

# Evolutionary Psychology

www.epjournal.net – 2013. 11(5): 1130-1139

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## Original Article

### Oral Sex, Semen Displacement, and Sexual Arousal: Testing the Ejaculate Adjustment Hypothesis

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**Abstract:** Male Indian Flying Foxes (*Pteropus giganteus*) that spend more time performing oral sex on a female also spend more time copulating with her. In humans, men who spend more time copulating with their regular partner also perform more “semen-displacing” copulatory behaviors (e.g., deeper, more vigorous penile thrusting). We investigated whether men who spend more time performing oral sex on their regular partner also spend more time copulating with her and perform more semen-displacing copulatory behaviors. We proposed and tested the ejaculate adjustment hypothesis for men’s copulatory behaviors: Men adjust their copulatory behaviors to increase their sexual arousal and consequent ejaculate quality, thereby increasing their chances of success in sperm competition. Two hundred and thirty-three men in a committed, heterosexual relationship responded to questions about their copulatory behavior and sexual arousal during their most recent sexual encounter with their long-term partner. The results indicated that men who spend more time performing oral sex on their partner also spend more time copulating with her, perform more semen-displacing copulatory behaviors, and report greater sexual arousal. We discuss limitations to the current research and highlight the heuristic value of sperm competition theory for understanding human sexual behaviors.

**Keywords:** sperm competition, oral sex, semen displacement, sexual arousal, semen quality

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## Introduction

Sperm competition occurs when a female copulates with two or more males within a sufficiently brief time period, resulting in the sperm of the different males simultaneously occupying the female's reproductive tract and competing 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 to whom he is genetically unrelated. The reproductive costs of cuckoldry have caused the evolution of male sperm competition tactics—adaptations that increase sperm competition success (Shackelford and Goetz, 2007). Males perform concurrently various sperm competition tactics to minimize their cuckoldry risk (Dickinson, 1986; Shackelford, Goetz, Guta, and Schmitt, 2006). In the current research, we 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 (Davies, 1983) prior to copulating with her. In the Indian Flying Fox (*Pteropus giganteus*), oral sex increases copulatory duration—a sperm competition tactic (Maruthupandian and 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). In humans, men who are at greater sperm competition risk (Pham and Shackelford, 2013a), and who perform more behaviors to decrease their sperm competition risk (Pham and Shackelford, 2013b), report greater interest in and spend more time performing oral sex on their regular partner. This research suggests that performing oral sex may be related to sperm competition risk and may relate to other anti-cuckoldry tactics.

Men may perform oral sex on their regular partner to minimize cuckoldry risk, but the specific function(s) of oral sex remains unclear: Men may perform oral sex on their regular partner to estimate sperm competition risk (Pham and Shackelford, 2013a; Thornhill, 2006), to influence female mechanisms that favor his sperm over another man's sperm (e.g., to induce uterine contractions, Baker and Bellis, 1993b; Pham, Shackelford, Sela, and Welling, 2013; Wildt, Kissler, Licht, and Becker, 1998), or to minimize her motivation to commit infidelity by increasing her relationship satisfaction (Pham and Shackelford, 2013b). All three functions support the broader hypothesis that oral sex functions to minimize cuckoldry risk.

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 Marimuthu, 2013). The current research investigates whether these findings extend to humans. We 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., we 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, and Del Valle, 2002). Deeper copulatory thrusts stimulate more nerve endings along the surface of the penis (Halata and Munger, 1986; Yang and Bradley, 1999), causing greater sexual arousal (Georgiadis and 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 and Simmons, 2005). Consistent with the ejaculate adjustment hypothesis, men at greater sperm competition risk ejaculate more sperm at next copulation (Baker and Bellis, 1993a). We 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).

## **Methods**

### *Participants*

We recruited from the community and university campuses 233 men in a committed, heterosexual, sexual relationship lasting at least 1 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; Pham and Shackelford, 2013a), 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 asked if they were at least 18 years of age, in a heterosexual, sexual, committed relationship lasting at least 1 year, and had sex with their partner at least once in the past 7 days. Those who qualified were asked to sign a consent form and to complete a questionnaire. Participants were asked to place the completed questionnaire in an envelope that they then sealed, and to place the consent form in a separate envelope, to retain anonymity.

## Results

To test Hypothesis 1, we 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 ( $\beta = .307$ ,  $t = 4.906$ ,  $p < .001$ ).

We conducted a principal components analysis to extract *semen displacement* and *sexual arousal* components (see Table 1 for component 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, we 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, we identified Component 2 as the *semen displacement* component. We used these two components as variables in tests of Hypotheses 2 and 3.

To test Hypothesis 2, we 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 semen-displacing copulatory behaviors also spend more time performing oral sex on her ( $\beta = .289$ ,  $t = 4.59$ ,  $p < .001$ ).

To test Hypothesis 3, we 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 ( $\beta = .230$ ,  $t = 3.58$ ,  $p < .001$ ).

**Table 1.** 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%

Note: Components obtained using Direct Oblimin rotation

## Discussion

The results of the current research support the hypothesis that men perform various sexual behaviors concurrently to increase their sperm competition success. Specifically, 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 research is our indirect, rather than direct, assessment of ejaculate quality. To test the ejaculate adjustment hypothesis, we 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; Zavos, 1985; Zavos and Goodpasture, 1989), sexual arousal is nevertheless a proxy measure. Future research could *directly* assess men's ejaculate quality.

Given the correlational design of the current research, we cannot conclude from the results that the duration of oral sex causes, or instead results from, greater sexual arousal. Cerdá-Molina, Hernández-López, de la O, Chavira-Ramírez, and Mondragón-Ceballos (2013) documented that men who smelled odors produced from the female genitals at high-fertility subsequently reported greater copulatory interest and experienced a surge in salivary testosterone, which suggests that oral sex causes 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 and Shackelford, 2013c), and her previous infidelity (McKibbin, Starratt, Shackelford, and Goetz, 2011). Future research could benefit from securing data regarding other cues to sperm competition risk when investigating men's 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, 1978; Murphy, 1973; Nishimura, Utsumi, Okano, and Iritani, 1991; Palagi et al., 2003; Sankar and Archunan, 2004; Soini, 1987). Previous research suggests that men can detect their partner's fertility status and adjust accordingly their anti-cuckoldry tactics (reviewed in Haselton and Gildersleeve, 2011). Men more frequently perform behaviors to reduce the likelihood of their partner's infidelity when she is at high fertility relative to low fertility (Gangestad, Thornhill, and 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 and Gangestad, 2006). 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 is also 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).

The current research 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 and Shackelford, 2006; Goetz et al., 2005; Pham and Shackelford, 2013a). The current research 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 research provides preliminary evidence that men adjust their copulatory behaviors to produce more competitive ejaculates.

**Received 14 November 2013; Revision submitted 28 November 2013; Accepted 30 November 2013**

## References

- Baker, R. R., and Bellis, M. A. (1993a). Human sperm competition: Ejaculate adjustment by males and the function of masturbation. *Animal Behaviour*, 46, 861-885.
- Baker, R. R., and Bellis, M. A. (1993b). Human sperm competition: Ejaculate manipulation by females and a function for the female orgasm. *Animal Behaviour*, 46, 887-909.
- 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.
- Davies, N. B. (1983). Polyandry, cloaca-pecking and sperm competition in dunnocks. *Nature*, 302, 334-336.
- 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. (1975). An examination of relationships between pleasantness, intensity, and concentration of 10 odorous stimuli. *Perception and Psychophysics*, 17, 492-496.
- 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.
- Gallup, G. G., and Burch, R. L. (2004). Semen displacement as a sperm competition strategy in humans. *Evolutionary Psychology*, 2, 12-23.
- Gallup, G. G., Burch, R. L., and 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., and Davis, J. A. (2003). The human penis as a semen displacement device. *Evolution and Human Behavior*, 24, 277-289.
- Gangestad, S. W., Thornhill R., and Garver-Apgar, C. E. (2002). Changes in women's sexual interests and their partner's mate-retention tactics across the menstrual cycle: Evolutionary Psychology – ISSN 1474-7049 – Volume 11(5). 2013.

- Evidence for shifting conflict of interest. *Proceedings of the Royal Society Biological Sciences*, 269, 975-982.
- Georgiadis, J. R., and Holstege, G. (2005). Human brain activation during sexual stimulation of the penis. *Journal of Comparative Neurology*, 493, 33-38.
- Goetz, A. T., and 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., Weekes-Shackelford, V. A., Euler, H. A., Hoier, S., Schmitt, D. P., and 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.
- Halata, Z., and Munger, B. L. (1986). The neuroanatomical basis for the protopathic sensibility of the human glans penis. *Brain Research*, 371, 205-230.
- Haselton, M. G., and Gangestad, S. W. (2006). Conditional expression of women's desires and men's mate guarding across the ovulatory cycle. *Hormones and Behavior*, 49, 509-518.
- Haselton, M. G., and Gildersleeve, K. (2011). Can men detect ovulation? *Current Directions in Psychological Science*, 20, 87-92.
- Johnston, R. E. (1974). Sexual attraction function of golden hamster vaginal secretion. *Behavioral Biology*, 12, 111-117.
- Kiddy, C. A., Mitchell, D. S., Bolt, D. J., and Hawk, H. W. (1978). Detection of estrus-related odors in cows by trained dogs. *Biology of Reproduction*, 19, 389-395.
- Kilgallon, S. J., and Simmons, L. W. (2005). Image content influences men's semen quality. *Biology Letters*, 1, 253-255.
- Maruthupandian, J., and Marimuthu, G. (2013). Cunnilingus apparently increases duration of copulation in the Indian flying fox, *Pteropus giganteus*. *PLoS One*, 8, e59743.
- McKibbin, W. F., Starratt, V. G., Shackelford, T. K., and 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.
- Murphy, M. R. (1973). Effects of female hamster vaginal discharge on the behavior of male hamsters. *Behavioral Biology*, 9, 367-375.
- Nishimura, K., Utsumi, K., Okano, T., and Iritani, A. (1991). Separation of mounting-inducing pheromones of vaginal mucus from estrual heifers. *Journal of Animal Science*, 69, 3343-3347.
- Palagi, E., Telara, S., and Tarli, S. B. (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.
- Pham, M. N., and Shackelford, T. K. (2013a). Oral sex as infidelity-detection. *Personality and Individual Differences*, 54, 792-795.
- Pham, M. N., and Shackelford, T. K. (2013b). Oral sex as mate retention behavior. *Personality and Individual Differences*, 55, 185-188.
- Pham, M. N., and 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., Sela, Y., and Welling, L. L. M. (2013). Is cunnilingus-assisted orgasm a male sperm-retention strategy? *Evolutionary Psychology*, 11, 405-414.
- Pound, N., Javed, M. H., Ruberto, C., Shaikh, M. A., and Del Valle, A. P. (2002). Duration of sexual arousal predicts semen parameters for masturbatory ejaculates. *Physiology and Behavior*, 76, 685-689.
- Sankar, R., and 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.
- Shackelford, T. K., and Goetz, A. T. (2007). Adaptation to sperm competition in humans. *Current Directions in Psychological Science*, 16, 47-50.
- Shackelford, T. K., Goetz, A. T., Guta, F. E., and Schmitt, D. P. (2006). Mate guarding and frequent in-pair copulation in humans: Concurrent or compensatory anti-cuckoldry tactics? *Human Nature*, 17, 239-252.
- Shackelford, T. K., Goetz, A. T., McKibbin, W. F., and 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., LeBlanc, G. J., Weekes-Shackelford, V. A., Bleske-Rechek, A. L., Euler, H. A., and Hoier, S. (2002). Psychological adaptation to human sperm competition. *Evolution and Human Behavior*, 23, 123-138.
- Simmons, L. W., and Fitzpatrick, J. L. (2012). Sperm wars and the evolution of male fertility. *Reproduction*, 144, 519-534.
- Smith, R. L. (1984). Human sperm competition. In R. L. Smith (Ed.), *Sperm competition and the evolution of animal mating systems* (pp. 601-659). New York: Academic Press.
- Snook, R. R. (2005). Sperm in competition: Not playing by the numbers. *Trends in Ecology and Evolution*, 20, 46-53.
- Soini, P. (1987). Sociosexual behavior of a free-ranging *Cebuella pygmaea* (Callitrichidae, platyrhini) troop during postpartum estrus of its reproductive female. *American Journal of Primatology*, 13, 223-230.
- Thornhill, R. (2006). Foreword: Human sperm competition and women's dual sexuality. In T. K. Shackelford and N. Pound (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., and Franklin, M. (2003). Major histocompatibility complex genes, symmetry, and body scent attractiveness in men and women. *Behavioral Ecology*, 14, 668-678.
- van Rouen, J. H., Slob, A. K., Gianotten, W. L., Dohle, G. R., van Der Zon, A. T. M., Vreeburg, J. T. M., and Weber, R. F. A. (1996). Sexual arousal and the quality of semen produced by masturbation. *Human Reproduction*, 11, 147-151.
- Wildt, L., Kissler, S., Licht, P., and Becker, W. (1998). Sperm transport in the human female genital tract and its modulation by oxytocin as assessed by hysterosalpingoscopy, hystero- and electrohysterography, and Doppler

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- sonography. *Human Reproduction Update*, 4, 655-666.
- Yang, C. C., and Bradley, W. E. (1999). Innervation of the human glans penis. *The Journal of Urology*, 161, 97-102.
- 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., and 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.