Running Head: HUMAN SPERM COMPETITION

Mate Retention, Semen Displacement, and Human Sperm Competition: Tactics to Prevent and Correct Female Infidelity

Aaron T. Goetz, Todd K. Shackelford, and Viviana A. Weekes-Shackelford

Florida Atlantic University

Harald A. Euler and Sabine Hoier

University of Kassel, Germany

David P. Schmitt

Bradley University

The first and second authors contributed equally to this article. Address correspondence to Aaron T. Goetz or Todd K. Shackelford, Florida Atlantic University, Department of Psychology, 2912 College Avenue, Davie, Florida 33314, United States; Tel 954-236-1179, Fax 954-236-1099, Email agoe1772@fau.edu (Goetz) or tshackel@fau.edu (Shackelford).

Abstract

Sperm competition is the competition between the sperm of two or more males to fertilize a female's egg(s). In humans, female physical attractiveness and personality characteristics that attract rival males may increase the likelihood of female sexual infidelity and, therefore, place her partner at a high recurrent risk of sperm competition. We examined how males under a high recurrent risk of sperm competition might solve the adaptive problems of preventing and correcting a female partner's sexual infidelity. Using a self-report survey, 463 males in committed, sexual relationships rated their partner's physical attractiveness and personality characteristics, and reported their use of tactics designed to prevent partner infidelity (mate retention tactics) and their use of specific copulatory behaviors arguably designed to remove or displace the semen of rival males (semen-displacing behaviors). As hypothesized, males mated to females who place them at a high recurrent risk of sperm competition were more likely to use mate retention tactics and to perform semen-displacing behaviors. Results suggest that preventative and corrective tactics are complementary tactics designed to solve the adaptive problem of sperm competition. Discussion addresses limitations of this study and directions for future work.

Key words: Human sperm competition, mate retention, semen displacement

Mate Retention, Semen Displacement, and Human Sperm Competition: Tactics to Prevent and Correct Female Infidelity

Competition between males to fertilize a female's egg(s) can occur before, during, and after copulation (Parker, 1970; and see Birkhead & Møller, 1998). When the sperm of two or more males simultaneously occupy the reproductive tract of a female and compete to fertilize her egg(s), sperm competition occurs (Parker, 1970). Sperm competition has been documented or inferred to exist in many species, ranging from molluscs (Baur, 1998) and insects (Simmons, 2001) to birds (Birkhead & Møller, 1992) and humans (Baker & Bellis, 1993, 1995).

For species that practice social monogamy, the mating system in which males and females form long-term pair bonds but also pursue extra-pair copulations (e.g., most birds and humans), female sexual infidelity creates the primary context for sperm competition (Birkhead & Møller, 1992; Smith, 1984). Males of such species may have adaptations that decrease the likelihood that a rival male's sperm will fertilize his partner's egg(s)—adaptations that decrease the likelihood of being cuckolded, unwittingly investing resources in genetically unrelated offspring. Baker and Bellis (1993), for example, demonstrated that human males may have physiological adaptations that function to increase the likelihood that their sperm will out-compete rival sperm to fertilize their partner's egg(s). In a study of couples in committed, sexual relationships, Baker and Bellis documented that, at the couple's next copulation, males inseminated more sperm when the couple had spent a lesser proportion of their time together since their last copulation. As the proportion of time together decreases, the likelihood of female infidelity increases, creating a higher risk of sperm competition (Baker & Bellis, 1995). Inseminating more sperm following a separation may function to outnumber or "flush out" rival

sperm that may be present in the reproductive tract of the female (Baker & Bellis, 1995; Parker, 1970).

This temporally variable risk of sperm competition produces specific physiological responses apparently designed to "correct" any female sexual infidelity that might have occurred while the couple was separated. Some males, however, may be mated to females who *recurrently* place them at a high risk of sperm competition. Female physical attractiveness and certain personality characteristics that attract rival males, for example, may increase the likelihood of female sexual infidelity and, therefore, place her partner at a high recurrent risk of sperm competition. Because a female's physical attractiveness indexes her reproductive value and fertility (Buss, 1994; Singh, 1993; Symons, 1979), physically attractive females are desired partners for long-term, short-term, and extra-pair mateships (Buss, 1989; Buss & Schmitt, 1993; Li, Bailey, Kenrick, & Linsenmeier, 2002; Regan, Levin, Sprecher, Christopher, & Cate, 2000). Accordingly, physically attractive females are more likely to have had males try to poach them away from their current partners (Schmitt & Buss, 2001), and males married to more physically attractive females devote more effort to retaining their mates (Buss & Shackelford, 1997).

Another set of factors that may place a male at a high recurrent risk of sperm competition is his partner's personality traits. The five-factor model of personality describes five dimensions of stable individual differences in personality (Surgency, Agreeableness, Conscientiousness, Emotional Stability, and Openness to Experience; Goldberg, 1982; Norman, 1963). Schmitt and Buss (2001) found positive relationships between a female's Surgency and Openness to Experience and the likelihood of having had someone try to poach her away from an existing mateship. Females who are dominant, independent, and sociable (high in Surgency) and curious, creative, and knowledgeable (high in Openness to Experience) are more likely to have received

mate poaching attempts. Similarly, Gangestad and Simpson (1990; and see Schmitt, 2002) found that females who are more socially dominant and extroverted (high in Surgency) were more willing to have sex without indicators of commitment and emotional closeness. Females who are higher in Surgency and Openness to Experience, therefore, are more often given the opportunity to engage in extra-pair copulations. No data exist on the relationship between physical attractiveness, Surgency, and Openness to Experience and the actual occurrence of infidelity, but because infidelity can only occur if the opportunity for infidelity exists, a greater opportunity for infidelity translates, on average, to a greater probability of infidelity. Although not all infidelity generates sperm competition, the occurrence of sperm competition depends, in large part, on female infidelity (Baker & Bellis, 1995; Smith, 1984).

In summary, males mated to females who are physically attractive or high in Surgency and Openness to Experience may face a high recurrent risk of sperm competition. Ancestral males mated to such females would have reaped reproductive benefits if they were able to prevent or correct their partner's sexual infidelity.

Mate Retention Tactics

One solution to the adaptive problem of sperm competition is for males to prevent a partner from being sexually unfaithful (Buss, 1988; Buss & Shackelford, 1997; Flinn, 1988). Buss (1988) identified 19 tactics that people use to guard or to retain their mates, ranging from vigilance over a partner's whereabouts to violence against rivals. Males and females, for example, give to their partners ornaments such as promise, engagement, or wedding rings that signal to others involvement in a romantic relationship. Also, males and females, but particularly males, attempt to prevent partner infidelity by concealing their partner (e.g., refusing to introduce a partner to same-sex friends).

Because only females of reproductive age are able to cuckold their partners, Buss and Shackelford (1997) predicted and documented that male mate retention tactics are more frequent and more intense with partners of high reproductive value, as indicated by the female's youth and physical attractiveness. Gangestad, Thornhill, and Garver (2002) demonstrated that males increase the frequency and intensity of their mate retention efforts during the follicular (high conception risk) phase of their partner's menstrual cycle. Because males adjust their mate retention efforts according to their partner's reproductive value and fertility, perhaps male mate retention tactics also are sensitive to the recurrent risk of sperm competition. This leads to the first hypothesis.

Hypothesis 1: Recurrent risk of sperm competition is related positively to the use of mate retention tactics.

Semen-Displacing Behaviors

Because tactics to prevent a female partner's infidelity are sometimes unsuccessful, male psychology may include mechanisms designed to "correct" a female partner's infidelity (LeBlanc, Shackelford, & Weekes, 1999; Shackelford, 2002). Inspired by Baker and Bellis's (1993) demonstration of male *physiological* adaptations to sperm competition, Shackelford et al. (2002) documented that human male psychology may include *psychological* adaptations to decrease the likelihood that a rival male's sperm will fertilize a female partner's egg(s). For example, males who spent a greater (relative to males who spent a lesser) proportion of time apart from their partner since the couple's last copulation rated their partners as more attractive and reported greater interest in copulating with their partners. As the proportion of time spent apart increases, so too does the likelihood of female infidelity (Baker & Bellis, 1995). Perceiving his partner as more attractive and having an increased interest in copulating with his partner may

motivate a male to copulate with his partner as soon as possible, placing his sperm in competition with any rival sperm that may be present in his partner's reproductive tract.

Sperm competition also may have fashioned a psychology that generated specific corrective behaviors designed to increase the likelihood that a male's ejaculate would out-compete a rival's ejaculate if the female had been inseminated recently by a rival (i.e., within the previous five to nine days; see Baker & Bellis, 1995; Smith, 1984). This could have been achieved by removing rival semen that was present in his partner's reproductive tract. There is both theory (Baker & Bellis, 1995; Smith, 1984) and preliminary evidence (Gallup, Burch, Zappieri, Parvez, & Stockwell, 2002) suggesting that the human penis may have evolved as a semen displacement device. Using artificial genitals and simulated semen, Gallup et al. (2002) empirically tested the hypothesis that the human penis was designed by sperm competition to displace semen deposited by other males in the reproductive tract of a female. The results indicated that artificial phalluses that had a glans and coronal ridge that approximated a real human penis displaced significantly more semen (91%) than did a phallus that did not have a glans and coronal ridge (35%). When the penis is inserted into the vagina, the frenulum of the coronal ridge makes possible semen displacement by allowing semen to flow back under the penis alongside the frenulum and collect on the anterior of the shaft behind the coronal ridge (Gallup et al., 2002; see Figure 1). Semen displacement only occurred, however, when phalluses were inserted at least 75% of the way into the artificial vagina.

That the penis must reach an adequate depth before semen is displaced suggests that successfully displacing rival semen requires specific copulatory behaviors. Following allegations of female infidelity or separation from their partners (contexts in which the likelihood of rival semen being present in the reproductive tract is relatively greater), both sexes report that males

thrusted deeper and more quickly at the couple's next copulation (Gallup & Burch, 2002; Gallup et al., 2002). In addition to thrusting deeply and quickly, other copulatory behaviors may be efficient semen-displacing behaviors. Changing sexual positions, for example, sometimes requires the penis to be pulled out of the vagina, potentially pulling out semen in the process. Also, males who thrusted for a longer time during sexual intercourse may have been able to displace more semen, thereby "correcting" a female's recent sexual infidelity. The link between the likelihood of female infidelity and semen-displacing behaviors leads to a second hypothesis.

Hypothesis 2: Recurrent risk of sperm competition is related positively to semen-displacing behaviors.

Tactic Complementarity

Baker and Bellis (1995) documented that, as female age increases (and reproductive value decreases), the rate of in-pair copulation decreases. High in-pair copulatory frequency has been proposed as a "corrective" measure in the context of sperm competition because the relative abundance of sperm from the primary male would outnumber rival male sperm due to differential insemination frequency (Parker, 1984). Although the corrective mechanism of frequent in-pair copulations is different than the proposed corrective mechanism of semen-displacing behavior (i.e., outnumbering rival sperm vs. displacing rival sperm), both tactics can produce the same result: decreasing the likelihood of cuckoldry. Buss and Shackelford (1997) documented that, as female partner's age increases, male mate retention efforts decrease. The findings from Baker and Bellis (1995) and Buss and Shackelford (1997) suggest that males mated to reproductively valuable females use preventative and corrective tactics simultaneously to solve the adaptive problem of sperm competition. There is corroborative, comparative evidence that several bird species that practice a socially monogamous mating system similar to

humans use mate retention and frequent in-pair copulation as complementary paternity guards (see, e.g., Dickinson & Leonard, 1996; Møller, 1987). This leads to a third hypothesis.

Hypothesis 3: Mate retention tactics and semen-displacing behaviors are complementary tactics designed to solve the adaptive problem of sperm competition. The use of mate retention tactics therefore will be related positively to semen-displacing behaviors.

In summary, we collected self-report data from several hundred males in committed sexual relationships living in the United States and Germany to test the hypotheses that males mated to females who place them at a high recurrent risk of sperm competition may solve this adaptive problem through preventative and corrective measures, and that the preventative and corrective measures are complementary, working together to solve the adaptive problem of sperm competition.

Methods

Participants

Four hundred sixty-three males in a committed, sexual relationship with a female participated in this study. Participants were drawn from universities and surrounding communities in the United States and Germany. The mean age of the participants was 24.2 years (SD = 7.9), and the mean age of the participants' partners was 23.0 years (SD = 7.3).

Materials

Participants completed a survey that included several sections. The first section requested demographic information, such as the participant's and partner's age. The second section asked four questions to assess partner attractiveness: How physically attractive do you think your partner is? How physically attractive do other men think she is? How sexually attractive do you think she is? How sexually attractive do other men think she is? Responses were recorded using

a Likert-type scale ranging from 0 (Not at all) to 9 (Extremely). The third section asked questions about the participant's most recent sexual encounter with his partner. Questions designed to assess the participant's copulatory behaviors asked for number of thrusts, deepest thrust, depth of thrusts on average, duration of sexual intercourse, and number of sexual positions initiated by the participant. Responses were recorded using a Likert-type scale ranging from 0 (Lesser/Shorter/Fewer than is typical of me) to 9 (Greater/Longer/More than is typical of me). The fourth section asked how often the participant performed 104 mate retention acts (from Buss, 1988) in the last month, ranging from 0 (Never) to 3 (Often). The final section assessed the participant's partner's standings on the major dimensions of personality, using Botwin, Buss, and Shackelford's (1997) 40-item instrument.

For the German participants, the survey was translated from English to German using the following procedure. A bilingual speaker translated the English language survey into German. A second bilingual speaker, unaware of the contents of the original English language survey, back-translated the German language survey into English. The few resulting translation discrepancies between the original survey and the back-translated survey were resolved between the two bilingual speakers.

Procedure

We sampled participants in two ways. About half the participants received nominal extra credit toward one of several social science courses in exchange for their participation. The remaining half of participants received credit toward a required research participation component of an introductory psychology course. Unfortunately, we did not code for method of data collection and, therefore, cannot include this as a variable in the statistical analyses.

Three criteria must have been met to qualify for participation: the prospective participant must be (1) male, (2) at least 18 years of age, and (3) currently involved in a committed romantic, sexual relationship with a woman. Prospective participants were aware of these participation criteria prior to appearing at a scheduled time and location. Upon the prospective participant's arrival at the schedule time and location, the researcher confirmed that the prospective participant met the three participation criteria.

If the participation criteria were met, the research assistant handed the participant a consent form, the survey, and a 9-inch X 12-inch brown security envelope. The participant was instructed to read and sign the consent form, complete the survey, place the completed survey in the envelope, and then seal the envelope. The participant was instructed not to seal the consent form inside the envelope to maintain anonymity. Finally, the participant was instructed to place the sealed envelope in a box that contained other sealed envelopes. The participant was asked to place the signed consent form in a separate envelope that contained other signed consent forms. The research assistant explained to the participant the purpose of the study, answered any questions, and thanked the participant for his participation.

Results

Several composite variables were created prior to analyses. Partner's attractiveness ($\alpha =$ .85) is the mean of four variables: participant's rating of partner's (a) physical attractiveness and (b) sexual attractiveness, and participant's rating of other males' assessments of partner's (c) physical attractiveness and (d) sexual attractiveness. Semen-displacing behavior ($\alpha = .75$) is the mean of five variables: (a) number of thrusts, (b) deepest thrust, (c) depth of thrusts on average, (d) duration of sexual intercourse, and (e) number of sexual positions initiated by the participant.

Each of the five variables ranged from 0 (Lesser/Shorter/Fewer than is typical of me) to 9 (Greater/Longer/More than is typical of me).

Nineteen mate retention tactics were created using the 104 mate retention acts according to Buss (1988), and the major dimensions of personality were created using Botwin et al.'s (1997) 40-item instrument. Alpha reliabilities for the 19 mate retention tactics varied in this study from $\alpha = .50$ to $\alpha = .84$ (see Table 2). A composite mate retention variable was created ($\alpha = .93$) by averaging responses on the 19 mate retention tactics. Alpha reliabilities for the target personality dimensions were: Surgency, $\alpha = .61$ and Openness to Experience, $\alpha = .63$. A composite recurrent risk of sperm competition variable was created ($\alpha = .53$) by averaging the partner's attractiveness variable, partner's Surgency, and partner's Openness to Experience. Partner's attractiveness was scaled differently from the personality measures, so the three variables were standardized prior to averaging.

Table 1 presents descriptive statistics for the target variables, collapsed across samples and separately for the United States and German samples. Table 1 also displays the results of independent means tests for the differences between the United States and German samples. The participants from the German sample were older than the participants from the United States sample, but their partners did not differ significantly in age. Relative to the German males, the United States males reported a higher recurrent risk of sperm competition, greater use of semen-displacing behaviors, and greater use of mate retention tactics. We analyzed the data separately by country and found that, for every within-country analysis, the results for the United States sample or for the German sample were statistically significant. For presentation efficiency and to capitalize on greater statistical power, we present only the results of analyses performed on data collapsed across country (country-level analyses are available upon request). Although the

hypotheses are directional, we use the more conservative two-tailed significance tests to evaluate the results.

Hypothesis 1 stated that recurrent risk of sperm competition is related positively to the use of mate retention tactics. Consistent with this hypothesis, recurrent risk of sperm competition correlated positively with the use of mate retention tactics, r (461) = .10 ($p < .05$). Males mated to females who place them at a higher recurrent risk of sperm competition reported more frequent use of mate retention tactics. Although the focus of Hypothesis 1 was the relationship between recurrent risk of sperm competition and the broad use of mate retention tactics, we also investigated the relationship between recurrent risk of sperm competition and each of the 19 mate retention tactics (see Table 2) reported by Buss (1988) and Buss and Shackelford (1997). Six of the 19 tactics showed significant positive correlations with recurrent risk of sperm competition (Resource Display, Sexual Inducement, Appearance Enhancement, Love and Care, Verbal Possession Signals, and Physical Possession Signals), and two of the 19 tactics showed significant negative correlations with recurrent risk of sperm competition (Concealment of Mate and Derogation of Mate).

Hypothesis 2 stated that recurrent risk of sperm competition is positively related to semen-displacing behaviors. Consistent with this hypothesis, recurrent risk of sperm competition correlated positively with semen-displacing behaviors, r (461) = .23 ($p < .001$). Males mated to females who place them at a higher recurrent risk of sperm competition reported performing more copulatory behaviors arguably designed to displace rival semen. For reportorial completeness, we also investigated the relationship between recurrent risk of sperm competition and each of the five individual semen-displacing behaviors (see Table 3). All five correlations were significant and positive, ranging from r (461) = .12 to r (461) = .25 (all ps < .05).

Hypothesis 3 stated that the use of mate retention tactics will be related positively to semen-displacing behaviors. Consistent with this hypothesis, the use of mate retention tactics correlated positively with semen-displacing behaviors, r (461) = .17 ($p < .001$). This positive correlation suggests that males used mate retention tactics and semen-displacing behaviors simultaneously. We also investigated the relationship between semen-displacing behaviors and each of the 19 mate retention tactics reported by Buss (1988) and Buss and Shackelford (1997; see Table 2). Ten of the 19 tactics were positively and significantly correlated with semen-displacing behaviors (Commitment Manipulation, Resource Display, Sexual Inducement, Appearance Enhancement, Love and Care, Verbal Possession Signals, Physical Possession Signals, Possessive Ornamentation, Intrasexual Threats, and Violence Against Rivals).

Discussion

Shackelford (2002) proposed three separate adaptive problems associated with sperm competition in human males: preventing a female partner's sexual infidelity, correcting a female partner's sexual infidelity, and anticipating a female partner's sexual infidelity (see also LeBlanc et al., 1999). The current study examined how males might solve the adaptive problems of preventing and correcting a partner's infidelity. More specifically, this study tested the hypotheses that males mated to females who have traits that recurrently place their partners at a high risk of sperm competition may solve this adaptive problem through preventative and corrective measures, and that the preventative and corrective measures are complementary, working together to solve the adaptive problem of sperm competition. Behaviors that functioned to prevent and correct a female partner's sexual infidelity would have been selected for in a socially monogamous species such as humans (Baker & Bellis, 1995; LeBlanc et al., 1999;

Shackelford, 2002; Smith, 1984). We demonstrated that human males perform both preventative and corrective behaviors when under a high recurrent risk of sperm competition.

Females who are physically attractive and have personality characteristics that attract rival males are more often given the opportunity to be sexually unfaithful, thereby placing their partners at a higher recurrent risk of sperm competition (Schmitt & Buss, 2001; see also Schmitt & Shackelford, 2002). The female partner's physical attractiveness, Surgency, and Openness to Experience index a male's recurrent risk of sperm competition. Males mated to such females may solve the adaptive problem of sperm competition through preventative and corrective measures. We operationalized preventative measures as the use of mate retention tactics (Buss, 1988), and we operationalized corrective measures as male copulatory behaviors consisting of relatively deep, numerous thrusts for a protracted period of time, and the initiation of different sexual positions—behaviors that may be effective at displacing rival semen present in the reproductive tract of a female.

The results supported the three hypotheses. Males mated to females who have traits linked to a higher probability of sexual infidelity more frequently use mate retention tactics apparently designed to thwart potential infidelity. Males mated to females who have traits linked to a higher probability of sexual infidelity also are more likely to perform copulatory behaviors arguably designed to displace rival male semen present in the female's reproductive tract. Finally, the current research suggests that mate retention tactics and semen-displacing behaviors are complementary tactics used simultaneously to reduce sperm competition risk and the consequences of sperm competition (e.g., cuckoldry).

The majority of copulations in humans are in-pair copulations (Baker & Bellis, 1995) and, therefore, semen-displacing behaviors performed by the primary male will usually displace

his own semen. We speculate, however, that over the vast expanse of evolutionary time, the costs of displacing a portion of one's own semen may have been outweighed by the tremendous reproductive benefits of displacing successfully a rival's semen (for a review of evolutionary cost-benefit analyses, see Tooby & Cosmides, 1992).

Examining the relationship between recurrent risk of sperm competition and each of the 19 mate retention tactics reveals that most of the relationships are positive, indicating that males mated to females who place them at high recurrent risk of sperm competition more frequently perform mate retention behaviors (see Table 2). Recurrent risk of sperm competition correlates positively with the mate retention tactic Sexual Inducement, for example. Sexual Inducement includes the following items: "He gave in to her sexual requests," "He performed sexual favors to keep his partner around," "He had a physical relationship with her to deepen their bond," and "He gave in to sexual pressure to keep her." Although the phrasing of these items suggests that Sexual Inducement is used more often by females, Buss (1988) found a sex difference in the opposite direction (i.e., males reported using Sexual Inducement more than females). From the perspective of sperm competition theory (Parker, 1970), the Sexual Inducement tactic can be interpreted as a "corrective" tactic designed to place a male's sperm in competition with any rival sperm that may be present in his partner's reproductive tract.

Recurrent risk of sperm competition also correlated positively with the mate retention tactic Love and Care. Love and Care includes the following items: "He told her that he loved her," "He went out of his way to be kind, nice, and caring," "He complimented her on her appearance," "He was helpful when she really needed it," and "He displayed greater affection for her." Glass and Wright (1985, 1992) documented that females who have extramarital affairs are more dissatisfied with their marriages than females who do not have affairs, and that the marital

dissatisfaction often provided the motivation to have the extramarital affairs (see also Buss, 2000). Males may be psychologically sensitive to the link between female relationship satisfaction and female infidelity and, therefore, perform Love and Care tactics that increase their partner's relationship satisfaction (see, e.g., Buss, 1994, 2000). Those males mated to females who are most likely to commit sexual infidelity may be most likely to display Love and Care toward their partner in an attempt to prevent her infidelity. The current results are consistent with this speculation.

Limiting factors such as time, energy, and resources do not allow males to perform every mate retention tactic all the time, and some tactics may be avoided deliberately. Recurrent risk of sperm competition correlated negatively, for example, with the mate retention tactic Derogation of Mate, which includes items such as, "He told other guys she was not a nice person," "He told other guys she was stupid," and "He told others she was a pain." Perhaps males mated to females who are more likely to commit sexual infidelity do not attempt to retain their mates by derogating their mates to competitors because this derogation may signal to competitors (i.e., rival males) impending relationship dissolution, prompting competitors to pursue the female. Directing rival males to a mate who is likely to commit sexual infidelity is unlikely to have been a reproductively profitable strategy.

Examining the relationship between recurrent risk of sperm competition and each of the five semen-displacing behaviors reveals that males mated to females who place them at high recurrent risk of sperm competition report that, during sexual intercourse with their partner, (a) they thrust more frequently (b) their deepest thrust is more deep, (c) the depth of their thrusts is much deeper on average, (d) the duration of sexual intercourse is much longer, and (e) they initiate more sexual positions than usual (see Table 3). That males report that their deepest thrust

is more deep than usual and that the depth of their thrusts is much deeper on average corroborates Gallup et al.'s (2002) demonstration that the penis must reach an adequate depth before semen is displaced. The other semen-displacing measures—number of thrusts, duration of sexual intercourse, and number of sexual positions initiated by the male—also may contribute to semen displacement. Thrusting more frequently during intercourse and a long duration of intercourse may afford a male more opportunity to displace rival semen, and because initiating different sexual positions sometimes requires the penis to be pulled out of the vagina, rival semen may be pulled out in the process.

Examining the relationship between semen-displacing behaviors and each of the 19 mate retention tactics reveals that all of the relationships are positive and most achieve statistical significance (see Table 2), suggesting that the two sets of behaviors are used simultaneously to solve the adaptive problem of sperm competition. This concurs with cross-species evidence that several bird species use preventative and corrective tactics as complementary paternity guards (see, e.g., Dickinson & Leonard, 1996; Møller, 1987).

Semen-displacing behaviors correlate positively with the mate retention tactic Sexual Inducement, for example. When males are giving in to their partners' sexual requests, performing sexual favors to keep their partners around, having a physical relationship with their partners to deepen their bond, and giving in to sexual pressure to keep their partner, they are performing semen-displacing behaviors during these acts. This relationship supports the interpretation of Sexual Inducement as a corrective tactic designed to place a male's sperm in competition with any rival sperm that may be present in his partner's reproductive tract.

Semen-displacing behaviors also correlate positively with the mate retention tactics Intrasexual Threats and Violence Against Rivals. Intrasexual Threats includes items such as, "He

yelled at the other guys who looked at her," "He stared coldly at the other guy who was looking at her," and "He told the other guy to 'stay away' form her." Violence Against Rivals includes items such as, "He hit the guy who made a pass at her," "He picked a fight with the guy who was interested in her," and "He vandalized the property of the guy who had made a pass at her." Males who perform copulatory behaviors arguably designed to displace rival male semen are simultaneously attempting to prevent partner infidelity by threatening and aggressing toward rival males.

An alternative explanation for the occurrence of semen-displacing behaviors in males who are mated to females who place them at high recurrent risk of sperm competition might be that such males thrust more deeply and frequently during sexual intercourse because they are extremely sexually aroused as a result of their partners' physical attractiveness (a key component of high recurrent risk of sperm competition). This alternative explanation is less tenable, however, when we note that males mated to females who place them at high recurrent risk of sperm competition also extend the duration of sexual intercourse. If males are thrusting more deeply and frequently because they are extremely sexually aroused, we would expect these copulatory behaviors to accelerate ejaculation, causing duration of sexual intercourse to be brief. In addition, a proponent of the "heightened sexual arousal" hypothesis must answer *why* males are more sexually aroused by physically attractive partners. Shackelford et al. (2002) argued that perceiving his partner as more attractive and becoming more sexually aroused may motivate a male to copulate with his partner as soon as possible, placing his sperm in competition with any rival sperm that may be present in his partner's reproductive tract.

Limitations and Future Research Directions

This study has several limitations. One limitation of this study is the homogeneity of the sample. The adaptations apparently designed to solve the adaptive problem of sperm competition are proposed to be universally present in male psychology. This study included mostly young males of similar educational background from two Western countries. Future research must sample males from different socio-economic, age, educational, ethnic, and cultural groups to allow for a clearer assessment of the universality of the proposed adaptations to human sperm competition (see, e.g., Schmitt et al., 2002).

A second limitation of this study is a design limitation. In this study, male copulatory behaviors were assessed as the behaviors performed at the most recent sexual intercourse with the participant's current partner. Although there is no reason to believe that the most recent sexual intercourse was unique, producing atypical copulatory behaviors, measurements of typical copulatory behaviors might have been more appropriate. Instead of assessing relative depth of thrusts at the last copulation, for example, assessing relative depth of thrusts across several copulations may better identify typical copulatory behaviors.

A third limitation of this study also is a design limitation. We present correlational analyses that prevent strong statements about casual relationships. We speculate that mateship to females who have traits linked to a higher probability of sexual infidelity *causes* males to perform mate retention tactics and semen-displacing behaviors. The data are consistent with this interpretation, but we cannot yet rule out an alternative, reverse causal relationship—that performing preventative and corrective measures causes males to select as mates females who have traits linked to a higher probability of sexual infidelity. A methodology that includes

repeated assessments of the key variables over time, such as a daily diary study, would allow for the identification of causal relationships.

An arguable design limitation of this research is the use of males' reports of their female partners' attractiveness and personality standings. Perhaps the results would have turned out differently if we had collected independent ratings on these key variables. This is not likely, however, because previous research indicates that males' ratings of their female partners' attractiveness and personality standings correlate positively with independent ratings (and with females' self-reports) on these variables (see, e.g., Botwin et al., 1997; Buss & Shackelford, 1997).

Although the correlations obtained between the target variables are small in magnitude and do not account for a large percentage of the variance, we nevertheless identified significant relationships in the hypothesized direction. We identified these hypothesized relationships despite experimental error, the error associated with participant recall, and other unknown sources of error.

There are several directions for future work. Future research should examine semen-displacing behaviors following an actual female sexual infidelity. This study examined the relationships between *likelihood* of female sexual infidelity (as assessed by her physical attractiveness and personality traits) and mate retention and semen-displacing behaviors. We expect that more intense mate retention and semen-displacing behaviors will be detectable under conditions of suspected or confirmed sexual infidelity.

Future research also might attempt to establish the female's role when males employ these preventative and corrective measures, particularly because the interests of males and females are often in conflict. If females are seeking genetic benefits in their extra-pair

copulations (Cashdan, 1996; Gangestad & Simpson, 2000; Scheib, 2001), for example, females who were inseminated recently by an extra-pair partner may resist or find unpleasant her partner's "corrective" semen-displacing behaviors.

Future research also should examine preventative and corrective measures as they relate to a temporally variable risk of sperm competition. The current study demonstrates that males may have psychological adaptations that attend to the recurrent risk of sperm competition. Risk of sperm competition can vary temporally as well. Shackelford et al. (2002) demonstrated that human male psychology may include mechanisms designed to attend to the risk of sperm competition as assessed by the proportion of time a couple has spent apart since their last copulation. We expect that the psychological adaptations that produce the preventative and corrective behaviors also are designed to attend to a temporally variable risk of sperm competition.

In conclusion, a wide variety of human male psychological adaptations may have been designed by selection due to sperm competition. To prevent sperm competition, males perform mate retention tactics apparently designed to reduce the likelihood of female sexual infidelity. Because preventative tactics are not fail-safe, however, males perform specific copulatory behaviors apparently designed to correct female sexual infidelity by displacing rival semen that may be present in the female's reproductive tract. These tactics accompany physiological adaptations (Baker & Bellis, 1993) and other psychological adaptations (Shackelford et al., 2002) to solve the adaptive problem of human sperm competition.

References

Baker, R. R., & Bellis, M. A. (1993). Human sperm competition: Ejaculate adjustment by males and the function of masturbation. *Animal Behaviour, 46*, 861-885.

Baker, R. R., & Bellis, M. A. (1995). *Human sperm competition*. London: Chapman & Hall.

Baur, B. (1998). Sperm competition in molluscs. In T. R. Birkhead & A. P. Møller (Eds.), *Sperm competition and sexual selection*. (pp. 255-305). San Diego: Academic Press.

Birkhead, T. R., & Møller, A. P. (1992). *Sperm competition in birds*. London: Academic Press.

Birkhead, T. R., & Møller, A. P. (Eds.). (1998). *Sperm competition and sexual selection*. San Diego: Academic Press.

Botwin, M. D., Buss, D. M., & Shackelford, T. K. (1997). Personality and mate preferences: Five factors in mate selection and marital satisfaction. *Journal of Personality, 65*, 107-136.

Buss, D. M. (1988). From vigilance to violence: Tactics of mate retention in American undergraduates. *Ethology and Sociobiology, 9*, 291-317.

Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences, 12*, 1-49.

Buss, D. M. (1994). *The evolution of desire*. New York: Basic Books.

Buss, D. M. (2000). *The dangerous passion*. New York: The Free Press.

Buss, D. M., & Schmitt, D. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review, 100*, 204-232.

Buss, D. M., & Shackelford, T. K. (1997). From vigilance to violence: Mate retention tactics in married couples. *Journal of Personality and Social Psychology, 72*, 346-361.

Cashdan, E. (1996). Women's mating strategies. *Evolutionary Anthropology, 5*, 134-143.

Dickinson, J. L., & Leonard, M. L. (1996). Mate attendance and copulatory behaviour in western bluebirds: Evidence of mate guarding. *Animal Behaviour, 52*, 981-992.

Flinn, M. V. (1988). Mate guarding in a Caribbean village. *Ethology and Sociobiology, 9*, 1-28.

Gallup, G. G., & Burch, R. L. (2002). The human penis as a semen displacement device: Male sexual behavior varies following separation from female partner. Poster presented at *14th Annual Human Behavior and Evolution Society Conference*, Rutgers University, New Brunswick, NJ.

Gallup G. G., Burch, R. L., Zappieri, M. L., Parvez, R. A., & Stockwell, M. L. (2002). The human penis as a semen displacement device. Manuscript under editorial review.

Gangestad, S. W., & Simpson, J. A. (1990). Toward an evolutionary history of female sociosexual variation. *Journal of Personality, 58*, 69-96.

Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behavior and Brain Sciences, 23*, 573-587.

Gangestad, S. W., Thornhill, R. & Garver, C. E., (2002). Changes in women's sexual interests and their partner's mate-retention tactics across the menstrual cycle: Evidence for shifting conflicts of interest. *Proceedings of the Royal Society of London, 269,* 975-982.

Glass, S. P., & Wright, T. L. (1985). Sex differences in the type of extramarital involvement and marital dissatisfaction. *Sex Roles, 12*, 1101-1119

Glass, S. P., & Wright, T. L. (1992). Justifications for extramarital relationships: The association between attitudes, behaviors, and gender. *Journal of Sex Research, 29*, 361-387.

Goldberg, L. R. (1982). From ace to zombie: Some explorations in the language of personality. In C. D. Spielberg & J. N. Butcher (Eds.), *Advances in personality assessment* (Vol. 1, pp. 203-234). Hillsdale, NJ: Erlbaum.

Gray, H., & Clemente, C. D. (Eds.). (1984). *Gray's anatomy of the human body* (30th ed.) New York: Lea & Febiger.

LeBlanc, G. J., Shackelford, T. K., & Weekes, V. A. (1999). Preventing, correcting, and anticipating sperm competition in humans. Paper presented at *11th Annual Human Behavior and Evolution Society Conference*, University of Utah, Salt Lake City, UT.

Li, N. P., Bailey, J. M., Kenrick, D. T., & Linsenmeier, J. A. W. (2002). The necessities and luxuries of mate preferences: Testing the tradeoffs. *Journal of Personality and Social Psychology, 82*, 947-956.

Møller, A. P. (1987). Mate guarding in the swallow *Hirundo rustica*. *Behavioral Ecology & Sociobiology, 21*, 119-123.

Norman, W. T. (1963). Toward an adequate taxonomy of personality attributes: Replicated factor structure in peer nominations and personality ratings. *Journal of Personality and Social Psychology, 66*, 574-583.

Parker, G. A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biological Review, 45*, 525-567.

Parker, G.A. (1984). Sperm competition and the evolution of animal mating strategies. In R. L. Smith (Ed.), *Sperm competition and the evolution of animal mating systems* (pp.1-60). London: Academic Press.

Regan, P. C., Levin, L., Sprecher, S., Christopher, F. S., & Cate, R. (2000). Partner preferences: What characteristics do men and women desire in their short-term sexual and long-term partners? *Journal of Psychology & Human Sexuality, 12*, 1-21.

Scheib, J. E. (2001) Context-specific mate choice criteria: Women's trade-offs in the contexts of long-term and extra-pair mateships. *Personal Relationships, 8*, 371-389.

Schmitt, D. P. (2002). Are sexual promiscuity and relationship infidelity linked to different personality traits across cultures? Findings from the International Sexuality Description Project. In W. Lonner, D. L. Dinnel, S. A. Hayes, & D. N. Sattler (Eds.), *OnLine Readings in Psychology and Culture*, Western Washington University, Department of Psychology, Center for Cross-Cultural Research Web site: http://www.wwu.edu/~culture.

Schmitt, D. P., Alcalay, L., Allik, J., Angleitner, A., Ault, L., Austers, I., Bennett, K. L., Bianchi, G., Boholst, F., Borg Cunen, M. A., Braeckman, J., Brainerd Jr., E. G., Caral, L. G. A., Caron, G., Casullo, M. M., Cunningham, M., Daibo, I., Desouza, E., De Backer, C., Diaz-Loving, R., Diniz, G., Durkin, K., Echegaray, M., Eremsoy, E., Euler, H. A., Falzon, R., Fisher, M. L., Fry, D. P., Fry, S. F., Ghayur, M. A., Giri, V. N., Golden, D. L., Grammer, K., Grimaldi, L., Halberstadt, J., Haque, S., Hefer, E., Herrera, D., Hertel, J., Hoffman, H., Hradilekova, Z., Hudek-Kene-evi, J., Jaafar, J., Jankauskaite, M., Kabangu-Stahel, H., Kardum, I., Khoury, B., Kwon, H., Laidra, K., Laireiter, A., Lakerveld, D., Lampart, A., Lauri, M., Lavallée, M., Lee, S., Leung, L. C., Locke, K. D., Locke, V., Luksik, I., Magaisa, I., Marcinkeviciene, J., Mata, A., Mata, R., McCarthy, B., Mills, M. E., Mkhize, N. J., Moreira, J., Moreira, S., Moya, M., Munyea, M., Noller, P., Olimat, H., Opre, A., Panayiotou, A., Petrovic, N., Poels, K., Popper, M., Poulimenou, M., P'yatokh, V., Raymond, M., Reips, U., Reneau, S. E., Rivera-Aragon, S., Rowatt, W. C., Ruch, W., Rus, V. S., Safir, M. P., Salas, S., Sambataro, F., Sandnabba, K. N., Schulmeyer, M. K., Schütz, A., Scrimali, T., Shackelford, T. K., Sharan, M. B., Shaver, P. R., Sichona, F., Simonetti, F., Sineshaw, T., Sookdew, R., Speelman, T., Sümer, H. C., Sümer, N., Supekova, M., Szlendak, T., Taylor, R., Timmermans, B., Tooke, W., Tsaousis, I., Tungaraza, F. S. K., Vandermassen, G., Vanhoomissen, T., Van Overwalle, F., Van

Wesenbeek, I., Vasey, P. L., Verissimo, J., Voracek, M., Wan, W. W. N., Wang, T., Weiss, P., Wijaya, A., Woertment, L., Youn, G., & Zupanèiè, A. (2002). Patterns of human mate poaching across 53 nations: The effects of sex, culture, and personality on romantically attracting another person's partner. Manuscript under editorial review.

Schmitt, D. P., & Buss, D. M. (2001). Human mate poaching: Tactics and temptations for infiltrating existing mateships. *Journal of Personality and Social Psychology, 80*, 894-917.

Schmitt, D. P., & Shackelford, T. K. (2002). Nifty ways to leave your lover: The tactics people use to entice and disguise the process of human mate poaching. Manuscript under editorial review.

Shackelford, T. K. (2002). Preventing, correcting, and anticipating female infidelity: Three adaptive problems of sperm competition. Manuscript under editorial review.

Shackelford, T. K., LeBlanc, G. J., Weekes-Shackelford, V. A., Bleske-Rechek, A. L., Euler, H. A., & Hoier, S. (2002). Psychological adaptation to human sperm competition. *Evolution and Human Behavior, 23*, 123-138.

Simmons, L. W. (2001). *Sperm competition and its evolutionary consequences in the insects*. Princeton, NJ: Princeton University Press.

Singh, D. (1993). Adaptive significance of waist-to-hip ratio and female physical attractiveness. *Journal of Personality and Social Psychology, 65*, 293-307.

Smith, R. L. (1984). Human sperm competition. In R. L. Smith (Ed.), *Sperm competition and the evolution of animal mating systems* (pp. 601-660). New York: Academic Press.

Symons, D. (1979). *The evolution of human sexuality*. New York: Oxford University Press.

Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind* (pp. 19-136). New York: Oxford University Press.

Table 1

Descriptive Statistics for Target Variables

	Sample						
	Total		United States		Germany		
Variable	Mean	*SD*	Mean	*SD*	Mean	*SD*	*t*
Participant's age (years)	24.18	7.89	23.71	8.18	26.29	6.0	−2.72**
Partner's age (years)	23.02	7.31	22.82	7.67	23.91	5.32	−1.23
Recurrent risk of sperm competition[a]	−0.03	0.73	0.02	0.72	−0.27	0.72	3.33***
Overall mate retention tactics[b]	0.68	0.36	0.74	0.44	0.44	0.25	7.41***
Semen-displacing behaviors[c]	5.47	1.19	5.58	1.20	4.96	0.99	4.38***

Note. For the total (United States and Germany) sample, $N = 463$; for the United States sample, $n = 379$; for the Germany sample, $n = 84$. The t values represent independent means tests of the difference between the United States and Germany. *SD* = Standard Deviation

a Standardized composite variable (see text), ranging form −3 (lowest recurrent risk of sperm competition) to 3 (highest recurrent risk of sperm competition).

b Composite variable (see text), ranging from 0 (least frequent use of mate retention tactics) to 3 (most frequent use of mate retention tactics).

c Composite variable (see text), ranging from 0 (least frequent use of semen-displacing behaviors) to 9 (most frequent use of semen-displacing behaviors).

** $p < .01$; *** $p < .001$ (two-tailed)

Table 2

Correlations between Mate Retention Tactics and Recurrent Risk of Sperm Competition, and between Mate Retention Tactics and Semen-displacing Behaviors

Mate retention tactic (alpha reliability)	Recurrent risk of sperm competition	Semen-displacing behaviors
Vigilance (.82)	.03	.09
Concealment of mate (.67)	−.11*	.09
Monopolization of mate (.72)	−.04	.07
Jealousy inducement (.70)	−.06	.01
Punishment of threat to infidelity (.81)	−.03	.09
Emotional manipulation (.80)	−.06	.07
Commitment manipulation (.50)	.08	.22***
Derogation of competitors (.76)	−.05	.01
Resource display (.84)	.23***	.24***
Sexual inducement (.64)	.11**	.15**
Appearance enhancement (.77)	.19***	.10*
Love and care (.66)	.26***	.16***
Submission and debasement (.68)	.01	.05
Verbal possession signals (.61)	.18***	.17***
Physical possession signals (.72)	.25***	.10*
Possessive ornamentation (.65)	.09	.19***
Derogation of mate (.70)	−.20***	.05
Intrasexual threats (.83)	.03	.10*
Violence against rivals (.80)	−.06	.13**

Note. $N = 463$.

* $p < .05$; ** $p < .01$; *** $p < .001$ (two-tailed)

Table 3

Correlations between Semen-displacing Behaviors and Recurrent Risk of Sperm Competition

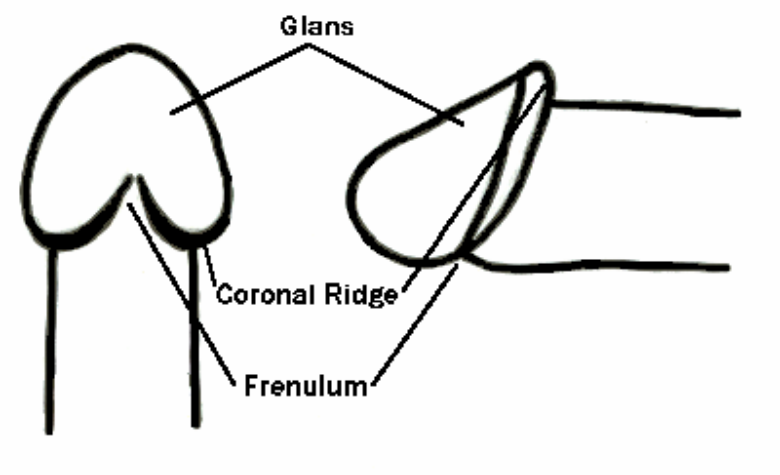
Semen-displacing behaviors	Recurrent risk of sperm competition
Number of thrusts	.18***
Deepest thrust	.25***
Depth of thrusts on average	.22***
Duration of sexual intercourse	.12**
Number of sexual positions initiated by the male	.13**

Note. $N = 463$. Each semen-displacing behavior is a relative measure; participants compared their copulatory behaviors at their most recent sexual intercourse with their partners to their typical copulatory behaviors.

** $p < .01$; *** $p < .001$ (two-tailed)

Figure Caption

Figure 1. Anatomical features of the human penis. Adapted from *Gray's Anatomy* (Gray & Clemente, 1984).


Glans
Coronal Ridge
Frenulum