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Human Precopulatory Sexual Conflict



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Introduction

In sexually reproducing species, some degree of cooperation between the sexes is an inevitable result of the dependence of each sex on the other for reproduction. Some degree of conflict should also be expected, however, because each member of a reproducing pair has conflicting genetic interests. This conflict is termed "sexual conflict" and is responsible for the evolution of an arms race, or antagonistic coevolution (Rowe and Day 2006), between the sexes, whereby the evolution of offensive and defensive adaptations in one sex creates the selection pressure for the evolution of counter-adaptations in the other and so on.

The two major categories of sexual conflict are "intralocus" and "interlocus" sexual conflict (Parker 2006; Rowe and Day 2006). Intralocus sexual conflict describes the contradictory effects of two autosomal alleles at a particular genetic locus within an individual. For example, males are usually physically stronger than females due to the selective effects of male-male competition on size and strength (Frontera et al. 1991). Conflict may therefore occur between a male-linked allele associated with greater physical strength and a female-linked allele associated with lesser physical strength. Interlocus sexual conflict describes conflict between sex-linked genes at different loci, usually manifested as conflict between the reproductive strategies of individual males and females. Both types of sexual conflict can be *precopulatory* (i.e., occurring prior to mating).

Precopulatory sexual conflict describes the costs that individuals of one sex inflict on individuals of the other sex prior to copulation. This is the period during which males and females are typically evaluating the suitability of their prospective mate(s). Because females invest more physiological and behavioral resources in childcare (Trivers 1972), they evolve strategies aimed at securing more parental investment from males than males are willing to apportion. Males, on the other hand, evolve strategies aimed at avoiding parental investment in favor of pursuing casual sexual encounters with multiple females. Therefore, much of precopulatory sexual conflict consists in the tension between female reluctance and male eagerness to engage in sexual intercourse.

Sexual conflict may create opportunities for sexual cooperation. For example, when male aggression is correlated with genetic worth or ability to secure resources, it may benefit a female to mate with a male exhibiting aggression even if he harms her in the process. The reason for this is that any son sired by such a male will likely inherit his father's traits (Eberhard 2005). If the son's aggression helps him to spread his mother's

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genes, such a benefit may outweigh a prospective mother's cost of mating with an aggressive male. Even if females are only benefited by male aggression because other females find aggressive males more attractive (a phenomenon referred to as the "sexy son" hypothesis; see Gwinner and Schwabl 2005), a female preference for aggressive males may evolve. According to Eberhard (2005), instances of sexual conflict may provide "the original 'nudges' that set off rounds of traditional Fiesherian runaway female choice" (p. S21). Thus, what may be an instance of sexual conflict may actually be, either in whole or in part, an instance of sexual cooperation. Albeit speculative, the courtship rituals of some species may reflect such conflict-turned-cooperation scenarios, as suggested by the manner in which a female resists a persistent suitor only to accept his advances once he has "proven" himself worthy (see Crean et al.'s 2000, discussion of female mate choice for large males in contexts of premating struggles between male and female seaweed flies). Another possibility is that male aggression is, in fact, costly to females, but the costs pale in comparison to the costs of resistance, which may involve harm or even death. As such, instances of sexual conflict may contain some degree of compromise and cooperation (Crean et al. 2000; Crean and Gilburn 1998; though see Parker's 2006, discussion of the decreased theoretical and empirical likelihood of sexual "concurrence" in comparison to sexual conflict).

Sexual Conflict Before Puberty

Sexual conflict pervades the entirety of the human lifespan. Even children and juveniles experience its effects. A good example of this is the practice of "*sim-pua*" marriages in Medieval China. *Sim-pua*, or "little daughter in law" practice, involved the adoption of a young, prepubescent girl by the parents of an infant son. The fact that such marriages were often unsuccessful is often presented in evolutionary discussions as an example of the "Westermarck effect" (Wolf 2005), which describes the activation of evolved incest avoidance mechanisms that prevent individuals who

grow up in the same household from being sexually attracted to one another. *Sim-pua* marriages are also a good example of sexual conflict between the reproductive interests of male children and female children. Insuring the virginity and betrothal of a prospective daughter-in-law to one's son may have conflicted with the reproductive interests of the daughter-in-law if the son in question was of low genetic worth or if he and his family were less wealthy than they claimed to be.

Similar conflicts may occur in cultures that practice bride pricing and dowries. For example, parents who are vying for the betrothal of their son or daughter to a girl or boy whose parents are asking for a bride price or dowry may exaggerate the actual worth of their son or daughter (who may turn out to be unhealthy, unkind, or lazy) or their resources (e.g., the livestock turn out to be sick, the land turns out to not be arable). In such instances, the reproductive interests of a girl may already be in conflict with the reproductive interests of a boy, even if those interests are represented by parents rather than the boy or girl in question. In effect, shared genes - and, hence, shared reproductive interests - among family members allow sexual conflicts between individuals to expand into conflicts between families.

An intriguing possibility is that unique imitative and linguistic abilities allowed humans to erect entire cultural systems as extended phenotypic expressions (see Dawkins 1982) of sexual conflict. In aforementioned examples of sim-pua marriages, dowries, and bride pricing, cultural traditions and explicit and implicit rules, norms, and principles are passed down alongside biologically older adaptations for sexual conflict. Certain Middle Eastern and African cultures, for example, enforce strict codes regulating interactions between men and women. Usually, the heavier burden is placed on girls and women. A girl who speaks to the wrong boy or a woman who wears something immodest is risking being harmed and even killed by a father, brother, husband, or entire community for having violated a law or tradition. An example of a more harmful cultural manifestation of sexual conflict is female genital mutilation, a cultural practice aimed at limiting a girl's sexuality by associating intercourse with excruciating physical pain. Effectively, such cultural traditions may be examples of society-spanning expressions of male adaptations for sexual conflict. Although a young girl and her parents perceive the alternative as much worse (i.e., prohibition from marriage and possible excommunication), female genital mutilation may nonetheless be situated in a context that favors male reproductive interests such as sexual proprietariness and decreased cuckoldry risk stemming from female pain during intercourse (Wilson and Daly 1998, 1993).

When examining such examples of culturespanning sexual conflict, it is important to note that male adaptations to sexual conflict might benefit some women (e.g., the male's female kin; Gwinner and Schwabl 2005) just as female adaptations to sexual conflict might benefit some men (e.g., the female's male kin). Thus, it is no surprise that women often enforce restrictions and punishments on girls and other women in cultures advocating female decency (BBC Monitoring 2016), just as it is no surprise that men enforce the criminalization and punishment of rapists and domestic abusers in cultures that value women's rights. This point also highlights the importance of not thinking of sexual conflict as a dualistic struggle between all men and all women. Humans are genetically heterogeneous creatures who can compete and cooperate with others regardless of their biological sex. As such, sexual conflict and its cultural expressions are simply the manifestations of the reproductive interests of individuals and not some universal patriarchies or matriarchies. From an evolutionary perspective, adaptations to sexual conflict are built by the differential survival and reproduction of individual men and women rather than by all men outcompeting all women or vice versa.

Sexual Conflict After Puberty

Men's sexual eagerness and women's sexual reluctance. The conflict between male eagerness and female reluctance to engage in casual sexual encounters is most clearly on display in a now classic study by Clark and Hatfield (1989). In the study, female college students were randomly approached by a male confederate, and male students were randomly approached by a female confederate who made various sexual propositions, ranging from less explicit (i.e., "Would you go out tonight?") to more explicit (i.e., "Would you go to bed with me?"). (Note that male and female confederate attractiveness was controlled for.) Unsurprisingly, all women refused the more explicit sexual offer, whereas a majority of men accepted it. It is easy to interpret Clark and Hatfield's findings in terms of sexual conflict dynamics. Specifically, by engaging in casual sex with the wrong man, a woman risks getting pregnant and being abandoned by the man – an outcome whose time and energy costs weigh heavily on the woman and her future offspring. A reluctance to engage in casual sex therefore evolved as part of women's arsenal in sexual conflict with men. Men, on the other hand, are reluctant to pass up any sexual opportunity, as doing so might jeopardize their reproductive interests - which are marked by increasing the quantity, as opposed to the quality, of sexual partners.

Men's eagerness to engage in sexual behavior is often in conflict with female reluctance. According to Haselton and Buss's "error management theory" (Haselton and Buss 2000), men are expected to maximize realized sexual opportunities and minimize missed sexual opportunities. In practice, this leads to men's overperception of women's sexual interest, even if it is nonexistent. Such overperceptions were responsible for an eventual lawsuit on the part of women employed at the Safeway supermarket chain who were told to smile and act friendly toward all customers (Haselton 2003). The problem was that some male customers interpreted the female employees' friendliness in sexual terms, which led to many awkward and a few relatively serious consequences, such as harassment. Along similar lines, Abbey (1982) revealed that male participants are more likely than female participants to report sexual intent in an actress's performance (but see Perilloux and Kurzban 2015, for an alternative interpretation of error management theory).

Women must also contend with error management, but their dilemma concerns maximizing opportunities to find a committed long-term partner and minimizing the possibility of falling for and possibly getting pregnant by - men who are not interested in commitment or paternal care. In practice, women realize this strategy with an enduring skepticism toward men's professions of love, devotion, and commitment (Haselton and Buss 2000). Men can presumably override this skepticism only if they lavish a sufficient amount of material and emotional investment on women to prove their honorable intentions. Inevitably, however, some men who are truly willing to commit are often passed over by women too skeptical to accept their shows of devotion as being genuine. Thus, women's underperception of men's commitment is often in conflict with men's eagerness to profess commitment (whether actual or false) in order to obtain or maintain sexual access to women.

In the context of romantic relationships, men's sexual eagerness and women's sexual reluctance manifest itself in sex differences in the preferred timing of sexual intercourse (Buss and Schmitt 1993). In general, a man is ready to have sex a week or so after first meeting a woman. Women, however, only reach the point of sexual readiness about 6 months into the relationship. This difference in the preferred timing of sex probably leads to many instances of precopulatory sexual conflict marked by men's pressuring of women into sexual activity and women's prolonged reluctance to acquiesce. Such divergent sexual strategies also fuel men's increased interest both in pornography and prostitution (Ellis and Symons 1990; Schmitt 2003), both of which may exacerbate existing tensions within a relationship by causing women to question men's level of commitment. On their part, women's increased interest in romance novels and films may create unrealistic expectations for men by causing women to demand greater displays of love and commitment than their partners can provide, which only adds to men's costs of pursuing sexual relationships with women.

Deception in the mating market. Sexual conflict in human mating often centers on men's and women's mate preferences. One such preference is the desire for physically attractive mates (Buss 1989; Jones et al. 2001). Other preferences include a desire for mates who have resources and a desire for mates who are capable of longterm romantic commitment (Buss 1989; Haselton et al. 2005). Evolutionarily, attractiveness is associated with genetic health and fertility (Jones et al. 2001; Pflüger et al. 2012). When judging the physical attractiveness of prospective mates, individuals are specifically attuned to features such as symmetry, averageness, clear skin, voluminous hair, and youthful eyes (Apicella et al. 2007; Fink et al. 2008; Gangestad et al. 1994; Mesko and Bereczkei 2004; Peshek et al. 2011). All of these features can be passed on to offspring and are the most prize-worthy outcomes of short-term mating, reproductively speaking. Having resources may likewise be associated with having good genes, but is also associated with being able to provide for one's offspring. Similarly, being willing to commit to, or form a pair-bond with, a romantic partner signals a prospective partner's willingness to stick around long enough to invest in any resultant offspring. As such, the ability and willingness to invest resources in one's partner and one's offspring are characteristics that are usually sought for in long-term mates.

Males tend to pursue a short-term mating strategy to a greater extent than females (even though the males of some species, such as human males, do invest in long-term mating and paternal care) (Trivers 1972). This is why men are generally more interested in prospective mates' physical attractiveness than are women (Buss 1989), whether in short-term or long-term relationships. Men's mate preferences focus on women's physical features such as youth, breast size, lumbar curvature, a 0.7 waist-to-hip ratio (i.e., an "hourglass" shape), and facial femininity (Burriss et al. 2011; Buss 1989; Karremans et al. 2010; Lewis et al. 2015; Zelazniewicz and Pawlowski 2011). Whereas women are generally more interested in long-term relationships and value characteristics such as maturity, ambition, industriousness, kindness, and commitment (Buss 1989; Buss and Schmitt 1993; Haselton et al. 2005; Lukaszewski and Roney 2010), they, too, engage in short-term mating and value men's characteristics such as height, masculinity, symmetry, and dominance (Gangestad et al. 2004; Pawlowski and Jasienska 2005; Penton-Voak et al. 2003; Quist et al. 2012). In general, women seek short-term mates either prior to finding committed partners or in order to procure good genes while deceiving existing committed partners (Pillsworth and Haselton 2006). In other words, sometimes a prospective mother's strategy may be to make sure that her offspring thrive in the genetic lottery regardless of who, if anyone, is providing paternal care.

When it comes to sexual conflict, men and women deceive each other about different things. This is suggested by Haselton et al.'s (2005) investigation into which types of deception men and women are differentially upset about. In general, men are more upset about women's false promises of sex (i.e., being "led on"), whereas women are more upset about men's exaggeration of their social status, resources, and willingness to commit. Although both short-term- and longterm-oriented men are upset about being led on, short-term-oriented men experience greater discomfort over this type of deception, which is likely a reflection of their greater interest in casual sexual opportunities with multiple women. Women's greater distress over men's exaggeration of commitment and - especially for women seeking long-term mates - inflation of status and resources suggests that women are primarily interested in finding long-term mates who are able and willing to provide paternal care. In short, what Haselton et al.'s study suggests is that deception is an integral aspect of human precopulatory sexual conflict and that men and women deceive each other by pretending to cooperate with each other's reproductive strategies.

Intrasexual competition and sexual conflict. When adaptations to sexual conflict are directed at other individuals whose behavior is likely to augment the reproductive success of an individual's would-be partner, it is helpful to consider this a form of *indirect* sexual conflict (see Thompson and Alvarado 2012, for a similar distinction between direct and indirect sexual coercion and the evolution of different adaptations in relation to each). All of the aforementioned examples constitute direct sexual conflict wherein males and females target their offensive and defensive adaptations at one another. Indirect sexual conflict entails that men and women target their attacks at their reproductive rivals. So, for example, when a male or female derogates or drives off an intended mate's other, otherwise valued, mating prospect, it can be said that the male or female is engaging in indirect sexual conflict. Although successfully driving off a competitor may indicate something about the successor's reproductive value, derogating rivals (which depends on cognitive and verbal abilities possessed by most humans) and seizing an opportunity to sabotage them (which depends highly on chance) are strategies that can be pursued by individuals of high and low reproductive value alike. Individuals of low reproductive value may even depend on these strategies to a greater extent than they do on strategies such as intrasexual physical combat and direct partner seduction - strategies that are more reflective of high reproductive value (see Miner et al. 2009b, for evidence that men of low mate value may rely on cost-inflicting, as opposed to benefitprovisioning, mate retention tactics).

Direct and indirect sexual conflict are often indistinguishable, as driving away reproductive rivals of high mate value inflicts a direct cost on one's intended future mate. Sometimes, the cost is also felt by the individual engaging in such aggressive tactics, in which case it is a nonadaptive byproduct of sexual conflict or intrasexual competition. For example, the mere act of battling or driving off a reproductive rival may be fatal to a potential mate, as instanced by the occasional killing of a female red-sided garter snake, recently arisen from hibernation, by a pack of male garters that coil up into a swarm of aggressive reptiles wrestling one another in a destructive melee that crushes the fought-over female in its depths (Arnqvist and Rowe 2013, pp. 49–50). The distinction between direct and indirect sexual conflict is valuable, however, because anticipating the two types of conflict allows scientists to formulate testable hypotheses about specific adaptations that may have been differentially selected for either type.

One tactic that humans use to drive away reproductive rivals is competitor derogation (Buss and Dedden 1990). In general, men are more prone to disparaging a male rival's income and willingness to commit, whereas women are more prone to disparaging a female rival's looks and sexual behavior (Buss and Dedden 1990; Fisher 2004; Schmitt and Buss 1996). The reason for this is that women prefer mates who have – or have the potential to acquire - resources and who are willing to enter into a committed relationship, whereas men prefer mates who are attractive and, in the context of a long-term relationship, are sexually faithful (an important factor for men given the evolutionarily recurrent threat of investing in genetically unrelated offspring). By derogating competitors, men and women are essentially engaging in competition with their reproductive rivals by disparaging them to their prospective mates. This competition is not as extreme as a barroom brawl, but it is competition nonetheless, and may engage multiple cognitive adaptations.

On the one hand, if a derogator is correct about her rival's deficiencies (e.g., her rival is not as young as she claims to be), then this may be valuable information for her prospective mate, who may take appropriate steps to avoid mating with her rival. If the derogator is higher in mate value than her rival, then her derogation of her rival's age was an instance of cooperation between her and her prospective mate. On the other hand, if her rival is in fact as young as she claims to be, then the derogator is inflicting a cost on her prospective mate by denying him a reproductively valuable mating opportunity. Such instances of competitor derogation can therefore be considered as specialized weapons employed by men and women in the context of sexual conflict.

Various emotional adaptations are likewise aimed at deterring one's future or current mate from mating with, or investing in, one's reproductive rivals. One such set of adaptations is associated with the experience of romantic jealousy. In general, men are much more likely to experience sexual jealousy, whereas women are much more likely to experience emotional jealousy (Buss et al. 1992). Sexual jealousy is felt as discomfort at the prospect that an intended or current romantic partner has had sex with someone else. Men's greater susceptibility to this form of jealousy arises from their vulnerability to cuckoldry (i.e., an instance of a female having sex with a male who is not her long-term partner). Humans, along with only a few other species, are marked by both maternal and paternal care. In most cultures, paternal care is an essential component of the total care received by a child (though it still does not measure up to the level of care provided by mothers). As a result of the high cost of paternal care, natural selection designed various psychological adaptations to ensure that a man does not waste resources on genetically unrelated children. One such adaptation is sensitivity to any prospect of sexual infidelity, i.e., sexual jealousy. Due to the recurrent evolutionary costs of relationship abandonment and a redirection of resources to other women and their children, however, women are more prone to emotional jealousy, which is felt as discomfort at the prospect that one's intended or current romantic partner has formed an emotional attachment (i.e., has fallen in love) with a reproductive rival. Both forms of jealousy may inflict costs on current or future romantic partners and can therefore be thought of as evolved, specialized emotions evoked in the context of sexual conflict.

As with many other sexually reproducing species, humans seek to neutralize their reproductive rivals by, among other methods, simply restricting their proximity to an intended mate, a technique known as "mate guarding." This can be done either by fighting off approaching rivals or by monitoring the movements of, or secluding, a prospective or current mate in order to make sure that he or she has no opportunity for a dalliance with a reproductive rival. Because males are typically stronger than females, they are more successful at mate guarding their prospective or current mate with threats and actual uses of force. Humans, for example, exhibit a continuum of mate-guarding behaviors, from benefitprovisioning, whereby individuals bestow gifts, care, and affection on partners in order to keep them happy, to cost-inflicting, whereby

individuals inflict verbal and physical abuse on partners to deter them from ending the relationship or to punish them for actual or perceived infidelity (Holden et al. 2014; Miner et al. 2009a, b). Note that, although research on mate guarding mostly examines interactions within existing sexually active relationships (hence the term *mate* guarding), similar tactics can be employed by individuals prior to copulation.

Even though men and women engage in both benefit-provisioning and cost-inflicting mateguarding behaviors, the costs of violent mate guarding are mostly felt by women (Whitaker et al. 2007). Notwithstanding that men and women engage in similar levels of domestic violence (and, in some studies, women are actually shown to be the primary culprits; Whitaker et al. 2007), it is women who bear the most serious injuries, including death, as a result of a partner's abuse (Daly and Wilson 1998). This is unsurprising given men's greater physical strength, on average, compared to women's. Of course, some men are more reproductively successful than others, and so they are expected to exhibit less jealousy and mate-guarding behaviors overall because they have no need of them. In partial support of this, tall men (who are high in mate value) exhibit less jealousy and engage in fewer benefit-provisioning mate-guarding behaviors (e.g., "love and care") than short men (Brewer and Riley 2009). Unlike short men, however, tall men engage in more costinflicting behaviors (e.g., monopolization of a partner's time). The authors hypothesize that this is because men of high mate value can more easily get away with guarding mates by engaging in costly mate-guarding behaviors, whereas men of low mate value might risk being abandoned by their partners if they were to engage in such behaviors. Other studies, however, suggest that men of low mate value are more likely to engage in cost-inflicting mate-guarding behaviors (such as verbal insults) than men of high mate value (Miner et al. 2009a, b).

Sexual harassment. Due to both methodological and political roadblocks, the evolutionary study of harmful sexual practices such as sexual harassment and sexual coercion continues to garner much controversy and debate. Nevertheless, notwithstanding the gap in our theoretical and empirical understanding of these phenomena, the evolutionary biological framework provides an important starting point for their scientific examination. However flawed the attempts at tracking harmful sexual behaviors through the lens of evolution by natural selection – and, in particular, the framework of sexual conflict - might be, such attempts are necessary if these behaviors are to be understood and remedied. As with any discussion of controversial topics with far-reaching social and political implications, it is important to keep in mind that any attempt at explaining such phenomena from a scientific perspective should not be conflated with an endorsement of them.

The definition of sexual harassment varies across time, region, and even across individuals. Nevertheless, its legal parameters within the United States often confine it to two more-orless independent categories: (1) quid pro quo sexual harassment, which involves pressuring someone into sexual activity with either threats (e.g., the loss of employment) or inducements (e.g., job promotion), and (2) the creation of a hostile environment via the persistent expression of unwelcome explicit or implicit sexual content (e.g., sexual jokes, suggestive comments about someone's clothing, etc.). Note that, although these categories are not the final word on what constitutes sexual harassment (as both the legal and lay understanding of sexual harassment continue to change), they are sufficient starting points for a discussion of how sexual conflict can illuminate instances of coercive sexual behavior.

Because men are generally more prone to favor casual sexual encounters and to pursue promiscuous sexual strategies to a greater extent than women, it is predicted that they would be the primary sexual harassment offenders. And, indeed, they are. As cited by Studd and Gattiker (1991), women – especially women who are young and single – are overwhelmingly more likely to report being victimized by workplace sexual harassment than men, and men are almost always the perpetrators. From an evolutionary perspective, be it quid pro quo or hostile environment sexual harassment, the fact that men are the primary culprits suggests that sexual harassment is a manifestation of men's evolved propensity to maximize sexual access to as many women as they can. As such, sexual harassment is an example of sexual conflict because it often exacts costs on its recipients.

In cases of quid pro quo sexual harassment, women who do not acquiesce to sexual advances may risk the loss of resources if their job security or career prospects are threatened. Women who do acquiesce to such advances, however, may risk unwanted pregnancy or the possibility of exposure to sexually and nonsexually transmitted diseases as the costs of maintaining their employment or furthering their career. Similarly, women who encounter a hostile work environment may suffer both financial and psychological costs due to the loss of productivity and emotional security. It is also possible that women may suffer reputational damage if they are perceived to not be "team players" due to their not taking part in crude office banter or sex talk - damage that could threaten both their career and mating prospects.

That sexual harassment may be a manifestation of sexual conflict is evidenced by instances of similar conduct that is less likely to be perceived as harassment when exhibited by attractive or high-status individuals. In examining sexual harassment vignette ratings, for example, LaRocca and Kromrey (1999) found that college students rated sexual advances as being less harassing when coming from attractive oppositesex individuals (e.g., female students rated attractive male professors as being less harassing than unattractive male professors). Similarly, female flight attendants reported less negative affective responses to verbal and physical sexual harassment exhibited by high-status pilots than by lowstatus airline workers such as cleaners and ticket agents (Littler-Bishop et al. 1982). These findings indicate that sexualized behaviors are only perceived as harassment when they are suggestive of sexual conflict - i.e., conflict between incompatible mating strategies. When there is no conflict, as when sexual overtures come from opposite-sex individuals who are of a high mate value, recipients are less likely to interpret such overtures as harassment.

Rape and sexual assault. The most extreme forms of sexual conflict are sexual assault and rape. Although women's sexual assault of men does occur, men's greater sex drive and women's decreased physical strength collude to make women's vulnerability to sexual assault and rape by men a more prevalent phenomenon. (Men's sexual assault and rape of other men are not presently discussed.) Furthermore, rape and sexual assault can be studied in the context of precopulatory sexual conflict because forced copulation need not occur for individuals' physiological and psychological adaptations associated with it, and in response to it, to be activated. For example, a man planning on committing a sexual assault in the future may very well be acting out a behavioral pattern that is a product of innumerable generations of sexual conflict between the sexes, even if the man happens to be arrested prior to committing the assault. Similarly, even if she is never attacked herself, a woman who is wary of strange men may be exhibiting a behavior pattern that was selected because it helped ancestral women to avoid unwanted sexual attacks. Despite the lack of an actual rape, each scenario highlights the possibility that specific precopulatory mechanisms (i.e., the planning of a sexual assault in the former scenario and its avoidance in the latter) selected in ancestral contexts of sexual conflict may be at play.

Whether rape is an adaptation whose selected function is to allow men to maximize their reproductive opportunities is still a topic of contention for both scientific and political reasons. Nevertheless, the prevalence of forced copulations among nonhuman animals attests to its occasional evolutionary advantages (Palmer 1989), which necessitates its inclusion in discussions of human sexual conflict. According to McKibbin et al. (2008), human rapists can be sorted into at least five categories: disadvantaged men (i.e., men who rape because they have no other avenue for consensual reproduction), specialized rapists (i.e., men who exhibit specific physiological and psychological adaptations for rape, such as greater arousal to sexually violent stimuli and discriminatory targeting of rape victims), opportunistic rapists (i.e., men who only exhibit sexually coercive behaviors in contexts where doing so poses fewer punitive risks, as in warfare – see Chang 1997, and Morris 1996), high-mating-effort rapists (i.e., men who are otherwise sexually successful, but who rely on sexual assault to obtain reproductive access to unwilling partners – see Lalumière et al. 1996), and partner rapists (i.e., men who rape their romantic partner when under threat of sperm competition following a partner's actual or perceived infidelity).

If rape and sexual assault were a regular part of life for ancestral women, it is likely that women evolved counter-adaptations aimed at preventing and countering such attacks. Hypothesizing this, McKibbin et al. (2009) developed a "rape avoidance inventory" by extracting four principle components from women's ratings of various rape avoidance behaviors. Each of these components may reflect a suite of specific defensive adaptations, and the components are as follows: "avoid strange men," which includes behaviors such as avoiding men with a reputation for sexual assault and not letting strange men into one's home; "avoid appearing sexually receptive," which includes behaviors such as avoiding wearing revealing clothes or drinking alcohol in unfamiliar places; "avoid being alone," which includes behaviors such as turning on the television or music when alone and not going out alone; and "awareness of surroundings/defensive preparedness," which includes behaviors such as looking around before getting out of the car and carrying a defensive weapon.

If the sexually coercive strategies on the part of men and the defensive strategies on the part of women constitute adaptive solutions to recurrent reproductive problems that members of each sex posed to members of the other sex over evolutionary time, then such solutions are examples of adaptations wrought by generations of sexual conflict. These strategies may even exhibit elements that are specifically tuned to the precopulatory period. For example, disadvantaged rapists and high-mating-effort rapists may exhibit adaptations specifically suited to assessing their own mate value and to responding to such an assessment by developing a sexually coercive mating strategy. Similarly, the development of specialized rape adaptations may depend on critical periods during which adolescent boys and young men are drawn toward, and positively rewarded by, violent sexual cues. In response, women may have evolved the ability to pick up on some of the specific cues given off by these men as a subcomponent of an avoidance-of-strange-men adaptation and may consequently avoid being alone or appearing sexually receptive when in the vicinity of these men. Opportunistic rapists may exhibit selective attunement to contexts wherein they could sexually coerce unconsenting women with impunity, and partner rapists may exhibit adaptive psychological and physiological precopulatory adaptations that are sensitive to contexts of partner infidelity and that bring about a more rapid sexual response as a result. In turn, women may discriminate between environments and contexts wherein they would be more or less vulnerable to rape and sexual assault and may modify their behavior accordingly. For example, women's awareness of their surroundings and attendant defensiveness may be activated in contexts wherein the costs of men's sexual violence are low or when their partners suspect them of infidelity.

Women's antirape adaptations, such as avoiding strange men, avoiding appearing sexually receptive, avoiding being alone, being aware of one's surroundings, and being prepared to defend oneself, all occur prior to the onset of forced copulation. In addition to McKibbin et al.'s (2008) proposed suite of women's antirape defenses. Thornhill and Thornhill (1990)advanced evidence for the adaptive function of psychological pain such as fear and social disturbance following sexual victimization. Specifically, Thornhill and Thornhill report that women of reproductive age (as opposed to prepubescent and postmenopausal women) and married women experienced more psychological pain after being raped than women who were neither of reproductive age nor married. The authors suggest that this is because psychological pain following a reproductively costly event functions to redirect one's efforts toward preventing such events in the future and that the evolutionary costs of rape are greatest for women of reproductive age (who suffer from the circumvention of mate choice) and married

women (who may suffer an increased risk of partner abandonment). As such, psychological pain following rape or sexual assault should likewise be counted as an adaptation for precopulatory sexual conflict, being as how it is aimed at preventing future instances of forced copulation.

Conclusion

The previous discussion suggests that much of human mating may be imbued with adaptations and counter-adaptations whose features were shaped by ancestral arms races between men's and women's competing reproductive strategies. Much is still unknown, however, about whether some of the previously mentioned examples particularly with respect to instances of rape and sexual assault - indicate the presence of specialized adaptations on the part of men and women. It may be that, for example, men's proclivity for sexual violence is not adaptive in itself but is rather a byproduct of a more general male proclivity for sexual variety. Likewise, women's antirape defenses may not be adaptive in and of themselves but may be extensions of more general defensive behaviors whose function is to ward of both human and nonhuman predators -behaviors that may be shared by both sexes. More research is needed in tracking both the evolutionary history of human sexual conflict and its physiological and psychological manifestations in modern humans.

References

- Abbey, A. (1982). Sex differences in attributions to friendly behavior: Do males misperceive females' friendliness? *Journal of Personality and Social Psychology*, 42, 830–838.
- Apicella, C. L., Little, A. C., & Marlowe, F. W. (2007). Facial averageness and attractiveness in an isolated population of hunter-gatherers. *Perception*, 36, 1813–1820.
- Arnqvist, G., & Rowe, L. (2013). *Sexual conflict*. Princeton: Princeton University Press.
- Brewer, G., & Riley, C. (2009). Height, relationship satisfaction, jealousy, and mate retention. *Evolutionary Psychology*, 7, 477–489.
- Burriss, R. P., Welling, L. L., & Puts, D. A. (2011). Men's attractiveness predicts their preference for female facial

femininity when judging for short-term, but not longterm, partners. *Personality and Individual Differences*, 50, 542–546.

- Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, 12, 1–49.
- Buss, D. M., & Dedden, L. A. (1990). Derogation of competitors. *Journal of Social and Personal Relationships*, 7, 395–422.
- Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review*, 100, 204–232.
- Buss, D. M., Larsen, R. J., Westen, D., & Semmelroth, J. (1992). Sex differences in jealousy: Evolution, physiology, and psychology. *Psychological Science*, *3*, 251–255.
- Chang, I. (1997). The rape of Nanking: The forgotten holocaust of WWII. New York: Basic Books.
- Clark, R. D., & Hatfield, E. (1989). Gender differences in receptivity to sexual offers. *Journal of Psychology and Human Sexuality*, 2, 39–55.
- Crean, C. S., & Gilburn, A. S. (1998). Sexual selection as a side-effect of sexual conflict in the seaweed fly, Coelopa ursina (Diptera: Coelopidae). *Animal Behaviour*, 56, 1405–1410.
- Crean, C. S., Dunn, D. W., Day, T. H., & Gilburn, A. S. (2000). Female mate choice for large males in several species of seaweed fly (Diptera: Coelopidae). *Animal Behaviour*, 59(1), 121–126.
- Daly, M., & Wilson, M. (1998). *Homicide*. Hawthorne: Aldine de Gruyter.
- Dawkins, R. (1982). *The extended phenotype*. Oxford: W. H. Freeman.
- Eberhard, W. G. (2005). Evolutionary conflicts of interest: Are female sexual decisions different? *The American Naturalist*, 165(S5), S19–S25.
- Ellis, B. J., & Symons, D. (1990). Sex differences in fantasy: An evolutionary psychological approach. *Journal of Sex Research*, 27, 527–556.
- Fink, B., Matts, P. J., Klingenberg, H., Kuntze, S., Weege, B., & Grammer, K. (2008). Visual attention to variation in female facial skin color distribution. *Journal of Cosmetic Dermatology*, 7, 155–161.
- Fisher, M. L. (2004). Female intrasexual competition decreases female facial attractiveness. *Proceedings of the Royal Society of London B: Biological Sciences*, 271, S283–S285.
- Frontera, W. R., Hughes, V. A., Lutz, K. J., & Evans, W. J. (1991). A cross-sectional study of muscle strength and mass in 45- to 78-yr-old men and women. *Journal of Applied Physiology*, 71, 644–650.
- Gangestad, S. W., Thornhill, R., & Yeo, R. A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology*, 15(2), 73–85.
- Gangestad, S. W., Simpson, J. A., Cousins, A. J., Garver-Apgar, C. E., & Christensen, P. N. (2004). Women's preferences for male behavioral displays change across

the menstrual cycle. *Psychological Science*, 15, 203–207.

- Gwinner, H., & Schwabl, H. (2005). Evidence for sexy sons in European starlings (*Sturnus vulgaris*). Behavioral Ecology and Sociobiology, 58(4), 375–382.
- Haselton, M. G. (2003). The sexual overperception bias: Evidence of a systematic bias in men from a survey of naturally occurring events. *Journal of Research in Personality*, 37, 34–47.
- Haselton, M. G., & Buss, D. M. (2000). Error management theory: A new perspective on biases in cross-sex mind reading. *Journal of Personality and Social Psychology*, 78(1), 81–91.
- Haselton, M. G., Buss, D. M., Oubaid, V., & Angleitner, A. (2005). Sex, lies, and strategic interference: The psychology of deception between the sexes. *Personality* and Social Psychology Bulletin, 31, 3–23.
- Holden, C. J., Shackelford, T. K., Ziegler-Hill, V., Miner, E. J., Kaighobadi, F., Starratt, V. G., Jeffery, A. J., & Buss, D. M. (2014). Husband's esteem predicts his mate retention tactics. *Evolutionary Psychology*, *12*, 655–672.
- Jones, B. C., Little, A. C., Penton-Voak, I. S., Tidderman, B. P., Burt, D. M., & Perrett, D. I. (2001). Facial symmetry and judgments of apparent health support for a "good genes" explanation of the attractiveness-symmetry relationship. *Evolution and Human Behavior*, 22, 417–429.
- Karremans, J. C., Frankenhuis, W. E., & Arons, S. (2010). Blind men prefer a low waist-to-hip ratio. *Evolution* and Human Behavior, 31, 182–186.
- Lalumière, M. L., Chalmers, L. J., Quinsey, V. L., & Seto, M. C. (1996). A test of the mate deprivation hypothesis of sexual coercion. *Ethology and Sociobi*ology, 17, 299–318.
- LaRocca, M. A., & Kromrey, J. D. (1999). The perception of sexual harassment in higher education: Impact of gender and attractiveness. *Sex Roles*, 40, 921–940.
- Lewis, D. M., Russell, E. M., Al-Shawaf, L., & Buss, D. M. (2015). Lumbar curvature: A previously undiscovered standard of attractiveness. *Evolution and Human Behavior*, 36, 345–350.
- Littler-Bishop, S., Seidler-Feller, D., & Opaluch, R. E. (1982). Sexual harassment in the workplace as a function of initiator's status: The case of airline personnel. *Journal of Social Issues*, 38, 137–148.
- Lukaszewski, A. W., & Roney, J. R. (2010). Kind toward whom? Mate preferences for personality traits are target specific. *Evolution and Human Behavior*, 31, 29–38.
- McKibbin, W. F., Shackelford, T. K., Goetz, A. T., & Starrat, V. G. (2008). Why do men rape? An evolutionary psychological perspective. *Review of General Psychology*, 12, 86–97.
- McKibbin, W. F., Shackelford, T. K., Goetz, A. T., Bates, V. M., Starrat, V. G., & Miner, E. J. (2009). Development and initial psychometric assessment of the rape avoidance inventory. *Personality and Individual Differences*, 46, 336–340.

- Mesko, N., & Bereczkei, T. (2004). Hairstyle as an adaptive means of displaying phenotypic quality. *Human Nature*, 15, 251–270.
- Miner, E. J., Shackelford, T. K., & Starratt, V. G. (2009a). Mate value of romantic partners predicts men's partnerdirected verbal insults. *Personality and Individual Differences*, 46, 135–139.
- Miner, E. J., Starratt, V. G., & Shackelford, T. K. (2009b). It's not all about her: Men's mate value and mate retention. *Personality and Individual Differences*, 47, 214–218.
- Monitoring, B. (2016, April 22). BBC News. Retrieved from http://www.bbc.com/news/world-middle-east-36101150
- Morris, M. (1996). By force of arms: Rape, war, and military culture. *Duke Law Journal*, 45, 651–781.
- Palmer, C. T. (1989). Rape in nonhuman animal species: Definitions, evidence, and implications. *The Journal of Sex Research*, 26, 355–374.
- Parker, G. A. (2006). Sexual conflict over mating and fertilization: An overview. *Philosophical Transactions* of the Royal Society B, 361, 235–259.
- Pawlowski, B., & Jasienska, G. (2005). Women's preferences for sexual dimorphism in height depend on menstrual cycle phase and expected duration of relationship. *Biological Psychology*, 70, 38–43.
- Penton-Voak, I. S., Little, A. C., Jones, B. C., Burt, D. M., Tiddeman, B. P., & Perrett, D. I. (2003). Female condition influences preferences for sexual dimorphism in faces of male humans (*Homo sapiens*). Journal of Comparative Psychology, 117, 264–271.
- Perilloux, C., & Kurzban, R. (2015). Do men overperceive women's sexual interest? *Psychological Science*, 26, 70–77.
- Peshek, D., Semmaknejad, N., Hoffman, D., & Foley, P. (2011). Preliminary evidence that the limbal ring influences facial attractiveness. *Evolutionary Psychology*, 9, 137–146.
- Pflüger, L. S., Oberzaucher, E., Katina, S., Holzleitner, I. J., & Grammer, K. (2012). Cues to fertility: Perceived attractiveness and facial shape predict reproductive success. *Evolution and Human Behavior*, 33, 708–714.
- Pillsworth, E. G., & Haselton, M. G. (2006). Male sexual attractiveness predicts differential ovulatory shifts in female extra-pair attraction and male mate retention. *Evolution and Human Behavior*, 27, 247–258.
- Quist, M. C., Watkins, C. D., Smith, F. G., Little, A. C., DeBruine, L. M., & Jones, B. C. (2012). Sociosexuality predicts women's preferences for symmetry in men's faces. *Archives of Sexual Behavior*, 41, 1415–1421.
- Rowe, L., & Day, T. (2006). Detecting sexual conflict and sexually antagonistic coevolution. *Philosophical Transactions of the Royal Society B*, 361, 277–285.
- Schmitt, D. P. (2003). Universal sex differences in the desire for sexual variety: Tests from 52 nations, 6 continents, and 13 islands. *Journal of Personality and Social Psychology*, 85, 85–104.
- Schmitt, D. P., & Buss, D. M. (1996). Strategic selfpromotion and competitor derogation: Sex and context

effects on the perceived effectiveness of mate attraction tactics. *Journal of Personality and Social Psychology*, 70, 1185–1204.

- Studd, M. V., & Gattiker, U. E. (1991). The evolutionary psychology of sexual harassment in organizations. *Ethology and Sociobiology*, 12, 249–290.
- Thompson, M. E., & Alvarado, L. C. (2012). Sexual conflict and sexual coercion in comparative evolutionary perspective. In T. K. Shackelford & A. T. Goetz (Eds.), *The Oxford handbook of sexual conflict in humans*. New York: Oxford University Press.
- Thornhill, N. W., & Thornhill, R. (1990). An evolutionary analysis of psychological pain following rape: I. The effects of victim's age and marital status. *Ethology and Sociobiology*, 11, 155–176.
- 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.
- Whitaker, D. J., Haileyesus, T., Swahn, M., & Saltzman, L. S. (2007). Differences in frequency of violence and reported injury between relationships

with reciprocal and nonreciprocal intimate partner violence. *American Journal of Public Health*, 97, 941–947.

- Wilson, M., & Daly, M. (1993). An evolutionary psychological perspective on male sexual proprietariness and violence against wives. *Violence and Victims*, 8(3), 271–294.
- Wilson, M., & Daly, M. (1998). Lethal and nonlethal violence against wives and the evolutionary psychology of male sexual proprietariness, Sage series on violence against women (Vol. 9, pp. 199–230). Thousand Oaks: Sage Publications.
- Wolf, A. P. (2005). Explaining the Westermarck effect, or, what did natural selection select for? In A. P. Wolf & W. H. Durham (Eds.), *Inbreeding, incest, and the incest taboo: The state of knowledge at the turn of the century*. Stanford: Stanford University Press.
- Zelazniewicz, A. M., & Pawlowski, B. (2011). Female breast size attractiveness for men as a function of sociosexual orientation (restricted vs. unrestricted). *Archives* of Sexual Behavior, 40, 1129–1135.