1994).

Biologists have identified two types of sexual conflict: intralocus sexual conflict and interlocus sexual conflict (for a review, see Arnqvist & Rowe, 2005). Intralocus sexual conflict occurs between traits common to males and females of which there is opposing selection. In humans, for example, wider hips are favored in females (but not males) to facilitate childbirth (Rice & Chippindale, 2008). Interlocus sexual conflict occurs when a trait is encoded by different genes in males and females, producing conflict in the outcome of male–female interactions. This form of conflict, which is the primary focus of evolutionary psychologists, encompasses much of what we think of when we think of sexual conflict in nonhuman species, such as sexual cannibalism, grasping and antigrasping organs, and love darts (see Koene, this volume).

Humans, of course, do not practice sexual cannibalism, we do not have grasping organs on our abdomens, and we do not produce love darts. In humans, traits produced by sexual conflict will often occur in the form of psychological mechanisms (see Gorelik & Shackelford, this volume). Later in this chapter, we review evidence for sexual conflict as reflected in the design of psychological mechanisms, but before doing so, we discuss the source of sexual conflict in humans.

## Why Sexual Conflict?

Sexual conflict in humans stems from an asymmetry in reproductive biology. Fertilization and gestation occur within females, and this form of sexual reproduction has two consequences that are relevant to sexual conflict in humans: asymmetric parental investment and paternity uncertainty.

*Sexual conflict associated with parental investment.* Internal fertilization and gestation produces a discrepancy in parents' investment in offspring (Trivers, 1972). Women's minimum obligatory investment (i.e., minimum parental investment needed to produce offspring) is significantly greater than men's, lasting at least nine months. In comparison, men's obligatory investment can end with a single copulation. This discrepancy in minimal obligatory investment has profound effects on the reproductive (or mating) strategies that men and women pursue (see Salmon & Crawford, this volume). Different mating strategies (e.g., being more short-term oriented or more long-term oriented) occur within the sexes (see Figueredo, Gladden, &

Beck, this volume; Gangestad & Simpson, 2000) but are especially pronounced between the sexes (Buss & Schmitt, 1993; Schaller & Murray, 2008; Schmitt, 2005). Because men's minimum obligatory investment is considerably less than women's, the costs associated with fast, indiscriminant mating are much greater for women than for men. Fast, indiscriminant mating could cost a woman substantial time, energy, and resources if conception occurs, whereas reproduction can be much less costly for a man (e.g., Bateman, 1948). Parental investment theory (Trivers, 1972), which states that the sex that makes the larger minimum obligatory parental investment will be the more sexually discriminating sex, whereas the sex that makes the smaller minimum obligatory parental investment will compete more intensely for access to the higher investing sex, predicts and accounts for much of the sexual conflict in humans. For example, parental investment theory predicts that sexual conflict will occur when men and women pursue their optimal mating strategy (i.e., the mating strategy yielding the highest return in reproductive currencies). Without the burden of a large obligatory investment, men (relative to women) would benefit more from short-term, low-investment strategies, and when compared with men, women would benefit more, on average, from long-term, high-investment strategies. These conflicting strategies account for myriad phenomena, but here we briefly discuss just two: sexual coercion and cognitive biases.

Sexual conflict associated with asymmetric minimum obligatory parental investment explains why, historically and cross-culturally, men are the perpetrators and why women are the victims of sexual coercion and rape. It is not yet known whether rape in humans is produced by an adaptation that was directly selected for or as a by-product of other psychological mechanisms (e.g., Camilleri & Quinsey, this volume; McKibbin, Shackelford, Goetz, & Starratt, 2008), but what is known is that sexual coercion is a consequence of conflict over sexual access. It follows from parental investment theory that men will have a stronger desire for sexual variety and will be more sexually persistent, whereas women will be more sexually restricted (Buss & Schmitt, 1993; Schaller & Murray, 2008; Schmitt, 2005).

Sexual conflict associated with parental investment also may account for a number of cognitive biases in men and women. Cognitive biases refer to inference-making mechanisms that bias cognition in favor of false positives or false negatives. As predicted by parental investment theory, men consistently

overperceive sexual interest in women (e.g., inferring sexual interest from a friendly smile) as this error was likely to have been less costly for our male ancestors than underperceiving sexual interest and missing a sexual opportunity (Abbey, 1982; Haselton, 2003; Haselton & Buss, 2000; Maner et al., 2005). Women are more likely to underperceive commitment in men (e.g., inferring that commitment displays are counterfeit), as this error was likely to have been less costly for our female ancestors than overperceiving men's commitment and risking desertion (Haselton & Buss, 2000).

*Sexual conflict associated with paternity uncertainty.* A second potential consequence of internal fertilization and gestation is paternity uncertainty. Due to internal fertilization and gestation, ancestral men could not have been certain that their children were, in fact, genetically their own. Ancestral women, having given birth, had maternity certainty. Internal fertilization and gestation imply that ancestral men could have faced paternity uncertainty, but did they? That is, were ancestral men the victims of cuckoldry—the unwitting investment of resources into genetically unrelated offspring? Even without direct observation of the ancestral environment, the answer is a resounding yes. When considering (a) cross-cultural infidelity and paternal discrepancy rates (reviewed above), (b) the cross-cultural ubiquity and power of male sexual jealousy (e.g., Buss, 2000; Daly et al., 1982; Schützwohl, this volume), (c) women's fertile-phase sexuality, which functions primarily in the context of extra-pair mating (e.g., Gangestad & Thornhill, 1998, 2008; Jones, DeBruine, Little, & Feinberg, this volume; Penton-Voak et al., 1999), (d) adaptations associated with sperm competition in humans (e.g., Goetz & Shackelford, 2006; McKibbin, this volume; Shackelford & Goetz, 2007; Shackelford, Goetz, McKibbin, & Starratt, 2007), (e) the matrilineal bias associated with grandparental and avuncular investment (e.g., Euler & Weitzel, 1996; Gaulin, McBurney, & Brakeman-Wartell, 1997; Jeon & Buss, 2007; Michalski & Shackelford, 2005), and paternity inferences and willingness to invest associated with paternal resemblance (Platek & Porter, this volume; Platek et al., 2003, 2004; Platek, Burch, Panyavin, Wasserman, & Gallup, 2002; Platek, Keenan, & Mohamed, 2005), it becomes clear that female infidelity and cuckoldry were recurrent features of our evolutionary history (see Emery Thompson & Alvarado, this volume, for a review of relevant theoretical and empirical work on non-human primates). The evolutionary consequences of female infidelity are

many, but here we briefly discuss one: the conflict that occurs during or after mating, known as sperm competition.

Sperm competition is the consequence of males competing for fertilizations (Parker, 1970; Smith, 1984). If females mate in a way that concurrently places sperm from two or more males in her reproductive tract, this generates several selection pressures on males. If these selection pressures are recurrent throughout a species' evolutionary history, males may evolve anatomical, physiological, and psychological adaptations to aid their sperm in outcompeting rivals' sperm in fertilizations. As discussed above, female infidelity was a recurrent feature of our evolutionary history, and research has begun to uncover men's anatomical, physiological (see Gallup, Burch, & Petricone, this volume), and psychological (see Kaighobadi, Shackelford, & Goetz, this volume) adaptations associated with sperm competition.

Anatomical adaptations owed to sperm competition might include men's relatively large testes and specific features of the penis. The relative size of human testes (0.08% of body weight) falls between the relative testes sizes of the highly promiscuous chimpanzee and the polygynous gorilla, suggesting intermediate levels of sperm competition in our evolutionary past. To test the hypothesis that the human penis has been shaped by natural selection to displace semen deposited by other men in the reproductive tract of a woman, Gallup et al. (2003) used artificial genitals and semen to simulate intercourse. The results indicated that artificial phalluses with a glans and coronal ridge that approximated a human penis displaced more simulated semen than did a phallus that did not have such features. When the penis is inserted into the vagina, the frenulum of the coronal ridge makes semen displacement possible by allowing semen to flow back under the penis alongside the frenulum and collect on the anterior of the shaft behind the coronal ridge.

Regarding physiological adaptations, there is evidence that men prudently allocate their sperm according to cues of sperm competition. Baker and Bellis (1989, 1993) documented a negative relationship between the proportion of time a couple has spent together since their last copulation and the number of sperm ejaculated at the couple's next copulation. As the proportion of time a couple spends together since their last copulation decreases, there is a predictable increase in the probability that the man's partner has been inseminated by another man. Additional analyses documented that the

proportion of time a couple spent together since their last copulation predicts sperm number ejaculated at the couple's next copulation, but not at the man's next masturbation (Baker & Bellis, 1993). Also in support of the hypothesis that men adjust their ejaculates in accordance with sperm competition theory, experimental evidence has demonstrated that men viewing images depicting cues to sperm competition produce more competitive ejaculates than men viewing comparable images in which cues to sperm competition are absent (Kilgallon & Simmons, 2005). Kilgallon and Simmons documented that men produce a higher percentage of motile sperm in their ejaculates after viewing sexually explicit images of two men and one woman (sperm competition images) than after viewing sexually explicit images of three women.

Inspired by Baker and Bellis's (1989, 1993) demonstration of male physiological adaptations to sperm competition, Shackelford and his colleagues (2002, 2007) documented that men may possess psychological adaptations to decrease the likelihood that a rival man's sperm will fertilize a partner's ovum. In two independent samples, men who spent a greater proportion of time apart from their partners since the couples' last copulation—and, therefore, face a higher risk of sperm competition—perceive their partners to be more sexually attractive, are more interested in copulating with their partners, report that their partners are more interested in copulating with them, and report greater distress and more sexual persistence in response to their partner's sexual rejection, relative to men who spent a lesser proportion of time apart from their partners. These effects were independent of men's relationship satisfaction, total time since last copulation, and total time spent apart, which rules out several alternative explanations. These perceptual changes may motivate men to copulate as soon as possible with their partners, thereby entering their sperm into competition with any rival sperm that may be present in their partners' reproductive tracts.

The question as to whether sperm competition has been an important selection pressure during human evolution remains somewhat controversial, and further research is needed to establish the extent to which this might be the case. As outlined above, however, there is accumulating evidence that aspects of male anatomy, physiology, and psychology may reflect adaptations to sperm competition (see also, Goetz, Shackelford, Platek, Starratt, & McKibbin, 2008).

## Concluding Comments

The evolutionary interests of human males and females are certainly asymmetrical, so there is no reason to doubt that sexual conflict occurred throughout our evolutionary history. Indeed, sexual conflict in humans is a growing field of study among evolutionary psychologists, and many researchers have studied conflict over sexual access (e.g., Crawford & Salmon, this volume; McKibbin et al., 2008), conflict that occurs during and after mating (e.g., Klusmann & Berner, this volume; Puts & Dawood, this volume; Shackelford & Goetz, 2007; Shackelford, Weekes-Shackelford, Schmitt, & Salmon, this volume), and conflict that occurs after conception (e.g., Anderson, Kaplan, & Lancaster, 2007; Kruger & Fitzgerald, this volume; Wade, this volume), for example.

Arnqvist and Rowe's (2005) reluctance to discuss sexual conflict in humans in their monograph, *Sexual Conflict*, might be attributable to the different empirical approaches employed by behavioral ecologists and evolutionary psychologists. Arnqvist and Rowe outlined six research methods that have been used to document sexual conflict, such as genetic experiments, phenotypic manipulations, experimental evolution, and comparative studies, and only a couple of these are readily applicable to human populations. Evolutionary psychologists are unable to use experimental evolution techniques and genetic engineering to study sexual conflict in humans, for example. They have at their disposal, however, additional methods that are well developed in research with human subjects but that cannot be employed readily by those who study nonhuman animals. Survey methodologies that secure self-reported perceptions and behavioral history provide a useful means to access human cognition and behavior. Methodologies measuring reaction time provide more objective access to perceptual and motivational processes. And more recently, neuroimaging techniques are allowing researchers to study the modular design of the human mind, identifying neural correlates of hypothesized psychological mechanisms. As evolutionary psychologists dedicated to understanding how the human mind has been shaped by selection, we are in a position to test hypotheses about how men's and women's minds have evolved to solve problems generated by the opposite sex.

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## References

- Abbey, A. (1982). Sex differences in attributions for friendly behavior: Do males misperceive females' friendliness? *Journal of Personality and Social Psychology*, 42, 830–838.
- Anderson, K. G. (2006). How well does paternity confidence match actual paternity? Evidence from worldwide nonpaternity rates. *Current Anthropology*, 48, 511–518.
- Anderson, K. G., Kaplan, H., & Lancaster, J. B. (2007). Confidence of paternity, divorce, and investment in children by Albuquerque men. *Evolution and Human Behavior*, 28, 1–10.
- Arnqvist, G., & Rowe, L. (2005). *Sexual conflict*. Princeton, NJ: Princeton University Press.
- Baker, R. R., & Bellis, M. A. (1989). Number of sperm in human ejaculates varies in accordance with sperm competition theory. *Animal Behaviour*, 37, 867–869.
- Baker, R. R., & Bellis, M. A. (1993). Human sperm competition: Ejaculate adjustment by males and the function of masturbation. *Animal Behaviour*, 46, 861–885.
- Bateman, A. J. (1948). Intrasexual selection in *Drosophila*. *Heredity*, 2, 349–368.
- Bellis, M. A., Hughes, K., Hughes, S., & Ashton, J. R. (2005). Measuring paternal discrepancy and its public health consequences. *Journal of Epidemiology & Community Health*, 59, 749–754.
- Benton, T. (2000). Social causes and natural relations. In H. Rose & S. Rose (Eds.), *Alas poor Darwin: Arguments against evolutionary psychology* (pp. 249–270). New York: Harmony Books.
- Buss, D. M. (1989). Conflict between the sexes: Strategic interference and the evocation of anger and upset. *Journal of Personality and Social Psychology*, 56, 735–747.
- Buss, D. M. (2000). *The dangerous passion*. New York: The Free Press.
- Buss, D. M. (2004). *Evolutionary psychology: The new science of the mind* (2nd ed.). Boston: Allyn & Bacon.
- Buss, D. M. (Ed.) (2005). *The handbook of evolutionary psychology*. Hoboken, NJ: John Wiley & Sons.
- Buss, D. M., Haselton, M. G., Shackelford, T. K., Bleske, A., & Wakefield, J. C. (1998). Adaptations, exaptations, and spandrels. *American Psychologist*, 53, 533–548.
- Buss, D. M., Larsen, R. J., Westen, D., & Semmelroth, J. (1992). Sex differences in jealousy: Evolution, physiology, and psychology. *Psychological Science*, 3, 251–255.
- Buss, D. M., & Schmitt, D. P. (1993). Sexual Strategies Theory: A contextual evolutionary analysis of human mating. *Psychological Review*, 100, 204–232.
- Buss, D. M., Shackelford, T. K., Kirkpatrick, L. A., Choe, J. C., Lim, H. K., Hasegawa, M., et al. (1999). Jealousy and the nature of beliefs about infidelity: Tests of competing hypotheses about sex differences in the United States, Korea, and Japan. *Personal Relationships*, 6, 125–150.
- Camilleri, J. A., & Quinsey, V. L. (2009). Testing the cuckoldry risk hypothesis of partner sexual coercion in community and forensic samples. *Evolutionary Psychology*, 7, 164–178.
- Cerda-Flores, R. M., Barton, S. A., Marty-Gonzales, L. F., Rivas, R., & Chakraborty, R. (1999). Estimation of nonpaternity in the Mexican population of Nuevo Leon: A validation study with blood group markers. *American Journal of Physical Anthropology*, 109, 281–293.
- Cosmides, L. (1989). The logic of social exchange: Has natural selection shaped how humans reason? Studies with the Wason selection task. *Cognition*, 31, 187–276.
- Cosmides, L., & Tooby, J. (1994). Origins of domain specificity: The evolution of functional organization. In L. A. Hirschfeld & S. A. Gelman (Eds.), *Mapping the mind: Domain specificity in cognition and culture* (pp. 85–116). New York: Cambridge University Press.
- Coyne, J. A. (2009). *Why evolution is true*. New York: Viking.
- Daly, M., & Wilson, M. I. (1999). Human evolutionary psychology and animal behavior. *Animal Behavior*, 57, 509–519.
- Daly, M., Wilson, M., & Weghorst, S. J. (1982). Male sexual jealousy. *Ethology and Sociobiology*, 3, 11–27.
- Darwin, C. (2006). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life* (1st ed.). In E. O. Wilson (Ed.), *From so simple a beginning: The four great books of Charles Darwin* (pp. 441–760). New York: Norton. (Original work published 1859)
- Dawkins, R. (2006). *The god delusion*. London: Bantam Press.
- Dawkins, R. (2009). *The greatest show on earth: The evidence for evolution*. New York: Free Press.
- Dennett, D. C. (1995). *Darwin's dangerous idea: Evolution and the meanings of life*. New York: Simon & Schuster.
- Euler, H. A., & Weitzel, B. (1996). Discriminative grandparental solicitude as reproductive strategy. *Human Nature-An Interdisciplinary Biosocial Perspective*, 7, 39–59.
- Fodor, J. A., (1983). *The modularity of mind*. Cambridge, MA: MIT Press.
- Gallup, G. G., Burch, R. L., Zappieri, M. L., Parvez, R. A., Stockwell, M. L., & Davis, J. A. (2003). The human penis as a semen displacement device. *Evolution and Human Behavior*, 24, 277–289.
- Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences*, 23, 573–587.
- Gangestad, S. W., & Thornhill, R. (1998). Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 265, 927–933.
- Gangestad, S. W., & Thornhill, R. (2008). Human oestrus. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 275, 991–1000.
- Gaulin, S. J. C., & McBurney, D. H. (2001). *Psychology: An evolutionary approach*. Upper Saddle River, NJ: Prentice Hall.
- Gaulin, S. J. C., & McBurney, D. H. (2008). *Evolutionary psychology* (2nd ed.). Upper Saddle River, NJ: Prentice Hall.
- Gaulin, S. J. C., McBurney, D. H., & Brakeman-Wartell, S. L. (1997). Matrilateral biases in the investment of aunts and uncles: A consequence of measure of paternity uncertainty. *Human Nature-An Interdisciplinary Biosocial Perspective*, 8, 139–151.
- Geher, G. (2006). Evolutionary psychology is not evil! (...And here's why...). *Psihologijske Teme*, 15, 181–202.
- Goetz, A. T., & Causey, K. (2009). Sex differences in perceptions of infidelity: Men often assume the worst. *Evolutionary Psychology*, 7, 253–263.
- Goetz, A. T., & Shackelford, T. K. (2006). Sexual coercion and forced in-pair copulation as sperm competition tactics in humans. *Human Nature-An Interdisciplinary Biosocial Perspective*, 17, 265–282.
- Goetz, A. T., & Shackelford, T. K. (2009). Sexual conflict in humans: Evolutionary consequences of asymmetric parental investment and paternity uncertainty. *Animal Biology*, 59, 449–456.
- Goetz, A. T., Shackelford, T. K., Platak, S. M., Starratt, V. G., & McKibbin, W. F. (2008). Sperm competition in

- humans: Implications for male sexual psychology, physiology, anatomy, and behavior. *Annual Review of Sex Research*, 18, 1–22.
- Gould, S. J. (2000). More things in heaven and earth. In H. Rose and S. Rose (Eds.), *Alas poor Darwin: Arguments against evolutionary psychology* (pp. 101–126). New York: Harmony Books.
- Hagen, E. H. (2005). Controversial issues in evolutionary psychology. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 145–173). Hoboken, NJ: John Wiley & Sons Inc.
- Hagen, L. K. (2008). The bilingual brain: Human evolution and second language acquisition. *Evolutionary Psychology*, 6, 43–63.
- Haselton, M. G. (2003). The sexual overperception bias: Evidence of a systematic bias in men from a survey of naturally occurring events. *Journal of Research in Personality*, 37, 43–47.
- Haselton M. G., & Buss, D. M. (2000). Error management theory: A new perspective on biases in cross-sex mind reading. *Journal of Personality and Social Psychology*, 78, 81–91.
- Hughes, S. M., Harrison, M. A., & Gallup Jr., G. G. (2004). Sex differences in mating strategies: Mate guarding, infidelity and multiple concurrent sex partners. *Sexualities, Evolution and Gender*, 6, 3–13.
- Jeon, J., & Buss, D. M. (2007). Altruism towards cousins. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 274, 1181–1187.
- Kilgallon, S. J., & Simmons, L. W. (2005). Image content influences men's semen quality. *Biology Letters*, 1, 253–255.
- Koehler, N., & Chisholm, J. S. (2007). Early psychosocial stress predicts extra-pair copulations. *Evolutionary Psychology*, 5, 184–201.
- Kurzban, R. (2002). Alas poor evolutionary psychology: Unfairly accused, unjustly condemned. *Human Nature Review*, 2, 99–109.
- Liddle, J. R., Bush, L. S., & Shackelford, T. K. (in press). An introduction to evolutionary psychology and its application to suicide terrorism. *Behavioral Sciences of Terrorism and Political Aggression*.
- Liddle, J. R., & Shackelford, T. K. (2009). Why evolutionary psychology is "true." A review of Jerry Coyne, *Why Evolution is True*. *Evolutionary Psychology*, 7, 288–294.
- MacDonald, K. B. (1991). A perspective on Darwinian Psychology: The importance of domain-general mechanisms, plasticity, and individual differences. *Ethology and Sociobiology*, 12, 449–480.
- MacDonald, K. B. (2007). Cross-cultural comparison of learning in human hunting: Implications for life-history evolution. *Human Nature*, 18, 386–402.
- Maner, J. K., Kenrick, D. T., Neuberg, S. L., Becker, D. V., Robertson, T., Hofer, B., et al. (2005). Functional projection: How fundamental social motives can bias interpersonal perception. *Journal of Personality and Social Psychology*, 88, 63–78.
- Mayr, E. (2001). *What evolution is*. New York: Basic Books.
- McBurney, D. H., Gaulin, S. J. C., Devineni, T., & Adams, C. (1997). Superior spatial memory of women: Stronger evidence for the gathering hypothesis. *Evolution and Human Behavior* 18, 165–174.
- McKibbin, W. F., Shackelford, T. K., Goetz, A. T., & Starratt, V. G. (2008). Why do men rape? An evolutionary psychological perspective. *Review of General Psychology*, 12, 86–97.
- Michalski, R. L., & Shackelford, T. K. (2005). Grandparental investment as a function of relational uncertainty and emotional closeness with parents. *Human Nature-An Interdisciplinary Biosocial Perspective*, 16, 293–305.
- Miller, S. L., & Maner, J. K. (2008). Coping with romantic betrayal: Sex differences in responses to partner infidelity. *Evolutionary Psychology*, 6, 413–426.
- Nelkin, D. (2000). Less selfish than sacred?: Genes and the religious impulse in evolutionary psychology. In H. Rose and S. Rose (Eds.), *Alas poor Darwin: Arguments against evolutionary psychology* (pp. 17–32). New York: Harmony Books.
- Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, 108, 483–522.
- Parker, G. A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biological Reviews*, 45, 525–567.
- Parker, G. A. (1979). Sexual selection and sexual conflict. In M. S. Blum & N. A. Blum (Eds.), *Sexual selection and reproductive competition in insects* (pp. 123–166). New York: Academic Press.
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K., et al. (1999). Female preference for male faces changes cyclically. *Nature*, 399, 741–742.
- Pinker, S. (1994). *The language instinct: How the mind creates language*. New York: William Morrow & Co.
- Pinker, S. (2002). *The blank slate: The modern denial of human nature*. New York: Penguin Books.
- Platek, S. M., Burch, R. L., Panyavin, I. S., Wasserman, B. H., & Gallup, G. G. (2002). Reactions to children's faces: Resemblance matters more for males than females. *Evolution and Human Behavior*, 23, 159–166.
- Platek, S. M., Critton, S. R., Burch, R. L., Frederick, D. A., Myers, T. E., & Gallup, G. G. (2003). How much resemblance is enough? Sex difference in reactions to resemblance, but not the ability to detect resemblance. *Evolution and Human Behavior*, 24, 81–87.
- Platek, S. M., Keenan, J. P., & Mohamed, F. B. (2005). Sex differences in neural correlates of child facial resemblance: An event-related fMRI study. *NeuroImage*, 25, 1336–1344.
- Platek, S. M., Raines, D. M., Gallup, G. G., Mohamed, F. B., Thomson, J. W., Myers, T. E., et al. (2004). Reactions to children's faces: Males are still more affected by resemblance than females are, and so are their brains. *Evolution and Human Behavior*, 25, 394–405.
- Rhodes, G. (2006). The evolutionary psychology of facial beauty. *Annual Review of Psychology*, 57, 199–226.
- Rice, W. R., & Chippindale, A. K. (2008). Intersexual ontogenetic conflict. *Journal of Evolutionary Biology*, 14, 685–693.
- Rose, H. (2000). Colonizing the social sciences. In H. Rose & S. Rose (Eds.), *Alas poor Darwin: Arguments against evolutionary psychology* (pp. 127–153). New York: Harmony Books.
- Sasse, G., Muller, H., Chakraborty, R., & Ott, J. (1994). Estimating the frequency of nonpaternity in Switzerland. *Human Heredity*, 44, 337–343.
- Schaller, M., & Murray, D. R. (2008). Pathogens, personality, and culture: Disease prevalence predicts worldwide variability in sociosexuality, extraversion, and openness to experience. *Journal of Personality and Social Psychology*, 95, 212–221.
- Schmitt, D. P. (2005). Sociosexuality from Zimbabwe to Zimbabwe: A 48-nation study of sex, culture, and strategies of human mating. *Behavioral and Brain Science*, 28, 247–311.

- Sell, A., Hagen, E., Cosmides, L., & Tooby, J. (2003). Evolutionary psychology: Applications and criticisms. In *Encyclopedia of Cognitive Science* (pp. 54–64). London: Macmillan.
- Shackelford, T. K., & Goetz, A. T. (2007). Adaptation to sperm competition in humans. *Current Directions in Psychological Science*, 16, 47–50.
- Shackelford, T. K., Goetz, A. T., McKibbin, W. F., & Starratt, V. G. (2007). Absence makes the adaptations grow fonder: Proportion of time apart from partner, male sexual psychology, and sperm competition in humans (*Homo sapiens*). *Journal of Comparative Psychology*, 121, 214–220.
- Shackelford, T. K., LeBlanc, G. J., Weekes-Shackelford, V. A., Bleske-Rechek, A. L., Euler, H. A., & Hoier, S. (2002). Psychological adaptation to human sperm competition. *Evolution and Human Behavior*, 23, 123–138.
- Shakespeare, T., & Erikson, M. (2000). Different strokes: Beyond biological determinism and social construction. In H. Rose & S. Rose (Eds.), *Alas poor Darwin: Arguments against evolutionary psychology* (pp. 229–247). New York: Harmony Books.
- Smith, R. L. (1984). Human sperm competition. In R. L. Smith (Ed.), *Sperm competition and the evolution of animal mating systems* (pp. 601–660). New York: Academic Press.
- Stieger, S., Eichinger, T., & Honeder, B. (2009). Can mate choice strategies explain sex differences? The deceived persons' feelings in reaction to revealed online deception of sex, age, and appearance. *Social Psychology*, 40, 16–25.
- Stone, E. A., Goetz, A. T., & Shackelford, T. K. (2005). Sex differences and similarities in preferred mating arrangements. *Sexualities, Evolution and Gender*, 7, 269–276.
- Symons, D. (1979). *The evolution of human sexuality*. New York: Oxford University Press.
- Symons, D. (1992). On the use and misuse of Darwinism in the study of human behavior. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 137–159). New York: Oxford University Press.
- Thornhill, R., & Palmer, C. T. (2000). *A natural history of rape: Biological bases of sexual coercion*. Cambridge, MA: MIT Press.
- Tooby, J., & Cosmides, L. (1990). The past explains the present: Adaptations in the structure of ancestral environments. *Ethology and Sociobiology*, 11, 375–424.
- Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–136). New York: Oxford University Press.
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 136–179). Chicago: Aldine.
- Weber, B. H., & Depew, D. J. (2003). *Evolution and learning: The Baldwin Effect reconsidered*. Cambridge, MA: MIT Press.
- Wiederman, M. W., & Kendall, E. (1999). Evolution and sex differences in sexual jealousy: Investigation with a sample from Sweden. *Evolution and Human Behavior*, 20, 121–128.
- Workman, L., & Reader, W. (2008). *Evolutionary psychology: An introduction* (2nd ed.). New York: Cambridge University Press.

# Sexual Conflict in Nonhuman Animals

Joris M. Koene

## Abstract

Although sexual reproduction is a joint effort of both sexes, they do not necessarily have the same evolutionary interests. As a consequence of the sexes' noncoinciding fitness optima, reproductive processes can become ongoing battles between the sexes to achieve their respective objectives. This chapter will cover these conflicts at different biological levels, will focus on the more recently worked-out examples, and will highlight differences between the types of sex that can be expressed, that is, separate sex, hermaphrodite, and parthenogen. To start off, several definitions and terms used in the animal literature, which are relevant when thinking about reproduction, are dealt with. Then, after covering intralocus sexual conflict, the chapter moves on toward interlocus conflicts at all the different episodes of reproduction, ranging from just after zygote formation up to parental care. Several examples return when covering the evolutionary consequences of sexual conflict before providing promising directions for further research.

**Key Words:** arms race, counter-adapt, haplo-diploid, hermaphrodite, interlocus, intra-locus, parental care, parthenogen, postconception, postcopulatory, precopulatory

## Introduction

The most bizarre and absurd behaviors found in the animal kingdom are, without much exception, somehow related to sex. Very often, these behaviors turn out to have evolved as a response to differences in interests between the mating partners. We have come a long way from Darwin's interpretation of reproduction as a joint venture between the sexes, to something quite the opposite, an ongoing battle between the sexes to achieve their often noncoinciding reproductive optima.

As Darwin (1871) noted, extravagant traits and displays are often used to attract mates. Besides such overt secondary sexual characters that result in sexual dimorphism (which Darwin focused on), we now know of many, often more covert, behaviors and attributes that are used to increase fertilization success, albeit via choice or manipulation. Whenever such a fertilization-enhancing strategy

is pursued at the expense of the opposite sex (i.e., the sexual partners), a conflict of interest occurs between the sexes.

As pointed out by Schärer & Janicke (2009), Charnov (1979, p. 2482) was first to fully appreciate the importance of the realization that "the interests of partners are often in conflict," and he referred to this as male–female conflict. In the same year, Parker (1979, p. 124) provided a concise, and often cited, definition of sexual conflict: "Conflict between the evolutionary interests of individuals of the two sexes". This definition, which is accurate to date, signifies that what is good for one sex can be bad for the other. This clearly distinguishes sexual conflict from sexual selection processes. Although in many cases the former may result from the latter, this is not necessarily the case, meaning that sexual conflict can also arise over traits that are not sexually selected in the first



place. This is easiest to envisage in a situation in which a trait has different optima for males and females. A good example is human hip bones: The pelvis is composed of different parts (the ilium, ischium, pubis, and sacrum) that are shaped differently in males and females. Obviously, the main reason for this difference is caused by the fact that females need to be able to give birth to offspring and therefore need wider hips (e.g., Hogervorst, Bouma, & De Vos, 2009).

In Figure 2.1, the general processes necessary for and involved in sexual conflict are schematically outlined. On the whole, sperm donors (males) want to ensure that the sperm that they donate will (eventually) fertilize eggs. To achieve this, they can evolve adaptations that increase fertilization chances. As we will see below, the most prominent of such adaptations range from immediately inducing egg laying in the partner, preventing the partner from remating with a competitor, increasing sperm storage, and decreasing sperm digestion. Whenever such an adaptation is not in the interest of the sperm recipient (female), for example, due to inflicted harm or a loss of choice and/or control over the production of her offspring, selection pressure will increase for counter-adaptations that will help to resist the strategy employed by the sperm donor. Clearly, this can then result in a continuous evolutionary cycle of adaptations and counter-adaptations that is usually referred to as

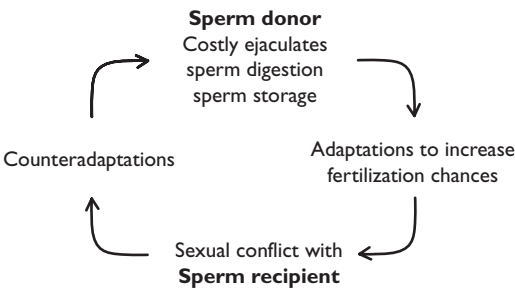
an evolutionary arms race between the sexes or antagonistic coevolution.

In recent decades, essentially since Charnov's and Parker's seminal papers (1979), much research has investigated these processes in animals. And the still growing field has already been extensively reviewed (e.g., Arnqvist & Rowe, 2005). Given this massive body of knowledge generated over the past decades, I can review but a small part of this here and therefore aim to concentrate on the more recently worked-out examples. In doing so, besides outlining the essential issues and factors for sexual conflict to occur, I will touch upon a number of different species, breeding systems, and reproductive processes. I will start by dealing with the different types of sexual breeding systems found in nature, to illustrate how the type of system may impact the form that sexual conflict takes. The subsequent sections then deal with intralocus sexual conflict and, subsequently, the different levels of interlocus sexual conflict. The chapter is then concluded with a discussion of the evolutionary consequences of sexual conflict and some promising future directions within this field of research.

### Breeding Systems

When thinking about nonhuman animals within the context of sexual conflict, it is essential to realize that different species may express different breeding systems. As we will see in the following, the type of breeding system is important for the shape that sexual conflict takes. For clarity, with the term breeding system, which is sometimes also referred to as mating system, I intend to indicate the expressed mode of sexual reproduction, such as whether males and females are present and whether mating occurs with one or several partners before the production of offspring. Since the nonhuman animal literature uses a number of specific terms and distinctions for differences in breeding system, for the purpose of this chapter I will first briefly highlight the most important, and sometimes obvious, ones here.

A first distinction that needs to be made is between the number of partners that are mated with during a lifetime. When mating only takes place with a single partner during an animal's lifetime, a species is referred to as monogamous. Monogamy is not necessarily restricted to one act of insemination during the animal's lifetime—many copulations can be performed with the single partner. As soon as matings occur with more than one partner, a species is said to be polygamous and, as a consequence, promiscuous. Whenever there is some form



**Fig. 2.1** Schematic illustration of the evolutionary causes and consequences of sexual conflict. Sperm donors (males) in nonmonogamous species are faced with investment in often costly ejaculates, and the selective storage and elimination of sperm in the sperm recipient (female). As a consequence, strategies that influence these processes in their favor will be selected for. However, these fertilization-enhancing strategies may not coincide with the sperm recipient's (female's) interests, thus generating sexual conflict. The evolutionary response of sperm recipients is then to evolve adaptations that will counter-act or resist (hence counter-adaptations). The latter then closes the evolutionary cycle, thus increasing the selection on sperm donors again to evolve more persuasive strategies, and so forth.

of a stable relationship, such systems can be split up into polyandry (one female with several males) or polygyny (one male with several females). Well-known examples of polygyny and polyandry, in some cases referred to as harems, can be found in lions, elephant seals, fish, and primates. However, it should be noted that often a stable relationship between males and females is not present, in which case the species is simply said to be polygamous.

A second useful distinction to make is between semelparity and iteroparity. A semelparous species reproduces only once in its lifetime, while an iteroparous species goes through many reproductive episodes. Important factors relating to these life history traits then become the investment in eggs within each reproductive episode, strategic ejaculate partitioning over different partners, the exact composition of the ejaculate besides sperm, the ability to retain (store) and eliminate (digest/eject) sperm, and whether some form of parental care is performed by one or both sexes.

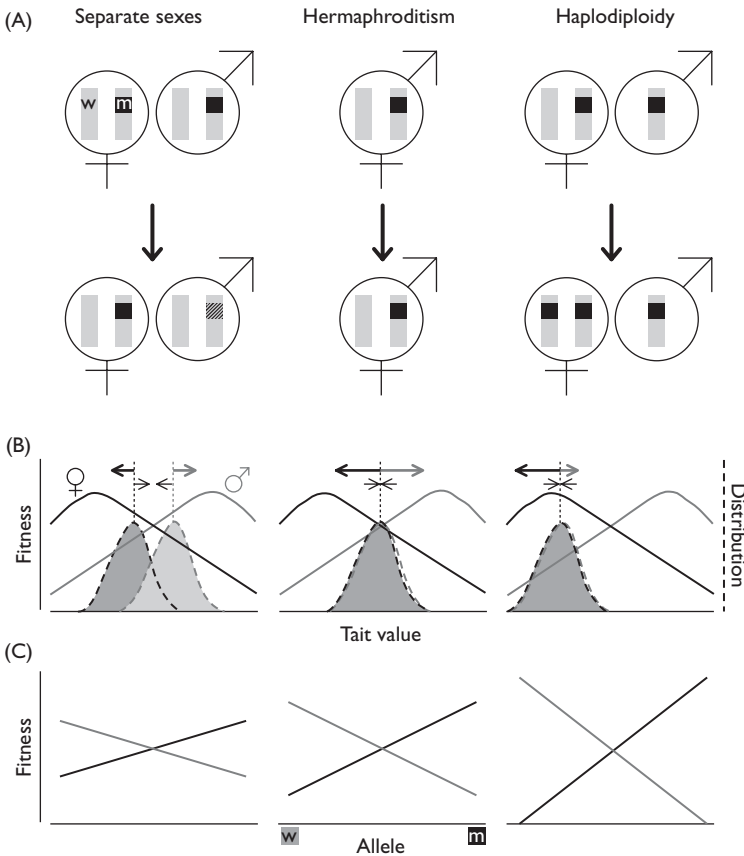
An important third distinction is based on the type of sex that is expressed. Next to the familiar situation with males and females, usually referred to as separate sexes but also gonochorism and dioecy, we can distinguish hermaphrodites and parthenogens. Hermaphroditism occurs when an individual is both male and female during its lifetime, which can be further subdivided. Sequential hermaphrodites start off their life in one sex and change to the opposite sex during their lifetime. This can go from male to female (protoandry) or vice versa (protogyny), while some species are also able to make this switch repeatedly. Simultaneous hermaphrodites express both sexes at the same time and thus possess functional male and female reproductive organs, which means they often have the ability to self-fertilize as well as cross-fertilize. Finally, parthenogenesis, although generally defined as the development of unfertilized eggs into offspring, is relevant here because it occurs in a number of different forms. It becomes relevant in a sexual conflict context as soon as sperm is required to trigger this developmental process. It is then often referred to as pseudogamy, gynogenesis, or sperm-dependent parthenogenesis, indicating that mating is required to get the sperm to initiate egg development (without the sperm DNA being used, but see D'souza, Storhas, Schulenburg, Beukeboom, & Michiels, 2004). Another relevant form of parthenogenesis is arrhenotoky (or arrhenotokous parthenogenesis), which occurs in haplo-diploids. In such animals, unfertilized eggs develop into males (and remain

haploid) while fertilized eggs become females (and are thus diploid).

## **Intralocus Conflict**

Sexual conflict can occur in two forms. Intralocus conflict will be covered in this section and interlocus conflicts will be covered subsequently. Intralocus conflict is defined to occur when males and females have different optima for a trait that is equally expressed in both sexes. Such a trait is generally expressed under the influence of one or several overlapping loci in the two sexes, thus entailing a genetic correlation between the sexes. A classic example for this is body size, which is sexually dimorphic in many species (Prasad, Bedhomme, Day, & Chippindale, 2007).

One way to exemplify intralocus conflict is to imagine a sexually antagonistic mutation that causes a certain trait to become beneficial for females and detrimental for males. We start with this in a separate sex situation as illustrated in Figure 2.2 (left panel). Although there is a detrimental effect for males, as long as the fitness benefit, averaged over the sexes, is positive, the mutation will be selected (Morgan, 1994; Rice, 1984) and thus pulled toward the female optimum (Figure 2.2B). However, there are a number of processes that can additionally influence the maintenance of the mutation. For example, evolution toward sex-specific regulation of the mutation will break down the strict intersexual genetic correlation and thus reduce the cost of carrying the mutated allele (Cox & Calsbeek, 2009; Ellegren & Parsch, 2007). As a consequence, selection against the trait in the negatively-affected sex will be reduced. Hence, the allele is said to be masked in one of the two sexes (sexual masking), but it remains present and polymorphism is maintained (Reinhold, 2000). Such sex-specific regulation or sexual masking results in shallower fitness correlations in Figure 2.2C; in other words, reduced intersexual genetic correlations (Bonduriansky & Chenoweth, 2009). It should be noted that (partially) resolving the conflict via sex-specific gene expression may still result in long-term fitness costs (Connallon, Cox, & Calsbeek, 2010). It has also been proposed that the confinement of sexually antagonistic genes to one sex may be partly responsible for the evolution of sex chromosomes (Rice, 1984; Mank & Ellegren 2009), which means that intralocus conflict could cause a high turnover of sex chromosomes, as was recently confirmed by a theoretical modeling study (Van Doorn & Kirkpatrick, 2007).



**Fig. 2.2** Illustration of the evolutionary outcome of intralocus sexual conflict in different breeding systems. Focus lies on a sexually antagonistic mutation (black square, m) that increases female fitness but decreases male fitness. A. Comparison of inheritance of the mutation after many generations. Only in the separate-sex situation can sexual masking of this allele occur due to sex-specific regulation (indicated by hatched mutation). Because the mutation is beneficial to females, sexual masking occurs in males in this example; in the reverse case it would occur in females. B. Fitness curves (solid line) and phenotype distributions (dashed line) for the sexually antagonistic trait. Thick black and gray arrows show female and male selection pressures, respectively. Thin black arrows display the constraint due to intersexual correlation. C. Fitness effects of the wild-type (w) and mutant allele (m) are shown for females and males. This figure is strongly inspired by the works of Bedhomme & Chippindale (2007), Bedhomme et al. (2009), Bonduriansky & Chenoweth (2009), and Kraaijeveld (2009).

Most species with separate sexes have sex chromosomes. However, if we take the above-mentioned alternative breeding systems into account, this changes the outcome of this form of sexual conflict (Figure 2.2, middle and right panel). For example, due to the lack of chromosomes that determine sex and the absence of the option of sexual masking in hermaphrodites and haplo-diploids, for both the maintenance of sexually antagonistic polymorphisms is much less likely. In addition, the genetic correlation between male and female traits in hermaphrodites is inherent to their breeding system and cannot be broken down (Anthes et al., 2010). Hence, although there is opposing selection for the trait affecting fitness, the trait distribution will never reach either optimum and fitness correlations remain steep (Figure 2.2B & 2.2C). Moreover, the mutation is subjected to selection in every individual, while for separate sexes this may be restricted to one sex. As a result, in hermaphrodites polymorphisms should reach fixation or loss faster, and hermaphrodites are therefore predicted to have fewer reproduction-related polymorphisms (Bedhomme et al., 2009; see also Abbott, 2011).

Thus, while in species with separate sexes the evolutionary optimum for a trait may be reached (Bonduriansky & Chenoweth, 2009), in hermaphrodites this cannot happen (Morgan, 1994; Bedhomme et al., 2009) as illustrated in Figure 2.2 (middle panel). What happens in haplo-diploids is again different—here the intralocus conflict seems to be mostly decided in favor of diploid females (Figure 2.2, right panel). As Kraaijeveld (2009) pointed out, this is essentially because the mutated allele will be present in females two-thirds of the time (because males are haploid) and hence will experience stronger selection via the diploid sex. This results in even steeper fitness correlations, and the opposing selection for the trait affecting fitness will in this case be won by the female as illustrated by the trait distribution reaching the female optimum and pulling the male's along (Figure 2.2B & 2.2C).

### Interlocus Conflict

Interlocus conflict occurs when the optimal expression of a trait encoded on a genetic locus for one sex negatively influences the expression of

a different trait on another locus in the opposite sex (Parker, 1979). The essential difference from intralocus conflict is that for interlocus conflict the two traits are genetically independent of each other and may only be expressed in one of the two sexes. There are many examples of species in which a form of interlocus conflict seems to occur. But it should be noted that in many cases the compelling experimental evidence showing that this is indeed a sexual conflict is lacking. Therefore, I will restrict discussion to recent examples in which the conflict situation has been worked out in detail. At the same time, I discuss examples that illustrate the different moments around copulation at which conflicts can arise and, where possible, highlight differences between breeding systems.

### **Precopulation—Prior to Sperm Transfer**

When referring to the act of copulation, what is meant here is the moment at which gametes are transferred. In the case of internally fertilizing animals, this refers to the moment at which sperm are introduced into the recipient's reproductive tract. In the case of externally fertilizing animals, this refers to the moment at which the male and/or female gametes are released. Anything that happens before that moment is considered as precopulatory.

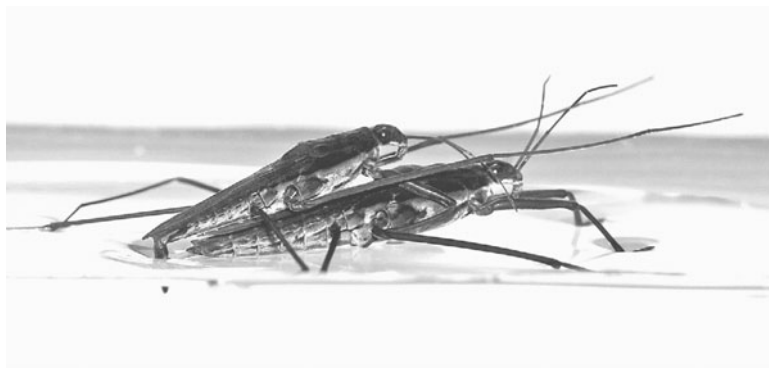
The separation that is generally made is between pre- and postcopulatory sexual selection processes. I will also use this conventional separation here, but it should be noted that sexual conflict can be far removed in time from the act of copulation. One such case is the recently discovered example that starts well before maturity, in utero, in the developing dizygotic twin embryos of Soay sheep, *Ovis aries* (Korsten, Clutton-Brock, Pilkington, Pemberton, & Kruuk, 2009). The conflict arises only when a male and female embryo are developing together in the uterus, and it is caused by the fact that males and females have different developmental requirements, for example, in terms of different sex-specific steroid hormone levels. Since the embryos will be competing for the common resources in the uterus, it is significant that some circulating hormones from the male fetus negatively affect development of the female fetus. This seems to have long-lasting consequences, since females that develop with a male cotwin are born with a reduced weight as compared with those that develop with a female cotwin. Such females also have lower first-year survival and therefore a lower lifetime breeding success (Korsten et al., 2009). The fact that this only happens in dizygotic twins

with opposite sexes indicates that this is a sexual conflict rather than a sibling conflict.

A second, rather gruesome example of sexual conflict that can also occur well before copulation is infanticide, for which lions are of course the classic nature documentary example. In such cases, newly resident males kill the females' current offspring to induce (re)mating and/or recommence ovulation in the female. Males benefit from this strategy since they ensure paternity and do not help with raising unrelated offspring. It goes without saying that this is likely to be more costly than beneficial for the females. Recent work in monkeys has revealed that there may be ways in which females can reduce the risk of infanticide, for example, by seeking protection from subordinate males that are potential fathers (e.g., Sooty mangabeys, *Cercocebus atys*, Fruteau, Range, & Noë, 2010; Chacma baboons, *Papio hamadryas ursinus*, Clarke, Henzi, & Barrett, 2009; Henzi, Clarke, Van Schaik, Pradhan, & Barrett, 2010).

The above is mostly based on observations and correlational data. However, infanticide also occurs in invertebrates, and here costs can be demonstrated more easily. A well-understood example comes from a spider, *Stegodyphus lineatus*. In this species, females guard sacs with fertilized eggs until they hatch. Normally, during this time they do not mate with other males. However, a male can get the female to mate again by removing her egg sac, and males do so actively (Schneider & Lubin, 1997). Males can gain from doing so because if they subsequently get to mate with the female they gain much of the paternity, while for females egg sac removal decreases her chances of successful reproduction (Schneider, 1999). Research on different populations indicates that the selective pressure on males to be able to win such struggles (which is aided by a relatively larger cephalothorax; Schneider & Lubin, 1997) depends on the size of the population. Under low density, males have a relatively larger cephalothorax to be able to win the rare encounters with females. Under high density, when encounters are frequent, females have a larger relative cephalothorax size to fend off males and avoid the cumulative costs of multiple mating (Maklakov, Bilde, & Lubin, 2006).

Another form of conflict that takes place prior to copulation revolves around the willingness to mate. In many species in which mating involves mounting by one individual (often the male) on top of the other (the female) behaviors can be observed that may be indicative of a reluctance in the mounted (female) to be inseminated or remated.



**Fig. 2.3** The mounting behavior of water striders, in this case the red-backed water strider *Gerris gracilicornis*. In the photograph the male is seen riding on the back of the female prior to copulation. The average size of these animals is between 12 and 15 mm. (Photo by Han & Jablonski, 2009, PLoS One 4, e5793.)

A few examples are the premating struggles in water striders (e.g., *Gerris odontogaster*; Arnqvist, 1992), bodily inflation in cane toads (e.g., *Bufo marinus*; Bruning, Phillips, & Shine, 2010), and shell shaking in hermaphroditic snails (*Physa acuta*; Facon, Ravigné, & Goudet, 2006).

In dung flies, *Sepsis cynipsea*, females appear to actively shake males from their back (Parker, 1972), and this can result in wing injury for females, but it is unclear whether there is a benefit for the male even though the alternative explanation that this is collateral damage due to precopulatory male–male competition seems more likely (Teuschl, Hosken, & Blanckenhorn, 2007). There are a few cases in which the actual costs of remating or insemination have been quantified. For example, in water striders, in which a male mounts on the female's back prior to copulation, the mating partners often have premating struggles prior to insemination (e.g., Han & Jablonski, 2009; Figure 2.3). One test of the effect of repeated mating for females was performed in the water strider *Aquarius paludum*. In this study, it was found that experimentally-increasing mating frequency with several different partners reduced egg production and hatching success (Ronkainen, Kaitala, & Kivelä, 2010). A second study investigated Zeus bugs, *Phoreticovelia disparata*. In this species males start guarding females when these are still juvenile, awaiting female maturity to assure paternity (Figure 2.4). The study manipulated the presence of males and found that male riding behavior, which is the way in which these males guard their mates, is costly for juvenile females in terms of survival (Jones, Elgar, & Arnqvist, 2010).

A similar situation seems to apply to the alfalfa leafcutting bee, *Megachile rotundata*. This is a haplodiploid insect in which males chase females and attempt to mate with them. Females generally mate once but can mate multiply and seem to resist mating attempts by struggling (using abdominal thrusts and leg kicks) to dislodge the male (Rossi,



**Fig. 2.4** Riding behavior of the Zeus bugs, *Phoreticovelia disparata*. The much smaller male guards a juvenile female until she becomes adult and ready to be inseminated. The animals measure around 1–2 mm. (Photo by Göran Arnqvist.)

Nonacs, & Pitts-Singer, 2010). Manipulation of the sex ratio revealed that the male behavior interferes with females' foraging and, as a result, offspring production (Rossi et al., 2010).

A final example of a precopulatory conflict is from simultaneously hermaphroditic land snails that “shoot” so-called love darts (Figure 2.5), although admittedly the costs have not been fully worked out yet. Dart shooting involves the forceful penetration of a calcareous dart-like structure through the partner's body wall (Figure 2.5). Because they mate simultaneously reciprocally, that is, exchange sperm, both mating partners do this before exchanging sperm, and these darts can remain lodged in the recipient (Koene & Chase, 1998). In the brown garden snail *C. aspersum*, it was revealed that the dart is used as a vehicle to transfer a substance from a set of glands into the blood of the mating partner that closes off the entrance to a sperm digestion organ (Adamo & Chase, 1990; Koene & Chase, 1998) and results in a higher proportion of paternity (Chase & Blanchard, 2006; Rogers & Chase, 2001).