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[in press, *Annual Review of Sex Research*, June 2007]

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

Aaron T. Goetz, Ph.D.
Florida Atlantic University
Department of Psychology
2912 College Avenue
Davie, Florida 33431
Office: 954-236-1179
Fax: 954-236-1099
E-mail: agoetz2@fau.edu

Todd K. Shackelford, Ph.D.
Florida Atlantic University
Department of Psychology
2912 College Avenue
Davie, Florida 33431
Office: 954-236-1179
Fax: 954-236-1099
E-mail: tshackel@fau.edu

Steven M. Platek, Ph.D.
University of Liverpool
School of Biological Sciences
Biological Sciences Building
Liverpool L69 7ZB, UK
Office: +44 (0) 151 795 4517
Fax: +44 (0) 151 795 4088
E-mail: splatek@liv.ac.uk

Valerie G. Starratt, M.A.
Florida Atlantic University
Department of Psychology
2912 College Avenue
Davie, Florida 33431
Office: 954-236-1179
Fax: 954-236-1099
E-mail: ystarrat@fau.edu

William F. McKibbin, M.A.
Florida Atlantic University
Department of Psychology
2912 College Avenue
Davie, Florida 33431
Office: 954-236-1179
Fax: 954-236-1099
E-mail: wmckibbi@fau.edu

Abstract

With the recognition, afforded by evolutionary science, that female infidelity was a recurrent feature of our evolutionary past has come the development of a unique 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. Males must compete for mates, but 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 two decades since Smith (1984) first argued that sperm competition occurs in humans, the application of sperm competition theory to humans has been enriched with exciting new ideas and discoveries. In this article, we review this recent theoretical and empirical work on human sperm competition, identify limitations and challenges of this research, and highlight important directions for future research.

Sperm Competition in Humans:

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Male competition for mates may take many forms. Males may compete by displaying the grandest plumage, having the largest antlers, or even fighting to the death (Alcock, 2004). They may even compete at the level of their sperm. This phenomenon is 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 *precopulatory* adaptations associated with intrasexual competition (e.g., horns on beetles, status seeking in men), researchers studying sperm competition aim to identify *postcopulatory* adaptations. Thus, an alternative way of thinking about sexual selection is that in some species there is not only a competition between males for mates, but a 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 the reproductive tract of a female, 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 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), does not capture the full spectrum of male anatomy, physiology, psychology, and behavior associated with sperm competition. In this article, we review the current state of knowledge regarding human sperm competition.

Sperm Competition as an Adaptive Problem in Humans

Smith (1984) presented theoretical arguments for the existence of sperm competition in humans. Sperm competition in humans requires that a woman copulates with more than one man within roughly a five-day period, although some have argued for a more conservative estimate (e.g., Gallup, Burch, & Berens Mitchell, 2006). 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 punish and discourage 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 anti-cuckoldry 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 is an emotion experienced when a valued relationship is threatened by a real or imagined rival, and 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 female infidelity likely occurred throughout human evolution with a frequency that would result in nontrivial levels of sperm competition. Finally, recent research that we review 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 do not have adaptations that have evolved to deal with particularly *high* levels of sperm competition, men may have adaptations that evolved to deal with *variable* levels 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. 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.

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 where overall levels are not especially high—but where sperm competition is a sufficiently frequent occurrence to select for mechanisms that allow prudent sperm allocation.

Studying humans, Baker and Bellis (1989, 1993a) 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 (Baker & Bellis, 1995; Shackelford et al., 2002). 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, 1989, 1995). 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 empirical research has focused on the psychological mechanisms that might be involved in regulating such responses. Adaptive changes in semen parameters can 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, LeBlanc, Weekes-Shackelford, Bleske-Rechek, Euler, and Hoier (2002) investigated the psychological responses of men to cues of sperm competition risk, arguing that there must be psychological mechanisms in men that evolved to motivate behavior that would have increased 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 that human male psychology may include *psychological* adaptations to decrease the likelihood that a rival man's sperm will fertilize a partner's ovum. Consistent with their 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 theory can account for the predictive utility of the proportion of time spent apart since the couple’s last copulation, independent of the total time since last copulation and independent of relationship satisfaction. 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 when there is a greater risk of sperm competition. Shackelford, Goetz, McKibbin, and Starratt (2007) documented that 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. These psychological mechanisms 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 committed an extra-pair copulation.

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 Baker and Bellis's (1993) "topping-up" model, a woman's primary partner should desire to maintain an optimum level of sperm in his partner'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, 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. We elaborate on this hypothesis in the section titled, *Sperm Competition and Men's Sexual Coercion in Intimate Relationships*.

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 the fact that men have testes that are larger relative to body size than those of monandrous species such as the gorilla and orangutan suggests that 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 multiply. When the degree of polyandry is considered along a continuum, it is likely that, although human males have not experienced levels of sperm competition as high as have been documented in some primate species, it is 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 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 male's genitals might remove rival sperm. He documented, for example, that the penis of the damselfly is equipped with spines that are able to remove up to 99% of the sperm stored in a female (Waage, 1979). Sperm displacement is not limited to damselflies, but is a sperm competition mechanism 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).

The human male's penis does not possess barbs and spines for removing rival sperm, but recent empirical evidence suggests that the human penis 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) hypothesis that the human penis may be designed to displace semen deposited by other men in the reproductive tract of a woman. Gallup and his colleagues (2003) documented that artificial phalluses that had a glans and a coronal ridge that approximated a real human penis displaced significantly more simulated semen than did a phallus that did not have a glans and a coronal ridge. 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, suggesting that successfully 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 in the reproductive tract is

relatively greater), both sexes report that men thrust deeper and more quickly at the couple's next copulation (Gallup et al., 2003). Such vigorous copulatory behaviors are likely to increase semen displacement.

In an independent test of the hypothesis that successfully displacing rival semen may require specific copulatory behaviors, Goetz and his colleagues (2005) investigated whether and how men under a high risk of sperm competition (i.e., men mated to women who have personality characteristics that attract mate poachers) might attempt to “correct” a female partner's sexual infidelity. Using a self-report survey, men in committed, sexual relationships reported their use of specific copulatory behaviors arguably designed to displace the semen of rival men. These copulatory behaviors included number of thrusts, deepest thrust, depth of thrusts, on average, and duration of sexual intercourse. An increase in these behaviors would afford a man a better chance to displace rival semen. As hypothesized, men mated to women who place them at a high recurrent risk of sperm competition were more likely to perform semen-displacing behaviors, suggesting that men perform specific copulatory behaviors apparently designed to correct female sexual infidelity by displacing rival semen that may be present in the woman's reproductive tract.

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 least conservative estimates of the frequency of extra-pair copulations are accepted. The consequences of such an effect might be minimized, however, if the temporal spacing between successive in-pair copulations is much greater than the spacing between copulations involving different men. Indeed, the refractory period may have been designed for this purpose (Gallup & Burch, 2004). The inability to maintain an erection following ejaculation

may function to minimize self-semen displacement. Furthermore, the costs associated with self-semen displacement might be minimal because ejaculation follows copulatory behavior that might have removed sperm. A savings account will not deplete if a deposit quickly follows each withdrawal.

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 competition 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 function to select as short-term sexual partners women who present the lowest risk of current or future sperm competition (Shackelford, Goetz, LaMunyon, Quintus, & Weekes-Shackelford, 2004). The risk of sperm competition for a man increases with a prospective short-term partner's involvement in one or more relationships. Women who are not in a long-term relationship and do not have casual sexual partners, for example, present a low risk of sperm competition. Consequently, 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. Other benefits are reaped from selecting uninvolved women as short-term sexual partners (e.g., avoiding retaliation by kin and resident males), but among those benefits are avoiding sperm competition.

An alternative explanation for the pattern of results is that by preferring unmated women, men can 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, would be least preferred according to this alternative hypothesis. The married potential sexual partner, however, was the least preferred. Men's preferences, therefore, suggest 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 men's sexual fantasies include more than sexual variety. Because sperm competition seems to have been a recurrent feature of human evolutionary history, it may be useful to interpret some facets of men's sexual fantasies 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. Hollywood seems

to be aware of this preference as well. A common scenario in many 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 an audience of one or more men observes the acts and becomes sexually aroused. Similarly, two women dancing seductively with one another tends to stimulate interest among observing men. It could be argued that the sight of two heterosexual women engaging in sexual behaviors is sexually arousing because it might suggest that both women are sexually available and copulation with both is possible. An interpretation informed by sperm competition theory, however, might argue that the sight of two heterosexual women engaging in sexual behaviors is sexually arousing because it is a cue to an absence of sperm competition. If given a choice, men might prefer to avoid sperm competition and thus be the sole fertilizers of a woman's egg(s). Thus, two women engaging in sexual behaviors may signal to men that the women are without male partners and, therefore, pose no risk of sperm competition. Although highly 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 is expected to be sexually arousing, it also has 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 to be sexually arousing because frequent copulation can be an effective method of paternity assurance. Pound (2002) 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. 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. 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 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. One might hypothesize that a man could produce even more competitive ejaculates when viewing images depicting cues to sperm competition that included a woman that resembled 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).

The idea that men might experience increased sexual motivation in response to cues of sperm competition risk also is supported by 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, it seems that in some contemporary societies some men do just this—perhaps because such men often report that they find the sight of their partner interacting sexually with other men to be sexually arousing (Talese, 1981). Moreover, they report that they experience increased sexual desire for their partner following her sexual encounters with other men, and some indicate that this increase in desire is particularly acute when they have witnessed their partner having sexual intercourse with another man (Gould, 1999). Thus, it appears that psychological cues to sperm competition might serve to antagonize the Coolidge effect.

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 in men associated with an increased risk of sperm competition, resulting in increased sexual arousal. For example, by “role-playing,” a man might get to 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 is exploiting 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 unconcerned with whether or not their female partners adopts a different role, this may constitute preliminary support for the

sperm competition risk hypothesis. Again, applying sperm competition theory to aspects of human sexual psychology and behavior may generate unique perspectives and hypotheses.

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 that they experience 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 serve to 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, circumstances involving actual sexual behavior should involve avoiding sperm competition (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 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 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, which is not maladaptive.

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 (i.e., point “e” above). “Swinger psychology” appears to generate maladaptive behavior. Swinger psychology, 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 have jealousy mechanisms that are activated given appropriate input (e.g., nontrivial cues to infidelity), and these men represent the middle of the jealousy distribution. Men at the positive tail of this distribution might become jealous by inappropriate or trivial cues—such men may be labeled morbidly jealous (Easton, Schipper, & Shackelford, in press). Thus, the “actual versus imagined behavior” hypothesis for why men appear to avoid and encourage sperm competition is appropriate given that swinger psychology is noise associated with developmental errors, mutation, and malfunctioning mechanisms.

Sperm Competition and Men’s Sexual Coercion in Intimate Relationships

Noting that instances of forced in-pair copulation (i.e., partner rape) followed extra-pair copulations in waterfowl and 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 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 (2006) 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 used more sexual coercion in their relationship are mated to women who had been or were likely to be unfaithful. Starratt, Goetz, Shackelford, and McKibbin (under review) 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 there currently are two general hypotheses to explain why many women experience sexual coercion by their intimate partners. The "domination and control" hypothesis, typically argued by feminists and standard social scientists, posits that sexual coercion in intimate relationships is motivated by men's attempts to dominate and control their partner 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 sperm competition hypothesis, again, proposes that sexual coercion in intimate relationships functions to introduce 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 further research needs to be conducted, the sperm competition hypothesis seems to

better account for men's sexual coercion in intimate relationships than the domination and control hypothesis.

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 might be implicated in the neural control of sperm competitive 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. When challenged with such a situation, activation was observed in the right superior temporal sulcus (STS) and amygdala. Rilling et al. (2004) suggest 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. A similar study, conducted in humans, documented similar activation (right amygdala) in men who were asked to read sentences that depicted their partner engaging in sexual infidelity (Takahashi et al., 2006). Because the amygdala is highly innervated with androgen receptors, one can conclude that increased anxiety and vigilance about partner infidelity could subsequently activate a system designed to act in response 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 observation of their mate engaged in a sexual infidelity.

This neural response system might be “on line” in men prior to 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. Interestingly, perceptions of attraction in men correlate with increased activity in the amygdala (Winston, O’Doherty, Kilner, Perrett, & Dolan, in press). Similarly, Winston et al. (in press) found increased anterior cingulate cortex (ACC) activation in men during rankings of attractiveness. The differential in ACC by sex activation is suggested by these authors to relate to differences in arousal that stem from internal monitoring. In other words, a man might employ this substrate as part of a mechanism enabled 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 prudent sperm allocation.

There are accumulating data implicating the superior temporal sulcus (STS) in decisions about social interactions (e.g, Frith & Frith 1999). Thus, the STS activation reported Rilling et al. and Winston et al. 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 adult’s, faces that share 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 future research is necessary to more fully understand how the neural networks cause sperm competition responses, behaviorally, physiologically, and psychologically, preliminary evidence suggests that the network will involved several key neurocognitive

mechanisms: 1) social evaluation of partners on the basis of presumed propensity towards trustworthiness and fidelity (STS), 2) decisions about attractiveness and relation to internal monitoring, or decisions about belief in suspicions (ACC, STS, medial prefrontal cortex), and 3) automatic response generators (amygdala) that serve to moderate prudent sperm allocation and behaviors involved in “correcting” a suspected or discovered partner infidelity (e.g., semen displacement, forced in-pair copulation, violence, or defection from pair bond). It is hypothesized that this specific network is specific to men and may be quickly called into action during all phases of anti-cuckoldry tactics (mate guarding, sperm competition, and parental investment decisions; see Platek & Shackelford, 2006).

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

Apart from the remarkable feat of traversing a hostile reproductive tract to fertilize an ovum or ova, sperm do some astonishing things. 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, 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 (i.e., existing in different morphologies or shapes and sizes). Previously interpreted as the result of developmental error (Cohen, 1973), Baker and Bellis (1988) proposed that sperm polymorphism was not due to meiotic errors, but instead reflected a

functionally adaptive “division of labor” between sperm. Baker and Bellis (1988) proposed two categories of sperm: “egg-getters” and “kamikaze” sperm. Egg-getters comprise the small proportion of sperm programmed to fertilize ova. Baker and Bellis (1988) argued that most of the ejaculate is composed of kamikaze sperm that function 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. Harcourt (1989) also argued that the presence of malformed sperm in the copulatory plugs of bats is a consequence of the malformed sperm’s poor mobility 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 (1989b) responded to Harcourt’s (1989) objections and elaborated on the Kamikaze Sperm Hypothesis. In their elaboration, Baker and Bellis (1989b) proposed a more active role for kamikaze sperm, speculating that evolutionary arms races between ejaculates could result in kamikaze sperm that incapacitate rival sperm with acrosomal enzymes or by inducing attack by female leucocytes. Baker and Bellis (1995) proposed specialized roles for

kamikaze sperm and identified two categories of kamikaze sperm: “blockers” and “seek-and-destroyers.” Baker and Bellis (1995) documented 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).

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 the findings of Baker and Bellis. 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 one to three hours, whereas Baker and Bellis (1995) allowed them to interact for fully three to six hours. Moore et al. (1999) offered theoretical reasons for this shorter interactive window (i.e., because one to three 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 warfare 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, three to six hour 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 we can draw a clear conclusion about the status of the hypothesis. Recent work by Kura and Nakashima (2000) might be viewed as encouraging for supporters of the hypothesis, however. Kura and Nakashima (2000) used theoretical and mathematical models to describe the conditions necessary for soldier sperm classes to evolve, and concluded that such conditions are not stringent and far from unlikely.

Future Directions

One possible future direction would be to demonstrate evidence that these sperm competition behaviors in humans serve the thus far theoretical function of increasing the probability of producing offspring. For instance, research has demonstrated evidence of prudent sperm allocation according to risk of sperm competition, where men inseminate more sperm when the risk is higher (Parker, 1982, 1990a, 1990b). It would be interesting to determine whether these behaviors actually translate into increased probability of insemination. Were this supported, 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, much of the work presented here is correlational in design. It will be important for future research to utilize experimental methods. For example, it has been shown that men at greater risk of sperm competition report their partner to be more attractive, and report that their partner finds them more attractive (Shackelford et al., 2002). It may be useful to manipulate experimentally

cues of sperm competition risk such that some men are exposed to cues of sperm competition whereas others are not. Men in the former, experimental condition are predicted to subsequently rate their partner to be more attractive and to report that their partner finds them more attractive, for example.

Concluding Remarks

Sperm competition and its effects have been documented or inferred to exist in dozens of non-human species, but researchers are beginning to uncover adaptations in humans that are 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 this article focuses on men's adaptations to sperm competition, women are not passive sperm receptacles. If sperm competition was a recurrent feature of human evolutionary history, we would expect to identify adaptations not only in men but also adaptations in women in response to sperm competition. In deed, 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 be met by numerous adaptations in women (e.g., Gallup & Burch, 2006). This is clearly an area for future work (and see Shackelford, Pound, & Goetz, 2005).

The likelihood or selective importance of sperm competition in humans was once 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, may not be as intense as in other species with adaptations to sperm competition. Recent work on the psychological, behavioral, and anatomical evidence of human sperm competition (reviewed in this article), however, was not considered in these previous critiques of human sperm competition. When considering all of the evidence of adaptations to sperm competition in humans, it is now reasonable to conclude that sperm competition is likely to have been a recurrent and selectively important feature of human evolutionary history.

Acknowledgements

We thank Gordon Gallup, Nicholas Pound, Rebecca Burch, and an anonymous reviewer for comments that greatly improved this article.

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