

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.

