

Original Article

Semen Displacement as a Sperm Competition Strategy in Humans

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Abstract: We examine some of the implications of the possibility that the human penis may have evolved to compete with sperm from other males by displacing rival semen from the cervical end of the vagina prior to ejaculation. The semen displacement hypothesis integrates considerable information about genital morphology and human reproductive behavior, and can be used to generate a number of interesting predictions.

Keywords: penis morphology, semen displacement, sperm competition, sperm retention, premature ejaculation, double mating, circumcision, penile hypersensitivity, refractory period, fertilization by proxy, last male precedence, infertility, self-semen displacement, semen coagulation, wife rape.

The human penis as a semen displacement device

The penis evolved as an internal fertilization device. There are, however, striking differences in penis morphology between different species (see Birkhead, 2000). In addition to the ostensible impact of female choice on the evolution of more elaborate male genitalia (Eberhard, 1996), there is reason to believe that sperm competition played a role in shaping the human penis. The human penis, with a relatively larger glans and more pronounced coronal ridge than is found in many other primates, may function to displace seminal fluid from rival males in the vagina by forcing it back over/under the glans. During intercourse the effect of repeated thrusting would be to draw out and displace foreign semen away from the cervix. As a consequence, if a female copulated with more than one male within a short period of time this would allow subsequent males to “scoop out”

semen deposited by others before ejaculating (Baker and Bellis, 1995).

To test this hypothesis, Gallup, Burch, Zappieri, Parvez, Stockwell, and Davis (2003) simulated sexual encounters using artificial models and measured the magnitude of artificial semen displacement as a function of phallus configuration, depth of thrusting, and semen viscosity. The displacement of simulated semen was robust across different prosthetic phalluses, different artificial vaginas, different semen recipes, and different semen viscosities. The magnitude of semen displacement was directly proportional to the depth of thrusting and inversely proportional to semen viscosity. By manipulating different characteristics of artificial phalluses, the coronal ridge and frenulum were identified as key morphological features involved in mediating the semen displacement effect.

Under conditions that raise the possibility of females engaging in extra-pair copulations (i.e., periods of separation from their partner, allegations of female infidelity), Gallup et al. (2003) also found that males appear to modify the use of their penis in ways that are consistent with the displacement hypothesis. Based on anonymous surveys of over 600 college students, many sexually active males and females reported deeper and more vigorous thrusting when in-pair sex occurred under conditions related to an increased likelihood of female infidelity.

Implications for species differences in penis length and morphology

Semen displacement as a means of competing with sperm from rival males is not an uncommon strategy in animals. The males of some species possess penile barbs, hooks, combs, or a textured glans to remove copulatory plugs and semen from the female reproductive tract (for a review see Baker and Bellis, 1995). In humans, the distinctive characteristics of the penis, relative to other primates, are its length, circumference, glans, and coronal ridge. In order for the human penis to serve as an efficient semen displacement device, it needs to be of sufficient size to fill the vagina and supplant foreign semen. The typical erect human penis ranges from 127mm to 178mm in length (Masters & Johnson, 1966), with an average circumference of 24.5mm (Wessells, Lue, and McAninch, 1996). In contrast with our closest living relative, the human penis is roughly twice as long and wide as that of the common chimpanzee (Short, 1980). The glans and coronal ridge of the human penis are also uniquely configured (Izor, Walchuk and Wilkins, 1981). The posterior portion of the human glans is larger in diameter than the penis shaft, and at the interface between the glans and the shaft the coronal ridge is positioned perpendicular to the shaft. Common chimpanzees have no clearly differentiated glans or coronal ridge (Kinzey, 1974).

As evidence that the human penis may have been shaped by the recurrent adaptive problem posed by sperm competition consider the following. Magnetic resonance imaging studies show that during coitus, the typical penis fills and expands the human vagina, and with complete penetration often pushes up against

the cervix (Weijmar Schultz, van Andel, Sabelis, and Mooyart, 1999). When ejaculation occurs, thrusting diminishes and vaginal penetration reaches its maximum point (Masters and Johnson, 1966). Not only does this serve to release semen in close proximity to the cervix, but data on ejaculatory pressure shows that the first several ejaculatory contractions project seminal fluid with such force that it can be expelled at a distance of 30-60cm if not contained in a vagina (Masters and Johnson, 1966). Thus, there appear to have been a series of adaptations that serve to confine or focus the release of semen to the uppermost portion of the vaginal tract, possibly as a means of making it less vulnerable to displacement by other males. A longer penis would not only have been an advantage for leaving semen in a less accessible part of the vagina, but by filling and expanding the vagina it also would aid and abet the displacement of semen left by other males as a means of maximizing the likelihood of paternity.

In addition to competing with sperm from rival males, there may be other benefits of deep semen placement. In contrast to organisms that walk on all fours, the assumption of an upright posture and the emergence of bipedalism brought the human female reproductive tract, and the vagina in particular, into a perpendicular orientation with gravity that is poorly suited to semen retention. Copulation in the ventral-ventral mode with the female in a supine position brings the female reproductive tract back into a more primitive parallel orientation with gravity, and enhances the likelihood that semen will be retained. However, due to the effects of gravity, the resumption of an upright posture following coitus has the potential to endanger semen retention. Consistent with this hypothesis, there are several mechanisms that appear to postpone getting up after a sexual encounter, such as post-copulatory petting, patterns of nocturnal copulation, and the sedative-like effects of orgasm (Gallup and Suarez, 1983). Likewise, a long penis that provides for the release of semen deep in the vagina could also serve as a hedge against semen loss.

Ordinal ejaculation effects

It follows from the semen displacement hypothesis that sperm competition among humans ought to involve ordinal ejaculation/mating order effects. Under conditions in which several males copulate with a female in close temporal proximity to one another the male who mated with the female last would have an advantage, known as last male precedence (see Birkhead, 2000). In the case of humans, the last male to copulate would be in a position to displace the semen left by previous males before inseminating the female with his own semen. This assumes, of course, that other factors such as sperm quality, ejaculate size, penis length, and female control of mating are constant. As yet, little research has been conducted on this topic, but in the sections that follow we elaborate a number of potentially testable implications of the semen displacement hypothesis.

Double Mating

For semen displacement to be adaptive it presupposes situations in which human females have sex with multiple (two or more) males in fairly close succession/temporal proximity to one another. Situations that satisfy this criterion include 1) consensual sex with multiple concurrent partners, 2) nonconsensual sex with multiple concurrent partners, and 3) multiple successive consensual and/or nonconsensual sexual encounters that occur within a relatively brief period of time. Examples include, group sex, gang rape, extra pair copulations, promiscuity, prostitution, and resident male insistence on sex in response to suspected infidelity (see subsequent section on female reproductive strategy). Instances of human heteroparity, or heteropaternal superfecundation, where members of a pair of fraternal twins are actually half sibs as a consequence of being conceived by different fathers, are well documented (e.g., Ambach, Parson, and Brezinka, 2000; Wenk, Houtz, Brooks, and Chiafari, 1992), and testify to the existence of double mating by females. It is also worth noting that patterns of consensual concurrent mating with multiple males by female chimpanzees, our closest living relatives, are common (Tutin, 1979), and as such may have been prevalent during earlier phases of human evolutionary history as well.

Effects of circumcision

What effect, if any, does the practice of surgically removing the foreskin have on the semen displacement properties of the human penis? For intact males, when the penis is fully erect the foreskin is pulled back over the glans and down the shaft of the penis. As a result, whether a man has been circumcised is often only apparent when the penis is flaccid. However, depending on how thick the foreskin is and how far it extends over the end of the glans, circumcision could affect the magnitude of semen displacement. During circumcision the foreskin is cut away from the shaft of the penis immediately behind the glans (Holman and Stuessi, 1999). As a consequence of removing the foreskin the circumference of the shaft posterior to the glans may be slightly reduced, causing the coronal ridge to be more pronounced and creating a larger area for semen to collect where it could be scooped back away from the cervix.

Laumann, Masi, and Zuckerman (1997) found that circumcised men masturbate more often and engage in more elaborate sexual behaviors. Anecdotal reports of adult circumcision by affected males and their partners also suggest that the procedure leads to changes in sexual behavior. Money and Davison (1983) and Fink, Carson, and De Vellis (2002) found that among males who underwent circumcision as adults, the majority reported a loss of penile sensitivity and a prolongation of sexual intercourse, and some reported less sexual gratification.

Anecdotal reports from females also bear on the semen displacement

properties of the circumcised penis. In a study of 139 women who had experienced intercourse with a number of both circumcised and uncircumcised partners, O'Hara and O'Hara (1999) found most (73%) reported that circumcised men thrust harder and deeper, and used more elongated strokes than their uncircumcised counterparts. The majority of the respondents preferred sex with uncircumcised males, citing greater displacement of vaginal secretions and resulting vaginal dryness, increased friction, and physical discomfort during intercourse with men that were circumcised. Among the minority of respondents who preferred circumcised partners (N = 20), the most common reason given was prolonged intercourse. But complaints about the loss of vaginal secretions, friction, and discomfort were still prevalent in this group. Perhaps due to reduced penile sensitivity, circumcised men thrust deeper and withdraw farther and thereby displace more vaginal fluids. O'Hara and O'Hara conclude that the loss of vaginal lubrication and discomfort is "because of the tight penile skin, the corona of the glans, which is configured like a one way valve, pulls the vaginal secretions out of the vagina when the shaft is withdrawn" (p. 82). Therefore, although practiced primarily for religious and/or hygienic reasons, an unintended consequence of circumcision may be to enhance the semen displacement properties of the human penis.

Another, albeit indirect, way to examine differences in the effectiveness of semen displacement would be to compare the incidence of cuckoldry between men that have and have not been circumcised. It follows from the displacement hypothesis that the risk of extra-pair paternity might vary with variation in semen displacement effectiveness. In addition to DNA testing to assess paternity, a less obtrusive (but far from perfect) measure of paternity would be to examine the extent to which children ostensibly sired by circumcised males exhibit a higher incidence of paternal resemblance (Platek, Burch, Panyavin, Wasserman, and Gallup, 2002).

The Piggy Backing Hypothesis

Another intriguing implication of the difference between circumcised and intact males is the question of self-cuckoldry. Put another way, is it possible (short of artificial insemination) for a women to become pregnant by a man she never had sex with? We think the answer is "yes."

If an uncircumcised man (Male B) were to have sex with a women (Female A) who recently had sex with another man (Male A), in the process of thrusting his penis back and forth in her vagina some of Male A's semen would be forced under Male B's frenulum, collect behind his coronal ridge, and be displaced from the area proximate to the cervix. After Male B ejaculates and substitutes his semen for that of the other male, as he withdraws from the vagina some of Male A's semen will still be present on the shaft of his penis and behind his coronal

ridge (see Ordinal Ejaculation Effects above). As his erection subsides the glands penis will withdraw under the foreskin, raising the possibility that some of Male A's semen could be captured underneath the foreskin and behind the coronal ridge in the process. Were Male B to then have sex with Female B several hours later, it is possible that some of the displaced semen from Male A would still be present under his foreskin and thus may be unwittingly transmitted to Female B who, in turn, could then be impregnated by Male A's sperm. Were Male B circumcised, this would be a far less likely outcome because the residual foreign sperm on his penis would not be afforded the protection by the foreskin from desiccation, light, and cooling and would likely perish during the interim separating sexual encounters with different partners.

The transfer of another male's semen from one female to the next as a consequence of genitals specialized for sperm removal, is also known as fertilization by proxy, and has been documented in insects (Haubruge, Arnaud, Mignon, and Gage, 1999). If the foreskin makes the human penis a vector for fertilization by proxy, why is the foreskin still there? We assume that during human evolutionary history the incidence of self-cuckoldry was not high enough to offset either the advantages of semen displacement or the advantages of the foreskin, which affords protection of the glans. Indeed, it is possible that the adaptive problems posed by the existence of piggybacking semen from rival males led to compensatory adaptations that incapacitate foreign sperm. For example, it would be interesting to determine if smegma, a glandular discharge that collects under the foreskin and lubricates the glans, has spermicidal properties. Alternatively, because smegma tends to be sticky and viscous it may entrap piggybacking sperm from rival males and minimize self-cuckoldry.

Adaptations to self-semen displacement

A potential pitfall of the displacement hypothesis is the problem posed by 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) strongly 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 is predicated on identifying putative collateral mechanisms that serve to minimize the likelihood of self-semen displacement.

Obvious candidate mechanisms 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 ensuing penile hypersensitivity, continued thrusting for many males can become unpleasant and even mildly aversive following ejaculation (e.g., Aversa, Mazzilli, Rossi, Delfino, Isidori, and Fabbri, 2000). Post-ejaculatory thrusting may also be

diminished as a consequence of an inability to sustain an erection. Typically within the first minute after ejaculation half of the erection is lost, and many males experience complete penile tumescence (Byer, Shainberg and Galliano, 1999). The refractory period, as measured by the inability to achieve another erection following ejaculation, varies with age, lasts from 30 minutes to 24 hours (Rathus, Nevid and Fichner Rathus, 2000), and also qualifies as an obvious adaptation that would serve to minimize self-semen displacement. It is interesting that the “Coolidge effect” as measured by an abbreviated refractory period, is usually a consequence of an opportunity to mate with a different female, and as such precludes the problem of self-semen displacement.

As still another corollary adaptation to self-semen displacement, we predict that males who continue to thrust past the point of ejaculation will show post-ejaculatory thrusting that is noticeably shallower and less vigorous. In contrast to deep thrusting, Gallup et al. (2003) found that shallow thrusting with prosthetic genitals failed to produce semen displacement.

Finally, one practical implication of this analysis of self-semen displacement would be to advise couples with infertility problems to refrain from engaging in post-ejaculatory thrusting. Indeed, it would be interesting to see if patterns of robust post-ejaculatory thrusting are more common among couples experiencing fertility problems.

Semen coagulation

Semen coagulates within seconds after ejaculation and then liquefies or decoagulates about 15-30 minutes later (Mandal and Bhattacharyya, 1985; Robert and Gagnon, 1999). While semen hyperviscosity is associated with infertility (Gonzales, Kortebani and Mazzolli, 1993), the first part of the ejaculate does not typically coagulate, only the last fraction (Baker and Bellis, 1995). Baker and Bellis speculate that this keeps the semen in place while sperm travel to the cervix, and at the same time prevents the passage of rival sperm from subsequent males.

As evidence that semen coagulation may have emerged (in part) as a sperm competition tactic that functions to block sperm from rival males, Dixon and Anderson (2002) examined semen coagulation and copulatory plugs in 40 species of primates. Coagulation rates were highest in species where females commonly mate with multiple partners, and lowest in those where females are primarily monogamous or belong to polygynous groups. Likewise, Mandel and Bhattacharyya (1986) measured semen coagulation in humans, and found that if the male had not ejaculated in the previous two days liquefaction times were significantly decreased. Thus, by implication, men who copulate frequently (which may include multi-partner matings) deposit semen that coagulates for longer periods of time.

The data derived from artificial genitals (Gallup et al., 2003) also show that viscous semen is more difficult to displace, and as a consequence another function of semen coagulation may be to minimize self-semen displacement and/or displacement by other males.

Implications for premature ejaculation

The latency between insertion of the penis into the vagina and the occurrence of ejaculation in humans ranges from 2 minutes to an hour (Michael, Gagnon, Laumann, and Kolata, 1994). The average duration of coitus is 7.9 minutes (Grenier and Byers, 2001), with 100 to 500 thrusts per encounter (Hrdy and Whitten, 1987). Premature ejaculation is one of the most common forms of male “sexual dysfunction,” affecting as many as one in four men (Laumann, Gagnon, Michael, and Michaels, 1994). Premature ejaculation takes two forms. The least common is when the male ejaculates prior to achieving intromission. The other is when ejaculation occurs upon or shortly after insertion of the penis into the vagina. Men who suffer from this form of premature ejaculation have an average ejaculation latency of 1.1 minutes following intromission (Spiess, Geer and O’Donohue, 1984).

Ejaculation that occurs outside the vagina is reproductively nonfunctional. However, after achieving intromission, selection may have operated to minimize the amount of time it takes to inseminate a female; i.e., premature ejaculation may have been ancestrally adaptive. Indeed, one article that champions this hypothesis is entitled “Survival of the Fastest” (Hong, 1984). This thesis is based on the fact that there are a number of potential costs associated with extended bouts of copulation. For example, the longer it takes to ejaculate the greater the risk of predation, the greater the likelihood of detection by jealous mates or offended kin, and the more one might have to contend with competition or interference from other sexually aroused males.

On the other hand, these potential costs have to be weighed against the existence of several compensatory benefits that might accrue to sexual encounters of longer duration. As the duration of coitus increases, the likelihood of female orgasm also increases, and it has been theorized that the vaginal and uterine contractions that accompany orgasm in females may be conducive to sperm uptake, transport, and retention (Baker and Bellis, 1993). From the standpoint of sperm competition, another benefit of extended periods of copulation would be more effective displacement of rival semen from the female reproductive tract. Indeed, premature ejaculation can be thought of as a failure to achieve semen displacement. This line of reasoning leads us to predict that among males with premature ejaculation, jealousy induction procedures (such as watching pornography which features infidelity) might antagonize such symptoms.

It is interesting that Spiess, Geer, and O’Donohue (1984) found men who

suffer from premature ejaculation had fewer sexual encounters. Indeed, the longer they went without intercourse, the more prone they were to premature ejaculation. Thus, sexually disadvantaged males appear to be at greater risk of premature ejaculation. Perhaps premature ejaculation functions as an adaptive mechanism that enables subordinate males to minimize the risk of detection and retaliation by dominant/rival males during opportunistic sexual encounters.

Impact of semen displacement on female reproductive strategy

On the basis of retrospective reports from both males and females, Gallup et al. (2003) found that human males often modify the use of their penis under conditions in which their long-term female partner may have been unfaithful. Using anonymous surveys of sexually active college students, it was determined that when males accused their partner of cheating, or when the couple had been separated for a period of time, many males thrust deeper, quicker, and more vigorously than during a typical sexual encounter.

Like many other features of the displacement hypothesis, this has interesting implications for future research. For example, we would predict that the sexual behavior of chronically or pathologically jealous men would feature strategies that might produce greater displacement; e.g., deeper and more vigorous thrusting. It would also be interesting to determine whether displacement behaviors are sensitive to contextual cues. Are there fluctuations in displacement behaviors that reflect cyclic changes in female receptivity? Do parameters of female attractiveness (facial features, waist to hip ratio, age, fecundity) affect displacement behaviors? Does variation in paternal resemblance among a male's ostensible offspring affect semen displacement behavior?

If females use extra-pair copulations with alpha males to cuckold their mates, the resident male's capacity for competing with and displacing the interloper's semen puts the reproductive best interests of the resident male and female at odds with one another. The effectiveness of sperm competition strategies in general, and semen displacement in particular, is time dependent (i.e., related to the elapsed time since the extra-pair copulation). Therefore, if semen displacement and other sperm competition strategies have been featured prominently during human evolutionary history, we would expect the desired timing of in-pair copulations by males and females following a female extra-pair encounter to be very different. Other things being equal, the effectiveness of sperm competition ought to be inversely proportional to the amount of time that has elapsed since insemination by the extra-pair male. Therefore, following an extra-pair encounter we would expect females to attempt to postpone copulation with the resident male, as an evolutionary strategy for minimizing sperm competition and increasing the likelihood of impregnation by the extra-pair male. Just the opposite strategy would hold true for males. We predict resident males who have

reason to suspect female infidelity would attempt copulation immediately with their partner following a possible extra-pair encounter, as an adaptation to displacing and substituting their semen for the interloper's. In support of both these predictions, Goetz and Shackelford (in press) have uncovered preliminary evidence that a substantial proportion of wife rapes involve husbands who suspect their wives had been unfaithful.

Thus, as illustrated by the different predictions we derive in this paper, the possibility that semen displacement may function as a sperm competition strategy among human males serves to both integrate many diverse features of human sexuality, and it can be used to generate a number of testable hypotheses.

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