THE EVOLUTIONARY PSYCHOLOGY OF ORAL SEX

by

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Michael Nghia Pham

ABSTRACT

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Cunnilingus—the oral stimulation of female genitals—is practiced across several human cultures and has been a recurrent feature of human evolution. Despite its ubiquity, little research has investigated the evolutionary functions of cunnilingus. The current research investigates the hypothesis that cunnilingus is an anti-cuckoldry behavior. Study 1 explores the infidelity-detection hypothesis of cunnilingus—that men perform cunnilingus to estimate the likelihood of their partner's recent sexual infidelity by detecting the presence of rival semen near her genitals. Studies 2 and 3 explore whether cunnilingus is a behavior that men perform to increase their sexual arousal and consequent ejaculate quality—a behavior designed to increase the likelihood of fertilizing ova. Study 4 explores whether men perform cunnilingus to minimize their partner's infidelity risk by increasing her relationship satisfaction. I document preliminary support for each of the proposed functions of cunnilingus. Further, the results across these studies support the broader hypothesis that cunnilingus is an anti-cuckoldry behavior.

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INTRODUCTION

Evolutionary psychology is the study of how evolution by natural selection has shaped the human mind. Like any biological adaptation, psychological adaptations were solutions to problems of survival and reproduction that have recurred over human evolution. The human mind houses specialized information processing systems that activate under specific conditions (i.e., domain-specific inputs), and that motivate the performance of behaviors designed to solve adaptive problems (Barrett & Kurzban, 2006). Because evolution is a slow and gradual process, modern humans still possess the same psychological adaptations that ancestral humans possessed, even though our modern ecology differs from the ecologies in which those adaptations evolved. Thus, investigating the structure and function of the modern human mind can provide insight into human evolutionary psychology.

Men have faced the adaptive problem of cuckoldry—the unwitting investment of resources into genetically unrelated offspring. Cuckoldry has likely recurred over human evolution. Current estimates document non-zero rates of discrepant social and genetic fatherhood (Anderson, 2006; Bellis, Hughes, Hughes, & Ashton, 2005; Wolf, Musch, Enczmann, & Fischer, 2012). A meta-analysis of 32 published studies documented that 3.1% of children are genetically unrelated to their social father (Voracek, Haubner, & Fisher, 2008). Anderson (2006) found that 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.

Male sexual jealousy provides further evidence that cuckoldry recurred over human evolution. The costs of cuckoldry far exceed the costs of losing a partner's resource investments. Indeed, men experience greater jealousy in response to a partner's sexual infidelity than to her emotional infidelity—a finding that has been replicated using several international samples, including the United States, Spain, Chile, Norway, the Netherlands, Korea, Japan, and Germany (Buss, Larson, Weston, & Semmelroth, 1992; Buss et al., 1999; Buunk, Angleitner, Oubaid, & Buss, 1996; Fernandez, Sierra, Zubeidat, & Vera-Villarroel, 2006; Kennair, Nordeide, Andreassen, Stronen, & Pallesen, 2011). Sexual jealousy motivates men to minimize the risk of their partner's infidelity, and jealousy is so strong, in fact, that it is a leading cause of partner-killing across cultures (Buss, 2006; Daly & Wilson, 1988). Male sexual jealousy could not have evolved without the evolutionary recurrence of cuckoldry (Buss, 2013).

Men possess adaptations designed to minimize their cuckoldry risk. Men prefer a potential long-term partner who will likely remain sexually faithful to them (Buss & Schmitt, 1993). Men who are currently mated perform behaviors to minimize the risk of their partner's infidelity (Buss, 1988; Buss & Shackelford, 1997)—a strategy I discuss in greater detail in Chapter 4. Female sexual infidelity does not always result in cuckoldry. Rather, cuckoldry occurs when rival sperm fertilizes her ova. In Chapters 1 through 3, I discuss how men's anti-cuckoldry tactics include post-copulatory strategies designed to minimize cuckoldry risk (Baker & Bellis, 1995; Shackelford et al., 2002). Finally, stepparents kill their children at higher rates than do genetic parents, which Wilson, Daly,

and Weghorst (1980) argue is an adaptation designed to minimize investing resources into genetically unrelated offspring. Thus, and as further evidence of the heavy costs of cuckoldry, men possess many adaptations to minimize the costs of cuckoldry. The current research investigates whether cunnilingus is also an anti-cuckoldry tactic.

Cunnilingus—the oral stimulation of female genitals—has been a prominent feature of modern and ancestral human sexuality. Cunnilingus occurs in many cultures (e.g., Guadamuz et al. 2006; Iwawaki and Wilson 1983; Lurie et al. 1995), including preindustrial cultures (Hewlett and Hewlett 2010), indicating that cunnilingus is not a culture-specific practice. Cunnilingus is depicted frequently in pornography, and the content of pornography is designed to appeal to evolved mechanisms (Malamuth, 1996). Cunnilingus is depicted in ancestral cave paintings (Angulo & García 2005). In fact, cunnilingus also occurs across many mammalian species (Maruthupandian & Marimuthu, 2013; Nishimura, Utsumi, Okano, & Iritani, 1991; Palagi et al., 2003; Soini, 1987), including dogs (Dunbar, 1977; Kiddy et al., 1978), hamsters (Mesocricetus auratus: Johnston, 1974; Murphy, 1973), bovine (Nishimura et al., 1991; Sankar & Archunan, 2004), ring-tailed lemurs (Lemur catta: Palagi et al., 2003), pygmy marmosets (Cebuella pygmaea: Soini, 1987), and Indian flying foxes (Pteropus giganteus: Maruthupandian & Marimuthu, 2013). Thus, evidence suggests an evolutionary history of cunnilingus not only in humans, but also in other mammals.

Individuals report various reasons for practicing cunnilingus. Cornell and Halpern-Felsher (2006) surveyed 425 young men and women who reported that they perform oral sex to retain virginity (because oral sex is sometimes not perceived as "real" sex; Sanders & Reinisch, 1999), to increase their sexual reputation, to sexually satisfy

their partner, and to avoid the risk of pregnancy and diseases associated with penilevaginal sex. The nationally representative National Health and Social Life Survey found that while 71% of men find performing cunnilingus either very appealing or somewhat appealing, and only 19% find it not at all appealing, 60% of women find receiving cunnilingus very appealing or somewhat appealing, and 28% report that it is not at all appealing (Laumann et al. 1992). Men's desire to gather the taste and smell of the female genitals is evidenced by the market demand for women's used underwear. Many customers request that women wear underwear for a few days before shipping them to the customer in a plastic ziplock bag to retain the genital scents (Ridley, 2015). It is not uncommon for customers to explicitly request that a woman masturbate while wearing the panties to increase the amount of female fluids that the panties capture (Ridley, 2015). Furthermore, these customers prefer panties worn by women who are young and attractive (i.e., fertile women: Nakano, 2014; Snow, 2015). Potentially, men's desire to perform cunnilingus may be related to experiencing sexual arousal as a function of the information they gather about the woman's fertility. This hypothesized function of cunnilingus would be similar to its function in other species in which mucous from female genitals contain pheromones that elicit mounting behaviors in males (Nishimura et al., 1991; Soini, 1987).

Despite the ubiquity of cunnilingus across cultures and human evolution, there exists little research on the evolutionary functions of cunnilingus in humans. Cunnilingus occurs most often in the context of romantic relationships. In fact, college women report having to *negotiate* with their sexual partner to receive cunnilingus during one night stands (Backstrom, Armstrong, & Puentes, 2012). Although we cannot directly observe

the human ancestral ecologies in which performing cunnilingus was adaptive, modern environments provide a useful starting point for investigation. Potentially, cunnilingus may have been a solution to the adaptive challenges men faced *specifically* in long-term relationships. One such challenge is cuckoldry. The current research investigates three anti-cuckoldry functions of cunnilingus.

In Chapter 1, I explore the infidelity-detection hypothesis of cunnilingus—that men perform cunnilingus to estimate the likelihood of their partner's recent sexual infidelity by detecting the presence of rival semen near her genitals. In Chapters 2 and 3, I explore whether cunnilingus is behavior that men perform to increase their sexual arousal and consequent ejaculate quality—a behavior designed to increase the likelihood of fertilizing ova. In Chapter 4, I explore whether men perform cunnilingus to minimize their partner infidelity risk by increasing her relationship satisfaction.

Three of my four studies include analyses of men's self-reports to investigate the evolutionary psychology of cunnilingus. Although this methodology has limitations (which I describe in each chapter), there are two important benefits. First, because I am investigating men's anti-cuckoldry psychology, it is more appropriate to measure men's perceptions of partner infidelity risk—rather than their actual partner infidelity risk—because the evolved mechanisms that produce anti-cuckoldry behaviors are activated as a function of their perceptions (i.e., inputs to those psychological mechanisms). If a man's partner surreptitiously commits sexual infidelity, but he does not discover or suspect her infidelity, then he would not deploy anti-cuckoldry tactics. Second, several researchers have documented that people can accurately report past sexual behaviors (Carballo-Dieguez, Remien, Dolezal, & Wagner, 1999; Masters & Johnson, 1966; reviewed in

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Allgeier & Allgeier, 2000), and self-reports are far less intrusive than actually observing sexual activity—a method that would cause participants to perform in unnatural ways.

Individuals are better at remembering details of more recent events than less recent events. To ensure that participants remember the details of their sexual activity, they report the performance of specific sexual behaviors during their most recent sexual encounter with their partner, relative to their typical sexual encounters.

CHAPTER 1

STUDY 1

Sperm competition occurs when a female copulates with two or more males within a sufficiently brief time period, resulting in the sperm from the different males competing to fertilize ova (Parker, 1970). Sperm competition has been documented or inferred to exist in many different species, including humans (Baker & Bellis, 1993a; 1993b; Birkhead & Møller, 1998; Smith, 1984; Shackelford et. al., 2002; 2007). Among socially monogamous species, female extra-pair copulations are the primary context of sperm competition (Smith, 1984).

Female infidelity is an important context for sperm competition in humans (Smith, 1984). Although humans typically form long term relationships, women occasionally pursue extra-pair copulations, placing their regular partner at risk for cuckoldry. The reproductive costs of cuckoldry may have produced adaptations designed to reduce the likelihood of cuckoldry (Shackelford, 2003). Some anti-cuckoldry mechanisms appear to be designed to prevent female infidelity by minimizing extra-pair copulation opportunities (Buss, 2002). Other anti-cuckoldry mechanisms appear to be designed to anticipate or to "correct" female infidelity, motivating the regular partner to enter his sperm into competition with rival male sperm that may already be present or that soon may be present in his partner's reproductive tract (Shackelford, 2003). Among men in committed relationships, those who spend a greater proportion of time apart from their partners since the couple's last copulation (and thus experience greater risk of sperm competition) ejaculate more sperm at the couple's next copulation (Baker & Bellis, 1993a). Inseminating more sperm increases a man's chances in the "sperm raffle" to fertilize his partner's ova, and has been documented in a wide range of taxa ranging from insects to humans (Baker & Bellis, 1993a; Parker, 1970). Men who spend a greater proportion of time apart from their partner since the couple's last copulation also report greater desire to copulate with their partner, find their partner to be more attractive, and report that other men find their partner to be more attractive (Shackelford et al, 2002; Shackelford, Goetz, McKibbin, & Starratt, 2007).

Men mated to more attractive women are at greater *recurrent* risk of sperm competition, because more attractive women are more likely to be pursued and successfully lured away by rival men (Goetz et al., 2005; Schmitt & Buss, 2001). Goetz et al. (2005) documented that men partnered to a more attractive woman (i.e., are at greater recurrent risk of sperm competition) perform deeper and more vigorous copulatory thrusts during sex with her, according to both men's reports and women's reports. These copulatory behaviors may function to displace from his partner's reproductive tract another man's semen, which complements the semen-displacing morphology of the human penis (Gallup et al., 2003).

Informed by sperm competition theory, Thornhill (2006) hypothesized that cunnilingus may function to detect the presence of rival semen following her sexual infidelity. Cunnilingus may allow men to taste and smell rival semen near or within the vagina, providing cues to a women's recent sexual history. This hypothesis was inspired by research on non-humans documenting the increased frequency of male genital licking and sniffing during female estrus—a period during which intense sperm competition occurs (Dugmore, Bailey, & Evans, 1984; Palagi, Telara, & Borgognini, 2003; Pennington, Albright, & Callahan, 1986). The infidelity-detection hypothesis may explain why men typically perform cunnilingus before (and not after) they ejaculate (Halpern & Sherman, 1979): Men's own semen might "mask" the odor of rival semen (but it is possible that men are simply repulsed by their own semen). Indirect evidence indicates that humans can smell the semen of others. For example, fertility clinicians record the odors they smell from semen as part of semen quality analysis (e.g., Mauras, Bell, Snow, & Winslow, 2005).

According to the infidelity-detection hypothesis, men experience physiological changes when performing cunnilingus on a woman who presents a high risk of sperm competition. For example, the female reproductive is an acidic environment (O'Connor, Kinchington, Kangro, & Jeffries, 1995). Humans possess specialized taste receptors that detect acidity—a system that evolved as an adaptation to avoid foods that were spoiled or unripe ("sour-like" taste: Huang et al., 2006). A system of detecting acidity in foods could be co-opted by the sexual arousal system to detect the acidity of non-food sources (e.g., female genital fluids). The alkalinity of human semen counteracts the acidic environment of the female reproductive tract (Tevi-Bénissan et al., 1997). This pH change may be detectable by men during cunnilingus. Change in pH is merely one example of how human semen changes the chemistry of the female genital taste and odor: Dozens of substances from human semen are absorbed through the epithelial lining of the female reproductive tract, some of which are even hypothesized to trigger ovulation (i.e.,

sperm competition risk: Burch & Gallup, 2006). In other words, the function of cunnilingus is not limited to the detection of rival semen, but also to the detectable effects that semen has on the female reproductive tract.

In the present study, I test the infidelity-detection hypothesis of oral sex: If cunnilingus functions to detect rival semen (including chemical changes to the female genitals caused by exposure to rival semen), then men at greater recurrent risk of sperm competition will report greater interest in performing cunnilingus on their partner (Prediction 1) and will perform cunnilingus for a longer duration (Prediction 2).

Men engage in lengthier durations of sexual intercourse with more attractive women (Goetz et al., 2005), so the predicted greater duration of cunnilingus for men at greater recurrent risk of sperm competition may be a byproduct of sexual intercourse duration. Men's relationship satisfaction and the length of the relationship also are correlated with the performance and frequency of oral sex (Santtila et al., 2008). I control statistically for these potential confounds in tests of the predictions.

Method

Participants

Two hundred and thirty-one men in a committed, sexual relationship lasting at least one year participated. All participants reported having had sex with their partner at least once in the past week. The mean participant age was 25.2 years (SD = 7.8) and the mean relationship length was 43.4 months (SD = 56.9).

Materials

Participants reported their age and current relationship length on a questionnaire. Following Shackelford et al. (2002, 2007), participants answered four questions about the attractiveness of their partner on a Likert-type scale ranging from 0 (*Not at all*) to 9 (*Extremely*): How (1) physically attractive and (2) sexually attractive do you find your partner? How (3) physically attractive and (4) sexually attractive do other men find your partner?

Participants answered questions about their most recent sexual encounter with their partner on a Likert-type scale, including: duration of sexual intercourse (0 = Lesstime than is typical, 9 = More time than is typical), own interest in performing oral sex (0 = Less interested or excited than is typical for me, 9 = More interested or excited than is typical for me), and duration of oral sex (0 = Less time than is typical for me, 9 = Moretime than is typical for me).

Participants answered four questions about their relationship satisfaction on a Likert-type scale ranging from 0 (*Not at all*) to 9 (*Extremely*): how (1) sexually satisfied, (2) emotionally satisfied, and (3) overall satisfied are you with your partner?, and (4) how committed are you to your partner?

Procedures

Potential male participants were recruited by word-of-mouth, flyers posted on campus bulletin boards, and announcements in psychology courses. Approximately 20-30 potential participants arrived to a laboratory where they were asked if they were at least 18 years of age and in a heterosexual committed relationship. Those who qualified received a consent form and a questionnaire packet to take home, so that they could privately provide their responses. At a time of their choosing, participants placed their signed consent form and completed questionnaire in separately sealed envelopes, and placed each in designated collection boxes—one box was dedicated to consent forms, and the other to questionnaires. The research team would periodically retrieve several completed questionnaires from these boxes.

Results

Following Goetz et al. (2005), I constructed a *relationship satisfaction* measure (α = .85) from the mean of four variables: sexual satisfaction, emotional satisfaction, overall satisfaction, and commitment to partner. Also following Goetz et al. (2005), I constructed a *recurrent risk of sperm competition* measure (α = .83) from the mean of four variables: how sexually and physically attractive the participant views his partner, and how sexually and physically attractive the participant believes other men view his partner. Before conducting analyses, I logarithmically transformed the relationship length variable to correct for significant skew (Tabachnick & Fidell, 2006).

Table 1 displays the zero-order correlations among the target variables. Recurrent risk of sperm competition was positively correlated with men's interest in performing cunnilingus and the duration of cunnilingus. Reports on the two oral sex variables also were correlated with reports on the potentially confounding variables: relationship satisfaction, relationship length, and duration of sexual intercourse. To identify the unique effects that recurrent risk of sperm competition may have on the two oral sex variables, I conducted multiple regression analyses to control for these potential confounds (see Table 2).

The results of the multiple regression analyses support Predictions 1 and 2: Men at greater recurrent risk of sperm competition reported greater interest in performing cunnilingus on their partner and performed cunnilingus for a longer duration, controlling for relationship length, relationship satisfaction, and duration of sexual intercourse.

Discussion

The results support the hypothesis that cunnilingus may function to detect female infidelity (Thornhill, 2006). Men mated to more attractive women—and, therefore, exposed to a greater recurrent risk of sperm competition—report greater interest in

Table 1

	1.	2.	3.	4.	5.
1. Recurrent Risk					
2. Relationship Satisfaction	.56**				
3. Relationship Length	20**	.00			
4. Duration of Intercourse	.23**	.16*	06		
5. Interest in performing oral sex	.26**	.23**	.01	.11	
6. Duration of oral sex	.24**	.12	07	.31**	.40**

Zero-order correlations among key variables.

N = 231 men, *p < .05, **p < .01. Relationship length is log transformed.

Table 2

Multiple regression analyses assessing relationships between recurrent risk of sperm competition and oral sex variables, controlling for relationship length, relationship satisfaction, and duration of intercourse.

	Recurrent Risk		Relationship Length		Relationship Satisfaction		Duration of Intercourse	
	В	t	В	t	B	t	В	t
Interest in oral sex	.20	2.48*	.05	.80	.11	1.37	.05	.75
Duration of oral sex	.19	2.40*	02	31	02	33	.27	4.27***

N = 231 men, * p < .05, **p < .01, ***p < .001. Relationship length is log transformed.

B = standardized beta coefficient, t = test statistic associated with B

performing cunnilingus on their partner and report performing cunnilingus for a longer duration, supporting Predictions 1 and 2. These effects remained even after controlling statistically for the potential confounds of relationship length, men's relationship satisfaction, and the duration of sexual intercourse.

An alternative explanation for the current results is that cunnilingus facilities sperm retention via orgasm, and that men at greater recurrent risk of sperm competition may be particularly likely to perform cunnilingus. Women who receive oral sex are more likely to experience orgasm at a given copulatory event than are women who do not receive oral sex (Backstrom et al., 2012), and women retain more sperm when they experience an orgasm temporally near their partner's ejaculation (Baker & Bellis, 1993b). Men who induce their partner's orgasm through cunnilingus and then soon after ejaculate into their partner's reproductive tract will have more sperm retained in her tract, thereby providing them with a competitive advantage in any ensuing sperm competition. According to the sperm retention hypothesis for cunnilingus, therefore, men at greater recurrent risk of sperm competition are predicted to be especially interested in performing cunnilingus on their partner to induce her orgasm, thereby facilitating preferential retention of their own sperm. The sperm retention hypothesis, but not the infidelity detection hypothesis, depends on cunnilingus resulting in orgasm. Future research therefore may be able to disentangle these hypotheses by securing data on whether cunnilingus resulted in orgasm.

Another explanation for the current results is that men perform cunnilingus on their partner to "sexually satiate" her. Sexually dissatisfied women are more susceptible to infidelity (Shackelford & Buss, 1997), and the frequency with which men perform cunnilingus on their partner is positively related to their partner's sexual satisfaction (Young, Denny, Young, & Luquis, 2000). Therefore, cunnilingus may be a tactic men use to minimize the likelihood that their partner will be sexually unfaithful. Future research might investigate whether sperm competition risk predicts men's interest in, and time spent, performing cunnilingus, *after* statistically controlling for their partner's sexual satisfaction.

In conclusion, cumulating evidence demonstrates the importance of sperm competition theory for understanding sexual conflict in intimate relationships (Shackelford & Goetz, 2012). Sperm competition theory helps to explain men's partnerdirected copulatory interest (Shackelford et al., 2002; 2007), intimate partner violence (Goetz & Shackelford, 2006), and partner sexual coercion and rape (Goetz, Shackelford, & Camilleri, 2008). I investigated the function of oral sex guided heuristically by sperm

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competition theory and provided preliminary support for the infidelity-detection hypothesis.

•

CHAPTER 2

STUDY 2

Sperm competition occurs when a female copulates with two or more males within a sufficiently brief time period, with the results that the sperm of the different males simultaneously occupy the female's reproductive tract and compete to fertilize ova (Parker, 1970). In humans, female infidelity is the most common context for sperm competition (Baker and Bellis, 1993a; Shackelford, Goetz, McKibbin, and Starratt, 2007; Shackelford et al., 2002; Smith, 1984). Men whose regular partner commits infidelity are at risk of cuckoldry—the unwitting investment of resources into genetically unrelated offspring. The reproductive costs of cuckoldry have caused the evolution of male sperm competition tactics—adaptations that increase sperm competition success (Shackelford & Goetz, 2007). Males perform concurrently various sperm competition tactics to minimize their cuckoldry risk (Dickinson, 1986; Shackelford, Goetz, Guta, & Schmitt, 2006). In the current study, I explore the co-occurrence of oral sex—a hypothesized anti-cuckoldry tactic—with other sperm competition tactics: prolonged copulation, semen-displacing copulatory behaviors, and ejaculate adjustment.

Oral sex may be related to sperm competition risk. *Male dunnocks (Prunella Modularis)* peck at a female's genitals to induce ejection of rival sperm prior to copulating with her (Davies, 1983). In the Indian Flying Fox (*Pteropus giganteus*), males who spend more time performing cunnilingus also spend more time copulating, and

prolonged copulations are a sperm competition tactic (Maruthupandian, & Marimuthu, 2013). Some non-human primates, particularly those that experience adaptive problems related to sperm competition, sniff and lick a female's genitals when she is near estrus—the period during which sperm can fertilize ova (Palagi, Telara, and Tarli, 2003; Soini, 1987). The results from Study 1 indicate that men at greater sperm competition risk report greater interest in and spend more time performing oral sex on their regular partner. These results also suggest that performing oral sex may be related to sperm competition risk and may relate to other anti-cuckoldry tactics.

Prolonged copulation may be a male-initiated sperm competition tactic. Males that spend more time copulating with a female may delay or thwart her copulation with other males (Cordero, 1990), deliver more sperm (Dickinson, 1986), influence female mechanisms that favor his sperm over another male's sperm (Eberhard, 1996), or displace another male's semen from the female's reproductive tract (Cordero, 1990; Gallup et al., 2003; Goetz et al., 2005). In humans, longer copulations may function to displace other men's semen: Men at greater sperm competition risk spend more time copulating with their regular partner, and perform more and deeper copulatory thrusts (Goetz et al., 2005), behaviors that complement the semen-displacing morphology of the human penis (Gallup et al., 2003). Furthermore, the period during which men lose their penile erection following ejaculation (i.e., post-ejaculatory refractory period) may function to prevent them from displacing their own semen (Gallup and Burch, 2004; Gallup, Burch, and Mitchell, 2006).

In some species, oral sex affords males longer copulatory duration, and this relationship has been interpreted with reference to sperm competition theory

(Maruthupandian and Marimuth, 2013). Study 2 investigates whether these findings extend to humans. I hypothesize that men who spend more time performing oral sex on their regular partner will also spend more time copulating with her (Hypothesis 1). Goetz et al. (2005) documented that men who spend more time copulating with their regular partner also perform more semen-displacing copulatory behaviors (e.g., deeper, more vigorous penile thrusting). Therefore, and following Goetz et al., I hypothesize that men who spend more time performing oral sex on their regular partner also will perform more semen-displacing copulatory behaviors (Hypothesis 2).

Findings from Goetz et al. (2005) are also consistent with an ejaculate adjustment hypothesis for male copulatory behaviors: Men adjust their copulatory behaviors to increase their sexual arousal and, consequently, produce higher quality ejaculates that are more likely to succeed in sperm competition (for a review of specific semen parameters predicting sperm competition success, see Simmons and Fitzpatrick, 2012; Snook, 2005). For example, men who spend more time masturbating during a masturbatory session produce ejaculates with greater sperm concentration, higher concentration of motile sperm, more motile sperm, and more total sperm (Pound, Javed, Ruberto, Shaikh, & Del Valle, 2002). Deeper copulatory thrusts stimulate more nerve endings along the surface of the penis (Halata & Munger, 1986; Yang & Bradley, 1999), causing greater sexual arousal (Georgiadis & Holstege, 2005). Men's self-reports of their sexual arousal and orgasm intensity correlate with the volume of their ejaculate (van Rouen et al., 1996), and men who view more sexually arousing pornographic images, compared to men who view less sexually arousing pornographic images, produce masturbatory ejaculates with a higher percentage of motile sperm (Kilgallon & Simmons, 2005). Consistent with the

ejaculate adjustment hypothesis, men at greater sperm competition risk ejaculate more sperm at next copulation (Baker & Bellis, 1993a). I therefore hypothesize that men who spend more time performing oral sex on their regular partner also will report greater sexual arousal when copulating with her (Hypothesis 3).

Method

Participants

I recruited from the community and university campuses 233 men in a committed, heterosexual, sexual relationship lasting at least one year. All participants reported having had sex with their partner at least once in the past week. The mean participant age was 25.4 years (SD = 7.8), the mean of their partner's age was 24.0 (SD = 7.0), and the mean relationship length was 48.2 months (SD = 56.0).

Materials

Participants reported their age, their partner's age, and current relationship length (in months) on a questionnaire. Following previous research (Goetz et al., 2005), men reported their copulatory behaviors during their most recent sexual encounter with their partner—compared to their typical sexual encounter—on a 10-point Likert-type scale: number of thrusts, depth of average and deepest thrust, duration of sexual intercourse, and time spent performing oral sex (0 = Lesser/Shorter/Fewer, 9 =

Greater/Longer/More).

Men reported their sexual arousal during their most recent sexual encounter with their partner—compared to their typical sexual encounter—on a 10-point Likert-type scale: orgasm intensity (0 = less intense; 9 = more intense), relief following ejaculation (0 = less relief, 9 = more relief), forcefulness of ejaculation (0 = less forceful, 9 = more forceful), sexual excitement (0 = less excited, 9 = more excited), feelings during intercourse (0 = worse, 9 = better), and penis sensitivity (0 = less sensitive, 9 = more sensitive).

Procedures

Potential male participants were recruited by word-of-mouth, flyers posted on campus bulletin boards, and announcements in psychology courses. Approximately 20-30 potential participants arrived to a laboratory where they were asked if they were at least 18 years of age and in a heterosexual committed relationship. Those who qualified received a consent form and a questionnaire packet to take home, so that they could privately provide their responses. At a time of their choosing, participants placed their signed consent form and completed questionnaire in separately sealed envelopes, and placed each in designated collection boxes—one box was dedicated to consent forms, and the other to questionnaires. The research team would periodically retrieve several completed questionnaires from these boxes.

Results

To test Hypothesis 1, I conducted a linear regression predicting the time men spend performing oral sex on their partner from the time they spend copulating with her. Consistent with Hypothesis 1, men who spend more time copulating with their partner also spend more time performing oral sex on her ($\beta = .307$, t = 4.906, p < .001).

I conducted a principal components analysis using direct oblimin rotation to extract *semen displacement* and *sexual arousal* components (see Table 3 for component

Table 3

Component loadings of key variables obtained by principal components analysis.

Variable	Mean (SD)	Component 1	Component 2
Feelings during intercourse	6.54 (1.64)	.89	01
Excitement during intercourse	6.37 (1.67)	84	03
Orgasm intensity	5.86 (1.92)	.81	.03
Forcefulness of ejaculation	5.60 (1.79)	.74	.06
Penis sensitivity	6.00 (1.70)	.72	08
Relief following ejaculation	6.16 (1.77)	.70	.14
Duration of copulation	5.49 (1.72)	15	.84
Number of thrusts	5.89 (1.55)	.00	.82
Depth of deepest thrust	5.92 (1.53)	.20	.71
Depth of average thrust	5.69 (1.41)	.17	.71
Time spent performing oral sex	5.59 (1.76)		
Eigenvalue		4.91	1.48
Variance explained		49.1%	14.8%

loadings). Because feelings during intercourse, excitement during intercourse, orgasm intensity, forcefulness of ejaculation, penis sensitivity, and relief following ejaculation loaded more heavily on Component 1 than Component 2, I identified Component 1 as the *sexual arousal* component. Because duration of copulation, number of thrusts, depth of deepest thrust, and depth of average thrust loaded more heavily on Component 2 than Component 1, I identified Component 2 as the *semen displacement* component. I used these two components as variables in tests of Hypotheses 2 and 3.

To test Hypothesis 2, I conducted a linear regression predicting the time men spend performing oral sex on their partner from their performance of semen-displacing copulatory behaviors. Consistent with Hypothesis 2, men who perform more semendisplacing copulatory behaviors also spend more time performing oral sex on her (β = .289, t = 4.59, p < .001).

To test Hypothesis 3, I conducted a linear regression predicting the time men spend performing oral sex on their partner from their sexual arousal. Consistent with Hypothesis 3, men who are more sexually aroused also spend more time performing oral sex on her ($\beta = .230$, t = 3.58, p < .001).

Discussion

The results of Study 2 support the hypothesis that men perform various sexual behaviors concurrently to increase their sperm competition success. Men who spend more time performing oral sex on their regular partner also spend more time copulating with her, perform more semen-displacing copulatory behaviors (i.e., more and deeper thrusts), and are more sexually aroused—thereby facilitating greater ejaculate quality.

Our measure of copulatory duration may have confounded our results: "*In* comparison to what is typical, how long did sexual intercourse with your partner last?" Participants may have included non-copulatory behaviors when responding to this question—including the time they spent performing oral sex on their partner. Future research assessing copulatory duration could state explicitly that copulatory duration includes only the time spent performing penile-vaginal penetration.

A further limitation of the current study is our indirect, rather than direct, assessment of ejaculate quality. To test the ejaculate adjustment hypothesis, I used men's self-reports of their sexual arousal as a proxy for ejaculate quality. Although previous research has documented a positive relationship between men's sexual arousal and ejaculate quality (Kilgallon and Simmons, 2005; van Rouen et al., 1996), sexual arousal is nevertheless a proxy measure. Future research could assess *directly* men's ejaculate quality.

Given the correlational design of the current study, I cannot conclude from the results that the duration of oral sex causes, or instead results from, greater sexual arousal. Future research could explore the direction of causality between these two variables by implementing experimental designs (e.g., manipulating men's exposure to sexually arousing pornographic content, then assessing the time they spend performing oral sex).

Goetz et al. (2005) secured men's ratings of their partner's attractiveness and her personality traits to assess their sperm competition risk. Men use other cues to estimate sperm competition risk, including the proportion of time they spend apart from their partner since the couple's last copulation (Shackelford et al., 2002, 2007), the time she spends with male friends (Pham & Shackelford, 2013), and her previous infidelity (McKibbin, Starratt, Shackelford, & Goetz, 2011). Future research could benefit from securing data regarding other cues to sperm competition risk when investigating men's sexual behaviors.

Similar to Study 1, the current study highlights the heuristic utility of sperm competition theory for understanding men's sexual behaviors. Men at greater sperm competition risk spend more time copulating with their regular partner, perform more and deeper copulatory thrusts, spend more time performing oral sex on her, and more frequently sexually coerce her (Goetz et al., 2005; Goetz and Shackelford, 2006). The current study adds to this literature by documenting that men who spend more time performing oral sex on their partner also spend more time copulating with her and perform more semen-displacing copulatory behaviors. Additionally, the current study provides preliminary evidence that men adjust their copulatory behaviors to produce more competitive ejaculates.

CHAPTER 3

STUDY 3

"Ejaculate quality" is a composite of ejaculate traits (e.g., sperm motility, sperm viability, sperm number) that affect fertilizing ability (Simmons & Fitzpatrick, 2012). Ejaculate volume is another trait indicator of quality. For example, non-sperm substances in semen—which comprise the majority of the ejaculate's volume—may promote fertilization by promoting sperm motility, reducing the risk of preeclampsia, and suppressing the female immune response that would otherwise attack foreign bodies including sperm (Burch & Gallup, 2006; Davis & Gallup, 2006). According to the World Health Organization (WHO, 2010), low volume ejaculates indicate infertility.

In humans, sexual arousal influences ejaculate volume between ejaculates within men, with greater sexual arousal associated with increased ejaculate volumes (WHO, 2010). For example, men produce ejaculates with greater volume from copulation (i.e., more arousing) than from masturbation (i.e., less arousing; Zavos, 1985; Zavos & Goodpasture, 1989), and during copulation uninterrupted until ejaculation (i.e., more arousing) than during *coitus interruptus* (i.e., less arousing; Zavos et al., 1994). Men produce higher quality masturbatory ejaculates when they spend more (versus less) time sexually aroused (Pound et al., 2002) and when they view more (versus less) sexually arousing stimuli (Joseph et al., 2015; Kilgallon & Simmons, 2005; Leivers et al., 2014). In Study 2, I documented that men who report greater sexual arousal report more intense orgasm and more forceful ejaculation. Men produce an ejaculate with greater volume (van Rouen et al., 1996). Thus, male sexual arousal is correlated positively with ejaculate quality.

Because there are non-trivial costs to producing high-quality ejaculates (WHO, 2010), men experience greater arousal when the reproductive benefits outweigh the costs of producing a higher quality, larger volume ejaculate. For example, men are sensitive to behavioral, visual, auditory, and olfactory cues to female fertility (Haselton & Gildersleeve, 2011). Men exposed to a woman's scent produced at high (versus low) fertility experience a testosterone surge and report greater sexual interest (Cerda-Molina et al., 2013; Doty et al., 1975; Miller & Manor, 2009), consistent with the idea that men are sexually aroused by high-fertility cues. Additionally, men are aroused by cues to sperm competition; Pham and Shackelford (2014) review evidence that men are sensitive to sociosexual, personality, visual, and olfactory cues to sperm competition. For example, pornography depicting two men with a woman is more arousing (McKibbin et al., 2013; Pound, 2002) and leads men to produce more competitive masturbatory ejaculates than pornography depicting multiple women (Kilgallon & Simmons, 2005). Men exposed to sperm competition cues (relative to men not exposed to sperm competition cues) report greater sexual interest (Camilleri & Quinsey, 2009; Pham & Shackelford 2013; Shackelford et al., 2002, 2007), greater sexual arousal (McKibbin et al., 2013; Pound, 2002), and produce higher quality ejaculates (Baker & Bellis, 1993a; Joseph et al., 2015; Kilgallon & Simmons, 2005; Leivers et al., 2014). Thus, men experience greater sexual arousal in sociosexual circumstances (e.g., higher conception risk, higher sperm competition risk) in which the reproductive benefits outweigh the costs of producing higher-quality, greater volume ejaculates.

Although humans and non-humans perform sexual behaviors that do not contribute directly to reproduction (e.g., cunnilingus, prolonged copulation), such behaviors might contribute indirectly to reproduction if they affect sexual arousal and consequent ejaculate volume. Sexual arousal fluctuates during the course of a single sexual event (Zavos et al., 1994). The current research investigates whether ejaculate volume is predicted by cunnilingus and by prolonged copulation in humans.

Males of many mammalian species perform cunnilingus in sociosexual circumstances (e.g., higher conception risk, higher sperm competition risk) in which the reproductive benefits outweigh the costs of producing higher-quality, greater volume ejaculates. For example, males perform cunnilingus to assess a female's fertility by sniffing and licking her genitals (i.e., cunnilingus) to gather scent cues to her fertility status. Male cotton-top tamarins (Saguinus Oedipus) that smell a female's scent marks produced at high-fertility-relative to at low-fertility-experience more frequent penile erections and perform more mounting behaviors (Ziegler et al., 1993). Gathering scent cues to fertility status also may explain why males of several mammalian species more frequently perform cunnilingus on high-fertility females than on low-fertility females, including dogs (Dunbar, 1977; Kiddy et al., 1978), hamsters (*Mesocricetus auratus*: Johnston, 1974; Murphy, 1973), bovine (Nishimura et al., 1991; Sankar & Archunan, 2004), ring-tailed lemurs (Lemur catta: Palagi et al., 2003), and pygmy marmosets (Cebuella pygmaea: Soini, 1987). Male Indian flying foxes (Pteropus giganteus) that spend more time performing cunnilingus on a female also spend more time copulating with her (Maruthupandian & Marimuthu, 2013), and Maruthupandian and Marimuthu have interpreted this relationship with respect to sperm competition theory. Thus, among mammals, cunnilingus may influence sexual arousal and consequent sperm competition tactics (e.g., mounting behaviors, copulatory thrusting, and ejaculate adjustment).

In humans, men may perform cunnilingus to increase their sexual arousal and consequent ejaculate volume, particularly in sociosexual circumstances (e.g., high conception risk, high sperm competition risk) in which the reproductive benefits outweigh the costs of producing higher quality ejaculates. In Study 2, I documented that men who report spending more time performing cunnilingus during their most recent sexual encounter report greater sexual arousal compared to their typical sexual encounters. Cunnilingus may also be more often employed in contexts that present greater sperm competition risk (reviewed in Pham & Shackelford, 2014). Men rate female genital odors that are produced during high-fertility (relative to low-fertility) as more pleasant smelling, experience a testosterone surge, and report greater sexual interest (Cerda-Molina et al., 2013; Doty et al. 1975). Men who report spending more time performing cunnilingus report greater sexual arousal (Pham et al., 2013), and cunnilingus may be related to conception risk and to sperm competition risk (reviewed in Pham & Shackelford 2014). Men who spend more time performing cunnilingus may receive more exposure to copulins—substances excreted by the vagina that may increase male sexual arousal (Juette, 1995; Steinbach et al., 2012). Men typically perform cunnilingus before they copulate and ejaculate (Halpern & Sherman, 1979), suggesting that cunnilingus may influence sexual arousal and consequent sperm competition tactics (e.g., copulatory thrusting, ejaculate adjustment).

Because cunnilingus increases male sexual arousal, and because male sexual arousal is correlated with ejaculate quality, I hypothesize that a man who spends more time performing cunnilingus will produce an ejaculate with greater volume (Hypothesis 1).

The ejaculate adjustment hypothesis of prolonged copulation proposes that men perform prolonged copulations to increase their sexual arousal and consequent ejaculate quality. Men who report their partner to be more sexually attractive (and, therefore, presenting greater sperm competition risk; Goetz et al., 2005) spend more time copulating at the couple's next copulation (Goetz et al., 2005), and men who masturbate to images of more (versus less) attractive women produce higher quality ejaculates (Leivers et al., 2014). Men who spend more time masturbating produce a higher quality ejaculate (Pound et al., 2002). Thus, prolonged copulation may increase sexual arousal and consequent ejaculate volume in a manner predicted by sperm competition theory. Thus, I hypothesize that a man who spends more time copulating will produce an ejaculate with greater volume (Hypothesis 2).

Humans and non-humans perform many behaviors during a single copulatory event (e.g., touching, kissing), each of which may affect male sexual arousal and copulatory behaviors. For example, bats that spend more time performing fellatio (*Cynopterus sphinx*; Tan et al., 2009) or cunnilingus (*Pteropus giganteus*; Maruthupandian & Marimuthu, 2013) spend more time copulating, and similar relationships were documented in Study 2. Therefore, in tests of the hypotheses, I control statistically for the total time the performers spend in physical contact.

I also control statistically for the female participants' age and attractiveness each of which is a cue to female fertility (Buss, 1989)—because males adjust their ejaculate quality as a function of their sexual partner's fertility (Goetz et al., 2005; Leivers et al., 2014). In particular, I focus on *body* attractiveness because body attractiveness (more than face attractiveness) provides information about a woman's current fertility (Confer et al., 2010). Indeed, men prioritize body attractiveness (over face attractiveness) when selecting short-term mating partners (Currie & Little, 2009; Confer et al., 2010)—the very mating context that pornography depicts.

Previous studies on humans that assess the relationship between sexual behavior and ejaculate quality relied on indirect measures of sexual behavior to protect participant privacy (e.g., researchers measure the time participants spend in a private room to indirectly assess the time they spend masturbating: Pound et al., 2002; participants selfreport whether they ejaculated via masturbation or via copulation: Dehghani et al., 2004). To address these limitations, I tested the hypotheses by securing more direct measures of sexual behaviors: Using content analysis of professional pornography scenes, coders assessed the time the male actor spent performing cunnilingus and performing vaginal penetration, the total time the partners spent in physical contact, and visually estimated ejaculate volume.

Method

I conducted a content analysis of professional pornography scenes. I implemented five inclusion criteria for selecting pornography scenes for analysis. First, I included only scenes depicting one man having sex with one woman because the number and sex of performers affect ejaculate quality (Kilgallon & Simmons, 2005). Second, I included only scenes in which the camera presented a clear view of the ejaculate. This criterion excluded scenes in which ejaculation occurred either inside the woman or outside the camera's view, or in which no ejaculation occurred. Third, because ejaculate volume varies between men (WHO, 2010), I selected only scenes starring one man—Bryan Matthew Sevilla (stage name: "James Deen")—for his prolific career in modern mainstream pornography (the Internet Movie Database credits him with 1,140 scenes at the time of data collection; Deen, 2014). Fourth, I included only scenes that began before performers made physical contact, and that ended after ejaculation. Fifth, I included only scenes in which the man did not wear a condom because condoms affect sexual arousal (see MacDonald et al., 2000). To secure scenes starring James Deen, I searched for "James Deen" on websites providing free access to pornography: keezmovies.com, pornhub.com, xnxx.com, xhamster.com, youporn.com, and xvideos.com. To ensure independence of observations, each scene depicted a different actress.

Six coders (two women, four men) coded a total of 100 scenes. All coders were blind to the hypotheses. Five of the six coders independently estimated the volume of the ejaculate (in teaspoons) and two of the six coders recorded the number of seconds the performers spent engaged in cunnilingus, vaginal penetration, and any physical contact. Multiple start-times and stop-times were documented when behaviors occurred more than once in a scene (e.g., actor performed cunnilingus, then performed vaginal penetration, then resumed cunnilingus) and the duration of these activities was summed if they occurred prior to ejaculation. Coders were instructed to estimate the total ejaculate volume by observing the number and quantity of each ejaculatory spurt, as they left the penis and as they appeared after landing. Each coder provided one estimate of ejaculate volume. Nine scenes were excluded because they could not be coded for all variables due to missing data (e.g., scenes were removed from websites during the data collection period), leaving 91 scenes for analyses.

I secured ratings of each actress's body attractiveness from pornstarnetwork.com—a mega-site containing 56 pornography websites and 11,300 pornography scenes (Pornstar Network, 2015). Users submit body attractiveness ratings of individual actresses on a 10-point system (1 = horrible, 10 = perfect). The website displays average ratings of each actress based on hundreds of user-submitted ratings.

I collected data from the Internet Adult Film Database (IAFD.com)—a website containing biographical information for over 100,000 adult performers (IAFD, 2015). For each actress, I recorded the year in which she was born and the year in which her scene was released. Using data from AIFD, I calculated each actress's age by subtracting the year in which the scene was released from the year in which the actress in that scene was born.

I constructed an estimated ejaculate volume variable from the mean of the estimates of ejaculate volume ($\alpha = 0.78$). I constructed three time variables (any physical contact, cunnilingus, penile-vaginal penetration) from the means of the estimates of each of those variables ($\alpha = 0.95$, 0.84, and 0.91, respectively). I used data secured from pornstarnetwork.com to measure each actress's body attractiveness.

I standardized each variable by subtracting the mean of the variable from each of its scores, and then dividing those scores by the variable's standard deviation. To test the hypothesis that a man who spends more time performing cunnilingus will produce an ejaculate with greater estimated volume (Hypothesis 1), I entered simultaneously into a linear multiple regression the age and attractiveness of the actress, the time spent performing cunnilingus, and the time spent in any physical contact (after subtracting from this variable the time spent performing cunnilingus) to predict estimated ejaculate volume. To test the ejaculate adjustment hypothesis for prolonged copulation (Hypotheses 2), I entered simultaneously into a linear multiple regression the age and attractiveness of the actress, the time spent performing vaginal penetration and the time spent in any physical contact (after subtracting from this variable the time spent performing vaginal penetration) to predict estimated ejaculate volume.

Results

Table 4 presents descriptive statistics and zero-order correlations among the key variables. Consistent with Hypothesis 1, when the actor spent more time performing cunnilingus, he produced an ejaculate with greater estimated volume ($\beta = 0.37$, t = 2.32, p < 0.05; see Table 5). Results were inconsistent with Hypothesis 2: When the actor spent more time performing vaginal penetration, he did not produce an ejaculate with greater estimated volume ($\beta = -0.03$, t = -0.25, p = 0.80; see Table 6).

Because of professional video editing, some scenes had interruptions. Such editing may have resulted in inaccurate coding of the target variables. Therefore, I conducted a separate set of analyses in which I excluded all scenes that contained video edited interruptions during sexual activity. After applying this exclusion criterion, I conducted the same analyses described above. Hypothesis 1 remained supported (n = 68, $\beta = 0.33$, t = 2.53, p < 0.05), and Hypothesis 2 remained unsupported (n = 68, $\beta = -0.06$, t= -0.41, p = 0.69).

Discussion

The results of the current research support the hypothesis that a man who spends more time performing cunnilingus produces an ejaculate with greater estimated volume (Hypothesis 1), even after controlling for potential confounds, including the total time the performers spent in physical contact, and the age and attractiveness of the actress. I did not find support for the hypothesis that a man who spends more time copulating will produce an ejaculate with greater estimated volume (Hypothesis 2).

Table 4

	Mean	SD	1.	2.	3.	4.	5.
1. Estimated	2.48	0.64		·····			
ejaculate volume	teaspoons						
2. Physical	1437.11	375.36	-0.02				
contact	seconds						
3. Cunnilingus	87.14	97.38	0.21	0.41**			
	seconds						
4. Penile-vaginal	689.33	324.69	0.02	0.21*	0.32**		
penetration	seconds						
5. Age	25.56 years	6.50	-0.08	0.12	0.26*	-0.00	
6. Attractiveness	9.14	1.07	0.04	-0.03	0.20	0.06	-0.04

Zero-order correlations among key variables.

Note: *n* = 85. **p* < .05, ***p* < .01

Table 5

Multiple regression analysis assessing the relationship between the time spent performing cunnilingus and estimated ejaculate volume, controlling statistically for the total time spent in physical contact and the age and attractiveness of the actress.

β	SE	t	<i>p</i> -value
0.27	0.12	2.32	0.02
-0.14	0.11	-1.27	0.21
-0.03	0.11	-0.23	0.82
-0.12	0.11	-1.12	0.26
	0.27 -0.14 -0.03	0.27 0.12 -0.14 0.11 -0.03 0.11	0.27 0.12 2.32 -0.14 0.11 -1.27 -0.03 0.11 -0.23

 β = standardized beta coefficient, S.E. = standard error of β , t = test statistic associated with β .

Table 6

Multiple regression analysis assessing the relationship between the time spent performing cunnilingus and estimated ejaculate volume, controlling statistically for the total time spent in physical contact and the age and attractiveness of the actress.

	β	SE	t	<i>p</i> -value
Cunnilingus	0.27	0.12	2.32	0.02
Age	-0.14	0.11	-1.27	0.21
Attractiveness	-0.03	0.11	-0.23	0.82
Physical Contact	-0.12	0.11	-1.12	0.26
Physical Contact	-0.12	0.11	-1.12	

 β = standardized beta coefficient, S.E. = standard error of β , t = test statistic associated with β .

An alternative hypothesis for prolonged copulation is that men perform prolonged copulations to spend more time displacing rival semen that may be in a woman's reproductive tract (Goetz et al., 2005). Gallup et al. (2003) used artificial genitals and artificial semen and provided evidence that the shape of the human penis facilitates semen-displacement from the vagina during copulatory thrusting. Goetz et al. (2005) found that men who perceive their partner to be more attractive (i.e., presenting greater sperm competition risk) perform more semen-displacement copulatory behaviors (e.g., deeper, more vigorous copulatory thrusts), including prolonged copulations. Although the results of the current research did not support the ejaculate adjustment hypothesis for prolonged copulation, future research can extend the results of Goetz et al. by conducting a content analysis of amateur pornography to assess whether men who copulate with a more attractive woman also spend more time copulating with her.

The current research is guided by a male perspective because male sexual arousal mediates the relationship between copulatory behaviors and ejaculate quality. However, women play significant roles in copulatory behavior. For example, men perform cunnilingus to satisfy a woman upon her request (Backstrom et al., 2012), and women can determine the duration of copulation depending on the sexual position (e.g., when a woman is mounted on top of a man). Women also have reproductive interests in their partner's ejaculate quality. When women's interests and men's interests are aligned (i.e., sexual cooperation), women may benefit from their partner's higher quality ejaculate (e.g., when a couple is attempting to conceive). Thus, the results of the current research should be interpreted not as the exclusive product of a male strategy, but instead as the

product of male and female sexual strategies that are variably in conflict or cooperation (see Shackelford & Goetz, 2012).

Professional pornography—in contrast with amateur pornography—uses superior camerawork and, therefore, produces higher-quality video of ejaculations. However, producers and directors of professional pornography may dictate the time professional actors spend performing sexual behaviors. Thus, the duration of sexual behaviors in professional pornography may not accurately reflect the duration of these behaviors in normal, natural circumstances. However, because ejaculate adjustment is an autonomic reflex—unconsciously controlled by the male sexual response cycle (Jones & Lopez, 2013)—the relationships between sexual behaviors and estimated ejaculate volume documented in the current research might be generalizable to normal, natural circumstances. Nevertheless, future research might attempt to replicate results of the current research using content analyses of amateur pornography.

There is significant variation in ejaculate quality between men (WHO, 2010). I controlled for this confound by conducting the current study on only one man. However, we should be cautious when generalizing these results to other men. Future research could conduct a content analysis on pornography in which each scene depicts a different man.

A limitation of the current research is reliance on visual estimates rather than actual assessments of ejaculate volume. However, the hypotheses (e.g., time spent performing cunnilingus is positively correlated with ejaculate volume) depend only on reliable estimates of volume—not on the accuracy of ejaculate volume estimates. In other words, it is irrelevant whether coders correctly identified ejaculate volumes in teaspoons, only that they correctly identified the relative differences in ejaculate volumes between scenes. The independent coders achieved reasonable inter-rater agreement in estimating ejaculate volume ($\alpha = 0.78$), indicating that these estimates can be made with sufficient reliability to warrant inclusion in empirical analyses. Nevertheless, future research could secure motion-capture video of participants during copulation to directly measure sexual behavior, and could collect the ejaculate (e.g., via condom) produced from that copulation to directly measure ejaculate volume.

I could not determine when the actor last ejaculated before each scene. The duration of abstinence is consistently one of the strongest predictors of ejaculate volume (WHO, 2010). Indeed, in studies that investigate the strategic adjustments in ejaculate quality, participants are instructed to abstain for at least 48 hours prior to submitting their ejaculates for analysis (Joseph et al., 2015; Kilgallon & Simmons, 2005; Leivers et al., 2014) Future replications of the current research could secure information about the most recent ejaculation prior to each copulation to increase the explanatory power of the models.

Humans are less dependent on chemosensory systems than are other primates (Gilad et al., 2003). Although I argue that cunnilingus is an adaptation in humans, it is possible that the relationship between cunnilingus and ejaculate quality in humans may be remnants of adaptations found in species closely related to humans (i.e., byproducts of phylogeny). Future research should replicate this study using non-human primate samples (e.g., using naturalistic observations of sexual behavior).

The quality of men's masturbatory ejaculates are dependent on several features of the pornography they consume, including cues to sperm competition (Kilgallon &

Simmons, 2015) and the actress's mate value (Leivers et al., 2014). Future research could extend our findings by investigating whether men produce different quality ejaculates depending on whether cunnilingus is depicted in the pornography they consume.

Variation in quality between ejaculates has been historically interpreted by andrologists as "noise," with the WHO (2010) recommending that clinicians secure two or three ejaculates from a man to determine his "true" fertility. However, a growing body of research indicates that men strategically adjust their ejaculates (reviewed in Pham & Shackelford, 2014)—including adjustments in non-sperm chemicals that affect fertilizing success (Burch & Gallup, 2006; Davis & Gallup, 2006). The current research contributes to this literature by documenting that men's pre-ejaculatory sexual behavior may affect ejaculate quality. Further, the current research contributes data from humans to the substantial non-human literature documenting that copulatory behaviors that do not contribute directly to reproduction contribute indirectly to reproduction by affecting sexual arousal and consequent ejaculate quality. Finally, the current research is the first to document a relationship between the time spent performing cunnilingus and ejaculate quality.

CHAPTER 4

STUDY 4

Female infidelity has been documented in dozens of cultures worldwide, and some published samples estimate that as many as 70% of women have committed infidelity at least once in their lifetime (Allen & Baucom, 2006; Buss, 1994; Schmitt, 2003; Wiederman & Hurd, 1999). Men who suspect or discover their partner's infidelity may suffer from physical and psychological problems, including major depression, anxiety, and relationship dissatisfaction (Cano & Leary, 2000; Betzig, 1989).

Men perform "mate retention" behaviors to reduce the likelihood of their partner's infidelity. Buss (1988) identified 19 mate retention "tactics" that range from subtle to overt (see Table 1). Buss organized these tactics into five "categories": Direct Guarding, Intersexual Negative Inducements, Intrasexual Negative Inducements, Positive Inducements, and Public Signals of Possession. Direct Guarding includes behaviors such as vigilance about one's partner's whereabouts and concealment of one's partner (e.g., "I called at unexpected times to see who my partner was with"). Intersexual Negative Inducements include behaviors that manipulate and derogate one's partner (e.g., "I threatened to harm myself if my partner ever left me"). Intrasexual Negative Inducements include behaviors intended to deter same-sex rivals from pursuing one's partner (e.g., "I told others my partner was a pain"). Positive Inducements include behaviors that increase the appeal of the current relationship to one's partner (e.g., "I bought my partner an expensive gift"). Public Signals of Possession include behaviors that display to others that one's relationship is exclusive and committed (e.g., "I held my partner's hand when others of my same sex were around").

Miner, Starratt, and Shackelford (2009) organized the five categories into two superordinate "domains"- cost-inflicting mate retention behaviors and benefitprovisioning mate retention behaviors. Direct Guarding, Intersexual Negative Inducements, and Intrasexual Negative Inducements comprise the cost-inflicting domain. Behaviors in this domain reduce the risk of partner infidelity by lowering one's partner's self-esteem, thereby causing her to feel undeserving of her current partner but especially of any other partner (Miner et al., 2009). In contrast, Positive Inducements and Public Signals of Possession comprise the benefit-provisioning domain. Behaviors in this domain reduce the risk of partner infidelity by increasing one's partner's relationship satisfaction (Miner et al., 2009).

Men may perform oral sex on their partner as a means of mate retention. The results of Study 1 document that men at greater risk of partner infidelity report greater interest in and spend more time performing oral sex on their partner. In contrast, men do not typically perform oral sex on a woman during a casual, sexual encounter (i.e. "a one night stand"; Backstrom et al., 2012; Lewis, Granato, Blayney, Lostutter, & Kilmer, 2011; Reiber & Garcia, 2010), a mating context that presents no risk of long-term partner infidelity. I hypothesize that men perform oral sex on their partner as a mate retention behavior. Specifically, I predict that men who report performing more mate retention behaviors, in general, will report greater interest in (Prediction 1) and spend more time performing (Prediction 2) oral sex on their partner.

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Oral sex may be a *benefit-provisioning* mate retention behavior. Miner et al. (2009) documented that men at greater risk of partner infidelity performed more benefitprovisioning mate retention behaviors, but *not* more cost-inflicting mate retention behaviors. Women who receive oral sex from their partner, relative to those who do not, report greater relationship satisfaction (Kaestle & Halpern, 2007; Santtila et al., 2008). Because greater partner relationship satisfaction is an outcome of benefit-provisioning mate retention, I hypothesize that men perform oral sex on their partner as part of a benefit-provisioning mate retention strategy. Specifically, I predict that men who report performing more benefit-provisioning mate retention behaviors, but *not* more costinflicting mate retention behaviors, will report greater interest in (Prediction 3) and spend more time performing (Prediction 4) oral sex on their partner.

Method

Participants

Three hundred and fifty-one men in a committed, sexual, heterosexual relationship participated in exchange for extra credit in a course. The mean participant age was 24.2 years (SD = 7.2) and the mean relationship length was 36.3 months (SD = 51.6).

Materials

Participants reported their age and current relationship length on a questionnaire. Participants completed the Mate Retention Inventory, which assesses performance of 104 mate retention behaviors (see Buss, 1988). On a scale from 0-3, participants reported how frequently they performed each behavior within the past month (0 = Never performed this act, 1 = Rarely performed this act, 2 = Sometimes performed this act, 3 = Often performed this act).

Participants answered questions about their most recent sexual encounter with their partner on a 0-9 scale: own interest in performing oral sex (0 = Less interested or excited than is typical for me, 9 = More interested or excited than is typical for me), and duration of oral sex (0 = Less time than is typical for me, 9 = More time than is typical for me).

Procedures

Potential male participants were recruited by word-of-mouth, flyers posted on campus bulletin boards, and announcements in psychology courses. Approximately 20-30 potential participants arrived to a laboratory where they were asked if they were at least 18 years of age and in a heterosexual committed relationship. Those who qualified received a consent form and a questionnaire packet to take home, so that they could privately provide their responses. At a time of their choosing, participants placed their signed consent form and completed questionnaire in separately sealed envelopes, and placed each in designated collection boxes—one box was dedicated to consent forms, and the other to questionnaires. The research team would periodically retrieve several completed questionnaires from these boxes.

Results

Following Buss (1988), I constructed 19 mate retention tactic variables from scores on the Mate Retention Inventory. I correlated scores for each mate retention tactic with scores on the two oral sex variables (see Table 7). Men who reported greater interest

Table 7

Mate retention tactics	Oral sex variables		Mate retention tactics	Oral sex variables	
	Interest	Duration		Interest	Duration
Vigilance	.00	.00	Violence	.05	.10
Concealment of	02	.04	Intrasexual Threats	.11*	.11*
Mate					
Monopolize Mate's	.03	02	Verbal Signals of	.24**	14**
Time			Possession		
Enhance Physical	.08	.11*	Physical Signals of	.22**	.12*
Appearance			Possession		
Punish Mate's	01	.08	Possessive	.18**	.10
Threat to Infidelity			Ornamentation		
Emotional	.08	.03	Derogation of	.10	.05
Manipulation			Competitors		
Commitment	.12*	.15*	Submission and	.10	.08
Manipulation			Debasement		
Derogation of Mate	04	02	Expressions of Love	.20**	.08
to Competitors			and Caring		
Resource Display	.11*	.14**	Threaten Infidelity	10	.00
Sexual Inducements	.12*	.12*			

Correlations between the two target oral sex variables and the 19 mate retention tactics.

n = 351 men. *p < .05, **p < .01

in performing oral sex on their partner also reported greater use of Intrasexual Threats, Resource Display, Sexual Inducements, Commitment Manipulation, Verbal Signals of Possession, Physical Signals of Possession, Possessive Ornamentation, and Expressions of Love and Care. Men who reported spending more time performing oral sex on their partner also reported greater use of Intrasexual Threats, Enhance Physical Appearance, Commitment Manipulation, Resource Display, Sexual Inducements, Verbal Signals of Possession, and Physical Signals of Possession.

Following Miner et al. (2009), I constructed a *benefit-provisioning mate retention* variable from the sum of responses to the items in the Positive Inducements and Public Signals of Possession categories ($\alpha = .92$). Also following Miner et al., I constructed a *cost-inflicting mate retention* variable from the sum of responses to the items in the Direct Guarding, Intersexual Negative Inducements, and Intrasexual Negative Inducements categories ($\alpha = .92$). I correlated scores on these two mate retention domains with responses on the two oral sex variables. Consistent with Predictions 3 and 4, men who reported performing more benefit-provisioning mate retention behaviors, but *not* more cost-inflicting mate retention behaviors, also reported greater interest in and spent more time performing oral sex on their partner (see Table 8).

Finally, I entered the *benefit-provisioning mate retention* and *cost-inflicting mate retention* variables into multiple regression equations to identify the unique effect each mate retention domain has on each of the two oral sex variables. Consistent with Predictions 3 and 4, men who reported performing more benefit-provisioning mate retention behaviors, but *not* more cost-inflicting mate retention behaviors, also reported greater interest in and spent more time performing oral sex on their partner (see Table 9).

Table 8

Correlations between scores on the two target oral sex variables with scores on five mate retention categories, two mate retention domains, and overall mate retention behaviors.

	Oral sex variables		
	Interest in performing	Duration of oral	
	oral sex	sex	
Mate retention categories			
Direct Guarding	.01	.00	
Intersexual Negative Inducements	.05	.07	
Intrasexual Negative Inducements	.06	.09	
Positive Inducements	.16**	.14**	
Public Signals of Possession	.26**	.15**	
Mate retention domains			
Benefit-provisioning	.23**	.16**	
Cost-inflicting	.04	.05	
Overall mate retention behaviors	.13*	.11*	

n = 351 men. *p < .05, **p < .01

Table 9

Multiple regression analyses assessing relationships between the two mate retention
domains (benefit-provisioning and cost-inflicting) and the two oral sex variables.

	Mate retention domains				
	Benefit-provisioning		Cos	st-inflicting	
Outcome variable	В	t	В	t	
Interest in performing	.12	4.85***	04	-2.25*	
oral sex					
Duration of oral sex	.08	2.93**	02	94	

n = 351 men. *p < .05, **p < .01, ***p < .001

B = unstandardized beta coefficient, t = test statistic associated with B

Discussion

The results are consistent with the hypothesis that men perform oral sex on their partner as part of a broader benefit-provisioning mate retention strategy. Men who report performing more mate retention behaviors, in general, and more benefit-provisioning mate retention behaviors, in particular, report greater interest in and spend more time performing oral sex on their partner.

The multiple regression analyses indicate that men who perform more costinflicting mate retention behaviors report *less* interest in performing oral sex on their partner. Although I did not predict this relationship, this result is consistent with previous research documenting that the frequency with which men perform benefit-provisioning behaviors is correlated *negatively* with their cost-inflicting behaviors (Miner et al., 2009). Men who provision their partner with benefits must expend resources (e.g., "I bought my partner an expensive gift"). In contrast, men who inflict costs on their partner expend fewer resources, but the costs men inflict on their partner may lower her relationship satisfaction and cause her to terminate the relationship. Therefore, men who have the resources to provision their partner with benefits also tend to avoid the risks associated with inflicting costs on her.

A limitation of the current study is the use of men's self-reports of their mate retention behaviors. Men may underreport the frequency with which they perform socially undesirable behaviors (e.g., "I told others of my same sex that my partner might have a sexually transmitted disease"). However, Shackelford, Goetz, and Buss (2005) documented that both men's and women's self-reports of their mate retention behaviors are positively correlated with their partner's reports of these behaviors. Nevertheless, future research may benefit from securing data from both men's self-reports and their partner's reports of men's mate retention behaviors.

The Mate Retention Inventory (Buss, 1988) assesses the frequency with which men perform various mate retention behaviors *within the past month*. I asked about men's oral sex behaviors during their *most recent copulation* to ensure that they best remembered the details of, and therefore reported most accurately, their oral sex behaviors. Future research investigating the relationship between men's mate retention behaviors and their oral sex behaviors may consider securing men's reports of their oral sex behaviors across multiple copulations *within the past month*, to ensure that measures of mate retention and oral sex assess behaviors that occur during the same time span. An evolutionary perspective provides a useful framework for researching infidelity. For example, men are more upset than woman about their partner's sexual infidelity (Buss et al., 1992; Shackelford & Goetz, 2012). Women but not men who commit sexual infidelity impose reproductive costs on their partner in the form of cuckoldry—the unwitting investment of time and resources into offspring to whom their partner is genetically unrelated. Future research investigating the function of oral sex as a mate retention behavior would profit from adopting an evolutionary perspective by assessing sex differences in oral sex behaviors as a consequence of perceived risk of partner sexual infidelity.

In conclusion, men perform a diverse array of behaviors designed to minimize the risk of their partner's infidelity. Men may appease, threaten, conceal, or emotionally manipulate their partner to dissuade her from committing infidelity (Buss, 1988). The current study provides preliminary support for the hypothesis that oral sex is part of a broader benefit-provisioning male mate retention strategy.

CONCLUSION

The results of the current research support the broader hypothesis that men perform cunnilingus as part of an anti-cuckoldry strategy. Specifically, men may perform cunnilingus to estimate partner infidelity risk (Study 1), to increase their sexual arousal and consequent ejaculate quality (Studies 2 and 3), and to minimize partner infidelity risk (Study 4).

Studies 1, 2, and 4 relied on men's self-reports of their past sexual behaviors. However, much research demonstrates that observer-reported sexual behaviors corroborate self-reported sexual behaviors—even when participants recall specific behaviors several months later (Allgeier & Allgeir, 2000; Crooks & Bauer, 2002; Hyde & DeLamater, 2003; Masters & Johnson, 1966; reviewed in Goetz et al., 2005). To ensure that men most accurately recalled the details of that encounter, I asked participants to recall their behaviors during their most recent sexual encounter. Nevertheless, future research could secure motion-capture video of participants during copulation to directly measure sexual behavior.

I cannot make strong conclusions about causation, given the correlational designs of these studies. For example, the results of the current research might be explicable, in part, as a consequence of men's personality traits. Men who are more altruistic and agreeable, for example, might be at lesser partner infidelity risk, more likely to provision their partner with benefits, more likely to experience heightened sexual arousal, and more likely to perform oral sex. The relationship between men's infidelity risk and their oral sex behaviors, therefore, may be spurious. Future research can assess whether priming men with thoughts of partner infidelity will influence their sexual behaviors.

In several non-human species, males lick and sniff a female's genitals (i.e., oral sex) to assess her fertility status. Males spend more time sniffing and licking the genitals of estrus (vs. non-estrus) females (Dunbar, 1977; Johnston, 1974; Kiddy, Mitchell, Bolt, and Hawk, 19878; Murphy, 1973; Nishimura, Utsumi, Okano, and Iritani, 1991; Palagi et al., 2003; Sankar and Archunan, 2004; Soini, 1987). Male cotton-top tamarins (*Saguinus Oedipus*) that smell a female's scent marks produced at high-fertility—relative to at low-fertility—experience more frequent penile erections and perform more mounting behaviors (Ziegler et al., 1993). Thus, cunnilingus may be a fertility-detection behavior in non-human species.

Indirect evidence suggests that cunnilingus also may be a fertility-detection behavior in humans. Haselton and Gildersleeve (2011) review evidence suggesting that men can detect their partner's fertility status and adjust accordingly their anti-cuckoldry tactics. Men perform more frequently behaviors to reduce the likelihood of their partner's infidelity when she is at high fertility relative to low fertility (Gangestad, Thornhill, & Garver-Apgar, 2002), and less attractive men (i.e., those at greater sperm competition risk; Gangestad et al., 2002) are more jealous and possessive when their partner is at high fertility relative to low fertility (Haselton & Gangestad, 2006). Cerda-Molina et al., (2013) found that men who smell vaginal odors produced at high-fertility (relative to low-fertility) also experience a surge in testosterone and report greater copulatory interest. Because previous research has identified olfactory mechanisms by which men detect women's fertility status (Thornhill et al., 2003), and because men report preferring the scent of vaginal fluid produced during high fertility relative to low fertility (Doty, 1975), men's oral sex behaviors may also function to gather information about their partner's health and fertility status. A fertility detection function of oral sex also is consistent with the broader hypothesis that men perform oral sex as an anti-cuckoldry tactic. Future research could investigate this function of oral sex by assessing men's oral sex behaviors, their partner's fertility status, and her age—given that her age affects her fertility (e.g., menopause).

In conclusion, men perform a diverse array of behaviors to minimize cuckoldry risk, ranging from pre-copulatory behaviors (e.g., mate retention tactics) to postcopulatory behaviors (e.g., sperm competition tactics). The current research adds to this growing body of literature by documenting that cunnilingus is also an anti-cuckoldry behavior.

APPENDIX

APPROVAL LETTER FROM THE HUMAN SUBJECTS INSTITUTIONAL REVIEW BOARD



Institutional Review Board for the Protection of Human Subjects

DATE:	September 21, 2015
TO:	Michael Pham
FROM:	Oakland University IRB
PROJECT TITLE:	The Evolutionary Psychology of Oral Sex
REFERENCE #:	800548-1
SUBMISSION TYPE:	New Project
ACTION:	DETERMINATION OF EXEMPT STATUS
DECISION DATE:	September 21, 2015
REVIEW CATEGORY:	Exemption category # 4

Thank you for your submission of New Project materials for this project. The Oakland University IRB has determined this project is EXEMPT FROM IRB REVIEW according to federal regulations.

The exemption is made with the understanding that NO CHANGES may be made in the procedures to be followed until such changes have been reviewed and approved by the IRB. Please use the "Protocol Amendment" form found in IRBNet to submit any proposed changes to the IRB. Do not collect data while the proposed changes are being reviewed. Data collected during this time cannot be used.

Please retain a copy of this correspondence for your record.

If you have any questions, please contact Stephanie Edwards at (248) 370-4329 or sedwards@oakland.edu. Please include your project title and reference number in all correspondence with this committee.

This letter has been electronically signed in accordance with all applicable regulations, and a copy is retained within Oakland University IRB's records.

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REFERENCES

- Allgeier, E. R., & Allgeier, A. R. (2000). Sexual interactions (5th ed.). Boston: Houghton Mifflin.
- Allen, E. S., & Baucom, D. H. (2006). Dating, marital, and hypothetical extradyadic involvements: How do they compare? *The Journal of Sex Research*, 43, 307-317.
- Anderson, K. (2006). How well does paternity confidence match actual paternity?. *Current Anthropology*, 47, 513-520.
- Angulo, J., & García, M. (2005). Sex in stone: Sexuality, reproduction, and eroticism in the Paleolithic epoch. Madrid: Luzán, 5.
- Backstrom, L., Armstrong, E. A., & Puentes, J. (2012). Women's negotiation of cunnilingus in college hookups and relationships. *Journal of Sex Research*, 49, 1-12.
- Baker, R. R., & Bellis, M. A. (1993a). Human sperm competition: ejaculate adjustment by males and the function of masturbation. *Animal Behaviour, 46*, 861–885.
- Baker, R. R., & Bellis, M. A. (1993b). Human sperm competition: Ejaculate manipulation by females and a function for the female orgasm. *Animal Behaviour*, 46, 887–909.
- Baker, R. R., & Bellis, M. A. (1995). Human sperm competition: Copulation, masturbation and infidelity. New York: Springer.
- Barrett, H. C., & Kurzban, R. (2006). Modularity in cognition: framing the debate. *Psychological Review*, 113, 628-647.
- Bellis, M. A., Hughes, K., Hughes, S., & Ashton, J. R. (2005). Measuring paternal discrepancy and its public health consequences. *Journal of Epidemiology and Community Health*, 59, 749-754.
- Betzig, L. (1989). Causes of conjugal dissolution: A cross-cultural study. Current Anthropology, 30, 654-676.
- Birkhead, T. R. & Møller, A. P., (Eds.). (1998). Sperm competition and sexual selection. London: Academic Press.

- 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: Evolutionary perspectives on male anti-cuckoldry tactics* (pp. 141-172). New York: Cambridge University Press.
- Buss, D. M. (1988). From vigilance to violence: Tactics of mate retention in American undergraduates. *Ethology and Sociobiology*, 9, 291-317.
- Buss, D. M. (1994). *The evolution of desire: Strategies of human mating*. New York: Basic Books.
- Buss, D. M. (2002). Human mate guarding. Neuroendocrinology Letters, 23, 23-29.
- Buss, D. M., Larsen, R. J., Westen, D., & Semmelroth, J. (1992). Sex differences in jealousy: Evolution, physiology, and psychology. *Psychological Science*, 3, 251-255.
- Buss, D. M., & Schmitt, D. P. (1993). Sexual Strategies Theory: An evolutionary perspective on human mating. *Psychological Review*, 100, 204-232.
- Buss, D. M., & Shackelford, T. K. (1997). From vigilance to violence: mate retention tactics in married couples. *Journal of Personality and Social Psychology*, 72, 346-361.
- Buss, D. M., Shackelford, T. K., Kirkpatrick, L. A., Choe, J. C., Lim, H. K., Hasegawa, M., ... & Bennett, K. (1999). Jealousy and the nature of beliefs about infidelity: Tests of competing hypotheses about sex differences in the United States, Korea, and Japan. *Personal Relationships*, 6, 125-150.
- Buunk, B. P., Angleitner, A., Oubaid, V., & Buss, D. M. (1996). Sex differences in jealousy in evolutionary and cultural perspective: Tests from the Netherlands, Germany, and the United States. *Psychological Science*, 7, 359-363.
- Camilleri, J. A., & Quinsey, V. L. (2009). Testing the cuckoldry risk hypothesis of partner sexual coercion in community and forensic samples. *Evolutionary Psychology*, 7, 164-178.
- Cano, A., & O'Leary, K. D. (2000). Infidelity and separations precipitate major depressive episodes and symptoms of nonspecific depression and anxiety. *Journal* of Consulting and Clinical Psychology, 68, 774-783.
- Carballo-Diéguez, A., Remien, R. H., Dolezal, C., & Wagner, G. (1999). Reliability of sexual behavior self-reports in male couples of discordant HIV status. *Journal of Sex Research*, 36, 152-158.

- Cerda-Molina, A. L., Hernández-López, L., de la O, C. E., Chavira-Ramírez, R., and Mondragón-Ceballos, R. (2013). Changes in men's salivary testosterone and cortisol levels, and in sexual desire after smelling female axillary and vulvar scents. *Frontiers in Endocrinology*, 4, 1-9.
- Cordero, A. (1990). The adaptive significance of the prolonged copulations of the damselfly, *Ischnura graellsii* (Odonata: Coenagrionidae). *Animal Behaviour*, 40, 43-48.
- Crooks, R. L., & Baur, K. (2002). *Our sexuality* (8th ed.). Pacific Grove, CA: Brooks/Cole.
- Davies, N. B. (1983). Polyandry, cloaca-pecking and sperm competition in dunnocks. *Nature*, *302*, 334-336.
- Davis, J. A., & Gallup, G. G. (2006). Preeclampsia and other pregnancy complications as an adaptive response to unfamiliar semen. In S. M. Platek & T. K. Shackelford (Eds.), *Female infidelity and paternal uncertainty* (pp. 191-204). New York: Cambridge University Press.
- Dehghani, V. A., Khalili, M. A., Khalili, M. A., Zamani, N., & Dreh-Zereshki, F. (2004). Comparison between semen parameters of ejaculates collected via masturbation versus coitus interruptus. Iranian Journal of Reproductive Medicine, 2, 9-11.
- Dickinson, J. L. (1986). Prolonged mating in the milkweed leaf beetle *Labidomera clivicollis clivicollis* (Coleoptera: Chrysomelidae): A test of the "sperm-loading" hypothesis. *Behavioral Ecology and Sociobiology*, 18, 331-338.
- Doty, R. L., Ford, M., Preti, G., & Huggins, G. R. (1975). Changes in the intensity and pleasantness of human vaginal odors during the menstrual cycle. *Science*, 190, 1316-1318.
- Dugmore, S. J., Bailey, K., & Evans, C. S. (1984). Discrimination by male ring-tailed lemurs (*Lemur catta*) between the scent marks of male and those of female conspecifics. *International Journal of Primatology*, 5, 235–245.
- Dunbar, I. F. (1977). Olfactory preferences in dogs: the response of male and female beagles to conspecific odors. *Behavioral Biology*, 20, 471-481.
- Eberhard, W. G. (1996). *Female control: Sexual selection by cryptic female choice*. Princeton, NJ: Princeton University Press.
- Fernandez, A. M., Sierra, J. C., Zubeidat, I., & Vera-Villarroel, P. (2006). Sex differences in response to sexual and emotional infidelity among Spanish and Chilean students. *Journal of Cross-Cultural Psychology*, 37, 359-365.

- Gallup, G. G., & Burch, R. L. (2004). Semen displacement as a sperm competition strategy in humans. *Evolutionary Psychology*, 2, 12-23.
- Gallup, G. G., Burch, R. L., & Mitchell, T. J. B. (2006). Semen displacement as a sperm competition strategy. *Human Nature*, 17, 253-264.
- 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.
- Gangestad, S. W., Thornhill R, & Garver-Apgar, C. E. (2002). Changes in women's sexual interests and their partner's mate-retention tactics across the menstrual cycle: Evidence for shifting conflict of interest. *Proceedings of the Royal Society Biological Sciences*, 269, 975-982.
- Georgiadis, J. R., & Holstege, G. (2005). Human brain activation during sexual stimulation of the penis. *Journal of Comparative Neurology*, 493, 33-38.
- 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.
- 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, 119-123.
- 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.
- Guadamuz, T. E., Kunawararak, P., Beyrer, C., Pumpaisanchai, J., Wei, C., & Celentano,
 D. D. (2010). HIV prevalence, sexual and behavioral correlates among Shan, Hill
 tribe, and Thai male sex workers in Northern Thailand. *AIDS Care*, 22, 597-605.
- Halata, Z., & Munger, B. L. (1986). The neuroanatomical basis for the protopathic sensibility of the human glans penis. *Brain Research*, 371, 205-230.
- Halpern, J., & Sherman, M. A. (1979). *Afterplay: A key intimacy.* New York: Pocket Books.
- Haselton, M. G., & Gildersleeve, K. (2011). Can men detect ovulation? *Current Directions in Psychological Science*, 20, 87-92.
- Hewlett, B. S., & Hewlett, B. L. (2010). Sex and searching for children among Aka foragers and Ngandu farmers of central Africa. *African Study Monographs*, 31, 107-125.

- Huang, A. L., Chen, X., Hoon, M. A., Chandrashekar, J., Guo, W., Tränkner, D, ... & Zuker, C. S. (2006). The cells and logic for mammalian sour taste detection. *Nature*, 442, 934-938.
- Hyde, J. S., & DeLamater, J. (2003). Understanding human sexuality (8th ed.). Boston: McGraw-Hill.
- Iwawaki, S., & Wilson, G. D. (1983). Sex fantasies in Japan. Personality and Individual Differences, 4, 543-545.
- James Deen [Internet]. Seattle (WA): IMDb. [Cited 2014 July 29]. Available from: http://www.imdb.com/name/nm1776976/
- Johnston, R. E. (1974). Sexual attraction function of golden hamster vaginal secretion. Behavioral Biology, 12, 111-117.
- Joseph, P. N., Sharma, R. K., Agarwal, A., & Sirot, L. K. (2015). Men ejaculate larger volumes of semen, more motile sperm, and more quality when exposed to images of novel women. *Evolutionary Psychological Science*, 1, 195-200.
- Juette A. (1995). Weibliche Pheromone Wirkung und Rolle von synthetischen "Kopulinen" bei der versteckten Ovulation des Menschen (Unpublished doctoral dissertation). University of Vienna, Vienna, Austria.
- Kennair, L. E. O., Nordeide, J., Andreassen, S., Stronen, J., & Pallesen, S. (2015). Sex differences in jealousy: A study from Norway. Nordic Psychology, 63, 20-34.
- Kaestle, C. E., & Halpern, C. T. (2007). What's love got to do with it? Sexual behaviors of opposite-sex couples through emerging adulthood. *Perspectives on Sexual and Reproductive Health*, 39, 134-140.
- Kilgallon, S. J., & Simmons, L. W. (2005). Image content influences men's semen quality. *Biology Letters*, 1, 253-255.
- Kiddy, C. A., Mitchell, D. S., Bolt, D. J., & Hawk, H. W. (1978). Detection of estrusrelated odors in cows by trained dogs. *Biology of Reproduction*, 19, 389-395.
- Koyama, N. (1988) Mating behavior of ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. *Primates*, 29, 163–175.
- Laumann, E. O., Gagnon, J. H., Michael, R. T., & Michaels, S. (1992). *National Health* and Social Life Survey [Data set]. Retrieved from http://popcenter.uchicago.edu/data/nhsls.shtml
- Leichliter, J. S., Chandra, A., Liddon, N., Fenton, K. A., & Aral, S. O. (2007). Prevalence and correlates of heterosexual anal and oral sex in adolescents and adults in the United States. *The Journal of Infectious Diseases, 196*, 1852-1859.

- 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.
- Lewis, M. A., Granato, H., Blayney, J. A., Lostutter, T. W., & Kilmer, J. R. (2012). Predictors of hooking up sexual behaviors and emotional reactions among U. S. college students. *Archives of Sexual Behavior*, 41, 1219-1229.
- Lurie, P., Eugenia, M., Fernandes, L., & Hughes, V. (1995). Socioeconomic status and risk of HIV-1, syphilis and hepatitis B infection among sex workers in São Paulo State, Brazil. *AIDS*, 9, 31-37.
- MacDonald, T. K., MacDonald, G., Zanna, M. P., & Fong, G. (2000). Alcohol, sexual arousal, and intentions to use condoms in young men: Applying alcohol myopia theory to risky sexual behavior. *Health Psychology*, 19, 290-298.
- Malamuth, N. M. (1996). Sexually explicit media, gender differences, and evolutionary theory. *Journal of Communication*, 46, 8-31.
- Mauras, N., Bell, J., Snow, B. G., & Winslow, K. L. (2005). Sperm analysis in growth hormone-deficient adolescents previously treated with an aromatase inhibitor: Comparison with normal controls. *Fertility and Sterility*, 84, 239-242.
- Maruthupandian, J., & Marimuthu, G. (2013). Cunnilingus apparently increases duration of copulation in the Indian flying fox, *Pteropus giganteus*. *PloS One*, *8*, e59743.
- Masters, W. H., & Johnson, V. E. (1966). *Human sexual response*. Boston: Little, Brown, & Co.
- 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 Human (*Homo sapiens*). Journal of Comparative Psychology, 125, 370-373.
- Miller, S. L., & Maner, J. K. (2009). Scent of a woman men's testosterone responses to olfactory ovulation cues. *Psychological Science*, 21, 276-283.
- Miner, E. J., Starratt, V. G., & Shackelford, T. K. (2009). It's not all about her: Men's mate value and mate retention. *Personality and Individual Differences*, 47, 214-218.
- Murphy, M. R. (1973). Effects of female hamster vaginal discharge on the behavior of male hamsters. *Behavioral Biology*, 9, 367-375.
- Nakano, K. (2014, December 3). http://www.tokyoreporter.com/2014/12/03/hitting-theskids-the-demise-of-japans-used-underwear-trade/. Retrieved November 1, 2015.

- Nishimura, K., Utsumi, K., Okano, T., & Iritani, A. (1991). Separation of mountinginducing pheromones of vaginal mucus from estrual heifers. *Journal of Animal Science*, 69, 3343-3347.
- O'Connor, T. J., Kinchington, D., Kangro, H. O., & Jeffries, D. J. (1995). The activity of candidate virucidal agents, low pH and genital secretions against HIV-1 in vitro. *International journal of STD & AIDS*, 6, 267-272.
- Palagi, E., Paoli, T., & Tarli, S. B. (2004). Reconciliation and consolation in captive Bonobos (*Pan paniscus*). *American Journal of Primatology*, 62, 15-30.
- Palagi, E., Telara, S. M., & Borgognini, T. (2003). Sniffing behavior in *Lemur catta*: Seasonality, sex, and rank. *International Journal of Primatology*, 24, 335-350.
- Parker, G. G. (1970). Sperm competition and its evolutionary consequences in the insects. *Biological Review*, 45, 525-567.
- Pennington, J. A., Albright, J. L. & Callahan, C. J. (1986). Relationship of sexual activities in estrous cows to different frequencies of observation and pedometer measurements. *Journal of Dairy Science*, 69, 2925-2934.
- Pham, M. N., & Shackelford, T. K. (2013a). Oral sex as infidelity-detection. *Personality* and Individual Differences, 54, 792-795.
- Pham, M. N., & Shackelford, T. K. (2013b). Oral sex as mate retention behavior. Personality and Individual Differences, 55, 185-188.
- Pham, M. N., & Shackelford, T. K. (2013c). 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.
- Pham, M. N., & Shackelford, T. K. (2014). Human sperm competition: A comparative evolutionary analysis. *Animal Behavior and Cognition*, 1, 410-422.
- Pham, M. N., Shackelford, T. K., Welling, L. L. M., Ehrke, A. D., Sela, Y., & Goetz, A. T. (2013). Oral sex, semen displacement, and sexual arousal: Testing the ejaculate adjustment hypothesis. *Evolutionary Psychology*, 11, 1130-1139.
- Pound, N. (2002). Male interest in visual cues of sperm competition risk. *Evolution and Human Behavior*, 23, 443-446.
- 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 and Behavior*, 76, 685-689.

- Reiber, C., & Garcia, J. R. (2011). Hooking up: Gender differences, evolution, and pluralistic ignorance. *Evolutionary Psychology*, *8*, 390-404.
- Ridley, J. (2015, August 16). Http://nypost.com/2015/08/16/i-pay-my-bills-by-sellingmy-used-panties/. Retrieved November 1, 2015.
- Sankar, R., & Archunan, G. (2004). Flehmen response in bull: Role of vaginal mucus and other body fluids of bovine with special reference to estrus. *Behavioural Processes*, 67, 81-86.
- Santtila, P., Wager, I., Katarina, W., Harlaar, N., Jern, P., Johansson, A., ... Sandnabba, N. K. (2008). Discrepancies between sexual desire and sexual activity: Gender differences and associations with relationship satisfaction. *Journal of Sex and Marital Therapy*, 34, 29-42.
- Schmitt, D. P. (2003). Universal sex differences in the desire for sexual variety: Tests from 52 nations, 6 continents, and 13 islands. *Journal of Personality and Social Psychology*, 85, 85-104.
- Schmitt, D. P., & Buss, D. M. (2001). Human mate poaching: tactics and temptations for infiltrating existing mateships. *Journal of Personality and Social Psychology*, 80, 894–917.
- Schurmann, C. (1982). Mating behaviour of wild orangutans. In de Boer, L. E. M., (Ed.). *The orang utan: Its biology and conservation* (pp. 269-284). The Hague, Netherlands: Junk Publishers.
- Shackelford, T. K. (2003). Preventing, correcting, and anticipating female infidelity: Three adaptive problems of sperm competition. *Evolution and Cognition*, 9, 90-96.
- Shackelford, T. K., & Buss, D. M. (1997). Susceptibility to infidelity in the first year of marriage. *Journal of Research in Personality*, 31, 193-221.
- Shackelford, T. K., & Goetz, A. T. (2007). Adaptation to sperm competition in humans. *Current Directions in Psychological Science*, 16, 47-50.
- 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., & Buss, D. M. (2005). Mate retention in marriage: Further evidence of the reliability of the Mate Retention Inventory. *Personality and Individual Differences*, 39, 415-425.

- 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, 214-220.
- Shackelford, T. K., Goetz, A.T., Guta, F. E., & Schmitt, D. P. (2006). Mate guarding and frequent in-pair copulation in humans: Concurrent or compensatory anticuckoldry tactics? *Human Nature*, 17, 239-252.
- 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, 123-138.
- Simmons, L. W., & Fitzpatrick, J. L. (2012). Sperm wars and the evolution of male fertility. *Reproduction*, 144, 519-534.
- Smith, R. L. (1984). Human sperm competition. In Smith, R. L. (Ed.), Sperm competition and the evolution of animal mating systems (pp. 601-659). New York: Academic Press.
- Snook, R. R. (2005). Sperm in competition: not playing by the numbers. *Trends in Ecology and Evolution*, 20, 46-53.
- Snow, A. (2015, June 13). http://www.thedailybeast.com/articles/2015/06/13/the-dirtypanties-black-market.html. Retrieved November 1, 2015.
- Soini, P. (1987). Sociosexual behavior of a free-ranging *Cebuella pygmaea* (Callitrichidae, platyrrhini) troop during postpartum estrus of its reproductive female. *American Journal of Primatology*, 13, 223-230.
- Steinbach, X., Oberzaucher, E., & Grammer, K. (2012). Human pheromones: Do "copulins" have an effect on men's testosterone levels and social behavior? XXI Biennial International Conference on Human Ethology. Vienna, Austria.
- Tabachnick, B. G., & Fidell, L. S. (2006). Using multivariate statistics (5th ed.). Boston, MA: Allyn & Bacon.
- Tan, M., Jones, G., Zhu, G., Ye, J., Hong, T., Zhou, S., ... Zhang, L. (2009). Fellatio by fruit bats prolongs copulation time. *PLoS ONE*, 4(10): e7595.
- Tevi-Bénissan, C., Belec, L., Levy, M., Schneider-Fauveau, V., Mohamed, A. S., Hallouin, M. C., ... & Grésenguet, G. (1997). In vivo semen-associated pH neutralization of cervicovaginal secretions. *Clinical and Diagnostic Laboratory Immunology*, 4, 367-374.

- Thornhill, R. (2006). Foreward: Human sperm competition and women's dual sexuality. In Shackelford, T. K. & Pound, N. (Eds.), *Sperm competition in humans: Classic and contemporary readings (v-xix)*. New York: Springer.
- Thornhill, R., Gangestad, S. W., Miller, R., Scheyd, G., McCollough, J. K., & Franklin, M. (2003). Major histocompatibility complex genes, symmetry, and body scent attractiveness in men and women. *Behavioral Ecology*, 14, 668-678.
- Smith, R. L. (1984). Human sperm competition. In Smith, R. L. (Ed.), Sperm competition and the evolution of animal mating systems (pp. 601-659). New York: Academic Press.
- van Rouen, J. H., Slob, A. K., Gianotten, W. L., Dohle, G. R., van Der Zon, A. T. M., Vreeburg, J. T. M., & Weber, R. F. A. (1996). Sexual arousal and the quality of semen produced by masturbation. *Human Reproduction*, 11, 147-151.
- Voracek, M., Haubner, T., & Fisher, M. L. (2008). Recent decline in nonpaternity rates: a cross-temporal meta-analysis 1, 2. *Psychological reports*, 103, 799-811.
- Wildt, L., Kissler, S., Licht, P., & Becker, W. (1998). Sperm transport in the human female genital tract and its modulation by oxytocin as assessed by hysterosalpingoscintigraphy, hysterotonography, electrohysterography and Doppler sonography. *Human Reproduction Update, 4*, 655-666.
- Wiederman, M. W., & Hurd, C. (1999). Extradyadic involvement during dating. *Journal* of Social and Personal Relationships, 16, 265-274.
- Wilson, M., Daly, M., & Weghorst, S. J. (1980). Household composition and the risk of child abuse and neglect. *Journal of Biosocial Science*, 12, 333-340.
- Wolf, M., Musch, J., Enczmann, J., & Fischer, J. (2012). Estimating the prevalence of nonpaternity in Germany. *Human Nature*, 23, 208-217.
- World Health Organization. (2010). WHO laboratory manual for the examination and processing of human semen (5th ed.). Geneva, Switzerland: WHO Press.
- Yang, C. C., & Bradley, W. E. (1999). Innervation of the human glans penis. *The Journal of Urology*, 161, 97-102.
- Young, M., Denny, G., Young, T., & Luquis, R. (2000). Sexual satisfaction among married women. *American Journal of Health Studies*, 16, 73-84.
- Zavos, P. M. (1985). Seminal parameters of ejaculates collected from oligospermic and normospermic patients via masturbation and at intercourse with the use of a Silastic seminal fluid collection device. *Fertility and Sterility*, 44, 517-520.

- Zavos, P. M., & Goodpasture, J. C. (1989). Clinical improvements of specific seminal deficiencies via intercourse with a seminal collection device versus masturbation. *Fertility and Sterility*, 51, 190-193.
- Zavos, P. M., Kofinas, G. D., Sofikitis, N. V., Zarmakoupis, P. N., & Miyagawa, I. (1994). Differences in seminal parameters in specimens collected via intercourse and incomplete intercourse (*coitus interruptus*). *Fertility and Sterility*, 61, 1174-1176.
- Ziegler, T. E., Epple, G., Snowdon, C. T., Porter, T. A., Belcher, A. M., & Küderling, I. (1993). Detection of the chemical signals of ovulation in the cotton-top tamarin, *Saguinus oedipus. Animal Behaviour*, 45, 313-322.