C23

CHAPTER

23

Sperm Competition

Valerie G. Starratt *and* Todd K. Shackelford

Abstract

Sperm competition is a form of intrasexual competition in which the sperm of two or more males concurrently occupy the reproductive tract of a single female and compete to fertilize an available ovum. As a nonmonogamous species, humans have been subject to selection pressures associated with sperm competition. Consequently, human males have evolved a variety of anatomical, physiological, and psychological adaptations to address associated adaptive problems. Some of these adaptations motivate avoidance of sperm competition by engaging in precopulatory intrasexual competition, which may limit the risk of exposure to sperm competition. Other adaptations promote engagement in sperm competition during copulation or postcopulation and function not by avoiding sperm competition but by increasing the likelihood of winning the competition and siring offspring. For example, men facing a perceived increase in risk of sperm competition are more likely to demonstrate an increased interest in sex with their long-term partner. We summarize previous research on adaptations to sperm competition in humans, and highlight several directions for future research.

Key Words: sperm competition, cuckoldry, semen displacement, ejaculate adjustment, forced in-pair copulation, sexual coercion, female-directed violence, cryptic female choice

C23.P1 Sperm competition occurs when the sperm of two or more males concurrently occupy the reproductive tract of a single female. The extent to which sperm competition occurs in sexually reproducing species varies, from virtually nonexistent in truly sexually monogamous species to extraordinary in polygynandrous species. As a nonmonogamous species, humans are subject to the risks of sperm competition. Some theorists argue that sperm competition has not been greatly influential over the course of human evolutionary history, and as evidence they point to historically and contemporary low discrepant paternity or cuckoldry rates in humans of around 1 to 2 percent (Greeff & Erasmus, 2015; Larmuseau et al., 2017; Larmuseau et al., 2013). Recent evidence indicates such rates may be culturally variable, and much higher in some cultures. For instance, extra-pair paternity is nearly 50 percent among Himba pastoralists of Namibia in southwest Africa (Scelza et al., 2020). In some cases, these instances of extra-pair paternity may not qualify

as cuckoldry, per se, as the men and women involved in such cases seem to be accurately aware of the mismatch (Scelza et al., 2020). Even outside of such explicit cases of extra-pair paternity, people estimate local cuckoldry rates to be upwards of 10 percent (Voracek et al., 2009). So, although there is some disagreement about a species-wide rate of cuckoldry or extra-pair paternity, it is undeniable that cuckoldry at least occasionally occurs in humans, today and for much of our recent evolutionary history. Consequently, the risk of sperm competition in humans is certainly greater than zero.

C23.P2 Compelling evidence for the influence of sperm competition in humans is also apparent in the suite of purported adaptations that reduce the costs associated with sperm competition (for men) or promote sperm competition (for women). Such adaptations manifest at many levels—including anatomical and physiological features as well as psychological motivations and behaviors—and can and do operate at every stage of the mating process.

C23.S1 ## Testes Size

C23.P3 One of the most consistently identified anatomical features associated with sperm competition risk is relative testes size, which is a ratio of combined testes mass to overall body mass. Across numerous nonmonogamous species, from butterflies (Gage, 1994) and fish (Stockley et al., 1997) to birds (Møller & Briskie, 1995), rodents (Ramm et al., 2005), and primates (Baker & Shackelford, 2018a, 2018b; Møller, 1988), interspecific differences in relative testes size correlate with interspecific differences in risk of sperm competition. Experimental evidence from *S. stercoraria* confirms that increases in testes size are consequent to increased sperm competition, such that increases in sperm competition cause subsequent increases in relative testes size (Hosken & Ward, 2001). Larger testes are an adaptation to increased risk of sperm competition given that larger testes produce larger ejaculates, which increases a male's chances of successful fertilization of an egg under circumstances of sperm competition (Møller, 1989). Among primates, human males have a relative testes size that is between gorillas' comparatively small testes (associated with very low sperm competition) and chimpanzees' comparatively large testes (associated with very high sperm competition). This suggests that human males, with intermediately sized testes, are subject to sperm competition at a rate between the highly competitive chimpanzees and the virtually noncompetitive gorillas (Baker & Shackelford, 2018a).

C23.S2 ## Semen Displacement

C23.P4 In addition to testes size, penis morphology may function as an adaptation to sperm competition. For example, the presence of penile spines (Orr & Brennan, 2016; Stockley, 2002) and the shape of the baculum (André et al., 2018; Stockley, 2012) are associated with greater sperm competition. Although human males have neither penile spines nor bacula, the shape of the human penis may similarly function as an adaptation to sperm competition. Specifically, the relatively greater penile girth (compared to humans' closest primate relatives) and the protrusion of the coronal ridge may function to displace semen

already present in the female reproductive tract (Gallup et al., 2003). That is, during intromission with a woman who has recently copulated with another man, the size (girth) and shape (prominent coronal ridge) of the human penis may function to push the rival male's sperm out of the female's reproductive tract. This would function as a valuable sperm competition tactic, as sperm that have been removed from the reproductive tract are no longer viable for fertilization, giving an advantage to the man who is doing the displacing over the male whose sperm has been displaced.

C23.P5 Behavioral evidence supports the hypothesis that semen displacement is a sperm competition tactic in humans. Men are more likely to engage in copulatory behaviors that facilitate displacement of rival semen when the risk of the presence of rival semen is higher. For example, men whose female partners have spent more time around rival males report greater sexual interest in their partners and greater distress following their partner's sexual rejection (DeLecce et al., 2017) and report copulatory behaviors that include deeper thrusting and a greater number of thrusts (Pham et al., 2017). A similar effect is evident among men who find themselves at greater risk of sperm competition given their partner's attractiveness and other individual difference traits related to an increased risk of a partner's extra-pair sex (Goetz et al., 2005). As these copulatory behaviors, including increased thrust frequency and deeper thrusting, have been demonstrated to displace comparatively greater amounts of semen (Gallup et al., 2003), the association of these behaviors with circumstances under which men are at greater risk of sperm competition further supports the role of semen displacement as an evolved response to sperm competition.

C23.P6 Of course, semen-displacing behaviors function to remove *any* semen currently in the female reproductive tract, even if that semen is one's own. As behaving in ways that could result in self-semen displacement would be disadvantageous, it would be reasonable to hypothesize that men may have adaptations to reduce the risk of self-semen displacement (Gallup & Burch, 2004). Indeed, such behaviors and physiological features have been documented. For instance, shortly following ejaculation, human males experience a significant loss of erectile volume, engage in reduced thrusting, and withdraw the penis from the vagina (Gallup et al., 2006), all of which are contrary to semen displacement and may function to reduce the likelihood of displacing one's own semen. It also has been argued that the postejaculatory refractory period, or the inability to achieve erection for some period of time following ejaculation, may function to reduce self-semen displacement (Gallup & Burch, 2004). If one cannot achieve the erection necessary to successfully copulate again following a successful copulation, then one is not at risk of inadvertently displacing one's own previously deposited semen. The fact that refractory periods are not immutable and may be overcome by the introduction of a novel female (i.e., the Coolidge effect; Vance & Shackelford, 2021) is suggestive of the functional value of such a refractory period in terms of reducing self-semen displacement.

C23.S3 **Sperm Quality and Ejaculate Adjustment**

C23.P7 In comparison to ova, sperm and seminal fluid are relatively inexpensive to produce in terms of metabolic expenditure (Hayward & Gillooly, 2011). However, *relatively inexpensive* does not mean *inconsequential*, and males are not expected to be indiscriminate in this expenditure. Rather, males are expected to adjust this expenditure to invest disproportionately in copulations for which sperm competition risk is higher. Indeed, at a species' level, sperm competition results in increased sperm quality along several parameters, including percentage of normal sperm, acrosome integrity, and motility (Gómez Montoto et al., 2011). Similar adjustments in sperm and ejaculate quality have been documented at an individual level, as well. For example, men who produced masturbatory ejaculates in response to sexually explicit visual materials adjust that ejaculate depending on the level of sperm competition depicted in that material. Specifically, men exposed to depictions of sperm competition produce masturbatory ejaculates with greater sperm motility (Kilgallon & Simmons, 2005). As sperm motility is positively associated with fertility (Tardif et al., 1999), producing an ejaculate with more motile sperm in the presence of sperm competition would be a valuable response to such conditions.

C23.P8 Other metrics relevant to the risk of sperm competition have been related to functional ejaculate adjustments. For example, high mate value men produce comparatively high-quality ejaculates, but only when produced in response to highly attractive women (Leivers et al., 2014). Given that highly attractive women are perceived to be particularly attractive as short-term mates (McDowell & Starratt, 2019) and are more likely to embrace a short-term mating strategy (Perilloux et al., 2013), they may represent a relatively high risk of sperm competition, at least in comparison to their less attractive counterparts. Higher mate value men are also more likely to pursue a slower life history strategy (McDowell & Starratt, 2021; Strouts et al., 2017) and, given that a slower life history strategy is associated with an increased focus on a long-term mating strategy and the consequential increased risk of sperm-competition-caused cuckoldry, men who report slower life history strategies also produce higher-quality ejaculates (Barbaro et al., 2019). In short, it is possible that men who find themselves at greater risk of sperm competition by forming long-term partnerships, and at greater risk of particularly high costs of sperm competition by forming partnerships with highly attractive women, may solve the adaptive problem of increased risk by producing high-quality ejaculates likely to be successful in sperm competition.

C23.P9 Beyond the influence of long-term versus short-term mating strategies and the attractiveness of one's partner, there are specific copulatory behaviors men perform that may affect ejaculate quality. In general, these copulatory behaviors may function to increase ejaculate quality by increasing male sexual arousal (Pound et al., 2002). One of the behaviors that may serve this purpose is the performance of cunnilingus, a behavior associated with increased sexual arousal in men and increased duration of subsequent copulation, both of which are associated with signals of increased ejaculate quality such as ejaculate

volume (Pham et al., 2016; Pham et al., 2013b). That is, men who perform oral sex on their partner may also experience increased sexual arousal and spend more time in copulation, which leads to the production of high-quality ejaculates (e.g., greater sperm number and faster sperm swimming speed) that presumably fare better in sperm competition.

C23.S4 **Copulation Frequency, Sexual Coercion, and Forced Copulation**

C23.P10 In addition to displacing rival semen and increasing ejaculate quality, males also may increase their chances of success in sperm competition by increasing the frequency of copulation with their partner. Indeed, men whose female partners spend more time around rival males—a circumstance that creates more opportunity for a woman to put her partner at risk of sperm competition—report greater in-pair copulation frequency, primarily when those women are perceived to be particularly attractive (Pham et al., 2014). The value of this increased copulation frequency may be twofold. First, as copulation frequency is positively related to relationship satisfaction (McNulty et al., 2016) and relationship satisfaction is negatively related to female extra-pair sexual activity (Atkins et al., 2001), it is possible that this increased frequency of in-pair copulation reduces the risk of sperm competition by increasing relationship satisfaction and consequently reducing the risk of a woman engaging in behaviors that would put her partner at risk of sperm competition.

C23.P11 Second, frequent copulations may decrease the likelihood that, should a female partner have engaged in an extra-pair copulation, the rival males' sperm will have an unchallenged chance at fertilization. This value of frequent in-pair copulation is evident in men's insistence on and persistence in pursuing copulation with a partner whom they believe may have engaged in extra-pair sexual activity. That is, men who are at greater risk of sperm competition are more likely to employ sexual coercion against their partners (Goetz & Shackelford, 2006; Lopes et al., 2019; Starratt et al., 2008). Additionally, following cues to increased sperm competition risk, men are more likely to report decreased copulatory duration (Barbaro et al., 2015). By engaging in forced in-pair copulation and reducing the amount of time to place his sperm in competition with any rival male sperm in his partner's reproductive tract, a man would be reducing the likelihood of cuckoldry should his partner's behavior have put him at risk of sperm competition (Shackelford et al., 2006). The reduced copulatory duration described here and the increased copulatory duration subsequent to increased cunnilingual duration described above may represent two distinct sperm competition tactics, with the former more likely to serve as a "corrective strategy" and the latter as a "preventative" strategy (Barbaro et al., 2015).

C23.P12 Partner-directed violence that is not specifically sexual also may function as a response to sperm competition, as female-directed violence positively correlates with frequency of in-pair copulations. That is, men who are more violent toward their partners also secure more copulations with those partners (Barbaro & Shackelford, 2016). That said, the nature of the violence may be tailored to different aspects of sperm competition risk. For example, while men who accuse their female partners of having been unfaithful are more

likely to sexually coerce their partners, men who find their partners to be already pregnant switch from sexual violence to nonsexual physical violence (Burch & Gallup, 2020). In other words, when the risk is that a female partner's behavior may have put a man at risk of sperm competition, he is more likely to engage in partner-directed sexual violence, which could function to place his sperm in competition with any existing rival males' sperm. However, when a partner's pregnancy is confirmed and the risk escalates from one of potential sperm competition to potential cuckoldry, men's behavior may shift from specifically sexual violence to nonsexual physical assault, which may more directly address the potential risk of his partner giving birth to a rival male's offspring (i.e., by causing miscarriage). Some evidence even suggests this nonsexual physical violence may be particularly targeted toward the pregnancy, with assaults to the abdomen and the developing fetus (Valladares et al., 2005).

C23.P13 These behavioral responses to sperm competition risk are expressions of men's evolved psychology designed to address such risk. That is, as men's risk of sperm competition increases, so too does their sexual interest in their partner, distress following their partner's sexual rejection, and persistence in pursuing sex with their partner following her sexual rejection (Shackelford et al., 2007), particularly when they perceive themselves to be at risk of a partner's infidelity (Starratt et al., 2013). Men at an increased risk of sperm competition also demonstrate increased mate-guarding behaviors, which function to reduce the likelihood of a partner engaging in behavior that would put a man at risk of sperm competition (Starratt et al., 2007). In short, men who perceive themselves to be at risk of sperm competition experience jealousy and emotional distress, which are amplified by a partner's sexual rejection and which motivate men to tenaciously pursue copulation with their partners, occasionally to the point forced sex.

C23.S5 ## Female Role in Sperm Competition

C23.P14 Men's sensitivity to a partner's sexual rejection and motivation to respond to that rejection with increased sexual persistence may be warranted in terms of risk of sperm competition. This is because women who have had sex with an extra-pair man may be likely to subsequently attempt delaying sex with their in-pair partner (Gallup et al., 2006). Such a delay would effectively prevent a woman's in-pair partner from successfully addressing this greater risk of sperm competition. This behavior of delaying in-pair copulation following extra-pair copulation may be but one way in which women influence sperm competition for the purpose of granting reproductive preference to some men over others. In fact, evidence suggests that females employ a wide array of strategies to exert control over males' sperm competition success, strategies sometimes referred to as cryptic female choice (Firman et al., 2017).

C23.P15 These female strategies to influence sperm competition include both behavioral strategies, such as in-pair copulation delay, and physiological mechanisms. An example of the latter is chemoattractant moderated sperm choice, in which the follicular fluid of a

particular woman differentially attracts sperm of some men over others in a manner that is independent of that woman's intentional mate choice (Fitzpatrick et al., 2020). Ova preferentially attract sperm from specific males, and the preferential treatment of those sperm appears to be independent of whether those sperm come from the woman's social partner or from an extra-pair partner. It is likely that these effects are the result of the influence of female reproductive fluid, including chemoattractants, on both sperm and seminal fluid. For example, female reproductive fluid can affect sperm motility, longevity, and capacitation and can influence seminal fluid such that it is more conducive to sperm viability (Gasparini et al., 2020).

C23.P16 It has also been suggested that female orgasm may function as a means of cryptic female choice via ejaculate manipulation, such that more sperm are retained in the reproductive tract when female orgasm occurs shortly before, during, or a brief time after male ejaculation (Baker & Bellis, 1993). Women who orgasm shortly before or less than an hour following male ejaculation, according to this hypothesis, retain more sperm from that ejaculate. That women are more likely to experience orgasm when their male partners are more attractive (Shackelford et al., 2000) and display lower fluctuating asymmetry (Thornhill, Gangestad, & Comer, 1995), two indicators of high mate value, suggests that women may preferentially retain sperm from particularly high value men. Retaining a greater portion of sperm from higher-quality men, of course, would subsequently increase the likelihood of successful fertilization by those more valuable men.

C23.P17 If female orgasm functions as a mechanism of cryptic female choice, then we might expect men to demonstrate interest in ensuring a female partner's orgasm, particularly when they are at greater risk of sperm competition. Indeed, evidence suggests that this is the case. For example, interest in a partner's orgasm is positively related to risk of sperm competition, particularly for men who are more highly invested in their long-term relationship (McKibbin et al., 2010). That is, men who perceive themselves to be at some risk of sperm competition and who are invested in maintaining a relationship with their current long-term partner are more likely to report an interest in ensuring their partner's copulatory orgasm, thereby potentially increasing their likelihood of successfully surviving sperm competition and decreasing the risk of suffering the negative effects of cuckoldry. This is not to suggest, however, that any potential value of female orgasm is restricted to its purported role in cryptic female choice. It also has been argued that female orgasm may function as a broader mate-retention strategy, such that women in relationships with men who demonstrate an interest in female orgasm and pursue behaviors to that end may remain more invested in and less likely to stray from those relationships (Pham et al., 2013a). In either case, men who are more successful in ensuring their female partner's copulatory orgasms may be at a reduced risk of encountering sperm competition and/or an increase likelihood of "winning" such a competition.

C23.P18 Impact and Influence of Sperm CompetitionAlthough there remains some debate as to the level of risk of sperm competition in humans, the preponderance of evidence indicates

that it has played an influential role in the evolution of human sexual physiology, psychology, and behavior. As the sex subject to both the negative consequences of losing sperm competition and the benefits of winning sperm competition, men have evolved physical adaptations that function to increase their chances of successfully navigating a high risk of sperm competition and psychological adaptations that motivate behaviors both for avoiding sperm competition and for being successful when it either cannot be avoided or

C23.T1

Table 23.1 Proposed Adaptations to Sperm Competition

Adaptation	Function
Precopulatory	
Large testes to body mass ratio	Larger testes produce larger ejaculates, which increase chances of successful fertilization
Penis morphology (e.g., coronal ridge protrusion)	Displacement of rival male semen from the female reproductive tract
Response to a partner's sexual rejection	Increased sexual interest, persistence, and distress following rejection increases likelihood of placing sperm in competition with potential rival sperm
Sexual coercion	Increases likelihood of placing sperm in competition with potential rival sperm
Mate guarding	Prevent partner from engaging in behavior that would increase risk of sperm competition
Copulatory	
Copulatory frequency	Increases likelihood of placing sperm in competition with potential rival sperm
Copulatory duration	quickly placing sperm in competition with potential rival sperm
Increased thrusting depth and frequency	displacement of rival male semen from the female reproductive tract
ejaculate adjustment	Ejaculate quality increases with the risk (high risk) and costs (high partner quality) of sperm competition
Chemoattractant moderated sperm choice	Cryptic female choice; female reproductive fluid preferentially attracts sperm from specific males
Female orgasm	Cryptic female choice; increased retention of sperm from high value males
Interest in ensuring female orgasm	Increase chance of preferential retention of own sperm over potential rival male sperm
Postcopulatory	
Female-specific refractory period	Reduce risk of self-semen displacement
Female-delayed in-pair copulation	Following extra-pair copulation, delaying in-pair copulation favors rival male sperm
Partner-directed nonsexual violence	Reduce risk of partner giving birth to rival male's offspring

when it would be reproductively valuable. On the other hand, as the sex that could almost invariably benefit from sperm competition, women have adaptations for both encouraging sperm competition among rival males and ensuring that the most valuable of those rivals is successful.

C23.S6 ## References

C23.P19 André, G. I., Firman, R. C., & Simmons, L. W. (2018). Phenotypic plasticity in genitalia: baculum shape responds to sperm competition risk in house mice. *Proceedings of the Royal Society of London B: Biological Sciences*, *285*, Article 20181086.

C23.P20 Atkins, D. C., Baucom, D. H., & Jacobson, N. S. (2001). Understanding infidelity: Correlates in a national random sample. *Journal of Family Psychology*, *15*(4), 735.

C23.P21 Baker, R. R., & Bellis, M. A. (1993). Human sperm competition: ejaculate manipulation by females and a function for the female orgasm. *Animal Behavior*, *46*, 887–909.

C23.P22 Baker, R. R., & Shackelford, T. K. (2018a). A comparison of paternity data and relative testes size as measures of level of sperm competition in the Hominoidea. *American Journal of Physical Anthropology*, *165*, 421–443.

C23.P23 Baker, R. R., & Shackelford, T. K. (2018b). Paternity data and relative testes size as measures of level of sperm competition in the Ceropithecoidea. *American Journal of Primatology*, *80*, Article e22937.

C23.P24 Barbaro, N., Pham, M. N., & Shackelford, T. K. (2015). Sperm competition risk and sexual coercion predict copulatory duration in humans. *Evolutionary Psychology*, *13*, 1–8.

C23.P25 Barbaro, N., & Shackelford, T. K. (2016). Female-directed violence as a form of sexual coercion in humans (*Homo sapiens*). *Journal of Comparative Psychology*, *130*, 321–327.

C23.P26 Barbaro, N., Shackelford, T. K., Holub, A. M., Jeffery, A. J., Lopes, G. S., & Zeigler-Hill, V. (2019). Life history correlates of human (*Homo sapiens)* ejaculate quality. *Journal of Comparative Psychology*, *133*, 294–300.

C23.P27 Burch, R. L., & Gallup, G. G. (2020). Abusive men are driven by paternal uncertainty. *Evolutionary Behavioral Sciences*, *14*, 197–209.

C23.P28 DeLecce, T., Barbaro, N., Mohamedally, D., & Shackelford, T. K. (2017). Husband's reaction to his wife's sexual rejection is predicted by the time she spends with her male friends but not her male coworkers. *Evolutionary Psychology*, *15*, 1–5.

C23.P29 Firman, R. C., Gasparini, C., Manier, M. K., & Pizzari, T. (2017). Postmating female control: 20 years of cryptic female choice. *Trends in Ecology & Evolution*, *32*, 368–382.

C23.P30 Fitzpatrick, J. L., Willis, C., Devigili, A., Young, A., Carroll, M., Hunter, H. R., & Brison, D. R. (2020). Chemical signals from eggs facilitate cryptic female choice in humans. *Proceedings of the Royal Society of London B: Biological Sciences*, *287*, Article 20200805.

C23.P31 Gage, M. J. G. (1994). Associations between body size, mating pattern, testis size and sperm lengths across butterflies. *Proceedings of the Royal Society of London B: Biological Sciences*, *258*, 247–254.

C23.P32 Gallup, G. G., & Burch, R. L. (2004). Semen displacement as a sperm competition strategy in humans. *Evolutionary Psychology*, *2*, 12–23.

C23.P33 Gallup, G. G., Burch, R. L., & Berens Mitchell, T. J. (2006). Semen displacement as a sperm competition strategy: Multiple mating, self-semen displacement, and timing of in-pair copulations. *Human Nature*, *17*, 253–264.

C23.P34 Gallup, G. G., Burch, R. L., Zappieri, M. L., Parvez, R. A., Stockwell, M. L., & Davis, J. A. (2003). The human penis as a semen displacement device. *Evolution and Human Behavior*, *24*, 277–289.

C23.P35 Gasparini, C., Pilastro, A., & Evans, J. P. (2020). The role of female reproductive fluid in sperm competition. *Philosophical Transactions of the Royal Society B*, *375*(1813), Article 20200077.

C23.P36 Goetz, A. T., & Shackelford, T. K. (2006). Sexual coercion and forced in-pair copulation as sperm competition tactics in humans. *Human Nature*, *17*, 265–282.

C23.P37 Goetz, A. T., Shackelford, T. K., Weekes-Shackelford, V. A., Euler, H. A., Hoier, S., Schmitt, D. P., & LaMunyon, C. W. (2005). Mate retention, semen displacement, and human sperm competition: A preliminary investigation of tactics to prevent and correct female infidelity. *Personality and Individual Differences*, *38*, 749–763.

C23.P38 Gómez Montoto, L., Magaña, C., Tourmente, M., Martin-Coello, J., Crespo, C., Luque-Larena, J. J., Gomendio, M., & Roldan, E. R. S. (2011). Sperm competition, sperm numbers and sperm quality in muroid rodents. *PLoS ONE*, *6*, Article e18173.

C23.P39 Greeff, J. M., & Erasmus, J. C. (2015). Three hundred years of low non-paternity in a human population. *Heredity*, *115*, 396–404.

C23.P40 Hayward, A., & Gillooly, J. F. (2011). The cost of sex: Quantifying energetic investment in gamete production by males and females. *PLoS ONE*, *6*, Article e16557.

C23.P41 Hosken, D. J., & Ward, P. I. (2001). Experimental evidence for testis size evolution via sperm competition. *Ecology Letters*, *4*, 10–13.

C23.P42 Kilgallon, S. J., & Simmons, L. W. (2005). Image content influences men's semen quality. *Biology Letters*, *1*, 253–255.

C23.P43 Larmuseau, M. H. D., Claerhout, S., Gruyters, L., Nivelle, K., Vandenbosch, M., Peeters, A., van den Berg, P., & Decorte, R. (2017). Genetic-genealogy approach reveals low rates of extrapair paternity in historical Dutch populations. *American Journal of Human Biology*, *29*, Article e23046.

C23.P44 Larmuseau, M. H. D., Vanoverbeke, J., Van Geystelen, A., Defraene, G., Vanderheyden, N., Metthys, K., Wenseleers, T., & Decorte, R. (2013). Low historical rates of cuckoldry in a Western European human population traced by Y-chromosome and genealogical data. *Proceedings of the Royal Society of London B: Biological Sciences*, *280*, Article 20132400.

C23.P45 Leivers, S., Rhodes, G., & Simmons, L. W. (2014). Context-dependent relationship between a composite measure of men's mate value and ejaculate quality. *Behavioral Ecology*, *25*, 1115–1122.

C23.P46 Lopes, G. S., Meneses, G. O., Cataldo, Q. F., Segundo, D. S. A., Fink, B., & Shackelford, T. K. (2019). Individual differences in men's use of partner-directed insults and sexual coercion: replication and extension in a South American sample. *Personality and Individual Differences*, *150*, Article 109480.

C23.P47 McDowell, J., & Starratt, V. G. (2019). Experimental examination and extension of the cheerleader effect. *Personality and Individual Differences*, *147*, 245–249.

C23.P48 McDowell, J., & Starratt, V. G. (2021). Positive correlation between high mate value and slow life history strategy is moderated by trait heritability. *Biodemography and Social Biology*, *66*, 21–39.

C23.P49 McKibbin, W. F., Bates, V. M., Shackelford, T. K., Hafen, C. A., & LaMunyon, C. W. (2010). Risk of sperm competition moderates the relationship between men's satisfaction with their partner and men's interest in their partner's copulatory orgasm. *Personality and Individual Differences*, *49*, 961–966.

C23.P50 McNulty, J. K., Wenner, C. A., & Fisher, T. D. (2016). Longitudinal associations among relationship satisfaction, sexual satisfaction, and frequency of sex in early marriage. *Archives of Sexual Behavior*, *45*, 85–97.

C23.P51 Møller, A. P. (1988). Ejaculate quality, testes size and sperm competition in primates. *Journal of Human Evolution*, *17*, 479–488.

C23.P52 Møller, A. P. (1989). Ejaculate quality, testes size and sperm production in mammals. *Functional Ecology*, *3*, 91–96.

C23.P53 Møller, A. P., & Briskie, J. V. (1995). Extra-pair paternity, sperm competition, and the evolution of testes size in birds. *Behavioral Ecology and Sociobiology*, *36*, 357–365.

C23.P54 Orr, T. J., & Brennan, P. L. (2016). All features great and small—The potential roles of the baculum and penile spines in mammals. *Integrative & Comparative Biology*, *56*, 635–643.

C23.P55 Perilloux, C., Cloud, J. M., & Buss, D. M. (2013). Women's physical attractiveness and short-term mating strategies. *Personality and Individual Differences*, *54*, 490–495.

C23.P56 Pham, M. N., DeLecce, T., & Shackelford, T. K. (2017). Sperm competition in marriage: Semen displacement, male rivals, and spousal discrepancy in sexual interest. *Personality and Individual Differences*, *105*, 229–232.

C23.P57 Pham, M. N., Jeffery, A. J., Sela, Y., Lynn, J. T., Trevino, S., Willockx, Z., Tratner, A., Itchue, P., Shackelford, T. K., Fink, B., & McDonald, M. M. (2016). Duration of cunnilingus predicts estimated ejaculate volume in humans: A content analysis of pornography. *Evolutionary Psychological Science*, *2*, 220–227.

C23.P58 Pham, M. N., Shackelford, T. K., Holden, C. J., Zeigler-Hill, V., Hummel, A., & Memering, S. L. (2014). Partner attractiveness moderates the relationship between number of sexual rivals and in-pair copulation frequency in humans (*Homo sapiens*). *Journal of Comparative Psychology*, *128*, 328–331.

C23.P59 Pham, M. N., Shackelford, T. K., Sela, Y., & Welling, L. L. M. (2013a). Is cunnilingus-assisted orgasm a male sperm-retention strategy? *Evolutionary Psychology*, *11*, 405–414.

C23.P60 Pham, M. N., Shackelford, T. K., Welling, L. L. M., Ehrke, A. D., Sela, Y., & Goetz, A. T. (2013b). Oral sex, semen displacement, and sexual arousal: Testing the ejaculate adjustment hypothesis. *Evolutionary Psychology*, *11*, 1130–1139.

C23.P61 Pound, N., Javed, M. H., Ruberto, C., Shaikh, M. A., & Del Valle, A. P. (2002). Duration of sexual arousal predicts semen parameters for masturbatory ejaculates. *Physiology & Behavior*, *76*, 685–689.

C23.P62 Ramm, S. A., Parker, G. A., & Stockley, P. (2005). Sperm competition and the evolution of male reproductive anatomy in rodents. *Proceedings of the Royal Society of London B: Biological Sciences*, *272*, 949–955.

C23.P63 Scelza, B. A., Prall, S. P., Swinford, N., Gopalan, S., Atkinson, E. G., McElreath, R., Sheehama, J., & Henn, B. M. (2020). High rate of extrapair paternity in a human population demonstrates diversity in human reproductive strategies *Science Advances*, *6*, Article eaay6195.

C23.P64 Shackelford, T. K., Goetz, A. T., Guta, F. E., & Schmitt, D. P. (2006). Mate guarding and frequent in-pair copulation in humans. *Human Nature*, *17*, 239–252.

C23.P65 Shackelford, T. K., Goetz, A. T., McKibbin, W. F., & Starratt, V. G. (2007). Absence makes the adaptations grow fonder: Proportion of time apart from partner, male sexual psychology, and sperm competition in humans (Homo sapiens). *Journal of Comparative Psychology*, *121*(2), 214.

C23.P66 Shackelford, T. K., Weekes-Shackelford, V. A., LeBlanc, G. J., Bleske, A. L., Euler, H. A., & Hoier, S. (2000). Female coital orgasm and male attractiveness. *Human Nature*, *11*, 299–306.

C23.P67 Starratt, V. G., Goetz, A. T., Shackelford, T. K., McKibbin, W. F., & Stewart-Williams, S. (2008). Men's partner-directed insults and sexual coercion in intimate relationships. *Journal of Family Violence*, *23*, 315–323.

C23.P68 Starratt, V. G., McKibbin, W. F., & Shackelford, T. K. (2013). Experimental activation of anti-cuckoldry mechanisms responsive to female sexual infidelity. *Personality and Individual Differences*, *55*(1), 59–62.

C23.P69 Starratt, V. G., Shackelford, T. K., Goetz, A. T., & McKibbin, W. F. (2007). Male Mate Retention Behaviors Vary with Risk of Partner Infidelity and Sperm Competition *Acta Psychologica Sinica*, *39*(3), 523–527.

C23.P70 Stockley, P. (2002). Sperm competition risk and male genital anatomy: comparative evidence for reduced duration of female sexual receptivity in primates with penile spines. *Evolutionary Ecology*, *16*, 123–137.

C23.P71 Stockley, P. (2012). The baculum. *Current Biology*, *22*, Article R1032.

C23.P72 Stockley, P., Gage, M. J. G., Parker, G. A., & Møller, A. P. (1997). Sperm competition in fishes: the evolution of testis size and ejaculate characteristics. *American Naturalist*, *149*, 933–954.

C23.P73 Strouts, P. H., Brase, G. L., & Dillon, H. M. (2017). Personality and evolutionary strategies: The relationships between HEXACO traits, mate value, life history strategy, and sociosexuality. *Personality and Individual Differences*, *115*, 128–132.

C23.P74 Tardif, S., Laforest, J. P., Cormier, N., & Bailey, J. L. (1999). The importance of porcine sperm parameters on fertility in vivo. *Theriogenology*, *52*, 447–459.

C23.P75 Thornhill, R., Gangestad, S. W., & Comer, R. (1995). Human female orgasm and mate fluctuating asymmetry. *Animal Behavior*, *50*, 1601–1615.

C23.P76 Valladares, E., Peña, R., Persson, L. Å., & Högberg, U. (2005). Violence against pregnant women: Prevalence and characteristics. A population-based study in Nicaragua. *BJOG: An International Journal of Obstetrics & Gynecology*, *112*, 1243–1248.

C23.P77 Vance, G., & Shackelford, T. K. (2021). The Coolidge effect. In J. Vonk & T. K. Shackelford (Eds.), *Encyclopedia of animal cognition and behavior*. Springer.

C23.P78 Voracek, M., Fisher, M., & Shackelford, T. K. (2009). Sex differences in subjective estimates of non-paternity rates in Austria. *Archives of Sexual Behavior*, *38*, 652–656.