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Sperm competition and its evolutionary consequences in humans

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Identifying sperm competition

Sexual selection is the mechanism that favors an increase in the frequency of alleles associated with reproduction (Darwin, 1871). Darwin distinguished sexual selection from natural selection, but today most evolutionary scientists combine the two concepts under the name, natural selection. Sexual selection is composed of intrasexual competition (competition between members of the same sex for sexual access to members of the opposite sex) and intersexual selection (differential mate choice of members of the opposite sex). Focusing mainly on precopulatory adaptations associated with intrasexual competition and intersexual selection, postcopulatory sexual selection was largely ignored even a century after the presentation of sexual selection theory. Parker (1970) was the first to recognize that male–male competition may continue even after the initiation of copulation when males compete for fertilizations. More recently, Thornhill (1983) and others (e.g. Eberhard, 1996) recognized that intersexual selection may also continue after the initiation of copulation when a female biases paternity between two or more males' sperm. The competition between males for fertilization of a single female's ova is known as *sperm competition* (Parker, 1970), and the selection of sperm from two or more males by a single female is known as *cryptic female choice* (Eberhard, 1996; Thornhill, 1983). Although sperm competition and cryptic female choice together compose postcopulatory sexual selection (see Table 6.1), sperm competition is often used in reference to both processes (e.g. Baker & Bellis, 1995; Birkhead & Møller, 1998; Simmons, 2001; Shackelford, Pound, & Goetz, 2005). In this chapter, we review the current state of knowledge regarding human sperm competition (and see Shackelford *et al.*, 2005).

Table 6.1. *Precopulatory and postcopulatory sexual selection.*

	Sexual selection	
	Intrasexual competition	Intersexual selection
Precopulatory	How do males compete for mates?	How do females select mates?
Postcopulatory	If two or more males have copulated with a female, how do males compete for fertilizations? (sperm competition)	If a female has copulated with two or more males, how does she select sperm? (cryptic female choice)

Sperm competition in non-human species

Examining the adaptive problems non-human species faced and the resultant evolved solutions to these problems can often provide insight into the adaptive problems and evolved solutions in humans (and vice versa). Shackelford and LeBlanc (2001) argued that because humans share similar adaptive problems with insects (e.g. mate retention) and birds (e.g. extra-pair copulations), humans, insects, and birds may share similar solutions to these adaptive problems. Shackelford and LeBlanc (2001) argued that applying a comparative evolutionary psychological approach to the study of evolved solutions to problems of sperm competition may lead to a better understanding of human sperm competition. We will therefore review some of the first work on sperm competition relevant to humans.

In species with internal fertilization, there exists the potential for sperm competition whenever a female mates with multiple males in a sufficiently short period of time so that live sperm from two or more males are present in her reproductive tract. One of the first hypotheses generated by sperm-competition theory was that males will deliver more sperm when the risk of sperm competition is high (Parker, 1982, 1990a). Across species, therefore, investment in sperm production is predicted to depend on the risk of sperm competition. Within species, males are predicted to allocate their sperm in a prudent fashion and inseminate more sperm when the risk of sperm competition is higher. In accordance with hypotheses generated by sperm-competition theory, investment in sperm production is greater in species for which the risk of sperm competition is higher. In primates (Harcourt *et al.*, 1981; Harvey & Harcourt, 1984; Short, 1979), birds (Møller, 1988a), ungulates (Ginsberg & Rubenstein, 1990), frogs (Jennions & Passmore, 1993), and butterflies (Gage, 1994) testis size (an index of investment in sperm production) is correlated positively with the frequency with which females engage in polyandrous matings. Recent work,

in addition, has demonstrated experimentally that exposure to mating environments with high levels of sperm competition can produce significant increases in testis size after only 10 generations in yellow dung flies (*Scathophaga stercoraria*; Hosken & Ward, 2001).

In addition to the evidence that investment in sperm production depends on the risk of sperm competition across species, evidence is accumulating that individual males are capable of prudent sperm allocation (for reviews see Parker *et al.*, 1997; Wedell, Gage, & Parker, 2002). Experiments have demonstrated that males in many species are capable of adjusting the number of sperm they deliver from one insemination to the next in response to cues of sperm-competition risk or intensity. Males need to rely on cues predictive of sperm-competition risk because this risk often cannot be assessed directly. Accordingly, there is experimental evidence that males of various species respond to cues of elevated sperm-competition risk in an adaptive fashion. Some of the cues used include male mating status, in species where it predicts the likelihood of mating with an already-mated female (Cook & Wedell, 1996), and female mating status where it is detectable (Gage & Barnard, 1996). In addition, males of various species appear to be sensitive to the mere presence of one or more rival males during a particular mating event. Field crickets (*Gryllobates supplicans*) and house crickets (*Acheta domesticus*), for example, increase the number of sperm they inseminate in proportion to the number of rivals present (Gage & Barnard, 1996). Of perhaps most relevance to the work on the responses of human males to cues of sperm competition risk is the finding that male rats (*Rattus norvegicus*) adjust the number of sperm they inseminate depending on the amount of time they have spent with a particular female prior to copulation (Bellis, Baker, & Gage, 1990). In addition, male rats inseminate more sperm when mating in the presence of a rival male (Pound & Gage, 2004).

For species that practice social monogamy, the mating system in which males and females form long-term pair bonds but also pursue extra-pair copulations, extra-pair copulations by females create the primary context for sperm competition (Birkhead & Møller, 1992; Smith, 1984). A male whose female partner engages in an extra-pair copulation is at risk of cuckoldry and its associated reproductive costs. These reproductive costs include loss of the time, effort, and resources the male spent attracting his partner, the potential misdirection of his current and future resources to a rival's offspring, and the loss of his mate's investment in any offspring he may have had with her in the future (Buss, 2004; Trivers, 1972). Because cuckoldry is so reproductively costly, males of paternally investing species are expected to possess adaptations that decrease the likelihood of being cuckolded.

Anti-cuckoldry tactics fall into three categories: *preventative tactics*, designed to minimize female infidelity; *sperm-competition tactics*, designed to minimize conception in the event of female infidelity; and *differential paternal investment*, designed to allocate paternal investment prudently in the event that female infidelity may have resulted in conception (Platek, 2003; Shackelford *et al.*, 2000; Wilson & Daly, 1992). It is expected that for a given mating interaction, the performance of these tactics will tend to proceed in the sequence outlined above. A male's best strategy is to prevent female infidelity and, if he is unsuccessful in preventing female infidelity, he would benefit by attempting to prevent conception by a rival male. If he is unsuccessful in preventing conception by a rival male, he would benefit by adjusting paternal effort according to available paternity cues. The performance of one tactic does necessitate the neglect of another tactic; indeed, a reproductively wise strategy would be to perform all three categories of anti-cuckoldry tactics.

Male swallows (*Hirundo rustica*), a socially monogamous species, have been observed performing preventative tactics, sperm-competition tactics, and differential paternal investment (Møller, 1985, 1987, 1988b; cited in Wilson & Daly, 1992). Male swallows guard their mates while they are fertile (Møller, 1987); they adjust their rate of in-pair copulation relative to the proximity of rival males (Møller, 1985); and they adjust paternal effort according to the observed frequency of their mate's extra-pair copulations (Møller, 1988b). Employing preventative tactics, sperm-competition tactics, and differential paternal investment to avoid the costs associated with cuckoldry, male swallows, as well as males of other bird species, possess an arsenal of anti-cuckoldry tactics. Before we examine men's anti-cuckoldry tactics and other adaptive solutions created by sperm competition, we must first consider whether sperm competition was an important selection pressure for humans.

Has sperm competition been an important selection pressure for humans?

The likelihood and selective importance of sperm competition in humans are issues of scholarly debate and controversy. Smith (1984) argued that the comparatively large size of the human penis, and the fact that human testes are somewhat larger in relation to body size than are those of monogamous primates (Short, 1981), suggests that sperm competition has been a recurrent feature of human evolutionary history. Smith (1984) argued that facultative polyandry (i.e. female sexual infidelity) would have been the most common reason for the simultaneous presence of live sperm from two or more men in the reproductive tract of an ancestral woman. Smith (1984) acknowledged that

other contexts in which sperm competition might have occurred include consensual communal sex, courtship, rape, and prostitution, but argued that these contexts may not have occurred with sufficient frequency over human evolutionary history to provide selection pressures for adaptations to sperm competition equivalent to female infidelity.

Evidence of an evolutionary history of female infidelity and sperm competition is provided by the ubiquity and power of male sexual jealousy. Male sexual jealousy could only evolve if female sexual infidelity was a recurrent feature of human evolutionary history (see e.g. Buss *et al.*, 1992; Daly, Wilson, & Weghorst, 1982; Symons, 1979), and female infidelity increases the likelihood that sperm from two or more men recurrently occupied the reproductive tract of a single woman. Indeed, based on past and present infidelity rates of men and women, it may be concluded that humans practice social monogamy. Because of female sexual infidelity, members of socially monogamous species are likely to face the adaptive problems associated with sperm competition (Birkhead & Møller, 1992; Smith, 1984).

Recent genetic studies provide additional evidence for a long evolutionary history of sperm competition in humans. Investigating genes that code for proteins involved in the production and function of sperm, Wyckoff, Wang, and Wu (2000) found that these genes have been evolving at a much faster rate than most other human genes. Wyckoff *et al.* (2000) concluded that this rapid genetic change could only have occurred if ancestral women had concurrent sexual partners often enough that sperm of different men competed to fertilize a woman's eggs.

Those questioning the application of sperm competition to humans (e.g. Birkhead, 2000; Dixson, 1998; Gomendio, Harcourt, & Roldán, 1998) contend 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 chapter), however, was not considered in these previous critiques of human sperm competition. When considering all of the evidence of adaptations to sperm competition in men and in women, it is reasonable to conclude that sperm competition is likely to have been a recurrent and selectively important feature of human evolutionary history.

DO WOMEN GENERATE SPERM COMPETITION?

Evolutionary accounts of human sexual psychology have tended to emphasize the benefits to men of short-term mating and sexual promiscuity (e.g. Buss & Schmitt, 1993; Symons, 1979). For men to pursue short-term sexual strategies, however, there must be women who mate non-monogamously

(Greiling & Buss, 2000). Moreover, if ancestral women never engaged in short-term mating, men could not have evolved a strong desire for sexual variety (Schmitt, Shackelford, & Buss, 2001b; Schmitt *et al.*, 2001a, 2003; Smith, 1984).

Ancestral women may have benefited from facultative polyandry in several ways (Smith, 1984; for a review, see Greiling & Buss, 2000). Some of the most important potential benefits include the acquisition of resources, either in direct exchange for sex with multiple men (Symons, 1979) or by creating paternity confusion as a means to elicit investment (Hrdy, 1981). Alternatively, ancestral women may have benefited indirectly by accepting resources and parental effort from a primary mate while copulating opportunistically with men of superior genetic quality (Smith, 1984; Symons, 1979). Furthermore, extra-pair sex might have been useful as insurance against the possibility that a primary mate was infertile, and in unpredictable environments it may be advantageous for women to ensure that offspring are sired by different men and are thus genetically diverse (Smith, 1984). Jennions and Petrie (2000) provide a comprehensive review of the genetic benefits to females of multiple mating.

Multiple mating by women is a prerequisite for sperm competition to occur, but not all patterns of polyandry will generate postcopulatory competition between men. For sperm competition to occur, women must copulate with two or more men in a sufficiently short period of time such that there is overlap in the competitive life spans of the rival ejaculates. The length of this competitive "window" might be as short as 2–3 days (Gomendio & Roldán 1993), or as long as 7–9 days (Smith, 1984). Using an intermediate estimate of 5 days, Baker and Bellis (1995) argued that the questionnaire data they collected on female sexual behavior indicated that 17.5% of British women "double-mated" in such a way as to generate sperm competition (in the absence of barrier contraception) at some point during the first 50 copulations in their lifetimes. Although questions have been posed about the accuracy of this estimate (e.g. Gomendio *et al.*, 1998), it is clear that women in contemporary human populations do frequently mate in a polyandrous fashion and thus potentially generate sperm competition in their reproductive tracts.

Large-scale studies of sexual behavior have not collected data on the frequency with which women double-mate specifically, but many have recorded how often they engage in concurrent sexual relationships more generally. Laumann *et al.* (1994), for example, found that 83% of respondents who report having had five or more sexual partners in the past year also report that at least two of these relationships were concurrent. Not all concurrent sexual relationships involve copulations with different men within a sufficiently short space of time to be considered double-matings, but it is likely that many do. For this

reason, some researchers have argued that the rate at which women participate in concurrent sexual relationships provides an index of the likelihood of sperm competition in a population. Gomendio *et al.* (1998), for example, argued that survey data indicate that only 2% of women in Britain have engaged in concurrent sexual relationships in the past year and, consequently, that sperm competition is likely to be a relatively infrequent occurrence. However, a major study of sexual behavior in Britain – the National Survey of Sexual Attitudes and Lifestyles conducted between 1999 and 2001 (Johnson *et al.*, 2001) – revealed that 9% of women overall, and 15% of those aged 16–24 years, reported having had concurrent sexual relationships with men during the preceding year.

It is likely that women's sexual behavior does sometimes generate sperm competition. Bellis and Baker (1990) argued that women “schedule” or time their copulations in a way that *actively promotes* sperm competition. Active promotion of successive insemination by two or more men may allow a woman to be fertilized by the most competitive sperm. Bellis and Baker (1990) documented that women are more likely to double-mate when the probability of conception is highest, suggesting that women may promote sperm competition. When the probability of conception is lower, in contrast, women separate in time in-pair and extra-pair copulations over a 5-day period, making sperm competition less likely. Bellis and Baker (1990) argued that the results cannot be attributed to men's preferences for copulation with women at peak fertility. According to Bellis and Baker (1990), if the results were due to men's preferences for copulation during peak fertility and not to women's active promotion of sperm competition, then in-pair copulations should occur more often during fertile phases of the menstrual cycle, just as was found for extra-pair copulations.

Bellis and Baker (1990) may have been too quick to dismiss the possibility that men prefer to copulate with a woman during peak fertility, however. Because women may be attempting to secure genetic benefits from their extra-pair partners (see Gangestad & Simpson, 2000; Greiling & Buss, 2000), women are predicted to prefer to copulate with extra-pair partners when conception is highest. A woman might simultaneously avoid copulation with an in-pair partner while seeking extra-pair sex. So, although her in-pair partner might prefer to copulate with her precisely during the peak fertility phase of her cycle, this may not be reflected in her actual pattern of copulations. Therefore, Bellis and Baker's (1990) finding that women are more likely to double-mate when the probability of conception is highest is consistent with the hypothesis that women sometimes actively promote sperm competition, but does not rule out the possibility that both in-pair and extra-pair partners prefer to copulate with a woman during her peak fertility.

POLYANDROUS SEX IN WOMEN'S FANTASIES

Sexual fantasy may provide a "window" through which to view the evolved psychological mechanisms that motivate sexual behavior (Ellis & Symons, 1990; Symons, 1979). A large empirical literature has addressed sex differences in sexual fantasy, and much of this work has been conducted from an evolutionarily informed perspective (see, e.g. Ellis & Symons, 1990; Wilson, 1987, 1997; Wilson & Lang, 1981; and see Leitenberg & Henning, 1995, for a broad review of empirical work on sexual fantasy). This work documents several marked sex differences in the content of sexual fantasies, consistent with hypotheses generated from Trivers' (1972) theory of parental investment and sexual selection. For example, given the asymmetric costs associated with sexual reproduction, sexual access to mates limits reproductive success for males more than for females. Consequently, it has been hypothesized that men more than women will have sexual fantasies that involve multiple, anonymous sexual partners who do not require an investment of time, energy, or resources prior to granting sexual access (e.g. Ellis & Symons, 1990), and empirical investigations have confirmed this hypothesis. Indeed, one of the largest sex differences occurs for fantasies about having sex with two or more members of the opposite sex concurrently, with men more than women reporting this fantasy (see review in Leitenberg & Henning, 1995).

Tests of the hypothesis that men more than women fantasize about concurrent sex with two or more partners have inadvertently provided data on women's polyandrous sexual fantasies. Although this work clearly indicates that men are more likely than women to report fantasies of concurrent sex with multiple partners, polyandrous sex is a reoccurring theme for some women. In a large survey study, for example, Hunt (1974) found that 18% of women report fantasies of polyandrous sex, imagining themselves as a woman having sex with two or more men concurrently. Wilson (1987) surveyed nearly 5000 readers of Britain's top-selling daily newspaper about their favorite sexual fantasy and performed content analyses on the responses of a random sub-sample of 600 participants. Polyandrous sex was the key element of the favorite sexual fantasy reported by 15% of female participants.

Studies using smaller samples of participants also provide evidence that polyandry is a common theme of women's sexual fantasies, albeit less common than for men. For example, Rokach (1990) reported that, although sex with more than one partner accounted for 14% of the sexual fantasies reported by a sample of 44 men, it accounted for 10% of the fantasies reported by a sample of 54 women. Person *et al.* (1989) and Pelletier and Herold (1988) documented that 27 and 29%, respectively, of the women sampled report fantasies of polyandrous

sex. And fully 41% of women sampled by Arndt, Foehl, and Good (1985) report fantasies involving sex with two men at the same time, and Price and Miller (1984) report that polyandrous sex was among the 10 most frequently reported fantasies in a small sample of college women. Indeed, polyandrous sex ranked as the third most frequent fantasy of black women and as the eighth most frequent fantasy of white women in this study.

If sexual fantasy reflects sexual desires and preferences that might sometimes be acted upon, then previous research indicates that polyandrous sex is not an unlikely occurrence, particularly given the well-established finding that women more than men are the “gatekeepers” of sexual access – including when, where, and the conditions under which sex occurs (see, e.g. Buss, 2004; Symons, 1979). If, as Symons (1979) has argued (and see Buss, 2004; Ellis & Symons, 1990), sexual fantasy provides a window through which to view evolved human psychology, then human female sexual psychology may include design features dedicated to the pursuit of polyandrous sex, with the consequence of promoting sperm competition.

Men’s adaptations to sperm competition

Sperm competition can take one of two forms: *contest competition*, in which rival ejaculates actively interfere with each other’s ability to fertilize an ovum or ova, and *scramble competition*, which is more akin to a simple race or lottery. In mammals, there are theoretical reasons to believe that most sperm competition takes the form of a scramble, and modeling studies and experimental findings support this view (Gomendio *et al.*, 1998). Male adaptations to scramble competition are likely to take the form of physiological, anatomical, and behavioral features that increase the male’s chances of fertilizing an ovum or ova in a competitive environment in which the ability to deliver large numbers of sperm is a crucial determinant of fertilization success.

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.

Compared to other primates, human ejaculates do not contain especially large numbers of sperm (Baker & Bellis, 1995; Dixson, 1998). Men, therefore, do not appear to be adapted to particularly high levels of sperm-competition. Nevertheless, it may be the case that men have physiological adaptations that allow them to allocate sperm prudently in the face of variable levels of sperm-competition risk. The only published evidence, however, indicating that men can adjust ejaculate composition in response to adaptively relevant aspects of their environment was provided by Baker and Bellis (1989a, 1993).

Baker and Bellis first reported that the number of sperm inseminated by men varied according to hypotheses generated by sperm-competition theory (Baker & Bellis, 1989a). For this study, 10 heterosexual couples provided semen specimens collected via masturbation and others collected during copulation. Although participants provided multiple specimens, the analysis was restricted to the first specimen provided in each of the two experimental contexts (masturbatory and copulatory). For the 10 copulatory specimens, there was a significant negative rank-order correlation between the percentage of time the couple had spent together since their last copulation and the estimated number of sperm in the ejaculate. That is, men who had spent the most time apart from their partners since their last copulation produced ejaculates containing the most sperm. Because the percentage of time spent apart from a partner is a reliable cue of the risk of female double-mating, these findings are consistent with the hypothesis that there is a positive association between the number of sperm inseminated and the risk of sperm competition (Parker 1970, 1982). What Baker and Bellis (1989a) reported, however, was a between-subjects relationship between sperm-competition risk and ejaculate composition. Baker and Bellis (1989a) did not provide direct evidence of prudent sperm allocation by men from one specimen to the next in response to variation in sperm competition risk. It could be the case that men who tended to produce larger ejaculates also tended to spend a greater proportion of their time between copulations apart from their partners. Moreover, this relationship could be mediated by between-male differences in testicular size and associated levels of testosterone production if variability in these variables predicts semen parameters and certain aspects of sexual behavior.

In a follow-up to this initial report, Baker and Bellis (1993) attempted to address the aforementioned problems by including in their analyses more than one ejaculate from each couple that participated in this second study. Twenty-four couples provided a total of 84 copulatory ejaculates. To assess whether the number of sperm inseminated by a man depended on the

percentage of time spent together since the last copulation with his partner, only those copulatory specimens that were preceded by an ejaculation also produced during an in-pair copulation (IPC) were included in the analyses (IPC-IPC ejaculates). Forty specimens produced by five men were included in the final analysis, and for these a non-parametric test based on ranks indicated a negative association between the number of sperm inseminated and the proportion of time the couple had spent together since their last copulation – evidence of prudent sperm allocation by men.

Although data were presented for the first IPC-IPC ejaculates produced by all 15 couples who provided copulatory specimens, an analysis similar to that presented in the 1989 paper was not reported. Shackelford and his colleagues (2005) conducted this analysis using the 1993 data, which revealed that, for the first IPC-IPC ejaculate produced by each couple, the negative rank-order correlation between the number of sperm inseminated by a man and the percentage of time spent together with his partner since their last copulation marginally statistically significant ($r = -0.50$; $P = 0.058$).

Aside from the small sample size used in Baker and Bellis' (1993) demonstration of prudent sperm allocation by individual men, a number of additional methodological concerns have led some researchers to be skeptical of the findings. One concern is the possibility that the people who participated in this intrusive research about some of their most private behaviors may not be representative of most people. Recruited from the staff and postgraduate students in a biology department, the participants might have had some knowledge of the experimental hypothesis. It is not clear, however, how such knowledge could affect semen parameters. Knowledge about the experimental hypothesis could have affected the sexual behavior of the participants, and there is some evidence that semen parameters are subject to behavioral influences (Pound *et al.*, 2002; Zavos, 1985, 1988; Zavos & Goodpasture 1989; Zavos *et al.*, 1994). However, evidence that men are able to adjust their semen parameters in response to the demand characteristics of an experiment would perhaps be more remarkable than evidence of prudent sperm allocation in the face of cues of sperm-competition risk.

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. Little attention has been paid, however, to 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 *et al.* (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.

Baker and Bellis (1993, 1995) operationalized risk of sperm competition as the proportion of time a couple has spent together since their last copulation. The proportion of time spent *apart* since the couple's last copulation is correlated negatively with the proportion of time that they have spent together and is arguably a more intuitive index of the risk of sperm competition and, therefore, Shackelford *et al.* (2002) used this in their work. Shackelford and his colleagues argued that the proportion of time spent apart is information that is processed by male psychological mechanisms that subsequently motivate a man to inseminate his partner as soon as possible, to combat the increased risk of sperm competition.

Total time since last copulation is not clearly linked to the risk of sperm competition. Instead, it is the proportion of time a couple has spent apart since their last copulation – time during which a man cannot account for his partner's activities – that is linked to the risk that his partner's reproductive tract might contain the sperm of rival males (Baker & Bellis, 1995). Nevertheless, total time since last copulation might have important effects on a man's sexual behavior. As the total time since last copulation increases, a man might feel increasingly "sexually frustrated" whether or not that time has been spent apart or together. To address the potential confound, Shackelford *et al.* (2002) assessed the relationships between male sexual psychology and behaviors predicted to be linked to the risk of sperm competition (as assessed by the proportion of time spent apart since last copulation), controlling for the total time since a couple's last copulation.

Shackelford *et al.* (2002) suggested that men might respond differently to cues of sperm-competition risk depending on the nature of their relationship with a particular woman. Satisfaction with, and investment in, a relationship are likely to be linked, with the result that a man who is more satisfied may have more to lose in the event of cuckoldry. For this reason, when examining the responses of men to increases in the proportion of time spent apart from their partner since their last copulation, Shackelford *et al.* controlled for the extent to which the participants were satisfied with their relationships.

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. 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.

Additionally, 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), a prediction first made by Baker and Bellis (1993). According to Baker and Bellis' (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 (2002) 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) 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 decline with the duration of the mateship (Klusmann, 2002).

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 (2002) 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, 2002). Because women more than men control sexual access, women's waning interest in sex translates into a decrease in sexual activity for both partners.

MEN'S REPRODUCTIVE ANATOMY AND COPULATORY BEHAVIOR

In primates, testis size relative to body weight also is correlated positively with the incidence of polyandrous mating (Harcourt *et al.*, 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 *et al.* (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 several primate species, it is unlikely that sperm competition was completely absent over human evolutionary history.

Human males have a penis that is longer than in any other species of ape (Short, 1979), but in relation to body weight it is no longer than the chimpanzee penis (Gomendio *et al.*, 1998). 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 in the context of scramble competition, which combines elements of a race and a lottery, because being able to place 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 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 coronal ridge makes semen displacement possible by allowing semen to flow back under the penis alongside the frenulum and collect on the anterior of the shaft behind the coronal ridge. Displacement of simulated semen 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 *et al.* (2005) investigated whether and how men under a high risk of sperm competition 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.

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 *et al.*, 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 do so in part to avoid 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 suggests both women are sexually available and copulation with both is imminent. 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 eggs. 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 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.

The idea that men might experience increased sexual motivation in response to cues of sperm-competition risk is also supported by anecdotal accounts of men who engage in "swinging" or "partner-swapping." Encouraging one's partner to copulate with other men is obviously a maladaptive strategy in that it clearly 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).

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 hear his partner talk 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.

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 *et al.*, 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 Baker and Bellis' (1988) 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 the 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 leukocytes. 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 (1995) 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' (1995) work, but failed to replicate the findings of Baker and Bellis (1995). 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 *et al.* (1999) 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 1–3 h, whereas Baker and Bellis (1995) allowed them to interact for fully 3–6 h. Moore *et al.* (1999) offered theoretical reasons for this shorter interactive window (i.e. because 1–3 h 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' (1995) longer, 3–6 h 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.

Aside from Moore *et al.*'s (1999) failure to replicate Baker and Bellis' (1995) findings, additional skepticism is generated by Baker and Bellis' (1995) failure to clearly specify how sperm can differentiate self-sperm from non-self-sperm. Given that sperm consist of a diminutive single-cell structure, a self-recognition system that must differentiate between not just different genes (because even sperm from a single male contain different combinations of genes), but different sets of competing genes (i.e. genes from another male) may be unlikely to have evolved. Moore *et al.*'s (1999) failure to replicate Baker and Bellis' (1995) findings and the absence of a clear self-recognition system is not fatal to the Kamikaze Sperm Hypothesis, but such concerns are cause for skepticism about its plausibility. 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. Kura and Nakashima (2000) concluded that such conditions are not stringent and far from unlikely.

Concluding remarks

This chapter reviews the mechanism of postcopulatory sexual selection first identified by Geoff Parker (1970): sperm competition. 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, and men's sexual arousal and sexual fantasies.

Although this chapter focuses on men's adaptations to sperm competition, women are not simply 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 in women. Indeed, intersexual conflict between ancestral males and females produces a coevolutionary 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. Women's adaptations to sperm competition are considered in Shackelford *et al.* (2005).

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