Sperm Competition in Humans: Implications for Male Sexual Psychology, Physiology, Anatomy, and Behavior

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With the recognition afforded by evolutionary science that female infidelity was a recurrent feature of our evolutionary past has come the development of a new area of study within 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. Just as males must compete for mates, if two or more males have copulated with a female within a sufficiently short period of time, the sperm from different males will compete for fertilizations. In the 2 decades since Smith (1984) first argued that sperm competition occurs in humans, this theory has been enriched with new ideas and discoveries. We review the recent theoretical and empirical work on human sperm competition, identify limitations and challenges of the research, and highlight important directions for future research.

Key words: anticuckoldry, evolutionary psychology, female infidelity, sexual conflict, sperm competition.

Male competition for mates may take many forms. For example, males may compete by displaying the grandest plumage, having the largest antlers, or even fighting to the death (Alcock, 2005). They may even compete at the level of their sperm, a phenomenon known as sperm competition. Broadly defined, sperm competition is intrasexual

(male-male) competition that occurs after the initiation of copulation. Whereas Darwin (1871) and others (see Andersson, 1994) 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 in some species there is a competition not only between males for mates, but also 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 her reproductive tract, this generates several selection pressures on males. If these selection pressures are recurrent throughout a species' evolutionary history, males will evolve tactics to aid their sperm in out-competing rivals' sperm in 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

Smith (1984) presented theoretical arguments for the existence of sperm competition in humans, which requires that a woman copulate with more than one man within roughly a 5-day period. Smith outlined several contexts in which sperm from two or more men might concurrently occupy the reproductive tract of a woman. Prostitution, communal sex (e.g., wife-swapping and orgies), courtship (e.g., short-term matings), rape, and female infidelity are contexts that can place the sperm of different men into competition. Prostitution and communal sex are relatively rare and probably did not represent a recurrent context over the evolutionary history of humans in which sperm competition could act as a selective force (Smith, 1984). Courtship, in the form of short-term matings, was likely more common than prostitution and communal sex, but the majority of women's multiple matings probably did not occur within a sufficiently short period of time to generate sperm competition.

Rape of females by males, however, probably was a recurrent feature of human evolutionary history, whether an adaptation or byproduct of other evolved mechanisms (Lalumière, Harris, Quinsey, & Rice, 2005; Smith, 1984; Thornhill & Palmer, 2000). Despite cultural institutions

that discourage and punish rape, rape of women by men is universal across cultures (see Lalumière et al., 2005, for a review). There also is a strong association between rape and war, a key feature of our evolutionary past (Gottschall, 2004; Thornhill & Palmer, 2000). These reports suggest that rape could have provided a recurrent context for sperm competition to act as a selection pressure on humans.

Female infidelity, however, is likely to have been the most common context for the concurrent presence of sperm from two or more men in the reproductive tract of a woman (Smith, 1984). Therefore, 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 around less than 1% to more than 30% with a mean of about 4% (Anderson, 2006; Bellis, Hughes, Hughes, & Ashton, 2005). 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. The tremendous variance in cuckoldry rates suggests that ancestral males would have benefited reproductively by possessing anticuckoldry tactics designed to thwart or "correct" incidences of female infidelity (see Platek & Shackelford, 2006, for overview).

Moreover, the cross-cultural ubiquity and power of male sexual jealousy provides evidence of an evolutionary history of female infidelity (and therefore, sperm competition), as jealousy, an emotion experienced when a valued relationship is threatened by a real or imagined rival, functions to maintain relationships by activating behaviors that deter rivals from mate poaching and deter mates from infidelity (e.g., Buss, Larsen, Westen, & Semmelroth, 1992; Daly, Wilson, & Weghorst, 1982; Symons, 1979). Female infidelity, of course, does not necessarily result in sperm competition, but likely it occurred throughout human evolution frequently enough to result in nontrivial levels of sperm competition. Finally, recent research reviewed below has identified several anatomical, physiological, psychological, and behavioral features that are parsimoniously explained if female infidelity occurred with sufficient frequency over human evolutionary history.

Men's Adaptations to Sperm Competition

Although men likely have not evolved to deal with particularly *high* levels of sperm competition, they may have evolved to deal with *variable* levels of sperm competition. Adaptations to variable levels of sperm competition are likely to take the form of physiological adaptations that

enable males to alter the number of sperm they inseminate according to variations in the risk or intensity of sperm competition. Sperm competition theory can be used to generate the hypothesis that, where the risk of sperm competition is *variable*, individual males will allocate their sperm prudently to inseminate more sperm when the risk is high.

Is There Evidence of Prudent Sperm Allocation by Men?

Sperm competition theory can be used to generate the predictions that, across species, investment in sperm production will depend on the level of sperm competition, and that, where the risk of sperm competition is variable, individual males will allocate their sperm in a prudent fashion and will, accordingly, inseminate more sperm when the risk is higher (Parker, 1982, 1990a, 1990b). It is possible that adaptations to variable levels of sperm competition will be seen in species when overall levels are not especially high—but when sperm competition is a sufficiently frequent occurrence to select for mechanisms that allow prudent sperm allocation.

Studying humans, Baker and Bellis (1989b, 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. Additional regression analyses documented that the proportion of time a couple spent together since their last copulation is a significant predictor of sperm number ejaculated at the couple's next copulation but not at the man's next masturbation (Baker & Bellis, 1989b, 1995). 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 (Baker & Bellis, 1995; Shackelford et al., 2002). Inseminating more sperm following separation from a partner may function to outnumber or dilute sperm from rival men that may be present in the reproductive tract of the woman.

Psychological Mechanisms Associated With Prudent Sperm Allocation

The findings of Baker and Bellis (1989a, 1993) suggest that men may be capable of such prudent sperm allocation, but it is not clear how men accomplish this. Recent research has focused on the psychological mechanisms that might be involved in regulating such responses. Adaptive changes in semen parameters serve no function unless they are accompanied by a desire to copulate with a partner when cues of sperm competition risk are present. Accordingly, Shackelford et al. (2002) investigated the psychological responses of men to cues of sperm competition risk, arguing that psychological mechanisms in men must have

evolved to motivate behavior, increasing the probability of success in sperm competition in ancestral environments.

Inspired by Baker and Bellis's (1993) demonstration of male *physiological* adaptations to sperm competition, Shackelford et al. (2002) documented possible *psychological* adaptations to decrease the likelihood that a rival's sperm will fertilize a partner's ovum. Consistent with predictions, Shackelford et al. (2002) found that a man who spends a greater (relative to a man who spends a lesser) proportion of time apart from his partner since the couple's last copulation (and, therefore, faces a higher risk of sperm competition) rates his partner as more attractive, reports that other men find his partner more attractive, reports greater interest in copulating with his partner, and reports that his partner is more interested in copulating with him. These effects were independent of relationship satisfaction, total time since last copulation, and total time spent apart, which rules out several alternative explanations (e.g., that men are simply "sexually frustrated"). These perceptual changes may motivate men to copulate as soon as possible with their partner, thereby entering their sperm into competition with any rival sperm that may be present in her reproductive tract. Shackelford and his colleagues argued that no existing theory other than sperm competition can account for these effects. Additionally, they argued that their findings support the hypothesis that men, like males of other socially monogamous but not sexually exclusive species, have psychological mechanisms designed to solve the adaptive problems associated with a partner's sexual infidelity.

Men are also distressed by, and more persistent in response to, a partner's sexual rejection in the presence of a greater risk of sperm competition. Men who spent a greater (relative to men who spend a lesser) percentage of time apart from their partner since last copulation reported greater distress, more persistence, and change in interest in sex with their partner following the partner's denial of a request for copulation (Shackelford, Goetz, McKibbin, & Starratt, 2007). These psychological mechanisms also may motivate a man to seek intercourse with his partner quickly, in an attempt to correct a situation of sperm competition that may occur if his partner has recently engaged in an extra-pair copulation.

In addition, psychological mechanisms associated with prudent sperm allocation may explain why men are continually interested in copulating with their partners throughout the duration of a mateship (Klusmann, 2002, 2006), a prediction first made by Baker and Bellis (1993). According to their "topping-up" model, a woman's primary partner should desire to maintain an optimum level of sperm in his part-

ner's reproductive tract as a sperm competition tactic. Surveying German participants, Klusmann (2006) documented that sexual desire for one's partner declines in women but remains constant in men for the duration of a mateship and interpreted the results in accordance with the topping-up model. Although men report that their sexual satisfaction (Klusmann, 2002, 2006) and the quality of marital sex (Chien, 2003) decline with the duration of the mateship, men's desire for sex with their partner does not (Klusmann, 2006).

The crux of the topping-up model is that continued sexual desire functions to motivate sexual activity throughout the mateship (i.e., sexual desire without sexual behavior would be an incomplete strategy). Klusmann (2006) found, however, that sexual activity declined in men and women with the duration of the mateship. This finding is not fatal to Klusmann's interpretation of the data or to Baker and Bellis's (1993) model when considering the fact that sexual activity typically requires a consenting partner. Over the duration of a mateship, women (but not men) experience decreased sexual desire and, accordingly, women (but not men) desire sex with their partner less often (Klusmann, 2006). Because women more than men control sexual access (see Klusmann, 2002), women's waning interest in sex translates into a decrease in sexual activity for both partners. Sexual rejection by a woman might signal to her partner strategic interference and could activate psychology and behavior associated with sexual coercion.

Sperm Competition and Men's Reproductive Anatomy and Copulatory Behavior

In primates, testis weight relative to body weight is correlated positively with the incidence of polyandrous mating (Harcourt, Harvey, Larson, & Short, 1981; Harvey & Harcourt 1984; Short, 1979). Smith (1984) argued that because men have larger testes relative to body size than those of monandrous species, such as the gorilla and orangutan, polyandry was an important selection pressure during human evolution. As Gomendio, Harcourt, and Roldán (1998) noted, however, human relative testis size is closer to these monandrous primates than to the highly polyandrous chimpanzee. Nevertheless, Gomendio et al.'s (1998) conclusion that humans are monandrous is not justified. Dichotomizing species into monandrous and polyandrous groups is not useful when there is continuous variation across species in the frequency with which females mate with multiple partners. When the degree of polyandry is considered along a continuum, ancestral human males experienced modest levels of polyandry. Thus, although human males have not experienced levels of sperm competition as high as have been documented in

some primate species, is it unlikely that sperm competition was completely absent over human evolutionary history.

Men's testes seem to be influenced by sperm competition. Might other features of their reproductive anatomy also be affected by an evolutionary history of sperm competition? In many nonhuman species, features of the penis may have evolved in response to the selective pressures of sperm competition. Waage (1979) was the first to study how males' genitals might remove rival sperm. He documented, for example, that the penis of the damselfly is equipped with spines able to remove up to 99% of the stored sperm (Waage, 1979). Sperm displacement is not limited to damselflies, but exists in many insect species. Although only 3% of bird species possess a penis (Briskie & Montgomerie, 1997), for these species the penis often has features designed to displace rival sperm. 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 (Coker, McKinney, Hays, Briggs, & Cheng, 2002; McCracken, Wilson, McCracken, & Johnson, 2001; cf. Briskie & Montgomerie, 1997).

Although the human male's penis does not possess barbs and spines for removing rival sperm, recent empirical evidence suggests that it may have evolved to function, in part, as a semen displacement device. Several arguments have been offered to explain how the length and shape of the human penis might reflect adaptation to an evolutionary history of sperm competition. A long penis may be advantageous because being able to deposit an ejaculate deep inside the vagina and close to the cervix may increase the chance of fertilization (Baker & Bellis, 1995; Short, 1979; Smith, 1984).

Additionally, it has been suggested that the length, width, and shape of the human penis indicate that it may have evolved to function as a semen displacement device. Using artificial genitals and simulated semen, Gallup et al. (2003) empirically tested Baker and Bellis's (1995) displacement hypothesis. Gallup and his colleagues (2003) documented that artificial phalluses with a glans and a coronal ridge approximating a real human penis displaced significantly more simulated semen than did a phallus without these features. When the penis is inserted into the vagina, the frenulum of the glans makes possible semen displacement 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 only occurred, however, when a phallus was inserted at least 75% of its length into the artificial vagina. Following allegations of female infidelity or separation from their partners, contexts for the likely presence of rival semen, both sexes reported

that men thrusted deeper and more quickly at the couple's next copula-
tion (Gallup et al., 2003). Such vigorous copulatory behaviors are likely
to increase semen displacement. In an independent test, Goetz and his
colleagues (2005) investigated whether and how men under a high risk
of sperm competition (i.e., men mated to women with personality char-
acteristics that attract mate poachers) might attempt to "correct" the
female partner's sexual infidelity. Using a self-report survey, men in
committed, sexual relationships reported their use of specific copulatory
behaviors, including number of thrusts, deepest thrust, average depth
of thrusts, and duration of sexual intercourse, behaviors arguably
affording a better chance to displace rival semen. As hypothesized, men
mated to women who place them at high recurrent risk of sperm compe-
tition were more likely to perform semen-displacing behaviors.

One concern with the hypothesis that the human penis has evolved
as a semen displacement device is that, during copulation, the penis
would frequently remove a man's own semen, even if the highest esti-
mates of the frequency of extra-pair copulations are accepted. Such con-
sequences might be minimized, however, if the time between successive
in-pair copulations is much greater than the time between copulations
involving different men. Indeed, the refractory period may have been
designed for this purpose (Gallup & Burch, 2004). The inability to main-
tain an erection following ejaculation may function to minimize dis-
placement of a man's own semen. Furthermore, the costs associated
with self-semen displacement might be minimal because ejaculation fol-
lows copulatory behavior that might have removed sperm.

Sperm Competition and Men's Mate Selection

As Baker and Bellis (1995) noted, an evolutionary history of sperm
competition may be responsible for myriad male behaviors related
directly and indirectly to mating. Research informed by sperm competi-
tion theory is just beginning to uncover those behaviors. Aspects of
men's short-term mate selection, for example, may have their origins in
sperm competition.

To avoid sperm competition or to compete more effectively, men may
have evolved mate preferences that select as short-term sexual partners
women who present the lowest risk of current or future sperm competi-
tion (Shackelford, Goetz, LaMunyon, Quintus, & Weekes-Shackelford,
2004). Because the risk of sperm competition for a man increases with a
prospective short-term partner's involvement in one or more relation-
ships, women who are not in a long-term relationship and do not have
casual sexual partners present a low risk of sperm competition. Conse-
quently, such women may be perceived as desirable short-term sexual

partners. Women who are not in a long-term relationship but who engage in short-term matings may present a moderate risk of sperm competition, because women who engage in short-term matings probably do not experience difficulty obtaining willing sexual partners. Women in a long-term relationship may present the highest risk of sperm competition. The primary partner's frequent inseminations might, therefore, make women in a long-term relationship least attractive as short-term sexual partners.

As predicted, Shackelford et al. (2004) found that men's reported likelihood of pursuing a short-term sexual relationship was lowest when imagining that the potential short-term partner is married, next lowest when imagining that she is not married but involved in casual sexual relationships, and highest when imagining that she is not married and not involved in any casual sexual relationships. These results suggest that, when selecting short-term sexual partners, men may do so in part to avoid sperm competition, even if they gain other benefits from selecting uninvolved women as short-term sexual partners, for instance, avoiding retaliation by kin and resident males.

Alternatively, men may prefer unmated women so as to avoid the costs associated with contracting a sexually transmitted disease (STD). The data, however, refute this alternative explanation. The potential short-term partner most likely to be infected with an STD would be the one having casual sex and, therefore, least preferred according to this alternative hypothesis; however, the married potential sexual partner was the least preferred. This study of men's preferences, therefore, suggests that avoiding STDs may be less important than avoiding sperm competition when selecting short-term partners.

Sperm Competition and Men's Sexual Arousal and Sexual Fantasies

It is well documented that men's sexual fantasies often involve multiple, anonymous partners (Ellis & Symons, 1990), but because these fantasies include more than sexual variety, it may be useful to interpret some of their facets in the light of sperm competition. Although never investigated empirically, one may assert with confidence that many men are sexually aroused by the exclusive sexual interaction between two women. A common scenario in mainstream movies and television shows, for example, involves two women, often implied or explicit heterosexuals, kissing or performing other sexual acts with one another while a male audience observes the acts and becomes sexually aroused. Similarly, two women dancing seductively with one another tends to stimulate interest among observing men. Perhaps this sight is sexually arousing because it suggests not only that both women are without

partners and sexually available, but also that copulation with both is possible. Bringing sperm competition theory to bear, however, might argue that sexual arousal occurs because the behavior cues an absence of sperm competition. Given a choice, men might prefer to avoid sperm competition and thus be the sole fertilizer of a woman's egg(s). Although speculative and difficult to test, this hypothesis serves to illustrate how the application of sperm competition theory to human mating psychology and behavior generates interesting and novel hypotheses.

Although the absence of sperm competition in a potential sexual partner may be sexually arousing, it has also been argued that the *presence* of sperm competition may result in sexual arousal. Pound (2002) argued that men should find cues of increased sperm competition risk sexually arousing because these call for frequent copulation as an effective method of paternity assurance. He further hypothesized that men, therefore, should be more aroused by pornography that incorporates cues of sperm competition than by comparable material in which such cues are absent. Indeed, content analyses of pornographic images on World Wide Web sites and of commercial "adult" video releases revealed that depictions of sexual activity involving a female and multiple males are more prevalent than those involving a male and multiple females. Strengthening his claim, an online survey of self-reported preferences and an online preference study that unobtrusively examined image selection behavior yielded corroborative results. Pound (2002) argued that the most parsimonious explanation for such results is that male arousal in response to visual cues of sperm competition risk reflects the functioning of psychological mechanisms that would have motivated adaptive patterns of copulatory behavior in ancestral males exposed to evidence of female promiscuity. This increased perception of sperm competition could antagonize the Coolidge effect. That is, whereas typically a male might be expected to show a decline in sexual interest in a sexual partner, visual cues of sperm competition could reduce this effect and increase sexual interest.

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 such cues are absent (Kilgallon & Simmons, 2005). Kilgallon and Simmons documented a higher percentage of motile sperm in men's ejaculates after they had viewed 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's ejaculates adjust in accordance with sperm competition theory. One might hypothesize that a man could produce even more competitive ejaculates when viewing images with cues

to sperm competition that included a woman resembling his partner. Computerized morphing techniques (e.g., Platek, Burch, Panyavin, Wasserman, & Gallup, 2002; Platek et al., 2003) could be used to test this hypothesis, but caution must be taken given the sometimes dangerous consequences of male sexual jealousy (Buss, 2000).

In addition to arousal, men might also experience increased sexual *motivation* or desire in response to cues of sperm competition risk, an idea supported by the anecdotal accounts of men who engage in "swinging" or "partner-swapping." Encouraging one's partner to copulate with other men appears to be a maladaptive strategy in that it increases the risk of cuckoldry; however, in some contemporary societies some men do just this—such men often report sexual arousal to the sight of their partner interacting sexually with other men (Talese, 1981). Moreover, they report increased sexual desire for their partner following such encounters with other men, and most acutely after witnessing their partner engaging in sexual intercourse (Gould, 1999).

Men may also voluntarily expose themselves to cues of sperm competition risk through their participation in sexual "role-playing" with their partner. Pretending to be someone other than himself may activate mechanisms associated with an increased risk of sperm competition, resulting in increased sexual arousal. For example, by role-playing, a man might see his partner behave as if she were copulating with another man. Alternatively, role-playing may be sexually arousing to men and women because it exploits mechanisms associated with sexual variety. Teasing the two hypotheses apart would require, among other tests, documenting how willing or excited men and women are to adopt a different role during role-playing. If the data revealed that when role-playing with their partners men are willing and excited to adopt a different role themselves, while simultaneously being unconcerned with whether or not their female partners do so, this evidence may constitute preliminary support for the sperm competition risk hypothesis.

Throughout this and the previous section, we discussed seemingly contradictory findings and hypotheses. We discussed (a) the findings of Shackelford and his colleagues (2004) who found that when selecting short-term sexual partners, men may do so in part to avoid sperm competition and (b) the speculative hypothesis that men's sexual arousal at the site of two women engaging in sexual behaviors may signal to men that there is no risk of sperm competition. We also discussed, however, (c) Pound's (2002) work showing that men found cues of increased sperm competition risk to be sexually arousing, (d) Kilgallon and Simmons's (2005) findings 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, (e) that a small percentage of men (e.g., swingers) report increased sexual desire for their partner following her sexual encounters with other men, and (f) the speculative hypothesis that some forms of role-playing might activate mechanisms in men associated with an increased risk of sperm competition. To understand why men might sometimes avoid sperm competition (as in "a" and "b" above), and at other times encourage sperm competition (as in "c" through "f" above), one must consider whether the circumstance involves actual or imagined behavior. If the circumstance involves actual behavior, encouraging sperm competition might be maladaptive and, thus, avoided (e.g., selecting short-term partners who present the lowest risk of sperm competition). If the circumstance involves imagined behavior (e.g., sexual fantasies), encouraging sperm competition is not maladaptive and indeed functions to increase sexual arousal. Sexual fantasies and sexual scenes involving cues to sperm competition increase sexual arousal, which subsequently increases sperm numbers and competitiveness (Pound, Javed, Ruberto, Shaikh, & Del Valle, 2002). That is, imagining or viewing cues to sperm competition can increase quantity and motility of sperm, markers of the competitiveness of an ejaculate. Thus, circumstances involving imagined behavior might involve encouraging sperm competition (e.g., viewing images or imagining scenarios depicting cues to sperm competition) as a means to increase sexual arousal and subsequent sperm quantity and quality.

This "actual versus imagined behavior" hypothesis, however, does not explain why some men (e.g., swingers) allow and encourage their partners to copulate with other men (point "e" above). "Swinger psychology," which appears to generate maladaptive behavior, however, is not typical of male psychology. Swingers occur very infrequently in the population (Talese, 1981) and probably represent the negative tail on a distribution of normal jealousy. That is, most men (the middle of the jealousy distribution) have jealousy mechanisms that are activated given appropriate input (e.g., nontrivial cues to infidelity). Men at the positive tail of this distribution might become jealous by inappropriate or trivial cues and may be labeled morbidly jealous (Easton, Schipper, & Shackelford, in press). Thus, the actual versus imagined behavior hypothesis is appropriate, given that swinger psychology may represent "noise" associated with developmental errors, mutation, and malfunctioning mechanisms.

Sperm Competition and Men's Sexual Coercion in Intimate Relationships

Noting that in waterfowl instances of forced in-pair copulation (i.e., partner rape) followed extra-pair copulations and considering reports

that forced in-pair copulation in humans often followed accusations of female infidelity, Thornhill and Thornhill (1992) and Wilson and Daly (1992) hypothesized that sexual coercion in response to cues of a partner's sexual infidelity might function in humans to force 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 (2006) found empirical support for this hypothesis in two studies. Specifically, men's sexual coercion in the context of an intimate relationship was related positively to their partners' infidelities. According to men's self-reports and women's partner-reports, men who used more sexual coercion in their relationship were mated to women who had been or were likely to be unfaithful. Starratt, Goetz, Shackelford, and McKibbin (2007) also reported that men who use certain types of insults against their partners, particularly accusations of sexual infidelity, are more likely to sexually coerce their partners. In other words, men who accuse their partners of having sex with one or more other men are more likely, relative to men who do not make those accusations, to sexually coerce their partners. Goetz and Shackelford (2007) have also documented that men's sexual coercion in intimate relationships is better predicted by women's infidelity than by men's controlling behavior, relationship violence, and dominant personality. This finding is important because two general hypotheses currently explain why many women experience sexual coercion by their intimate partners. The "domination and control" hypothesis, typically argued by feminists and traditional social scientists, posits that sexual coercion in intimate relationships is motivated by men's attempts to dominate and control their partners and that this expression of power is the product of men's social roles (e.g., Basil, 1999; Brownmiller, 1975; Gage & Hutchinson, 2006; Johnson, 1995). The other hypothesis, the sperm competition hypothesis, proposes that sexual coercion in intimate relationships functions to force a male's sperm into his partner's reproductive tract at a time when there is a high risk of cuckoldry, such as when a man suspects his partner has been sexually unfaithful. Although men's sexual coercion of their intimate partner involves domination and control, its function may be rooted in sperm competition.

What Are the Neurocognitive Correlates of Sperm Competition?

Although there is accumulating evidence that males prudently allocate sperm and engage differential psychological strategies that appear to be designed as a response to female infidelity, the neural correlates of such strategies have only recently been investigated. If, as hypothesized above, prudent sperm allocation is related to perceptions of infidelity,

then two recent studies suggest a network of brain substrates that, in the context of sperm competition, might be implicated in the neural control of physiological changes. Rilling, Winslow, and Kilts (2004) used positron emission tomography (PET) to measure brain activation when male rhesus macaques were allowed to observe their exclusive female mating partner engaging in copulation with a rival male. In this situation, activation was observed in the right superior temporal sulcus (STS) and amygdala. Rilling et al. suggested that activation of these areas might relate to similar reports of humans experiencing increased vigilance and anxiety under conditions of purported sexual infidelity by their partners. In a similar study conducted with humans, Takahashi et al. (2006) documented comparable activation (right amygdala) in men who were asked to read sentences that depicted their partner engaging in sexual infidelity. Because the amygdala is highly innervated with androgen receptors, increased anxiety and vigilance about partner infidelity could subsequently activate a system designed to respond to possible sperm competition. This hypothesis was partially supported by Rilling et al. (2004), who also demonstrated increases in circulating testosterone levels when macaques were challenged with the situation described above.

In fact, this neural response system might be "on line" in men prior to any observation or suspicion of infidelity. Shackelford et al. (2002) found that perceptions of mate attractiveness increase as a function of time spent apart from a partner, and Winston, O'Doherty, Kilner, Perrett, and Dolan (in press) recently found that such perceptions of attraction correlate with increased activity in the amygdala . Similarly, Winston et al. found increased anterior cingulate cortex (ACC) activation in men during rankings of attractiveness, and these authors relate the differential in ACC by sex activation to differences in arousal stemming from internal monitoring. In other words, a man might employ this substrate as part of a mechanism enabling him to make appropriate arousal valuations under circumstances when he suspects or has directly observed his partner's infidelity. This arousal might then lead to increased execution of sperm competitive behaviors and, possibly, to prudent sperm allocation.

Some data are accumulating that implicate the superior temporal sulcus (STS) in decisions about social interactions (e.g., Frith & Frith, 1999). Thus, the STS activation reported by Rilling et al. (2004) and Winston et al. (in press) might reflect the degree to which evaluations about infidelity and trustworthiness are made. Processing associated with social evaluation might also feed into the ACC. Platek, Keenan, and Mohamed (2005) identified a sex difference in activation of the ACC

in response to children's, but not adults', faces that share the subject's facial resemblance. Because facial resemblance appears to serve as an indicator of paternity (Platek et al., 2002, 2003, 2004), this finding suggests that the ACC might serve as a broad scale evaluation substrate for fidelity judgments.

Although further research is necessary to understand fully how the neural networks cause sperm competition responses—behaviorally, physiologically, and psychologically—preliminary evidence suggests that the networks will involve several key neurocognitive mechanisms: (a) social evaluation of partners on the basis of presumed propensity toward trustworthiness and fidelity (STS), (b) decisions about attractiveness and relation to internal monitoring, or decisions about belief in suspicions (ACC, STS, medial prefrontal cortex), and (c) automatic response generators (amygdala) that serve to moderate prudent sperm allocation and behaviors to "correct" a suspected or discovered partner infidelity (e.g., semen displacement, forced in-pair copulation, violence, or defection from pair bond). This network, apparently specific to men, may be quickly called into action during all phases of anticuckoldry tactics (mate guarding, sperm competition, and parental investment decisions; see Platek & Shackelford, 2006).

Is There Evidence of Contest Competition between Men's Ejaculates?

Even apart from the remarkable feat of traversing a hostile reproductive tract to fertilize an ovum or ova, sperm do some astonishing things. For example, sperm of the common wood mouse (*Apodemus sylvaticus*) have a hook that allows the sperm to adhere to one another to form a motile "train" of several thousand sperm (Moore, Dvorakova, Jenkins, & Breed, 2002). These trains display greater motility and velocity than single sperm, thereby facilitating fertilization. This cooperative behavior between sperm of a single male reveals that sperm are capable of complex behavior. Might mammalian sperm display equally complex behavior *in the presence of rival sperm*?

Baker and Bellis (1988) proposed that, in mammals, postcopulatory competition between rival male ejaculates might involve more than just scramble competition and that rival sperm may interfere actively with each other's ability to fertilize ova. Mammalian ejaculates contain sperm that are polymorphic, that is, existing in different morphologies or shapes and sizes. These occurrences were previously interpreted as the result of developmental error (Cohen, 1973). Baker and Bellis (1988), however, proposed that sperm polymorphism was not due to meiotic errors but instead reflected a functionally adaptive "division of labor" between sperm. They proposed two categories of sperm: "egg-get-

ters" and "kamikaze" sperm, the first comprising the small proportion of sperm programmed to fertilize ova. Kamikaze sperm, though, compose most of the ejaculate, functioning to prevent other males' sperm from fertilizing the ova by forming a barrier at strategic positions within the reproductive tract. Preliminary evidence for the Kamikaze Sperm Hypothesis came from the observation that the copulatory plugs of bats are composed of so-called "malformed" sperm (Fenton, 1984), and from documentation that, in laboratory mice, different proportions of sperm morphs are found reliably at particular positions within the female reproductive tract (Cohen, 1977).

Harcourt (1989) challenged Baker and Bellis's (1988) Kamikaze Sperm Hypothesis. Harcourt argued that "malformed" sperm were unlikely to have adaptive functions, citing evidence from Wildt et al. (1987) that, in lions, inbreeding results in an increase in the proportion of deformed sperm. Harcourt (1989) argued that, if deformed sperm were produced by an adaptation, inbreeding would not increase the expression of the trait, but instead would decrease it. Further he argued that the presence of malformed sperm in the copulatory plugs of bats is a consequence of the malformed sperm's poor motility and, therefore, that plug formation was not a designed function of deformed sperm. Following Cohen (1973), Harcourt (1989, p. 864) concluded that "abnormal sperm are still best explained by errors in production."

Baker and Bellis (1989a) responded to Harcourt's (1989) objections and elaborated on the Kamikaze Sperm Hypothesis. They proposed an even more active role for kamikaze sperm, speculating that evolutionary competition between ejaculates could result in kamikaze sperm that incapacitate rival sperm with acrosomal enzymes or by inducing attack by female leucocytes. In later work, they identified specialized roles for kamikaze sperm: "blockers" and "seek-and-destroyers," documenting that, when mixing ejaculates from two different men in vitro, agglutination and mortality of sperm increased. Baker and Bellis interpreted these findings as an indication that, when encountering sperm from another male, some sperm impede the progress of rival sperm (blockers) and some sperm attack and incapacitate rival sperm (seek-and-destroyers). The Kamikaze Sperm Hypothesis and the reported interaction of rival sperm have generated substantial criticism, however (see, e.g., Birkhead, Moore, & Bedford, 1997; Short, 1998). One criticism was that Baker and Bellis did not adequately label the sperm during the interactions so that it was not possible to determine if rival sperm were interacting or if self-sperm were interacting.

Moore, Martin, and Birkhead (1999) performed the first and, thus far, only attempt to replicate some of Baker and Bellis's (1995) work,

but failed to replicate their findings. It should be noted, however, that only a few of the predictions derived from the Kamikaze Sperm Hypothesis were tested by Baker and Bellis (1995) and even fewer were tested by Moore et al. (1999). After mixing sperm from different men and comparing these heterospermic samples to self-sperm (i.e., homospermic) samples, Moore et al. (1999) observed no increase in aggregation and no greater incidence of incapacitated sperm in the heterospermic samples. Moore and his colleagues did not replicate exactly the methodological procedures used by Baker and Bellis (1995), however. Heterospermic and homospermic samples, for example, were allowed to interact for just 1 to 3 hours, whereas Baker and Bellis (1995) allowed them to interact for fully 3 to 6 hours. Moore et al. (1999) offered a theoretical reason for this shorter interactive window—1 to 3 hours is the time that sperm normally remain in the human vagina—but perhaps this interval was too restrictive. Upon insemination, sperm have one of two initial fates: Some are ejected or secreted from the vagina and some travel quickly from the vagina to the cervix and uterus. Perhaps the majority of sperm competition takes place in the cervix and uterus, locations in the reproductive tract where sperm are able to interact for a prolonged period. If this is the case, Baker and Bellis's (1995) longer interactive window would be more valid ecologically. In addition, both Baker and Bellis (1995) and Moore et al. (1999) investigated sperm interactions in vitro, and one cannot be sure that sperm in a petri dish behave precisely as they do in the human vagina. Clearly, more work remains before a clear conclusion about the status of the hypothesis can be drawn. Yet, recent work by Kura and Nakashima (2000) might be viewed as encouraging for supporters of the hypothesis, however. Using theoretical and mathematical models to describe the conditions necessary for sperm classes to evolve, they concluded that such conditions are stringent and unlikely.

Future Directions

One possible research direction would be to demonstrate that these sperm competition behaviors in humans serve the function, thus far theoretical, of increasing the probability of producing offspring. Researchers have already established prudent sperm allocation according to risk of sperm competition (Parker, 1982, 1990a, 1990b), but do these behaviors actually increase the probability of fertilization? Were this so, these findings would not only add to the support for sperm competition theory in humans, but also could have practical medical implications for couples with fertility problems. Also, because much of the work presented here is still correlational, it will

be important for future researchers to use experimental methods. For example, it has already been shown that men at greater risk of sperm competition report their partner to be more attractive and that their partner finds them more attractive (Shackelford et al., 2002). Experimentally manipulating cues of sperm competition risk such that some men are exposed to these cues whereas others are not should confirm the previous results.

Concluding Remarks

Sperm competition and its effects have been documented or inferred to exist in dozens of nonhuman species, but researchers are beginning to uncover adaptations in humans that are also most parsimoniously explained by sperm competition theory. In humans, sperm competition may have influenced reproductive anatomy and physiology, men's attraction to and sexual interest in their partners, men's copulatory behaviors, men's short-term mate selection, men's sexual arousal and sexual fantasies, and men's sexual coercion in intimate relationships.

Although in this article we have focused on men's adaptations to sperm competition, women are not passive sperm receptacles. If sperm competition has been a recurrent feature of human evolutionary history, we would expect to identify adaptations not only in men but also in women in response to sperm competition. Indeed, intersexual conflict between ancestral males and females produces a co-evolutionary arms race between the sexes, in which an advantage gained by one sex selects for counter-adaptations in the other sex (see, e.g., Rice, 1996). Thus, men's numerous adaptations to sperm competition are likely to have been met by numerous adaptations in women (e.g., Gallup & Burch, 2006). Research on female adaptation is clearly an area for future work (see Shackelford, Pound, & Goetz, 2005).

The likelihood or selective importance of sperm competition in humans was once only an issue of scholarly debate and controversy. Those questioning the application of sperm competition to humans (e.g., Birkhead, 2000; Dixson, 1998; Gomendio et al., 1998) contended that sperm competition in humans, although possible, might not be as intense as in other species showing adaptations. However, recent work on the psychological, behavioral, and anatomical evidence of human sperm competition reviewed in this article had not been considered in these previous critiques. Taking into consideration the developing evidence of adaptations to sperm competition in humans makes it now reasonable to conclude that sperm competition is likely to have been a recurrent and selectively important feature of human evolutionary history.

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