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CHAPTER 15

Human Sperm Competition

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SPERM COMPETITION WAS first defined as "the competition within a single female between the sperm from two or more males for the fertilization of the ova" (Parker, 1970, p. 527). As a form of sexual selection that occurs after the initiation of copulation (termed postcopulatory sexual selection), sperm competition has caused the evolution of adaptations in many taxa (Birkhead, Hosken, & Pitnick, 2009; Birkhead & Møller, 1998). These adaptations in males increase their probability of fertilization when sperm competition occurs, and in females allow them to bias paternity toward favorable males (Eberhard, 1996).

SPERM COMPETITION IN NONHUMAN SPECIES

Sperm competition has been reported in many species, from molluscs (Baur, 1998) and insects (Simmons, 2001) to birds (Birkhead & Møller, 1992) and mammals (Gomendio, Harcourt, & Roldán, 1998). In species with internal fertilization, sperm competition can occur when a female mates with multiple males within a sufficiently short time period so that sperm from two or more males simultaneously occupy her reproductive tract. Although the outcome of such competition depends on many factors (e.g., mating order, male accessory secretions, and the shape, number, and size of female sperm storage organs), the number of sperm transferred is often the most important factor and, consequently, a male can increase the probability of fertilizing ova by inseminating more sperm (Parker, 1970, 1990a). However, because the costs of ejaculate production are nontrivial (e.g., Dewsbury 1982; Pitnick, Markow, & Spicer, 1995), males must trade off ejaculate production costs against the benefits of delivering more sperm in an ejaculate. Thus, one of the first hypotheses generated by sperm competition theory was that males will deliver more sperm when sperm competition risk is higher (Parker, 1982, 1990a). Across species, therefore, sperm competition risk should predict investment in sperm production, whereas within-species males are predicted to exhibit prudent sperm allocation, inseminating more sperm when the risk

of sperm competition is higher (Parker, Ball, Stockley, & Gage, 1997). Consistent with the first prediction, investment in sperm production is greater in species with higher levels of sperm competition (e.g., Gage, 1994; Harcourt, Harvey, Larson, & Short, 1981; Møller, 1988). In nematodes, where sperm size correlates with sperm competitiveness (LaMunyon & Ward, 1998), species with greater sperm competition risk produce larger, more costly, sperm (LaMunyon & Ward, 1999). Moreover, experimental exposure to higher levels of sperm competition leads to the evolution of increased testis size in yellow dung flies within 10 generations (*Scathophaga stercoraria*) (Hosken & Ward, 2001) and experimental removal of sperm competition in fruit flies results in the evolution of lower investment in sperm production (Pitnick, Miller, Reagan, & Holland, 2001).

Within species, individual males in many species are capable of prudent sperm allocation (for reviews, see delBarco-Trillo, 2011; Kelly & Jennions, 2011) and adjust the number of sperm they deliver during each insemination in response to auditory, chemosensory, tactile, or visual cues of sperm competition. Prudent sperm allocation has been demonstrated in many taxa, but perhaps rats (*Rattus norvegicus*) are of most relevance to humans. Male rats adjust the number of sperm they inseminate depending on the amount of time they have spent "guarding" a particular female prior to copulation (Bellis, Baker, & Gage, 1990) and when mating in the presence of a rival male (Pound & Gage, 2004). In another mammalian example, male voles (*Microtus pennsylvanicus*) deliver more sperm when exposed to the odor of another male (delBarco-Trillo & Ferkin, 2004).

For males, lack of success in sperm competition means loss of fertilization opportunities. However, in species with substantial paternal investment, males also risk cuckoldry—the unwitting investment of resources into genetically unrelated offspring—and the associated loss of the time, effort, and resources spent attracting a partner (Trivers, 1972). Both males and females of socially monogamous species pursue extra-pair copulations, and female sexual infidelity creates the primary context for sperm competition (Birkhead & Møller, 1992; Smith, 1984). Consequently, selection pressures associated with sperm competition can generate adaptations that function to maximize sperm competition success, thereby minimizing cuckoldry risk.

HAS SPERM COMPETITION BEEN AN ADAPTIVE PROBLEM FOR HUMANS?

Smith (1984) argued that female infidelity was the most common ancestral context for sperm competition in humans, whereas other contexts (e.g., consensual communal sex, courtship, rape, prostitution) may not have occurred with sufficient frequency over human evolution to provide selection pressures for adaptations to sperm competition comparable to female infidelity.

Male anatomy and physiology provide evidence of an evolutionary history of sperm competition. Across primate species, relative testis size and the number of sperm per ejaculate correlate positively with the degree of polyandry, which determines sperm competition risk (Harcourt et al., 1981; Harcourt, Purvis, & Liles, 1995; Short, 1979). As a proportion of body mass, human testes are larger than those in monandrous species such as the gorilla and orangutan but smaller than testes in the highly polyandrous chimpanzee (Harcourt et al., 1995). Similarly, human ejaculates contain an intermediate number of sperm. Smith (1984) argued that these traits

indicate polyandry, and, therefore, that sperm competition was an important selection pressure during human evolution.

DO WOMEN HAVE ADAPTATIONS TO INDUCE SPERM COMPETITION?

Evolutionary analyses of human sexual psychology have emphasized the benefits to men of short-term mating and sexual promiscuity (Buss & Schmitt, 1993; Symons, 1979). However, for men to successfully pursue short-term sexual strategies, there must be women who mate nonmonogamously (Greiling & Buss, 2000). Ancestral women may have benefited from facultative polyandry in several ways (reviewed in Greiling & Buss, 2000). First, they may acquire resources, either in direct exchange for sex (Symons, 1979) or by creating paternity confusion to elicit investment (Hrdy, 1981). Second, women may secure genetic benefits for their offspring by copulating opportunistically outside their pair bond with men of superior genetic quality (Smith, 1984; Symons, 1979; reviewed in Jennions & Petrie, 2000).

Multiple mating by women is a necessary—but not sufficient—condition for sperm competition to occur. Women must copulate with two or more men *within a sufficiently short time period* such that there is temporal overlap in the competitive lifespans of the rival ejaculates. Several studies indicate that the length of this competitive window is 5 days (Wilcox, Dunson, Weinberg, Trussell, & Baird, 2001; Wilcox, Weinberg, & Baird, 1998). Using an estimate of 5 days, Baker and Bellis (1995) documented that 17.5% of British women self-report "double-mating" 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.

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 reporting five or more sexual partners in the past year also reported that at least two of these relationships were concurrent. Moreover, a 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. Not all concurrent sexual relationships involve double matings, but it is likely that many do.

Based on survey findings that women report more frequent double matings when conception rate is higher, Bellis and Baker (1990) argued that women "schedule" their copulations in a way that *actively promotes* sperm competition and thus encourages fertilization by the most competitive sperm. Bellis and Baker argued that this finding cannot be attributed to men's preferences for copulation with women at peak fertility, because it arose from increases in the frequency of extra-pair copulations. A general male preference for copulation at times of high conception risk would be expected to also increase the frequency of in-pair copulations during this time. Bellis and Baker may have been too quick to dismiss the possibility that men prefer to copulate with a woman during peak conception risk, however. If women pursue extra-pair copulations to secure genetic benefits from extra-pair partners (e.g., Gangestad & Simpson, 2000), then, while pursuing extra-pair partners, they should simultaneously avoid in-pair copulations (Gallup, Burch, & Mitchell, 2006). Consequently, the absence of a

spike of in-pair copulations at times of high conception risk may not reflect the motivation of the in-pair male.

POLYANDROUS SEX IN WOMEN'S FANTASIES

Sexual fantasy may provide insight into the psychological mechanisms that motivate sexual behavior (Ellis & Symons, 1990; Symons, 1979). Empirical studies have addressed sex differences in sexual fantasy (reviewed in Leitenberg & Henning, 1995), many of which have been guided by an evolutionary perspective (e.g., Ellis & Symons, 1990; Wilson, 1987). Given the asymmetric costs of sexual reproduction, female reproduction is limited by the ability to bear and rear offspring, whereas male reproduction is limited by sexual access to females (Trivers, 1972). 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 (Ellis & Symons, 1990), and empirical investigations have confirmed this hypothesis. Indeed, one of the largest sex differences occurs for fantasies about 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, nevertheless, provided data on women's polyandrous sexual fantasies. Large-scale surveys indicate that some women report fantasies of polyandrous sex, imagining themselves as a woman having sex with two or more men concurrently: 18% in the United States (Hunt, 1974) and 15% in the United Kingdom (Wilson, 1987). Similarly, smaller studies find that 15% to 41% of women report sexual fantasies involving two or more men concurrently (Arndt, Foehl, & Good, 1985; Davidson, 1985; Pelletier & Herold, 1988; Person, Terestman, Myers, Goldberg, & Salvadori, 1989; Sue, 1979). 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. Price and Miller (1984) report that polyandrous sex was among the 10 most frequently reported fantasies in a sample of college women.

If women's sexual fantasies reflect sexual desires and preferences that might sometimes be acted upon, then polyandrous sex is not an unlikely occurrence, given that women more than men are the "gatekeepers" of sexual access—including when, where, and the conditions under which sex occurs (Symons, 1979). If, as Symons (1979) argued, sexual fantasy provides a window through which to view evolved human psychology, then human female sexual psychology may include mechanisms that motivate polyandrous sex, with the consequence of promoting sperm competition.

MEN'S ADAPTATIONS TO SPERM COMPETITION

There are theoretical reasons to believe that mammalian sperm competition takes the form of *scramble competition* in which sperm are "lottery tickets" for the prize of fertilizing ova, 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 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 investment in sperm production will vary with sperm competition risk across species (Parker, 1982, 1990a, 1990b), and anatomical, physiological, and behavioral adaptations to *high* levels of sperm competition that deliver large numbers of competitive sperm. Sperm competition theory also predicts that, when sperm competition risk varies between matings, males will allocate resources prudently, adjusting the number of sperm inseminated at each copulation. Prudent sperm allocation occurs even in species in which overall levels of sperm competition are not especially high—but sufficiently variable to select for the evolution of such facultative mechanisms.

Ejaculates are costly to produce for human males. Frequent ejaculation, especially more frequent 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. 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). Baker and Bellis (1993a) suggest, however, that these lost sperm are older and less competitive, and that noncopulatory ejaculations increase the number of younger, highly-competitive sperm ejaculated at the next copulation. Given the cost of ejaculates, human males may have evolved the ability to modulate ejaculated sperm numbers depending on sperm competition risk at copulation. The number of sperm in a man's ejaculate varies considerably between ejaculates (e.g., Mallidis, Howard, & Baker, 1991). Although clinicians treat this intra-individual variability as "noise" when determining the "true" values of a man's semen parameters, sperm competition theory predicts that some of this variability might reflect prudent sperm allocation in response to the temporal risk of sperm competition.

Evidence indicating that men adjust ejaculate composition in response to sperm competition risk was first reported in several articles by Baker and Bellis. In the first report for a sample of copulatory ejaculates (Baker & Bellis, 1989), one from each of 10 couples, there was a negative rank-order correlation ($r_s = -0.95$) between "objective" sperm competition risk—the percentage of time the couple had spent *together* since their last copulation—and the number of sperm in the ejaculate. No such relationship was identified for masturbatory ejaculates. Baker and Bellis (1989) argued that objective sperm competition risk indexes risk of female double mating and, therefore, that 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. Their study was based on a single ejaculate per couple, with the finding that men who had spent the most time apart from their partners since their last copulation produced copulatory ejaculates containing the most sperm. It could be that men who tend to produce larger ejaculates also tend to spend a greater proportion of their time between copulations apart from their partners.

Baker and Bellis (1993a) addressed the aforementioned problems by including in their analyses multiple ejaculates from each participating couple. For a sample of 40

specimens produced by five men, nonparametric analyses indicated a negative association between the number of sperm inseminated and objective sperm competition risk. Although Baker and Bellis argued that these results demonstrated prudent sperm allocation in response to a cue of increased sperm competition risk, alternative interpretations are possible. For example, changes in ejaculate composition may depend on changes in female sexual behavior induced by partner absence providing different stimuli prior to, and at the time of, ejaculation. This may be significant because quality differences between ejaculates obtained via uninterrupted coitus and those obtained via *coitus interruptus* (Zavos, Kofinas, Sofikitis, Zarmakoupis, & Miyagawa, 1994) indicate that sexual stimuli present at the moment of ejaculation may be important determinants of sperm numbers.

PHYSIOLOGICAL MECHANISMS ASSOCIATED WITH PRUDENT SPERM ALLOCATION

Although the findings of Baker and Bellis (1993a, 1995) suggest that men are capable of prudent sperm allocation, the physiological mechanisms involved in the adaptive regulation of ejaculate composition are poorly understood. However, factors known to affect semen parameters may provide some clues. In longitudinal studies, individual men exhibit substantial variability in ejaculate parameters such as volume and sperm concentration (e.g., Mallidis et al., 1991), in part because both parameters are affected by the duration of ejaculatory abstinence (e.g., Blackwell & Zaneveld, 1992). There also is evidence that the context in which an ejaculate is produced is important. For example, ejaculates produced during copulation are superior to those produced via masturbation (Zavos, 1985), having greater volumes, greater sperm numbers, and higher grades of sperm motility (Sofikitis & Miyagawa, 1993; Zavos & Goodpasture, 1989).

The mechanisms that cause copulatory ejaculates to contain more sperm than masturbatory ejaculates are not fully understood, but the greater intensity and duration of precoital stimulation increases the number of motile sperm with normal morphology in copulatory ejaculates (Zavos, 1988). There is mixed evidence on whether sexually stimulating visual material can improve semen parameters for masturbatory ejaculates (Handelsman et al., 2013; van Rooijen et al., 1996; Yamamoto, Sofikitis, Mio, & Miyagawa, 2000), but there is a positive association between the duration of pre-ejaculatory sexual arousal and sperm concentration for masturbatory ejaculates when multiple specimens are collected from individual men (Pound, Javed, Ruberto, Shaikh, & Del Valle, 2002) although this is not apparent in between-male studies (Elzanaty, 2008; Handelsman et al., 2013).

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 (for review, see Pound, 2002). Given the relationship between duration of pre-ejaculatory sexual arousal and variation in ejaculate sperm counts across species, males may achieve adaptive changes in ejaculate composition through behavioral changes that prolong arousal prior to ejaculation (Pham, Shackelford, Welling et al., 2013; Pound, 2002).

PSYCHOLOGICAL MECHANISMS ASSOCIATED WITH PRUDENT SPERM ALLOCATION

Males in many nonhuman species can adjust the number of sperm they inseminate in response to sperm competition risk. Baker and Bellis (1993a) suggest that human

males share this capacity. Shackelford et al. (2002) investigated men's psychological responses to sperm competition risk, hypothesizing that psychological mechanisms evolved to motivate male behavior to increase the probability of success in sperm competition. For men, the absence of a regular partner (e.g., objective sperm competition risk) may provide key information processed by psychological mechanisms and which subsequently motivates a man to inseminate his partner as soon as possible, to combat the increased risk of sperm competition (Shackelford et al., 2002). Nevertheless, total time since last copulation might have important effects on a man's sexual behavior, perhaps increasing feelings of sexual frustration whether that time has been spent apart or together.

Shackelford et al. (2002) assessed the relationships between male sexual psychology and behaviors predicted to be linked to objective sperm competition risk, while controlling for the total time since a couple's last copulation. Shackelford et al. 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. (2002) controlled for the extent to which the participants were satisfied with their relationships.

Shackelford et al. (2002) and Shackelford, Goetz, McKibbin, and Starratt (2007) found that men who spend a greater proportion of time apart from their partner since their last copulation (and, therefore, faced greater sperm competition risk) rate her as more attractive, report that other men find her more attractive, report greater interest in copulating with her, and indicate that she is more interested in copulating with him, but only among men who perceive that she spends more time *with other men* (Pham & Shackelford, 2013a). Starratt, McKibbin, and Shackelford (2013) documented that men experimentally primed with thoughts of partner infidelity report greater partner-directed copulatory interest. Taken together, these findings suggest that men are sensitive to cues to sperm competition risk and adjust accordingly their partner-directed copulatory interest.

The *cuckoldry risk hypothesis* predicts that men at greater sperm competition risk are more likely to sexually coerce their partner (Goetz & Shackelford, 2006; Lalumiere, Harris, Quincy, & Rice, 2005; Thornhill & Thornhill, 1992; Wilson & Daly, 1992). In socially monogamous birds, forced in-pair copulations often follow immediately a female's extra-pair copulation (Bailey, Seymour, & Stewart, 1978; McKinney & Stolen, 1982). In humans, research documents a positive relationship between men's partner-directed sexual coercion and their partner's infidelity risk. Men who rape their female partners often accuse their partner of infidelity prior to the act (Finkelhor & Yllo, 1985; Russell, 1982). Female victims of intimate partner violence rate their abusers as more sexually jealous when the abuse also includes rape (Frieze, 1983; Gage & Hutchinson, 2006). Men who report sexually coercing their partner are more likely to report perceiving their partners as being unfaithful, and women who report being sexually coerced are more likely to report being unfaithful (Goetz & Shackelford, 2006). Even after controlling for men's dominant personalities and controlling behaviors, men's sexual coercion tactics are positively correlated with their perception or knowledge of partner infidelity (Goetz & Shackelford, 2009). Men's sexual coercion is positively correlated with the occurrence of partner-directed insults involving accusations of

their partner's infidelity (Starratt, Goetz, Shackelford, & Stewart-Williams, 2008). The proportion of time spent apart from a partner since the couple's last copulation predicts men's partner-directed sexual coercion, but *only* among men who perceive a greater risk of partner infidelity (McKibbin, Starratt, Shackelford, & Goetz, 2011).

Men's partner-directed copulatory interest in response to sperm competition risk may manifest as frequent copulations. In many socially monogamous birds, males use frequent copulations to increase rates of sperm transfer into the female reproductive tract, thereby increasing their chances of success in sperm competition (Birkhead, Atkin, & Moller, 1987; McKinney, Cheng, & Bruggers, 1984). Similarly in humans, men at greater sperm competition risk (Kaighobadi & Shackelford, 2008; Pham et al., 2014), and men who more frequently perform behaviors to minimize sperm competition risk (Shackelford, Goetz, Guta, & Schmitt, 2006), also perform more frequent copulations with their partner.

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 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 longer 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 closer to the cervix may increase the chance of fertilization (Baker & Bellis, 1995; Short, 1979; Smith, 1984).

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. found that artificial phalluses with a glans and a coronal ridge approximating a human penis displaced more simulated semen than did a phallus lacking these features. They suggested that when the penis is inserted into the vagina, space around the frenulum allows semen to flow back under the penis and collect behind the coronal ridge, facilitating its extraction. Displacement of simulated semen only occurred, however, 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 more deeply and more quickly at the couple's next copulation (Gallup et al., 2003). Such copulatory behaviors may increase semen displacement.

In an independent test of the hypothesis that displacing rival semen may require specific copulatory behaviors, Goetz et al. (2005) investigated whether and how men under a higher risk of sperm competition might attempt to "correct" a female partner's sexual infidelity. Men in committed, sexual relationships reported their performance of specific copulatory behaviors arguably designed to displace the semen of rival men. As hypothesized, men who mated to women who place them at higher recurrent risk

of sperm competition were more likely to perform semen-displacing behaviors, including an increase in number of thrusts, deepest thrust, average depth of thrusts, and duration of sexual intercourse.

Sperm competition theory has informed research on other male sexual behaviors, such as oral sex. Evidence suggests that oral sex was a recurrent feature of human evolution, occurring in most cultures and in several other species (see Pham & Shackelford, 2013a, 2013b). It is frequently depicted in modern pornography (Mehta & Plaza, 1997), and appears in Paleolithic cave paintings (Angulo & Garcia, 2005). However, whether oral sex is an adaptation is unclear. Previous researchers have suggested that men perform oral sex to (a) assess a partner's reproductive health (Baker, 1996), (b) detect rival male semen in the vagina (Baker, 1996; Kohl & Francoeur, 1995; Thornhill, 2006), (c) manipulate female mechanisms that may bias the outcome of sperm competition (Pham, Shackelford, Sela, & Welling, 2013), (d) sexually satisfy the woman, thereby reducing the likelihood of her mating with another man (Pham & Shackelford, 2013c), or (e) increase male sexual arousal and consequent semen quality (Pham, Shackelford, Welling et al., 2013). Additionally, oral sex may facilitate "fertility-detection": Men use olfactory cues to detect women's fertility status (reviewed in Haselton & Gildersleeve, 2011), and men report vaginal fluid is more pleasant smelling when produced at high fertility versus low fertility (Cerdeña-Molina, Hernández-López, de la O, Chavira-Ramírez, & Mondragón-Ceballos, 2013).

THE INFLUENCE OF SPERM COMPETITION ON MEN'S MATE SELECTION

To minimize sperm competition risk, men may have evolved mate preferences that function to select as short-term sexual partners women who present a lower risk of sperm competition (Shackelford, Goetz, LaMunyon, Quintus, & Weekes-Shackelford, 2004). Men's risk of sperm competition increases with a prospective short-term partner's involvement in one or more relationships. Women who are not in a long-term relationship and who 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 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 casual sexual relationships. These results suggest that when men are presented with different mating options, they are less sexually aroused by options that reflect higher sperm competition risk. However, exposed to high sperm competition risk—such as when their regular partner commits infidelity—men are more sexually aroused to high sperm competition risk (Shackelford et al., 2002, 2007).

THE INFLUENCE OF SPERM COMPETITION ON MEN'S SEXUAL AROUSAL AND SEXUAL FANTASIES

Men's sexual fantasies often involve multiple, anonymous partners (Ellis & Symons, 1990; Symons, 1979). These fantasies tend to be embodied in pornography produced for men, incorporating multiple, low-investment matings with highly fertile women (Malamuth, 1996). However, much pornography contains visual cues of sperm competition risk. Pound (2002) analyzed pornographic images on Internet sites and showed that depictions of sexual activity involving a woman and multiple men are more prevalent than those involving a man and multiple women. Similar results were found in both an online survey of self-reported preferences and in a preference study that unobtrusively examined image selection behavior. McKibbin, Pham, and Shackelford (2013) reported that the number of images on adult DVD covers depicting multimale interactions with one woman predicted DVD sales rank better than the number of images depicting multifemale interactions with one man. Finally, anecdotal reports from the "swinging" or "partner-swapping" community suggest that men often experience intense sexual arousal in response to the sight of their partner interacting sexually with other men (Gould, 1999; Talese, 1981).

Pound (2002) argued that males should find mate sharing to be aversive because of the potential loss of paternity to a competitor's ejaculate. However, sexual arousal in response to cues of sperm competition risk may be produced by a paternity assurance mechanism because it may motivate earlier or more frequent copulation. Moreover, increased arousal in response to cues of sperm competition risk may play a proximate role in ejaculate adjustment mechanisms (Pound, 2002). Consistent with this hypothesis, Kilgallon and Simmons (2005) reported that men who view pornography depicting two men interacting with one woman (cueing sperm competition), relative to men who view pornography depicting three women (cueing absence of sperm competition) ejaculate a higher percentage of motile sperm. Thus, although men should avoid sexual instances with risk of sperm competition, they may actually prefer the arousal associated with the same instances when experiencing the fantasies involved in viewing pornography.

WOMEN'S ADAPTATIONS TO SPERM COMPETITION

If sperm competition was a recurrent feature of human evolutionary history, women may have adaptations that allow them to influence its outcome. Specifically, women may have evolved mechanisms to determine which men achieve paternity; that is, adaptations for both precopulatory and postcopulatory choice. In this context, "postcopulatory female choice" refers to female influence that follows initiation of copulation (Eberhard, 1996).

PRECOPULATORY FEMALE CHOICE: PROMOTING AND AVOIDING SPERM COMPETITION

Bellis and Baker (1990) documented that women in committed relationships are more likely to double mate when the probability of conception is higher. This observation suggests that women have psychological adaptations that promote sperm competition, with the result that their ova will be fertilized by the most competitive sperm. For example, although women's sexual attraction to their regular partner remains

unchanged across their fertility cycle, they are more sexually attracted to, and fantasize about, men *other than* their regular partner during periods of higher conception risk (Gangestad, Thornhill, & Garver, 2002; Pillsworth & Haselton, 2006), suggesting that women may promote sperm competition during these periods. However, under certain conditions, it may be advantageous for women to *avoid* sperm competition. Gallup et al. (2006) documented that women delay copulations with their regular partner following their extra-pair copulation. Favoring copulation with an extra-pair partner to the exclusion of a primary partner reduces competition for the extra-pair sperm when conception is more likely. 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 have been selected to be sensitive to their partner's increased interest in extra-pair copulation near ovulation (Gangestad et al., 2002), women may have postcopulatory adaptations that favor sperm from one man over another.

POSTCOPULATORY FEMALE CHOICE: A FUNCTION FOR FEMALE COITAL ORGASM?

One such female postcopulatory adaptation to sperm competition may be orgasm. The human clitoris and penis develop from the same embryonic tissue, prompting Symons (1979) and Gould (1987) to argue that female orgasm is a by-product of male orgasm. Others have hypothesized that female orgasm may be an adaptation (e.g., Alexander, 1979; Baker & Bellis, 1993b; Hrdy, 1981; Smith, 1984). Women experience oxytocin surges during orgasm, which may promote pair bonding and repeated copulations with a man (reviewed in Puts, Dawood, & Welling, 2012). Female coital orgasm also may afford 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 (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.

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 coital orgasm. Coital orgasms that occurred between 1 minute before and 45 minutes after their partner ejaculated were associated with greater sperm retention than orgasms that occurred earlier than 1 minute before their partner ejaculated. Baker and Bellis also provided evidence that women with a regular partner and one or more extra-pair partners had fewer high-retention orgasms with their regular partner and more high-retention orgasms with their extra-pair partners.

Missing from Baker and Bellis's (1993b) study, however, was an explicit demonstration of higher sperm retention associated with partners of higher genetic quality. Thornhill, Gangestad, and Comer (1995) established this link and documented that women mated to men with lower fluctuating asymmetry (indicating relatively high genetic quality) reported more copulatory orgasms than did women mated to men with higher fluctuating asymmetry. Women mated to men with lower fluctuating asymmetry did not simply have more orgasms, but specifically reported more copulatory orgasms likely to result in greater sperm retention. Another indicator

of genetic quality and related to fluctuating asymmetry is physical attractiveness. Shackelford et al. (2000) found that women mated to more physically attractive men were more likely to report achieving orgasm at their most recent copulation than were women mated to less attractive men.

Although orgasm as an adaptation for postcopulatory female choice between rival ejaculates is plausible, the functional significance of the female orgasm is still hypothetical (Pound & Daly, 2000). Baker and Bellis's (1995) evidence that women retain more sperm if they experience orgasm between 1 minute before and 45 minutes after their partner ejaculates than at other times (or not at all) assumes that the number of sperm ejaculated is identical regardless of whether or when the woman has an orgasm. This assumption may be incorrect, however, because the duration of pre-ejaculatory sexual arousal is positively associated with the number of sperm ejaculated (Pound, 2002; Zavos, 1988).

Men's interest in whether their partner achieves orgasm suggests that female orgasm may be an adaptation (see Thornhill et al., 1995). Consistent with this, McKibbin, Bates, Shackelford, Hafen, and LaMunyon (2010) found that sperm competition risk moderates the association between men's relationship investment and their interest in their partner's copulatory orgasm. In some cultures, men do not appear concerned about whether their partners experience orgasm (Symons, 1979), but these may be cultures where sperm competition risks are lowered through other mechanisms; for example, in many cultures, female sexuality (and female orgasm) is suppressed through punishment of female promiscuity (reviewed in Baumeister & Twenge, 2002).

Women may pretend orgasm to appease their partner, suggesting the existence of female counteradaptations to men's interest in their orgasm (Thornhill et al., 1995). Women may pretend orgasm to signal their relationship satisfaction to their partner, thereby minimizing the likelihood of their partner's infidelity (Muehlenhard & Shippee, 2010). Women who perceive a greater risk of partner infidelity are more likely to pretend orgasm (Kaighobadi, Shackelford, & Weekes-Shackelford, 2012). A tendency to pretend orgasm with a desired partner would seem to be inconsistent with the hypothesized sperm retention function of genuine orgasm. If female orgasm functioned to retain, preferentially, sperm from men of high genetic quality, we might predict that women would pretend orgasm more frequently with men of lower genetic quality to "avoid" retaining his sperm from genuine orgasm, simultaneously satisfying him, possibly to continue securing nongenetic benefits. To reconcile these differences, future research should investigate whether the frequency with which women pretend orgasm correlates with measures of their partner's genetic quality (e.g., masculinity, muscularity, fluctuating asymmetry; Frederick & Haselton, 2007).

Direct evidence of preferential use of sperm by females is absent in humans, particularly because it is 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. Although there have been 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 offspring paternity (see Eberhard, 1996). Because much of postcopulatory competition occurs in the reproductive tract, it is likely that human females have evolved adaptations in response to sperm competition.

This chapter focuses on men's adaptations, which reflects the historical and current state of research and theory. Intersexual conflict between ancestral males and females,

however, produces a coevolutionary arms race between the sexes, in which an advantage gained by one sex selects for counteradaptations in the other sex (Rice, 1996; Shackelford & Goetz, 2012). Thus, men's numerous adaptations to sperm competition are likely to be met by numerous adaptations in women, including female orgasm (reviewed in Puts et al., 2012), and manipulating the timing of their copulations with their regular partner and with a potential extra-pair partner (Gallup et al., 2006).

CONCLUDING REMARKS

We describe the far-reaching consequences of female infidelity and consequent sperm competition. First identified in nonhuman species in the 1970s, and not considered in humans until the 1980s, evolutionary-minded researchers are only beginning to uncover its possible role in shaping human anatomy, physiology, and psychology. 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, so understanding its role will be challenging but necessary if we are to achieve a comprehensive understanding of human sexuality.

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