

Sexual Conflict in Humans

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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 adaptedness.

Environment of evolutionary adaptedness. The importance of identifying the relevant features of the environment of evolutionary adaptedness 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 (Platak & Porter, this volume; Platak et al., 2003, 2004; Platak, Burch, Panyavin, Wasserman, & Gallup, 2002; Platak, 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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