

Adaptation to Sperm Competition in Humans

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ABSTRACT—*With the recognition, afforded by recent evolutionary science, that female infidelity was a recurrent feature of modern humans' evolutionary history has come the development of a unique area in the study of human mating: sperm competition. A form of male–male postcopulatory competition, sperm competition occurs when the sperm of two or more males concurrently occupy the reproductive tract of a female and compete to fertilize her ova. Males must compete for mates, but if two or more males have copulated with a female within a sufficiently short period of time, sperm will compete for fertilizations. Psychological, behavioral, physiological, and anatomical evidence indicates that men have evolved solutions to combat the adaptive problem of sperm competition, but research has only just begun to uncover these adaptations.*

KEYWORDS—*sperm competition; anti-cuckoldry; sexual conflict; female infidelity; evolutionary psychology*

Male flour beetles sometimes fertilize females with a rival male's sperm. This "fertilization by proxy" occurs when the mating male's aedeagus (reproductive organ) translocates the sperm of another male into the female's reproductive tract (Haubruge, Arnaud, Mignon, & Gage, 1999). The sperm of a male that a female has copulated with can adhere to a subsequent male's aedeagus because these insects' genitalia have chitinous spines designed to facilitate removal of rival male sperm prior to deposition of self-sperm into a female's reproductive tract. This phenomenon was predicted and observed by researchers who study sperm competition. Although not yet documented empirically, humans also may experience fertilization by proxy (Gallup & Burch, 2004). More generally, a rapidly growing literature indicates that sperm competition has been an important selection pressure during human evolution.

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Sperm competition is intrasexual (male–male) competition that occurs after the initiation of copulation. Whereas Darwin and others identified *pre*copulatory adaptations associated with intrasexual competition (e.g., horns on beetles, status seeking in men), researchers studying sperm competition aim to identify *post*copulatory adaptations. Thus, an alternative way of thinking about sexual selection is that there is not only competition between males for mates, but competition between males for fertilizations.

Sperm competition is the inevitable consequence of males competing for fertilizations. If females mate in a way that concurrently places sperm from two or more males in their reproductive tracts, this generates selection pressures on males. If these selection pressures are recurrent throughout a species' evolutionary history, males will evolve tactics to aid their sperm in outcompeting rivals' sperm for fertilizations. These tactics may take the form of anatomical, physiological, and psychological adaptations. Although revolutionary for its time, the first definition of sperm competition, "the competition within a single female between the sperm of two or more males for the fertilization of the ova" (Parker, 1970, p. 527), does not capture the full spectrum of male anatomy, physiology, psychology, and behavior associated with sperm competition.

SPERM COMPETITION AS AN ADAPTIVE PROBLEM IN HUMANS

For species that practice social monogamy—the mating system in which males and females form long-term pair bonds but also pursue extra-pair copulations (i.e., "affairs")—it is the extra-pair copulations by females that creates the primary context for sperm competition. A male whose female partner engages in an extra-pair copulation is at risk of cuckoldry—the unwitting investment of resources into genetically unrelated offspring—and its associated costs, which include loss of the time, effort, and resources the male spent attracting his partner and the misdirection of his current and future resources to a rival's offspring. Consequently, in species with paternal investment in offspring, selection often favors the evolution of adaptations that decrease

the likelihood of being cuckolded. Anti-cuckoldry tactics fall into three categories: *preventative tactics*, designed to prevent female infidelity; *sperm competition tactics*, designed to minimize conception risk in the event of female infidelity; and *differential paternal investment*, designed to allocate paternal investment prudently in the event that female infidelity may have resulted in conception.

The extent to which sperm competition occurred in ancestral human populations would have depended largely on rates of female sexual infidelity and cuckoldry. Current estimates of worldwide cuckoldry rates range from 1.7% to 29.8% (Anderson, 2006). Although current estimates of cuckoldry rates provide only a proxy of the occurrence of cuckoldry throughout human evolutionary history, even the most conservative estimates of these rates would have generated sufficient selection pressures on males to avoid the costs of cuckoldry. Moreover, the ubiquity and power of male sexual jealousy provides evidence of an evolutionary history of female infidelity and thus perhaps also of sperm competition. Male sexual jealousy can evolve only if female sexual infidelity was a recurrent feature of human evolutionary history, and female infidelity increases the likelihood that sperm from two or more men occupied concurrently the reproductive tract of a particular woman. This suggests that sexual selection, in the form of sperm competition, has been an important selection pressure during recent human evolution. If this is the case, then specific adaptations to sperm competition may have evolved.

ADAPTATIONS TO SPERM COMPETITION IN HUMANS

In this section, we discuss adaptations men may have evolved in response to an evolutionary history of sperm competition. We limit our discussion of these adaptations to testis size, ejaculate adjustment, semen displacement, sexual arousal, and forced in-pair copulation, as these adaptations have been investigated more rigorously than others.

Testis Size

Across a range of animal species, males have relatively larger testes in species with more intense sperm competition. Because larger testes produce more sperm, a male with larger testes can better compete by inseminating a female with more sperm. Among the great apes, testes size varies predictably with the risk of sperm competition. In gorillas, female promiscuity and sperm competition are rare, and the gorilla's testes are relatively small, making up just 0.03% of their body weight. Chimpanzees, in contrast, are highly promiscuous and, accordingly, males have relatively large testes, making up 0.30% of their body weight. The size of human testes falls between these two extremes at 0.08% of body weight, suggesting intermediate levels of female promiscuity and sperm competition in our evolutionary past (Shackelford & Goetz, 2006).

Ejaculate Adjustment

The number of sperm recruited into a given ejaculate is not constant. Although the physiology is not well understood, there is evidence that sperm number can be adjusted even moments before ejaculation (reviewed in Shackelford, Pound, & Goetz, 2005). A key hypothesis derived from sperm competition theory is that males will adjust the number of sperm they inseminate into a female as a function of the risk that their sperm will encounter competition from the sperm of other males. Baker and Bellis (1993) documented a negative relationship between the proportion of time a couple has spent together since their last copulation and the number of sperm ejaculated at the couple's next copulation. As the proportion of time a couple spends together since their last copulation decreases, there is a predictable increase in the probability that the man's partner has been inseminated by another male. Additional analyses documented that the proportion of time a couple spent together since their last copulation negatively predicts sperm number ejaculated at the couple's next copulation, but not at the man's next masturbation (Baker & Bellis, 1993). Inseminating into a female more sperm following a separation may function to outnumber or "flush out" sperm from rival men that may be present in the reproductive tract of the woman.

Inspired by Baker and Bellis's (1993) demonstration of male physiological adaptations to sperm competition, Shackelford et al. (2002) documented that human male psychology may include psychological adaptations to decrease the likelihood that a rival man's sperm will fertilize a partner's ovum. For example, men who spent a greater proportion of time apart from their partners since the couples' last copulation—and, therefore, face a higher risk of sperm competition—report that their partners are more sexually attractive, have more interest in copulating with their partners, and believe that their partners are more interested in copulating with them, relative to men spent a lesser proportion of time apart from their partners. These effects were independent of relationship satisfaction, total time since last copulation, and total time spent apart, which rules out several alternative explanations (although other plausible alternative mechanisms remain to be evaluated). These perceptual changes may motivate men to copulate as soon as possible with their partners, thereby entering their sperm into competition with any rival sperm that may be present in their partners' reproductive tracts.

Semen Displacement

Features of the penis may have evolved in response to the selective pressures of sperm competition. The penis of the damselfly is equipped with spines that can remove up to 99% of the sperm stored in a female, and the penis of the tree cricket is designed structurally to remove rival sperm prior to insemination of the male's own ejaculate. Spines, ridges, and knobs on the penis of some waterfowl are positioned in a way to displace

rival sperm, and these protuberances are larger in species for which the intensity of sperm competition is greater.

The human penis does not have barbs and spines for removing rival sperm, but recent evidence suggests that the human penis may have evolved to function, in part, as a semen-displacement device. Using artificial genitals and simulated semen, Gallup et al. (2003) tested the hypothesis that the human penis is designed to displace semen deposited by other men in the reproductive tract of a woman. The results indicated that artificial phalluses with a glans and coronal ridge that approximated a human penis displaced more simulated semen than did a phallus that did not have such features. When the penis is inserted into the vagina, the frenulum of the coronal ridge makes semen displacement possible by allowing semen to flow back under the penis alongside the frenulum and collect on the anterior of the shaft behind the coronal ridge. Displacement of simulated semen occurred when a phallus was inserted at least 75% of its length into the artificial vagina.

That the penis must reach an adequate depth before semen is displaced suggests that displacing rival semen may require specific copulatory behaviors. Following allegations of female infidelity or separation from their partners (contexts in which the likelihood of rival semen being present is relatively greater), both men and women report that men thrust the penis more deeply and more quickly into the vagina at the couple's next copulation (Gallup et al., 2003), behaviors likely to increase semen displacement. In an independent study, Goetz et al. (2005) investigated men's copulatory behaviors when under a high risk of sperm competition. Men mated to women who placed them at high risk of sperm competition were more likely to use specific copulatory behaviors arguably designed to displace rival semen (e.g., more frequent thrusts, deeper thrusts) than were men mated to women who did not place them at high risk of sperm competition.

Sexual Arousal

Men's sexual fantasies often involve sex with multiple, anonymous partners—behavior that would have had fitness payoffs in ancestral environments. It has been suggested, however, that although men might desire and seek sexual variety and the absence of competition with other men, cues of sperm competition risk also might be sexually arousing. Because sexual arousal increases the rate of sperm transport in the vas deferens, Pound (2002) argued that ancestral males might have benefited from being aroused to cues of sperm competition. When faced with cues of sperm competition, sexual arousal would have resulted in an increase in sperm transport upon ejaculation, thus enabling men to compete more effectively in such contexts.

Pound hypothesized that men, therefore, will be more aroused by sexually explicit images incorporating cues of sperm competition than by comparable material in which such cues are absent. Content analyses of sexually explicit images on Internet

sites and of commercial “adult” video releases revealed that depictions of sexual activity involving a woman and multiple men are more prevalent than those involving a man and multiple women, indicating that the former category may be preferred by men. Additionally, an online survey of self-reported preferences and an online preference study that unobtrusively assessed image selection yielded corroborative results. Pound argued that the most parsimonious explanation for these results is that male sexual arousal in response to visual cues of sperm competition reflects the functioning of psychological mechanisms that would have motivated adaptive patterns of copulatory behavior in ancestral males exposed to evidence of female promiscuity.

Pound's hypothesis recently has been supported by experimental evidence that men viewing images depicting cues to sperm competition produce more competitive ejaculates than men viewing comparable images in which cues to sperm competition are absent (Kilgallon & Simmons, 2005). Kilgallon and Simmons documented that men produce a higher percentage of motile sperm in their ejaculates after viewing sexually explicit images of two men and one woman (sperm competition images) than after viewing sexually explicit images of three women. More generally, these results support the hypothesis that men adjust their ejaculates in accordance with sperm competition theory.

Forced In-Pair Copulation

Noting that instances of forced in-pair copulation (i.e., partner rape) followed extra-pair copulations in waterfowl and anecdotal reports that forced in-pair copulation in humans often followed accusations of female infidelity, Thornhill and Thornhill (1992) hypothesized that sexual coercion in response to cues of a partner's sexual infidelity might function in humans to introduce a man's sperm into his partner's reproductive tract at a time when there is a high risk of extra-pair paternity. Goetz and Shackelford (2006a) found empirical support for this hypothesis. In two studies, Goetz and Shackelford found that men's sexual coercion in the context of an intimate relationship was related positively to his partner's infidelities. According to men's self-reports and women's partner-reports, men who use more sexual coercion in their relationships are mated to women who have been or are likely to be unfaithful. The hypothesis that sexual coercion and forced in-pair copulation may be a sperm competition tactic has been supported directly and indirectly in at least half a dozen studies (reviewed in Goetz & Shackelford, 2006b).

CONCLUSION AND FUTURE DIRECTIONS

Sperm competition was first identified as a form of postcopulatory competition between males by Geoff Parker in the 1970s. Since then, evolutionary biologists and behavioral ecologists have described many anatomical, physiological, and behavioral adaptations to sperm competition in many nonhuman species. The question as to whether sperm competition has been an

important selection pressure during human evolution remains somewhat controversial, and further research is needed to establish the extent to which this might be the case. As outlined in this article, however, there is mounting evidence that aspects of men's sexual psychology and behavior, such as their attraction to and sexual interest in their partners, their copulatory behaviors, and sources of sexual arousal, may reflect adaptations to sperm competition.

Although we focused on men's adaptations to sperm competition, women are not passive sperm receptacles. An important avenue for future research is to identify adaptations not only in men but also in women. Sexual conflict between males and females produces a coevolutionary arms race between the sexes, in which an advantage gained by one sex selects for counteradaptations in the other sex. Thus, men's adaptations to sperm competition are likely to be met by counteradaptations in women (e.g., mechanisms that increase retention of sperm inseminated by men with "good genes"; see Shackelford et al., 2005), and the study of such mechanisms is an important direction for future research.

Recommended Reading

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