

Original Article

Human Sexual Conflict from Molecules to Culture

Gregory Gorelik, Department of Psychology, Florida Atlantic University, Boca Raton, FL, USA; Email: gregory.gorelik33@gmail.com (Corresponding author).

Todd K. Shackelford, Oakland University, Department of Psychology, Rochester, MI, USA.

Abstract: Coevolutionary arms races between males and females have equipped both sexes with mutually manipulative and defensive adaptations. These adaptations function to benefit individual reproductive interests at the cost of the reproductive interests of opposite-sex mates, and arise from evolutionary dynamics such as parental investment (unequal reproductive costs between the sexes) and sexual selection (unequal access to opposite-sex mates). Individuals use these adaptations to hijack others' reproductive systems, psychological states, and behaviors—essentially using other individuals as extended phenotypes of themselves. Such extended phenotypic manipulation of sexual rivals and opposite-sex mates is enacted by humans with the aid of hormones, pheromones, neurotransmitters, emotions, language, mind-altering substances, social institutions, technologies, and ideologies. Furthermore, sexual conflict may be experienced at an individual level when maternal genes and paternal genes are in conflict within an organism. Sexual conflict may be physically and emotionally destructive, but may also be exciting and constructive for relationships. By extending the biological concept of sexual conflict into social and cultural domains, scholars may successfully bridge many of the interdisciplinary gaps that separate the sciences from the humanities.

Keywords: sexual conflict, extended phenotype, arms race, parental investment, sexual selection, culture

Introduction

From molecules to culture, conflict surrounds us. The beauty, grandeur, and complexity of our existence are outcomes of innumerable conflicts of interest—conflicts fought over eons between our ancestors and their rivals, as well as opposing genetic interests within individual organisms. The victors of these conflicts survived and reproduced, imparting to us a legacy of traits that led to their victory. For better or worse,

the biological weapons with which our ancestors overcame their foes are with us still. We use these weapons when our immune systems battle parasites and pathogens (Zakharova, 2009), when we manipulate nature to yield its resources (Kuznar, 2001), outmaneuver our reproductive rivals (Buss and Dedden, 1990; Buss, 1988), or seduce members of the opposite sex (Bleske-Rechek and Buss, 2006). Our abilities to think, feel, speak, and act, have all been forged in the fires of natural and sexual selection. With them, we are able to confront the conflicts that bombarded our ancestors for millions of years.

The battle between the sexes is one of the most incessant of evolutionary conflicts. Whether we are dealing with members of our own sex or of the opposite sex, friends or relatives, foes or allies, sexual conflict is ever-present. Being a crucial sieve by which our ancestors' passed their genes into succeeding generations, sexual reproduction is responsible for many of our adaptations and can explain much of our daily functioning. Evolutionarily, it is not "survival" of the fittest that matters, but "reproduction" of the fittest. Of course, sometimes a cigar is just a cigar, and not every aspect of our being is libido-driven. However, the genes responsible for building us travelled through innumerable border crossings of sexual reproduction in preceding generations. Their evolutionary success depended on their contribution to the development of phenotypic networks that enabled their replication through the gateways of sexual reproduction. These phenotypes encompass molecular-level processes (Anderson et al., 2007), tissue and organ morphologies and functions (Gallup, Burch, and Mitchell, 2006), psychological traits and behaviors (Shackelford et al., 2002), and higher-level cultural and societal dynamics (Chang, Wang, Shackelford, and Buss, 2011; Shackelford, Weekes-Shackelford, and Schmitt, 2005). Sexual conflict pervades these levels and can illuminate much of human nature.

In this article, we illustrate how sexual conflict is expressed at many levels of human functioning and portray how divergent sexual interests exert their power over humans by describing sexual conflict's spheres of influence. Beginning our discussion with foundational biological concepts and theories, we continue by highlighting the molecular, anatomical, and physiological aspects of human reproduction, proceed with an analysis of human thoughts, emotions, and speech, and culminate by discussing aspects of popular culture, politics, media, religion, and other societal phenomena. We do not restrict our analysis of human functioning to any one domain at a time, as each domain influences, and is influenced by, many other domains of human development. Instead, we maintain the common thread of sexual conflict to anchor and clarify our discussion. We engage a variety of fields and academic disciplines, from the biological to the psychological and social sciences. In so doing, we are aware of our limitations and hope that scholars from these diverse fields will forgive but correct our misconceptions and oversights. We are also aware of our Darwinian bias but are confident that this perspective unites many of the social and natural sciences and provides an explanatory framework for human nature that ties us to all plant and animal life. We encourage researchers and theoreticians to consider the ideas presented here and test whatever novel hypotheses this discussion may inspire.

Concepts and Definitions

What is Sexual Conflict?

Since the dawn of sexual reproduction, males and females have been embroiled in an incessant evolutionary struggle. The reasons for this struggle are numerous but can be traced to a set of key insights derived from evolutionary biology and expounded in the theory of parental investment (Trivers, 1972). According to this theory, the sex with the greater reproductive effort required to produce offspring should also be choosier when it comes to selecting mates. In most mammalian species, females invest more time, energy, and resources in reproduction and parenting than do males. This sexual inequality has led to an evolutionary divergence of interests between female hesitancy and male readiness to copulate (Haselton and Buss, 2000), and is responsible for the emergence of sexual conflict. In addition to sex differences in parental investment, the degree of sexual conflict in a population may be influenced by the operational sex ratio (i.e., the proportion of sexually mature males to females in a population) and sex differences in reproductive rate (Clutton-Brock and Parker, 1992).

Sexual conflict was fought across evolutionary time and is fought presently when individuals employ their evolved mechanisms against members of the opposite sex, whether in the nightclub, in the bedroom, in the kitchen, or in court. Thus, many of our physical and psychological sex differences can be explained by the action of innumerable coevolutionary arms races that have raged for millions of years between males and females, whereby an adaptation benefitting the reproductive interests of one sex evolves at a cost to the other sex. This is the classic definition of sexual conflict (Lessells, 2006). In our discussion, we also include conflicts between members of one's own sex over sexual access to members of the opposite sex as a constituent component of sexual conflict.

We must not conflate our discussion of sexual conflict with concepts derived from the various fields of social science or gender studies, although we aim to integrate many of these fields into an evolutionary framework. Contrary to popular opinion within some of these disciplines (Evans, 2009), males do not usually benefit other males at the expense of females as a whole, or vice versa, as selection only builds adaptations that function to further the reproductive interest of individuals, or even selfish genetic elements within individuals (Burt and Trivers, 2006). Although we discuss male and female adaptations, these adaptations do not benefit each sex at a group level. Of course, individual interests may at times coincide and individuals may thereby benefit by cooperating with individuals that have similar interests. In this way, patriarchal cultures may advance the reproductive interests of men as a group, just as matrilineal population demographics may benefit the reproductive interests of women as a group (Figueredo et al., 2001), but it is individual males and females who ultimately reap the reproductive benefits.

Individual reproductive interests are sometimes furthered by cooperating with other organisms, whether of the same or of a different species (West, Griffin, and Gardner, 2007). For cooperative traits to evolve, their reproductive benefits must exceed their costs. For instance, individuals of opposite sexes may mutually benefit their genetic interests by reproducing with each other in the context of a long-term or a short-term relationship (although one of the partners may derive greater benefits than the other partner and may employ deceptive tactics to maintain the relationship). In such cases, sexual conflict is minimized because each side benefits from the reproductive venture. Hence, deception and

manipulation, though not eliminated entirely, are not as apparent. Likewise, individuals of the same sex may cooperate through various means of social support and reciprocity (“friendship”) to acquire opposite-sex mates (Shackelford and Buss, 1996). Adaptations that generate cooperation, like adaptations that generate conflict, are manifest at many levels of analysis, whether cellular or cultural, and one cannot discuss sexual conflict without touching on sexual cooperation. In many ways, conflict and cooperation are opposite sides of the same coin, in that our mates and friends may sometimes be used as weapons against individuals with whom we are in conflict. Therefore, when cooperating with some individuals, one often inflicts costs on others (Olson and Blumstein, 2009). Even within a relationship, there is a mixture of conflict and cooperation across a variety of spatial and temporal contexts (Gallo and McClintock, 1965).

Why Sex?

Why reproduce sexually? Wouldn't it be wiser to clone oneself *ad infinitum*? Why bother spending so much time and energy on finding sexual partners, only to contribute half of one's genes into the resultant offspring? At first glance, sex seems evolutionarily wasteful. One intriguing explanation that is in line with the theme of sexual conflict is “The Red Queen Hypothesis” (Ridley, 1993), named after a character in Lewis Carroll's *Through the Looking-Glass*. Just as Alice is forced by the Red Queen to run without getting anywhere, selection continuously tweaks our adaptations without there being any overall improvement in their effectiveness. Although organisms evolve over time—modifying their weapons, building up their defenses—their enemies evolve at a similar pace. As a result, organisms are no better at fighting off parasites, predators, prey, or sexual rivals, than were their ancestors. To stay afloat in the evolutionary game, organisms must have what it takes to outmaneuver their rivals, but one's rivals endure similar pressures to outmaneuver their competitors. This leads to a coevolutionary struggle between organisms with competing interests.

One of the most pervasive struggles is fought between hosts and parasites (Zakharova, 2009). Parasites reproduce more quickly than their hosts, enabling the evolution of parasitic weaponry that is especially suited to successfully manipulating and sometimes attacking and harming hosts. In turn, hosts come under selection pressures to modify their genetic combination to thereby thwart their evolving parasites. Thus, the best way to pass host genes into the next generation may be to recombine them with the genes of another organism, thereby curbing the destructive power of parasites. As parasites perfect their weaponry against hosts, hosts must ceaselessly find other organisms with whom to recombine their genes in every generation—genes that are already vulnerable to the destructive effects of rapidly evolving parasites. So our biological drive to find mates, court them, and battle sexual competitors to maintain them, may be a result of continuous arms races between ourselves and our parasites. A disturbing implication of this hypothesis is that individuals themselves may be parasitic upon members of the opposite sex. Assuming that males and females have different reproductive interests, mating may entail the exploitation of opposite-sex organisms as vehicles to transport one's genes into the next generation. This dynamic is especially salient in barnacle species in which dwarf males attach themselves to much larger females in an almost-parasitic effort to fertilize their eggs (Urano et al., 2009; for other examples of intersexual manipulation in non-humans, see Arnqvist and Rowe, 2005).

Sexual Selection

The evolutionary need to escape from parasites via sexual reproduction has brought about a further set of selection pressures. Not only does an organism have to outmaneuver its own parasites, but also it must choose sexual partners who are themselves free of parasites (or are insensitive to their harmful effects; see Getty, 2002) and are without harmful genetic mutations (Møller and Cuervo, 2003). This selection of sexual partners is a direct form of “sexual selection” (Darwin, 1871; Miller, 2000), as opposed to an indirect form, in which a struggle for mating opportunities between individuals of the same sex leads to the selection of traits that prove useful in such struggles. Indirect sexual selection may help to explain why males tend to be physically larger than females, including in our own species (Bukowski et al., 2007). As male-male competition raged across evolutionary time, the victors were usually larger and imparted their greater size to their offspring. Thus, it is not only the inanimate environment that organisms must adapt to in order to survive and reproduce; they also must have what it takes to overcome sexual rivals or impress members of the opposite sex if they are to leave behind any progeny.

Direct sexual selection often leads to the evolution of fitness indicators—relatively gaudy, energy-consuming traits or behaviors that communicate an organism’s developmental stability. Members of each sex use these phenotypic cues to judge the parasite load or genetic health of potential mates. A large and colorful tail, full female breasts and buttocks, or an intelligent and agile mind (Miller, 2000), may communicate the genetic health of a potential mate by advertising a developmental history unperturbed by parasites, as evidenced by the successful development of such costly handicaps (Zahavi, 1975). In this way, seemingly useless and even harmful traits may be inherited because of what they signal to members of the opposite sex. Although we may not consciously understand the messages that these traits convey, we find some traits attractive and others unattractive because such reactions enabled our ancestors to choose the sexual partners that were likely to yield healthy offspring that would develop into sexy adults.

Although physical attractiveness is usually correlated with genetic and bodily health, sometimes simply possessing “sexiness” may be enough to attract a mate (Cornwell and Perrett, 2008), even if one’s overall success at survival or parasite resistance is sub-par. Scholars should consider this possibility when accounting for the presence of seemingly useless and even harmful human traits. To stress the point again, the crucible of evolution is *reproduction*, not survival. Likewise, and in line with parental investment theory, members of the lesser-investing sex (usually males) who may not possess high-quality genes may nonetheless attract sexual partners if they are willing and able to invest in childrearing. Therefore, possessing and displaying material resources and empathetic qualities that communicate nurturance, may be the product of an evolved, long-term mating strategy, notably for males (Khallad, 2005; Kruger, 2008).

All of the preceding mating strategies are employed by humans in one form or another. They vary between individuals and may even vary within individuals as individuals develop throughout the lifespan or their environmental circumstances call for a change in mating strategy (Del Giudice, 2009). With the evolution of fitness indicators, sexual conflict has brought about novel ways to manipulate and deceive mates and competitors. If an organism can get away with brandishing fitness indicators that are not as costly to produce and maintain as the “real things”, then their deceptive qualities may be seized upon by selection and proliferate within subsequent populations. With the evolution

of deceptive signals of mate quality, the sexes must evolve ever-more sophisticated mechanisms by which to judge the true quality of their suitors. Such a scenario is consistent with the “chase-away” model of sexual selection (Holland and Rice, 1998), which posits that members of one sex may evolve exaggerated signaling systems that take advantage of the signal-receiving mechanisms of the other sex. Exaggerated male signals lead to the coevolution of female insensitivity to these signals. Females are predicted to be the winners of such coevolutionary contests because males must ultimately pay the reproductive costs of developing and maintaining their burdensome signaling systems. As later discussed, our own species has taken deceptive fitness signaling to insidious degrees with the help of cultural products and modern market economies (Miller, 2009). In the following section, we expound on the many spheres of sexual conflict between men and women, from molecules to culture.

Spheres of Sexual Conflict

We live our lives ignorant of the majority of the agents that manipulate and deceive us. These agents are no Iron Age gods, haunting us from the supernatural realm. They are part of the natural environment into which we are born. Their influence stems from the molecular to the global. Their manipulative powers have been perfected over eons of evolutionary time. With each generation they get more efficient at exploiting us. However, we are not passive automatons who allow ourselves to be idly manipulated by these ancient puppeteers. With every generation, we sharpen our scissors and attempt to cut free of the strings that bind us. With each successive turn of the evolutionary wheel, we become the tiniest-bit better at throwing off our shackles. With each bout of selection, we have acquired stronger defenses, and more manipulative weaponry of our own. What worked in prior generations was imparted to us—gifts from an ancestral legacy of survival and reproduction.

Whether we realize it or not, we, our spouses, our families, our friends, and our colleagues, are all hidden troves of manipulative intentions and schemes. In the following sections, we discuss the myriad ways by which men and women manipulate and deceive one another. We begin with a discussion of sexual conflict as manifested at the molecular stage and follow the argument outward into widening spheres of influence. It is important to keep in mind that our phenotypes do not end with our individual bodies—i.e., our adaptations are not restricted to our physical frame. Our skin, our organs, our eyes, and our genitals are only one level of phenotypic expression. According to Dawkins (1982), organisms can evolve extended phenotypes, or adaptations that go beyond their bodies. Thus, anthills and termite mounds are ant and termite adaptations, respectively, even though they are not parts of ant and termite body frames. Similarly, organisms can evolve manipulative adaptations by which they control the behavior of other organisms, in essence using other organisms as extended phenotypes. For example, our coughing and sneezing can be seen as adaptations on the part of our bodies to rid ourselves of viruses. Taken from the perspective of a virus, however, our coughing and sneezing may be the best avenues by which it can spread and infect other humans. This makes us, and our coughing and sneezing, in particular, extended phenotypic viral adaptations. In what follows, we apply the notion of the extended phenotype to human sexual behavior, whereby men and women are shown to possess adaptations by which they attempt to manipulate and control the

physiological, psychological, and behavioral functions of one another. From gametes to social institutions, our manipulative extended phenotypes pervade our bodies, minds, and cultures.

Molecular Manipulation

The hidden layers of human sexuality are slowly coming into focus. One of the most astonishing findings has been the extent to which we use molecular means to manipulate our sexual partners and defend against their manipulative ploys on us (e.g., Gallup, Burch, and Platek, 2002; Goetz et al., 2005). Male and female reproductive systems are equipped by selection to counteract the negative effects of the other sex's reproductive strategies. Thus, we all possess molecular mechanisms by which we attempt to take advantage of our sexual partners' reproductive systems. Semen contains chemical properties that hijack women's physiological and psychological functions. Women, in turn, evolved the presence of stalwart guards, barricades, and anatomical obstacle courses to prevent all but the best reproductive contenders through, while minimizing the costs of male molecular manipulation (see Baker and Bellis, 1993a, 1993b, 1995).

It appears as if our reproductive systems function under the evolutionary rationale of differential parental investment. Women are at an increased risk of squandering valuable time and resources on rearing genetically inferior offspring, or offspring that will lack adequate paternal support. As a result, female reproductive anatomy and chemistry is adept at retaining the most viable sperm from the most viable male contender. In true Red Queen fashion, the male predisposition to spread their seed far and wide has enabled male anatomy and chemistry to keep up in the evolutionary arms race by evolving ways to usurp competitor sperm and unconsciously influence the physiological mechanisms of female reproductive choice (e.g., Gallup, Burch, and Platek, 2002; Goetz et al., 2005).

Research suggests that the per-copulation risk of pregnancy is higher for rape than for consensual sex (Gottschall and Gottschall, 2003). There may be other explanations and criticisms of such findings, but if true, we must further examine the possibility that some men may have evolved predatory adaptations that are activated during coercive sexual encounters with women (Gottschall and Gottschall, 2003). The evidence for this comes from findings demonstrating the presence of follicle-stimulating-hormone (FSH) and luteinizing hormone (LH) in semen. These hormones normally function to stimulate the maturation of an egg and its subsequent release. That semen contains these hormones is indicative of their manipulative function in stimulating female ovulation. Rapists may possess higher concentrations of these hormones than non-rapists, or men's concentrations of FSH and LH may increase when in coercive sexual encounters with women. Both scenarios require further investigation. Likewise, we encourage researchers to measure the amounts of FSH and LH in semen to investigate whether male FSH and LH levels are sufficiently high to induce female ovulation. Far from legitimizing rape, such evolutionary possibilities need further study if we are to help prevent future instances of sexual coercion. The time has come to abandon the naturalistic fallacy and accept that biological truths do not necessarily equate to moral truths. That male or female anatomy, physiology, and psychology may be host to evolved coercive mechanisms says nothing about their moral legitimacy.

Although essential for the normal sexual maturation of both sexes, FSH and LH are present in every man's semen and may function to facilitate female ovulation. The uterus, on the other hand, is home to immunological agents that attack unrecognized intruders. To counteract such defenses, selection has provided men with immunosuppressant seminal compounds. Furthermore, the presence of female infidelity throughout human evolutionary history has equipped both sexes with numerous weapons and defenses (see Baker and Bellis, 1993a, 1993b, 1995). The female reproductive tract, for instance, is apparently designed by selection to weed out all but the best genetic suitors (Baker and Bellis, 1993b). Female orgasm may play a role in this by causing greater retention of sperm from a high quality male (see Puts and Dawood, 2006). If an instance of female orgasm comes across as genuine, then a male is more likely to assume that his reproductive endeavors were met with success. Thus, women who "fake it" in the bedroom may be employing a deceptive strategy with a long evolutionary history, designed by selection to secure material resources from men who cannot otherwise provide genetically fit offspring. By faking an orgasm, ancestral women may have deceived men into apportioning investment to offspring that may not have been theirs.

Men, on the other hand, possess seminal compounds that neutralize competitor sperm and limit future access of other men's gametes to the woman's ova by blocking access to her reproductive tract with a post-ejaculatory plug (Baker and Bellis, 1993b, 1995). Likewise, penile foreskin may be an adaptation for entrapping and extracting competitor semen residing in a woman's reproductive tract (as discussed later, this function of male genitalia may cast light upon cultural practices of genital mutilation; Wilson, 2008). Though not quite as romantic as medieval knights battling one another or undertaking a dangerous quest in the hopes of winning the heart of a fair maiden, molecular sexual conflict exhibits no less drama.

In applying the extended phenotype model to human sexuality, we can posit that selection pressures evaluate human reproductive success by how well individuals of each sex can manipulate members of the opposite sex. This manipulation is both physiological and psychological. For example, other compounds in semen may act as antidepressants that affect female psychology as would an addictive drug, and women may seek sexual encounters with men to experience the associated euphoria (Gallup, Burch, and Platek, 2002). An ultimate evolutionary rationale for this euphoria may be that it signals a man's genetic quality. Thus, women may be unconsciously seeking the cheerfulness associated with the seminal properties of a fit male or a male with economic resources (a similar evolutionary rationale may explain the psychological effect of a woman's orgasm on her mating choices; Puts and Dawood, 2006).

We suspect that some men take advantage of women's psychological states by manipulatively (and unconsciously) increasing the antidepressant properties of their semen in order to maintain sexual access to them. In other words, men may biochemically hijack women's psychological states and behaviors with their semen. If so, men may not be aware that their own bodies are playing out the results of evolutionary arms races between deceptive seminal signaling and defensive female physiology and psychology. As with most issues discussed in this article, sexual conflict is mostly unconscious, even if it concerns our psychology. Selection does not favor awareness of one's reproductive physiology, psychology, and behavior; instead, it favors traits and behaviors that increase the probability that an individual will develop and behave in a way that would have been

reproductively advantageous in ancestral environments. However, some individuals may achieve conscious understanding of their reproductive behaviors. A study of the reproductive behavior of professionals in biological and evolutionary fields may reveal some interesting findings regarding the effects of “Darwinian awareness” on an individual’s love life.

Men and women benefit themselves by using each other as extended phenotypes. In this way, much of our subjective functioning and experience may be under the influence of other organisms. The extent of this manipulation is difficult to gauge and is a task worthy of scholars from diverse fields of expertise. Much of this manipulation is enacted via pheromones, hormones, neurotransmitters, and other molecules. In the following section, we discuss ways by which men and women psychologically manipulate each other with thoughts, emotions, and words. This type of sexual manipulation works in tandem with molecular manipulation and its implicit nature may not become apparent unless examined through an evolutionary lens. That is, by manipulating the emotional states of others via facial expressions, verbal and non-verbal communication, behavioral mimicry (Chartrand and Bargh, 1999), and other means, individuals can indirectly influence others’ neurotransmitter and hormone systems in an extended phenotypic manner. An individual’s development across the lifespan may entail the gradual emergence and refinement of evolved manipulative weaponry, as well as a broadening of phenotypic power to include social and cultural spheres. Likewise, the emergence of defenses against manipulation depends on a species-typical developmental process. Anatomical, physiological, and psychological weapons and defenses rely on life experience and attunement to cultural information for optimal functioning (Laland, 2008). Hence, human sexual conflict cannot be abstracted into separate domains, whether genetic, molecular, psychological, or cultural, and entails their collective contribution throughout ontogeny (Bjorklund and Pellegrini, 2002). We encourage biologists and psychologists to measure the effects of these varied influences on the evolution and development of manipulative and defensive human adaptations. Although every domain of human functioning has an effect on other domains, we nevertheless examine sexual conflict within a few key realms of human experience, and explore some of the interactions between and within these domains. Our discussion of human sexual conflict is far from exhaustive. Instead, we hope to unveil a world beset on all sides by veiled intentions, masked seducers, and hidden influences, where nothing is what it appears to be.

Sexual Conflict, Psychology, and Human Behavior

Although men may not hail from Mars, nor women from Venus, we nonetheless think, feel, and behave somewhat differently, oftentimes at the expense of our opposite-sex partners. The following discussion centers on the variety of contexts within which these psychological sex differences are manifested, usually triggered by cues of sexual conflict. As opposed to molecular and anatomical sexual conflict, psychological sexual conflict entails a different level of analysis and may be just as unconscious. Although certain aspects of our psychological treatment of sexual conflict are speculative, future investigations into these dynamics may yield fruitful results for researchers in the social and biological sciences. Furthermore, we restrict our discussion of sexual conflict to

heterosexual relationships, although an evolutionary analysis of homosexuality and sexual conflict should not be neglected by scholars.

Sexual conflict takes on psychological dimensions when it is manifested in the expression of certain thoughts, emotions, and behaviors. Thus, sexual differences at the molecular and anatomical levels are reflected at the level of mental functions. Men's psychology was shaped by selection to be interested in novel sexual partners and to assume that a woman may be interested in sex, whether she is or is not (Haselton and Buss, 2000). For ancestral males, this would have been a profitable reproductive strategy as it was likely to increase a man's genetic representation in the next generation. Women, on the other hand, were selected to be wary of casual sexual encounters and to assume that a man is uninterested in a long-term relationship, whether he is or is not (Haselton and Buss, 2000). For ancestral females, this reproductive strategy would have been beneficial to their genetic interests as they were thereby less likely to invest in genetically inferior offspring or grant sexual access to males that were unwilling to provide for them or their children.

Psychological adaptations to sexual conflict are directed at negotiating interpersonal relationships with opposite-sex mates and same-sex competitors. These dynamics bring about such phenomena as mate guarding (Shackelford et al., 2006), and sexual and emotional jealousy (Buss et al., 1999), when there is conflict, and reciprocity, status, knowledge, and protection, when there is cooperation. For example, men may engage in nurturing and benefit-apportioning behaviors to prevent partner sexual infidelity, but also may employ coercive and cost-inducing tactics for the same purpose (Miner and Shackelford, 2010). Furthermore, female-directed sexual coercion and rape are more likely to occur soon after a suspected infidelity, because the risk of sperm competition is greater during this period (Camilleri and Quinsey, 2009a, 2009b; Goetz and Shackelford, 2006, 2009; Goetz, Shackelford, and Camilleri, 2008). Intimate partner violence, however, is likely to be employed by men to prevent future instances of infidelity (Kaighobadi, Shackelford, and Goetz, 2009) as opposed to punishment for a past or current affair. It also seems that physical violence is more likely to be perpetuated against women of lower mate value by men who are also of lower mate value (Kaighobadi, Shackelford, and Goetz, 2009). In contrast to women of higher mate value, these women are less likely to be chosen as long-term partners by high-status men and so are more likely to reap reproductive benefits by engaging in short-term extra-pair copulations with reproductively valued men. As a result, their low-status partners may be under an evolutionary incentive to employ physical violence to prevent them from cheating.

Both sexes are threatened by a long-term partner's sexual and emotional infidelity, but the costs are not equal. Men are more likely to prevent and punish sexual infidelity by their partners, whereas women are more concerned with their partner's emotional infidelity (Buss et al., 1999). Female sexual infidelity is reproductively costly to male partners, as men risk apportioning investment to offspring to whom they are not genetically related. On the other hand, because male emotional infidelity may lead to the diversion of his financial support and commitment to another woman and her children, women may have come under selection pressure to employ psychological and behavioral tactics aimed primarily at preventing emotional infidelity. Thus, members of an individual's own sex or of the opposite sex can pose substantial risks to an individual's reproductive success and so a variety of physiological, psychological, and behavioral adaptations may function to influence the behavior of same-sex and opposite-sex reproductive rivals.

Now is a fine time to qualify the role of sexual conflict in human interaction. Adaptations that were selected to facilitate fitness in ancestral times may not be serving this function currently. Thus, when speaking of “adaptive” traits, we mean “adaptive” in the historical sense. Likewise, individuals may not always exhibit physiologies, psychologies, or behaviors characteristic of their sex. Although sex differences are often documented cross-culturally and across a variety of contexts, this is not always the case. Our discussion of adaptations describes the general physiological and psychological differences between men and women as a whole, not between any particular man or woman, and should be read as a theoretical treatment of the evolution of sex differences as they relate to sexual conflict. Our intent is to address the relative frequency with which certain traits and behaviors are associated with a particular sex, and we do not thereby endorse any Platonic ideals distinguishing males from females. Some women may be just as interested in casual sex as most men, and some men may be just as interested in committed long-term relationships as most women. Nevertheless, sexual conflict, and the permutations thereof, can explain some typical features of human sexuality.

As with molecular sexual conflict, much of psychological sexual conflict involves manipulation, counter-manipulation, and defense against manipulation. Humans are exceptional at using deceptive cues, the psychological means by which we manipulate one another, to initiate extended phenotypic exploitation of other humans. It can be argued that our emotional expressions are directed toward the use of others as extended phenotypes of ourselves. This extended phenotypic manipulation of others can be cooperative as well as conflicting. For example, when a woman cries, she may either be signaling a genuine instance of discomfort or danger (which may imperil her reproductive value to a man), or she may be using this emotional display to take control of a man’s mental state and behavior, at his reproductive cost (see Gelstein et al., 2011). The same can be said about a man who is attempting to seduce a woman; his thoughts, emotions, mannerisms, and words may be honest signals of his genetic worth or relationship commitment in one context, or these may be deceptive ploys used to initiate sex at the woman’s reproductive expense in a different context. The contexts in which individuals deceive each other vary by sex because some of the adaptive problems encountered by men and women were different throughout evolutionary history (see Haselton et al., 2005). Men are more likely to deceive women about their resource holdings (i.e., driving a Ferrari while living in squalor), social status (i.e., pretending to have friends or connections), relationship commitment (i.e., saying “I will stay with you forever”), or emotional fidelity (i.e., saying “She means nothing to me” when referring to another woman). Women, in contrast, are more likely to deceive men about their readiness to have sex (i.e., saying “I want you so bad”), age and beauty (i.e., with clothing, makeup, or cosmetic surgery), or sexual fidelity (i.e., saying “I would never have sex with him” when referring to another man). Such evolutionarily-relevant instances of deception are enacted to further one’s reproductive interests at the expense of the reproductive interests of opposite-sex individuals. In general, men manipulate women’s behaviors to maximize sexual access to them, whereas women manipulate men’s behaviors to extract material and social resources from them (Tooke and Camire, 1991).

Men and women employ various means of psychological and behavioral manipulation when competing with same-sex rivals for mating opportunities. For instance, men may enact mate-guarding behaviors to monopolize their partners’ time or sequester them from other men, while increasing the frequency of sexual intercourse with them

(Shackelford et al., 2005). Such behavioral manipulation may reflect aspects of sperm competition. By preventing their partner from copulating with sexual rivals and at the same time increasing the frequency with which they inseminate their partner, men may decrease the likelihood that a rival's sperm will be present in their partner's reproductive tract. In this way, men increase the likelihood that they are the genetic sire of their partner's offspring. Women, on the other hand, may surreptitiously engage in extra-pair copulations and deceive their long-term partners about offspring paternity. In this way, they are able to extract material resources from their long-term partners while extracting good genes from their paramours. As with heart rate and respiration, these behaviors are enacted by individuals without any conscious awareness of their evolutionary purpose.

Men and women may also manipulate each other's mating decisions more directly by derogating their intrasexual rivals (Buss, 1988; Buss and Dedden, 1990). Men do this by derogating other men's economic and social standing when referring to their sexual competitors as "losers", for example. They may likewise refer to other men as "assholes" who are not interested in long-term commitment. Such behaviors are used by men to dissuade women from associating with and possibly mating with other men. Women, on the other hand, are likely to derogate their intrasexual competitors' appearance and sexual behavior by criticizing other women's weight or by calling them "whores". In this way, verbal manipulation may be a uniquely human adaptation for manipulating the behavior of other humans. Thus, while molecules such as pheromones are used by many animals to manipulate one another molecularly, words and facial expressions may offer additional means of manipulation for our species, and the ability to "charm" others may be important for successful human interaction.

The use of language in mating contexts has yet to be fully accounted for by scientists interested in human reproductive behavior. In contrast to this lack of an evolutionary approach to human communication, mating calls and threats directed at sexual rivals are well demonstrated in birds and non-human primates (e.g., Krebs and Dawkins, 1984; Dawkins and Krebs, 1978). We suggest that humans use language for similar (as well as for more uniquely human) reproductive ends. Thus, linguistics may benefit from an evolutionary examination of verbal structure and function. Considered from the perspective of the extended phenotype, words may be another mechanism by which organisms hijack the minds and bodies of other organisms.

In line with research on animal signaling (Krebs and Dawkins, 1984; Dawkins and Krebs, 1978), communication between organisms is as likely to entail manipulation as it is cooperation, and perhaps more so. Articulate human speech, like birdsong, may signal an individual's genetic fitness to a prospective mate or it may relay honest information about an individual's reproductive intentions (e.g., whether a man is willing to invest in a long-term romantic relationship and in his future offspring), but it may also be used as a deceptive tactic that manipulates a prospective mate's behavior in an extended phenotypic fashion. Much of the time, the distinctions between the various uses of speech are fuzzy. Therefore, it is sometimes difficult to distinguish genuine communication from deceptive manipulation. Often, the line between the two is blurred and effective deception may itself function as a fitness indicator when acquiring mates and friends. As discussed in the following paragraphs, the ability to deceive one's self so as to better deceive others may be a naturally and sexually selected trait. Thus, individuals who successfully seduce mates or manipulate others may enjoy the same, if not greater, reproductive benefits as individuals

who are completely cooperative and genuine. Of course, no individual is completely deceptive or completely cooperative, and one's strategies may shift with changing contexts. As a social species, humans likely possess numerous cooperative adaptations (i.e., empathy, love, guilt, righteousness, and other social emotions; Nesse, 2007), but may also possess deceptive adaptations.

Ironically, deception may sometimes be employed during cooperative interaction. Perhaps the ability to deceive during courtship is itself an unconsciously communicated fitness signal. Flirtation could be a game of deception in which each party is aware of the other's sexual intentions but the indirect means by which these intentions are playfully communicated are under constant evaluation. Therefore, the ability to deceive effectively may be considered charming or sexy. Although this is a speculative hypothesis, ancestral male deception during courtship may have inflicted a cost on ancestral females, but as the coevolutionary arms race between men and women advanced, enhancement of deceptive tactics placed women under selection pressure to be attracted to men who were skilled at deception (as these men were more likely to sire reproductively successful offspring). In this way, instances of sexual conflict may sometimes evolve into instances of sexual cooperation. An examination of whether individuals are attracted to certain deceptive traits or behaviors in mates may shed light on whether deception may play an adaptive role in courtship.

Most individuals with whom we interact have reproductive interests that are in some way antithetical to ours, and so a moderate amount of deception and manipulation is expected within social contexts, particularly when individuals are genetically unrelated (relative to other individuals). Of course, the ways by which we deceive and manipulate one another vary by circumstance and type of relationship. In familial contexts, for example, there are instances in which the reproductive interests of family members do not overlap, as is evident in parent-offspring relationships (Apostolou, 2009). In such contexts, offspring may manipulate their parents for material or social resources or for the right to choose their own mates. In contrast, parents may seek to limit resources to their offspring or to influence their offspring's mating decisions to suit parental genetic interests. Thus, although individuals may be genetically related, their reproductive interests may not coincide.

Within friendship contexts, individuals depend on each other for survival and reproduction and are therefore invested in each other's reproductive well-being. This mutualism may take the form of direct or indirect reciprocity and may entail the use of friends for one's reproductive benefit. For example, men may use male friends as "wing-men" when attempting to court women. Women, in contrast, may use female friends as guards against unwanted male attention. The latter role led to the coinage of the term "cockblocker" in American slang, which refers to an individual who threatens another's access to a sexual prospect (although speculative, expressions with original reference to non-human animals, such as "ass", "cock", "pussy", "bitch", and "stud", may hint at an evolutionary function of speech for dehumanizing competitors and sexual conquests). This individual may even be a friend who is consciously or unconsciously seeking to further his or her own reproductive interests at the expense of the reproductive interests of a same-sex friend. Although direct violence may occur, other expressions of sexual rivalry, such as snide comments or humorous insults, are common in mating competition contexts. Among men, these tactics may be considered behavioral manifestations of sperm competition,

whereby men vie with other men for sexual access to women. Among women, such behaviors are employed when there is competition for access to genetically fit or resourceful men. Thus, sexual conflict may be fought within physiological, anatomical, psychological, behavioral, and verbal domains. Linguists and communication experts are encouraged to perform content analyses of context-dependent linguistic communication from an evolutionary perspective. Such analyses may go a long way toward the naturalization of linguistics and may raise our awareness of what we say and how we say it.

Self-Deception

One effective method by which humans may become better deceivers is through self-deception (von Hippel and Trivers, 2011). The evolutionary rationale for self-deception has its roots in coevolutionary arms races. As detectors improve their abilities to spot deception and punish it accordingly, deceivers come under selection pressures to devise sophisticated methods to conceal their deception (oftentimes, detection and deception are enacted by the same individual in different contexts). Believing the truth of one's own lies may help to convince others of their veracity and so self-deception may evolve. Some degree of self-deception may be active in most human relationships as it may aid in efficient human interaction, whether cooperative or competitive. Sexual relationships, in particular, may exhibit unique instances of self-deception. Parental investment theory provides clues to when self-deception is most active. A man, for example, may only be interested in a sexual encounter with a particular woman whereas that woman may desire a long-term romantic commitment. In such a scenario, it may be in the man's reproductive interests to deceive the woman into having sex with him. To the extent that he can convince himself that he wants a long-term romantic commitment, his self-deceptive behavior may help to persuade the woman that his intentions are sincere, and so self-deception may indirectly become a sexually selected trait. Likewise, a woman may consciously convince herself that she loves a man while unconsciously being drawn to his material or social resources. Further scientific study of self-deception in human mating may be useful for tracking its cooperative and competitive instances. Although behaviors may be labeled as "deceptive" or "self-deceptive", the experienced conscious phenomena may be quite genuine and indistinguishable from the experience of "true love". Therefore, when we are discussing deception, we are referring to the evolutionary rationale behind certain classes of human experience and are not judging the subjective experiences themselves. Likewise, what may be considered conflict from an evolutionary perspective may be accepted and desired from the perspective of subjective human experience.

Self-deception may also be evident in cooperative sexual relationships. For example, individuals may convince themselves that their romantic partner is more attractive, kinder, smarter, or wealthier than they actually are. Such false beliefs may help to preserve one's commitment to a sexual partner and may thus benefit both parties within a long-term sexual relationship (Maner, Gailliot, and Duvall, 2007; Maner, Gailliot, and Miller, 2009). Certain contexts are likely to trigger this type of self-deception, as when one is exposed to attractive opposite-sex individuals who threaten commitment to one's current partner. In such instances, individuals may use self-deception to downplay the attractive qualities exhibited by other, opposite-sex mating options.

With self-deception, humans can suppress their reproductive agendas from themselves. Self-deception and deception by other individuals underscore the possibility

that we all may be manipulating one another without realizing it. At times, our deceptive tactics may be detected by others as well as ourselves. When this happens, conflict between individuals and within individuals is made salient and depression, heartache, regret, or relationship dissolution may follow. Although speculative, it is possible that individuals use alcohol and other drugs to better enable self-deception (see Strom and Barone, 1993, for evidence of increased self-deception in alcoholics). Thus, when in pursuit of mates, drinking alcohol may help to lower one's inhibitions by deluding individuals about their true reproductive interests. Other substances, like cannabis, may have the opposite effect in that they enhance an individual's awareness of themselves and their motives.

Adaptive Drug Use

If certain drugs can enhance an individual's creative thinking, and if creativity is a sexually selected trait (Griskevicius, Cialdini, and Kenrick, 2006), then some mind-altering drugs may aid an individual's reproductive prospects by exposing him or her to an altered perspective of reality. Furthermore, individuals may signal their psychological stability to other individuals by consuming potent psychoactive chemicals. By engaging in such costly displays of fitness, individuals may be signaling their value to mates and acquaintances (i.e., by remaining sane, economically productive, and socially functional after ingesting LSD, an individual may gain social and sexual status). Müller and Schumann (2011) propose a similar, though not identical, hypothesis that speaks to the extended phenotypic use of drugs by humans. What Müller and Schumann suggest is that humans may use drugs as instruments to change their mental states in the service of furthering survival and reproduction-related goals. For example, alcohol ingestion promotes social disinhibition. An individual may thus use alcohol as an instrument to change his or her mental state to engage in social and sexual relationship building. Although we appreciate Müller and Schumann's argument, the physical, psychological, and social harm that drugs pose may sometimes be central to their role as costly fitness indicators, and not simply the byproducts of the beneficial aspects of drugs. Regarding sexual conflict, individuals may be using drugs as manipulative mechanisms by which they can more effectively seduce or deceive current and future sexual partners (e.g., drinking alcohol for its confidence-boosting psychological effects in social contexts—a phenomenon colloquially referred to as “liquid confidence”). Of course, there may be individual, ethnic, and cultural variations in the effects that various substances have on the brain. Furthermore, the issue of whether different psychoactive substances may serve evolved human functions remains unresolved. Obviously, some mind-altering chemicals are simply hijacking the psychological circuits by which individuals feel happiness and other positive emotions, and so individuals are maladaptively conditioned to pursue the highs associated with taking such drugs. In short, mind-altering plants and chemicals can be considered human extended phenotypes if they somehow benefit human reproductive interests (interestingly, humans can be considered extended phenotypic means by which domesticated plants reproduce themselves). We concede that more empirical work is needed to corroborate these claims, however.

The use of mind-altering substances depends on an individual's culture and the nature of mind-alteration within his or her cultural context. Many adaptations, including adaptations associated with sexual conflict, develop and are expressed with the aid of environmental input, including culture. For example, the cultural innovation of grain harvesting may have facilitated the biological innovation of alcohol tolerance. In turn, this

biological innovation may have facilitated refinement of harvesting methodology and alcohol production. With increasing population densities following the onset of agriculture and animal domestication, new genetic variants may have proliferated and have been selected to thrive within the rapidly-changing social environment of the past 10,000 years (Cochran and Harpending, 2009). Thus, genes are imbedded within cultural contexts, and both depend on each other for the evolution and development of human adaptations. In the following section, we discuss the myriad ways by which sexual conflict is culturally expressed. In particular, we focus on the lack of demarcation between biology, psychology, and culture—all are implicated in the developmental and evolutionary processes of adaptation construction. Sexual conflict is evident at cultural levels of analysis and the use of cultural capital as an extended human phenotype deserves attention.

Human Culture and Sexual Conflict

The ability to transmit non-genetic information across space and time is not unique to humans. Humans, however, have taken the relevant adaptations to extraordinary heights with the accumulation of culture. The amount of cultural information available for individual consumption increases rapidly as knowledge accumulates within and across generations. Thus, the invention of the wheel was a necessary precondition for the invention of the automobile. Just as individuals inherit genes, they inherit cultures, and shared culture may help individuals to accomplish joint tasks such as hunting or shelter construction. Cultural change is much more rapid than genetic change, yet like genes, culture may exhibit features of sexual conflict. Economic, political, religious, and media institutions provide numerous examples of human sexual conflict as manifested within the cultural sphere.

Culture may be considered an extended phenotype that is used by humans to influence the minds of other humans, whether for cooperative or competitive purposes. Thus, by listening to a certain type of music, liking a certain actor, or subscribing to a certain philosophy or worldview, individuals may form cooperative friendships with other individuals who are like-minded. In this sense, they may establish symbiotic relationships with other individuals by tailoring their extended phenotypes to others' extended phenotypes. Individuals also may seek to attract mates by advertising their reproductive fitness via costly forms of cultural display and consumer behavior (Miller, 2009). Such manipulation of cultural products, services, and information may function as an extended phenotype that influences the reproductive behavior of current and future mates. Thus, the efficient and agile use of various forms of culture to signal intelligence, social savvy, and other physical and psychological traits associated with reproductive fitness and resource-holding, may be a sexually-selected adaptation. However, such cultural signals may be deceptive if they illegitimately inflate the signaler's mate value. Genuine and deceptive signals of wealth and status (i.e., knockoff Prada bags and Rolex watches) may be used to intimidate same-sex rivals or to attract friends and mates. Whether such signals are effective in furthering the signaler's reproductive strategy is a different issue.

The expression of religious faith provides a clear example of extended phenotypic cultural processes. Individuals may subscribe to a religious worldview and enact certain religious rituals in an attempt to convey a costly signal of sacrifice to other individuals who share the same religious beliefs (Atran, 2002). For example, the cross-cultural evolution of

ritual genital mutilation, including penile circumcision and more extreme forms such as cliterodectomy, may function to culturally demonstrate commitment to one's religion or community (Wilson, 2008). Aside from immediate costs such as pain, discomfort, infection, or injury, genital mutilation may carry long-term reproductive costs as well. For instance, male reproductive efficiency may suffer as male morphological and physiological adaptations to sperm competition are physically altered. Furthermore, women who undergo cliterodectomy suffer from long-term physical, psychological, and reproductive consequences. Pain during sexual intercourse may carry the added cost of limiting female reproductive choice in addition to the obvious emotional and cognitive tolls that it takes on girls in the developing and even parts of the developed world. However, as horrible as they are, the costs of genital mutilation may function as honest signals of social commitment, with possible long-term reproductive benefits stemming from in-group reciprocity and protection.

Given how prevalent deception and manipulation is in human interaction, we posit that costly cultural signals of commitment may sometimes function as manipulative ploys by which some individuals limit the reproductive success of their rivals. It is incumbent on scholars to construct evolutionary models of the distribution of competitive and cooperative cultural strategies within a population. Thus, although culturally-induced costly signals, such as genital mutilation, may be used by individuals to communicate group commitment and initiate cooperative relationships with other group members, they also may be evidence of extended phenotypic manipulation of individuals by other individuals who want to curb their competitors' reproductive success.

Many religious institutions endorse rules and values associated with monogamy and modesty. Similarly to genital mutilation, adoption of a monogamous and sexually modest lifestyle (i.e., the wearing of the full-bodied burqa by Muslim women) may function as a costly signal of group commitment, but may also be imposed on sexual rivals to limit their reproductive success. Again, religious beliefs, rituals, and practices may function as extended phenotypes that enhance an individual's cohesion with his or her community, but also may be imposed by others to the reproductive cost of those who are indoctrinated, persuaded, or physical threatened by such beliefs, rituals, and practices. Therefore, instances of religious manipulation and hypocrisy may exemplify the deceptive use of ideology to further one's reproductive success at the expense of one's fellow group members. We encourage biologists and population geneticists to collaborate with psychologists and sociologists to produce a scientific account of cultural norms, values, beliefs, rituals, and institutions, to understand the manipulative and cooperative dynamics inherent within human culture.

The media may likewise reflect and perpetuate various manifestations of sexual conflict. Individuals may use media outlets as extended phenotypic means by which to influence the reproductive behaviors of other individuals. Although culturally novel, global communication channels such as the telephone, the television, and the internet, may be cultural tools that are useful in modern contexts of sexual conflict. According to Salmon and colleagues (Salmon, Crawford, Dane, and Zuberbier, 2008; Salmon, Crawford, and Walters, 2008; Salmon, Figueredo, and Woodburn, 2010), the high prevalence of attractive females in media such as periodicals, television, and film, may have the effect of inducing anorexia and bulimia in female consumers of this information. Anorexia and bulimia may have historically served to decrease female fertility. Thus, a woman's self-induction of

reduced fertility through a decrease in nutritional intake may have functioned to prevent impregnation by inferior men or to decrease the physical, psychological, and reproductive costs of intense female-female competition over mating opportunities. Therefore, deceptive displays of intense female-female competition (i.e., the false presentation by the media that the average woman is as attractive as Jennifer Aniston or Katy Perry) may function as extended phenotypic means by which women manipulate the reproductive systems of other women through the psychological induction of eating disorders. Whether such manipulation is intentional deserves further theoretical and empirical study. More generally, scholars should investigate whether some elements of modern culture may function as designed weaponry that is used to manipulate the behavior of sexual rivals and mates, while other cultural elements may have this effect, albeit incidentally.

Manifestations of sexual conflict depend on social context, culture, and regional demographics. Most psychological adaptations are expressed within particular cultural contexts and depend on culture for their development and functioning. Thus, the degree of patriarchy and matrilocality within a given region may determine the extent and form of sexual conflict within that region (see Figueredo et al., 2001). From an evolutionary perspective, when a culture is patriarchal, the men within that culture are embedded within a social system that benefits their evolved reproductive interests more than it benefits the reproductive interests of women. Patriarchies may develop in contexts in which sons are more likely to inherit the wealth of fathers than are daughters. As this cultural practice spreads across a society, men may form cooperative social networks based on reciprocal exchange of resources, and so an economic and social system favoring men may develop.

Social and cultural systems associated with patriarchy coevolve with genes to create male and female phenotypes that function within such cultures. Although modern feminism had its rise in the 20th century, female-female cooperation against male interests may be millions of years old. Thus, women may form close-knit ties with other women to deter unwanted male attention, and physical or sexual violence by men. Female cooperative networks, however, are usually not as large as male networks and hierarchies, and so economic and political resources become unevenly distributed in patriarchies. Women, however, may continue to possess some degree of economic power granted them by the evolution of relatively concealed ovulation. The benefiting function of concealed ovulation for women is an increase in control over reproductive decisions. Thus, women may choose to initiate long-term mating relationships with highly resourceful, yet reproductively less fit men, while having short-term sexual relationships with reproductively more fit men. Because of concealed ovulation, men who are less fit, yet resourceful, may be unable to identify when conception may have occurred and so may be manipulated by women into investing in offspring to whom they are not genetically related. Thus, women may be able to rear genetically-fit children who are cared for and protected by resourceful men.

The power of female social networks is manifest in matrilocal cultures, where daughters remain close to their mothers, and often live with them after marriage (Figueredo et al., 2001). Matrilocal cultures enable women to maintain reproductive power, as women may thus accumulate more economic resources as well as protection from their female relatives. Likewise, institutional and legal means of extracting child support from men may further alleviate the reproductive burdens felt by women (see Shackelford, Weekes-Shackelford, and Schmitt, 2005). Thus, although individual men and women may be looking out for their own reproductive interests, social practices and institutions may form

that either favor most men or most women within a given society. These cultural practices coevolve with genes (Laland, Odling-Smee, and Myles, 2010) and lead to the evolution and development of extended phenotypes that are adapted to function within cooperative and competitive intrasexual networks.

In cases of culture, individual-level sexual conflict is evident at the level of social structures, institutions, practices, and beliefs. Thus, gender politics may be a different level of analysis for the same phenomena that can be understood from other theoretical perspectives, such as sperm competition, parental investment, and sexual selection. We encourage sociologists, political scientists, cultural anthropologists, and feminism theorists to enrich their theoretical understanding of culture with more evolutionarily-oriented perspectives. Likewise, biologically-minded scholars in the natural and social sciences may become better informed by extending their perspectives into established structures within the humanities, as well as more culturally-concerned disciplines within the social sciences. Not all sub-disciplines or theoretical and empirical perspectives may experience a seamless synthesis, but this should not dissuade communication across different fields of study. Although some tensions may persist, all scholars may benefit from such an enlargement of intellectual scope.

Concluding Remarks

Sexual conflict pervades many layers of human experience and results from millions of years of coevolution between the sexes. Thus, male-female arms races function across different levels of analysis, from molecules to societies and cultures. Sexual conflict may even be exhibited within individuals. Research on genetic imprinting (Patten and Haig, 2008; Haig, 2006; Úbeda and Haig, 2003; Haig, 2000) indicates that a father's genes and a mother's genes do not always coincide peacefully within an individual offspring. Thus, certain behaviors on the part of the offspring—such as extracting more nutrients and resources from the mother than the mother is willing to apportion—may partly be explained by the action of paternal genetic interests vying for control of the offspring's behavior against maternal genetic interests, and vice versa. Our children, therefore, may function as extended phenotypes of ourselves, just as we may function as extended phenotypes of our own mothers and fathers. In a more general sense, individuals may be imparting their offspring with a legacy of sexual conflict. The offspring, in turn, will impart the legacy of their sexual conflict to their own offspring. This conflict is felt through and through, not just with regard to other individuals, whether mates, friends, or sexual rivals, but also with regard to oneself.

The internal struggles of a man's motivation to have sex with novel sexual partners, against his motivation to attract and maintain a long-term partner, and a woman's struggles between her desire to maintain a loving and nurturing relationship with an investing husband, and her sexual desires for other, more attractive men, demonstrate the pervasiveness of internal sexual conflict. In a way, our culture may provide the psychological tools by which internal and external forms of sexual conflict are played out and perceived. For example, one's preferences for long-term romantic commitment may motivate interest in cultural or religious traditions wherein monogamy is venerated. On the other hand, one's persistent desire for casual sexual relationships may find cultural expression through pornography or various fetishes.

Although there are manifestations of sexual conflict that are morally abhorrent, such as misogyny, spousal abuse, child neglect, rape, and partner homicide, other manifestations of sexual conflict may make life quite interesting. The mating game, in particular, may function as an adult playground wherein one must battle romantic rivals and aspects of oneself, and seduce future lovers with one's looks, wits, status, possessions, and charm. Likewise, games of strategic deception and manipulation, if not taken to an extreme, may add much spice and excitement into a couple's love life.

Evolutionary conflicts are inescapable, whether between parasites and hosts, or between men and women. Many of our physical and psychological traits exist because they enabled our ancestors to outmaneuver romantic rivals and gain access to mates. The future manifestations of sexual conflict, either within an individual's life, or within a particular culture, are unpredictable. However, the presence of sexual conflict may still be discerned across political, economic, cultural, and personal domains.

Received 01 August 2011; Revision submitted 25 November 2011; Accepted 26 November 2011

References

- Anderson, M.J., Chapman, S.J., Videan, E.N., Evans, E., Fritz, J., Stoinski, T.S., Dixon, A.F., and Gagneux, P. (2007). Functional evidence for differences in sperm competition in humans and chimpanzees. *American Journal of Physical Anthropology*, *134*, 274-280.
- Apostolou, M. (2009). Parent-offspring conflict over mating: The case of short-term mating strategies. *Personality and Individual Differences*, *47*, 895-899.
- Arnqvist, G., and Rowe, L. (2005). *Sexual conflict*. Princeton, NJ: Princeton University Press.
- Atran, S. (2002). *In gods we trust: The evolutionary landscape of religion*. Oxford: Oxford University Press.
- Baker, R.R., and Bellis, M.A. (1993a). Human sperm competition: Ejaculate adjustment by males and the function of masturbation. *Animal Behaviour*, *46*, 861-885.
- Baker, R.R., and Bellis, M.A. (1993b). Human sperm competition: Ejaculate manipulation by females and a function for the female orgasm. *Animal Behaviour*, *46*, 887-909.
- Baker, R.R., and Bellis, M.A. (1995). *Human sperm competition: Copulation, masturbation, and infidelity*. London: Chapman and Hall.
- Bjorklund, D.F., and Pellegrini, A.D. (2002). *The origins of human nature: Evolutionary developmental psychology*. Washington, DC: American Psychological Association.
- Bleske-Rechek, A., and Buss, D.M. (2006). Sexual strategies pursued and mate attraction tactics deployed. *Personality and Individual Differences*, *40*, 1299-1311.
- Bukowski, R., Smith, G.C.S., Malone, F.D., Ball, R.H., Nyberg, D.A., Comstock, C.H., Hankins, G.D.V., Berkowitz, R.L., Gross, S.J., Dugoff, L., Craigo, S.D., Timor-Tritsch, I.E., Carr, S.R., Wolfe, H.M., and D'Alton, M.E. (2007). Human sexual size dimorphism in early pregnancy. *American Journal of Epidemiology*, *165*, 1216-1218.
- Burt, A., and Trivers, R.L. (2006). *Genes in conflict: The biology of selfish genetic elements*. Cambridge: Harvard University Press.

- Buss, D.M. (1988). The evolution of human intrasexual competition: Tactics of mate attraction. *Journal of Personality and Social Psychology*, *54*, 616-628.
- Buss, D.M., and Dedden, L.A. (1990). Derogation of competitors. *Journal of Social and Personal Relationships*, *7*, 395-422.
- Buss, D.M., Shackelford, T.K., Kirkpatrick, L.A., Choe, J.C., Lim, H.K., Hasegawa, M., Hasegawa, T., and Bennett, K. (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., and Quinsey, V.L. (2009a). Individual differences in the propensity for partner sexual coercion. *Sexual Abuse: A Journal of Research and Treatment*, *21*, 111-129.
- Camilleri, J.A., and Quinsey, V.L. (2009b). Testing the cuckoldry risk hypothesis of partner sexual coercion in community and forensic samples. *Evolutionary Psychology*, *7*, 164-178.
- Chang, L., Wang, Y., Shackelford, T.K., and Buss, D.M. (2011). Cultural evolution and cultural continuity across a quarter of a century: An illustration using Chinese mate preferences. *Personality and Individual Differences*, *50*, 678-683.
- Chartrand, T. L., and Bargh, J. A. (1999). The chameleon effect: The perception-behavior link and social interaction. *Journal of Personality and Social Psychology*, *76*, 893-910.
- Clutton-Brock, T.H., and Parker, G.A. (1992). Potential reproductive rates and the operation of sexual selection. *The Quarterly Review of Biology*, *67*, 437-456.
- Cochran, G., and Harpending, H. (2009). *The 10,000 year explosion: How civilization accelerated human evolution*. New York: Basic Books.
- Cornwell, R.E., and Perrett, D.I. (2008). Sexy sons and sexy daughters: The influence of parents' facial characteristics on offspring. *Animal Behavior*, *76*, 1843-1853.
- Darwin, C. (1871). *The descent of man, and selection in relation to sex*. London: Charles Murray.
- Dawkins, R. (1982). *The extended phenotype*. Oxford: W. H. Freeman.
- Dawkins, R., and Krebs, J.R. (1978). Animal signals: Information or manipulation? In J.R. Krebs and N.B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (pp. 282-309). Oxford, UK: Blackwell Scientific Publications.
- Dawkins, R., and Krebs, J.R. (1979). Arms races between and within species. *Proceedings of the Royal Society of London B*, *205*, 489-511.
- Del Giudice, M. (2009). Sex, attachment, and the development of reproductive strategies. *Behavioral and Brain Sciences*, *32*, 1-67.
- Evans, S.M. (2009). Sons, daughters, and patriarchy: Gender and the 1968 generation. *American Historical Review*, *114*, 331-347.
- Figueredo, A.J., Corral-Verdugo, V., Frías-Armenta, M., Bachar, K.J., White, J., McNeill, P.L., Kirsner, B.R., Castell-Ruiz, I.P. (2001). Blood, solidarity, status, and honor: The sexual balance of power and spousal abuse in Sonora, Mexico. *Evolution and Human Behavior*, *22*, 295-328.
- Gallo, P.S., and McClintock, C.G. (1965). Cooperative and competitive behavior in mixed-motive games. *The Journal of Conflict Resolution*, *9*, 68-78.
- Gallup, G.G., Burch, R.L., and Mitchell, T.J.B. (2006). Multiple mating, self-semen displacement, and timing of in-pair copulations. *Human Nature*, *17*, 253-264.

- Gallup, G.G. Jr., Burch, R.L., and Platek, S.M. (2002). Does semen contain antidepressant properties? *Archives of Sexual Behavior*, *39*, 289-291.
- Gelstein, S., Yeshurun, Y., Rozenkrantz, L., Shushan, S., Frumin, I., Roth, Y., and Sobel, N. (2011) Human tears contain a chemosignal. *Science*, *331*, 226-230.
- Getty, T. (2002). Signaling health versus parasites. *The American Naturalist*, *159*, 363-371.
- Goetz, A. T., and Shackelford, T. K. (2006). Sexual coercion and forced in-pair copulation as sperm competition tactics in humans. *Human Nature*, *17*, 265-282.
- Goetz, A.T., and 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., and Camilleri, J.A. (2008). Proximate and ultimate explanations are required for a comprehensive understanding of partner rape. *Aggression and Violent Behavior*, *13*, 119-123.
- Goetz, A.T., Shackelford, T.K., Weekes-Shackelford, V.A., Euler, H.A., Hoier, S., Schmitt, D.P., et al. (2005). Mate retention, semen displacement, and human sperm competition: a preliminary investigation of tactics to prevent and correct female infidelity. *Personality and Individual Differences*, *38*, 749-763.
- Gottschall, J.A., and Gottschall, T.A. (2003). Are per-incident rape-pregnancy rates higher than per-incident consensual pregnancy rates? *Human Nature*, *14*, 1-20.
- Griskevicius, V., Cialdini, R.B., and Kenrick, D.T. (2006). Peacocks, Picasso, and parental investment: The effects of romantic motives on creativity. *Journal of Personality and Social Psychology*, *91*, 63-76.
- Haig, D. (2000). The kinship theory of genomic imprinting. *Annual Review of Ecology and Systematics*, *31*, 9-32.
- Haig, D. (2006). Intragenomic politics. *Cytogenetic and Genome Research*, *113*, 68-74.
- Haselton, M.G., and 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.
- Haselton, M.G., Buss, D.M., Oubaid, V., and Angleitner, A. (2005). Sex, lies, and strategic interference: The psychology of deception between the sexes. *Personality and Social Psychology Bulletin*, *31*, 3-23.
- Holland, B., and Rice, W.R. (1998). Perspective: Chase-away sexual selection: Antagonistic seduction versus resistance. *Evolution*, *52*, 1-7.
- Kaighobadi, F., Shackelford, T.K, and Goetz, A.T. (2009). From mate retention to murder: Evolutionary psychological perspectives on men's partner-directed violence. *Review of General Psychology*, *13*, 327-334.
- Khallad, Y. (2005). Mate selection in Jordan: Effects of sex, socio-economic status, and culture. *Journal of Social and Personal Relationships*, *22*, 155-168.
- Krebs, J.R., and Dawkins, R. (1984). Animal signals: Mind reading and manipulation. In J.R. Krebs and N.B. Davies (Eds.), *Behavioral ecology: An evolutionary approach* (pp. 380-402). Oxford, UK: Blackwell Scientific Publications.
- Kruger, D.J. (2008). Male financial consumption is associated with higher mating intentions and mating success. *Evolutionary Psychology*, *6*, 603-612.
- Kuznar, L.A. (2001). Ecological mutualism in Navajo corrals: Implications for Navajo environmental perceptions and human/plant coevolution. *Journal of Anthropological Research*, *57*, 17-39.

- Laland, K.N. (2008). Exploring gene-culture interactions: Insights from handedness, sexual selection and niche-construction case studies. *Philosophical Transactions of the Royal Society B*, *363*, 3577-3589.
- Laland, K.N., Odling-Smee, J., and Myles, S. (2010). How culture shaped the human genome: Bringing genetics and the human sciences together. *Nature Reviews: Genetics*, *11*, 137-148.
- Lessells, C. (Kate). M. (2006). The evolutionary outcome of sexual conflict. *Philosophical Transactions of the Royal Society B*, *361*, 301-317.
- Maner, J.K., Gailliot, M.T., and DeWall, C.N. (2007). Adaptive attentional attunement: Evidence for mating-related perceptual bias. *Evolution and Human Behavior*, *28*, 28-36.
- Maner, J.K., Gailliot, M.T., and Miller, S.L. (2009). The implicit cognition of relationship maintenance: Inattention to attractive alternatives. *Journal of Experimental Social Psychology*, *45*, 174-179.
- Miller, G.F. (2000). *The mating mind: How sexual choice shaped the evolution of human nature*. London: Heinemann.
- Miller, G.F. (2009). *Spent: Sex, evolution, and consumer behavior*. New York: Viking.
- Miner, E.J., and Shackelford, T.K. (2010). Mate attraction, retention, and expulsion. *Psychothema*, *22*, 9-14.
- Møller, A.P., and Cuervo, J.J. (2003). Sexual selection, germline mutation rate and sperm competition. *BMC Evolutionary Biology*, *3*, 6-16.
- Müller, C.P., and Schumann, G. (2011). Drugs as instruments: A new framework for non-addictive psychoactive drug use. *Behavioral and Brain Sciences*, *34*, 293-347.
- Nesse, R.M. (2007). Runaway social selection for displays of partner value and altruism. *Biological Theory*, *2*, 143-155.
- Olson, L.E., and Blumstein, D.T. (2009). A trait-based approach to understand the evolution of complex coalitions in male mammals. *Behavioral Ecology*, *20*, 624-632.
- Puts, D.A., and Dawood, K. (2006). The evolution of female orgasm: Adaptation or byproduct? *Twin Research and Human Genetics*, *9*, 467-472.
- Patten, M.M., and Haig, D. (2008). Reciprocally imprinted genes and the response to selection on one sex. *Genetics*, *179*, 1389-1394.
- Ridley, M. (1993). *The red queen: Sex and the evolution of human nature*. New York: Viking.
- Salmon, C., Crawford, C., Dane, L., and Zuberbier, O. (2008). Ancestral mechanisms in modern environments: impact of competition and stressors on body image and dieting behavior. *Human Nature*, *19*, 103-117.
- Salmon, C., Crawford, C.B., and Walters, S. (2008). Anorexic behaviour, female competition, and stress: Developing the Female Competition Stress Test. *Evolutionary Psychology*, *6*, 96-112.
- Salmon, C., Figueredo, A.J., and Woodburn, L. (2010). Life history strategy and disordered eating behavior. *Evolutionary Psychology*, *7*, 585-600.
- Shackelford, T.K., and Buss, D.M. (1996). Betrayal in mateships, friendships, and coalitions. *Personality and Social Psychology Bulletin*, *22*, 1151-1164.

- Shackelford, T. K., Goetz, A. T., Guta, F. E., and Schmitt, D. P. (2006). Mate guarding and frequent in-pair copulation in humans: Concurrent or compensatory anti-cuckoldry tactics? *Human Nature, 17*, 239-252.
- Shackelford, T.K., LeBlanc, G.J., Weekes-Shackelford, V.A., Bleske-Rechek, A.L., Euler, H.A., and Hoier, S. (2002). Psychological adaptation to human sperm competition. *Evolution and Human Behavior, 23*, 123-138.
- Shackelford, T.K., Weekes-Shackelford, V.A., and Schmitt, D.P. (2005). An evolutionary perspective on why men refuse or reduce their child support payments. *Basic and Applied Social Psychology, 27*, 297-306.
- Strom, J., and Barone, D.F. (1993). Self-deception, self-esteem, and control over drinking at different stages of alcohol involvement. *Journal of Drug Issues, 23*, 705-714.
- Tooke, W., and Camire, L. (1991). Patterns of deception in intersexual and intrasexual mating strategies. *Ethology and Sociobiology, 12*, 345-364.
- Trivers, R.L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man, 1871-1971* (pp. 136-179). Chicago: Aldine-Atherton.
- Úbeda, F., and Haig, D. (2003). Dividing the child: Genomic imprinting and evolutionary games. *Genetica, 117*, 103-110.
- Urano, S., Yamaguchi, S., Yamato, S., Takahashi, S., and Yusa, Y. (2009). Evolution of dwarf males and a variety of sexual modes in barnacles: An ESS approach. *Evolutionary Ecology Research, 11*, 713-729.
- von Hippel, W., and Trivers, R. (2011). The evolution and psychology of self-deception. *Behavioral and Brain Sciences, 34*, 1-16.
- West, S.A., Griffin, A.S., and Gardner, A. (2007). Evolutionary explanations for cooperation. *Current Biology, 17*, R661-R672.
- Wilson, C.G. (2008). Male genital mutilation: An adaptation to sexual conflict. *Evolution and Human Behavior, 29*, 149-164.
- Zahavi, A. (1975). Mate selection: A selection for a handicap. *Journal of Theoretical Biology, 53*, 205-214.
- Zakharova, L.A. (2009). Evolution of adaptive immunity. *Biology Bulletin, 36*, 107-116.