Semen Displacement as a Sperm Competition Strategy

Multiple Mating, Self-Semen Displacement, and Timing of In-Pair Copulations

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Using a sample of 652 college students, we examined several implications of the hypothesis that the shape of the human penis evolved to enable males to substitute their semen for those of their rivals. The incidence of double mating by females appears sufficient to make semen displacement adaptive (e.g., one in four females acknowledge infidelity, one in eight admit having sex with two or more males in a 24-hour period, and one in 12 report involvement in one or more sexual threesomes with two males). We also document several changes in post-ejaculatory behavior (e.g., reduced thrusting, penis withdrawal, loss of an erection) which may have evolved to minimize displacement of the male's own semen. Consistent with predictions derived from a theoretical model (Gallup and Burch 2006), we discovered that most females report waiting at least 48 hours following an instance of infidelity before resuming sex with their in-pair partners.

KEY WORDS: Cuckoldry; Double mating; Genital morphology; Paternity; Post-ejaculatory changes; Sperm competition

In humans, ovulation is not accompanied by salient external signals and fertilization occurs internally. As a consequence, females have a considerable reproduc-

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tive advantage over males. Whereas maternity is always certain, males have to contend with uncertain paternity—in other words, the possibility of their partners producing offspring sired by other males. Gallup and Burch (2006) present four categories of human paternal assurance strategies that may have evolved to deal with this problem and minimize the chances of males investing in offspring other than their own (see also Shackelford, Pound, and Goetz 2005).

The first and perhaps most obvious class of paternal assurance strategies involves *insemination prevention,* which includes mate guarding (Buss 2002), male sexual jealousy (Daly et al. 1982), and various other techniques (e.g., chastity belts, infibulation) used to discourage or preclude female infidelity. However, if these tactics fail and the female is inseminated by another male, there is a second class of *counter-insemination* strategies, which include sperm competition (e.g., Shackelford 2003) and semen displacement (Baker and Bellis 1995). These function to reduce the likelihood of conception by the rival male. Should these mechanisms fail and the female is impregnated by another man, the third category of paternal assurance strategies involves *pregnancy termination,* which can involve pregnancy-induced domestic violence (Burch and Gallup 2004) and coitus-induced uterine contractions that interfere with embryo implantation (for details, see Gallup and Burch 2006). Finally, if the pregnancy prevails and a child is born, the remaining class of paternal assurance strategies involves *differential investment* by the resident male, which can include neglect, abandonment, child abuse, or even infanticide. There is growing evidence, for example, that males are sensitive to paternal resemblance and invest preferentially in infants with whom they share facial features (Platek et al. 2003).

The focus of this paper is on counter-insemination strategies—more specifically, mechanical means by which semen from rival males may be displaced from the cervical area of the vagina, thereby enabling the male to substitute his semen for those of his rivals. A leading candidate mechanism mediating semen displacement is the shape and/or configuration of the human penis (Baker and Bellis 1995). Compared with the penis of our closest living relative, the chimpanzee, the human penis is longer, wider, and includes a distinctively bulbous glans or head. At the junction between the shaft of the penis and the head is a protrusion which encircles the base of the glans called the coronal ridge. According to the semen displacement hypothesis, thrusting of the penis back and forth in the vagina forces foreign semen behind the glans. As a result, the coronal ridge acts to scoop semen left by other males away from the cervix, enabling the male to replace rival semen with his own.

By simulating sexual intercourse using artificial genitals, this hypothesis was recently tested under laboratory conditions (Gallup et al. 2003). To assess semen displacement, different latex vaginas were loaded with a fixed volume of simulated semen. Artificial phalluses of different shapes and sizes were then inserted into the vaginas and the volume of simulated semen displaced from the cervical end of the vagina was measured. The displacement of simulated semen varied as a function of

the shape of the phallus, with those resembling the human penis producing significantly greater displacement. The volume of semen displacement was also proportional to the depth of thrusting, and the presence of the coronal ridge proved to be an important morphological feature involved in promoting semen displacement. Based on surveys administered to sexually active participants, Gallup et al. (2003) also found compensatory changes in male sexual behavior under conditions that increase the likelihood of insemination by rival males. Following allegations of female infidelity or periods of separation, the majority of males and females reported increases in both the depth and vigor of thrusting (see also Goetz et al. 2005).

The present study was conducted to examine additional implications of the semen displacement hypothesis. First, this hypothesis implies that patterns of female multiple mating were present during human evolution; in other words, there were recurrent situations in which females were inseminated by two or more males in relatively close temporal proximity. Another implication of this hypothesis is that there are mechanisms that become operational during the post-ejaculatory period that function to minimize displacement of the male's own semen. Finally, the ever-present prospect of counter-insemination strategies by the resident male may have affected female reproductive strategies in ways that favor rival semen.

METHODS

The subjects consisted of 652 undergraduate college students from the State University of New York at Albany and the State University College at Oswego, New York. Those that reported being homosexual were excluded from the analyses, resulting in 479 female and 117 male respondents. Subjects were asked to fill out an anonymous survey that was approved by the respective local Institutional Review Boards concerning targeted features of their sexual behavior and sexual experiences. The survey consisted of questions that could be answered "yes" or "no" ("Have you ever experienced sexual intercourse?"), open-ended questions (e.g., "How often do you have sexual intercourse?"), and questions with Likert-like response alternatives (e.g., "When cheating on my partner, my orgasm is: (*a*) less intense, (*b*) about the same intensity, (*c*) more intense, (*d*) I do not experience an orgasm").

RESULTS

The majority of males (88.2%) and females (87.5%) reported having experienced sexual intercourse. Most of the males (62.6%) and females (72.6%) also reported being in a committed sexual relationship. For those in committed relationships, males reported a mean frequency of sexual intercourse of 2.33 times per week (s.d. = 1.89) and females reported having sex 2.87 times per week (s.d. = 2.01).

Multiple Mating by Females

Multiple mating means having sex under conditions that could lead to the presence of viable semen from more than one male in the female reproductive tract. We used a conservative definition of multiple mating as having sex with two or more males within 24 hours of one another (see Discussion).

Among females who were sexually active the mean number of lifetime sexual partners was 5.31 (s.d. = 5.30). Almost one in four females (24.9%) who had been in a committed relationship reported at least one extra-pair copulation. In response to the question "Have you ever had sex with two or more males within 24 hours?" more than one in eight females (13.4%) indicated that they had. As to the issue of concurrent sex with multiple partners, approximately one in 12 females (8.3%) admitted to having participated in at least one sexual threesome involving two males. Finally, one in 33 females (3.1%) indicated participation in group sex with three or more male partners.

Mechanisms That Minimize Self-Semen Displacement

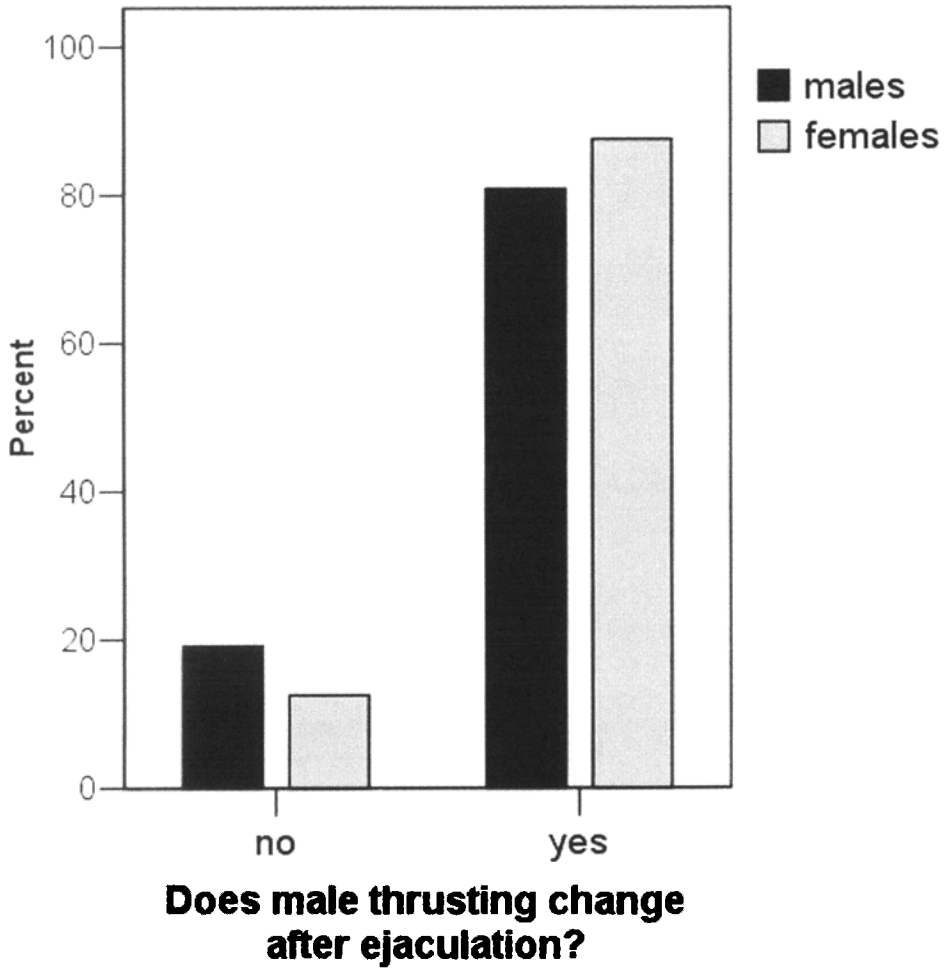
In response to the question "Does thrusting change after ejaculation?" the majority of males and females indicated that it does (Figure 1). In terms of the specific changes, 88.1% of the males and 86.2% of the females report that the speed of thrusting diminishes following ejaculation. Also, most respondents (62.0% of the males and 60.1% of the females) indicated that thrusting becomes noticeably shallower.

In response to the question "Do you know when your partner ejaculates?" 92.5% of the females said they did. Interesting effects emerged in response to the follow-up question, "How do you know when your partner ejaculates?" (Table 1). Four of the eight indicators involved penile changes: diminished thrusting, changes in thrusting depth, loss of thrusting rhythm, and loss of an erection. Indeed, penile changes were listed as the principal means of inferring ejaculation by almost half (44.5%) of the females. A reduction in the speed of thrusting was the second most common indicator listed by females as the cue that enabled them to sense ejaculation on the part of their partner(s).

Experiencing penis hypersensitivity following orgasm was reported by 60.4% of the males, and most males indicated that the increase in genital sensitivity they experience following orgasm occurs within 30 seconds. As an ostensible consequence of penile hypersensitivity, more than a third of the males (35.6%) and 42.0% of the females report that the penis is typically withdrawn from the vagina within a "few seconds" after ejaculation. Almost three out of four males (74.6%) and females (72.7%) report penis withdrawal within one minute.

Loss of penile tumescence following ejaculation is another common post-ejaculatory response which may function to diminish displacement of the male's own

Figure 1. Percentages of males and females who notice a difference in thrusting following ejaculation.



semen. Whereas only 6.7% of the males acknowledge losing their erection within a few seconds, almost four times as many females (23.0%) report the loss of their partner's erection within a few seconds ($\chi^2 = 10.65, p < .05$). The loss of an erection within a minute after ejaculation was reported by roughly the same proportion of males (44.9%) and females (48.3%) in our sample, and almost all the females (92.6%) indicated that their partner's erection is lost within a few minutes (Figure 2).

The inability to achieve another erection, known as the refractory period, also bears on the question of self-semen displacement (Gallup and Burch 2004). For females who responded (14.7%) to the open-ended question "After the erection is lost, how soon until another erection occurs?" the mean refractory period was 59.0 minutes with a range of 5 to 480 minutes.

Table 1. How Do You Know When Your Partner Ejaculates?

Ejaculatory Cue	*Percent**
Changes in face or body	31.6
Changes in thrusting speed	19.9
Feel the ejaculate	16.2
Changes in thrusting depth	14.7
Partner tells me	13.2
Feel my partner's orgasm	9.9
Loss of thrusting rhythm	7.0
Loss of erection	2.9

* The sum of the percentages exceeds 100 because respondents could indicate more than one cue.

Timing of In-Pair Copulations Following Extra-pair Encounters

Whereas only one in seven (15.4%) males reported an extra-pair copulation, one in four (24.9%) females reported having sex with one or more other males while being in a committed relationship ($\chi^2 = 3.72$, $p < .05$). As evidence that a sexual encounter with another male makes females relatively refractory for an in-pair en-

Figure 2. Percentages of males and females reporting that loss of penile tumescence as a function of time since ejaculation.

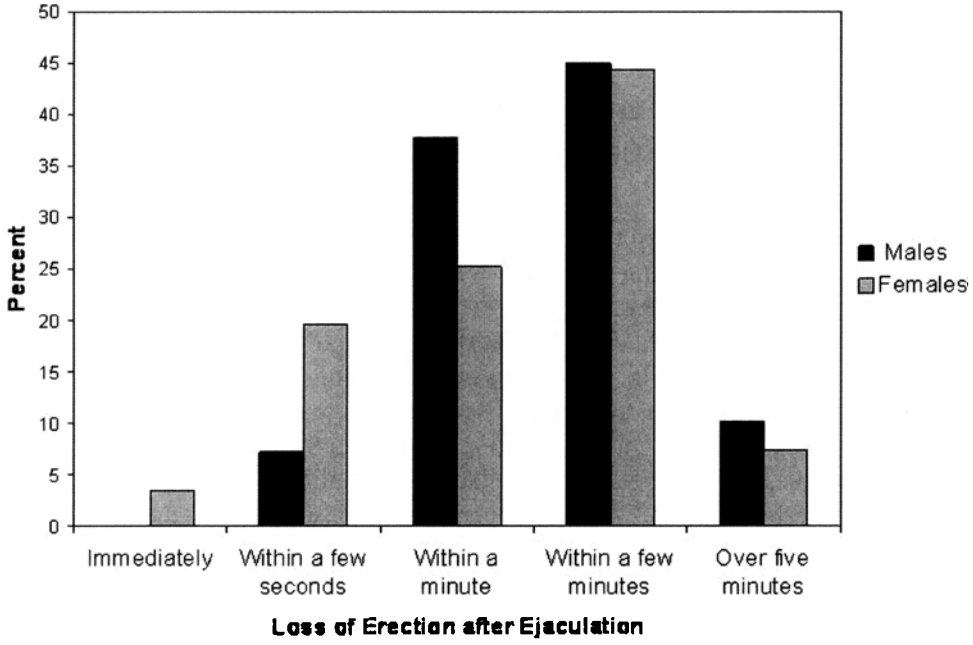
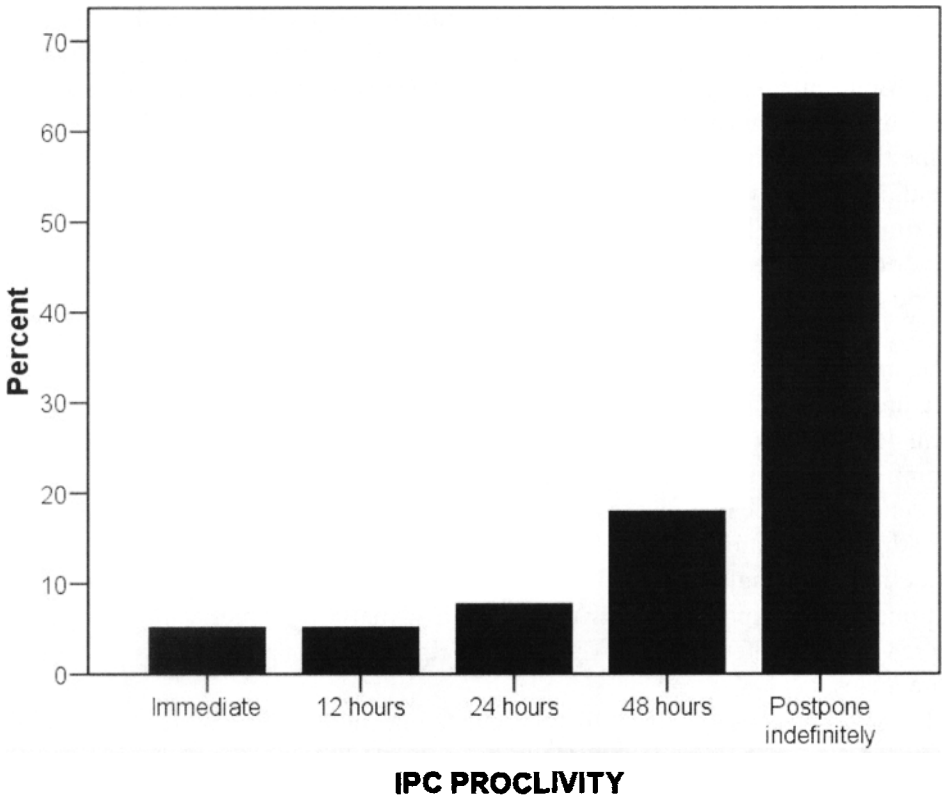


Figure 3. Percentages of females waiting various lengths of time to have sex with their in-pair partner following sex with another male.



counter, almost two thirds (64.1%) of the females who ever cheated reported attempting to postpone having sex indefinitely with their committed partner following an extra-pair copulation (Figure 3).

When asked if they had "ever thought that their romantic partner was cheating on them," 48.0% of the males and 42.7% of the females indicated having had suspicions of sexual infidelity by their partners. The reasons given for suspecting infidelity included attempts by their partner to avoid them (reported by 41.6% of the males and 26.3% of the females), and lack of sexual desire by their partner (reported by 37.5% of males and 12.1% of females).

Whereas only 15.4% of the males described the orgasm they experienced as a result of an extra-pair copulation as being more intense than an in-pair copulatory orgasm, three times as many females (47.9%) reported more intense orgasms as a consequence of having sex with someone else while being in a committed relationship ($\chi^2 = 13.08, p < .001$).

DISCUSSION

Were there occasions during human evolutionary history when females had sex with multiple males in close temporal proximity? Both sperm competition and semen displacement presuppose what Baker and Bellis (1995) term "double mating," whereby females have sexual encounters with multiple males within a limited time frame that leads to the presence of viable sperm from more than one male in the female reproductive tract. There is little consensus, however, about the extent of this time frame. Whereas Baker and Bellis define double mating as having sex with two or more males within a period of three days, Smith (1984) argues for a period extending as long as seven to nine days.

Evidence concerning the effects of temperature shows that while human sperm can survive in vitro for as long as 24–48 hours at room temperature, at body temperature survival rarely exceeds 12 hours (Appell, Evans, and Blandy 1977; Makler et al. 1981). As a consequence, we adopted a conservative definition of double mating as having sex with two or more males within 24 hours. Nonetheless, the incidence of double mating among college females in our sample was still substantial. Almost one in four coeds who had been in committed relationships admitted to infidelity, one in eight reported having sex with two or more males within 24 hours, and one in 12 acknowledged involvement in sexual threesomes with two males. There were even a few females who had participated in group sex involving three or more males.

There are reasons to believe that these data may underestimate the incidence of double mating in the population (Gallup and Burch 2006). First, even with the assurance of confidentiality and anonymity, females have little to gain by being candid about their sexual indiscretions. Second, undergraduates may be relatively naive and sexually inexperienced compared with more mature women. For instance, using a more heterogeneous sample that included older females, Baker and Bellis (1995) found that approximately 30% report having had sex with two males within 24 hours. Among chimpanzees, our closest living relatives, concurrent mating by females with multiple male partners is common (Tutin 1979). For several days each month when female chimpanzees are in estrus, it is not unusual for them to be inseminated repeatedly by most of the available males in the vicinity. Therefore, it is reasonable to suppose that the incidence of double mating may not have been uncommon during earlier phases of human evolution.

In a recent review of the literature on human nonpaternity, Anderson (2006) has shown that nonpaternity, as an index of infidelity among females, is a cross-cultural universal. Based on nonpaternity rates, the incidence of female infidelity does not appear to vary significantly as a function of either culture or geography. However, Anderson found that the incidence of nonpaternity does vary as a function of paternal confidence. Among males with high paternity confidence, the rate of nonpaternity is about 2%, whereas among males with low paternity confidence

it is 15 times higher (30%). Thus, there may be psychological mechanisms that function to inform males about variation in the likelihood/risk of nonpaternity.

One problem with the semen displacement hypothesis is that the penis would not only serve to displace semen left by other males, but the same fate would be met by the male's own semen. What is to prevent the penis from displacing the male's own semen? As we predicted (Gallup and Burch 2004), the results of this survey provide evidence for an ensemble of post-ejaculatory mechanisms that may minimize this problem. Both male and female respondents noted that thrusting becomes shallower following ejaculation. Under laboratory conditions with artificial genitals, we found that shallow thrusting greatly diminishes, if not eliminates, the displacement effect (Gallup et al. 2003). Likewise, respondents report that speed of thrusting also diminishes following ejaculation. Almost two-thirds of the males report experiencing penile hypersensitivity following ejaculation, and, as a consequence, most of the male and female respondents indicated that the penis is withdrawn from the vagina shortly after ejaculation. As further evidence for post-ejaculatory changes that negate continued thrusting, one in four females report the loss of their partner's erection within a few seconds after ejaculation, and almost all of the females noted the loss of their partner's erection within a few minutes following ejaculation (Figure 2). Finally, according to the females, the average amount of time required for their partner to achieve another erection following ejaculation was approximately one hour. In the context of sperm competition theory, it is interesting to note that the length of the refractory period may vary as a function of the sociosexual context. In pigtailed macaques, for example, the refractory period is reduced by as much as 60% of normal control values if males observe another monkey copulating with their female partners (Busse and Estep 1984).

When it comes to infidelity, the reproductive interests of males and females are sometimes at odds. Sperm competition and semen displacement may represent counter-insemination strategies that increase the likelihood of paternity by resident males. Therefore, it is possible that females have evolved compensatory reproductive strategies that give priority to rival male semen. That is, if females had extra-pair copulations during human evolutionary history that functioned to cuckold their mates and thereby enabled them to produce offspring sired by higher-quality males and/or achieve greater genetic variance among their offspring, then we might expect females to have been selected to postpone copulation with their resident partner following a sexual encounter with another male (Gallup and Burch 2006).

In support of this expectation, we found that more than 80% of the females who committed infidelity said that they waited at least 48 hours following an extra-pair copulation before having sex with their in-pair partner. But do females delay in-pair copulations following extra-pair copulations longer than they do following in-pair copulations? Two thirds of the females in our sample reported attempting to postpone sex indefinitely with their committed partner following an instance of infidelity (Figure 3). If females attempted to delay sex as long as possible with their committed sexual partners following in-pair copulations, chances are they would

not be able to maintain those relationships. Thus, reluctance to have sex with their in-pair partner on the heels of infidelity may be a unique adaptation that functions to minimize sperm competition and semen displacement, and thereby enhance the female's chances of conceiving by the rival male. It is interesting that this effect may have exerted reciprocal selection pressure on males to evolve counter adaptations (see also Goetz and Shackelford, this issue). For instance, almost half of both the male and female respondents in our survey reported suspicions of infidelity, and more than 30% of the males indicated that their suspicions were triggered by an apparent lack of sexual desire on the part of their female partners.

The reluctance on the part of females to have sex with their in-pair partners following extra-pair encounters also has implications for sperm competition theory. Contrary to the hypothesis and data presented by Baker and Bellis (1995) suggesting that females sometimes promote sperm competition between in-pair and extra-pair partners, our results suggest that females may take steps to minimize sperm competition. Whereas females may have something to gain by using high-quality extra-pair males to sire some of their offspring, they have nothing to gain from sperm competition per se.

Finally, it is interesting to note that three times as many females as males reported experiencing more intense orgasms as a result of extra-pair copulations in contrast to in-pair copulations. Baker and Bellis (1995) speculated that female orgasm may increase the chances of conception as a consequence of vaginal and uterine contractions that facilitate the movement of sperm up through the female reproductive tract. If that turns out to be the case, more intense female orgasms could selectively promote conception by rival males.

Our use of single-item assessments of unknown reliability and our reliance on data collected from college students represent potential limitations of the present study. As to the question of reliability, however, it is important to note that our results are based on a large sample of respondents, and the results were consistent (both within and between sexes) across many of the questions (e.g., Figures 1 and 2). But how representative are the results? In many respects, our data on double mating among females are comparable to those obtained by Baker and Bellis (1995) using a much more heterogeneous sample that included more mature respondents. Likewise, in terms of more traditional measures of sexual behavior among college students (e.g., the proportion of students who have engaged in sexual intercourse, frequency of intercourse, and number of sex partners), our sample is comparable to those in other recent studies (see, for example, Douglas et al. 1997; Laumann et al. 1994; Poulson et al. 1998; Weinberg, Lottes, and Shaver 1995).

In conclusion, the incidence of double mating by female college students, the variety of changes reported by both males and females in post-ejaculatory behavior, and the apparent attempt by females to postpone in-pair copulation following extra-pair encounters are all consistent with a history of human sperm competition in general and semen displacement in particular.

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