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Changes in women's sexual interests and their partners' mate-retention tactics across the menstrual cycle: evidence for shifting conflicts of interest

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Because ancestral women could have obtained genetic benefits through extra-pair sex only near ovulation, but paid costs of extra-pair sex throughout the cycle, one might expect selection to have shaped female interest in partners, other than primary partners, to be greater near ovulation than during the luteal phase. Because men would have paid heavier costs if their partners had extra-pair sex near ovulation, one might also expect selection to have shaped males' efforts to track their primary partners' whereabouts to be increased near ovulation, relative to the luteal phase. Women filled out questionnaires about their sexual interests and their partners' mate-retention tactics twice: once within 5 days before a lutenizing hormone surge and once during the luteal phase. Results showed that: (i) women reported greater sexual interest in, and fantasy about, non-primary partners near ovulation than during the luteal phase; (ii) women did not report significantly greater sexual interest in, and fantasy about, primary partners near ovulation; (iii) women reported that their primary partners were both more attentive and more proprietary near ovulation.

Keywords: sexual conflicts; intersexual selection; evolutionary psychology; extra-pair sex; mate guarding; sexual desires

1. INTRODUCTION

Two sexually reproducing parents clearly have a shared genetic interest in the well-being of an offspring, an interest particularly evident in species in which many parents cooperatively care for offspring. Humans appear to be just such a species (Kaplan *et al.* 2000; but Hawkes *et al.* (1991) offers an alternative view). Even when sharing the arduous tasks of caring for offspring, however, parents also often have genetic conflicts. For instance, females may sometimes benefit reproductively from having males other than social partners sire offspring (e.g. to increase the genetic quality or diversity in offspring; Jennions & Petrie 2000), but retaining the investment of social partners. Male social partners may enhance their reproductive interests by reducing the probability of investment in offspring that are not their own, for example, by reducing their mates' prospects of having sex with other males, or by monitoring cues indicating that they may have done so (Johnstone & Keller 2000). Intersexual conflict may lead to adaptations that benefit the sex of the adaptation's owner, but at the expense of the other sex (Rice 1996; Rice & Holland 1998).

In socially monogamous birds, species-wide sexual monogamy is relatively rare. The median extra-pair paternity rate is 10–15% and rates over 20% are not uncommon (Birkhead & Møller 1995; Petrie & Kempenaers 1998). In some species, at least, sexual selection of good genes appears to account for female choice of sires (Møller & Alatalo 1999). Though the sexes behave in ways that mutually benefit both reproductively, some behaviours of one sex (here, females) appear to work against the interests of the other (cf. Shellman-Reeve & Reeve 2001).

Non-paternity rates among purported mother–father pairs vary across modern human populations, perhaps from 1 to 30% (MacIntyre & Sooman 1991). For instance, recent studies estimated non-paternity rates of 1% in Switzerland (Sasse *et al.* 1994) and 12% in Monterey, Mexico (Cerda-Flores *et al.* 1999). In the latter study, the estimated rate among a low socio-economic status subgroup was 20% (see also Beckerman *et al.* 1998; Hill & Hurtado 1996). The extra-pair paternity in ancestral environments need not have been high for intersexual coevolution to have produced adaptations in women to *selectively* seek sex with extra-pair partners and counter-adaptations in men to reduce their mates' opportunities and desires to do so.

If the benefits and costs of specific cognitive, emotional and overt behavioural responses varied across contexts ancestrally, selection might be expected to shape psychological adaptations to produce them contingent on context. Suppose that ancestral women could have secured a better genetic complement for their offspring from extra-pair males, at the expense of the reproductive interests of their social partners who impose a cost on such behaviour when they observe it (e.g. by deserting). Because women obtain genetic benefits only when fertile, but could pay the cost throughout the cycle, selection may have shaped female interest in men who possess indicator traits of good genes such that it *changes* across the cycle: increases when women are fertile (the few days to a week prior to ovulation; Jöchle 1973) and decreases when not.

In fact, female preferences do change in systematic ways across the cycle. Women prefer the scent of men who evidence developmental stability (by virtue of symmetry;

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Gangestad & Thornhill 1998; Rikowski & Grammer 1999; Thornhill & Gangestad 1999*b*), but only during the fertile phases of their cycles. Developmental stability is thought to be a component of broadly defined developmental health, as affected by pathogens, toxins, or mutations (Møller & Swaddle 1997). Women also prefer more masculine male facial features when fertile (Penton-Voak *et al.* 1999; Penton-Voak & Perrett 2000; Johnston *et al.* 2001). Facial masculinity is affected by androgen production during development, which may be a costly signal of (again, broadly defined) good condition (Thornhill & Gangestad 1993, 1999*a*; Mueller & Mazur 1997; Penton-Voak & Perrett 2001).

One might also suspect that women would be particularly likely to engage in extra-pair sex when fertile (though selectively with certain men, and depending on the characteristics of, and potential cost of losing, a mate). Penton-Voak *et al.* (1999) found that women's preference for facial masculinity increased only when judging men as potential short-term mates. Grammer *et al.* (1997) found that women are more likely to visit a singles-scene nightclub without a primary mate during the fertile phase of their cycle. A survey of women in the UK showed that women's extra-pair sex (6% of copulations reported by women with primary partners) occurred more often on high-fertility days, whereas the frequency of in-pair sex was more evenly distributed across the cycle (Bellis & Baker 1990).

Because women's extra-pair sex when fertile may have been both more frequent and more costly to their in-pair partners, selection may have also shaped counter-adaptations in men, leading them to be particularly vigilant of their mates' whereabouts and creating a desire to monopolize their time during this period, responding to whatever residual cues of the fertile state (including behavioural ones) might exist, despite no obvious overt signs of ovulation. Using observational methods, Flinn (1988) showed that men in a Caribbean village were more vigilant of fertile female partners than ones not fertile (post-menopausal or pregnant). No previous study, to our knowledge, has examined whether men's vigilance changes with female fertility across the menstrual cycle.

The present study was conducted to test the prediction that women's sexual desires for partners, other than a primary partner, increase when they are fertile, as well as whether men are particularly vigilant of their partners' whereabouts and activities at this time. Bellis and Baker's findings do not directly address questions of women's sexual attraction to, or desires for, men other than a primary partner. Possibly, for instance, women experience greater generalized sexual desire mid-cycle (Regan 1996) and therefore initiate more sex during this period (Adams *et al.* 1978; cf. Persky *et al.* 1978). Because in-pair partners themselves are likely to have greater opportunity to initiate more sex than an extra-pair partner, women may initiate a greater proportion of their extra-pair than in-pair sex, generating Bellis and Baker's pattern of findings.

Participants were women not taking contraceptive hormones who, on two occasions, filled out a questionnaire concerning their sexual desires and their partners' behaviour: once just prior to ovulation and once during the mid-to-late luteal phase. We predicted that:

(i) women's sexual desires for, and fantasies about, men other than primary romantic partners would be greater prior to ovulation than during the luteal phase;
(ii) though some women's desires for primary partners (particularly those of certain characteristics) might well be expected to also increase during the fertile phases, women's sexual desires for, and fantasies about, men other than primary partners would increase to a greater degree;
(iii) women would report their primary partners to engage in mate retention tactics, such as monitoring their whereabouts and monopolizing their time to a greater extent, prior to ovulation than during the luteal phase.

2. MATERIAL AND METHODS

(a) *Participants*

Participants were 51 undergraduate women at the University of New Mexico who satisfied a research requirement, or earned extra credit for a psychology class by participating. None had used hormone-based contraceptives (e.g. pills, Depo-Provera) in the past month and, on the basis of a nationally marketed ovulation detector (Ovusign), all were judged to have experienced a lutenizing hormone (LH) surge (preceding ovulation by 24–48 h in most instances) between 5 days after and 1 day before participating in one questionnaire session (see below). Two recent studies found that ovulation detection kits that, like ours, use a urinary stick to detect an LH surge, yielded 97–100% concordance with actual ovulation detected by ultrasonography, much higher than tests using cervical mucus, basal body temperature, or salivary ferning (Guida *et al.* 1999; Guermandi *et al.* 2001). Of a larger sample recruited for the study ($n = 118$), 28 showed no evidence of surging within 5 days, 12 showed no evidence of surging but did not report for testing on one or more of the 5 days, 22 failed to complete the multisession study (e.g. because they dropped the class, started using the pill or, in one case, became pregnant) and one's current romantic partner was female. Another four women tested positive for an LH surge, but were inadvertently scheduled incorrectly. Because these women did not report on a period that was clearly non-fertile, they were excluded from the sample. All results reported in this article are based on the remaining sample of 51 women (or appropriate subsamples; see below).

The mean age of the women was 19.6 yr (s.e. = 3.3, range 18–34 yr); 47% identified themselves as Caucasian, 43% Hispanic, 4% Asian American, 2% African American and 4% another ethnicity. (All means and standard deviations are calculated on the full sample unless otherwise noted.) All claimed to be heterosexual (48) or bisexual (3); all of the latter had had sex with a man within the past year and none indicated having a same-sex primary partner at the time of the study. In total, 24 women claimed to have a single, primary relationship and another seven had primary partners but did not regard the relationship to be exclusive. (This subsample of 31 women having primary partners was used in certain analyses). Of the remaining women, some were dating, but did not regard one partner as a primary partner. Fourteen (27%) were virgins, including six with a primary partner (19%). On average, women had 3.3 sex partners per lifetime (s.d. = 7.1). Eight (16%) had never been unfaithful to a primary partner and 4 out of 31 (13%)

had been unfaithful to their current primary partner, including 1 out of 24 (4%) who said they were exclusively dating one person and 3 out of 7 (42%) who did not say so.

(b) *Procedure*

Participants reported for three main sessions: a first introductory session and two questionnaire sessions: one conducted within 5 days before an LH surge and one conducted in the mid-to-late luteal phase.

(i) *Introductory session*

Following informed consent at the first session, women filled out a number of brief questionnaires, including a basic demographic information sheet and a sexual and relationship history. The relationship history questionnaire asked about whether they were dating one person exclusively, married, living with a partner, seeing multiple persons (even if regarding one as primary), or dating no one. Women also filled out information about their contraceptive use and menstrual cycle.

(ii) *Scheduling and LH testing*

At the end of the introductory session, a female researcher scheduled a day for the next session. Women in the follicular phase of their cycle were scheduled for a high-fertility session as their next session. Women in the luteal phase were scheduled for a low-fertility session. At, or after, that next session, women were scheduled in person, or by phone, for their final session (a low-fertility session for women who first completed a high-fertility session, a high-fertility session for women who first completed a low-fertility session).

High-fertility sessions were scheduled between 17 and 19 days prior to the anticipated end of their cycle, based on the expectation that ovulation occurs, on average, 14–15 days prior to the beginning of the next cycle (Jöchle 1973). Two days prior to the expected LH surge (about 16 days prior to the end of cycle), women were scheduled for ovulation detection. For these brief sessions, they reported to our laboratory and provided a urine sample, which was tested by using the Ovusign ovulation detection kit. Women were tested for up to five consecutive days in total, or until they tested positive for an LH surge, whichever occurred first. For weekend testing, women were given kits, which they returned the following Monday.

On average, an LH surge occurred 1.8 days following the high-fertility questionnaire session (range: 1 day prior to 5 days after; s.e. = 1.8). Unprotected sex up to 5–7 days prior to ovulation may result in conception and hence most, if not all, of these individuals should have been in a fertile state at the time of the session (Jöchle 1973; Wilcox *et al.* 1995). Because conception risk may increase up to, or near, the point of ovulation (Wilcox *et al.* 1995) however, the number of days a woman filled out her questionnaire prior to the LH surge was entered as a variable of interest in all analyses (days to LH surge).

Low-fertility sessions were targeted to be at least a week following an LH surge. Attempts were made to avoid the final 3 days of the cycle (and the potential effects of premenstrual symptoms). On average, women were tested 10.9 days following their LH surge (s.d. = 3.9) and 8.1 days prior to the beginning of their next cycle (or anticipated start of the next cycle; s.d. = 5.6). One woman (2% of the sample) was tested on the day that she began her next menstrual cycle and three (6%) were tested on one of the preceding two days.

(iii) *Sessions 2 and 3*

During the high-fertility and low-fertility sessions, women filled out questionnaires (in addition to rating photos of men as part of a related project). The completed questionnaires can be found in an electronic appendix available on The Royal Society's Publications Web site.

We first asked participants to rate how much they had engaged in each of 35 behaviours or feelings *in the past two days* on a 4-point (0, not at all; 1, once; 2, a few times; 3, more than a few times) rating scale. The first 21 items concerned a variety of feelings that probed their general mood state and interpersonal behaviours, which we generally did not anticipate would change across the menstrual cycle (e.g. 'felt happy for no good reason', 'felt sad for no good reason', 'felt worried about my safety', 'became angry with someone', 'felt insecure'). Of the final 14 items, 13 concerned sexual behaviour, feelings, attractions and fantasies:

(i) one item asked about sexual desire in general ('felt strong feelings of sexual desire');
(ii) two items concerned attraction to or fantasy about a current sex partner ('felt strong sexual attraction toward my primary current partner', 'fantasized about sex with a current partner');
(iii) three items concerned attraction to or fantasy about a person other than a primary current partner ('felt strong sexual attraction toward someone other than a current partner', 'fantasized about sex with a stranger or acquaintance/past partner');
(iv) two items also concerned attraction to persons other than current partners, but in particular ways ('felt sexually aroused by the sight of someone very physically attractive [other than a primary current partner]', 'felt sexually aroused by the scent of someone [other than a primary current partner]');
(v) five items concerned sex with primary partners and other individuals, which were not the main concern of this study but that we will briefly mention in our results ('had sex with a primary current partner/someone other than a primary current partner', 'experienced orgasm with a primary current partner/someone other than a primary current partner', 'initiated sex [was the one who was sexually aggressive]');
(vi) the remaining item concerned flirtation ('flirted with someone other than a current partner').

To test primary hypotheses concerning targets of sexual attraction, two parallel composites were formed for the responses at each session: (i) *sexual attraction to and fantasy of partner*: a composite of the responses to items concerning sexual attraction to, or fantasy about, a current primary partner (applicable for individuals with a current partner); (ii) *sexual attraction to and fantasy of others*: a composite of the responses to items concerning sexual attraction to, or fantasy about, someone other than a current partner. An additional, larger composite concerning attraction toward a person other than a primary partner was formed by combining the three items in composite (ii) (above) with the two additional items concerning sexual arousal to the sight of a physically attractive person or the scent of someone (see (iv) above). Because this third composite contained items not parallel to that in the composite concerning attraction to a primary partner, it was not used in direct comparisons with sexual interest in a primary partner. Naturally, results emerging

from this five-item composite are not independent from results from the three-item composite but, because the former may be a more comprehensive measure of sexual interest in a non-primary partner, we report on both measures for reasons of completeness.

A second questionnaire was adapted from an instrument developed by Steven Gangestad and Todd Shackelford (unpublished data) to assess mate retention tactics. Women were asked to rate the extent to which their primary partner had engaged in 41 behaviours related to mate retention *within the past two days* on a 4-point scale (0, not at all; 1, once; 2, a few times; 3, more than a few times). (Women without a primary partner did not respond to this questionnaire.) The item responses aggregate into 11 content-defined clusters:

(i) vigilance (seven items, e.g. 'called me at unexpected times to see who I was with');
(ii) monopolization (five items; 'spent as much free time with me as he could so I couldn't meet other men');
(iii) proprietariness (four items; 'got angry if he saw me walking alone with another man');
(iv) spoiling (three items; 'tried to be as nice as he could to please me');
(v) expressed dependency (four items; 'cried to keep me with him');
(vi) self-congratulation (two items; 'told me I'll never find someone who will treat me as well as he treats me');
(vii) mate discreditation (four items; 'reminded me in subtle ways that while my wishes and concerns are important, as the man in the relationship his wishes and concerns are relatively more important');
(viii) public mate deprecation (two items; 'bad mouthed me to other men so they wouldn't be interested in me');
(ix) intrasexual derogation (four items; 'intentionally bad mouthed other men in front of me to make himself look better');
(x) intrasexual threat (three items; 'confronted someone who made a pass at me');
(xi) extra-pair sexual attention (three items; 'showed interest in other women to make me angry').

Not surprisingly, given the short time-frame in question (not a constraint on the original measure), some items received low endorsement rates and, hence, some clusters had very low internal consistency reliabilities (in particular, public mate deprecation and intrasexual threat had internal consistency reliabilities near zero; mate discreditation's mean α was 0.46). Eight clusters had mean reliabilities greater than 0.6 (and averaging 0.73). To reduce the measures, we performed a principal components analysis (combining the high-fertility and low-fertility samples). Eigenvalue scree suggested two components (together accounting for 59% of the the total variance), which were extracted and rotated using a direct oblimin criterion. The two components are very similar to those emerging from other principal components or factor analyses of this measure (Cousins 1999; S. Gangestad and T. Shackelford, unpublished data). The first was marked by proprietariness, vigilance, mate discreditation, self-congratulation, intrasexual threat and extra-pair sexual attention and can be interpreted as *proprietariness*. The second was marked by monopolization, spoiling and expressed dependency and can be interpreted as *attentiveness*. The two components correlated substantially with one another: 0.47. Our primary analyses concerned three measures within each session: (i) total mate retention tactics, a sum of all item responses; (ii) proprietariness, a sum of the 27 items contained within the subscales defining it; (ii) attentiveness, a sum of the 12 items contained within its defining subscales. Internal consistency reliabilities for these composites were good: 0.93/0.90, 0.92/0.91 and 0.86/0.79 for the three measures, respectively (high/low fertility).

In a separate sample of 203 dating couples (for a description of the sample, see Gangestad & Thornhill (1997)), we examined agreement between a male's self-report and his partner's report of his mate-retention behaviour on our measure. For the overall measure, $r = 0.48$, $p < 0.000\,01$. For proprietariness and attentiveness, $r = 0.43$ and 0.50, $p < 0.000\,01$. Correlations for individual item clusters averaged 0.43 and all were significant (range: 0.27–0.52, all $p < 0.0001$). Hence, partner reports on men's behaviour reliably predict men's own reports.

3. RESULTS

Analyses were performed on two overlapping samples: first, all 51 women and, second, the 31 women with primary relationship partners (some hypotheses concern only these women). For all main analyses, we included two between-subject factors and one covariate: (i) whether they were in a primary relationship that they indicated to be exclusive (exclusive primary versus none); (ii) the order in which they did the sessions (high-fertility session done first versus low-fertility session done first); (iii) the number of days prior to the LH surge that they did the high-fertility session (a covariate). All analyses also included the within-subject factor of fertility status (high versus low fertility). Where appropriate, we included the within-subject factor of target of attraction (primary current partner versus other). All primary analyses were run on SPSS-PC 10.0 GLM repeated measures.

For all tests of the predicted effects, directed *t*-tests were used. Directed tests detect hypothesized directional effects with power greater than two-tailed tests yet, unlike one-tailed tests, allow one to reject the null hypothesis in an unpredicted direction. Following convention, we split the α level of 0.05 into 0.04/0.01 (predicted/unpredicted tail; reported p values for predicted effects were multiplied by 5/4 so that the critical p is 0.05; Rice & Gaines 1994). Two-tailed tests were used for all other analyses.

(a) *Hypothesis 1: changes in attraction to men other than primary partners*

Our first hypothesis states that women's sexual attraction to and fantasy about men, other than primary partners, will be greater when they are fertile than when not. (Naturally, for women without current partners, this would include all men.) Analyses using both the three-item and five-item composites of 'sexual attraction to and fantasy about others' strongly supported this hypothesis: $t_{45} = 3.21$, $p = 0.002$ and $t_{45} = 3.68$, $p = 0.0004$, for the main effects of fertility status. (Sample size was 50; one participant did not fully complete this section of the questionnaire.) Estimated marginal means on the measures were 65–80% higher during the high-fertility phase (0.92 versus 1.67 and 1.68 versus 2.63 for the two measures).

For the five-item measure, the 'fertility status × exclusive primary relationship' and 'fertility × days to LH surge'

interactions were also significant, $F_{1,45} = 4.96$ and 4.40, $p = 0.031$ and 0.042. Fertility status had a greater effect for those women not claiming to be in exclusive relationships. Moreover, the effect of fertility status was strengthened when women were assessed during the high-fertility phase closer in time to ovulation (and hence strengthened as true conception risk increased). This interaction effect is not unexpected, as theory anticipates that these effects should track true conception risk.

Analyses on the subsample of 31 women who had primary partners also strongly supported the hypothesis. These women reported greater attraction toward, and fantasy about, another man during the high-fertility phase ($t_{26} = 3.57$, $p = 0.0009$ and $t_{26} = 3.20$, $p = 0.002$, for the three-item and five-item composites, respectively). Estimated marginal means were *ca.* 80–160% higher during the high-fertility phase (0.77 versus 2.04 and 1.61 versus 2.88). For these analyses, the 'fertility status by days to LH surge' interaction was also significant ($F_{1,26} = 5.48$, $p = 0.027$ and $F_{1,26} = 5.42$, $p = 0.028$).

For the three-item composite, the 'days to LH surge' effect and 'fertility status × exclusive primary relationship × days to LH surge' interaction were significant ($F_{1,26} = 4.71$, $p = 0.039$ and $F_{1,26} = 4.42$, $p = 0.045$). The 'days to LH surge' effect indicated that overall attraction to and fantasy about extra-pair partners increased with propinquity to ovulation, which, as just noted above, was largely driven by increases during the high-fertility phase. The three-way interaction effect indicated that the strengthening of the fertility status effect by propinquity to ovulation was greatest for women whose primary relationships were not exclusive.

(b) *Hypothesis 2: comparisons with changes in attraction to primary partners*

We found no evidence that women experience greater sexual attraction to, and fantasy about, their primary partners during the days leading to ovulation than in the mid-to-late luteal phase ($t_{26} = 1.05$, ns ($N = 31$)). The observed increase in marginal means from the luteal to the fertile phase was 18% (2.63–3.08). No other significant effects emerged from this analysis.

To test whether women's sexual attraction to, and fantasy about, men other than current partners especially increase in the days prior to ovulation, compared with attraction to, and fantasy about, current partners, we performed an analysis with two within-subject factors: fertility status and partner–other attraction. Again, 'exclusive primary relationship' and 'order' were treated as between-subject factors and 'days to LH surge' was entered as a covariate. Only the 31 women with primary partners were included in the analysis. The hypothesized greater effect of fertility status on attraction to, and fantasy about, a man other than a primary partner, compared with a current partner, would be reflected in a 'fertility status × partner–other' two-way interaction. This interaction was indeed significant ($t_{26} = 1.96$, $p = 0.038$). A significant fertility status effect also emerged ($F_{1,26} = 6.47$, $p = 0.017$), with greater sexual attraction and fantasy in the fertile phase (though, as just noted, driven largely by effects on attraction to individuals other than current partners). A 'partner–other' effect reflected the fact that women overall reported more interest in a primary partner than other males ($F_{1,26} = 17.73$, $p = 0.0003$). An unexpected (and possibly spurious) 'order × partner–other' effect also emerged ($F_{1,26} = 5.81$, $p = 0.023$).

(c) *Hypothesis 3: changes in women's reports of their partners' mate-retention tactics*

Women, then, are especially likely to be attracted to, and fantasize about, sex with men other than current partners in the days just prior to ovulation, even if these internal events very rarely lead women to actually engage in sex with the targets of their attraction. Do men selectively engage in tactics to decrease their partners' opportunities to interact with other men, or increase the likelihood of detecting interactions between their partners and other men during their partners' fertile period? To address this question, we performed analyses on women's reports of their primary partners' mate-retention tactics. (Sample size was 27; four women with primary partners did not fully complete this questionnaire.) As proposed, there emerged a main effect of fertility status on men's total mate-retention tactics ($t_{22} = 3.15$, $p = 0.003$), such that women reported higher frequencies of these partner acts when fertile than when not. Exclusive primary relationship had a main effect as well ($F_{1,22} = 9.65$, $p = 0.005$), such that women not in exclusive relationships reported that their primary partners engaged in the tactics more than women in exclusive relationships. Exclusive primary relationship did not significantly moderate the fertility status effect, however ($F_{1,22} = 0.48$, n.s.). The covariate had an effect ($F_{1,22} = 4.44$, $p = 0.047$), such that men were said to engage in the tactics more when women were assessed closer to ovulation. The analysis also yielded an unexpected and difficult-to-explain 'order × fertility status' effect ($F_{1,22} = 8.56$, $p = 0.008$), such that women who went through the high-fertility session first experienced a greater effect of fertility status.

To further explore these effects, separate analyses were performed on the proprietariness and attentiveness subcomponents. Results revealed effects on both components. Women reported that their partners engaged in more tactics associated with proprietariness during the fertile phase than the luteal phase ($t_{22} = 2.31$, $p = 0.019$; marginal means: 8.69 and 6.85, respectively). Similarly, they reported that their partners engaged in more tactics associated with attentiveness in the days leading to ovulation ($t_{22} = 2.20$, $p = 0.024$; marginal means: 10.66 and 8.29 for fertile versus luteal phase, respectively). Women not in exclusive relationships claimed that these men engaged in greater degrees of both sets of tactics ($F_{1,22} = 6.76$ and 8.30, $p = 0.016$ and 0.009, respectively), though exclusivity of the relationship did not moderate the fertility status effects ($F_{1,22} = 1.20$ and 0.00, n.s.). Order moderated the fertility status effect on proprietariness ($F_{1,22} = 5.26$, $p = 0.032$). Exploratory analyses on the eight reliable, individual item clusters were performed as a follow-up. The most dramatic and complex effects occurred on vigilance. Women reported men to be more vigilant (e.g. calling or checking up on them unexpectedly, looking through personal belongings) during the fertile than non-fertile phase ($t_{22} = 3.89$, $p = 0.0004$). Women in non-exclusive relationships reported that partners were particularly likely to engage in vigilance ($F_{1,22} = 20.82$, $p < 0.0001$). The vigilance of these women's partners was

also significantly more affected by women's fertility status ($F_{1,22} = 10.30$, $p < 0.004$). Days to LH surge had a main effect ($F_{1,22} = 11.12$, $p = 0.003$) and also interacted with fertility status ($F_{1,22} = 7.16$, $p = 0.014$) and relationship exclusivity ($F_{1,22} = 4.52$, $p = 0.045$). These effects reveal a pattern in which women report their partners to be particularly vigilant as ovulation nears, with propinquity to ovulation particularly affecting the vigilance of men in non-exclusive relationships.

Fertility status also significantly affected women's reports of their partners' monopolization (of time) and spoiling ($t_{22} = 2.55$ and 2.05, $p = 0.011$ and 0.032). Women reported that men were particularly interested in monopolizing their time, and motivated to please them, during the high-fertility phase. No significant effects of fertility status were observed for the remaining item clusters.

(d) *Predictors of men's mate-retention tactics*

Men could be motivated to spend time with their partners near the time of peak conception risk in the cycle for reasons other than a motive to limit their opportunities to interact with other men. For instance, they may experience a greater interest in sexual activity with their partner (possibly owing to selection for sperm competition). If men are concerned about their partners' interactions with other men, one might expect that they should be particularly vigilant and monopolizing of their partners' time when they suspect that their partner may be interested in other men. Consistent with this idea, we saw above that men appear to be most vigilant regarding their partners' whereabouts when they do not have an exclusive relationship with their primary partner. To explore more specifically the links between women's sexual attraction to men other than their partners and changes in men's mate-guarding prior to partners' ovulation, we regressed changes in men's mate-retention tactics as a function of their partners' fertility status (i.e. a difference score) on changes in women's attraction to, and fantasy about, their partner and changes in their attraction to, and fantasy about, others. Order was also entered as a control variable. Women's heightened attraction to, and fantasy about, others pre-ovulation positively predicted men's heightened mate-retention tactics pre-ovulation ($t_{23} = 3.01$, $p = 0.006$; $\beta = 0.56$; $N = 27$). Changes in women's attraction to, and fantasy about, their partner had a marginally significant negative effect on changes in men's mate-retention tactics ($t_{23} = -1.71$, $p = 0.100$; $\beta = -0.32$). Large increases in men's proprietariness during the fertile phase were significantly associated with their partners' increased attraction to other men ($p = 0.031$); the relationship was marginally significant for men's attentiveness ($p = 0.096$). These findings are consistent with the idea that increases in men's mate guarding prior to ovulation are partly motivated by increased concerns about partners' interactions with other men.

(e) *General mood and behavior*

Another possibility is that men want to spend more time with their partners near ovulation because their partners are in a better, more prosocial mood at that time. Of the 21 items concerning women's feelings and behaviour across the previous 2-day period, only two were significantly affected by women's fertility status: 'spent time with a current romantic partner' ($F_{1,45} = 4.42$, $p = 0.041$) and 'worried that I had offended someone' ($F_{1,45} = 5.23$, $p = 0.027$, $N = 50$). Higher frequencies were associated with high-fertility status. Analyses on the subsample of 31 women with primary partners yielded similar results. The first effect is not surprising (see § 3c) and the second is not strong evidence that women are friendlier prior to ovulation.

(f) *General sexual desires and behaviour*

Women did not endorse significantly higher levels of overall sexual desire when fertile ($F_{1,46} = 0.28$, n.s., and $F_{1,26} = 0.46$, n.s., for the full sample of 51 and the 31 with primary partners, respectively). Women with primary partners did not claim to have significantly more sex with their partners when fertile ($F_{1,26} = 2.70$, $p = 0.112$), though fertility status did significantly interact with days to LH surge to predict frequency of sex ($F_{1,26} = 9.31$, $p = 0.005$). As ovulation neared, women had more sex with their partners. Accordingly, a main effect of days to LH surge was also observed ($F_{1,26} = 4.80$, $p = 0.038$). No woman claimed to have had sex with a non-primary partner.

Women did claim to initiate sex with their partners more when fertile ($F_{1,26} = 4.43$, $p = 0.046$), especially when assessed near ovulation ($F_{1,26} = 7.28$, $p = 0.012$). Days to LH surge had a significant main effect on female-initiated sex ($F_{1,26} = 12.70$, $p = 0.002$).

To explore the links between female-initiated sex and their sexual attractions and fantasy, we regressed changes in female-initiated sex as a function of their sexual attraction to, and fantasy about, their partners as well as others, also controlling for days to LH surge. Women's sexual attraction to, and fantasy about, their partner predicted the increased frequency of sex that they initiated at a marginally significant level ($t_{26} = 1.90$, $p = 0.068$). Their sexual attraction to, and fantasy about, others did not ($t_{26} = 0.36$, n.s.). Although, on average, women do appear to initiate more sex with their partners prior to ovulation, this effect appears to be largely unrelated to women's increased interest in, and fantasy about, men other than a current partner.

We also examined whether men's mate-retention tactics were associated with female-initiated sex. Controlling for days to LH surge, we regressed changes in female-initiated sex with each of the mate-retention measures. Of those significantly associated with fertility status, the only one that improved prediction at even a marginally significant level did so negatively. The *more* men increased their attempts to monopolize their partners' time prior to ovulation, the *less* their partners initiated sex with them ($t_{22} = -1.95$, $p = 0.063$, partial $r = -0.37$). The subset of women who drive the effect of fertility status on female-initiated sex appears to be different from the subset of women whose partners attempt to monopolize their time, possibly because they have partners with different qualities from those who increase mate-retention tactics with ovulation (i.e. ones who are not as concerned about their partners' potential infidelity). As alluded to above (§ 1), the evolutionary perspective that we draw on expects that women who have masculine and intrasexually competitive partners should experience increased, not decreased,

interest in their partners (Furlow *et al.* 1998; Manning & Wood 1998; see Simpson *et al.* (1999) for links between symmetry and intrasexual competitiveness). One provisional observation, consistent with this notion, is that the only mate-retention cluster whose fertility-related increases were *positively* associated with fertility-associated changes in female-initiated sex was intrasexual threats (partial $r_{23} = 0.47$, $p = 0.017$). Because this association was not predicted *a priori* and emerged from exploratory analyses, it must be viewed as merely suggestive.

4. DISCUSSION

Based on specific notions of intersexual selection, we predicted that women would experience increased sexual interest in men other than primary partners when fertile, and to a degree greater than they experience increased sexual interest in their partners. These predictions were supported. Naturally, we do not know the features of men that women found attractive and fantasized about during the fertile phase. Previous research, however, suggests that these men were, on average, relatively facially masculine and developmentally stable.

Cycle effects on probability of extra-pair sex (Bellis & Baker 1990) may be mediated by changes in the preferences of women, with women being more attracted to certain men (who typically are not primary partners) in the days preceding ovulation. Nonetheless, women's heightened attraction to other men may lead them to actually have extra-pair sex during this period only rarely, as women may experience (and, ancestrally, experienced) substantial costs from extra-pair sex, which they are expected to consider.

Although women did not report increased sexual attraction to, and fantasy about, their primary partners, they did claim to initiate sex with them more often, when fertile (also Adams *et al.* 1978). This effect, however, was unrelated to women's heightened attraction to, and fantasy about, men other than their partners, when fertile. As noted above, one should expect women who have partners that are most attractive to women when fertile (e.g. facially masculine men) to be more attracted to their partners at that time. Possibly, these women are responsible for the effect of fertility status on female-initiated sex, an issue to be explored in future research.

The proximate factors responsible for changes in women's preferences and sexual interests across the menstrual cycle remain unknown. Obvious candidates are the effects of circulating hormones, whose levels change across the cycle (e.g. oestrogen) on neural targets.

Women's reports of their partners' behaviour also supported the prediction that, as a counter-strategy, men would engage in more mate-retention tactics in the days prior to their partners' ovulation. The largest effect of fertility status was on men's vigilance—monitoring their mates' whereabouts and activities. That effect was greatest for primary partners of women who did not claim that the relationship was exclusive, and strengthened as women neared ovulation. Men whose mate-retention tactics increased most dramatically in the days preceding their partners' ovulation had partners who especially expressed sexual attraction to, and fantasy about, other men and, hence, perhaps had the most to worry about with respect to potential competitors.

These findings beg the question: what cues do men use to detect the period of risk? One possibility is that they can use visual or olfactory cues (e.g. changes in their partners' fluctuating asymmetry (Manning *et al.* 1996); or scent (Singh & Bronstad 2001)). Another is that men respond to their partners' behaviour (e.g. increased interest in other men or increased desire to spend time away on the part of women), which could account for the links between women's heightened interest in other men and their partners' mate-retention tactics.

One obvious limitation of the current study is that we obtained reports of men's vigilance from women. As noted above, in a separate sample of 203 couples, male and female partner reports agreed well beyond chance levels and, hence, one should expect that men would, on average, see themselves as similar to what women said about them in this study. Moreover, because women observe the male acts that they report, it is not clear that women's reports should be trusted any less than men's reports as to what they say and do. Nonetheless, a future study should obtain reports from both partners. If the effects transpire to be due to changes in women's perceptions rather than men's actual behaviour, that result would be very interesting.

More generally, the current study reinforces the utility of looking at human romantic relationships partly as the outcome of genetic conflicts of interest. Previous work has revealed some not-so-subtle ways that intersexual selection due to these conflicts shaped psychological design (Buss 2000). The current study illustrates, in addition, the subtlety of human adaptive design.

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