

Evolution and Human Behavior 27 (2006) 247-258

Evolution and Human Behavior

Male sexual attractiveness predicts differential ovulatory shifts in female extra-pair attraction and male mate retention

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Initial receipt 1 July 2005; final revision received 11 October 2005

Abstract

Because ancestral women faced trade-offs in choosing mates, they may have evolved to pursue a dual-mating strategy in which they secured investment through one partner and obtained good genes through others. The dual-mating theory predicts that women will display greater interest in extra-pair sex near ovulation, especially if they are mated to a primary male partner who is low in sexual attractiveness. Forty-three normally ovulating women rated their partner's sexual attractiveness and separately reported their own desires and their partner's mate retention behaviors at high and low fertility (confirmed using luteinizing hormone tests). In the high-fertility session relative to the low, women who assessed their partners as being lower in sexual attractiveness reported greater extra-pair desires and more expressed love and attention from their male partners. Women's desire for their own partners did not differ significantly between high and low-fertility sessions.

Keywords: Ovulatory cycle; Mate guarding; Sexual conflict; Conception; Sexual desire; Female sexuality

1. Introduction

Females can benefit by selecting mates who offer material benefits to offspring, such as parental care and food resources (Trivers, 1972), and by selecting mates who offer benefits

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^{1090-5138/06/\$ –} see front matter @ 2006 Elsevier Inc. All rights reserved. doi:10.1016/j.evolhumbehav.2005.10.002

that can be genetically transmitted to offspring (Jennions & Petrie, 2000; Kokko, Brooks, Jennions, & Morley, 2003; Møller & Alatalo, 1999). In principle, women could benefit from both material and heritable benefits conferred by male partners, but both sets of features may be difficult to find in the same mate. Men who display indicators of good genes are highly attractive as sex partners; hence, they can, and often do, pursue a short-term mating strategy that tends to be associated with reduced investment in mates and offspring (Gangestad & Simpson, 2000; Gangestad & Thornhill, 1997). Therefore, women may often be forced to make strategic trade-offs by selecting long-term social partners who are higher in investment attractiveness than sexual attractiveness (Gangestad & Simpson, 2000).

These trade-offs may have selected for a psychology of dual mating, which leads women to seek primary partners who provide investment while seeking good genes through extra-pair mating. Indeed, rates of human extra-pair paternity are substantial, with current estimates ranging from lows around 1% to highs of more than 55% in some populations (Anderson, 2005). In sum, there are conditions under which a dual-mating strategy may have evolved, and there is evidence that human extra-pair mating occurs.

1.1. Predictions

1.1.1. Shifts in extra-pair desire

A key prediction of the dual-mating hypothesis is that attraction to extra-pair mates should increase as women near ovulation. Results from previous studies have been somewhat mixed, with most documenting greater attraction to extra-pair mates when women are in the ovulatory phase of their cycles (Gangestad, Thornhill, & Garver, 2002; Haselton & Gangestad, in press) and one suggesting that women are more attracted to their primary partner at peak fertility within the cycle (Pillsworth, Haselton, & Buss, 2004). In light of these conflicting findings, Pillsworth et al. (2004) suggested that future research should explicitly examine male sexual attractiveness to test the hypothesis that a woman's pursuit of an extra-pair vs. an in-pair conceptive strategy is conditional on how sexually attractive her partner is relative to other men. Consistent with this proposal, in a daily diary study, Haselton and Gangestad (in press) found that increases in extra-pair desires at high fertility were greatest for women who rated their partners as low in sexual vs. investment attractiveness. Similarly, Gangestad et al. (2005) found that women with partners high in fluctuating asymmetry reported greater attraction to extra-pair men, and less attraction to their own partners, when near ovulation. In the current study, we further examined this hypothesis by seeking to replicate the finding of Haselton and Gangestad (in press) using a more rigorous luteinizing hormone (LH) method of fertility assessment. We also advanced two additional predictions, which are discussed hereafter.

1.1.2. Shifts in in-pair desire

According to the good genes model, women whose long-term partners display indicators of good genes do not benefit from engaging in a dual-mating strategy; thus, we predicted that women's reported desire for their primary partner would also result from the interaction of fertility and partner's sexual attractiveness, such that ovulatory increases in in-pair desires will be reported more by women with partners who are high in sexual attractiveness.

1.1.3. Shifts in partner mate guarding and positive inducements to fidelity

Female affairs can be extremely costly to male partners, and men are therefore expected to possess evolved counter-strategies designed to protect them from cuckoldry. Mate retention strategies may be either prohibitive—such as restricting a partner's movements—or persuasive—such as engaging in attentive and solicitous behavior toward the partner. Gangestad et al. (2002) found that women reported increases in both their partners' proprietary behaviors and attentiveness as a function of fertility. In the current study, we predicted that women's reports of their partners' mate-guarding tactics would increase during the fertile phase of the cycle, and that this effect would be stronger for women who rated their partners as less sexually attractive, as these are the women most likely to pursue a dualmating strategy.

2. Methods

2.1. Participants

Participants were 43 women recruited from a large university in the Southwestern United States who either satisfied a research requirement or were paid for their participation, and who reported that they were currently involved in a romantic relationship. None had used hormonal contraceptives in the 3 months prior to participation, and all reported having regular menstrual cycles between 24 and 36 days in length (mean=29.56, S.D.=2.95). Using a nationally marketed ovulation test (ClearBlue), all participants were assessed to have a LH surge between 2 days prior and 4 days following one of their laboratory sessions (see data hereafter). Tests such as these that measure LH levels in urine are 97% concordant with ovulation as confirmed by ultrasonography (Guermandi et al., 2001). Low-fertility sessions were scheduled to occur after the likely day of ovulation, excluding menstrual days and the 3 days preceding menstruation (to avoid premenstrual effects). Eighty women were originally recruited for the study, but 37 were ineligible for inclusion in analyses because they failed to complete the multisession study (n=22), showed no evidence of an LH surge within six testing days (n=5), participated in the high-fertility session more than 4 days before a surge in LH was detected (n=1), or were scheduled inaccurately for low-fertility sessions (with that session falling either within the 3 days prior to menstruation or within what might have been an ovulatory phase, n=9). In sum, of the women who completed all parts of the study, 74.1% were eligible for inclusion in analyses. This retention rate is comparable to those of previous studies with similar methods (e.g., Gangestad et al., 2002, reported a 61.4% retention rate).

The mean age of participants in the sample was 21.43 years (S.D.=5.35, range 18–46); 8.1% identified themselves as Asian-American, 25.6% as Caucasian, 9.3% as Hispanic, 2.3% as African-American, 2.3% as Middle Eastern, and 2.3% as another ethnicity. All women in the sample identified themselves as "currently in a romantic relationship," with a median relationship length of 15.55 months (mean=28.34 months, S.D.=35.77, range=.1-144 months). Twenty-six (60.46%) women had engaged in sexual intercourse with their current partner; of those who had not, 15 (34.88% of the sample) were virgins. On average,

women had a total of 2.45 sex partners to date (S.D.=4.94, range=0–25). Four out of 43 women (9.3%) had engaged in sexual intercourse with someone other than their current partner while involved in the current relationship.

2.2. Procedure

Participants came to the laboratory for three sessions: an initial session and two follow-up sessions. The follow-up sessions were scheduled according to each participant's menstrual cycle, with one session occurring during the ovulatory phase of her cycle and the other occurring during the luteal phase (information on phase scheduling appears hereafter).

2.2.1. Initial session

Participants answered questions about their health (e.g., medications they were taking), cycle regularity, cycle length, and anticipated next date of menstrual onset. Participants then completed several computer-based questionnaires that included basic demographic information, relationship and sexual histories, and several items concerning their assessments of their relationship and current partner.

Items assessing partner mate value (after Haselton, 2003) varied along two primary dimensions: sexual attractiveness and investment attractiveness. Sexual attractiveness (α =.83) was the aggregate of the following: "Compared with most men, how attractive is your partner's body to women?" "Compared with most men, how attractive is your partner's face to women?" "Compared with most men, how sexy would women say your partner is?" Investment attractiveness (α =.71) was the aggregate of the following: "Compared with most men, what is your partner's present financial status?" "Compared with most men, what is your partner's estimated future financial status?" "Compared with most men, how high is your partner in social status at the present time?" "Compared with most men, what is your partner's estimated future social status?" and "How intelligent would women say your partner is, compared to most men?" Each of the items was rated on a scale of 1-9 (1="extremely low" or "not at all sexy/intelligent/etc.," 5="average," and 9="extremely high" or "extremely sexy/ intelligent/etc."). Intelligence has been argued to be a sexually selected fitness indicator (Furlow, Armijo-Prewitt, Gangestad, & Thornhill, 1997; Miller, 2000), and it is also linked with financial success (Neisser et al., 1996). Because intelligence was correlated more strongly with the investment attractiveness items than with the sexual attractiveness items, and its inclusion in the investment attractiveness composite increased the reliability of the investment attractiveness measure, we included it in the investment attractiveness composite. Dropping intelligence from the composite did not affect the patterning of results reported below.

Sexual satisfaction was assessed with five items created for the purpose of this study. Each item asked women to assess their primary partner relative to other men with whom they had sexual experience (α =.91): "Relative to sex with other men, how enjoyable is sex with your current partner?" "... how passionate is sex with your current partner?" "... how attentive to your needs is your partner during sex?" "... how satisfying is sex with your current partner?" during sex?" "... how satisfying is sex with your current partner?" Women were directed to answer these questions with regard to all sexual activity (including kissing,

touching, etc.), whether or not they had ever engaged in sexual intercourse. Items were rated on a 1–7 scale (1=not at all enjoyable/etc., 4=average, 7=extremely enjoyable/etc.).

2.2.2. Scheduling and LH testing

We followed the methods of Gangestad et al. (2002). In the initial session, if a participant was currently in the follicular phase of her cycle (more than 17 days prior to the anticipated start of her next menstruation), she was scheduled for a high-fertility session; if she was in the luteal phase of her cycle (between 4 and 17 days before menstruation), she was scheduled for a low-fertility session. Women expecting menstrual onset within 3 days were scheduled for high-fertility sessions. About half of the participants completed their high-fertility session first (n=23, 53.49%), and about half completed their low-fertility session first (n=20, 46.51%).

High-fertility sessions were scheduled to occur between 16 and 19 days prior to the expected end of the cycle, with the expectation that ovulation normally occurs 14-15 days prior to the onset of menses (Weinberg, Gladen, & Wilcox, 1994; Wilcox, Weinberg, & Baird, 1995). Women were scheduled to complete urine tests beginning 2 days before their highfertility session and continuing for at least 5 days, or until a surge was detected; on these days participants reported to the laboratory and were given an unlabeled midstream urine test designed to detect the presence of LH in the urine. Participants were blind to the purpose of the tests. An LH surge usually occurs 24–48 h prior to ovulation; thus, it was expected that a surge would be observed for most women on or shortly following their scheduled highfertility session. Luteinizing hormone surge was observed, on average, 0.98 days following the scheduled high-fertility session (S.D.=1.42; range, 2 days prior to 4 days following). Conception may occur as a result of intercourse up to 5–7 days prior to ovulation (Jochle, 1973; Wilcox et al., 1995); hence, all of the women included in this study are presumed to have been in a fertile state at the time of their high-fertility session. Because the probability of conception increases as ovulation nears, the estimated number of days prior to ovulation (days-to-LH-surge minus 2) was included as a control variable in analyses. Inclusion of this variable (with day of ovulation=0) allowed us to estimate high- vs. low-fertility effects at the day of ovulation.

Low-fertility sessions were scheduled to occur 3–10 days prior to the next expected menstrual onset. On average, women were tested 6.61 days prior to the end of their menstrual cycle (S.D.=1.93), excluding one women whose low-fertility session was conducted during the follicular rather than the luteal phase (23 days before expected menstruation or 9 days before estimated day of ovulation). This session was far enough from the predicted date of ovulation to be nonfertile (Wilcox et al., 1995) and was thus retained in the analyses.

2.2.3. Sessions 2 and 3

During the high-fertility and low-fertility sessions, participants completed a series of computer-based questionnaires about their current feelings, desires, and recent experiences with their primary partners and with other men.

Participants were asked to rate, on a scale of -4 (far less than usual) to +4 (far more than usual, 0=about average) how much they had experienced certain events over the last 48 h,

Measure	Items	α at high fertility	α at low fertility
Extra-pair desire	Been physically attracted to someone you did not know Been physically attracted to an acquaintance Been physically attracted to a friend or coworker	.70	.85
In-pair desire	Felt sexually attracted to your partner	_	_
General desire	Had persistent sexual thoughts Had sexual thoughts Had sexual fantasies Experienced sexual desire	.93	.94
Partner solicitousness	Given you attention Expressed commitment to you Expressed feelings of love to you Expressed sexual attraction to you	.94	.90
Partner jealousy	Acted jealous about your casual interactions with other people Monopolized your time Acted possessive of you	.80	.90

Measures in surveys administered at high and low fertility

relative to other days. The items of interest were interspersed with other items that were not theoretically predicted to vary across the menstrual cycle, and for which few significant effects emerged, with no clear pattern across like items (e.g., "felt happy" or "felt sad"). Table 1 presents items used to test our predictions with composite reliabilities at both high and low fertility.

3. Results

Table 1

3.1. Statistical analyses

We conducted analyses using repeated general linear models (SPSS 12.0) on the dependent variables of interest. Fertility status (measured as low vs. high phases of the cycle) was a repeated factor in all analyses. In our focal analyses, we entered partner's sexual attractiveness and investment attractiveness—which were of primary interest in tests of predictions—as quantitative predictor variables, along with the number of days prior to ovulation in the high-fertility session, and session order (high vs. low first).

In a second set of analyses, we added several control variables to examine whether the effects of primary interest were robust to the inclusion of variables that might be confounded

with partner's sexual attractiveness. Whether a woman had ever had sexual intercourse with her partner (yes vs. no) was entered as a factor and therefore controlled. Sexual satisfaction and relationship length were also added as quantitative control variables. These quantitative variables were zero centered so that the main effect of fertility status would be estimated for mean levels of these predictors. Our consent procedures made it clear that women could skip items that they did not wish to respond to and still remain in the study. There are, therefore, some missing data, and the degrees of freedom for the reported analyses vary accordingly.

We followed the recommendations of Rice and Gaines (1994) by implementing directed tests for predicted effects. These tests allocate a probability of .04 (of a total .05) to the predicted tail and .01 to the unpredicted tail. For unpredicted effects, we used two-tailed tests. Reported p values reflect these criteria.

One woman had an extremely low partner's sexual attractiveness score (3.54 S.D. below the mean), raising the possibility that her datum might skew estimates of effects. We therefore winsorized the data, which entailed truncating only this score to meet the next lowest score (1.74 S.D. below the mean; Howell, 1992). Presented analyses include the truncated score. The two key interactions of sexual attractiveness and cycle phase remain when the original score is included in analyses.

3.2. Shifts in extra-pair and in-pair desires

3.2.1. Are ovulatory increases in extra-pair desires greater for women with less sexually attractive partners?

As predicted, the effect of fertility status on extra-pair desires was moderated by partner's sexual attractiveness [F(1,38)=5.54, p=.015, partial r=-.36; see Fig. 1]. Women who perceived their partners as low in sexual attractiveness were particularly likely to report increases in extra-pair desires at high fertility. There was no interaction of phase and partner's investment attractiveness on extra-pair desires [F(1,38)=.05, ns]. Overall, women tended to report greater extra-pair desires at high fertility (marginal mean=0.27) than at low fertility

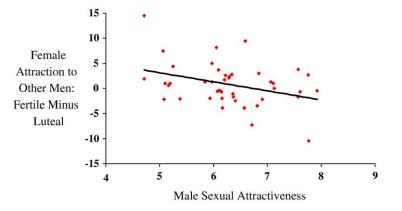


Fig. 1. Relationship between male sexual attractiveness and ovulatory shifts in women's attraction to extra-pair men. n=43, partial r=-.36, p=.015; points represent residual scores after controlling for investment attractiveness, order of session (high vs. low fertility first), and estimating effect of phase at the day of ovulation (based on LH assay).

(marginal mean=-0.48), but this effect was not statistically significant [F(1,38)=.70, ns]. No other effects were significant.

With the other covariates added, the interaction of fertility status and partner's sexual attractiveness remained robust [F(1,30)=6.28, p=.011], and the main effect of fertility status began to approach significance [F(1,30)=1.88, p=.113]. Partner's investment attractiveness had a marginal main effect, such that women with more investing partners reported lower overall extra-pair desires [F(1,30)=3.84, p=.059]. No other main effects or interactions were significant.

3.2.2. Are there ovulatory increases in in-pair desires?

There were no significant cycle effects or interactions involving partner quality on in-pair desires, in either the focal analysis or in the secondary analysis in which potential confounds were controlled (all p values>.20).

3.3. General sexual desire

We did not find main effects of phase or interactions with partner's sexual or investment attractiveness on women's reports of general sexual desire (all p values>.50). In the secondary analysis, we observed a significant phase by sexual satisfaction interaction [F(1, 29)=4.88, p=.035], such that women who were more sexually satisfied showed a greater increase in sexual desire at high fertility than those less sexually satisfied. No other main effects or interactions were significant. In sum, a generalized increase in desire at high fertility was not found in this sample, nor did we find that fertility interacted with partner's sexual attractiveness; hence, general desire does not appear to be able to explain the target-specific shifts we have observed.

3.4. Mate retention

3.4.1. Do less sexually attractive men increase their mate-guarding efforts more when their partners are fertile?

There was a significant interaction of partner's sexual attractiveness and fertility on women's reports of their partners' expressed love and attention giving [F(1,34)=5.93, p=.013, partial r=-.39; see Fig. 2]. Less sexually attractive partners increased their mate retention efforts more at high fertility. There was also a significant main effect of partner's investment attractiveness on women's reports of positive attention by their partners [F(1,34)=4.78, p=.036], such that partners higher in investment attractiveness tended to engage more in positive mate retention efforts. No other effects were significant.

With possible confounds controlled, the observed interaction of phase and partner's sexual attractiveness remained significant [F(1,26)=3.40, p=.048], and the relationship between partner's investment attractiveness and positive mate retention dropped to nonsignificant [F(1,26)=1.91, p=.179]. There were no other significant main effects or interactions.

In contrast to these robust effects, no significant effects were observed for partner jealousy and mate guarding in either the focal or the secondary analysis. Because ovulatory increases

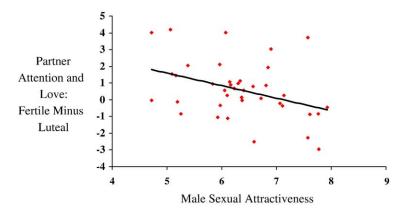


Fig. 2. Relationship between male sexual attractiveness and ovulatory shifts in male mate retention. n=39, partial r=-.39, p=.02; points represent residual scores after controlling for investment attractiveness, order of session (high vs. low fertility first), and estimating effect of phase at the day of ovulation (based on LH assay).

in jealousy were observed in a previous study (Gangestad et al., 2002), we also examined the individual items within the composite. None of these effects were significant in either the focal or the secondary analyses.

In sum, men who were rated as less sexually attractive were reported to increase attention to and expressed love for their partners near ovulation, as predicted. Jealousy, in contrast, produced no such effects, suggesting that the ovulation-contingent mate retention efforts observed in this sample were limited to positive inducements to fidelity.

4. Discussion

According to the good genes model, a dual-mating strategy is advantageous only if a woman's partner lacks cues to good genes. We therefore predicted that women with less sexually attractive partners (those likely to display fewer cues to good genes) would show ovulatory increases in extra-pair desires. The good-genes model predicts that this effect will be specific to sexual attractiveness and will not be observed for partners lacking investment cues. This differential pattern of effects is, in fact, what we found. Sexual attractiveness, but not investment attractiveness, interacted with fertility status to predict extra-pair desires; women rating their partners as least sexually attractive showed the greatest increases in extrapair desires. We predicted and found parallel results for partner mate retention. Less sexually attractive men—those for whom female infidelity may be of greatest concern—were reported to increase their mate retention efforts more at high fertility. We did not find evidence of ovulatory increases in male jealousy or interactions of partner's sexual attractiveness and cycle phase predicting male jealousy; thus, in this study, mate retention effects were limited to positive inducements to fidelity.

We predicted a reversed pattern for in-pair desires, such that women with sexually attractive partners would show increases in attraction to partners at high fertility. We did not confirm this prediction. It is possible that this effect, if it exists, is smaller in magnitude than the predicted effect of sexual attractiveness on extra-pair desires (see Gangestad et al., 2005) and, thus, more difficult to detect.

Male sexual attractiveness is correlated with many other variables, and thus, we cannot be certain that our effects are driven by it. However, when we controlled for several variables that may be associated with male sexual attractiveness, including female sexual satisfaction and relationship length, our effects remained robust. Our results are also cross-validated by the findings of Gangestad et al. (2005) who documented that women mated to relatively asymmetrical partners showed greater ovulatory increases in extra-pair desires than did women mated to symmetrical partners.

Like Gangestad et al. (2002) and Haselton and Gangestad (in press), we did not observe a main effect of fertility on general sexual desire, nor did we find an interaction of partner's sexual attractiveness and fertility in predicting generalized desire. This is noteworthy, as it helps to rule out the alternative explanation that target-specific cycle shifts are produced by generally elevated sexual desire. This does not appear to be the case in any of these studies. We did observe an interaction of sexual satisfaction and fertility on general desire. Given the number of tests we conducted by virtue of controls for confounds, this effect could be spurious. If robust, it may reflect a greater sensitivity in sexually satisfied women to changes in sexual functioning near ovulation (e.g., increases in the frequency of orgasms) relative to the luteal phase (Clayton, Clavet, McGarvey, Warnock, & Weiss, 1999).

A limitation of this study is that reports of male mate retention are made by female partners rather than by male partners themselves. Other studies have demonstrated that male and female partners' reports of male mate retention behaviors tend to agree (Dobash, Dobash, Cavanagh, & Lewis, 1998; Gangestad et al., 2002). Nonetheless, this is a clear avenue for future research. In addition, although there was considerable range in the ages of the women in our sample and in the length of their relationships, our participants were, on average, relatively young and their relationships were relatively new. It is possible that shifting relationship dynamics across the cycle vary depending on female age or relationship length, and a systematic investigation of this question may also be fruitful.

In sum, this study provides additional evidence for the good genes hypothesis of female extra-pair mating. This study also provides evidence for the texture and subtlety of adaptations underlying partner choice and relationship dynamics—not only do women's desires and men's mate retention efforts vary across the cycle (Gangestad et al., 2002), but the degree to which they change varies with theoretically relevant characteristics of male partners.

Acknowledgments

We thank Dave Frederick, Sheila Allameh, Anna Berezovskaya, Lani Cante, Elizabeth Carlin, Sarah Dodd, Bahar Ebrat, Erika Forster, Lisa Marchlewicz, Lisa Newon, and Carolyn Pratt for their generous assistance in collecting the data; Paul Andrews, Steve Gangestad, and Christine Garver-Apgar for helpful advice on high- and low-fertility scheduling; April

Bleske-Rechek, Dan Fessler, and two anonymous reviewers for comments on an earlier draft; the UCLA Experimental Biological Anthropology group for discussion of the ideas contained in this manuscript; and the UCLA Statistical Consulting Center for statistical advice. We gratefully acknowledge Unipath Diagnostics for their generous donation of ClearBlue ovulation detection kits.

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