

CHAPTER 12

Female Infidelity and Sperm Competition

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THE TERM *SPERM COMPETITION* brings to mind an image of tiny sperm, battling with one another to fertilize a female's egg. The first definition of sperm competition—"the competition within a single female between the sperm from two or more males for the fertilization of the ova" (Parker, 1970, p. 527)—implies that sperm competition is an interaction among males' sperm, devoid of male and female anatomy, physiology, psychology, and behavior. Nothing could be further from the truth. An interactive competition among sperm is just one of many aspects of sperm competition. Broadly defined, sperm competition is sexual selection after the initiation of copulation, or *postcopulatory* sexual selection (influences during copulation are still referred to as *postcopulatory*; see Eberhard, 1996; LaMunyon & Eisner, 1993). As with *precopulatory* sexual selection, the *postcopulatory* form can occur intrasexually (male-male interactions) or intersexually (male-female interactions).

Whereas Darwin (1871) and others (see Andersson, 1994, for a review) have identified *precopulatory* adaptations associated with intrasexual competition and intersexual selection, sperm competition investigators aim to identify *postcopulatory* adaptations. The study of sperm competition, therefore, involves examining (1) how males compete to fertilize a female's egg(s) once the initiation of copulation has occurred and (2) how females nonrandomly bias paternity between two or more males' sperm (Eberhard, 1996).

SPERM COMPETITION IN NONHUMAN SPECIES

Sperm competition has been documented or inferred to exist in many species, ranging from molluscs (Baur, 1998) and insects (Simmons, 2001) to birds (Birk-

head & Møller, 1992) and mammals (Gomendio, Harcourt, & Roldán, 1998). In species with internal fertilization, there is the potential for sperm competition to occur 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. The outcome of such competition may depend on many factors, including mating order effects; male accessory secretions; the shape, number, and size of female sperm storage organs; and female manipulation of sperm. However, the number of sperm transferred may be one of the most important factors. A particular male can increase the probability of siring a female's offspring by inseminating more sperm, and a male that transfers very few sperm will generally experience little success in sperm competition (Parker, 1970, 1990a).

Although sperm are normally thought of as inexpensive to produce, the metabolic costs of ejaculate production are nontrivial. Across many species, these costs are attributable to the sheer numbers of sperm ejaculated, in addition to costs associated with the production and maintenance of the requisite physiological machinery (Dewsbury, 1982; Nakatsuru & Kramer, 1982). It is not uncommon for investment in sperm to depend on male body size in invertebrates (LaMunyon & Ward, 1998; Pitnick & Markow, 1994), suggesting that sperm production is limited by available resources. Repeated ejaculation can even lead to sperm depletion in some mammals (Ambriz et al., 2002). For males, therefore, there is a trade-off between ejaculate production costs and the potential benefits of delivering large numbers of sperm in any particular ejaculate.

One of the first hypotheses generated by sperm competition theory was that males deliver more sperm when the risk of sperm competition is higher (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 to 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 (e.g., Gage, 1994; Harcourt, Harvey, Larson, & Short, 1981; Møller, 1988). In nematodes, where sperm size correlates with sperm competitiveness, species with greater risk of sperm competition produce larger, but more costly, sperm (LaMunyon & Ward, 1998, 1999). 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). The reverse is also true: Experimental removal of sperm competition in fruit flies has resulted in the evolution of lower investment in sperm production (Pitnick, Miller, Reagan, & Holland, 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 (Parker, Ball, Stockley, & Gage, 1997; Wedell, Gage, & Parker, 2002). 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. Males need to rely on cues predictive of sperm competition risk because this risk often cannot be assessed directly. Any auditory, chemosensory, tactile, or visual stimuli that reliably predict whether a female's reproductive tract (in the case of internal fertilizers) or the

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spawning area (in the case of external fertilizers) contains or will soon contain sperm from rival males could be used as cues to the risk of sperm competition.

There is experimental evidence that males of various species respond to cues of elevated sperm competition risk in an adaptive fashion (e.g., Gage, 1991; Gage & Baker, 1991). Of most relevance to humans 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 this experiment, rats were housed in mixed-sex pairs but prevented from mating by wire mesh dividing each cage. When allowed to mate, males inseminated less sperm when copulating with a female that they had accompanied during the 5 days preceding her estrus than when mating with a female accompanied by a different male during those 5 days. Bellis et al. (1990) interpreted this finding as evidence of prudent sperm allocation, because time spent with a female prior to copulation can be thought of as "guarding" time, and "unguarded" females are more likely to contain sperm from one or more rival males.

Sperm competition can be far more costly than the loss of fertilizations to other males. Males of many species invest more than sperm during and/or after mating, and the loss of a fertilization may result in cuckoldry. Cuckoldry is a reproductive cost inflicted on a male by a female's sexual infidelity or promiscuity. In some species, the losses incurred extend after copulation due to long-term investment in unrelated offspring. This is the case for species that practice social monogamy, the mating system in which males and females form long-term pair bonds. Although it was once thought that sperm competition was rare in species that are socially monogamous, it is now clear that both males and females in these species pursue extra-pair copulations, and female sexual infidelity creates the primary context for sperm competition (Birkhead & Møller, 1992; Smith, 1984). In addition to the resources lost providing paternal care for an unrelated offspring, a male suffers the loss of the time, effort, and resources spent attracting his partner (Buss, 2004; Trivers, 1972). Because cuckoldry is so costly, males of paternally investing species are expected to have adaptations that decrease the likelihood of being cuckolded.

HAS SPERM COMPETITION BEEN AN ADAPTIVE PROBLEM FOR HUMANS?

The issue of whether sperm competition has been an important selective force during human evolution is controversial. Smith (1984) argued that facultative polyandry (i.e., female infidelity) would have been the most common context for the simultaneous presence of live sperm from two or more men in the reproductive tract of an ancestral woman. Other contexts in which sperm competition might have occurred include consensual communal sex, courtship, rape, and prostitution, but Smith (1984) 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.

Male morphology can also provide evidence of an evolutionary history of sperm competition. Across primate species, relative testicular size correlates positively with the degree of polyandry, which determines sperm competition (Harcourt et al., 1981; Harcourt, Purvis, & Liles, 1995; Short, 1979). Among gorillas (*Gorilla gorilla*), for instance, female promiscuity and sperm competition are rare, and the male gorilla's testes are relatively tiny, composing 0.018% of body weight.

Orangutans (*Pongo pygmaeus*), whose mating system falls between dispersed and polygyny and results in intermediate risk of sperm competition, have testes that compose 0.047% of body weight. Chimpanzees (*Pan troglodytes*) are highly promiscuous and males have relatively large testes, composing 0.268% of body weight. Because human testes are of intermediate size compared to other primates, composing 0.062% of body weight (Dixson, 1998; Harcourt et al., 1981), Smith (1984) argued that polyandry, and, therefore, sperm competition, was an important selection pressure during human evolution.

Evidence of an evolutionary history of female infidelity and sperm competition also 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, Larsen, Westen, & Semmelroth, 1992; Daly, Wilson, & Weghorst, 1982; Symons, 1979), and female sexual infidelity increases the likelihood that sperm from two or more men simultaneously occupied the reproductive tract of a single woman. Based on past and present infidelity rates of men and women, it may be concluded that, although humans practice social monogamy, they are somewhat sexually promiscuous. Because of female sexual infidelity, males are likely to face the adaptive problems associated with sperm competition (Birkhead & Møller, 1992; Smith, 1984).

Evidence of adaptations to sperm competition in men and women indicates that sperm competition has been a continuous selection pressure during human evolution. This chapter reviews evidence of physiological, psychological, and behavioral mechanisms that are most parsimoniously explained as evolutionary responses to sperm competition.

DO WOMEN GENERATE SPERM COMPETITION?

Evolutionary accounts of human sexual psychology have emphasized 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 nonmonogamously (Greiling & Buss, 2000). Moreover, if ancestral women never engaged in short-term mating, men could not have evolved a strong desire for sexual variety in the absence of coercion or rape—contexts that would not require females to voluntarily engage in short-term mating (Schmitt et al., 2003; Smith, 1984).

Ancestral women may have benefited from facultative polyandry in several ways (for a review, see Greiling & Buss, 2000). Some of the most important potential benefits include the acquisition of resources, either in exchange for sex with multiple men (Symons, 1979) or by creating paternity confusion as a means to elicit investment (Hrdy, 1981). Ancestral women also may have benefited by accepting resources and parental effort from a primary mate while copulating opportunistically with men of superior genetic quality (Smith, 1984; Symons, 1979). 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 are sufficient for postcopulatory competition among 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 to 3 days (Gomendio & Roldán, 1993) or as long as 7 to 9 (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, Gagnon, Michael, and Michaels (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. Moreover, 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 ages 16 to 24 years reported having had concurrent sexual relationships with men during the preceding year.

Bellis and Baker (1990) argued that women "schedule" 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 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 argued that the results cannot be attributed to men's preferences for copulation with women at peak fertility. According to Bellis and Baker, 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, e.g., Gangestad & Simpson, 2000), women are predicted to prefer to copulate with extra-pair partners when conception is highest. A woman might simultaneously avoid copulation with a genetically inferior in-pair partner, although her in-pair partner might prefer to copulate with her precisely during the peak fertility phase of her cycle. Therefore, Bellis and Baker's 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; 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. Given the asymmetric costs associated with sexual reproduction, female reproduction is limited by the ability to bear and rear offspring, whereas males are limited by sexual access to females. Consequently, it has been hypothesized that men more than women 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: Men report this fantasy much more than do women (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 certainly something about which women fantasize. 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 5,000 readers of Britain's top-selling daily newspaper about their favorite sexual fantasy and performed content analyses on the responses of a random subsample 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. 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, Terestman, Myers, Goldberg, and Salvadori (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. Davidson (1985) and Sue (1979) report that smaller but still sizable percentages (17% and 15%, respectively) of women recall fantasies involving sex with two or more men concurrently, 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 African American women and as the eighth most frequent fantasy of European American women in this study.

If sexual fantasy reflects sexual desires and preferences that might sometimes be acted on, 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, 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 akin to a 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 success.

IS THERE EVIDENCE OF PRUDENT SPERM ALLOCATION BY MEN?

Sperm competition theory predicts that, across species, investment in adaptations to sperm production varies with the risk of sperm competition (Parker, 1982, 1990a, 1990b), and adaptations to *high* levels of sperm competition include anatomical, physiological, and behavioral traits that facilitate the delivery of large numbers of highly competitive sperm. Sperm competition theory also predicts that, where the risk of sperm competition varies from mating to mating and where male adaptations to sperm are costly, individual males modulate their adaptations to sperm competition in a prudent fashion. When the risk varies, the modulations are likely to take the form of adjustments in the number of sperm inseminated. It is possible that the ability to modulate sperm competition adaptations will be seen even in species where the overall levels of sperm competition are not especially high—but where the costs of the adaptations are sufficiently pronounced to cause the evolution of mechanisms that allows prudent sperm allocation. Across primate species, relative testicular size (and, therefore, sperm numbers) correlates positively with the degree of polyandry (Harcourt et al., 1981; Short, 1979). Human ejaculates contain intermediate numbers of sperm compared to other primates (Short, 1979; Smith, 1984). Although much variation exists, the mean number of sperm per ejaculate for gorillas, orangutans, humans, and chimpanzees is 65, 91, 175, and 603 million, respectively (Smith, 1984).

Ejaculates do appear to be costly for human males to produce. Frequent ejaculation, especially occurring more frequently than every other day, results in decreased sperm counts (Tyler, Crockett, & Driscoll, 1982), suggesting limits to sperm production. Men hardly seem limited by sperm production, however, given the apparent wastage of sperm that occurs in humans. Sperm are continuously lost in the urine, and entire ejaculates are lost during nocturnal emissions and masturbation, although masturbatory ejaculates contain fewer sperm than do copulatory ejaculates (Zavos & Goodpasture, 1989). It has been suggested, however, that these lost sperm are older and less competitive (Baker & Bellis, 1993a) and that noncopulatory ejaculations increase the number of younger, highly competitive sperm ejaculated at the next copulation. Given the cost of human ejaculates and the fact that sperm competition risk varies from copulation to copulation depending on the sociosexual context, human males may have evolved the ability to modulate adaptations to sperm competition. The number of sperm contained in a man's ejaculate varies considerably from one ejaculate to the next (Mallidis, Howard, & Baker, 1991; Schwartz, Laplanche, Jouannet, & David, 1979). Although clinicians treat this intraindividual variability as "noise" or as a

barrier to determining the "true" values of a man's semen parameters, predictions generated by sperm competition theory have led researchers to examine the possibility that some of this variability might reflect prudent sperm allocation in the face of variations in the temporal risk of sperm competition. Whether or not such variation is patterned adaptively in contemporary environments, it is possible that it may reflect the functioning of mechanisms that evolved to deal with variations in the risk of sperm competition in ancestral environments.

Men display prudent sperm allocation in at least one fundamental sense: Sperm are not emitted continuously but, instead, are ejected during discrete ejaculatory events that occur in response to sexual stimulation of sufficient intensity and duration. The only published evidence, however, indicating that men adjust ejaculate composition in response to adaptively relevant aspects of the sociosexual environment was reported in a series of papers by Baker and Bellis.

In 1989, Baker and Bellis first reported that the number of sperm inseminated by men varied according to hypotheses generated by sperm competition theory (Baker & Bellis, 1989b). For this study, 10 couples provided semen specimens collected via masturbation and others collected during copulation. In each case, participants used nonsterile condoms to collect the specimens and provided information about the time since their last ejaculation, the time since their last copulation, and the percentage of time spent together with their partner since the last copulation. 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 ($r_s = -.95$) between the percentage of time the couple had spent *together* since their last copulation and the estimated number of sperm in the ejaculate. No such relationship was identified for masturbatory ejaculates. If the percentage of time spent apart from a partner is a reliable cue of the risk of female double-mating, then 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 (1989b) reported, however, was a between-subjects relationship between sperm competition risk and ejaculate composition—an observation that, for a sample of 10 couples, men who had spent the most time apart from their partners since their last copulation produced copulatory ejaculates containing the most sperm. Baker and Bellis 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 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 (1993a) addressed 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 nonparametric test based on ranks indicated a significant negative association between the number of sperm inseminated and the proportion of time the couple had spent together since their last copulation.

Aside from the small sample size used in Baker and Bellis's (1993a) demonstration of prudent sperm allocation by individual men, there are methodological issues that may threaten the reliability, validity, and generalizability of the results. 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, Javed, Ruberto, Shaikh, & Del Valle, 2002; Zavos, 1988; Zavos, Kofinas, Sofikitis, Zarmakoupis, & Miyagawa, 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.

Baker and Bellis (1993a) argued that increases in the number of sperm inseminated by a man in response to a decrease in the proportion of time spent together with his partner since the couple's last copulation reflects prudent sperm allocation in response to a cue of increased sperm competition risk. Several alternative interpretations are possible, however. For example, changes in ejaculate composition may be secondary to changes in female sexual behavior induced by partner absence. Women who have spent a smaller proportion of time together with their partner since the couple's last copulation may behave differently during intercourse and thus provide different stimuli prior to, and at the time of, ejaculation. This may be significant because evidence that human ejaculates obtained via uninterrupted coitus have higher semen volume, total sperm number, and sperm motility than those obtained via *coitus interruptus* (Zavos et al., 1994) indicates that sexual stimuli present at the moment of ejaculation may be important determinants of ejaculate composition.

Also, changes in semen parameters following a period of partner absence might not function primarily as a response to the risk that a partner contains sperm from a rival male but as a consequence of an extra-pair copulation during that period of absence. It is possible that changes in semen parameters occur following a period of partner absence because past absence may predict future absence (Gomendio et al., 1998). Thus, increases in the number of sperm delivered might serve simply to maximize the chances of conception during a future period of partner absence during which ovulation might occur.

PHYSIOLOGICAL MECHANISMS ASSOCIATED WITH PRUDENT SPERM ALLOCATION

The findings of Baker and Bellis (1993a, 1995) suggest that men may be capable of prudent sperm allocation, but it is not clear how men accomplish this. The physiological mechanisms involved in the regulation of ejaculate composition are poorly understood, but clues to their possible nature might be derived from observations of the factors known to affect semen parameters.

In studies in which men provide multiple semen specimens over several days or weeks, there is substantial intraindividual variability in parameters such as ejaculate volume and sperm concentration (Mallidis et al., 1991; Schwartz et al., 1979), in part because both parameters are affected by the duration of ejaculatory abstinence (Blackwell & Zaneveld, 1992; Matilsky et al., 1993). There also is evidence that the context in which an ejaculate is produced is important. For example, ejaculates produced during copulation and collected in nonspermicidal condoms are generally superior to those produced via masturbation (Zavos, 1985). Compared to masturbatory ejaculates, copulatory ejaculates have greater volumes, greater total sperm numbers, and a higher grade of sperm motility (Zavos & Goodpasture, 1989). The percentage of motile and morphologically normal sperm also is higher for copulatory ejaculates, and these ejaculates consequently perform better on various sperm function tests (Sofikitis & Miyagawa, 1993).

The mechanisms that cause copulatory ejaculates to contain more sperm than masturbatory ejaculates are not fully understood, but the difference may be attributable, in part, to the greater intensity and duration of sexual arousal that typically precedes copulatory ejaculation. One study indicated that sexual stimulation, in the form of sexually explicit videotapes, can improve semen parameters for masturbatory ejaculates (Yamamoto, Sofikitis, Mio, & Miyagawa, 2000), but this contradicts a previous finding (van Rooijen et al., 1996). An increase in the duration of precoital stimulation increases the number of motile sperm with normal morphology in copulatory ejaculates (Zavos, 1988). There also is a positive association between the duration of preejaculatory sexual arousal and sperm concentration for masturbatory ejaculates (Pound et al., 2002).

Relationships between semen quality and the duration of sexual arousal also have been documented in domesticated farm animals when specimens are collected for artificial insemination (e.g., bulls: Almquist, 1973; boars: Hemsworth & Galloway, 1979; and stallions: Weber, Geary, & Woods, 1990). Given the relationship between duration of preejaculatory sexual arousal and variation in ejaculate sperm counts across species, it is possible that males achieve adaptive changes in ejaculate composition through behavioral changes that prolong arousal prior to ejaculation. The idea that males delay intromission and ejaculation in response to cues of sperm competition risk is counterintuitive, however, because it is known that they are likely to experience increased sexual motivation at such times (see Pound, 2002). Perhaps more important, mammalian sperm competition is likely a race as well as a lottery. It, therefore, may be costly to prolong ejaculatory latency and thus delay insemination. Whether the increase in sperm numbers with prolonged arousal has an adaptive function is not clear, but this increase may depend on the same physiological mechanisms involved in adaptive increases in sperm numbers in other circumstances. An understanding of how sexual arousal can improve semen quality, therefore, can shed light on some of the possible sites where adaptive regulation might take place.

PSYCHOLOGICAL MECHANISMS ASSOCIATED WITH PRUDENT SPERM ALLOCATION

Males in many nonhuman species are capable of adjusting the number of sperm they inseminate in response to cues of sperm competition risk, and the available evidence indicates that this is something that men also are able to do

(Baker & Bellis, 1993a). 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 (1993a, 1995) operationalized risk of sperm competition as the proportion of time a couple has spent together since their last copulation and examined changes in semen parameters associated with variations in this index, which, they argued, is inversely related to the risk of sperm competition. 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. Shackelford et al. (2002) 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 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 proportion of time apart from his partner since their last copulation (and, therefore, faces a higher risk of sperm competition) rates his partner as more attractive, feels that other men find his partner more attractive, reports greater interest in copulating with his partner, and believes that his partner is more interested in copulating with him. The effects of the proportion of time spent apart are independent of the total time since the last copulation and independent of relationship satisfaction. These 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.

THE INFLUENCE OF SPERM COMPETITION ON MEN'S REPRODUCTIVE ANATOMY AND COPULATORY BEHAVIOR

Human testis size suggests an evolutionary history of intermediate levels of sperm competition (Smith, 1984), and other aspects of male reproductive anatomy may provide insights as well. 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 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).

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 et al. 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 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 occurred, however, only when a phallus was inserted at least 75% of its length into the artificial vagina, suggesting that successful displacement of 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 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. (2003) 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. 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 such as an increase in number of thrusts, deepest thrust, average depth of thrusts, duration of sexual intercourse, and number of sexual positions initiated by the male, 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 thrusting is terminated immediately after ejaculation, and 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, personal communication, July 2002). The inability to maintain an erection following ejaculation may function to minimize self-semen displacement. In addition, the costs of displacing a portion of one's own semen may have been outweighed by the tremendous reproductive benefits of displacing successfully a rival male's semen (for a review of evolutionary cost-benefit analyses, see Tooby & Cosmides, 1992).

THE INFLUENCE OF SPERM COMPETITION ON 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 these 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 sexual arousal and reported likelihood of pursuing a short-term sexual relationship were 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.

THE INFLUENCE OF SPERM COMPETITION ON 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.

Anecdotal evidence suggests that many men are sexually aroused by the exclusive sexual interaction between two women. Indeed, a common scenario in movies and television shows involves two women (often implied or explicit heterosexuals) kissing or performing other sexual acts with each other while an audience of one or more men observe the acts and become sexually aroused. 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 may signal to men that the women are without male partners and, therefore, pose no risk of sperm competition.

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 sexually arousing because frequent copulation can be an effective method of paternity assurance. Pound 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 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.

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." 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 men indicate that this increase in desire is particularly acute when they have witnessed their partner having sexual intercourse with another man (T. Gould, 1999).

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, Dvorkova, Jenkins, & Breed, 2002). These trains display greater motility and velocity than single sperm, facilitating fertilization. This cooperative behavior among 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 among rival male ejaculates might involve more than just scramble competition and that rival sperm might 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 proposed that sperm polymorphism was not due to meiotic errors, but instead reflected a functionally adaptive "division of labor" among sperm. Baker and Bellis 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 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) argued that "malformed" sperm were unlikely to have adaptive functions, citing evidence that, in lions, inbreeding results in an increase in the proportion of deformed sperm (Wildt et al., 1987). Harcourt 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 (1989a) responded to Harcourt's (1989) objections and elaborated on the kamikaze sperm hypothesis. In their elaboration, Baker and Bellis (1989a) 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) reported 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).

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 find incapacitation affects associated with the presence of rival sperm. After mixing sperm from different men and comparing these heterospermic samples to self-sperm (i.e., homospermic) samples, Moore et al. observed no increase in aggregation and no greater incidence of incapacitated sperm in the heterospermic samples. Moore et al. did not replicate precisely the methodological procedures used by Baker and Bellis (1995), however. Heterospermic and homospermic samples, for example, were allowed to interact for just 1 to 3 hours, whereas Baker and Bellis (1995) allowed them to interact for fully 3 to 6 hours. Moore et al. offered theoretical reasons for this shorter interactive window (i.e., because 1 to 3 hours is the time that sperm normally remain in the human vagina), but perhaps this interval was too short. 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, 3- to 6-hour interactive window is more valid ecologically.

Aside from Moore et al.'s (1999) failure to replicate Baker and Bellis's (1995) findings, additional skepticism is generated by Baker and Bellis's failure to clearly specify how sperm can differentiate self-sperm from non-self-sperm. Given that sperm consist of a diminutive single-cell devoid of many of the cytoplasmic contents found in their somatic counterparts, a self-recognition system that must differentiate among 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 failure to replicate Baker and Bellis's (1995) findings and the absence of a clear self-recognition system is not necessarily fatal to the kamikaze sperm hypothesis, but such concerns are cause for skepticism about its plausibility, especially for the proposed seek-and-destroy sperm morphs. More work remains before we can draw a conclusion about the status of the hypothesis.

WOMEN'S ADAPTATIONS TO SPERM COMPETITION

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. Given that selection will produce adaptations in females that allow them to influence paternity, the role of the female in sperm competition is as important as the role of the male. Female influence may be exerted before, during, and after copulation. Female choice that precedes copulation is known as "precopulatory female choice," whereas "postcopulatory female choice" refers to female influence that follows initiation of copulation (Eberhard, 1996). An evolutionary history of sperm competition, therefore, is expected to have produced precopulatory and postcopulatory female adaptations.

PRECOPULATORY FEMALE CHOICE: PROMOTING AND AVOIDING SPERM COMPETITION

Bellis and Baker (1990) documented that women are more likely to engage in successive copulations with in-pair and extra-pair partners in a short time interval when the probability of conception is highest, suggesting that women may have psychological adaptations that motivate active promotion of sperm competition, thus allowing their eggs to be fertilized by the most competitive sperm. It is possible that human female psychology also includes mechanisms designed to motivate the avoidance of sperm competition under certain conditions. Gangestad, Thornhill, and Garver (2002), for example, documented that, as women enter the high conception phase of their menstrual cycle, they are sexually attracted to, and fantasize about, men *other than* their regular partner. These results suggest that women are sensitive to the fact that favoring genes of an extra-pair partner over a primary partner is accomplished by copulation with only the extra-pair partner and not the primary partner when the likelihood of

conception is high. Thus, women's sexual attraction to and fantasy about men other than their regular partner may qualify as a precopulatory female adaptation. But because men, in turn, have been selected to be sensitive to their partner's increased interest in extra-pair copulation near ovulation (Gangestad et al., 2002), women may possess postcopulatory adaptations designed to selectively favor sperm from one man over another.

POSTCOPULATORY FEMALE CHOICE: A FUNCTION FOR FEMALE COITAL ORGASM?

One such postcopulatory adaptation in women may be orgasm. Both the female clitoris and the male penis develop from the same embryonic organ, prompting Symons (1979) and S. J. Gould (1987) to argue that female orgasm is a by-product of male orgasm. Others have hypothesized, however, that female orgasm has an adaptive function (e.g., Alexander, 1979; Baker & Bellis, 1993b; Fox, Wolff, & Baker, 1970; Hrdy, 1981; Smith, 1984). A leading functional hypothesis is that female coital orgasm was designed in the context of sperm competition as a mechanism of selective sperm retention (Baker & Bellis, 1993b; Smith, 1984). Female orgasm causes the cervix to dip into the seminal pool deposited by the male at the upper end of the vagina, and this may result in the retention of a greater number of sperm (see research reviewed in Baker & Bellis, 1993b, 1995). Baker and Bellis (1993b) and Smith (1984) contend that by strategic timing of orgasm, women may select preferentially the sperm of extra-pair partners, who are likely to be of higher genetic quality than in-pair partners.

In a test of this hypothesis, Baker and Bellis (1993b) estimated the number of sperm in ejaculates collected by condoms during copulation and by vaginal "flowbacks" (i.e., ejected seminal and vaginal fluids) when condoms were not used and documented that women influence the number of sperm retained in their reproductive tract through the presence and timing of a coital orgasm. Coital orgasms that occurred between one minute before and 45 minutes after their partner ejaculated were linked with significantly greater sperm retention than coital orgasms that occurred earlier than one minute before their partner ejaculated. Analyzing women's copulatory behavior, Baker and Bellis also provided evidence that women with a regular partner and one or more extra-pair partners had significantly fewer high sperm retention orgasms with their regular, primary partner and more high sperm retention orgasms with their extra-pair partners.

Missing from Baker and Bellis's (1993b) study, however, was the explicit demonstration of higher sperm retention associated with partners of higher genetic quality. Thornhill, Gangestad, and Comer (1995) established this link. Thornhill et al. documented that women mated to men with low fluctuating asymmetry (indicating relatively high genetic quality) reported significantly more copulatory orgasms than did women mated to men with high fluctuating asymmetry (indicating relatively low genetic quality). Women mated to men with low fluctuating asymmetry did not simply have more orgasms, but specifically reported more copulatory orgasms likely to result in greater sperm retention. Another indicator of high genetic quality and related to fluctuating asymmetry is physical attractiveness. Replicating Thornhill et al.'s work, Shackelford et al. (2000) found that

women mated to more physically attractive men were more likely to report having a copulatory orgasm at their most recent copulation than were women mated to less attractive men.

Although the hypothesis that female orgasm is an adaptation for postcopulatory female choice between rival ejaculates is plausible, the functional significance of the female orgasm is still hypothetical (Pound & Daly, 2000). While Baker and Bellis (1995) documented that women retain more sperm if they experience orgasm between one minute before and 45 minutes after their partner ejaculates than if they orgasm earlier than one minute before or not at all, Baker and Bellis assume that the number of sperm ejaculated is identical regardless of whether or when the woman has an orgasm. This assumption may be false, however, particularly because the duration of preejaculatory sexual arousal has been shown to correlate positively with the number of sperm ejaculated (Pound, 1999; Zavos, 1988). Moreover, it has yet to be demonstrated that female orgasm influences conception rates. If female orgasm causes the cervix to dip into the seminal pool, causing greater numbers of sperm to be retained, it would follow that the likelihood of conception will increase accordingly, but this has not been tested empirically. The observation that men are often concerned with whether their partner achieves orgasm and the observation that women often fake orgasm to appease their partner further suggests that female orgasm may have adaptive value (see Thornhill et al., 1995).

Direct evidence of preferential use of sperm by females is absent in humans, particularly because it is methodologically difficult to study female influence of sperm behavior within the female reproductive tract. Even in nonhuman animals, evidence of female manipulation of sperm is scarce and circumstantial. Although there have been rare observations of females discarding stored sperm when mating with a new partner (Davies, 1985; Etman & Hooper, 1979), most studies infer female manipulation based on patterns of sperm storage or patterns of offspring paternity (see, e.g., Eberhard, 1996). Because much of postcopulatory competition is played out in the reproductive tract, it is likely that human females have evolved a host of adaptations in response to sperm competition.

Far fewer adaptations to sperm competition have been proposed in women than in men. The fact that the bulk of this chapter focuses on men's adaptations is an accurate reflection of the historical and current state of research and theory in the field. 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 counteradaptations 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.

CONCLUSIONS

In this chapter, we have attempted to describe the far-reaching consequences of female infidelity, specifically sperm competition. Sperm competition and its effects were not discussed directly in the nonhuman literature until the 1970s and were ignored in humans well into the 1980s. Evolutionary-minded researchers are only beginning to uncover the anatomical, physiological, and psychological features produced by an evolutionary history of sperm competition. Sperm competition may have influenced men's and women's 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. Discovering the ways in which sperm competition may have designed human anatomy, physiology, and psychology will be challenging but necessary if we are to achieve a comprehensive understanding of human sexuality.

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