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The semen-displacement hypothesis: semen hydraulics and the intra-pair copulation proclivity model of female infidelity

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Introduction

Among sexually reproducing species, the penis evolved as an internal fertilization device. But across different species, penises exist in a bewildering array of shapes and sizes (see Eberhard, 1985). Among primates, the human penis is distinctive by virtue of both its size and its enlarged glans and protruding coronal ridge (see Gallup & Burch, 2004). There has been some speculation that the human penis evolved not only as an internal fertilization device, but also as a mechanism for displacing semen left by rival males in the female reproductive tract (e.g. Baker & Bellis, 1995).

In a series of studies designed to simulate sexual intercourse under laboratory conditions using artificial genitals, we found that when latex vaginas contained simulated semen, phalluses that approximated the configuration of the human penis displaced 80% or more of the semen by drawing it away from the cervical end of the vagina (Gallup *et al.*, 2003). Through a series of experimental manipulations, we determined that the coronal ridge may be an important feature of the penis in mediating semen displacement. Thus, as a mechanical means of affecting sperm competition, the human penis may enable successive males to displace foreign semen from the female reproductive tract and substitute their semen for those of their rivals.

In a survey of over 600 college students, reported in the same paper (Gallup *et al.*, 2003), we found that, following periods of separation or allegations of female infidelity, both males and females report that penile thrusting is noticeably deeper and more vigorous. Therefore, how men unwittingly use their penis also may be related to its semen-displacement properties, and the parameters of penile thrusting appear to vary as a function of the likelihood that there may be semen from other males in the female reproductive tract.

In a more recent paper, we derived and expanded on a number of other theoretical implications that follow from the proposition that the unique configuration of the human penis evolved to compete with semen left in the vagina by other males (Gallup & Burch, 2004). Included among the predictions we made are the following. If several males copulate with the same female in a short period of time (e.g. 24 h), the last male to inseminate the female has the best chance of paternity (referred to as ordinal ejaculation effects or last-male precedence; Gallup & Burch, 2004). Because of the possibility that males may unwittingly piggyback foreign semen from one vagina to the next, females that copulate with uncircumcised partners are at risk of fertilization by proxy and resulting impregnation by males they have never had sex with. Likewise, we argued that, in one sense, premature ejaculation can be thought of as a failure to achieve semen displacement, and we speculated that jealousy-induction procedures might work to antagonize this problem. Finally, because of the prospect of displacing their own semen, we predicted that males who show vigorous post-ejaculatory thrusting are at risk of infertility as a consequence of displacing their own semen.

In this chapter, we expand on some of these and other implications of the semen-displacement hypothesis. We also present preliminary data from several surveys we have conducted that bear on some of the predictions that follow from this hypothesis.

Semen hydraulics

One way to think about semen displacement is in terms of semen hydraulics, or the flow and resistance of seminal fluid as it passes through confined spaces. For our purposes, there are three applications of semen hydraulics that relate to human reproductive competition: semen viscosity, semen displacement, and semen retention.

One of the principal parameters of semen hydraulics is *semen viscosity*. There is considerable individual variation among men in semen viscosity (Gonzales, Kortebani, & Mazzolli, 1993), and the viscosity of semen has been implicated as a factor in male fertility. Semen hyperviscosity has been linked to infertility

and is often one of the initial assessments performed by infertility clinics (Gonzales, Kortebani, & Mazzolli, 1993; Gopalkrishnan, Padwal, & Balaiah, 2000). Thick or viscous semen appears to entrap sperm and impair their ability to swim up through the female reproductive tract.

There also is a relationship between semen viscosity and *semen displacement*. In our attempt to model semen displacement under laboratory conditions, we examined the effect of variation in simulated semen viscosity (Gallup *et al.*, 2003). Using different levels of semen viscosity and several different phalluses, we determined that the magnitude of semen displacement was inversely proportional to semen viscosity; that is, viscous semen was less subject to displacement. Thus, there would appear to be a trade-off between semen viscosity and semen displacement. Viscous semen deposited deep inside the vaginal tract would be less accessible and more difficult for other males to displace. However, because semen hyperviscosity compromises sperm motility, there is probably a trade-off between semen displacement and fertility with respect to semen viscosity; that is, the benefits of semen viscosity as a means of minimizing displacement are offset by the fertility costs that are incurred as a consequence.

The same constraints hold true for *semen retention*. With the assumption of an upright posture during human evolution and the emergence of patterns of bipedal locomotion, the female reproductive tract has been brought into a perpendicular orientation with gravity and as such is poorly suited to the retention of semen (Gallup & Suarez, 1983). In most quadruped species (including most primates), copulation occurs in the dorsal–ventral mode with the male mounting the female from behind, and under these conditions the female reproductive tract is in a parallel orientation to gravity. The problems posed by semen retention in bipedal humans appear to have impacted human sexual behavior. One of the most common, cross-cultural means of affecting copulation in humans is in face-to-face or frontal encounters that occur in the ventral–ventral mode, with the female in a supine position and the male on top (Ford & Beach, 1951). In this position the woman's reproductive tract is brought back into a more primitive, parallel orientation with gravity and as such may be better suited to semen retention. Because the orientation of the female reproductive tract may be important to the retention of semen, we predict that couples that frequently use the female superior position will be at greater risk of experiencing infertility problems.

It follows from this analysis that we expect to find a variety of corollary postcopulatory adaptations in humans that function to postpone the assumption of an upright posture following insemination. With regard to the timing of copulation, humans tend to show a nocturnal copulation bias (Ford & Beach,

1951). By copulating preferentially at night, the likelihood of remaining in a prone position for an extended period of time afterward is enhanced. The sedative-like effects of orgasm would further promote remaining in a prone position following a sexual encounter (Gallup & Suarez, 1983), particularly under conditions in which sexual partners sleep together (Hughes, Harrison, & Gallup, 2004). The fact that some human females are capable of experiencing multiple orgasms may cause these sedative-like effects to summate and further promote remaining in a supine position for an extended period of time after sex.

Postcopulatory behavior

In addition to the premium that would accrue to depositing semen in the most inaccessible parts of the vagina and thereby minimizing the likelihood of displacement by rival males, the same logic holds for semen retention. Semen deposited deep within the vaginal tract would have a retention advantage, and this may have produced additional selective pressure for the evolution of a longer penis (see Gallup & Burch, 2004; Gallup & Suarez, 1983). As implied by our discussion of semen hydraulics, another important parameter of semen retention involves postcopulatory behavior. What females do after they copulate can have important implications for semen retention.

As one test of this hypothesis, we examined differences in postcopulatory behavior among people from different races (Stockwell *et al.*, 2001). There are substantial differences in penis size across different racial groups, with African-Americans having, on average, longer penises (e.g. Gebhard & Johnson, 1979). To see if these differences evolved to compensate for differences in what females do after they copulate, we surveyed over 500 undergraduates regarding their ethnic background, sexual practices, and the behavior of their partners. Consistent with the hypothesis that semen deposited deep within the vaginal tract would be afforded a retention advantage, African-American women were more likely than Caucasian and Asian women to get up and do other things right after having sexual intercourse. After sex, African-American women were more likely than women of other ethnic backgrounds to report taking a shower, getting dressed, going home, or going to work. They were also less likely to remain in a prone position and to cuddle with their partners after sex.

In light of the dual function of the penis as both a means of maximizing semen retention and displacing semen from rival males, it is notable that there are independent data implicating higher levels of female infidelity among African-Americans based on the existence of ethnic differences in jealousy and partner abuse. In a recent study by McFarlane and Wilson (2000), the majority of victims of domestic violence were African-American. Likewise, Straus and Gelles

(1986) have shown that rates of overall violence against females are higher among African-American men, and family violence that ends in homicide is higher as well (Wilson & Daly, 1992). In a sample of 780 college students, we also found significant race differences in domestic violence (Stockwell *et al.*, 2000), with a higher incidence of abusive acts directed toward female partners among African-Americans than women of other ethnic groups.

Double-mating

The semen-displacement hypothesis assumes that there were recurrent situations during human evolutionary history in which females had sex with two or more males in fairly close temporal proximity to one another. We listed the following situations as ones that satisfy this criterion: (1) consensual sex with multiple concurrent partners, (2) nonconsensual sex with multiple concurrent partners, and (3) successive consensual or nonconsensual sexual encounters with multiple partners that occur within a relatively brief period of time (Gallup & Burch, 2004). Contemporary examples of female double-mating include threesomes, group sex, gang rape, extra-pair copulations, promiscuity, and prostitution.

Using the definition of double-mating as a woman having sexual intercourse with a man while another man's ejaculate is still present in her reproductive tract, Baker and Bellis (1995) surveyed over 3500 women through a British magazine. They found that the lifetime number of sexual partners varied considerably; after 3000 copulations, the percentage of women who had over 100 partners was the same as those who only had one (5.6%). They also found that as women age, and as they have more children, the incidence of extra-pair copulations increases.

The incidence of double-mating in Baker and Bellis' British sample also depended upon sexual experience; roughly one out of six women double-mated within their first 50 copulations, one-half double-mated within their first 500 copulations, and over 80% had double-mated by the time they had experienced 3000 copulations. After 500 copulations, one in 200 women reported being inseminated on at least one occasion by two different men within 30 min of one another. Approximately 30% of women in the Baker and Bellis sample reported having been inseminated by two males within 24 h.

In a recent attempt to examine the incidence of double-mating in a contemporary sample of college students, we found that 18%, or over one out of six of the female respondents ($n = 136$), and 10% of the males ($n = 44$) reported having had at least one extra-pair copulation while being in a committed relationship (Gallup, Burch, and Beren Mitchell, 2005). In terms of sex with successive

partners, one out of 10 (10.4%) females acknowledged having had intercourse with more than one male in a 24-h period, 3.5% reported having sex with more than one male in 12 h, and 2.6% admitted to having sex with two or more men within 8 h or less. In response to questions about concurrent (rather than successive) encounters with multiple sex partners, 8.1%, or one out of 12 females, reported having engaged in a threesome, and 5.9% of the females acknowledged having participated in group sex with three or more partners. These data suggest that the incidence of double-mating among female college students is substantial. Moreover, these data should be treated as conservative estimates of double-mating. First, even under conditions of anonymity, women have little to gain (and far more to lose) by being completely candid and forthright about their sexual indiscretions. Second, college students in their late teens and early twenties are relatively inexperienced in the sexual domain as compared to older, more mature women.

Adaptations to self-semen displacement

If the human penis evolved to displace semen left by other males, what is to prevent this adaptation from displacing the male's own semen? The data derived from artificial genitals (Gallup *et al.*, 2003) suggest that continued thrusting beyond the point of ejaculation would lead to displacement of the male's own semen. Therefore, the tenability of the displacement hypothesis depends on identifying evolved collateral mechanisms that serve to minimize post-ejaculatory thrusting and thereby reduce the likelihood of self-semen displacement.

Candidate mechanisms identified by Gallup and Burch (2004) that appear to preclude or at least diminish self-semen displacement include the following post-ejaculatory changes: (1) penile hypersensitivity, (2) loss of an erection, and (3) the refractory period. Due to enhanced post-ejaculatory increases in penile hypersensitivity, continued thrusting for many males can be unpleasant following ejaculation. Post-ejaculatory thrusting can also be diminished as a consequence of an inability to sustain an erection. Many males lose penile tumescence after they ejaculate. The refractory period, as measured by the inability to achieve another erection following ejaculation, also may function to minimize self-semen displacement.

As another adaptation to self-semen displacement, we predicted that males who do not withdraw and continue to thrust past the point of ejaculation would show post-ejaculatory thrusting that was shallower and less vigorous. In contrast to deep thrusting, we found that shallow thrusting with prosthetic genitals failed to produce semen displacement (Gallup *et al.*, 2003). In a recent survey

administered to 180 sexually active college students, we discovered that 72% of the males and 87% of the females reported that thrusting became noticeably shallower and less intense following ejaculation (Gallup *et al.*, 2005). Therefore, there is evidence for the existence of a variety of mechanisms in human males that operate to minimize self-semen displacement.

The intra-pair copulation (IPC) proclivity model of female infidelity

One way to think about semen displacement in particular, and sperm competition in general, is in terms of the competing reproductive interests of men and women. If a woman in a committed relationship engages in an extra-pair copulation, not only might this pit the semen of the resident male against the semen of the rival male, it also raises a number of interesting issues relative to the timing and topography of subsequent, and perhaps compensatory, inseminations by the resident male.

The effectiveness of sperm competition and semen displacement as means of competing for paternity is critically related to the elapsed time since the extra-pair encounter. In order to substitute their semen for those of their rivals, we expect resident males to show a high propensity to initiate relatively immediate copulation with their partner under conditions in which they have reason to question her fidelity. On the other hand, if females (consciously or not) engage in extra-pair copulations as a means of using high-quality and/or genetically different males to cuckold their mates, then because of sperm competition and the potential for semen displacement to prevent impregnation, we expect females to have been selected to avoid copulating with their in-pair partners on the heels of an extra-pair copulation. In other words, females should attempt to avoid sex with their committed partners for a period of time following an incidence of infidelity as a means of unwittingly maximizing the likelihood of impregnation by the extra-pair male.

Figure 7.1 represents a depiction of these hypothetical sex differences in the propensity to engage in intra-pair copulations as a function of the elapsed time since the female's sexual encounter with another male. The resident male's insistence on relatively immediate copulation with his partner following a perceived instance of female infidelity is consistent with the importance of minimizing the time between her encounter with the interloper and the application of sperm-competition mechanisms and semen displacement as a means of preventing paternity by his rival.

There is evidence that even sexual intercourse itself may interfere with embryo implantation, which typically occurs within about 24 h of conception.

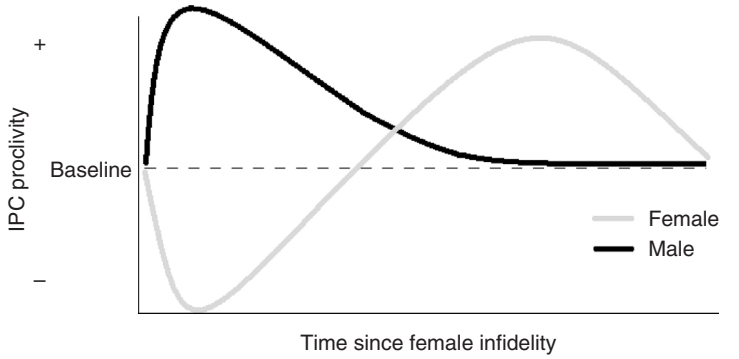

Figure 7.1 The intra-pair copulation (IPC) proclivity model of female infidelity.

It has been known for some time that sexual intercourse, and especially the occurrence of female orgasm, has the effect of increasing uterine myometrial activity (Fox, Wolff, & Baker, 1970). Recent data derived from *in vitro* fertilization embryo-transfer studies indicate that these coitus-induced uterine contractions in human females can interfere with early embryo implantation (Tremellen *et al.*, 2000). Our earlier findings, that males thrust deeper and more vigorously following periods of separation from their partners and following allegations of infidelity (Gallup *et al.*, 2003), may bear on this effect. Not only would deeper and more vigorous penile thrusting effect more complete displacement of rival semen, it may also function to enhance uterine contractions and thereby increase the likelihood of blocking or preventing early embryo implantation. Thus, under conditions of female infidelity, the importance of a short-latency, male-initiated intra-pair copulation may be three-fold. In addition to the operation of (1) sperm competition and (2) semen displacement as a means of minimizing conception by rival males, (3) by promoting uterine contractions, sexual intercourse itself along with the occurrence of female orgasm has the potential to interfere with early implantation of embryos conceived by rival males.

Because of male counter-insemination tactics, we expect females to have been selected to refrain from or at least postpone copulation with the resident male following an extra-pair encounter as a means of enhancing the likelihood of paternity by the rival male. As we have suggested (Gallup & Burch, 2004), if you combine a male's insistence for sex with the female's reluctance for sex, it is a recipe for sexual coercion and rape. Indeed, in support of our analysis, Goetz and Shackelford (see Chapter 5 in this volume) have evidence that the incidence of wife rape is enhanced under conditions in which males believe their wives have been unfaithful.

As a preliminary test of our prediction about females becoming refractory for intra-pair copulations following extra-pair copulations, we recently attempted to measure changes among college females in the propensity to engage in an intra-pair copulation as a function of the time since an instance of infidelity (Gallup *et al.*, 2005). In response to questions about infidelity, 84.2% of the females ($n = 136$) indicated that they would wait at least 48 h or longer before resuming sex with their committed, in-pair partners. Thus, consistent with our model, reluctance to engage in an intra-pair copulation following an extra-pair copulation appears to be a robust and widespread phenomenon among college females which, coupled with the fact that females are more likely to have extra-pair copulations during the ovulatory phase of their cycles and are less likely to use contraceptives (Baker & Bellis, 1995), suggests that women behave (wittingly or not) in ways that enhance the likelihood of conception by extra-pair males.

Another interesting prediction that can be derived from this model concerns the female's recovery and, indeed, eventual resurgence of intra-pair copulation receptivity. Should impregnation and implantation occur as a consequence of an extra-pair encounter, it becomes important for the female to resume copulation with the resident male to mask or obscure the possibility of failed paternity. Thus, the model (see Figure 7.1) not only predicts an eventual return to intra-pair copulation proclivity baseline by both males and females, but as the time since the extra-pair copulation continues to increase, females are predicted to initiate patterns of copulation with the resident male. In other words, if a woman has been impregnated by another man, it becomes important to take steps (consciously or not) to ensure that paternity in the eyes of the resident male is assured. The frequent anecdotal reports that positive feelings toward their committed partners are enhanced as a consequence of partner swapping (Fang, 1976; Wachowiak & Bragg, 1980), may be a byproduct of this compensatory increase in sexual attraction that females experience toward their committed partners on the heels of extra-pair sexual encounters.

Paternal-assurance tactics

To frame the issue of semen displacement as a sperm-competition mechanism in broader perspective, we next comment briefly on the rich ensemble of evolved strategies that may function to assure human paternity. As shown in Table 7.1, there appear to be at least four major categories of paternal-assurance tactic that have emerged during human evolutionary history.

The first and most obvious paternal assurance tactics are those that involve *insemination-prevention strategies*. These include putting a premium on virginity in a bride (for evidence, see Hughes & Gallup, 2003), mate guarding and mate

Table 7.1. *Human paternal-assurance tactics.*

Insemination-prevention strategies
• Preference for virgin brides
• Mate guarding
• Male sexual jealousy
• Mechanical and surgical intervention
• Frequent copulation
Counter-insemination strategies
• Sperm competition
• Semen displacement
Pregnancy-termination strategies
• Coitus-induced uterine contractions
• Pregnancy-induced domestic violence
Postpartum investment strategies
• Paternal resemblance
• Child abuse
• Infanticide

monitoring, mechanical (e.g. chastity belts) and surgical techniques (e.g. infibulation) designed to dissuade female infidelity (Daly, Wilson & Weghorst, 1982), engaging in frequent copulation (Shackelford, 2003), and male sexual jealousy (Daly, Wilson & Weghorst, 1982), all of which function to reduce the likelihood of cuckoldry by minimizing the woman's exposure to semen from rival males. However, if these mechanisms fail and insemination of the female occurs as a consequence of an extra-pair copulation, *counter-insemination strategies*, such as sperm competition (Baker & Bellis, 1995; Birkhead, 2000) and semen displacement (Gallup *et al*., 2003), come into play. If these counter-insemination tactics fail and impregnation occurs as a consequence of female infidelity, there also appears to be a class of *pregnancy-termination strategies*. These tactics include coitus-induced uterine contractions that interfere with early embryo implantation (Tremellen *et al*., 2000), and instances of pregnancy-induced domestic violence. There is growing evidence that males who question their partner's fidelity show an increase in spouse abuse during pregnancy, and the abuse is often directed toward the female's abdomen (Burch & Gallup, 2000). Finally, in instances of failed paternity, where children sired by rival males are born, a set of *postpartum investment strategies* come into play. These include the recent discovery that males, but not females, make hypothetical investment decisions that favor children with whom they share facial characteristics (e.g. Platek *et al*.,

2003). Likewise, instances of male-initiated child abuse (e.g. Burch & Gallup, 2000) and infanticide by non-genetic fathers (Daly & Wilson, 1988) serve to reduce and even terminate investment in children of dubious paternity.

The existence of such a wide and diverse array of paternal-assurance tactics suggests strongly that female infidelity was widespread, and as a consequence competition among males for paternity was a prominent, recurring feature of human evolutionary history.

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