[in press, February 2026: DeLecce, T. & Shackelford, T. K. (2026). Sexual conflict. In G. Geher, A. Gallup, and S. Karthikeyan (Eds.), *Oxford Handbook of Evolutionary Psychology*. New York: Oxford University Press.]

Sexual Conflict

Tara DeLecce & Todd K. Shackelford

Oakland University

Abstract

For purposes of this chapter, "sexual conflict" refers to any type of conflict that arises between members of the animal kingdom (including humans) as the result of misalignment of male and female reproductive interests. Across the animal kingdom, mating is not an entirely cooperative process. Instead, mating typically includes conflict and, over evolutionary time, arms races between males and females to achieve their (sometimes) discrepant reproductive goals. Such conflict can be manifested in many forms but falls into two broad categories: precopulatory conflict and post-copulatory conflict. By focusing on both nonhuman and human animals, this chapter provides an overview of the most researched forms of sexual conflict based on established theories in the field. This chapter is further divided into theories and behaviors that best address expressions of sexual conflict in males (e.g., sperm competition) and in females (e.g., cryptic female choice).

Keywords: sexual conflict; sperm competition; cryptic female choice; error management theory; sexual coercion

Sexual Conflict

Introduction

Sexual conflict has been defined as "a conflict between the evolutionary interests of individuals of the two sexes" (Parker, 2006, p. 235). Evolutionary interests in this case refer to reproductive interests in terms of transmitting genes to the next generation, with many forms of sexual conflict stemming from males' greater emphasis on *quantity* in terms of reproduction and the concomitant transmission of genes to the next generation and females' greater emphasis on the *quality* of the genes transmitted. In this chapter, sexual conflict will be reviewed both at the *precopulatory level* and *postcopulatory level*. Within these two broad types of sexual conflict, subsections will outline both common behaviors and theories applied to explain them, and how these behaviors often differ between males and females.

In most species (including humans), such differences in male and female genetic interests are generated by anisogamy, or the difference in size and metabolic energy involved in the production of male and female gametes and, consequently, sex differences in minimal obligatory parental investment (Bateman, 1948; Trivers, 1972).

For males, the optimal mating strategy is often to maximize their number of sexual partners due to their small gamete size and low obligatory minimum parental investment. For females, the optimal mating strategy often is to mate only with a few partners of high genetic quality due to females' larger, metabolically expensive gametes and greater obligatory minimum parental investment that, especially in mammals, typically includes gestation and lactation (Lessells, 2006).

This biological reality of reproductive differences between males and females of many species means that there are numerous circumstances in which the reproductive success of a male

occurs at the expense of the female's reproductive success and vice versa, which over evolutionary time can lead to sexually antagonistic coevolution that can favor the evolution of traits that are advantageous for one sex and detrimental to the other sex (Parker & Partridge, 1998). Such antagonistic coevolution in mating strategies has been observed both before copulation occurs during the initial mate attraction and/or courtship phase and after mating has commenced (either during copulation or after copulation has been completed).

Precopulatory sexual conflict – Theories

Error management theory

Over evolutionary history, humans have faced recurring problems that created selection pressures that crafted adapted solutions. Such problems include identifying mating opportunities and staying alive by avoiding aggressive encounters and infectious diseases. Due to these recurrent adaptive problems, error management theory (Haselton & Buss, 2000; Lewis, et al., 2022; Ng, 2025) contends that human psychology has evolved cognitive biases aimed at securing matings and survival even at the expense of perceptual accuracy. These cognitive biases are commonly observed in mating contexts and are one cause of sexual conflict.

From an evolutionary perspective, successful reproduction is a key outcome, so cognition and behaviors that increase the likelihood of successful reproduction will be selected for and retained in the population. Error management theory has identified two main cognitive biases related to mating. The first is male over-perception of female sexual interest. There is an asymmetry in parental investment between the sexes (Trivers, 1972), such that women have greater minimum investment in offspring (in the form of an egg, plus gestation and lactation) compared to men. Consequently, ancestral men had fewer restrictions on their reproductive potential and increases their reproductive success by engaging in multiple short-term matings (Trivers, 1972; Janicke, et al., 2016). Therefore, from a man's perspective, missing an

opportunity for a sexual encounter would be more detrimental in fitness terms than assuming there is an opportunity when there is none (Camilleri, et al., 2009).

One result is that men are commonly observed to over-perceive sexual interest during interactions with women. Early research on the sexual over-perception bias suggested that men (relative to women) infer greater sexual interest from women when observing ambiguous social cues (Abbey, 1982; Haselton & Buss, 2000); however, more contemporary research shows that the male over-perception bias is not as robust as was initially indicated (Brandner, et al., 2021). For example, when men observe two people of opposite sex in an ambiguous interaction, men rate the woman to be expressing greater sexual interest in her male interaction partner than women observing the same interaction (Abbey, 1982). This effect also occurs in self-report scenarios and vignettes, in addition to observations (Haselton & Buss, 2000). This perception bias has been replicated across several studies as reported in a meta-analysis (La France, et al., 2009). More recent research, though, reports mixed results in detecting the sexual over-perception bias. This could be due to earlier research failing to account for the role of individual differences. One relevant individual difference may be self-perceived mate value, which has been found to moderate the strength of the male over-perception bias (Brandner, et al., 2021; Samara, et al., 2021).

The second of these mating-related cognitive biases is women's tendency to underestimate a man's willingness to commit early on in a relationship (Haselton & Buss, 2000). This bias has been hypothesized to prevent women from selecting long-term mates that are likely to abandon them and their children. From an evolutionary perspective, it is a better mating strategy to be overly demanding about a man's willingness to commit and delay copulation until such a willingness is established than to inadvertently reproduce without paternal care (which

decreases survival prospects for offspring). As found for men's biased perceptions of women's sexual interest, women underestimate men's commitment willingness in self-report situations (Haselton & Buss, 2000; Brown & Olkov, 2011) and in face-to-face interactions (Friesen, et al., 2005). Women even perceive highly physically attractive men as less attractive as another means of maintaining skepticism in terms of male mate value when no information about commitment-willingness is available (Lewis, et al., 2022). Additional evidence for the commitment skepticism bias is the finding that postmenopausal women are less likely than reproductive aged women to underestimate men's commitment early on in relationships (Cyrus, et al., 2011).

Taking together men's and women's cognitive mating biases, men's bias toward sexual interest from women can lead to behaviors that conflict with women's strategy of waiting to assess male commitment before mating, and these conflicts include sexual harassment and/or intimidation.

Because measuring cognition in nonhuman species is more difficult than doing so in humans, this section focuses on human cognitive biases. However, this next portion of the chapter will include discussion of behaviors in nonhuman species (in addition to those observed in humans) as part of precopulatory sexual conflict.

Precopulatory sexual conflict – Male tactics

Sexual harassment

In nonhuman animals, sexual harassment refers to a male's repeated, aggressive attempts to mate with a female who attempts to escape, sometimes leading to forcible or coerced copulation (Clutton-Brock & Parker, 1995). Since such behaviors align more closely with sexual coercion and rape in humans, nonhuman sexual harassment will be addressed in the section of this chapter focused on sexual coercion and rape in humans. In humans, sexual harassment is less

closely linked with direct sexual coercion and refers to any unwanted behavior interpreted by the target as sexual, but often focuses on sexual comments, prolonged staring, or touching of sexual body parts such as breasts, buttocks, or the crotch area (Hennekam & Bennett, 2017). Research on perpetrators and targets of sexual harassment suggests that sexual harassment is a manifestation of male sexual psychology, as the perpetrators are overwhelmingly male, and the victims are overwhelmingly females between the ages of 20 and 35 years, physically attractive, and single (Kennair & Bendixen, 2012; Studd & Gattiker, 1991; Klümper, & Schwarz, 2020; Luthar & Luthar, 2008).

Another aspect of sexual harassment that is consistent with the contention that it is a form of sexual conflict is the finding that women experience the same act (e.g., unwanted sexual comments) as more upsetting than men do; moreover, men often have difficulty understanding why these harassing acts are upsetting to women (Bohns & DeVincent, 2018; Buss, 2016b). Similarly, both men and women are more likely to perceive ambiguous comments as sexual harassment when a man expresses them to a woman than when a woman expresses the same comments to a man (Hehman, et al., 2022). This suggests that there is a problem with cross-sex "mind reading" in this context, as each sex is biased to perceive these situations in terms of their own mating desires and goals.

There also are moderating factors that can affect both perpetrators' and targets' reactions to sexual harassment. Research has documented that not all men are equally likely to engage in sexual harassment. Men who primarily pursue a short-term mating strategy are more likely to be perpetrators (Kennair & Bendixen, 2012), and men who score highly on the Dark Tetrad personality traits of narcissism, Machiavellianism, psychopathy, and sadism also are more likely to be perpetrators (Pryor, et al., 2024; Zeigler-Hill, et al., 2016).

For victims of sexual harassment, the distress of the sexual harassment varies as a function of the perpetrator's social status, such that persistent sexual advances from garbage collectors, for example, are more upsetting than the same advances from medical students or successful musicians (Colarelli & Haaland, 2002). Recent research has found that sexual harassment is perceived as less harmful when the perpetrator is physically attractive, and this effect is observed for both men and women (Klümper, & Schwarz, 2020). The finding that the distress of the harassment varies with male perpetrator status and/or attractiveness is consistent with women's interest in retaining choice and only mating with males of high genetic quality.

Precopulatory sexual conflict – Female tactics

Avoidance of sexually aggressive males

Because males of most species are more sexually aggressive than females, female human and nonhuman animals deploy tactics to avoid sexual aggression, coercion, or rape before the opportunity arises in order to retain mate choice. One way that females avoid sexual harassment by unwanted males is to inhabit places where such males are less likely to be found.
In several nonhuman species such as humpback whales (*Megaptera novaeangliae*), lions (*Panthera leo*), tigers (*Panthera tigris*), polar bears (*Ursus maritimus*), and brown bears (*Ursus arctos*; Clark & Stirling, 1998; Dejante, et al., 2024; Derville, et al., 2018; Penteriani, et al., 2024; Singh, et al., 2014), females inhabit spaces where males are less likely to be present to thereby avoid interactions with males, especially if they are pregnant or have reproduced recently.

Similarly, human females avoid situations that might be risky in terms of sexual aggression. For instance, women report avoiding activities such as walking in dimly lit areas or going to bars alone, avoiding strange men, and being prepared and/or being aware of their

surroundings such as by looking around before exiting a car or carrying pepper spray (Bröder & Hohmann, 2003; Chavanne & Gallup, Contreras-Merino, et al., 2024; 1998; McDonald, et al., 2015; McKibbin, et al., 2009). Another study revealed that women who report greater fear of rape also report consuming more true crime media than women with a lesser fear of rape, and true crime media consumption may reflect a desire to learn strategies to escape sexually aggressive attacks (McDonald, et al., 2021). Additionally, women are more likely to engage in these avoidance strategies when they are virginal (Prokop, 2013) or not using oral contraceptives, which further supports the contention that such behaviors are reproductively motivated (Bröder & Hohmann, 2003).

Formation of alliances with other females

Another tactic that reduces the likelihood of sexual aggression from males is to form female coalitions, or at the very least to spend time in areas with a female-biased sex ratio. For instance, in leaf beetles (*Leptinotarsa undecimlineata*), females move to plants with more females than males to avoid male harassment (Muniz, et al., 2018). In several other species such as lions, guppies (*Poecilia reticulata*), bottlenose dolphins (*Tursiops truncatus*), and botos (*Inia geoffrensis*), sex segregation is observed, with female avoidance of male sexual aggression a noted cause (Chakrabarti, et al., 2021; Darden & Croft, 2008; Galezo, et al., 2018; Martin & da Silva, 2004).

In species in which females do not just aggregate together but actively form coalitions to defend against male sexual coercion such as hyenas (*Crocuta crocuta*) and bonobos (*Pan paniscus*), sexual aggression from males is drastically reduced as a result (Paoli, 2009; Strauss & Holecamp, 2019; Tokuyama & Furuichi, 2016). Among human females, sexual coercion is less

likely when women live in groups with kin or are socially connected and spend less time socially isolated (Cense & Brackenridge, 2001; Smuts, 1992).

Seeking male protection from sexually aggressive males

Another method to avoid male sexual aggression is to establish relationships with other males who can provide protection against sexually coercive males – this idea has been coined the "bodyguard hypothesis" (Wilson & Mesnick, 1997). In several birds and primates, females compete with one another for access to dominant males that offer protection from mating attempts by lower ranking, younger, or otherwise undesirable males (Cox & Le Boeuf, 1977; Pizzari & Birkhead, 2000; Smit & Robbins, 2024). While such male-female relationships have not been studied as extensively in humans, some research suggests that a woman's husband may serve as a "bodyguard" in this context as unmarried women are 2.7 times more likely to experience sexual harassment and sexual coercion attempts than are married women (while also controlling for the women's age and socioeconomic status; Wilson & Mesnick, 1997).

Newer research in this area also suggests that men who are visibly perceived as physically stronger also are perceived as better community leaders, and these perceptions are especially pronounced in dangerous/unstable (or otherwise known as "desperate") ecologies where the risk of aggression from other men is higher (Brown et al., 2024). Despite female attempts to avoid sexually aggressive males, the nature of the antagonistic coevolution between males and females in terms of reproductive goals means that females' avoidance attempts are not always successful. The next section on postcopulatory sexual conflict discusses the dynamics (both theoretical and empirical) involved in these occasions.

Postcopulatory sexual conflict – Theories

Sperm competition theory

For males, the most pressing recurring ancestral problem in terms of postcopulatory sexual conflict is ensuring paternity instead of allowing that achievement to go to a rival male. Part of the process of achieving paternity often includes sperm competition. Sperm competition occurs when one female copulates with two or more males within a sufficiently brief period, resulting in sperm of the different males competing to fertilize ova (Parker, 1970; 2020). Among socially monogamous species – animals that form long-term bonds and occasionally pursue extra-pair copulations (EPCs) – sperm competition most commonly occurs when females pursue EPCs (Baker & Bellis, 1993; Smith, 1984). A paternally investing male whose regular partner pursues EPCs is at risk of cuckoldry – unwitting investment of resources into offspring to whom he is genetically unrelated. According to sperm competition theory, the costs of cuckoldry may have driven the evolution of male sperm competition tactics – strategic adjustments in psychology, behavior, and physiology that increased sperm competition success for ancestral males. Because males have finite resources for survival and reproduction, they judiciously deploy sperm competition tactics: Males attend to specific sperm competition cues and adjust accordingly their sperm competition tactics.

Cuckoldry is likely to have recurred not just in nonhuman species but also over the course of human evolution. Research documents non-zero rates of discrepant social and genetic fatherhood (Anderson, 2006; Bellis, Hughes, et al., 2005; Larmuseau, Matthijs, & Wenseleers, 2016; Wolf, Musch, Enczmann, & Fischer, 2012). A meta-analysis of 32 published studies reported that 3.1% of children are genetically unrelated to their social father (Voracek, Haubner, & Fisher, 2008).

However, non-Western samples may face higher cuckoldry rates. Scelza and colleagues (2020) reported that 48% of children in a sample of the indigenous Himba in northern Namibia

are genetically unrelated to their social father. Anderson (2006) showed that, across 67 studies involving men from various regions in North America, South America, South Africa, and Europe, 29.8% of men with low paternity confidence (e.g., those disputing paternity), compared to 1.7% of men with high paternity confidence, are genetically unrelated to their child. These results suggest that men's perceived cuckoldry risk may reasonably predict their actual cuckoldry risk. Additionally, male sexual jealousy has been interpreted as evidence that cuckoldry recurred over human evolution. Jealousy motivates men to minimize the risk of their partner's EPCs, and jealousy often is so strong that it is a leading cause of partner-killing and interpersonal violence across cultures (Buss, 2006; Daly & Wilson, 1988). Male sexual jealousy likely could not have evolved in the absence of the evolutionary recurrence of cuckoldry (Buss, 2013).

Cryptic female choice

Once sperm have entered the female reproductive tract, sexual conflict continues as females can counteract male sperm competition tactics and can bias how sperm in the reproductive tract is used and thus influence paternity in their favor. Specifically, postcopulatory sexual conflict focuses on identifying and selectively favoring sperm of the highest quality for fertilization, whereas other precopulatory female mate choice mechanisms facilitate receipt of direct benefits for the female, such as increased access to resources (Eberhard, 1996; Kruger & Hughes, 2010; Kustra & Alonzo, 2023; Thornhill, 1983). Such female mechanisms of postcopulatory sexual conflict are predicted by cryptic female choice, often viewed as a means for polyandrous females to control paternity when premating choice is difficult or constrained (Firman, et al., 2017).

Because sperm utilization occurs internally in females of many species, it is more difficult to investigate empirically than are male postcopulatory sexual conflict tactics, and,

therefore, the function of cryptic female choice is still debated (Slatyer, et al., 2012). However, multiple functions (that are unlikely to be mutually exclusive) have been proposed. Specifically, cryptic female choice may facilitate fertilization by sperm harboring traits of good male genetic quality (e.g., good immune function) which is coined the "good sperm hypothesis." Relatedly, the "sexy sperm hypothesis" suggests that fertilization success is favored for males with good ejaculate traits (e.g., greater progressive motility). Another proposed function of cryptic female choice is to facilitate genetic compatibility between males and females (Firman, et al., 2017). Greater genetic compatibility in parents produces higher quality offspring (Eberhard, 1996; Firman, et al., 2017).

Recent research has found support for the genetic compatibility explanation for cryptic female choice. Experiments investigating a wide range of species, including field crickets (*Gryllus bimaculatus*), red junglefowl (*Gallus gallus*), house mice (*Mus musculus*), guppies, and the Mediterranean orb-web spider (*Cyrtophora citricola*), have all shown that sperm from nonrelatives are preferred (either in terms of sperm retention or *in vitro* sperm selection for paternity) compared to sperm from genetic relatives, suggesting that cryptic female choice is, in part, an inbreeding avoidance mechanism (Firman & Simmons, 2015; Gasparini & Pilastro, 2011; Gasparini, et al., 2020; Tregenza & Wedell, et al., 2002; Welke & Schneider, 2009).

Cryptic female choice also has evolutionary consequences for males. Usually, males attempt to dissuade or discourage a female from remating after copulation so that there is no (or reduced) sperm competition. For instance, males may spend up to seven days guarding females after copulation (sometimes by remaining in copulatory positions) to prevent remating with rival males, as seen in several insect species, including firebugs (*Pyrrhocoris apterus*), ladybirds

(*Menochilus sexmaculatus*), and jumping spiders (*Phidippus clarus*) (Chaudhary & Mishra, 2015; Elias, et al., 2014; Schöfl & Taborsky, 2002).

Another method to prevent remating is the use of copulatory plugs, as observed in several rodent species (Mangels, et al., 2016), and the use of a "soft plug" has been suggested in humans (Dixson & Anderson, 2002). Yet another counter-tactic to reduce or prevent female remating is the inclusion of substances in seminal fluid that reduce female mating motivation, as documented in several insect species, including fruit flies (*Drosophila melanogaster*; Chen, 1996; Scolari, et al., 2021). Now that the theoretical background for this antagonistic coevolution at the postcopulatory level has been outlined, the following sections will detail the behavioral tactics used by males to gain an edge in postcopulatory sexual conflict, followed by a discussion of female countertactics to thwart the effectiveness of these male tactics.

Postcopulatory sexual conflict – Male tactics

In-pair male copulatory interest

Males may possess a sperm competition psychology – a set of information-processing mechanisms that motivate males to strategically deploy sperm competition tactics. These mechanisms are activated when males perceive sperm competition cues (e.g., female attractiveness: Cornwallis & O'Connor, 2009; presence of rival males: DeLecce, et al., 2025; Nicholls, et al., 2001) and produce outputs that function as sperm competition tactics (Goetz, et al., 2007).

Among many non-human species, males attend to the presence of rival males and adjust accordingly their sperm competition tactics (Candolin & Reynolds, 2002; Gage & Barnard, 1996; Magris, 2021; Nicholls, et al., 2001). For instance, in house mice, male mating motivation increases under situations in which competition is high (e. g. extra-territorial copulations; Ramm

& Stockley, 2014). Human males at greater objective sperm competition risk (e.g., spending more time away from their regular female; regular partner spends more time with male friends and/or colleagues) report greater in-pair copulatory interest, and greater distress (e.g., anger, upset, frustration, and persistence) if their regular partner denies their in-pair copulation request (Shackelford, et al., 2002, 2007), but only among men who perceive that their female partner spends more time with male friends (i.e., sexual rivals; Pham & Shackelford, 2013a; DeLecce, et al., 2017). Men register greater sperm competition risk when their regular partner is absent because it is during her absence that they cannot account for her sexual behavior with other men. Additionally, men experimentally primed with thoughts of partner infidelity reported distress if their regular partner denies their copulatory request (Starratt, et al., 2013). These studies suggest a male sperm competition psychology that regulates in-pair copulatory interest as a function of sperm competition risk.

In-pair copulation frequency

Frequent in-pair copulation may function as a sperm competition tactic. A male who performs frequent in-pair copulations maintains large numbers of viable sperm in his partner's reproductive tract, increasing his chances of success in sperm competition across her fertility cycle. In many avian species, males at greater sperm competition risk copulate more frequently with their regular partner (Crowe, et al., 2009; Hoi, et al., 2013). For example, male Montagu harriers (*Circus pygagus*) experimentally exposed to a rival male, relative to no rival males, performed more frequent in-pair copulations (Mougeot, et al., 2001). Thus, males may strategically adjust copulation frequency according to sperm competition risk.

In humans, frequent in-pair copulations also may function as a sperm competition tactic. For example, a man copulates more frequently with his regular partner if she is more attractive

(Kaighobadi & Shackelford, 2008), if she has more male friends and male coworkers (i.e., potential sexual rivals; Pham et al., 2014), and if he performs more mate guarding behaviors (Shackelford, et al., 2006). Additionally, frequent copulation as a sperm competition tactic may explain why men (but not women) report continued sexual desire toward their regular partner over the duration of a romantic relationship (Klusmann, 2002, 2006; McNulty, et al., 2019).

Sexual coercion and rape

Males at greater sperm competition risk may perform sexual coercion to force their sperm into competition with rival sperm that may be, or will be, in her reproductive tract. In nonhuman animals, the term "sexual harassment" is often loosely defined and frequently overlaps with sexual coercion, as both may involve physically aggressive mating attempts that precede or facilitate forced copulation (Capozzo et al., 2008; Smit, 2025).

For instance, among fallow deer (*Dama dama*) and small tortoiseshell butterflies (*Aglais urticae*), males initiate physical contact or attempt copulation with resisting females until they concede as a means to stop the copulation attempts (Baker, 1972; Clutton-Brock, et al., 1988).

Among socially monogamous birds, forced in-pair copulations occur predictably (and immediately) following events that index cuckoldry risk (e.g., territorial intrusions by rival males, female absence, partner-observed female EPCs; Barash, 1977; Cheng, Burns, & McKinney, 1983; reviewed in Goetz & Shackelford, 2006). Human females whose regular partner is unattractive report lower sexual desire for their regular partner and greater interest in extra-pair copulations during periods of conception risk (Gangestad, et al., 2005). Thus, males may sexually coerce their regular partner as a sperm competition tactic. This is yet another result of sexual conflict (Shackelford & Goetz, 2012).

Rape and sexual assault are not uncommon occurrences, with a recent report from the National Sexual Violence Resource Center estimating its prevalence to be between 9.7 and 20.5 per 1,000 women (Cantor, et al., 2023), although rape has historically and continues to be underreported (Fisher, et al., 2025). The ability to estimate prevalence is especially complicated by the fact that women who have experienced rape often do not acknowledge it as such and instead label it in other terms such as "sexual miscommunication." For example, a meta-analysis on rape occurrences labeled differently found that 60.4% of victims do not acknowledge that they were rape victims, with this phenomenon being significantly more common among college-educated women compared to non-college-educated women (Wilson & Miller, 2016).

However, the documented evidence on rape and sexual assault that is available suggests that human males who engage in sexual coercion also are more likely to accuse their regular partner of EPCs around the time they engage in this act (Finkelhor & Yllo, 1985; He & Tsang, 2017; Russell, 1982). According to both men's reports and women's reports, men who are sexually coercive toward their regular partner also are more likely to accuse her of sexual infidelity (Starratt, et al. 2008). Among physically abused women, those whose regular partner performed forced copulations also report that he is more sexually jealous (Frieze, 1983; Gage & Hutchinson, 2006). Men who report sexually coercing their regular partner also report greater suspicion of her having committed sexual infidelity, and women who report a greater likelihood of pursuing EPCs also report that their regular partner is more sexually coercive (Arnocky, et al. 2015; Goetz & Shackelford, 2006; 2009). Among men convicted of physically assaulting their regular partner, those who engaged in sexual coercion, relative to those who did not, experienced greater cuckoldry risk events prior to the assault (Camilleri & Quinsey, 2009). Men exposed to greater objective sperm competition risk may be more likely to engage in sexual coercion, but

evidence shows this effect appears limited to those who also perceive a heightened likelihood of partner infidelity. Therefore, perception matters (McKibbin, et al., 2011; reviewed in Goetz, et al., 2008).

Outside of intimate partner rape and now considering serial rapist scenarios, research suggests that men who have previously achieved short-term mating success are more likely to self-report routinely engaging in both verbal and physical sexual coercion (Lalumiere, et al., 1996). Similarly, men who admitted via self-report to be perpetrators of sexual assault also report having a higher number of lifetime sexual partners compared to men who have not reported perpetrating sexual assault (Ellis, et al., 2009). These data contrast with an earlier hypothesis suggesting that men with poor mating prospects (dubbed "the mate deprivation hypothesis") would be most likely to engage in sexual coercion and rape (Thornhill & Thornhill, 1992).

Additionally, some evidence suggests that pregnancy is statistically more likely to occur from instances of rape compared to instances of consensual intercourse, and one explanation for this finding is that rapists may more frequently target women at high-fertility than women at low-fertility (Gottschall & Gottschall, 2003). Research also suggests that women at high-fertility dress more provocatively (Haselton, et al., 2007) and walk more sexually (Guéguen, 2012), and individuals generally agree on the "ease of rape" when judging the walk of featureless avatars (Gunns, et al., 2002).

Prudent sperm allocation

Sexual conflict based on male reproductive concerns occurs not only in terms of copulatory behavior, but also in terms of biology, and even at the microscopic level. Sperm are considered "tickets" for the "lottery prize" of fertilizing ova (Parker, 1970; Wedell, et al. 2002). Males at greater sperm competition risk ejaculate more sperm to increase the probability that

their own sperm – and not rival sperm – fertilize ova (Wedell, et al., 2002). For example, among many avian species, males at greater sperm competition risk ejaculate more sperm at the next copulation (Nicholls, et al., 2001; Pizzari, et al., 2003). Human males at greater "objective" sperm competition risk – the proportion of time they spend apart from their regular partner since their last in-pair copulation – ejaculate more sperm at their next in-pair copulation (Baker & Bellis, 1993a). Males may also adjust other ejaculate parameters in response to sperm competition risk. Human males produce masturbatory ejaculates containing a greater percentage of motile sperm when viewing male-male-female ("MMF") pornography (i.e., indexing the presence of sperm competition), than when viewing female-female-female ("FFF") pornography (i.e., indexing the absence of sperm competition; Kilgallon & Simmons, 2005).

Whether humans can adjust their ejaculate (engage in prudent sperm allocation) in a manner predicted by sperm competition theory remains debated. For example, critics have cited the decline in ejaculate quality during recent decades as evidence against the existence of human sperm competition (e.g., Auger, et al., 1995; Cannarella, et al., 2023).

In terms of direct empirical evidence, a recent study by Pham and colleagues (2018) revealed that there were no significant differences in ejaculate quality between men primed with sperm competition and those in a control condition via written vignettes. However, written vignettes may be less effective for evoking expected differences in ejaculates than are audiovisual stimuli. The fact that Kilgallon and Simmons (2005) found differences in ejaculates between conditions using visual stimuli supports this speculation.

In another, more recent study by DeLecce and colleagues (2025) involving copulatory ejaculate quality among heterosexual couples, there were findings that both supported and contradicted sperm competition theory. Specifically, the time that couples spent apart from one

another since their last copulation did not predict ejaculate quality at their next copulation, and rapid progressive motility (a parameter linked to fertilization success) was higher for men who perceived their regular partner as more faithful (e.g., low sperm competition risk). However, these same data also revealed that overall sperm concentration was higher when men perceived more potential sexual rivals (e.g., male friends and coworkers). One possible reason for different results in this study compared to those of Baker and Bellis could be the increased precision in semen analysis among live sperm that was done via electro-optical technology, signal conversion, and the application of proprietary algorithms that was not available in the 1990s when Baker and Bellis were conducting their research. Nevertheless, given these inconsistent findings regarding ejaculate adjustment as predicted by sperm competition theory, further research is required to clarify the role of prudent sperm allocation in humans.

Semen displacement

Another anti-cuckoldry tactic that affects sperm directly is semen displacement, as males from several non-human species have adaptations to displace rival semen from a female's reproductive tract. For example, male tree crickets (*Truljalia hibinosis*) can remove nearly 90% of a rival's ejaculate from a female's reproductive tract during copulation (Ono, et al., 1989). Humans also may have adaptations for semen displacement. Using artificial human penises, artificial female reproductive tracts, and semen-like fluid,

Gallup et al. (2003) provided evidence that the human penis may be able to displace semen from the female reproductive tract during copulatory thrusting via the use of artificial genitals and artificial semen-like fluid. Despite the suggestion of displacement ability in this study, this methodology has limitations in that it did not examine displacement in real genitals. Men perform more semen-displacing copulatory behaviors (e.g., deeper and more thrusts, as

reported by both men and their partners) when they are at a greater recurrent risk of sperm competition (Goetz, et al., 2005; Pham, et al., 2017), and when they accuse their regular partner of infidelity (Gallup, et al., 2003). Additionally, men experience post-ejaculatory events that prevent them from displacing their own semen, including decreased copulatory interest with the same woman (reviewed in Gallup & Burch, 2004), but not with novel women (i.e., Coolidge Effect; O'Donohue & Plaud, 1991).

An alternative explanation is that men who suspect partner infidelity may be engaging in such copulatory behaviors to facilitate their partner's orgasm, as increasing their partner's orgasm frequency may increase her sexual satisfaction and thus decrease her motivation to seek extra-pair partners. Additionally, Baker and Bellis (1993b) provided evidence that women who experience orgasm near the time of their partner's ejaculation retain more of his sperm in their reproductive tract, potentially increasing his chances of success in sperm competition.

However, Pham and colleagues (2017) reported that deeper thrusts were not associated with the likelihood of female orgasm. Additionally, men were generally poor at knowing if their partner had a copulatory orgasm. These data support the explanation that the purpose of deeper copulatory thrusts may be semen displacement. Deeper thrusts need not coincide with female reproductive interests, but surely with male reproductive interests. The hypothesis that deeper thrusts are motivated by male reproductive interests related to semen displacement rather than increasing female orgasm likelihood also has been supported by Gallup and colleagues (2003; but also reviewed by Borgerhoff-Mulder & Rauch, 2009), who reported that both male and female members of couples report deeper and faster thrusting after allegations of female infidelity; however, there is no difference in orgasmic experiences (either male or female).

Postcopulatory sexual conflict – Female tactics

Strategic timing of copulations and promiscuous mating

When females are unlikely to succeed in avoiding sexually aggressive males, reduce the risk of infanticide, and/or bias paternity in a way that facilitates female genetic interests, they can mate with multiple males in a strategic manner. For instance, among several primate species, females who mate promiscuously with multiple males face less risk of injury by appeasing aggressive males and thereby reducing the risk of infanticide by such males after reproduction (Smit, 2025). Among rodents, the production of litters sired by multiple males by definition entails paternity confusion and reduces the risk of infanticide by males with whom the female copulated (and who therefore may have sired one or more of the litter; Ishibashi & Saitoh, 2008). Females can also time multiple matings in a manner that biases paternity in favor of more desired males over undesired males. For example, some female primates mate only with dominant males during peak fertility, as reflected in female genital swelling, but also allow subordinate males to copulate when at non-peak fertility (Nunn, 1999).

In humans, sperm competition occurs when a woman "double-mates" or copulates with two or more men within about five days (sperm remain alive in the female reproductive tract for about five days; Baker & Bellis, 2014). Using data collected from a nationwide survey of British women, Baker and Bellis (2014) reported the percentage of women who ever double-mated as a function of their sexual experience, operationalized as lifetime number of copulations. For women reporting fewer than 50 lifetime copulations, 17.5% reported having double-mated at least once. This percentage sharply increases with sexual experience: 71.8% of women reporting more than 1,000 lifetime copulations reported double-mating at least once. Among American college women, 13.4% reported having copulated with two men within a 24-hour period at least once, and 8.3% reported having copulated with two men simultaneously at least once. In

addition, women with a regular partner who double-mate with extra-pair partners often wait at least 48 hours after EPCs to resume copulations with their regular partner, which suggests that this delay is a strategic maneuver to bias paternity in favor of extra-pair males (Gallup, et al., 2006).

The temporal window for human sperm competition may extend beyond the temporal window for sperm viability. For example, dead sperm may block cervical pathways for sperm of subsequent ejaculates (Baker & Bellis, 2014). Additionally, research has yet to investigate the extent to which non-sperm substances in semen (e.g., spermicidals; Baker & Bellis, 2014) might influence the outcome of human sperm competition or the duration that these substances remain potent in the female reproductive tract. For example, it has been speculated that hormones in seminal fluid (namely follicle-stimulating hormone and leutenizing hormone) in the female reproductive tract may trigger ovulation (reviewed in Burch & Gallup, 2006; Gallup, Burch, & Petricone, 2012).

Additional information about women's propensity for (or at least attitudes about) double-mating can be gleaned from reports of their sexual fantasies. Price and Miller (1984) ranked the content of women's sexual fantasies by popularity and found that sexual fantasies involving sperm competition were among the top 10 most popular fantasies. For example, many women report fantasies about having sex with more than one male simultaneously, which is very likely to facilitate sperm competition (in the absence of condoms). Women also commonly reported fantasies of having sex with someone other than their current partner, which also might facilitate sperm competition between her regular partner and her extra-pair partner. In another, more recent study, sexual fantasies involving intercourse with more than one man at a time again was commonly reported, with 56.5% of women reported having fantasized about sex with two men

and 28.9% of women reported having fantasized about sex with more than three men (Joyal, et al., 2015).

Strategic female orgasm

The timing and occurrence of female orgasm may play a role in postcopulatory sexual conflict. The function of female orgasm is still debated, as some researchers view the female orgasm as a byproduct of the male orgasm, whereas other researchers propose that female orgasm fulfills an adaptive function (Baker & Bellis, 1993a; Lloyd, 2005; Puts, et al, 2012; Symons, 1979). The specifics of this debate are beyond the scope of this chapter; however, some research suggests that female orgasm increases sperm retention and, consequently, the likelihood of conception (Zervomanolakis, et al, 2007). In brief, orgasm releases oxytocin into the bloodstream, which then triggers uterine contractions, and these contractions aid transmission of seminal fluid through the uterus to the oviducts (Kunz, et al., 2007; Zervomanolakis, et al, 2007). This hypothesized function of female orgasm is referred to as the "upsuck hypothesis" (Fox, et al., 1970).

Some researchers theorize that, in addition to increasing the probability of conception, female orgasm acts as an indicator to females of male genetic quality, and that (in the case of humans) only men of high quality can induce orgasms (also known as the sire choice hypothesis; Gallup & Frederick, 2010; Gallup et al., 2018; Smith, 1984; Thornhill, et al., 1995). Due to women's lower potential reproductive output relative to men's (Trivers, 1972), women are more selective when choosing a sire for their offspring, to increase the genetic quality of offspring and, therefore, the likelihood of their offspring surviving to reproductive age. If female copulatory orgasm is more likely to occur with men of higher genetic quality, this may aid women in biasing paternity in their favor by choosing a high-quality sire for their offspring.

Some research indicates an association between men's genetic quality and their likelihood of inducing orgasm in their female partners. Physical attractiveness is often considered a proxy for genetic quality (Grammer, et al., 2003), and male physical attractiveness has positively predicted female orgasm occurrence across several independent studies. For example, Shackelford and colleagues (2000) found that male attractiveness (as perceived by their female partner) predicted the likelihood of women's orgasm during their last copulation with their regular partner. Another study reported that more physically attractive men (as assessed by self-ratings and independent ratings) are more likely to induce orgasms in their regular female partners (according to self-reports from female partners) during copulation (Puts, Welling, Burriss, and Dawood, 2012). More recent research has come to similar conclusions, with women who report higher male partner ability to induce orgasm also perceive such partners to be more physically attractive and healthy (da Silva, et al., 2025).

Another putative measure of genetic quality is fluctuating asymmetry. During development, the presence of environmental and genetic perturbations (e.g., mutations and pathogens) leads to the production of more asymmetrical features in adulthood (Gangestad, Thornhill, & Yeo, 1994). When there is natural resistance to these developmental stresses (e.g., low mutation load and good immune functioning), morphological symmetry is maintained. Thus, low fluctuating asymmetry is considered an honest indicator of genetic quality (Gangestad, et al, 1994).

Male fluctuating asymmetry is associated with female orgasm likelihood. Thornhill and colleagues (1995) found that women mated to men of lower fluctuating asymmetry are more likely to experience copulatory orgasms with their partners than are women mated to men of higher fluctuating asymmetry. Masculinity is also thought to be positively correlated with

genetic quality as an indicator of immunocompetence (Foo, et al., 2020; Folstad & Karter, 1992), and research has documented that women are more likely to experience copulatory orgasms with more masculine men (as indicated by ratings of facial masculinity from men's regular female partners and independent ratings; Puts, et al, 2012). Additionally, these orgasms are more likely to occur at a time in the copulatory session which coincides with the window of time conducive to greater sperm retention.

Conclusion

Due to biological factors like anisogamy, male and female reproductive interests are sometimes at odds with one another which produces sexual conflict. Males and females have evolved tactics to bias the outcome of sexual conflict in their favor, with countertactics evolved in the opposite sex to thwart the effectiveness of these tactics. Specifically, males benefit from mating more widely and thus are more sexually coercive while also attempting to reduce cuckoldry risk. Females, on the other hand, benefit from being more discriminating in their mate choice due to their greater minimum obligatory parental investment and less potential reproductive output. Therefore, females attempt to counter male sexual aggression and have adaptations that affect the timing of copulations and the use of sperm in the reproductive tract to bias paternity toward males of higher genetic quality. The nature of the antagonistic coevolution of tactics in sexual conflict ensures that neither sex has a permanent edge in this ever-changing but never-ending conflict.

References

Abbey, A. (1982). Sex differences in attributions for friendly behavior: Do males misperceive females' friendliness? *Journal of Personality and Social Psychology*, *42*(5), 830 – 838. https://doi.org/10.1037/0022-3514.42.5.830

Anderson, K. (2006). How well does paternity confidence match actual paternity? Evidence from worldwide nonpaternity rates. *Current Anthropology*, *47*(3), 513-520. https://doi.org/10.1086/504167

Arnocky, S., Sunderani, S., Gomes, W., & Vaillancourt, T. (2015). Anticipated partner infidelity and men's intimate partner violence: The mediating role of anxiety. *Evolutionary Behavioral Sciences*, *9*(3), 186 - 196. DOI:10.1037/ebs0000021

Auger, J., Kunstmann, J. M., Czyglik, F. & Jouannet, P. (1995). Decline in semen quality among fertile men in Paris during the past 20 years. *New England Journal of Medicine, 332*(5), 281–285. DOI: 10.1056/NEJM199502023320501

Baker, R. R. (1972). Territorial behaviour of the nymphalid butterflies, *Aglais urticae* (L.) and *Inachis io* (L.). *Journal of Animal Ecology 41*(2), 453–469. https://www.jstor.org/stable/3480

Baker, R. R., & Bellis, M. A. (1993a). Human sperm competition: Ejaculate adjustment by males and the function of masturbation. *Animal Behaviour*, *46*(5), 861-885. https://doi.org/10.1006/anbe.1993.1271

Baker, R. R., & Bellis, M. A. (1993b). Human sperm competition: Ejaculate manipulation by females and a function for the female orgasm. *Animal Behaviour*, *46*(5), 887-909. https://doi.org/10.1006/anbe.1993.1272

Baker, R., & Bellis, M. A. (2014). *Human sperm competition: Copulation, masturbation and infidelity*. London: Chapman & Hall.

Barash, D. P. (1977). Sociobiology of rape in mallards (*Anas platyrhynchos*): responses of the mated male. *Science*, *197*(4305), 788-789. DOI: 10.1126/science.197.4305.788

Bateman, A. J. (1948). Intra-sexual selection in Drosophila. *Heredity*, *2*(3), 349-368.

Bellis, M. A., Hughes, K., Hughes, S., & Ashton, J. R. (2005). Measuring paternal discrepancy and its public health consequences. *Journal of Epidemiology & Community Health, 59*(9), 749-754. DOI:10.1136/jech.2005.036517

Bohns, V. K., & DeVincent, L. A. (2019). Rejecting unwanted romantic advances is more difficult than suitors realize. *Social Psychological and Personality Science*, *10*(8), 1102-1110. https://doi.org/10.1177/1948550618769880

Borgerhoff-Mulder, M., & Rauch, K. L. (2009). Sexual conflict in humans: variations and solutions. *Evolutionary Anthropology*, *18*(5), 201-214. https://doi.org/10.1002/evan.20226

Brandner, J. L., Pohlman, J., & Brase, G. L. (2021). On hits and being hit on: Error management theory, signal detection theory, and the male sexual overperception bias. *Evolution and Human Behavior*, *42*(4), 331-342. https://doi.org/10.1016/j.evolhumbehav.2021.01.002

Bröder, A. & Hohmann, N. (2003). Variations in risk taking behavior over the menstrual cycle: an improved replication. *Evolution and Human Behavior 24*(6), 391–398. https://doi.org/10.1016/S1090-5138(03)00055-2

Brown, C. M., & Olkhov, Y. M. (2015). Functional flexibility in women's commitment-skepticism bias. *Evolutionary Psychology*, *13*(2), 283-298. https://doi.org/10.1177/147470491501300201

Brown, M., Boykin, K., & Difiore, F. (2024). Coalitional value of formidable men in hostile and desperate ecologies. *EvoD Journal*, *14*(1), 1-13. http://evostudies.org/evos-journal/about-the-journal/

Burch, R. L., & Gallup, G. G. (2006). The psychobiology of human semen. In S. M. Platek & T. K. Shackelford (Eds.), *Female infidelity and paternal uncertainty* (pp. 141-172). New York: Cambridge University Press.

Buss, D. M. (2006). *The murderer next door: Why the mind is designed to kill*. New York: Penguin.

Buss, D. M. (2013). Sexual Jealousy. *Psychological Topics*, *22*(2), 155-182.

Camilleri, J. A., & Quinsey, V. L. (2009). Testing the cuckoldry risk hypothesis of partner sexual coercion in community and forensic samples. *Evolutionary Psychology*, *7*, 147470490900700203. https://doi.org/10.1177/147470490900700203

Camilleri, J. A., Quinsey, V. L., & Tapscott, J. L. (2009). Assessing the propensity for sexual coaxing and coercion in relationships: Factor structure, reliability, and validity of the Tactics to Obtain Sex Scale. *Archives of Sexual Behavior*, *38*(6), 959-973. https://doi.org/10.1007/s10508-008-9377-2

Candolin, U., & Reynolds, J. D. (2002). Adjustments of ejaculation rates in response to risk of sperm competition in a fish, the bitterling (*Rhodeus sericeus*). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*(1500), 1549-1553. https://doi.org/10.1098/rspb.2002.2055

Cannarella, R., Gül, M., Rambhatla, A., & Agarwal, A. (2023). Temporal decline of sperm concentration: The role of endocrine disruptors. *Endocrine*, *79*(1), 1-16. https://doi.org/10.1007/s12020-022-03136-2

Cantor D., Edwards W. S., Giambo P., Steiger D. M., Yan T., Hicks W., Sun H., DeMatteis J., Westat Inc. (2023). *National crime victimization survey redesign field test Topline report: Comparing condition 1 and condition 2 by interleaving treatment (NCJ 303980)*. https://www.ojp.gov/pdffiles1/bjs/grants/303980.pdf

Cappozzo, H. L., Tu´ nez, J. I. & Cassini, M. H. (2008). Sexual harassment and female gregariousness in the south American sea lion, *Otaria flavescens*. *Naturwissenschaften 95*, 625–630. https://doi.org/10.1007/s00114-008-0363-2

Cense, M. & Brackenridge, C. (2001). Temporal and developmental risk factors for sexual harassment and abuse in sport. *European Physical Education Review, 7*(1), 61–79. https://doi.org/10.1177/1356336X010071006

Chakrabarti, S., Bump, J. K., Jhala, Y. V. & Packer, C. (2021). Contrasting levels of social distancing between the sexes in lions. *iScience, 24*(5), 102406. https://doi.org/10.1016/j.isci.2021.102406

Chaudhary, D. D., & Mishra, G. (2015). Prolonged matings in a ladybird, *Menochilus sexmaculatus*: a mate guarding mechanism? *Journal of Asia-Pacific Entomology*, *18*(3), 453-458. https://doi.org/10.1016/j.aspen.2015.05.003

Chavanne, T. J. & Gallup, G. G. (1998). Variation in risk taking behavior among female college students as a function of the menstrual cycle. *Evolution and Human Behavior 19*(1), 27–32. https://doi.org/10.1016/S1090-5138(98)00016-6

Chen, P. S. (1996). The accessory gland proteins in male Drosophila: structural, reproductive, and evolutionary aspects. *Experientia*, *52*, 503-510. https://doi.org/10.1007/BF01969718

Cheng, K. M., Burns, J. T., & McKinney, F. (1983). Forced copulation in captive mallards III. Sperm competition. *The Auk*, *100*(2), 302-310. https://doi.org/10.1093/auk/100.2.302

Clark, D. A., & Stirling, I. (1998). Habitat preferences of polar bears in the Hudson Bay lowlands during late summer and fall. *Ursus*, *10,* 243-250. https://www.jstor.org/stable/3873132

Clutton-Brock, T. H., & Parker, G. A. (1995). Sexual coercion in animal societies. *Animal Behaviour*, *49*(5), 1345-1365. https://doi.org/10.1006/anbe.1995.0166

Clutton-Brock, T. H., Green, D., Hiraiwa-Hasegawa, M. & Albon, S. D. (1988). Passing the buck: resource defence, lek breeding and mate choice in fallow deer. *Behavioral Ecology and Sociobiology 23*, 281–296. https://doi.org/10.1007/BF00300575

Colarelli, S. M., & Haaland, S. (2002). Perceptions of sexual harassment: An evolutionary perspective. *Psychology, Evolution & Gender*, *4*(3), 243-264. https://doi.org/10.1080/14616661.2002.10383127

Contreras-Merino, A. M., Farhane-Medina, N. Z., & Castillo-Mayén, R. (2024). Unmasking street harassment in Spain: Prevalence, psychological impact, and the role of sexism in women's experiences. *Sex Roles*, *90*(9), 1136-1153. https://doi.org/10.1007/s11199-024-01500-2

Cornwallis, C. K., & O'Connor, E. A. (2009). Sperm: seminal fluid interactions and the adjustment of sperm quality in relation to female attractiveness. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1672), 3467-3475. https://doi.org/10.1098/rspb.2009.0807

Cox, C. R. & Le Boeuf, B. J. (1977). Female incitation of male competition: a mechanism in sexual selection. *The American Naturalist, 111*(978), 317–335. https://doi.org/10.1086/283163

Crowe, S. A., Kleven, O., Delmore, K. E., Laskemoen, T., Nocera, J. J., Lifjeld, J. T., & Robertson, R. J. (2009). Paternity assurance through frequent copulations in a wild passerine with intense sperm competition. *Animal Behaviour*, *77*(1), 183-187. https://doi.org/10.1016/j.anbehav.2008.09.024

Cyrus, K., Schwarz, S., & Hassebrauck, M. (2011). Systematic cognitive biases in courtship context: women's commitment–skepticism as a life-history strategy?. *Evolution and Human Behavior*, *32*(1), 13-20. https://doi.org/10.1016/j.evolhumbehav.2010.07.006

da Silva, C. S. A., Mafra, A. L., & Valentova, J. V. (2025). Evolutionary role of the female orgasm: Insights into mate choice and beyond. *Archives of Sexual Behavior*, *54*(1), 323-334. https://doi.org/10.1007/s10508-024-03011-3

Darden, S. K. & Croft, D. P. (2008). Male harassment drives females to alter habitat use and leads to segregation of the sexes. *Biology Letters, 4*(5), 449–451. https://doi.org/10.1098/rsbl.2008.0308

Daly, M. & Wilson, M. (1988). *Homicide.* Hawthorne, NY: Aldine.

Dejeante, R., Loveridge, A. J., Macdonald, D. W., Madhlamoto, D., Valeix, M. & Chamaille´-Jammes, S. (2024). Counter-strategies to infanticide: the importance of cubs in determining lion habitat selection and social interactions. *Journal of Animal Ecology 93*(2), 159–170. https://doi.org/10.1111/1365-2656.14045

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*(2), 1-5. https://doi.org/10.1177/1474704917705062

DeLecce, T., Vance, G. S., Zeigler-Hill, V., Welling, L. L., & Shackelford, T. K. (2025). Ejaculate adjustment in response to sperm competition risk in humans. *Archives of Sexual Behavior*, *54*(1), 277-287. https://doi.org/10.1007/s10508-024-03030-0

Derville, S., Torres, L. G. & Garrigue, C. (2018). Social segregation of humpback whales in contrasted coastal and oceanic breeding habitats. *Journal of Mammalogy, 99*(1), 41–54. https://doi.org/10.1093/jmammal/gyx185

Dixson, A. F., & Anderson, M. J. (2002). Sexual selection, seminal coagulation and copulatory plug formation in primates. *Folia Primatologica*, *73*(2-3), 63-69. https://doi.org/10.1159/000064784

Eberhard, W. G. (1966). *Female control: sexual selection by cryptic female choice*. Princeton University Press.

Elias, D. O., Sivalinghem, S., Mason, A. C., Andrade, M. C., & Kasumovic, M. M. (2014). Mate-guarding courtship behaviour: tactics in a changing world. *Animal Behaviour*, *97*, 25-33. https://doi.org/10.1016/j.anbehav.2014.08.007

Ellis, L., Widmayer, A., & Palmer, C. T. (2009). Perpetrators of sexual assault continuing to have sex with their victims following the initial assault: Evidence for evolved reproductive strategies. *International Journal of Offender Therapy and Comparative Criminology*, *53*(4), 454-463. https://doi.org/10.1177/0306624X08316711

Finkelhor, D., & Yllo, K. (1985). *License to rape: Sexual abuse of wives.* New York: Holt, Rinehart, & Winston.

Firman, R.C. and Simmons, L.W. (2015) Gametic interactions promote inbreeding avoidance in house mice. *Ecology Letters, 18*(9), 937–943. https://doi.org/10.1111/ele.12471

Firman, R. C., Gasparini, C., Manier, M. K., & Pizzari, T. (2017). Postmating female control: 20 years of cryptic female choice. *Trends in Ecology and Evolution, 32*(5), 368 – 382. DOI: 10.1016/j.tree.2017.02.010

Fisher, B. S., & Gross, R. L. (2025). The Evolution of the Measurement of Rape and Sexual Assault Over 50 Years: Milestones, Definitions, Operationalizations, and Classifications. *Journal of Contemporary Criminal Justice*, *41*(1), 166-195. https://doi.org/10.1177/10439862241290352

Foo, Y. Z., Simmons, L. W., Perrett, D. I., Holt, P. G., Eastwood, P. R., & Rhodes, G. (2020). Immune function during early adolescence positively predicts adult facial sexual dimorphism in both men and women. *Evolution and Human Behavior*, *41*(3), 199-209.

Folstad, I., & Karter, A. J. (1992). Parasites, bright males, and the immunocompetence handicap. *The American Naturalist*, *139*(3), 603-622. https://doi.org/10.1086/285346

Fox, C. A., Wolff, H. S., & Baker, J. A. (1970). Measurement of intra-vaginal and intra-uterine pressures during human coitus by radio-telemetry. *Reproduction*, *22*(2), 243-251. https://doi.org/10.1530/jrf.0.0220243

Friesen, M. D., Fletcher, G. J., & Overall, N. C. (2005). A dyadic assessment of forgiveness in intimate relationships. *Personal Relationships*, *12*(1), 61-77. https://doi.org/10.1111/j.1350-4126.2005.00102.x

Frieze, I. H. (1983). Investigating the causes and consequences of marital rape. *Signs: Journal of Women in Culture and Society*, *8*(3), 532-553. https://doi.org/10.1086/493988

Gage, A. J., & Hutchinson, P. L. (2006). Power, control, and intimate partner sexual violence in Haiti. *Archives of Sexual Behavior*, *35*, 11-24. https://doi.org/10.1007/s10508-006-8991-0

Gage, A. R., & Barnard, C. J. (1996). Male crickets increase sperm number in relation to competition and female size. *Behavioral Ecology and Sociobiology*, *38*, 349-353. https://doi.org/10.1007/s002650050251

Galezo, A. A., Krzyszczyk, E. & Mann, J. (2018). Sexual segregation in indo-Pacific bottlenose dolphins is driven by female avoidance of males. *Behavioral Ecology, 29*(2), 377–386. https://doi.org/10.1093/beheco/arx177

Gallup Jr, G. G., & Burch, R. L. (2004). Semen displacement as a sperm competition strategy in humans. *Evolutionary Psychology*, *2*, 147470490400200105. https://doi.org/10.1177/147470490400200105

Gallup, G. G., Jr., & Frederick, D. A. (2010). The science of sex appeal: An evolutionary perspective. *Review of General Psychology, 14,* 240–250. http://dx.doi.org/10.1037/a0020451

Gallup, G. G., Burch, R. L., & Mitchell, T. J. B. (2006). Semen displacement as a sperm competition strategy: Multiple mating, self-semen displacement, and timing of in-pair copulations. *Human Nature*, *17*, 253-264. https://doi.org/10.1007/s12110-006-1008-9

Gallup Jr, G. G., Burch, R. L., & Petricone, L. R. (2012). Sexual conflict, infidelity, and vaginal/semen chemistry. In T. K. Shackelford & A. T. Goetz (Eds.), *The Oxford handbook of sexual conflict in humans* (pp. 217-231). New York: Oxford University Press.

Gallup Jr, G. G., Towne, J. P., & Stolz, J. A. (2018). An evolutionary perspective on orgasm. *Evolutionary Behavioral Sciences*, *12*(1), 52 – 69. https://doi.org/10.1037/ebs0000104

Gallup Jr, 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*(4), 277-289. https://doi.org/10.1016/S1090-5138(03)00016-3

Gangestad, S. W., Thornhill, R., & Yeo, R. A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology*, *15*(2), 73-85. https://doi.org/10.1016/0162-3095(94)90018-3

Gangestad, S. W., Thornhill, R., & Garver-Apgar, C. E. (2005). Women's sexual interests across the ovulatory cycle depend on primary partner developmental instability. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1576), 2023-2027. https://doi.org/10.1098/rspb.2005.3112

Gasparini, C. and Pilastro, A. (2011) Cryptic female preference for genetically unrelated males is mediated by the ovarian fluid in the guppy. *Proceedings of the Royal Society of London B, 278*(1717), 2495–2501. https://doi.org/10.1098/rspb.2010.2369

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), 20200077. https://doi.org/10.1098/rstb.2020.0077

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. https://doi.org/10.1007/s12110-006-1009-8

Goetz, A. T., & Shackelford, T. K. (2009). Sexual coercion in intimate relationships: A comparative analysis of the effects of women's infidelity and men's dominance and control. *Archives of Sexual Behavior*, *38*, 226 - 234. https://doi.org/10.1007/s10508-008-9353-x

Goetz, A. T., Shackelford, T. K., & Camilleri, J. A. (2008). Proximate and ultimate explanations are required for a comprehensive understanding of partner rape. *Aggression and Violent Behavior*, *13*(2), 119-123. https://doi.org/10.1016/j.avb.2008.02.002

Goetz, A. T., Shackelford, T. K., Platek, S. M., Starratt, V. G., & McKibbin, W. F. (2007). Sperm competition in humans: Implications for male sexual psychology, physiology, anatomy, and behavior. *Annual Review of Sex Research*, *18*(1), 1-22. https://doi.org/10.1080/10532528.2007.10559845

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*(4), 749-763. https://doi.org/10.1016/j.paid.2004.05.028

Gottschall, J. A., & Gottschall, T. A. (2003). Are per-incident rape-pregnancy rates higher than per-incident consensual pregnancy rates? *Human Nature*, *14*, 1-20. https://doi.org/10.1007/s12110-003-1014-0

Grammer, K., Fink, B., Møller, A. P., & Thornhill, R. (2003). Darwinian aesthetics: sexual selection and the biology of beauty. *Biological Reviews*, *78*(3), 385-407. https://doi.org/10.1017/S1464793102006085

Guéguen, N. (2012). Gait and menstrual cycle: Ovulating women use sexier gaits and walk slowly ahead of men. *Gait & Posture*, *35*(4), 621-624. https://doi.org/10.1016/j.gaitpost.2011.12.011

Gunns, R. E., Johnston, L., & Hudson, S. M. (2002). Victim selection and kinematics: A point-light investigation of vulnerability to attack. *Journal of Nonverbal Behavior*, *26*, 129-158. https://doi.org/10.1023/A:1020744915533

Haselton, M. G., & Buss, D. M. (2000). Error management theory: a new perspective on biases in cross-sex mind reading. *Journal of Personality and Social Psychology*, *78*(1), 81 – 91. https://doi.org/10.1037/0022-3514.78.1.81

Haselton, M. G., Mortezaie, M., Pillsworth, E. G., Bleske-Rechek, A., & Frederick, D. A. (2007). Ovulatory shifts in human female ornamentation: Near ovulation, women dress to impress. *Hormones and Behavior*, *51*(1), 40-45. https://doi.org/10.1016/j.yhbeh.2006.07.007

He, S., & Tsang, S. (2017). Perceived female infidelity and male sexual coercion concerning first sex in Chinese college students' dating relationships: The mediating role of male partners' attachment insecurity. *Personality and Individual Differences*, *111*, 146-152. https://doi.org/10.1016/j.paid.2017.02.016

Hehman, J. A., Salmon, C. A., Pulford, A., Ramirez, E., & Jonason, P. K. (2022). Who perceives sexual harassment? Sex differences and the impact of mate value, sex of perpetrator, and sex of target. *Personality and Individual Differences*, *185*, 111288. https://doi.org/10.1016/j.paid.2021.111288

Hennekam, S., & Bennett, D. (2017). Sexual harassment in the creative industries: Tolerance, culture and the need for change. *Gender, Work & Organization*, *24*(4), 417-434. https://doi.org/10.1111/gwao.12176

Hoi, H., Krištofík, J., & Darolová, A. (2013). Experimentally simulating paternity uncertainty: immediate and long-term responses of male and female reed warblers Acrocephalus scirpaceus. *PLoS One*, *8*(4), e62541. https://doi.org/10.1371/journal.pone.0062541

Ishibashi, Y. & Saitoh, T. (2008). Effect of local density of males on the occurrence of multimale mating in gray-sided voles (*Myodes rufocanus*). *Journal of Mammalogy 89*(2), 388–397. https://doi.org/10.1644/07-MAMM-A-036.1

Janicke, T., Häderer, I. K., Lajeunesse, M. J., & Anthes, N. (2016). Darwinian sex roles confirmed across the animal kingdom. *Science Advances*, *2*(2), e1500983. DOI: 10.1126/sciadv.1500983

Joyal, C. C., Cossette, A., & Lapierre, V. (2015). What exactly is an unusual sexual fantasy? *The Journal of Sexual Medicine*, *12*(2), 328-340. https://doi.org/10.1111/jsm.12734

Kaighobadi, F., & Shackelford, T. K. (2008). Female attractiveness mediates the relationship between in-pair copulation frequency and men's mate retention behaviors. *Personality and Individual Differences*, *45*(4), 293-295. https://doi.org/10.1016/j.paid.2008.04.013

Kennair, L. E. O., & Bendixen, M. (2012). Sociosexuality as predictor of sexual harassment and coercion in female and male high school students. *Evolution and Human Behavior*, *33*(5), 479-490. https://doi.org/10.1016/j.evolhumbehav.2012.01.001

Kilgallon, S. J., & Simmons, L. W. (2005). Image content influences men's semen quality. *Biology Letters*, *1*(3), 253-255. https://doi.org/10.1098/rsbl.2005.0324

Klümper, L., & Schwarz, S. (2020). Oppression or opportunity? Sexual strategies and the perception of sexual advances. *Evolutionary Psychological Science*, *6*(2), 142-153. https://doi.org/10.1007/s40806-019-00215-y

Klusmann, D. (2002). Sexual motivation and the duration of partnership. *Archives of Sexual Behavior*, *31*, 275-287. https://doi.org/10.1023/A:1015205020769

Klusmann, D. (2006). Sperm competition and female procurement of male resources. *Human Nature*, *17*, 283-300. https://doi.org/10.1007/s12110-006-1010-2

Kruger, D. J., & Hughes, S. M. (2010). Variation in reproductive strategies influences post-coital experiences with partners. *Journal of Social, Evolutionary, and Cultural Psychology*, *4*(4), 254 – 264. https://doi.org/10.1037/h0099285

Kustra, M. C., & Alonzo, S. H. (2023). The coevolutionary dynamics of cryptic female choice. *Evolution Letters*, *7*(4), 191-202. https://doi.org/10.1093/evlett/qrad025

Kunz, G., Beil, D., Huppert, P., & Leyendecker, G. (2007). Oxytocin–a stimulator of directed sperm transport in humans. *Reproductive Biomedicine Online*, *14*(1), 32-39. https://doi.org/10.1016/S1472-6483(10)60761-4

La France, B. H., Henningsen, D. D., Oates, A., & Shaw, C. M. (2009). Social–sexual interactions? Meta-analyses of sex differences in perceptions of flirtatiousness, seductiveness, and promiscuousness. *Communication Monographs*, *76*(3), 263-285. https://doi.org/10.1080/03637750903074701

Lalumière, M. L., Chalmers, L. J., Quinsey, V. L., & Seto, M. C. (1996). A test of the mate deprivation hypothesis of sexual coercion. *Ethology and Sociobiology*, *17*(5), 299-318. https://doi.org/10.1016/S0162-3095(96)00076-3

Larmuseau, M. H., Matthijs, K., & Wenseleers, T. (2016). Cuckolded fathers rare in human populations. *Trends in Ecology & Evolution*, *31*(5), 327-329. DOI: 10.1016/j.tree.2016.03.004

Lessells, C. K. M. (2006). The evolutionary outcome of sexual conflict. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*(1466), 301-317. https://doi.org/10.1098/rstb.2005.1795

Lewis, D. M., Al-Shawaf, L., Semchenko, A. Y., & Evans, K. C. (2022). Error Management Theory and biased first impressions: How do people perceive potential mates under conditions of uncertainty?. *Evolution and Human Behavior*, *43*(2), 87-96. https://doi.org/10.1016/j.evolhumbehav.2021.10.001

Lloyd, E. A. (2005). *The case of the female orgasm: Bias in the science of evolution*. Harvard University Press.

Luthar, H. K., & Luthar, V. K. (2008). Likelihood to sexually harass: A comparison among American, Indian, and Chinese students. *International Journal of Cross Cultural Management*, *8*(1), 59-77. https://doi.org/10.1177/1470595807088322

Magris, M. (2021). Strategic adjustment of ejaculate quality in response to variation of the socio-sexual environment. *Behavioral Ecology and Sociobiology*, *75*(6), 1 - 24. https://doi.org/10.1007/s00265-021-03032-1

Mangels, R., Tsung, K., Kwan, K., & Dean, M. D. (2016). Copulatory plugs inhibit the reproductive success of rival males. *Journal of Evolutionary Biology*, *29*(11), 2289-2296. https://doi.org/10.1111/jeb.12956

Martin, A. R. & da Silva, V. M. F. (2004). River dolphins and flooded forest: seasonal habitat use and sexual segregation of botos (Inia geoffrensis) in an extreme cetacean environment. *Journal of Zoology, 263*(3), 295–305. https://doi.org/10.1017/S095283690400528X

McDonald, M. M., James, R. M., & Roberto, D. P. (2021). True crime consumption as defensive vigilance: Psychological mechanisms of a rape avoidance system. *Archives of Sexual Behavior*, *50*(5), 2085-2108. https://doi.org/10.1007/s10508-021-01990-1

McDonald, M. M., Donnellan, M. B., Cesario, J., & Navarrete, C. D. (2015). Mate choice preferences in an intergroup context: Evidence for a sexual coercion threat-management system among women. *Evolution and Human Behavior*, *36*(6), 438-445. https://doi.org/10.1016/j.evolhumbehav.2015.04.002

McKibbin, W. F., Starratt, V. G., Shackelford, T. K., & Goetz, A. T. (2011). Perceived risk of female infidelity moderates the relationship between objective risk of female infidelity and sexual coercion in humans (Homo sapiens). *Journal of Comparative Psychology*, *125*(3), 370-373. https://doi.org/10.1037/a0023146

McKibbin, W. F., Shackelford, T. K., Goetz, A. T., Bates, V. M., Starratt, V. G., & Miner, E. J. (2009). Development and initial psychometric assessment of the rape avoidance inventory. *Personality and Individual Differences*, *46*(3), 336-340. https://doi.org/10.1016/j.paid.2008.10.026

McNulty, J. K., Maxwell, J. A., Meltzer, A. L., & Baumeister, R. F. (2019). Sex-differentiated changes in sexual desire predict marital dissatisfaction. *Archives of Sexual Behavior*, *48*(8), 2473-2489. https://doi.org/10.1007/s10508-019-01471-6

Mougeot, F., Arroyo, B. E., & Bretagnolle, V. (2001). Decoy presentations as a means to manipulate the risk of extrapair copulation: an experimental test of paternity assurance strategies in a semi-colonial raptor, the Montagu's Harrier Circus pygargus. *Behavioural Ecology*, *12*(1), 1-7. https://doi.org/10.1093/beheco/12.1.1

Muniz, D. G., Baena, M. L., Macı´as-Ord_on˜ez, R. & Machado, G. (2018). Males, but not females, perform strategic mate searching movements between host plants in a leaf beetle with scramble competition polygyny. *Ecology and Evolution, 8*(11), 5828–5836. https://doi.org/10.1002/ece3.4121

Ng, Y. L. (2025). An error management approach to the human alarm system for correct and incorrect news content involving direct life-threatening risks. *Journal of Risk Research*, *28*(5), 1-17. https://doi.org/10.1080/13669877.2025.2512079

Nicholls, E. H., Burke, T., & Birkhead, T. R. (2001). Ejaculate allocation by male sand martins, *Riparia riparia*. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1473), 1265-1270. https://doi.org/10.1098/rspb.2001.1615

Nunn, C. L. (1999). The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal Behaviour 58*(2), 229–246. https://doi.org/10.1006/anbe.1999.1159

O'Donohue, W., & Plaud, J. J. (1991). The long-term habituation of sexual arousal in the human male. *Journal of Behavior Therapy and Experimental Psychiatry*, *22*(2), 87-96. https://doi.org/10.1016/0005-7916(91)90003-N

Ono, T., Siva-Jothy, M. T., & Kato, A. K. I. (1989). Removal and subsequent ingestion of rivals' semen during copulation in a tree cricket. *Physiological Entomology*, *14*(2), 195-202. https://doi.org/10.1111/j.1365-3032.1989.tb00952.x

Paoli, T. (2009). The absence of sexual coercion in bonobos. In *Sexual coercion in primates and humans: An evolutionary perspective on male aggression against females* (eds M. N. Muller and R.W. Wrangham), pp. 410–423. Cambridge: Harvard University Press. doi.org/10.4159/9780674054349-016

Parker, G. A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biological Reviews*, *45*(4), 525-567. https://doi.org/10.1111/j.1469-185X.1970.tb01176.x

Parker, G. A. (2006). Sexual conflict over mating and fertilization: an overview. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*(1466), 235-259. https://doi.org/10.1098/rstb.2005.1785

Parker, G. A. (2020). Conceptual developments in sperm competition: a very brief synopsis. *Philosophical Transactions of the Royal Society B*, *375*(1813), 20200061. https://doi.org/10.1098/rstb.2020.0061

Parker, G. A., & Partridge, L. (1998). Sexual conflict and speciation. Philosophical Transactions of the Royal Society of London. *Series B: Biological Sciences, 353*(1366), 261-274. https://doi.org/10.1098/rstb.1998.0208https://doi.org/10.1098/rstb.1998.0208https://doi.org/10.1098/rstb.1998.0208

Penteriani, V., Kojola, I., Heikkinen, S., Find'o, S., Skuban, M., Fedorca, A., Garcı´a-S_anchez, P., Fedorca, M., Zarzo-Arias, A., Balbontı´n, J. & Delgado, M. d. M. (2024). Livin' on the edge: reducing infanticide risk by maintaining proximity to potentially less infanticidal males. *Animal Behaviour 210*, 63–71. https://doi.org/10.1016/j.anbehav.2024.01.021

Pham, M. N., & Shackelford, T. K. (2013a). The relationship between objective sperm competition risk and men's copulatory interest is moderated by partner's time spent with other men. *Human Nature*, *24*, 476-485. https://doi.org/10.1007/s12110-013-9181-0

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*(3), 328-331. https://doi.org/10.1037/a0036602

Pham, M. N., Barbaro, N., Holub, A., Holden, C. J., Mogilski, J. K., Lopes, G. S., Nicolas, S. C. A., Sela, Y., Shackelford, T. K., Zeigler-Hill, V. & Welling, L. L. M. (2018). Do men produce higher-quality ejaculates when primed with thoughts of partner infidelity? *Evolutionary Psychology, 16*, 1-7. https://doi.org/10.1177/1474704918757551

Pizzari, T. & Birkhead, T. R. (2000). Female feral fowl eject sperm of subdominant males. *Nature, 405*, 787–789. https://doi.org/10.1038/35015558

Pizzari, T., Cornwallis, C. K., Løvlie, H., Jakobsson, S., & Birkhead, T. R. (2003). Sophisticated sperm allocation in male fowl. *Nature*, *426*, 70-74. https://doi.org/10.1038/nature02004

Price, J. H., & Miller, P. A. (1984). Sexual fantasies of Black and of White college students. *Psychological Reports*, *54*(3), 1007-1014. https://doi.org/10.2466/pr0.1984.54.3.1007

Prokop, P. (2013). Rape avoidance behavior among Slovak women. *Evolutionary Psychology*, *11*(2), 365-382. https://doi.org/10.1177/147470491301100207

Pryor, J. B., Stutterheim, S. E., & Lemmens, L. H. (2024). The relationships of sexually harassing behaviors to organizational context factors and working men's dark personality traits. *Aggressive Behavior*, *50*(2), e22142. https://doi.org/10.1002/ab.22142

Puts, D. A., Dawood, K., & Welling, L. L. (2012). Why women have orgasms: An evolutionary analysis. *Archives of Sexual Behavior*, *41*, 1127-1143. https://doi.org/10.1007/s10508-012-9967-x

Puts, D. A., Welling, L. L., Burriss, R. P., & Dawood, K. (2012). Men's masculinity and attractiveness predict their female partners' reported orgasm frequency and timing. *Evolution and Human Behavior*, *33*(1), 1-9. https://doi.org/10.1016/j.evolhumbehav.2011.03.003

Ramm, S. A., & Stockley, P. (2014). Sequential male mate choice under sperm competition risk. *Behavioral Ecology*, *25*(3), 660-667. https://doi.org/10.1093/beheco/aru037

Russell, D. E. H. (1982). *Rape in marriage.* New York: Macmillan Press.

Samara, I., Roth, T. S., & Kret, M. E. (2021). The role of emotion projection, sexual desire, and self-rated attractiveness in the sexual overperception bias. *Archives of Sexual Behavior*, *50*(6), 2507-2516. https://doi.org/10.1007/s10508-021-02017-5

Scelza, B. A., Prall, S. P., Swinford, N., Gopalan, S., Atkinson, E. G., McElreath, R., ... & Henn, B. M. (2020). High rate of extrapair paternity in a human population demonstrates diversity in human reproductive strategies. *Science Advances*, *6*(8), eaay6195. DOI: 10.1126/sciadv.aay6195

Schöfl, G., & Taborsky, M. (2002). Prolonged tandem formation in firebugs (*Pyrrhocoris apterus*) serves mate-guarding. *Behavioral Ecology and Sociobiology*, *52*(, 426-433. https://doi.org/10.1007/s00265-002-0524-9

Scolari, F., Khamis, F. M., & Pérez-Staples, D. (2021). Beyond sperm and male accessory gland proteins: exploring insect reproductive metabolomes. *Frontiers in Physiology*, *12*, 729440. https://doi.org/10.3389/fphys.2021.729440

Shackelford, T. K., & Goetz, A. T. (Eds.). (2012). *The Oxford handbook of sexual conflict in humans.* New York, Oxford University Press.

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. https://doi.org/10.1007/s12110-006-1007-x

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), 214-220. DOI:10.1037/0735-7036.121.2.214

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. https://doi.org/10.1007/s12110-000-1015-1

Shackelford, T. K., LeBlanc, G. J., Weekes-Shackelford, V. A., Bleske-Rechek, A. L., Euler, H. A., & Hoier, S. (2002). Psychological adaptation to human sperm competition. *Evolution and Human Behavior*, *23*(2), 123-138. https://doi.org/10.1016/S1090-5138(01)00090-3

Singh, R., Nigam, P., Qureshi, Q., Sankar, K., Krausman, P. R. & Goyal, S. P. (2014). Strategy of female tigers to avoid infanticide. *Current Science 107*(9), 1595–1597. https://www.jstor.org/stable/24107222

Slatyer, R. A., Mautz, B. S., Backwell, P. R., & Jennions, M. D. (2012). Estimating genetic benefits of polyandry from experimental studies: a meta-analysis. *Biological Reviews*, *87*(1), 1-33. https://doi.org/10.1111/j.1469-185X.2011.00182.x

Smit, N. (2025). Strategies, costs, and counter-strategies to sexual coercion. *Biological Reviews.* https://doi.org/10.1111/brv.70013

Smit, N. & Robbins, M. M. (2024). Female gorillas compete for food and males. *Evolution and Human Behavior, 45*(5), 106611. https://doi.org/10.1016/j.evolhumbehav.2024.106611

Smith, R. L. (1984). Human sperm competition. In R. L. Smith (Ed.), *Sperm competition and the evolution of animal mating systems* (pp. 601-659). New York: Academic Press.

Smuts, B. (1992). Male aggression against women: an evolutionary perspective. *Human Nature 3*, 1–44. https://doi.org/10.1007/BF02692265

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. https://doi.org/10.1016/j.paid.2013.02.005

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. https://doi.org/10.1007/s10896-008-9153-z

Strauss, E. D. & Holekamp, K. E. (2019). Social alliances improve rank and fitness in convention-based societies. *Proceedings of the National Academy of Sciences 116*(18), 8919–8924. https://doi.org/10.1073/pnas.1810384116

Studd, M. V., & Gattiker, U. E. (1991). The evolutionary psychology of sexual harassment in organizations. *Ethology and Sociobiology*, *12*(4), 249-290. https://doi.org/10.1016/0162-3095(91)90021-H

Symons, D. (1979). *The evolution of human sexuality*. New York: Oxford University Press.

Thornhill, R. (1983). Cryptic female choice and its implications in the scorpionfly Harpobittacus nigriceps. *The American Naturalist*, *122*(6), 765-788. https://doi.org/10.1086/284170

Thornhill, R., & Thornhill, N. W. (1992). The evolutionary psychology of men's coercive sexuality. *Behavioral and Brain Sciences*, *15*(2), 363-375. https://doi.org/10.1017/S0140525X00069120

Thornhill, R., Gangestad, S. W., & Comer, R. (1995). Human female orgasm and mate fluctuating asymmetry. *Animal Behaviour*, *50*(6), 1601-1615. https://doi.org/10.1016/0003-3472(95)80014-X

Tokuyama, N. & Furuichi, T. (2016). Do friends help each other? Patterns of female coalition formation in wild bonobos at Wamba. *Animal Behaviour 119*(), 27–35. https://doi.org/10.1016/j.anbehav.2016.06.021

Tregenza, T. and Wedell, N. (2002) Polyandrous females avoid costs of inbreeding. *Nature, 415*, 71–73. https://doi.org/10.1038/415071a

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), Sexual selection and the descent of man (pp. 1871-1971). Chicago: Aldine.

Voracek, M., Haubner, T., & Fisher, M. L. (2008). Recent decline in nonpaternity rates: a cross-temporal meta-analysis. *Psychological Reports*, *103*(3), 799-811. https://doi.org/10.2466/pr0.103.3.799-811

Wedell, N., Gage, M. J., & Parker, G. A. (2002). Sperm competition, male prudence and sperm-limited females. *Trends in Ecology & Evolution*, *17*(7), 313-320. DOI: 10.1016/S0169-5347(02)02533-8

Welke, K. & Schneider, J. M. (2009). Inbreeding avoidance through cryptic female choice in the cannibalistic orb-web spider *Argiope Iobata. Behavioral Ecology, 20*(5), 1056 – 1062. https://doi.org/10.1093/beheco/arp097

Wilson, M., & Mesnick, S.L. (1997). An empirical test of the bodyguard hypothesis. In: Gowaty, P.A. (eds) *Feminism and evolutionary biology*. Boston, MA: Springer. https://doi.org/10.1007/978-1-4615-5985-6_21

Wilson, L. C., & Miller, K. E. (2016). Meta-analysis of the prevalence of unacknowledged rape. *Trauma, Violence, & Abuse*, *17*(2), 149-159. https://doi.org/10.1177/1524838015576391

Wolf, M., Musch, J., Enczmann, J., & Fischer, J. (2012). Estimating the prevalence of nonpaternity in Germany. *Human Nature*, *23*(2), 208-217. https://doi.org/10.1007/s12110-012-9143-y

Zeigler-Hill, V., Besser, A., Morag, J., & Campbell, W. K. (2016). The Dark Triad and sexual harassment proclivity. *Personality and Individual Differences*, *89*, 47-54. https://doi.org/10.1016/j.paid.2015.09.048

Zervomanolakis, I., Ott, H. W., Hadziomerovic, D., Mattle, V., Seeber, B. E., Virgolini, I., ... & Wildt, L. (2007). Physiology of upward transport in the human female genital tract. *Annals of the New York Academy of Sciences*, *1101*(1), 1-20. https://doi.org/10.1196/annals.1389.032