

Conditional expression of women's desires and men's mate guarding across the ovulatory cycle

Martie G. Haselton^{a,*}, Steven W. Gangestad^b

^a *Communication Studies and Department of Psychology, University of California, Los Angeles, Center for Behavior, Evolution and Culture, 3130 Hershey Hall, 415 Portola, Los Angeles, CA 90095, USA*

^b *Department of Psychology, University of New Mexico, Albuquerque, NM 87131, USA*

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Abstract

Thirty-eight normally cycling women provided daily reports of sexual interests and feelings for 35 days. Near ovulation, both pair-bonded and single women reported feeling more physically attractive and having greater interest in attending social gatherings where they might meet men. Pair-bonded women who were near ovulation reported greater extra-pair flirtation and greater mate guarding by their primary partner. As predicted, however, these effects were exhibited primarily by women who perceived their partners to be low on hypothesized good genes indicators (low in sexual attractiveness relative to investment attractiveness). Ovulation-contingent increases in partner mate guarding were also moderated by female physical attractiveness; midcycle increases in mate guarding were experienced primarily by less attractive women, whereas more attractive women experienced relatively high levels of mate guarding throughout their cycle. These findings demonstrate ovulation-contingent shifts in desires and behaviors that are sensitive to varying fitness payoffs, and they provide support for the good genes hypothesis of human female extra-pair mating. The daily assessment method provides an important supplement to existing studies using scheduled laboratory visits as the purpose of the study (examining cycle-related variation) is not known by participants.

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Across myriad species, the psychological mechanisms underlying mating behavior appear to produce conditional strategies. The leading explanation for conditional strategies is specialized psychological design shaped through selection (see, e.g., Thornhill, 1990). Such design leads an organism to vary its behaviors in response to features that recurrently covaried with the relative payoffs of alternative tactics in ancestral conditions. Behavioral ecologists have documented adaptive, conditional mating strategies in a wide variety of species that guide the allocation of effort to mating versus parenting, the production of male versus female offspring, the number offspring produced, and the timing of reproduction within the lifespan, to name a few (for examples, see Alcock, 2001).

In this paper, we test predictions about human female desires and male mating tactics that vary depending upon a woman's fertility status across the cycle. We test further predictions that

these conditional effects are themselves conditional on a particular set of hypothesized cues to variable fitness payoffs: the qualities women and men perceive in their primary mates.

There is wide agreement that mate choice adaptations in females have evolved to select males who will confer benefits on offspring, through direct and indirect routes (Kokko et al., 2003). For instance, in humans and in many socially monogamous bird species, males may invest parental care or confer heritable genetic benefits (*good genes*) on offspring (for overviews of the literature, see Gangestad and Simpson, 2000; Jennions and Petrie, 2000; Kokko et al., 2003; Møller and Alatalo, 1999). Females could benefit from both paternal care and good genes offered by long-term male partners; however, because males displaying indicators of genetic quality are attractive, they are in demand as sex partners, and they shift their efforts toward mating at the expense of providing parental care. In the collared flycatcher, for example, males who sport a large forehead patch—a sexually selected indicator of genetic quality (e.g., Sheldon et al., 1997)—invest less in offspring (Qvarnström, 1999). In

* Corresponding author. Fax: +1 310 206 2371.

E-mail address: haselton@ucla.edu (M.G. Haselton).

humans, symmetry is a hypothesized indicator of good genes (e.g., Gangestad and Thornhill, 1998), symmetry is associated with male sexual attractiveness (e.g., Scheib et al., 1999), and more symmetrical men tend toward a short-term reproductive strategy (Gangestad and Thornhill, 1997).

The mating market is driven by supply and demand, and therefore not all women will attract long-term mates offering good genes. Ancestrally, these women may have benefited from a strategy in which they secured investment from a long-term mate and obtained genetic benefits from extra-pair partners. A woman could obtain genetic benefits of extra-pair mating only when fertile, but its costs (e.g., as a result of partner jealousy) extended throughout her cycle. Therefore, evolved design for extra-pair mating to obtain genetic benefits should cause increased extra-pair desires as women approach ovulation, when the probability of conception is highest.

Women's preferences for hypothesized indicators of good genes—including facial masculinity (Johnston et al., 2001; Jones et al., 2005; Penton-Voak et al., 1999; Penton-Voak and Perrett, 2000), vocal masculinity (Feinberg et al., in press; Puts, 2005), body scents associated with symmetry (Gangestad and Thornhill, 1998; Rikowski and Grammer, 1999), and behavioral displays of intrasexual competitiveness (Gangestad et al., 2004)—do indeed peak near ovulation. These shifts appear when women rate men's short-term sexual attractiveness; studies have not detected changes in long-term mating preferences (Gangestad et al., 2004; Penton-Voak et al., 1999). Additionally, women's extra-pair desires and commitment to their primary partners change across the cycle. Gangestad et al. (2002) found that women reported greater attraction to extra-pair mates in the ovulatory relative to the luteal phase of the cycle. Similarly, Jones et al. (2005) showed that women's reported commitment to their partners was weakest on low progesterone days of the cycle (when fertility is high). Gangestad et al. (2002) also found that women reported that their partners were more vigilant of their whereabouts and monopolizing of their time when fertile, a pattern suggesting sexually antagonistic coevolution of female strategy and male counter-strategy.

In addition to obtaining intrinsic good genes, extra-pair mating could function to obtain compatible genes, diverse genes, and non-genetic ancestral benefits (e.g., mate-switching, paternity confusion; see Greiling and Buss, 2000; Zeh and Zeh, 2001). The intrinsic good genes explanation appears to account best for cycle-related changes in preferences documented to date (see Gangestad and Thornhill, 2004), though additional tests—such as our study—are needed. Multiple functions of extra-pair mating are possible.

We made several novel predictions that apply only to pair-bonded women and several that apply to all women in our sample.

Prediction 1. (pair-bonded women): male sexual attractiveness moderates ovulatory shifts in female extra-pair desires.

Prediction 2. (pair-bonded women): male sexual attractiveness moderates ovulatory shifts in male mate guarding.

The benefits of extra-pair mating for good genes outweigh its costs only for women with primary partners who offer relatively low genetic benefits to offspring. Hence, we predicted that the ovulatory cycle shift in women's extra-pair desires and flirtation is strongest for women who perceive their partners as low in sexual attractiveness. Similarly, men who lack sexual attractiveness should be most at risk of cuckoldry; thus, we predicted that these men particularly increase mate guarding when their partners are near ovulation.

Prediction 3. (pair-bonded women): female physical attractiveness is associated with relatively high levels of male mate retention effort across the cycle.

Male mate guarding functions to protect paternity and prevent the loss of a mate to competitors. Physically attractive women are valued on the mating market (possibly due to fertility cues; e.g., Symons, 1979, 1995) and are more likely to be targets of *mate poaching* attempts (Schmitt and Buss, 2001); thus, we predicted that physically attractive women experience greater mate guarding by their male partners. Although the benefits of protecting against mate loss and cuckoldry are high, engaging in mate guarding also carries costs of increased intrasexual conflict (Flinn, 1988) and opportunity costs (Alberts et al., 1996). For men with attractive mates, the net benefit of mate guarding may extend throughout the cycle (protecting against both mate loss and cuckoldry) more so than for men with less attractive mates, who may allocate effort more selectively and concentrate their efforts near ovulation, when the risk of cuckoldry is highest. We therefore investigated whether the ovulation-contingent effect on mate retention is moderated by female attractiveness—with the expectation that the ovulatory effect would be strongest for less attractive women.

Prediction 4. (pair-bonded women): relationship dynamics shift as a function of a woman's position within the cycle.

Ovulatory changes in female extra-pair desires and commitment to partners, in concert with changes in male mate guarding, suggest shifting conflicts of interest. Because women become more reproductively valuable to their partners near ovulation, these shifting relationship dynamics may lead women to feel greater desirability or power relative to their partners near ovulation. Shifts in relationship dynamics may furthermore be greatest in couples in which men are particularly possessive of their mates midcycle: when women are mated to men who are not seen as particularly sexually attractive or possibly when women are less attractive themselves (see paragraph above). Therefore, we predicted that male sexual attractiveness, and possibly female physical attractiveness, will moderate the effect of fertility status on female feelings of desirability and power in relationships.

Prediction 5. (pair-bonded and single women): women's subjective feelings of attractiveness increase near ovulation.

A long evolutionary history of female infidelity may have selected for male sensitivity to cues to ovulation. The coevolved

female response, in turn, is to conceal or obscure these cues to preserve female choice (Benshoof and Thornhill, 1979; Symons, 1979). Any cues associated with ovulation should therefore be subtle, and perhaps most obvious to the woman herself. Emerging evidence suggests two subtle cues. First, women's body scent is rated as most attractive during the high fertility phase of the cycle (Doty et al., 1975; Singh and Bronstad, 2001; Thornhill et al., 2003). Second, there may be subtle visual cues. Skin lightness is associated with youth and attractiveness (Symons, 1995), and skin color shifts slightly throughout the cycle, becoming lightest near ovulation (Van den Berghe and Frost, 1986). Recent evidence also suggests that facial photographs of women taken during high and low fertility phases of the cycle can be discriminated from each other (Roberts et al., 2004). If women are sensitive to these changes in themselves (or to other changes not yet documented), or to the differential reactions of the men around them, their subjective feelings of attractiveness and sexiness should also vary across the cycle (also see Discussion for an alternative rationale for this prediction).

Prediction 6. (pair-bonded and single women): near ovulation, women's desire to attend social gatherings where they might meet men increases.

Fessler (2003) compiled and reviewed evidence indicating that, in human and non-human females, feeding behavior decreases near ovulation, whereas females' ranging activities and women's participation in volunteer social activities increase. He hypothesized that decreases in feeding behavior reflect diminished motivational salience of goals related to non-mating activities. For pair-bonded women, these changes may serve to increase searching for potential alternative sires for their offspring (see Prediction 1). For single women, these changes may also facilitate searching to find the best possible mate, as selection (e.g., on allocation of cognitive effort and salience of cues relevant to reproduction) may have led women to be most proficient at evaluating potential mates when fertile. We predicted, therefore, that women's desire to go out to social gatherings where they might meet men is greater in the high fertility than in the low fertility phase of the cycle.

Method

Participants

Participants were 38 heterosexual women who participated for research credit in a psychology class at a large university in the United States. Twenty-five of the women classified themselves as currently involved in a "committed romantic relationship," and these women comprised the sample in the pair-bonded analyses. Thirty-seven of the participants were between 17 and 22 years old; one participant was 43 years old ($M = 19.50$, $SD = 4.05$; when the 43-year-old was dropped from analyses, all of the predicted effects reported below remained statistically significant; the reported analyses include all participants). All participants reported that they were not taking oral or other hormonal contraceptives. Based on the size of the sample of pair-bonded women ($n = 25$) and results of Gangestad et al. (2002), we estimated 85–90% power to detect similar effects. If the hypothesized cycle effects on self-perceived attractiveness and desire to meet men are similar in size, power is greater for tests of the predictions involving the full sample ($n = 38$).

Procedure

Daily questionnaires

Participants were given 35 dated questionnaires to complete alone at night before going to sleep and return every few days via campus mail. On a separate form, they reported menstrual onset and duration. The importance of completing the questionnaires daily was emphasized in one-on-one orientation sessions. Participants were told to not go back to complete questionnaires for missed days. Participants received a daily reminder email or phone call. On average, women returned 31.1 daily reports; missed days were scattered across the cycle and thus did not markedly compromise sampling of days within the high and low fertility phases. In total, 8.2% of fertile days and 7.0% of luteal phase days were missed, $t(37) = 0.57$, ns. During debriefing, participants verbally reported their impressions about the purpose of the study. Three thought that it might concern changes in feelings near the onset of menses; none guessed that the hypotheses concerned changes in feelings or experiences around the time of ovulation.

Phase estimation

We generated two sets of scores for each participant, an average of (1) all fertile days and (2) all infertile days following ovulation and excluding premenstrual and menstrual days. We used the reverse cycle day (RCD) method to predict the day of ovulation (methods using day-in-cycle have been used with success to predict other effects of theoretical interest, e.g., DeBruine et al., 2005; Gangestad and Thornhill, 1998; Jones et al., 2005). Fertile days included the day 15 days prior to the first day of the next cycle (estimated day of ovulation) and the previous 4 days (Lenton et al., 1984, also see Wilcox et al., 2001). Infertile days typically included 9 days: those between the estimated day of ovulation and 3 days prior to menstrual onset, excluding the 2 days immediately following ovulation (e.g., RCD 13 and 12), which could possibly include the day of ovulation.

Dependent variables

Participants provided ratings by indicating "Relative to other days, over the last 24 hours, how much have you..." They selected numerical ratings for each item from a 9-point scale with three anchors: $-4 =$ "far less than usual," $0 =$ "about average" and $+4 =$ "far more than usual." To test the predictions, we summed related items within days. Seven items assessed flirtation and attraction to others: "flirted with men you do not know," "flirted with male acquaintances," "flirted with friends or co-workers," "been attracted to a man you did not know," "been attracted to a male acquaintance," "been attracted to a male friend or co-worker," and "noticed attractive men around campus or around town" (α high fertility = 0.94; α low fertility = 0.93). Seven items assessed subjective attractiveness: "felt that you looked physically attractive (facial attractiveness)," "felt that you looked physically attractive (body attractiveness)," "felt that you looked physically attractive (overall attractiveness)," "felt sexually desirable," "felt sexually attractive," "looked hot," and "felt unattractive" (reverse scored) (α high = 0.92; α low = 0.77). Four items measured general sexual desire: "had persistent sexual thoughts," "had sexual thoughts," "had sexual fantasies," and "experienced sexual desire" (α high = 0.84; α low = 0.93). Two items assessed desire to go out and meet men. Women were asked to "Imagine that you have no work to do tonight and a few of your good female friends ask you to go out with them tonight..." "relative to other days, how much would you be interested in going out tonight with your friends to a dance club [big party] where you might meet men?" (α high = 0.92; α low = 0.97).

Pair-bonded women made additional reports of relationship feelings and events. Two items assessed partner jealousy and possessiveness, and four assessed love and attention: "Relative to other days, how much has your partner... acted jealous of your casual interactions with other people" and "acted possessive of you" (Jealous/Possessive, α high = 0.89; α low = 0.98); "given you attention," "expressed commitment to you," "expressed feelings of love for you," "expressed sexual attraction to you" (Love/Attention; α high = 0.89; α low = 0.97). Two items assessed relative power/desirability: "Today I have felt like..." $-4 =$ "my partner is much more desirable than me"; $0 =$ "I am about equally as desirable as my partner"; $+4 =$ "I am much more desirable than my partner." And, "Over the last 24 hours, who do you think had more power in your relationship?"; $-4 =$ "my partner had far more power in our relationship"; $0 =$ "we were about equal" $+4 =$ "I had far more power in our relationship" (α high = 0.74; α low = 0.65).

Individual differences variables

In initial testing, participants provided several self and partner assessments. On a 9-point scale, they rated their own attractiveness along two dimensions: “Compared with women you know who are about your age, how attractive is your body [face] to men?” ($\alpha = 0.81$). In the orientation session, the experimenter also rated participants’ facial, body, and overall attractiveness ($\alpha = 0.92$). The self and experimenter ratings were correlated ($r = 0.47$, $P = 0.028$) and hence were standardized and averaged. Participants completed a measure of the degree to which their partner invests in their relationship (the Partner Specific Investment Inventory; PSI; Ellis, 1998) and rated their commitment, sexual satisfaction, emotional satisfaction, and overall satisfaction in their relationship on seven-point scales.

Women also rated their partner’s sexual attractiveness and attractiveness as a long-term mate. Sexual attractiveness ratings were: “How would you rate your partner’s desirability as a short-term mate (e.g., a partner in a one-night sexual encounter or brief affair), relative to you?”; and “How would you judge this person’s physical attractiveness, relative to you? (1 = less desirable [attractive] than I; 5 = about equally desirable [attractive]; 9 = more desirable [attractive] than I). Long-term/investment ratings were: “How would you rate your partner’s desirability as a long-term mate (e.g., a partner in a long-term committed relationship or marriage), relative to you?”; and “How would you judge this person’s likely future professional success, relative to you? (1 = less desirable [successful] than I; 5 = about equally desirable [successful]; 9 = more desirable [successful] than I). These measures correlated negatively though non-significantly, $r = -0.33$, $P = 0.11$. We created two summary variables using these items, overall mate value (long-term attractiveness plus sexual attractiveness) and sexual-versus-investment attractiveness (sexual attractiveness minus long-term attractiveness). In creating the latter, we reasoned that preferred long-term mates will have a host of qualities that would also be preferred in a short-term mate (e.g., physical attractiveness) and vice versa; a difference score should better tap the extent to which a mate specifically has the qualities particular to good long-term mates (e.g., willingness to invest) or particular to good short-term mates (sexual attractiveness). The best estimate of overall attractiveness should be the sum of the two. The critical sexual-versus-investment attractiveness variable, key to several predictions, is in effect the sum of two difference scores: relative short-term versus long-term mate attractiveness and relative physical attractiveness vs. financial prospects. These two items correlated 0.48, and the reliability of the two-item measure was 0.64.

In debriefing, seven participants in the pair-bonded category indicated that they had broken up with their partners during the study, although most of them (71%) continued to interact with them and to provide daily partner ratings. Breakup status was statistically controlled in the analyses.

Statistical analyses

Following recommendations by Rice and Gaines (1994), we implemented directed tests for predicted effects by allocating a probability of 0.04 (of a total α of 0.05) to the predicted direction and 0.01 to the unpredicted direction. For unpredicted effects, we used two-tailed tests. P values reflect these criteria.

To test predictions for pair-bonded women, we conducted repeated-measures general linear models (SPSS 11.5) on the dependent variables of interest (e.g., flirtation and attraction to others, possessiveness and jealousy). These variables were measured at both high-fertility and low-fertility phases and, hence, Fertility Status was a repeated factor. We then included three quantitative predictor variables: Male partners’ Sexual-versus-Investment Attractiveness, Male partners’ Overall Mate Value, and Female Physical Attractiveness. In addition, whether women had broken up with their partners was included as a factor. All quantitative variables were zero-centered so that the main effect of the repeated factor (fertility status) would be estimated for mean levels of these predictors. Due to consent procedures allowing women to skip questions they did not want to answer for some dependent measures, between 1 and 3 women’s data were missing, leaving 22–24 women in these analyses.

We also report analyses controlling for two additional variables, male Partner Specific Investment (PSI, Ellis, 1998) and female sexual satisfaction, each of which could be confounded with partner sexual attractiveness. These controls did not markedly change the predicted effects (see below). We could not control for all possible confounding variables in the analyses, given sample size.

We did examine the correlations between the critical male sexual-versus-investment attractiveness variable and other potentially important variables: relationship length, level of commitment, overall satisfaction, and emotional satisfaction. None of these correlations was statistically significant, $r = 0.20$, 0.14, -0.11 , -0.06 , respectively, all $P > 0.3$. These variables hence cannot account for the effects of Male Sexual-versus-Investment Attractiveness. As one reviewer noted, women’s attractiveness may also be confounded with their partner’s sexual attractiveness; because Female Physical Attractiveness was included in all analyses, it was also statistically controlled.

To test predictions pertaining to both pair-bonded and single women, we conducted repeated measures GLM analyses with fertility status (fertile vs. luteal) as the repeated factor. Relationship Status (pair-bonded vs. single) was included as a factor and Female Physical Attractiveness as a quantitative predictor variable.

Results

Predictions for pair-bonded women

Prediction 1: does male sexual attractiveness moderate the association between women’s cycle phase and extra-pair desires?

As predicted, the effect of Fertility Status was powerfully moderated by Male Sexual-versus-Investment Attractiveness, $F(1,19) = 9.47$, $P = 0.004$ (see Fig. 1). When women were mated to men with low Sexual-versus-Investment Attractiveness, they were particularly likely to experience increased attraction to men other than their partner when fertile. Women mated to men with high sexual-versus-investment attractiveness showed no tendency to be more attracted to men other than primary partners midcycle. Fig. 1 shows one individual reporting an extreme shift. The Male Sexual-versus-Investment Attractiveness interaction remained with this individual removed, $F(1,18) = 5.10$, $P = 0.036$.

There was no significant effect of Fertility Status, $F(1,19) = 1.10$, ns. Women reported more flirtation with and attraction to other men when fertile (marginal mean = 1.62) than when non-fertile (0.78), but not significantly so. No other main effects or interactions with fertility status were significant, all $P > 0.080$.

To assess whether the Fertility Status \times Male Sexual vs. Investment Attractiveness interaction could be explained by

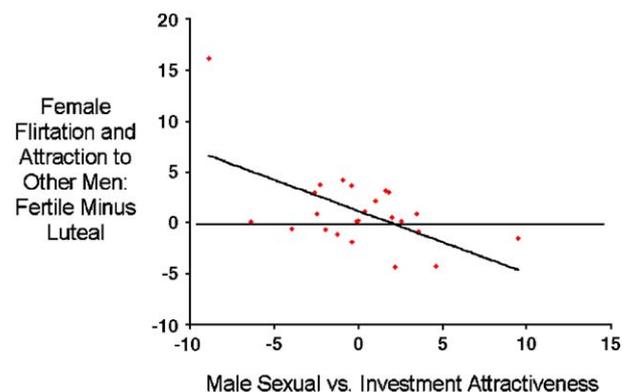


Fig. 1. Scatterplot of shift in women’s flirtation and attraction to men other than a primary partner (fertile–luteal) as a function of men’s relative sexual-versus-investment attractiveness. These values are residuals (centered around the sample mean), with Male Overall Mate Value, Female Physical Attractiveness, and breakup status partialled out. The partial correlation is -0.58 , $P = 0.004$. $n = 24$.

specific confounding variables, we added two predictor variables: Male PSI and Female Sexual Satisfaction with the relationship. Once again, the predicted Fertility Status \times Male Sexual-versus-Investment Attractiveness interaction emerged, $F(1,16) = 10.12$, $P = 0.004$. No other main effects or interactions were observed, all $P > 0.069$.

In summary, results supported the hypothesis: women mated to men relatively low in sexual attractiveness experience greater increases in attraction to men other than their primary partners in the high fertility phase of their cycle.

Prediction 2: does male sexual attractiveness moderate the association between women's cycle phase and male jealousy and possessiveness?

Women reported their partners to be more jealous and possessive when they were fertile (marginal mean = 0.71) than when non-fertile (-0.58), $F(1,17) = 3.87$, $P = 0.041$, replicating the finding of Gangestad et al. (2002).

We also observed the predicted Fertility Status \times Male Sexual-versus-Investment Attractiveness interaction, $F(1,17) = 3.68$, $P = 0.045$. Men low on sexual attractiveness, relative to attractiveness as a long-term partner, were reported to increase their jealous and possessive behaviors midcycle more than sexually attractive men (see Fig. 2).

Men rated as particularly good mates overall were less jealous and possessive overall, $F(1,17) = 11.64$, $P = 0.003$. Possibly, their lack of possessiveness may contribute to their partners' perceptions that they are good mates. Alternatively, women who choose partners who are particularly good mates may behave in ways interpreted to indicate greater faithfulness and commitment, leading partners to be less jealous and possessive in general.

Women in relationships that broke up reported that their partners were more jealous and possessive than partners in intact relationships (marginal means = 0.75 vs. -0.61 , respectively), $F(1,17) = 9.95$, $P = 0.006$.

In a subsequent analysis, we added two potential confounds: Male PSI and Female Sexual Satisfaction. The predicted interaction between Fertility Status and Male Sexual-versus-

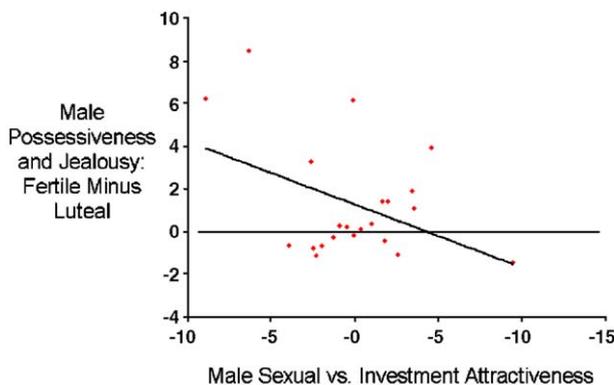


Fig. 2. Scatterplot of shift in men's possessiveness and jealousy across the cycle (fertile-luteal) as a function of men's relative sexual-versus-investment attractiveness. These values are residuals (centered around the sample mean value), with Male Overall Mate Value, Female Physical Attractiveness, and breakup status controlled. The partial correlation is -0.42 , $P = 0.045$. $n = 22$.

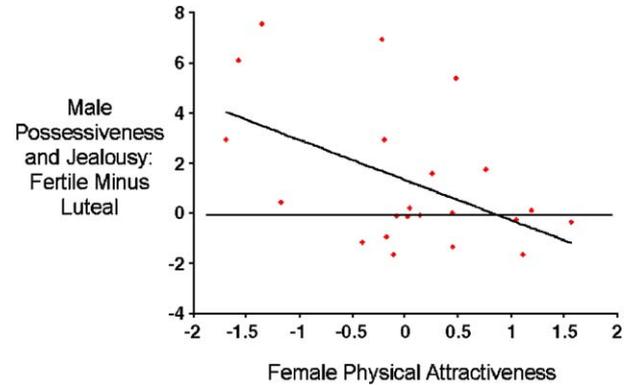


Fig. 3. Scatterplot of shift in men's possessiveness and jealousy across the cycle (fertile-luteal) as a function of female physical attractiveness. These values are residuals (centered around the sample mean value), with Male Overall Mate Value, Male Sexual-versus-Investment Attractiveness, and breakup status controlled. The partial correlation is -0.50 , $P = 0.019$. $n = 22$.

Investment Attractiveness strengthened somewhat when these variables were controlled, $F(1,14) = 6.33$, $P = 0.016$. The main effects of Male Overall Mate Value and breakup status also remained significant, $F(1,14) = 11.89$, $P = 0.004$, and $F(1,14) = 12.42$, $P = 0.003$.

Sexual Satisfaction significantly interacted with Fertility Status, $F(1,14) = 5.35$, $P = 0.037$. Male partners of highly sexually satisfied women were particularly likely to become jealous and possessive midcycle. This is an unpredicted effect and one that could be spurious given the number of unpredicted associations examined by virtue of our controls for potential confounds. If robust, a possible explanation is that women with partners who are relatively high in investment as compared with sexual attractiveness (those for whom the cycle shifts in extra-pair attraction and partner jealousy are greatest) report higher sexual satisfaction because their partners are more attentive to their sexual needs.

In summary, the results support our second prediction: men who are low on sexual attractiveness evidence the greatest increases in jealousy and possessiveness from the luteal to the fertile phase of their partners' cycles.

Prediction 3: is female physical attractiveness associated with relatively high levels of male mate possessiveness across the cycle?

As predicted, in the analysis on Male Jealousy and Possessiveness, Female Physical Attractiveness had a large main effect, $F(1,17) = 16.02$, $P < 0.001$. The Fertility Status \times Female Physical Attractiveness interaction was also significant, $F(1,17) = 5.64$, $P = 0.019$ (see Fig. 3). Men with attractive partners were more jealous and possessive overall, but the jealousy of men with less attractive partners shifted more as a function of their partners' fertility status. Simple main effects analyses revealed that Female Physical Attractiveness strongly predicted male jealousy during the luteal phase, $t(17) = 3.46$, $P = 0.003$, but not during the fertile phase, $t(17) = 0.31$, ns.

With Male PSI and Female Sexual Satisfaction also controlled, both the main effect of Female Physical

Attractiveness and its interaction with Fertility Status remained robust, $F(1,14) = 16.04$, $P < 0.001$, and $F(1,14) = 6.40$, $P = 0.015$, respectively.

In summary, the results support the prediction: the jealousy and possessiveness of men with physically attractive partners are generally higher than those of men with less attractive partners. The results also suggest that the jealousy and possessiveness of men with attractive partners extend across the cycle more so than the jealousy and possessiveness of men with less attractive partners, which is greatest when their partners are fertile.

What are the effects of fertility status, male sexual attractiveness, and female physical attractiveness on male positive inducements to fidelity?

In exploratory analyses, we examined whether comparable effects would be found on male positive inducements to female fidelity, as reflected in women's reports of love and attention received from partners.

Fertility Status did not have a main effect, $F(1,17) = 1.38$, ns. Female Physical Attractiveness had a marginally significant overall effect, $F(1,17) = 3.24$, $P = 0.089$, and a marginally significant interaction with Fertility Status, $F(1,17) = 3.79$, $P = 0.068$. Men mated to more attractive women tended to be more attentive overall, but this effect was larger in the luteal phase than in the fertile phase; simple main effects: luteal phase: $t(17) = 2.26$, $P = 0.038$; fertile phase, $t(17) = 0.13$, ns. This effect parallels the interaction effect of female attractiveness and fertility status on jealousy and possessiveness. Men perceived to be higher in overall mate value, relative to self, tended to be claimed to be less loving and attentive overall, $F(1,17) = 3.96$, $P = 0.063$. No other interactions were significant, all $F(1,17) < 1.32$, ns.

When sexual satisfaction and male investment were included as predictors, the interaction between Female Physical Attractiveness and Fertility Status reached statistical significance, $F(1,14) = 6.32$, $P = 0.025$. The main effects of Male Overall Mate Value and Female Physical Attractiveness did not reach statistical significance, $F(1,14) = 3.68$, $P = 0.076$, and $F(1,14) = 3.2$, $P = 0.099$, respectively.

Prediction 4: do women feel greater desirability or power near ovulation?

As predicted, women tended to report feeling greater power and desirability, relative to their partners, when they were fertile than when non-fertile (marginal means = 0.16 and -0.50 , respectively), $F(1,17) = 3.44$, $P = 0.051$.

As also anticipated, the effect of fertility status was especially carried by women with partners not particularly attractive as short-term mates themselves, relative to their long-term mate attractiveness, $F(1,17) = 5.73$, $P = 0.018$ (see Fig. 4), and by less attractive women, $F(1,17) = 4.32$, $P = 0.033$. These interactions were also significant when Male PSI and Female Sexual Satisfaction were added as predictors, $F(1,14) = 4.19$, $P = 0.038$, and $F(1,14) = 4.95$, $P = 0.027$, respectively.

No main effects of the individual differences measures emerged.

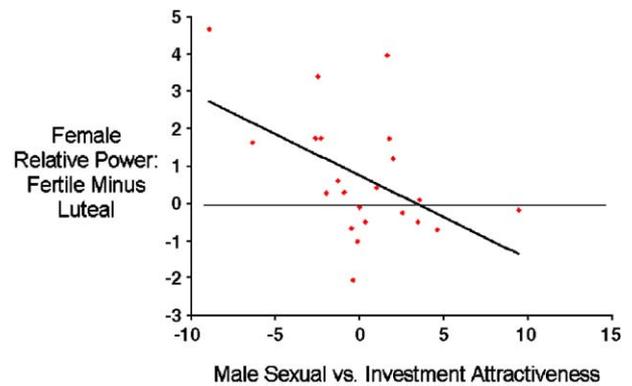


Fig. 4. Scatterplot of shift in women's relative power and desirability across the cycle (fertile–luteal) as a function of men's relative sexual-versus-investment attractiveness. These values are residuals (centered around the sample mean value), with Male Overall Mate Value, Female Physical Attractiveness, and breakup status controlled. The partial correlation is -0.50 , $P = 0.017$. $n = 22$.

General desire

We made no predictions about changes in overall sexual desire but examined them. We found no effect of fertility status, $F(1,17) = 0.40$, ns, or its interaction with Male Overall Mate Value ($F[1,17] = 3.20$, $P = 0.092$), Male Sexual-versus-Investment Attractiveness ($F[1,17] = 2.44$, ns), or Female Physical Attractiveness ($F[1,17] = 0.69$, ns). Female Physical Attractiveness had a main effect, $F(1, 17) = 6.23$, $P = 0.023$; more attractive women reported greater sexual desire. The differential effects of general sexual desire and extra-pair desire suggest that shifts in women's desires across the cycle are target-specific (cf. Chivers et al., 2004).

Might men be tracking shifts in female flirtatious behavior?

Women's fertility status, in concert with their own attractiveness and characteristics of male partners, affected their attraction to other men and their partner's jealousy, as our hypotheses predict. An issue not directly addressed by our hypotheses is how mating adaptations in men accomplish the differential allocation of mate retention efforts across the cycle so that increased efforts coincide with the period of highest conception risk. A natural question raised by our results is whether the increased jealousy expressed by men at high fertility can possibly be attributed to changes in their partner's flirtatious behaviors (with increased flirtation resulting in increased jealousy), or whether men are using other cues more directly linked with ovulation, such as women's body scent, to adjust their mate retention efforts. To explore this question, we simply correlated changes in women's flirtation and attraction to men from the luteal to the fertile phase with changes in male possessiveness/jealousy from the luteal to the fertile phase. In fact, these changes tended to be positively correlated, $r = 0.34$, $P = 0.069$ (directed test). When the analysis was limited only to overt female behavior (items measuring only flirtation from the flirtation and attraction composite), this result was somewhat stronger, $r = 0.41$, $P = 0.032$ (directed test). These positive associations between flirtation and attraction and male mate guarding are consistent with a similar

result found by Gangestad et al. (2002) and with the possibility that men do track cues of women's attraction to other men and adjust their mate retention efforts accordingly (though they naturally do not rule out other cues that could mediate changes in male mate guarding across the female cycle). The correlation between changes in women's flirtation and attraction to other men and changes in men's love toward them across the ovulatory cycle fell short of significance, $r = 0.24$, ns, as did the association between men's love and the flirtation items alone, $r = 0.24$, ns.

Predictions for pair-bonded and single women

Prediction 5: do women feel more attractive and sexy near ovulation?

Women were predicted and found to report feeling more attractive and sexually desirable when fertile (marginal mean = 2.45) than during the luteal phase (marginal mean = 0.93; $F[1,34] = 6.82$, $P = 0.008$). This effect was not moderated by either relationship status ($F[1,34] = 0.06$, ns) or female physical attractiveness ($F[1,34] = 0.36$, ns). Although there is evidence that features associated with attractiveness change across the cycle (e.g., scent as rated by men, Singh and Bronstad, 2001, Thornhill et al., 2003), no study has before explored or documented an ovulatory shift in women's self-perceived attractiveness. This finding could reflect sensitivity in women to objective changes in their own attractiveness to men or it could serve a motivational function, as we discuss below.

Prediction 6: are women more interested in going out to places where they could meet men near ovulation?

Women were predicted and found to report greater interest in going out to places where they might meet men (dance clubs and parties) when fertile (marginal mean = 0.11) than when non-fertile (marginal mean = -0.87; $F(1,34) = 5.99$, $P = 0.012$). This effect was not moderated by women's relationship status ($F[1,34] = 0.59$), ns, or their physical attractiveness ($F[1,34] = 2.45$, $P = 0.13$).

Discussion

Women's reproductive biology has imposed heavy obligatory costs of parental investment and strong selection for a discriminating sexual psychology. This proposal, coupled with the fact that the period of maximal fertility within a woman's cycle is fleetingly brief, suggests that the expression of a woman's mating adaptations may be sensitive to or contingent upon her fertility status. This study provided evidence for this general thesis.

This study also supported a specific hypothesis about mating design in human females. Prior research using longitudinal laboratory methods showed that pair-bonded women experience increases in their desire for extra-pair sex near ovulation (Gangestad et al., 2002, 2005b; also see Bellis and Baker, 1990); another study using somewhat weaker cross-sectional methods did not find this effect (Pillsworth et al., 2004). We tested a prediction specific to a good genes account of increases

in extra-pair desires at midcycle that may help to explain why women show varying patterns of desire across the cycle. Specifically, we predicted and found that women with partners low in sexual-versus-investment attractiveness would be those for whom the ovulatory increase in extra-pair desires is greatest. Our finding is bolstered by another recent study, which found that women paired with long-term partners who are relatively asymmetrical report greater increases in extra-pair attraction midcycle compared to women with symmetrical partners (Gangestad et al., 2005b). In concert, these two sets of findings provide a key piece of evidence for the good genes model of human extra-pair mating.

This study also provided evidence for shifting conflicts of interest between women and their primary partners. Women reported their partners to be more jealous and possessive and themselves to feel greater power in their relationships at midcycle, effects also moderated by male sexual attractiveness—ovulatory shifts were greater for women with partners low in sexual attractiveness relative to investment attractiveness, as the good genes hypothesis predicts. As male jealousy was reported by female partners, we cannot be certain that changes in male behavior are actual rather than merely perceived, though other evidence indicates that partners' reports of jealousy tend to agree (Gangestad et al., 2002; Dobash et al., 1998). We also observed converging effects of fertility across the cycle on reports of male jealousy/possessiveness, which women tend to find aversive, and love/attentiveness, which women tend to find pleasant. This would seem to weigh against an alternative explanation based on shifts in women's global feelings about their social partners near ovulation (e.g., that they are more easily irritated by them).

A colleague who commented on an earlier draft of this paper proposed an alternative explanation for the finding that women with less sexually attractive partners experience ovulatory increases in extra-pair desires: because women experience fewer orgasms during sex with partners high in fluctuating asymmetry (who are less sexually attractive; Gangestad et al., 1994; Shackelford et al., 2000; Thornhill et al., 1995), these women could be less sexually satisfied and more prone to look elsewhere during periods of increased desire. Two of our other findings argue against this explanation. First, our findings involving extra-pair desires remained robust after controls for female sexual satisfaction. Second, we examined but did not find cyclic shifts in women's reports of generalized desire. We do not assert based on this null finding that generalized desire does not change across the cycle; indeed, other studies have found this effect (e.g., Wallen, 1995). We do argue that the lack of robust effects of generalized desire indicates that the extra-pair desire findings in our study are not attributable to generally elevated feelings of sexual desire in our participants. The differential effects of extra-pair desires and generalized desires also suggest that researchers should ask target-specific questions when assessing changes in women's sexual thoughts and feelings, as assessments of generalized desire might not fully capture the subtlety of cyclic shifts.

Other competing explanations of female extra-pair mating also do not fit well with our findings. A mate-switching account

(Greiling and Buss, 2000), which proposes that women are seeking new *long-term* social mates, does not straightforwardly predict ovulatory effects nor does it predict ovulatory effects conditional on male sexual attractiveness. Moreover, whereas Jones et al. (2005) found that women's commitment to their partners was lower on high fertility days within the cycle, they did not find cyclic differences in women's general happiness in their relationships, which further suggests that the female temptation to stray is not the result of motivations to switch mates. The genetic diversity hypothesis (see, e.g., Jennions and Petrie, 2000) suggests that women seek extra-pair matings as a bet-hedging strategy so that all of their offspring are not eliminated at once by a single disease; this hypothesis also does not lead to expectations about the effects of male sexual attractiveness on extra-pair desires. The paternity confusion hypothesis (e.g., Hrdy, 2003) is challenged by our findings—if women seek to confuse men about true paternity, matings need to only be scattered across the cycle and across several possible sires rather than concentrated during periods of high fertility and especially when a woman's social partner lacks sexual attractiveness.

Naturally, we cannot rule out all other possible interpretations of our effects. Sexual attractiveness in men is reasonably hypothesized to be an indicator of genetic fitness (ancestrally, even if not now), but we cannot be certain that it is. The key is not whether there are other potential causes of sexual attractiveness—very clearly, there are (e.g., Kokko et al., 2003)—but rather whether any of these alternatives could generate and account for our specific findings concerning ovulatory cycle variation (or, for that matter, the many other studies that have documented ovulatory cycle shifts in female mate preferences or sexual interests; e.g., Gangestad et al., 2005a).

One alternative explanation that cannot be ruled out is the possibility that, rather than tapping intrinsic good genes, our measure of sexual attractiveness taps compatible genes—those that work well with the mate chooser's genes rather than individuals in general (e.g., Jennions and Petrie, 2000; Zeh and Zeh, 2001). Wedekind et al. (1995), for instance, found that women find the scent of men who do not share with them major histocompatibility (MHC) alleles more attractive; MHC dissimilarity presumably constitutes compatible genes (see Penn and Potts, 1999). Because our measure of male sexual attractiveness was an assessment made by the female partner rather than an assessment by outside observers, our measure may at least partly reflect attractiveness due to compatibility. This compatible genes interpretation—another form of good genes argument—could also lead to the prediction that partner-assessed male sexual attractiveness will be associated with greater flirtation with and attraction to extra-pair men when women are fertile. Thornhill et al. (2003) found no evidence that normally ovulating women particularly prefer the scent of MHC compatible men when in the fertile phase of their cycles, but their findings do not rule out the possibility that MHC compatibility could nonetheless moderate changes in female sexual interest across the cycle. This alternative good genes account, then, deserves further investigation.

We did not detect robust moderator effects of overall male mate value (sexual attractiveness plus investment attractiveness) on female extra-pair attraction and male mate guarding. In collared flycatchers, females do not strongly prefer males with large forehead patches as social partners (presumably because males with small patches make up for their lack of good genes with increased paternal investment), and the overall value of males as social partners does not predict female extra-pair mating. Rather, females are most likely to seek extra-pair matings when their social partners have small forehead patches and tend to invest relatively heavily in offspring (Michl et al., 2002). Of course, not all bird species show this pattern; but, if we are correct that human females have also been selected to trade off good genes for investment in primary partners and to seek extra-pair matings when their primary partners are low in sexual attractiveness, the collared flycatcher model may offer insights into the human data.

Ancestral men needed to allocate time to multiple fitness-relevant activities with demands that were often in conflict. Increased efforts devoted to mate guarding, for example, would result in corresponding decreases in other activities, such as resource acquisition. It is likely that the ancestral benefits of mate retention extending throughout a woman's cycle were higher for men with physically attractive mates, as attractiveness signaled greater youth and fertility and hence greater reproductive opportunity (and the potential for reproductive loss). We therefore predicted and found that men's efforts devoted to mate retention would be higher when directed toward more attractive partners. We also found that men's mate retention efforts were most strongly linked to fertility in the menstrual cycle when their mates were relatively low in physical attractiveness. Women high in attractiveness reported relatively high levels of mate guarding throughout the cycle. Parallel results were observed for male partners' positive inducements to female fidelity (expressed love and attention).

This study also documented two new effects of cycle-based fertility status among both pair-bonded and single women. Women felt more sexually attractive and had a greater desire to go out and meet men at midcycle. These effects could serve motivational functions. Like men, ancestral women needed to accomplish diverse tasks ranging from childcare, to food acquisition, to mating actions involved in the choice of partners and the timing of reproduction. Because the costs and benefits of women's mating actions are greatest when they are most fertile, selection may have designed adaptations in women that increase the motivational strength of mating decisions near ovulation. Indeed, this is one interpretation of evidence that female calorie intake is reduced and ranging activities increased near ovulation (Fessler, 2003). Female self-perceived attractiveness is associated with stronger preferences for symmetry and masculinity in male faces (Little et al., 2001). Therefore, enhanced feelings of attractiveness might also serve a related function: to lead women to be more selective when most fertile in their cycle.

A limitation of this study is our use of female assessments rather than more objective measures of male partners' sexual and investment attractiveness. Additional data using such

measures would provide further evidence in favor of the hypotheses (see, e.g., our discussion of the compatible genes alternative above), but we also hasten to add that cues to male sexual and investment attractiveness must be perceived and processed by the female psychology in order to have effects on female behavior; thus, future studies gathering objective assessments should also assess female perceptions.

We detected many significant effects in this study despite a fairly modest sample size, perhaps partly because we sampled observations from women across an entire cycle, a within-subject design allowing for fairly good estimation of cycle variation for individual women. The fact that effects were detected despite modest sample size may also attest to their size. This study is the first to use a daily report method to test evolutionary hypotheses about cycle shifts. A drawback of laboratory studies in which women are scheduled at high and low fertility points in their cycle, and in which hormonal assays are used (e.g., Gangestad et al., 2002), is that participants may realize that researchers intend to compare their responses during different points in the cycle (e.g., if participants detect that session scheduling is based on information, they provided about their cycles or that the urine tests measure hormone levels). The diary method we used is valuable supplement to other methods because the intention to compare low and high fertility days is not obvious to participants (indeed, none of our participants suspected that we were examining midcycle shifts). Because we did not conduct hormonal assays, we could not pinpoint the precise day of ovulation in our participants. Still, it is very likely that our 5-day high fertility windows substantially overlapped with true 5-day windows in our sample. Moreover, any lack of overlap would weaken our ability to detect effects; it is hard to imagine how minor inaccuracies in our estimation of days of ovulation using the reverse cycle method could have led us to detect effects not real.

A key question left unanswered by this research concerns the hormonal mechanisms likely to underpin these effects. Analyses of women's attraction to the scent of symmetrical men found that changes across the cycle appear to be best accounted for by facilitative effects of testosterone and suppressive effects of progesterone (as estimated by mean changes in these and other hormones, such as estrogen, across the cycle; Garver-Apgar, Gangestad, and Thornhill, unpublished data). Changes in women's preference for vocal masculinity (Puts, 2005), facial masculinity (Jones et al., 2005), and facial self-resemblance (DeBruine et al., 2005) also show patterns that are best explained by changes in progesterone across the cycle. And, Gangestad et al. (2002) found that changes in women's extra-pair desires across the ovulatory and luteal phases were stronger for women tested nearer to the day of luteinizing hormone surge. Testosterone, progesterone, and luteinizing hormone are therefore all candidate mechanisms, and future research should examine which of these specific hormones, or ratios of hormones, underlie cyclic shifts in women's desires. A related question concerns whether variations in hormones across individual women's cycles (between-cycle variation) or across women (between-woman variation)

affect women's sexual preferences and sexual interests in ways similar to the within-cycle variations we report. As men's behavior in response to women may also be sensitive to physiological or behavioral byproducts of female hormone levels, men's behavior toward their partners may also vary with variations in specific hormones. These questions suggest clear avenues for future research.

At a more general level, the results of this study provide further evidence for the subtlety and intricacy of adaptive design for mating in humans. They suggest that ovulatory cycle shifts in female sexual interests and male mate guarding are themselves dependent upon contextual cues, including characteristics of the partner. It is not at all evident that this adaptive information processing could be achieved by general cognitive abilities not structured or specialized to solve particular adaptive problems specific to mating and differentiated by sex (cf. Wood and Eagly, 2002). These findings provide evidence, therefore, for the basic premise that humans possess domain-specific adaptations dedicated to sex-specific problems of mating (Buss, 1991; Symons, 1979; Tooby and Cosmides, 1992).

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References

- Alberts, S.C., Altmann, J., Wilson, M.L., 1996. Mate guarding constrains foraging activity of male baboons. *Anim. Behav.* 51, 1269–1277.
- Alcock, J., 2001. *The Triumph of Sociobiology*. Oxford Univ. Press, Oxford.
- Bellis, M.A., Baker, R.R., 1990. Do females promote sperm competition? Data for humans. *Anim. Behav.* 40, 997–999.
- Benshoof, L., Thornhill, R., 1979. The evolution of monogamy and the loss of estrus in humans. *J. Soc. Bio. Struct.* 2, 95–106.
- Buss, D.M., 1991. Evolutionary personality psychology. *Annu. Rev. Psychol.* 45, 459–491.
- Chivers, M.L., Reiger, G., Latty, E.J., Bailey, J.M., 2004. A sex difference in the specificity of sexual arousal. *Psychol. Sci.* 15 (736), 744.
- DeBruine, L.M., Jones, B.C., Perrett, D.I., 2005. Women's attractiveness judgments of self-resembling faces change across the menstrual cycle. *Horm. Behav.* 47, 379–383.
- Dobash, R.E., Dobash, R.P., Cavanagh, K., Lewis, R., 1998. Separate and intersecting realities: a comparison of men's and women's accounts of violence against women. *Viol. Women* 4, 382–414.
- Doty, R.L., Ford, M., Preti, G., Huggins, G.R., 1975. Changes in the intensity and pleasantness of human vaginal odors during the menstrual cycle. *Science* 190, 1316–1317.
- Ellis, B.J., 1998. The partner-specific investment inventory: an evolutionary approach to individual differences in investment. *J. Perspsi* 66, 383–442.

- Feinberg, D.R., Jones, B.C., Law Smith, M.J., Moore, F.R., DeBruine, L.M., Cornwell, R.E., Hillier, S.G., Perrett, D.I. in press. Menstrual cycle, trait estrogen level and masculinity preferences in the human voice.
- Fessler, D.M.T., 2003. No time to eat: an adaptationist account of periovulatory behavioural changes. *Q. Rev. Biol.* 78, 3–21.
- Flinn, M.V., 1988. Mate guarding in a Caribbean village. *Ethol. Sociobiol.* 9, 1–28.
- Gangestad, S.W., Simpson, J.A., 2000. The evolution of human mating: trade-offs and strategic pluralism. *Behav. Brain Sci.* 23, 675–687.
- Gangestad, S.W., Thornhill, R., 1997. The evolutionary psychology of extrapair sex: the role of fluctuating asymmetry. *Evol. Hum. Behav.* 18, 69–88.
- Gangestad, S.W., Thornhill, R., 1998. Menstrual cycle variation in women's preference for the scent of symmetrical men. *Proc. R. Soc. London, B* 265, 927–933.
- Gangestad, S.W., Thornhill, R., 2004. Female multiple mating and genetic benefits in humans: investigations of design. In: Kappeler and, P.M., van Schaik, C.P. (Eds.), *Sexual Selection in Primates: New and Comparative Perspectives*. Cambridge Univ. Press, Cambridge, pp. 90–116.
- Gangestad, S.W., Thornhill, R., Yeo, R.A., 1994. Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethol. Sociobiol.* 15, 73–85.
- 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. *Proc. R. Soc. London, B* 269, 975–982.
- Gangestad, S.W., Simpson, J.A., Cousins, A.J., Garver-Apgar, C.E., Christensen, P.N., 2004. Women's preferences for male behavioral displays change across the menstrual cycle. *Psychol. Sci.* 15, 203–207.
- Gangestad, S.W., Thornhill, R., Garver-Apgar, C.E., 2005a. Adaptations to ovulation. In: Buss, D.M. (Ed.), *Handbook of Evolutionary Psychology*. Wiley, New York, pp. 344–371.
- Gangestad, S.W., Thornhill, R., Garver-Apgar, C.E., 2005b. Women's sexual interests across the ovulatory cycle depend on primary partner fluctuating asymmetry. *Proc. R. Soc. London, B* 272, 2023–2027.
- Greiling, H., Buss, D.M., 2000. Women's sexual strategies: the hidden dimension of extra-pair mating. *Pers. Individ. Differ.* 28, 929–963.
- Hrdy, S.B., 2003. The optimal number of fathers: evolution, demography, and history in the shaping of female mate preferences. In: Scher, S.J. (Ed.), *Evolutionary Psychology: Alternative Approaches*. Kluwer, Dordrecht, Netherlands, pp. 111–133.
- Jennions, M.D., Petrie, M., 2000. Why do females mate multiply?: A review of the genetic benefits. *Biol. Rev.* 75, 21–64.
- Johnston, V.S., Hagel, R., Franklin, M., Fink, B., Grammer, K., 2001. Male facial attractiveness: evidence for hormone mediated adaptive design. *Evol. Hum. Behav.* 23, 251–267.
- Jones, B.C., Little, A.C., Boothroyd, L., DeBruine, L.M., Feinberg, D.R., Law Smith, M.J., Cornwell, R.E., Moore, F.R., Perrett, D.I., 2005. Commitment to relationships and preferences for femininity and apparent health in faces are strongest on days of the menstrual cycle when progesterone level is high. *Horm. Behav.* 48, 283–290.
- Kokko, H., Brooks, R., Jennions, M.D., Morley, J., 2003. The evolution of mate choice and mating biases. *Proc. R. Soc. London, B* 270, 653–664.
- Lenton, E.A., Landgren, B.M., Sexton, L., 1984. Normal variation in the length of the luteal phase of the menstrual cycle: identification of the short luteal phase. *Br. J. Obstet. Gynaecol.* 91, 685–689.
- Little, A.C., Burt, D.M., Penton-Voak, I.S., Perrett, D.I., 2001. Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proc. R. Soc. London, B* 268, 39–44.
- Møller, A.P., Alatalo, R.V., 1999. Good-genes effects in sexual selection. *Proc. R. Soc. London, B* 266, 85–91.
- Michl, G., Torok, J., Griffith, S.C., Sheldon, B.C., 2002. Experimental analysis of sperm competition mechanisms in a wild bird population. *Proc. Natl. Acad. Sci. U. S. A.* 99, 5466–5470.
- Penn, D., Potts, W., 1999. The evolution of mating preferences and major histocompatibility complex genes. *American Nat.* 153, 145–164.
- Penton-Voak, I.S., Perrett, D.I., 2000. Female preference for male faces changes cyclically: further evidence. *Evol. Hum. Behav.* 21, 39–48.
- Penton-Voak, I.S., Perrett, D.I., Castles, D., Burt, M., Koyabashi, T., Murray, L.K., 1999. Female preference for male faces changes cyclically. *Nature* 399, 741–742.
- Pillsworth, E.G., Haselton, M.G., Buss, D.M., 2004. Ovulatory shifts in female sexual desire. *J. Sex Res.* 41, 55–65.
- Puts, D.A., 2005. Mating context and menstrual phase affect female preferences for male voice pitch. *Evol. Hum. Behav.* 26, 388–397.
- Qvarnström, A., 1999. Different reproductive tactics in male collared flycatchers signalled by size of secondary sexual character. *Proc. R. Soc. London, B* 266, 2089–2093.
- Rice, W.R., Gaines, S.D., 1994. 'Heads I win, tails you lose': testing directional alternative hypotheses in ecological and evolutionary research. *Trends Ecol. Evol.* 9, 235–237.
- Rikowski, A., Grammer, K., 1999. Human body odour, symmetry, and attractiveness. *Proc. R. Soc. London, B* 266, 869–874.
- Roberts, S.C., Havlicek, J., Flegr, J., Hruskova, M., Little, A.C., Jones, B.C., Perrett, D.I., Petrie, M., 2004. Female facial attractiveness increases during the fertile phase of the menstrual cycle. *Proc. R. Soc. London, B* 271, S270–S272 (Suppl.).
- Scheib, J.E., Gangestad, S.W., Thornhill, R., 1999. Facial attractiveness, symmetry, and cues of good genes. *Proc. R. Soc. London* 1318–1321.
- Schmitt, D.P., Buss, D.M., 2001. Human mate poaching: tactics and temptations for infiltrating existing relationships. *J. Pers. Soc. Psychol.* 80, 894–917.
- Shackelford, T.K., Weekes-Shackelford, V.A., LeBlanc, G.J., Bleske, A.L., Euler, H.A., Hoier, S., 2000. Female coital orgasm and male attractiveness. *Hum. Nat.* 11, 299–306.
- Sheldon, B.C., Merila, J., Qvarnström, A., Gustafsson, L., Ellegren, H., 1997. Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character. *Proc. R. Soc. London, B* 264, 297–302.
- Singh, D., Bronstad, P.M., 2001. Female body odour is a potential cue to ovulation. *Proc. R. Soc. London, B* 268, 797–801.
- Symons, D., 1979. *The Evolution of Human Sexuality*. Oxford Univ. Press, New York.
- Symons, D., 1995. Beauty is in the adaptations of the beholder: the evolutionary psychology of human female sexual attractiveness. In: Abramson, P., Pinkerton, S. (Eds.), *Sexual Nature/Sexual Culture*. University of Chicago Press, Chicago, pp. 80–118.
- Thornhill, R., 1990. The study of adaptation. In: Bekoff, M., Jamieson, D. (Eds.), *Interpretation and Explanation in the Study of Behavior*, Vol. II. Westview Press, pp. 31–62.
- Thornhill, R., Gangestad, S.W., Comer, R., 1995. Human female orgasm and mate fluctuating asymmetry. *Anim. Behav.* 50, 1601–1615.
- Thornhill, R., Gangestad, S.W., Miller, R., Scheyd, G., McCollough, J., Franklin, M., 2003. MHC, symmetry and body scent attractiveness in men and women (*Homo sapiens*). *Behav. Ecol.* 14, 668–678.
- Tooby, J., Cosmides, L., 1992. The psychological foundations of culture. In: Barkow, J.H., Cosmides, L., and, J. (Eds.), *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. Oxford Univ. Press, New York, pp. 19–136.
- Wallen, K., 1995. The evolution of female sexual desire. In: Abramson, P., Pinkerton, S. (Eds.), *Sexual Nature, Sexual Culture*. University of Chicago Press, Chicago, pp. 57–79.
- Wilcox, A.J., Duncan, D.B., Weinberg, C.R., Trussell, J., Baird, D.D., 2001. Likelihood of conception with a single act of intercourse: providing benchmark rates for assessment of post-coital contraceptives. *Contraception* 63, 211–215.
- Van den Berghe, P.L., Frost, P., 1986. Skin color preference, sexual dimorphism and sexual selection: a case of gene-culture co-evolution? *Ethn. Racial Stud.* 9, 87–113.
- Wedekind, C., Seebeck, T., Bettens, F., Paepke, A.J., 1995. MHC-dependent mate preferences in humans. *Proc. R. Soc. London, B* 260, 245–249.
- Wood, W., Eagly, A.H., 2002. A cross-cultural analysis of the behavior of men and women: implications of the origins of sex differences. *Psychol. Bull.* 128, 699–727.
- Zeh, J.A., Zeh, D.W., 2001. Reproductive mode and the genetic benefits of polyandry. *Anim. Behav.* 61, 1051–1063.