The Scent of Symmetry: A Human Sex Pheromone that Signals Fitness?

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A previous study by the authors showed that the body scent of men who have greater body bilateral symmetry is rated as more attractive by normally ovulating (non-pill-using) women during the period of highest fertility based on day within the menstrual cycle. Women in low-fertility phases of the cycle and women using hormone-based contraceptives do not show this pattern. The current study replicated these findings with a larger sample and statistically controlled for men's hygiene and other factors that were not controlled in the first study. The current study also examined women's scent attractiveness to men and found no evidence that men prefer the scent of symmetric women. We propose that the scent of symmetry is an honest signal of phenotypic and genetic quality in the human male, and chemical candidates are discussed. In both sexes, facial attractiveness (as judged from photos) appears to predict body scent attractiveness to the opposite sex. Women's preference for the scent associated with men's facial attractiveness is greatest when their fertility is highest across the menstrual cycle. The results overall suggest that women have an evolved preference for sires with good genes. © 1999 Elsevier Science Inc.

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Several lines of evidence indicate that olfactory cues or pheromones may play a major role in the human sexual selection system. First, although adults of both sexes report that body scent of others significantly affects their sexual interest, women report a stronger effect than men (Franzoi and Herzog 1987; Herz and Cahill 1997; Regan and Berscheid 1995). Indeed, Herz and Cahill found that women report olfactory information to be the single most important sensory input in mate selection and sexual arousal, whereas men rated visual and olfactory cues as about equally important. Second, evidence suggests that the importance of male scent in women's sexual interest and arousal varies across the menstrual cycle. Normally ovulating women, i.e., reproductive-age women who are not using oral contraceptives that eliminate ovulation, differentially evaluate androstenone, a substance in human scent, across different phases of the menstrual cycle, with most favorable evaluations near ovulation (Grammer 1993). Moreover, women's olfactory sensitivity to androstenol and related chemicals appears to be enhanced before ovulation, near the peak of fertility (Doty 1981;Vierling and Rock 1967; although see Amoore et al. 1975; see also Pause et al. 1996). Androstenol, a chemical precursor of androstenone, importantly contributes to body odor (giving it a musky smell; see review by Gower and Ruperelia 1993), and its production is highly sexually dimorphic, which implicates sexual selection, with men excreting in urine about three times more than women (Brooksbank 1962; Brooksbank and Haslewood 1961).

Evidence indicates that women's sexual interest also changes across the menstrual cycle. Their sexual desire and rate of extrapair copulations (EPCs) appear to peak during the midfollicular to ovulatory phases, the interval during which fertility reaches a maximum (Baker and Bellis 1995; Regan 1996), which when coupled with the above, suggests a third connection between sex pheromones and human sexual selection. Specifically, the fact that both EPCs and positive evaluation of sexually dimorphic substances in human sweat peak near maximal menstrual-cycle fertility suggests that selection has led to a preference in women for their offspring's sire and that the preference may include an olfactory component.

One possible function of the preference may be to motivate matings with males who possess good genes (genes that increase offspring viability or other components of offspring fitness, such as sexual attractiveness, offspring sex ratio, and so on) during the fertile phase of the menstrual cycle. Good-genes sexual selection, especially viability-based sexual selection, is important in a variety of animal species. Partial reviews of evidence for good-genes sexual selection can be found in Andersson 1994; Kirkpatrick 1996; Møller and Thornhill 1998a; Petrie and Kempenaers 1998; Petrie et al. 1998; Wilkinson et al. 1998. Møller and Alatalo's (1999) exhaustive meta-analysis of data from animals revealed a significant, average, positive correlation between magnitude of expression of secondary sexual traits favored by sexual selection and offspring survival.

FLUCTUATING ASYMMETRY

A potentially important phenotypic marker of good genes is low fluctuating asymmetry (FA). FA is nondirectional deviation from perfect bilateral symmetry in traits that are, on average, bilaterally symmetric. FA reflects ability to deal with stresses, both genetic and environmental, during ontogeny. Individual FA, then, is developmental maladaptation owing to the individual's inability to achieve perfect symmetry given environmental and genetic perturbations during traits' ontogeny (review in Møller and Swaddle 1997).

Genetic perturbations known to generate FA include mutations, inbreeding, homozygosity, and genetic disturbance due to incomplete coadaptation among genes seen when directional selection increases the frequency of previously rare alleles (Møller and Swaddle 1997). FA variation should reflect heritable fitness much of the time, often making FA an indicator of genetic quality and leading to selection for mate preferences based on FA or on traits such as scents that may covary with FA. The composite of human traits we have measured (see following) has a heritability of about .30, according to Livshits and Kobyliansky (1991). This estimate rises to about .5 when error in trait measurement is considered (Gangestad and Thornhill 1999).

Meta-analyses and other literature reviews indicate that FA negatively predicts fitness components such as growth rate, longevity, fecundity, and health status across a wide variety of species (Leung and Forbes 1996; Møller 1997, in press; Thornhill and Møller 1997). Moreover, a meta-analysis of data from 42 species reveals that, on average, individuals with relatively low FA experience greater mating success or attractiveness to the opposite sex (Møller and Thornhill 1998b) and low FA in signaling traits across species appears to be more predictive of sexual attractiveness than trait size (Thornhill and Møller 1998). Given FA's heritability in general across species (Møller and Thornhill 1997a, 1997b), good-genes sexual selection, including viability-based good-genes sexual selection, probably contributes importantly to the greater mating success enjoyed by more symmetric individuals.

In humans, too, FA is probably involved in viability-based good-genes sexual selection. In both sexes, low FA is associated with increased genetic, physical health, and mental health, including cognitive skill and IQ (Furlow et al. 1997; Shackelford and Larsen 1997; review in Thornhill and Møller 1997). Also, symmetric men are more muscular and vigorous (Gangestad and Thornhill 1997a), have lower basal metabolic rate (Manning et al. 1997), and may be larger in body size (Manning 1995; Gangestad and Thornhill 1997a) than asymmetric men. In men also, low FA has been shown to predict components of mating success, such as a relatively high number of sexual partners, earlier age of first sex, quicker sexual access to a new romantic partner (Baker 1997; Gangestad and Thornhill 1997a; Thornhill and Gangestad 1994), facial attractiveness (Baker 1997; Gangestad et al. 1994; Thornhill and Gangestad 1994; but see also Gangestad and Thornhill 1997b), number of EPC partners, and number of times chosen as an EPC partner (Gangestad and Thornhill 1997b). Moreover, men's symmetry predicts a relatively high frequency of their sexual partners' copulatory orgasms (Thornhill et al. 1995). Female copulatory orgasm may be a mechanism of cryptic female choice in contexts in which women mate with multiple partners (Baker and Bellis 1995).

The effect of symmetry on sexual attractiveness appears to be stronger in men than in women, and it is only in men that symmetry predicts the components of mating success mentioned immediately before (Gangestad and Thornhill 1997a). This difference is not surprising given that sexual selection has been stronger in males than females in human evolutionary history (Buss 1994; Symons 1979), apparently because of the sexual disparity in minimal parental investment for successful reproduction (Symons 1979; Trivers 1972). Parental investment theory specifically predicts that sexual selection stemming from variance in genetic quality will be strongest on males in species in which males invest less than females (Gangestad 1993; Trivers 1972).

BODY SCENT AND FA

In addition to the three lines of evidence mentioned indicating that sex pheromone is involved in the human sexual selection system, a previous study by the authors provided data supporting the hypothesis that olfactory stimuli pertaining to men's phenotypic and genetic quality, measured by degree of body FA, positively affect men's sexual attractiveness to women (Gangestad and Thornhill 1998a). That study showed that non-pill-using women's preferences for the scent of male symmetry is directly associated with women's probability of conception inferred from days since last menstruation. When non-pill-using women's fertility was near zero, they showed no systematic preference for either symmetric or asymmetric men's scent. As their probability of conception increased (in the mid-to-late follicular phase), so too did their preference for symmetric men's scent. The Pearson product-moment correlation between women's actuarial probability of conception (based on tabled medical data) and women's preference for symmetric men's scent was a substantial .54 ($N = 28$ women, 41 men).

This paper reports the results of a second, methodologically similar study. The main goals of this study were two-fold. First, we wished to see if the first study would replicate and thereby assess the reliability of its main finding using a larger sample. Second, we wished to extend the findings of the first study in three important ways. In the first study, we did not statistically control for certain potential confounds, such as hygienic practices, and thus could not rule out the possibility that symmetric men simply showered more or used more fragrances (despite our instructions that they not do so). In the current study, we examined those potential confounds. Moreover, in this study we examined whether women prefer the scents of visually attractive men (based on facial photographs) as well as symmetric men. One theory of facial attractiveness is that it reflects, in part, genetic differences in fitness and, from the standpoint of selection, is preferred partly for that reason (Gangestad 1993; Thornhill and Gangestad 1993). If so, women might be expected to particularly prefer the scents of facially attractive men when women are fertile. Finally, the first study did not explore men's evaluation of the body scent of symmetric or facially attractive women, and we examine these associations in this paper. We discuss also the possibility that a human sex pheromone related to symmetry honestly signals phenotypic and genetic quality.

METHODS

Research participants were 80 men and 82 women. Ages ranged from 17 to 33 years for men (mean and $SD = 20.4$ and 2.9) and 17 to 53 years for women (mean and $SD =$

22.3 and 6.8). Self-reported ethnicities of men were 55% Caucasian, 30% Hispanic, 8% African American, 4% Asian, 4% Native American; of women, 52% Caucasian, 32% Hispanic, 6% African American, 2% Asian, and 7% Native American. Participants received experimental course credit in an introductory psychology course in return for their participation in the research (Gangestad and Thornhill 1998a). Recruitment postings specifically asked for women who did not use hormone-based contraception (i.e., a pill or DepoProvera). Nonetheless, we asked women whether they used a contraceptive of this sort and found that some did (see following).

Symmetry Measurement

Participants reported in unisex groups of up to four for an initial session. After reading and signing an informed consent form, each participant was given a brief questionnaire on demographic and other information (e.g., age, height, weight, sexual orientation, socioeconomic status of family of origin, lifetime number of sex partners). One at a time, they were taken into an adjoining room, where the right and left sides of the following 10 characters were measured using a digital caliper, sensitive to 0.01 mm: ear length, ear width, elbow width, wrist width, ankle width, foot breadth, and lengths of all fingers excluding the thumb. In previous samples ($N >$ 700), these characters have been shown to exhibit very little directional asymmetry and slight leptokurtosis, as expected of FA (Furlow et al. 1997; Gangestad and Thornhill 1999). To assess and increase reliability, we measured each character twice. In addition, a facial photograph was taken with a 35-mm camera (50-mm lens), placed approximately 2.5 feet from the participant's face (using 400 ASA color film).

After measurements were taken and the questionnaire was completed, each participant was given a clean, unworn, white, cotton, Hanes-brand T-shirt and provided with explicit wearing instructions. Each was told that he or she should wear the T-shirt a particular 2 nights (identical for each sex) while sleeping. Each was instructed to wash his or her bed sheets with unscented laundry detergent (provided by us) prior to those 2 nights and, during the 2-day period, refrain from the following: (1) using scented soaps, deodorant, or fragrance such as perfume, cologne, or aftershave, and instead use only unscented soap (which we provided); (2) eating garlic, onion, green chile, pepperoni, pungent spices, herbs, strong cheeses, cabbage, celery, asparagus, yogurt, and lamb; (3) drinking alcohol or using recreational drugs; (4) smoking tobacco; (5) engaging in sex with another person; and (6) sleeping with another person. Each participant was further instructed to place the T-shirt in a plastic bag (provided and identified with an arbitrary code number) during the day, when not worn, and return the shirt, in the bag, the morning following the second night at 9 a.m. Of male participants, 74 (92%) returned their shirts on time; of female participants, 78 (95%) returned their shirts on time. When participants dropped off their shirts, each filled out a brief questionnaire about any guidelines, if any, they had violated during the 2-day period when shirts were worn during sleep. They were told that there is no loss of experimental course credit for violating any of our instructions, but we wanted to determine if any had been violated. The questionnaire also obtained information about bathing frequency and use of scented soap and shampoo during the 2-day period involving wearing the shirts. Because we had told participants that, should they happen to use deodorants during the day, they should shower before putting on the shirt, we asked whether they had showered immediately before putting on the shirt.

Scent Attractiveness Ratings

At 10 a.m. of the morning each sex returned shirts, the opposite-sex participants began reporting in groups of up to five. Following informed consent, each woman or man was placed in a separate room for rating the T-shirts. Shirts had been separated into groups of approximately 10 and each group placed in a box. In addition to the shirts worn by men and women, one unworn shirt was included in the sample. Boxes were circulated through the sample of raters present during a session. Although no attempt was made to fully randomize the order in which raters smelled shirts, it is likely that no two raters smelled them in precisely the same order. For each shirt, raters were asked to open the plastic bag and without touching the shirt, smell the shirt, and then rate it on three dimensions: (1) pleasantness, on a scale of 1 = very unpleasant to 10 = very pleasant; (2) sexiness, on a scale of 1 = very unsexy to 10 = very sexy; and (3) intensity, where 1 = not at all intense to 10 = very intense. They were instructed to roll the top of the bag shut before putting it back in its box and moving onto the next shirt. All researchers presenting shirts to participants for smelling were unaware of the symmetry scores of the participants who had worn them.

Women raters were also given a brief questionnaire to fill out, which assessed (1) whether the woman currently used a contraceptive pill or other hormone-based contraceptive; (2) the first day of the woman's last menstrual period (women were provided a calendar to assist with this task); and (3) the typical length (in days) of the woman's menstrual cycle.

In total, rating sessions lasted about 1 hour and were conducted from 8 a.m. until 3 p.m. the day following the collection of the T-shirts.

Despite our instructions, the smell of fragrance (from perfume, soap, or lotion) or smoke was evident on some shirts. Scent raters were asked to indicate if they smelled a nonhuman odor on any of the shirts. Guided by these comments, three experimenters systematically smelled shirts and confirmed ones that had such odors. Of women's shirts, 14 had the smell of fragrance and one smelled of smoke. Of men's shirts, two smelled of fragrance and four smelled of smoke. These shirts were eliminated from all analyses.

Facial Attractiveness Ratings

We recruited 14 women and 15 men unfamiliar with the research to rate participants' facial attractiveness based on the facial photograph. Ratings were made on 1 (least attractive) to 10 (most attractive) scale. Raters were instructed to not rate pictured individuals who they recognized. All opposite-sex ratings were averaged to yield an index of facial attractiveness. Internal consistency of these indices was high: for male participants, alpha = .87; for female participants, alpha = .93. (We used opposite-sex ratings only, although mean ratings made by the two sexes were highly correlated: for male participants, $r = .85$; for female participants, $r = .86$; both $p < .00001$.)

Data Treatment: Symmetry

The multiple (2) asymmetry measurements were checked for reliability. Intraclass correlations of the two measured signed asymmetries for men's individual traits ranged from .78 to .91, $F(79,80) = 8.00$ to 21.10, $p < .00001$; mean intraclass $r = .85$; for women, .76 to .90, $F(80,81) = 7.31$ to 19.98, $p < .00001$; mean intraclass $r = .84$. For unsigned asymmetries, these correlations for men ranged from .60 to .83, $F(79,80) = 4.00$ to 10.61, $p < .00001$; mean intraclass $r = .73$, and for women, from .58 to .87, $F(80,81) = 3.80$ to 14.47, $p < .00001$; mean intraclass $r = .74$.

Previous work has demonstrated that these traits exhibit at most small directional asymmetry (Furlow et al. 1997). None of the signed trait asymmetries exhibited significant platykurtosis, which would indicate antisymmetry. Mean g_2 was .50 for men and 1.48 for women, and hence distributions were slightly leptokurtic, as expected of FA (Gangestad and Thornhill 1999).

To guard against the effects of large asymmetries due to injury, FA of traits that participants reported as injured by break or sprain were excluded in these analyses if they were greater than the mean (56 of 1,620 observations [3.5%]). For measurement purposes, the mean FA for the trait was substituted in these instances (Thornhill and Gangestad 1994). This procedure is essentially equivalent to eliminating these traits from analyses.

An aggregated FA score was calculated in two different ways. First, each trait's absolute asymmetry was divided by the mean trait size ([R + L]/2) for that participant, and the FA of all 10 characters summed to yield an overall index (relative FA). Second, each trait's absolute asymmetry was standardized (divided by) the sample mean of trait size and summed to yield an overall index (absolute FA). These two measures correlated .99 with each other and yielded nearly identical results. Thus, we report results for just one measure (the first). The intraclass correlation across the two measurements for the summed index was .83 for men, $F(79,80) = 10.55$, $p < .00001$, and .84 for women, $F(80,81) = 11.81$, $p < .00001$.

Data Treatment: Scent Attractiveness

Four men and two women reported a homosexual or bisexual orientation. Because this study examined attractiveness of scent in a heterosexual situation, analyses included only the olfactory responses of the exclusively heterosexual participants.

Of the 72 heterosexual women who reported, 16 currently used a pill or related contraceptive (e.g., DepoProvera), one had recently taken a morning-after pill, two did not have menses for medical reasons, two were postmenopausal, one was pregnant, and two did not complete the rating sheet. For the remaining 48 women, we estimated fertility risk (probability of conception following sex) on the basis of their day of the cycle and conception values reported in the medical literature (Jöchle 1973; illustrated in Figure 2 of Box 6.10 in Baker and Bellis 1995). We did so in two ways, one based on a forward method, the other on a backward method (Baker and Bellis 1995). For the former, we simply took the day of the cycle that women were at on the day of smelling based on their reported first day of last menstruation and used the actuarial table to estimate probability of conception. For the latter method, we took into account women's reported cycle length (mean and $SD = 28.5$ and 3.5; women reported this to us at two different sessions, and the two reports correlated 0.80, $p < .0001$; we used the average). Women who have longer cycles, on average, ovulate later in the cycle than women who have shorter cycles (Baker and Bellis 1995). We assumed that the typical day of ovulation was about 15 days prior to the end of their typical cycle (e.g., day 14 in a 29-day cycle) and that the average day of women that actuarial tables are based on is day 14. Women's probability of conception was then based on how far along they had come toward or after their assumed day of ovulation and the actuarial tabled values for women in general. The two methods yielded values that correlated 0.82, $p < .0001$, and results based on each were highly similar. As each method may have some validity that the other lacks, we averaged the two sets of values for our main analyses. (Full results are available from the authors.) The minimum value was .01, the maximum .39 (approximately day 12 of the cycle). Fertility risk steeply rises from near zero to near .2 shortly after the average end of menses (days 5 to 6) and sharply falls from more than .2 to less than .1 immediately after mean ovulation (day 14). Only during days 6 through 14 is fertility risk at least .15. Thirteen women reported being in this range. For convenience, we refer to this group as "high fertility risk." Within it, the mean fertility risk was estimated to be .28 (range .16–.39) The remaining women had a mean fertility risk of .03 (range .01–.11). We refer to this group as "low fertility risk." The mean cycle length of normally cycling women was 28.6 days (range 22–39). Knowledge of actual ovulation point, unavailable in our study, would be ideal for analysis of women's menstrual cycle stage. Our specification of cycle stage based on self-reported cycle point and overall fertility risk reported in the medical literature undoubtedly introduced error in estimated fertility for many women participants. Thus, any significant patterns found should be viewed as underestimates of the actual relationship, as it is very unlikely that error introduced by our method spuriously generates significant relationships.

The mean correlation between individual participants' "pleasantness" and "sexiness" ratings was .85 for women raters and .82 for men. Hence, these ratings were averaged for each sex into a total attractiveness index for reported analyses. Analyses on specific ratings yielded highly similar results.

RESULTS

Although unsigned FA tends to be non-normally distributed (Swaddle et al. 1994), Monte Carlo analyses reveal that significance tests on parametric correlations involving FA are robust (Gangestad and Thornhill 1998b); hence, we performed standard parametric analyses. For predicted effects, we used directed tests (Rice and Gaines 1994), which use a p value of .04 for a predicted relationship and .01 for a relationship opposite of prediction (rather than .025 for each, as with a two-tailed test). In cases in which we predicted no relationship, two-tailed tests were applied.

For men, FA predicted lifetime number of sex partners, $r = -.34$, $p = .001$ (with age partialed out). This result replicates previous findings (Baker 1997; Gangestad and Thornhill 1997b; Thornhill and Gangestad 1994) and, hence, appears to be a robust effect. Women's FA did not predict their number of partners, $r = .00$, *NS.* Sample correlations of men's and women's facial attractiveness with lifetime number of partners were positive but not significant, $r = .19$, $p = .052$, and $r = .18$, $p = .058$. Neither men's nor women's FA significantly predicted their facial attractiveness in this sample, $r = -.10$ and $-.04$, respectively. Two prior studies showed a significant negative relationship between men's body asymmetry and their facial attractiveness (Gangestad et al. 1994; Thornhill and Gangestad 1994), although one study showed a near-zero correlation (Gangestad and Thornhill 1997b). The correlation of $-.10$ in the current sample is close to the weighted average of all our estimates. In light of all evidence, it appears that men's body asymmetry negatively but weakly predicts their facial attractiveness (see also Baker 1997). The correlation between weight and FA was $-.10$ for men and .10 for women. Again, other studies have shown an association between these variables in the same direction as in our sample and significant for men but not women (Gangestad and Thornhill 1997a; Manning et al. 1997). Like the association between FA and facial attractiveness, this association may be negative but fairly weak.

For each sex, we performed two complementary sets of analyses on body scent attractiveness. The first treated shirt wearers as the unit of analysis and examined associations of wearers' FA and facial attractiveness with mean scent attractiveness ratings by opposite-sex individuals. The second treated scent raters as the unit of analysis and examined variations in how individual ratings were associated with the opposite sex's FA and facial attractiveness. For women rating male scents, the primary analysis was an examination of how women's probability of conception, based on their day in the cycle, covaried with their preference for symmetric and facially attractive men's scents.

Women's Attraction to Male Scent: Men as the Unit of Analysis

For our first set of analyses, we split women into the two groups of normally ovulating women discussed earlier: high fertility risk and low fertility risk. Mean attractiveness rating for each male's scent was calculated within each group. Each total index had a reasonably high internal consistency (alpha = .66 and .90, respectively, the latter higher largely because there were about three times as many women in the low-fertility-risk group), indicating that women's ratings tended to covary within groups.

The mean (± *SD*) scent ratings given by high and low fertility women were 4.99 ± .88 and 4.81 ± .86, respectively. On average, the two groups of women did not rate men's scent attractiveness significantly different, $t_{46} < 1$, *NS.* The high-fertility-risk women rated the scent of the unworn T-shirt as significantly more attractive than did the low-fertility-risk women (mean ± *SD* = 5.42 ± 1.43 and 4.06 ± 1.83, respectively, $t_{45} = 2.64$, $p = .011$). We did not find this effect in our earlier study and its significance, if any, is unknown.

Analyses of FA. Based on previous work, we predicted that men's FA would correlate more negatively with the mean attractiveness ratings of high-fertility-risk women than those of low-fertility-risk women. This prediction was confirmed. Whereas low-fertility-risk women's ratings were slightly positively associated with men's FA ($r = .04$), high-fertility-risk women's ratings were somewhat negatively associated with men's FA ($r = -.15$). The difference between these correlations was highly significant, $t_{65} = 2.56$, $p < .006$ (test between dependent correlations; Cohen and Cohen 1975). At the same time, neither correlation itself was significantly different from zero (for high-fertility-risk women, $p = .10$).

To examine the effects of potential confounding factors, we correlated men's responses to the questionnaire about hygiene, other practices, and rule violations (e.g., consuming certain foods or alcohol) during the 2 days with their rated scents. One variable predicted the attractiveness of men's scent particularly well: men who bathed or showered more often had more favorable scents to women, $r = .42$, $p < .01$. Once this variable was controlled for, no other variables significantly predicted additional variance in men's scent attractiveness. To control for this variable, we correlated high- and low-fertility-risk women's attractiveness ratings with men's FA with number of showers/baths partialed out. (One other variable, men's use of scented shampoo, predicted women's ratings of men's scent, although not when men's showering was partialed out. Controlling for this variable as well in our analyses rendered results almost identical to those reported.)

Results revealed once again a significant difference between the correlations, $t_{64} = 2.37$, $p = .010$. Moreover, whereas low-fertility-risk women's ratings were uncorrelated with men's FA ($r = -.03$, *NS*), men's FA was significantly related to high-fertility-risk women's ratings in the predicted negative direction ($r = -.22$, $p = .033$).

A more conservative analysis removed men who reported using any fragrance or scented deodorant whatsoever during the 2-day period (even if they showered immediately before wearing the shirt), leaving 49 men who said they did not. When number of showers was statistically controlled for, men's FA significantly predicted high-fertility-risk women's ratings of scent attractiveness in this sample of men ($r = -.33$, $p = .011$), but not low-fertility-risk women's ratings ($r = -.09$, *NS*). These two correlations significantly differed from one another, $t_{45} = 2.80$, $p = .004$, and are similar to those we previously reported on a separate sample ($-.31$ and $-.02$; Gangestad and Thornhill 1998a).

Analyses of physical attractiveness. We performed a parallel set of analyses using men's rated facial attractiveness rather than FA as a predictor. Men's facial attractiveness correlated .20 and .10 with high-fertility-risk and low-fertility-risk women's ratings of their scent, respectively, both nonsignificant. When men's number of showers taken was partialed out, the correlation between men's facial attractiveness and mean rating by high-fertility-risk women increased to .25, $p = .022$. The r value between men's facial attractiveness and mean rating by low-fertility-risk women was .16, *NS.* These two correlations did not significantly differ from one another, however, $t_{64} = 1.05$, *NS.* Limiting the sample of men to those who claimed to have used no fragrances yielded a correlation between men's facial attractiveness and scent attractiveness as assessed by high-fertility-risk women of .28, $p = .030$. Once again, the correlation of facial attractiveness with mean scent rating made by low-fertility-risk women was nonsignificant ($r = .17$), but did not significantly differ from that with mean scent rating made by high-fertility-risk women ($t_{45} = 1.07$, *NS*).

Additional analyses. Low-fertility-risk and high-fertility-risk women's ratings of men's scent attractiveness were highly correlated, $r = .78$, $p < .0001$. Clearly, then, a set of cues affected both sets of women in similar ways. Nonetheless, given the difference in correlation with men's FA between the two groups of women's ratings, it appears that some variance in high-fertility-risk women's evaluations was due to factors not affecting (or affecting to a lesser degree) low-fertility-risk women's evaluations. To examine the association between men's FA and variation in women's ratings unique to the high-fertility-risk group, we partialed low-fertility-risk women's ratings out of the correlation between high-fertility-risk women's ratings and men's FA and found partial $r = -.31$, $p = .006$. With low-fertility-risk women's ratings controlled, the correlation between high-fertility-risk women's scent attractiveness ratings and men's facial attractiveness was .31, $p = .006$.

Moreover, additional analyses showed that the correlations of high- and low-fertility-risk women's ratings with men's hygienic practices or rule violations did not differ for any variable, whether the variable significantly covaried with men's scent attractiveness or not, all $t_{65} \leq 1.12$, *NS*; mean absolute difference in correlations = .04. Furthermore, neither men's symmetry nor men's facial attractiveness significantly covaried with any of these variables, all $|r| < .17$, *NS.* These results bolster the notion that differences in hygiene or other practices across men do not account for differences in high and low-fertility-risk women's ratings in relation to men's symmetry.

For exploratory purposes, we correlated men's mean scent rating with their age, weight, and self-reported socioeconomic status of family of origin (on a 5-point scale, where 5 = upper class, 3 = middle class, 1 = lower class). With number of showers partialed out, these correlations were not significant, partial $r = -.22$, $-.18$, and .12, respectively, all *NS.* Nor did any of these correlations differ across ratings made by high-fertility-risk and low-fertility-risk women, all $t < 1$, *NS.* Analyses comparing scent attractiveness across ethnicities revealed no significant differences, *F*94,63) < 1, *NS.*

Women's Attraction to Male Scent: Women as the Units of Analysis

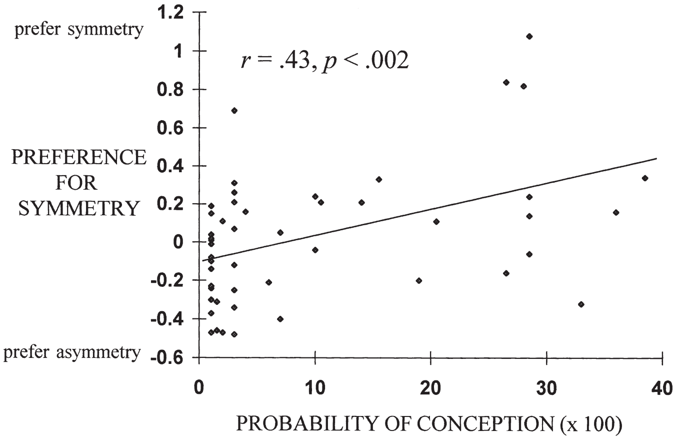
Analyses of FA. Because these analyses examined changes in women's scent preferences as a function of the menstrual cycle based on rough and fixed categories of fertility risk, a second set of analyses treating individual women as the unit of analysis was performed. Each woman's scent attractiveness ratings were regressed on men's FA. The unstandardized regression slope that resulted reflected changes in an individual woman's ratings as a function of men's FA. Because a negative slope reflects preferences for the scent of symmetric men, the sign of this regression slope was reversed. The resultant variable was then treated as an estimate of "preference for symmetry." These analyses parallel those performed in our previous work (Gangestad and Thornhill 1998a).

Normally ovulating (non-pill-using) women's preference for symmetry was correlated with estimated fertility risk based on women's day in the menstrual cycle. The correlation was highly significant, $r = .43$, $p = .001$ ($N = 48$). As can be seen in Figure 1, the greater the fertility risk of a woman, the greater her preference for scent associated with male symmetry. The intercept of the least-squares regression line is nearly zero, meaning that women with no fertility risk favored the scents of neither symmetric men nor asymmetric men. As estimated fertility risk increased, however, women preferred the scents of symmetric men.

To control for fragrance use and hygiene, we performed the same analysis (1) using only men who said they did not use fragrances at all during the two day period and (2) partialing out the effects of men's number of showers (i.e., each woman's preference for symmetry score was based on regressions controlling for the effect of men's bathing on her ratings of scent attractiveness). The correlation between women's preference for symmetry and fertility risk was even stronger in this analysis, $r = .49$, $p = .0001$. This finding indicates that the association between women's preference for symmetry and their probability of conception is not due to a correlation of men's symmetry with either their fragrance use or bathing (Figure 2). The effects that these variables have on scent attractiveness appear to be independent of the effects of symmetry.

Analyses of physical attractiveness. Just as we constructed a measure of women's preference for the scent of symmetry by regressing each woman's scent ratings on male FA, we constructed a measure of non-pill-using women's preference for the scents of

FIGURE 1. Normally ovulating (non-pill-using) women's preference for the scent of symmetry as a function of their probability of conception, based on values reported in the medical literature (Baker and Bellis 1995; Jöchle 1973).



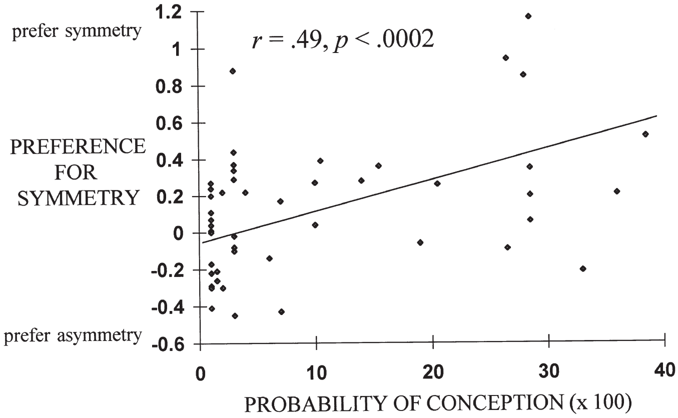


FIGURE 2. Normally ovulating (non-pill-using) women's preference for the scent of symmetry as a function of their probability of conception, with men's fragrance use and shower-taking controlled. Men who said they used fragrance were eliminated. Number of showers by men was partialed out of the regression of each woman's scent ratings on male FA.

facially attractive men by regressing each woman's scent ratings on men's facial attractiveness. We then correlated this measure with women's actuarial probability of conception. The correlation was .29, $p = .023$. Women with a higher fertility risk preferred the scents of facially attractive men more than women with a lower fertility risk. Limiting the set of men to those who said they used no fragrances and partialing men's shower-taking out of these analyses did not change these results: $r = .29$, $p = .022$. These results suggest that preference for the scent of facially attractive men increases with fertility risk, whereas analyses comparing the correlations of facial attractiveness with scent ratings made by high- and low-fertility-risk women yielded no significant difference. It should be noted that one difference between these analyses is that, because more women are low fertility risk, the reliability of the average ratings made by these women is higher than the reliability of the average ratings made by high-fertility-risk women in the analysis treating men as units of analysis, reducing power to detect a difference between correlations in that analysis. For this reason, the analysis treating women as the units of analysis may be expected to be more sensitive to detecting an effect.

Additional analyses. For exploratory purposes, we correlated women's preference for the scent of symmetry with a number of additional variables: women's age, own FA, and number of self-reported sex partners. No variable reliably predicted preference for symmetry. Statistically controlling women's probability of conception or men's hygiene and fragrance use did not change this result, all $|r| \leq .27$, *NS.*

We correlated women's preference for facial attractiveness with the same variables. No correlation was significantly different from zero, all $|r| \leq 0.15$, *NS.*

Women's Attraction to Male Scent: Women Using Hormone-Based Contraception

As we specifically sought to recruit normally ovulating women, this research was not designed to examine the preferences of women using hormone-based contraception (see Gangestad and Thornhill 1998a for a discussion of these women's preferences). Nonetheless, 16 women reported using these contraceptives (11 a pill, 5 DepoProvera). The internal consistency (alpha) of scent ratings made by these women was .85. The mean scent attractiveness rating they gave the shirts was 4.21, which did not significantly differ from the mean ratings given by high or low fertility risk, normally ovulating women, $t_{27} = 2.03$ and $t_{49} = 1.73$, *NS*. The sample of women who specifically had a DepoProvera shot rated the shirts' attractiveness just 3.78 on average, which did significantly differ from the mean ratings given by high and low-fertility-risk women, $t_{16} = 2.40$ and $t_{38} = 2.15$, $p < .05$. As this sample was very small and this analysis post hoc, however, these results are only suggestive and require replication.

As expected, these women's mean scent attractiveness ratings did not significantly correlate with men's FA, $r = -.05$, *NS* ($-.05$ and $-.01$ for women on a pill and DepoProvera, respectively, *NS*), or men's facial attractiveness, $r = .03$, *NS* (.02 and .04 for women on a pill and DepoProvera, respectively, *NS*).

To examine whether pill-using women's preferences for symmetry show the same changes across the menstrual cycle as we observed for those of normally ovulating women, we correlated their preference for symmetry with the fertility risk they would have were they normally ovulating, based on their day in the cycle. As expected, the correlation was nonsignificant, $r = -.35$, *NS* ($N = 10$). Excluding men who reported using a fragrance and controlling for men's number of showers and scented shampoo did not alter this result, $r = -.21$, *NS*. Despite the small sample size, these correlations significantly differed from the comparable correlations for normally ovulating women ($z = 2.11$ and 1.84, respectively, $p = .017$, .033). These findings suggest that changes in normally ovulating women's preferences for the scent of symmetry across the menstrual cycle are due to changes that occur in connection with normal ovulation and not to changes that are entrained with menstruation independent of normal ovulation (see also Gangestad and Thornhill 1998a).

The correlation between pill-using women's fertility risk were they normally ovulating (based on their day in the cycle) and preference for the scent of facially attractive men was not significant, $r = -.25$ and $-.35$, *NS*, based on the full sample and the restricted sample with shower-taking partialed out, respectively. These correlations did not differ significantly (or did so only marginally) from the comparable correlations for normally ovulating women, $z = 1.38$ and 1.65, $p = .084$, .050), although, due to the small size of the sample of pill-using women, these analyses have little power to detect differences.

Intensity Ratings of Male Scents

Internal consistencies (alpha) of women's intensity ratings of male scents were .54 and .86, respectively, for high- and low-fertility-risk women (again, the latter larger mostly because of the much greater number of low-fertility-risk women). Women's intensity ratings of men's scents were largely independent of their olfactory attractiveness ratings. Across women, the mean correlation between these two judgments was .13, $t = 1.71$, *ns*. Men's FA did not significantly correlate with either high-fertility-risk or low-fertility-risk women's intensity ratings, $r = -.13$ and .01, *NS.* Nor did these two correlations significantly differ from one another, $t_{65} = 1.18$, *NS.* Similarly, men's facial attractiveness did not significantly predict the intensity ratings of either high- or low-fertility-risk women, $r = -.07$ and $-.11$, *NS*, test for difference: $t_{65} < 1$, *NS.* Limiting these analyses to the group of men who said they used no fragrances whatsoever produced nearly identical results.

Previous research has suggested that women's sensitivity to male scents varies across the menstrual cycle (see introduction). We therefore performed an a priori contrast between the mean intensity ratings made by high-fertility-risk women (5.80) and those made by normally cycling, low-fertility-risk women (5.11) and women using a hormone-based contraceptive (5.57). No difference was detected, $t_{61} = 1.13$, *NS.* Furthermore, actuarial probability of conception did not significantly predict mean intensity rating within the group of normally ovulating women, $r = .24$, $p = .096$. More importantly, probability of conception did not covary with the extent to which men's symmetry or facial attractiveness predicted individual women's intensity ratings, $r = .16$ and .09, *NS.* Not surprisingly, then, when intensity ratings were statistically controlled for in deriving individual women's preference for the scent of symmetry and facial attractiveness, the correlations of these preferences with women's probability of conception were not highly affected; both remained significant, $r = .41$, $p = .001$, and $r = .26$, $p = .036$, respectively. Thus, these findings provide no evidence that the association between women's fertility risk and their preference for male symmetry is mediated by a general increased sensitivity to smells during the fertile period.

Men's Attraction to Women's Scent: Women as the Unit of Analysis

In total, 61 men rated 65 women's shirts. The internal consistency of men's ratings was high (alpha = .90). The average of these ratings was 4.80. This value did not differ from the mean ratings given men's scents by either high- or low-fertility-risk women, $t_{72} < 1$ and $t_{97} < 1$, *NS.* Men's mean rating of the unworn shirt was 4.39.

Women's mean scent attractiveness to men did not significantly correlate with women's FA, $r = -.04$, *NS*, age, $r = .02$, *NS*, or facial attractiveness, $r = .18$, *NS* (with age partialed out; in this sample, age correlated $-.43$ with women's facial attractiveness, $p = .0002$). When the sample of women was restricted to those who did not use any fragrance whatsoever, women's facial attractiveness predicted their scent attractiveness, $r = .23$, $p = .031$. Both FA and age remained unassociated with women's scent attractiveness, $r = .03$ and $-.03$, *NS.*

Women's self-reports about hygiene and rule compliance were analyzed in relation to their mean scent attractiveness to the men. No significant correlations emerged and thus we did not follow up our analysis with partial correlational analyses controlling for these variables.

For exploratory purposes, we correlated women's scent attractiveness with their weight, socioeconomic status of family of origin, and (for those women normally ovulating: $N = 55$) actuarial probability of conception based on day of the cycle (see earlier). No significant associations emerged, $r = -.08$, $-.11$, and $-.18$, *NS*. Within the set of women who claimed to use no fragrances, the correlations were $-.10$, $-.09$, and $-.02$, respectively, *NS*. Women's scent attractiveness did vary as a function of their ethnicity, $F(4, 60) = 3.51$, $p = .012$ (even if the alpha level is Bonferroni adjusted for family-wise error rate given tests on four variables, this effect is significant). No post hoc Scheffé comparisons were significant, but it is perhaps notable that women in the least represented groups (African Americans, Asians, and Native Americans) received the highest scent attractiveness ratings (5.29, 5.00, and 5.24, respectively vs. 4.56 for Caucasian women and 4.88 for Hispanic women). The reliability and significance of this effect may be explored in future research.

Men's Attraction to Women's Scent: Men as the Unit of Analysis

Individual men's ratings of women's scent were regressed on women's FA and the slope of the best fit line, with sign reversed, was used as a measure of men's preference for the scent of symmetry. Preference for symmetry was then correlated with men's age, own FA, and number of sex partners (age adjusted). Bonferroni adjustment for family-wise error gives an alpha criterion of .017. Men's FA significantly predicted their preference for symmetry, such that symmetric men tended to rate symmetric women's scents relatively more favorably, $r = -.32$, $p = .009$. Neither men's number of sex partners nor their age significantly predicted their preference for symmetry, $r = -.23$, $p = .063$, and $r = -.14$, *NS*, respectively. When the analysis was restricted to women who claimed to have used no fragrances, however, the correlation between men's FA and their preference for the scent of symmetry fell short of significance, $r = -.22$, $p = .074$.

Intensity Ratings of Women's Scents

Internal consistency (alpha) of men's intensity ratings of female scents was .91. Across women the mean and $SD = 5.00$ and .68. On average, male scents were rated as more intense (mean $\pm$ $SD = 5.34 \pm .68$) than female scents, $t_{130} = 2.88$, $p = .005$. Men tended to rate more attractive scents as more intense, although this correlation was quite small; on average across individual men, $r = .15$, $t_{60} = 3.02$, $p = .004$. Correlations between female scent intensity (averaged across all male raters) and a variety of female characteristics were computed. No significant correlation was observed for female FA ($-.06$), age (.01), facial attractiveness ($-.07$, with age partialed out), weight (.14), or socioeconomic status of family of origin ($-.06$). Women's scent intensity did significantly covary inversely with their actuarial probability of conception, $r = -.36$, $p = 0.015$. This correlation was not significant, however, in the sample of women who claimed to have used no fragrance whatsoever, $r = -.16$, *NS*. Bonferroni adjustment of alpha for the number of correlations involving female scent intensity we computed renders all correlations nonsignificant.

DISCUSSION

This research used T-shirts worn by each sex for 2 nights of sleep and then smelled by the opposite sex to examine the relationship between heterosexual attractiveness of one's body odor and one's body FA. The results indicate a sex difference in this relationship. Compared to the body scent of relatively asymmetric men, relatively symmetric men's scent is more attractive to normally ovulating (non-pill-using) women during their period of peak fertility based on menstrual cycle point. Yet non-pill-using women show no odor preference related to male body symmetry during menstrual cycle times of low fertility. Moreover, women using hormone-based contraception do not show the preference. By contrast, we found no evidence that men find the scent of symmetric women more attractive. That fertile women prefer the scent of male symmetry has now been found in two separate studies (also see Gangestad and Thornhill 1998a). This relationship was also reported by Rikowski and Grammer (1998) from their methodologically similar T-shirt study in Austria involving a relatively small sample of research subjects. When all three studies are considered, the effect of men's symmetry on fertile women's scent attractiveness ratings appears quite robust. These findings may partially explain why women report in multiple studies that scent of a man is central in their mate choice and sexual desire (see introduction).

Definitive evidence for a scent associated with men's symmetry would involve the isolation of the chemical and the use of appropriate control odors for eliminating potential confounds such as novelty. That evidence has not yet been found; hence, we cannot say with absolute certainty that there exists a chemical emitted by men that women use to discriminate men who have and have not experienced developmental imprecision. Nonetheless, the current evidence strongly suggests that there is such a chemical(s). Apparently, the attractiveness of the symmetry scent to women does not arise from hygienic differences between men in relation to their symmetry (e.g., number of times they showered). Partialing out factors relating to men's hygiene affecting women's ratings of men's scent actually increased the effect of women's probability of conception on their scent preferences for symmetry, indicating that these factors affect women's preferences independently of symmetry. Nor does it appear to arise from not following our research guidelines for diet, alcohol and drug use, or sleeping behavior over the period in question. The symmetry of men was unknown to the scent-rating women and the researchers involved in collecting the scent ratings. The raters and the researchers only received plastic bags, each containing a T-shirt and labeled with a subject number. Although women exhibit increased olfactory sensitivity during the fertile aspect of the menstrual cycle (Doty 1981; Kohl and Francoeur 1995; Vroon 1997), the odor preference for symmetry shown by normally ovulating women cannot readily be explained by an increased general olfactory sensitivity or response with high fertility. In our first study and in the current study, there was no significant relationship between women's intensity ratings of the shirts and male symmetry. In sum, we know of no explanation of our results other than that normally ovulating women use a chemical(s) in men's sweat or skin as a basis for discriminating men who have and have not experienced perturbations that generate FA.

In this study, we found no evidence that fertile women differentially evaluated scent that might conceivably be associated with a number of other male traits studied, including age, weight, or socioeconomic status. As women's probability of conception increased, however, so too did their preference for the scent of facially attractive men. This pattern was also reported by Rikowski and Grammer (1998). Possibly, some components of men's facial attractiveness may have evolved through good-genes sexual selection such that facial attractiveness is an ancestral marker of good genes, just as low FA may be (Gangestad 1993; Gangestad and Simpson 1990; Thornhill and Gangestad 1993). In this sample, men's FA did not significantly correlate with their facial attractiveness. Future work might aim to identify which male facial features are associated with low FA and are associated with scents that women prefer during peak fertility.

Although women's FA did not predict their scent attractiveness to men, we found some evidence that women's scent attractiveness and facial attractiveness are positively correlated. We found no significant correlation in the full sample, but a significant positive association was found within the sample of women who stated that they used no fragrance whatsoever. Rikowski and Grammer (1998) reported the same association between women's facial attractiveness and scent attractiveness in their Austrian sample. Hence, women's facial attractiveness and scent attractiveness may functionally convey overlapping information, and future work might aim to identify more precisely the nature of the overlap.

Women's Scent Preference: For High Genetic Quality Sires?

Women's self-reported sexual desire peaks at the fertile time of the menstrual cycle (Regan 1996). Evidence suggests that women also engage in more mating effort at midcycle. Women attending both nightclubs and university classes wear clothing that reveals more skin at self-reported midcycle (E. Hill, unpublished data; Grammer et al. 1997) and their skin exposure in public is directly related to salivary estradiol (Grammer et al. 1997; also K. Grammer and J. Dittami, unpublished data).

Our results indicate that women have a specific preference for scent associated with male symmetry during the fertile time in their menstrual cycle. These results and results mentioned immediately before indicating significant increases in women's sexual desire and associated mating effort at the fertile time of the cycle imply a preference in women that functions to select a sire for their offspring rather than a preference for a mate that will invest in a woman and her offspring. That historical selection on males in the context of mates' EPC was effective is seen in men's adaptation to prevent cuckoldry: facultative adjustment of ejaculate size based on probability of EPC (Baker and Bellis 1995) and men's sexual proprietariness and associated mate guarding tactics (Buss 1994; Wilson and Daly 1992). Increasing evidence indicates that women have adaptation for EPC and that it relates, in part, to obtaining a genetic sire rather than only an additional or different male investor. Benshoof and Thornhill (1979) proposed that women's concealment of ovulation is an adaptation for obtaining good genes and other benefits by EPCs (also see Baker and Bellis 1995; Hrdy 1981; Symons 1979). Concealed ovulation disguises variation in female fertility and thus reduces pair-bond males' ability to mate guard effectively. Women engage in more EPCs, but not more in-pair copulations, at peak fertility (Baker and Bellis 1995). Indeed, the peak rate of EPCs (occurring around the 10th day of the cycle) is about 2.5 times the minimal rate of EPCs (occurring the last week of the cycle). Moreover, women with a primary mate are most likely to attend a singles-scene nightclub without the mate near peak fertility (K. Grammer, unpublished data). Also, there is evidence that pair-bonded women choose symmetric men as EPC partners, and given that symmetric men invest less in their romantic relationships than asymmetric men (Gangestad and Thornhill 1997a), these choices are probably not for increased male investment (Gangestad and Thornhill 1997b). Finally, Baker and Bellis (1995) provide evidence that female copulatory orgasm may be involved in selective sperm retention, and it may be involved in selective pair bonding as well (Thornhill et al. 1995). Either of these two selective mechanisms, or both, would give an advantage to the sperm of certain men over others when women have multiple mates. Women's pattern of orgasm appears to favor EPC partner's sperm over in-pair partner's sperm (Baker and Bellis 1995). We previously reported that women are more likely to experience copulatory orgasm with relatively symmetric male partners than with asymmetric partners (Thornhill et al. 1995).

Regarding concealed ovulation in women, our study suggests that men cannot detect the fertile point in a woman's cycle by the attractiveness of her body scent. We found that men's attractiveness ratings of women's body scent were unrelated to women's probability of conception based on cycle day. There is some evidence, however, that men respond sexually to copulins, which are present in women's vaginal secretions (Grammer and Jutte 1997).

Sexual selection theory predicts that females will have evolved to seek mates with high genetic quality pertaining to offspring viability (Andersson 1994; Gangestad 1993; Trivers 1972; Williams 1966). There is increasing evidence that female mate choice is based on heritable viability in a diversity of species (see references in introduction). Humans may be a species in which this kind of mate choice is highly developed because the relatively limited intensity of sexual selection in humans stemming from biparental care may be conducive to the maintenance of consistent heritability of viability (Møller and Thornhill 1998b; Pomiankowski and Møller 1995). However, EPCs leading to offspring production in pair-bonding species increase the intensity of sexual selection considerably (Møller 1998). A factor that may elevate the importance of EPCs in humans is that the sexes have evolved in groups of closely associated individuals. The close proximity of males and females may lower the costs of EPCs for both sexes (Benshoof and Thornhill 1979). Another factor that may make EPCs important for women is that pair bonding limits female choice for good genes when male investment in a female and male genetic quality do not coincide as may be the case in humans and some bird species. Møller and Thornhill (1998b) provide evidence across pair-bonding bird species that females engage in more offspring production with sexually attractive extrapair bond males when attractive males invest less than unattractive males. This pattern of attractive males investing less may occur in humans, because, as mentioned earlier, we have found that symmetric men invest less time, money, honesty, and sexual exclusivity in their romantic relationships.

This is not to say that women do not often seek material or direct benefits by EPCs. They do apparently. Hill and Hurtado (1996) in a study of Ache Indians and Beckerman et al. (1998) in a study of the Barí provide evidence that extramarital copulations by women enhance offspring survival, apparently as a result of the greater parental investment from multiple "fathers." Yet female preference for male-provided resources does not negate an important role for good-genes sexual selection when fitness is heritable. Considerable genetic variation in fitness is seen in most natural populations (Burt 1996; Gangestad 1997; Kirkpatrick 1996). FA is a useful measure of overall fitness and is significantly heritable (see introduction).

The results from this and our prior study of the scent of male symmetry (Rikowski and Grammer 1998), studies of women's sexual desire and EPC behavior, the literature on the relationship between FA and phenotypic and genetic quality, and the negative relationship in men between symmetry and relationship investment support the hypothesis that women have an olfactory preference at the fertile part of their menstrual cycle for symmetric men because the preference resulted in offspring with fitter genes in human evolutionary historical environments. It is conceivable that the olfactory preference functions to secure mates who are physical protectors of women instead of sires with good genes. Smuts and Smuts (1993) have summarized ethnographic data indicating that protection by a pair-bond mate may reduce sexual coercion by other males. Our prior studies have shown that although symmetric men invest less with respect to certain types of investment, they perceive themselves and are perceived by their romantic partners as better protectors of the female partner (Gangestad and Thornhill 1997a). Also, symmetric men engage in more fights with other men than asymmetric men (Furlow et al. 1998). Protection of the female is a form of male investment that least interferes with a man's access to partners other than his pair-bond mate because his protective ability is attractive to women in general and, compared to investment in the form of time, honesty, and sexual exclusivity, competes with male pursuit of additional partners to a lesser degree. Thus, female preference for male protection is not necessarily an explanation that is exclusive of good-genes mate choice. Symmetric men may have more protection ability and better genes for offspring fitness.

It is also conceivable that symmetric men may be preferred by women at mid-cycle because of a preference for adequate sperm. Manning et al. (1998) (also Baker 1997) have shown a positive correlation between ejaculate size, sperm quality, and body symmetry in men. This, too, however, is not necessarily an alternative to good genes.

One possible good-genes mechanism is that symmetric men may have particularly rare major histocompatibility (MHC) genotypes making them attractive to many fertile women. MHC loci are involved in recognizing antigens and thereby initiating the immune response. It has been proposed by several workers that heterozygosity at MHC may defend against parasites (see Penn and Potts 1998 for review; also Wedekind and Füri 1997; Wedekind et al. 1995). Wedekind et al. (1995) and Wedekind and Füri (1997) found that normally ovulating women, but not women on the pill, prefer the scent of men who possess dissimilar MHC genotypes, and hence men with rare MHC genotypes are expected to be attractive to relatively many women. If having many rare MHC alleles is associated with high parasite resistance, then symmetric men may have more rare MHC alleles. (See Thornhill and Møller 1997 for review of human health, including infectious disease, in relation to symmetry.) The MHC effect, however, works in both directions in that both sexes prefer the scent of MHC dissimilar individuals (Ober et al. 1997; Wedekind and Füri 1997). Our results indicate that only women have the symmetry-scent preference. Thus, it may be that aspects of the genome other than MHC are responsible for the preference. The symmetry-scent preference may reflect assessment of potential sires in terms of overall genetic quality pertaining to viability.

It has been suggested to us that MHC-based scent preferences are incompatible with good-genes preferences. This is not the case. MHC preference may function to avoid inbreeding or to produce an offspring with optimal genotype against certain parasites (see review in Penn and Potts 1998). Separate mate choice adaptation may focus on different problems facing offspring, such as other components of viability. Mate choice adaptations are anticipated to be involved in tradeoffs of benefits, just as are other types of adaptations. Also, the circumstances of a mate chooser (e.g., her genotype, health, and so on) may affect the priority given to a particular benefit obtained from mate choice. Thus, the self-referential component of MHC preference probably applies to many mate-choice domains.

Multiple lines of research indicate that women's sexual scent preferences are influenced by the contraceptive pill.Wedekind et al. (1995) and Wedekind and Füri (1997) have shown that only non-pill-using women prefer MHC-dissimilar scents; pill users prefer MHC-similar scents. Apparently, the pill changes the hormonal milieu in a way that mimics pregnancy and thereby affects preference for MHC types. Our research on the scent of male symmetry shows that the scent is attractive only to non-pill users with high conception probability. An interesting question is whether the pill influences women in ways that interfere with their choice of sire. Baker and Bellis (1995) have found that women are significantly more likely to use contraception during in-pair copulation than during EPC. This effect may result, in part, from pill-using women being less motivated to EPC as a result of the pill reducing their interest in men who are physically or olfactorily attractive.

Symmetry Pheromone as Handicap Signal

Honest signal theory—the handicap theory that Amotz Zahavi (1975) originated in the mid-1970s—is now widely recognized as the theory of signals in biology. The theory has been applied widely and successfully to visual and acoustical communication systems. It has rarely been discussed in connection with chemosensory systems (for sex pheromones, see Eisner and Meinwald 1995; Pagel 1993; Penn and Potts 1998; Zahavi and Zahavi 1997; intercellular pheromonal signals, Møller and Pagel 1998; Pagel 1993).

We hypothesize that the chemical(s) involved in fertile women's preference for the scent of symmetry is an honest signal of phenotypic and genetic quality of men, just as body symmetry itself appears to be (also Gangestad and Thornhill 1998a). Because all males would gain a mating advantage by producing attractive scent, selection on females to use cues of true quality, and selection on signalers to produce these cues, would result in an honest signal—that is, one that cannot be faked by low-quality males (Grafen 1990; Zahavi 1975; Zahavi and Zahavi 1997). Thus, we are suggesting that the chemical is a signal in that it reflects adaptation for influencing others—in this case, male adaptation that influences female mating and orgasmic decisions. This is in contrast to the chemical being merely an incidental effect to which the opposite sex responds, as is seen with sex attractants produced by certain female insects. In these insects, selection has apparently not operated on senders (females), but has acted effectively on males for tracking any chemical that is associated with a female (Thornhill and Alcock 1983); the males have adaptation for olfactory response to females, but females lack specializations for storing or dispensing scent. In the human case, we hypothesize male adaptation for signaling with the chemical and female adaptation for receiving and processing the signal and for mate and sire choice decisions based on the signal.

Current knowledge of chemical communication pertaining to human sexuality suggests some honest signaling possibilities for the pheromone of male symmetry. Androstenol and androstenone, two chemicals known to be involved in human scent, are associated with and probably derived from other androgens such as testosterone and dehydroepiandrosterone (Kohl and Francoeur 1995). Because androgens may be handicaps on the immune systems (Folstad and Karter 1992; Wedekind 1992), androstenol and/or androstenone levels may signal health, including developmental health or symmetry. A related possibility is that the abundance or type of bacteria on the skin that contributes to the scent of male sweat (Gower and Ruperelia 1993) may vary as a function of male health and thus male symmetry. A third possibility relates to certain fatty acids in sweat that are known to contribute to its odor (Gower and Ruperelia 1993). If differences in metabolic rate that are apparently related to male symmetry (Manning et al. 1997) generate different amounts or kinds of fatty acids (or androgen-related chemicals), this would imply honest chemical signaling of symmetry and thereby phenotypic and genetic quality. Any of these hypothetical honest chemical signals may be dispersed or stored in structures that are adaptations for it. It has been repeatedly suggested that there may be human axillary adaptations of hair and vascularization for dispersal of scent and of glands for storing it (Kohl and Francoeur 1995; Vroon 1997).

The Term Pheromone

The scenario for the scent of symmetry we have described is consistent with the concept of a male sex pheromone related to symmetry. The term pheromone is often used to include not only olfactory signals but olfactory stimuli that affect another individual when there is no olfactory signaling adaptation in the sender. This use is common in the insect literature. Other researchers, however, especially those studying mammalian olfaction, only use the term pheromone for chemicals that cause an automatic behavioral or developmental response that they view to be cued by the chemical involved alone and without influence by other information. A “large degree of genetic programming which is influenced minimally by experience” is often part of this perspective (Beauchamp et al. 1976: 145). The true pheromone in this case is seen as being comparable to an ethological “releaser.” In this terminology, other chemicals that are pheromone-like are referred to as primers or primer pheromones, because they may or may not bring about a behavioral response dependent on additional cues, such as hormonal state and experience of the receiver. Such a view often limits pheromones to invertebrates and primers to vertebrates, especially the higher vertebrates, because the latter’s intelligence and flexible behavior is thought to complicate interpretations of their responses. Flexible behavior is interpreted as indicative of a lack of a large degree of genetic programming and of a primary role for experiential influences, especially learning, in behavioral response to odors (Beauchamp et al. 1976). There is debate in the literature about whether mammals, especially primates (including humans), have real pheromones or only primers (Beauchamp et al. 1976).

Although taxonomies of proximate causes (individual’s developmental experiences, physiological status, and so on) of responses to chemical cues given off by conspecifics are useful in understanding between-species variation in pheromonal systems, the notion that insects do chemical communication in a simple, automatic, and genetically determined way and without information other than the pheromonal chemical itself, but mammals, and especially humans, often do not, is misguided. In insects, pheromonal responses are strategic (i.e., based on specialized adaptation), just like those of mammals, and, as in mammals, involve multiple informational domains including physiological state and experiences of pheromone-receiving individuals. (For example, see Thornhill 1984 for discussion of a relatively well worked out sex pheromonal system in scorpionflies where the primer concept applies given the detailed knowledge of the system.) The term pheromone is a perfectly good one to describe the chemosensory system of humans that our results indicate exists, as well as the human scent systems involving MHC (see earlier), kin recognition (Schaal and Porter 1991), menstrual synchrony (Stern and McClintock 1998), and so on (Schaal and Porter 1991). The notions that “degree of genetic programming” has validity for any trait of the individual organism or that experience does not apply to traits of insects (or applies less) reflect misunderstandings of ontogeny. In actuality, the adaptations involved in detecting olfactory cues, whether possessed by invertebrates or humans, are the result of genetic causes and a multitude of environmental causes (experiences) acting in inseparable concert.

Humans are the second species in which data indicate that the scent of symmetric males is more attractive to females than the scent of asymmetric males. Thornhill (1992) found that symmetric male scorpionflies (*Panorpa japonica*) produce relatively attractive scent; in this case the scent arises from a scent-dispersing organ present only in males that is elaborately specialized for pheromone production and release. We anticipate on theoretical grounds that the “scent of symmetry” effect will be widespread in sexual pheromone systems across animal species because of symmetry’s positive relationship with developmental stability and thus with phenotypic quality in many species. This relationship is expected to provide the basis for the evolution of pheromonal honest signal systems. Indeed, such systems need not be limited to sexual pheromones, but are likely to be evolutionarily stable in all forms of social interaction (nepotism, reciprocity, mate choice, intrasexual competition).

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REFERENCES

Amoore, J.E., Pelosi, P., and Forrester, L.J. Specific anosmias to 5 alpha-androst-16-en-3-one and alpha-pentadecalactone: the urinous and musky primary odours. *Chemical Sens Flavour* 2:401–425, 1975.

Andersson, M. *Sexual Selection.* Princeton, NJ: Princeton University Press, 1994.

Baker, R.R. Copulation, masturbation and infidelity: state-of-the art. In *New Aspects of Human Ethology.* A. Schmitt, K. Atzwanger, K. Grammer, and K. Schafer (Eds.). New York: Plenum Press, 1997, pp. 163–188.

Baker, R.R., and Bellis, M.A. *Human Sperm Competition: Copulation, Masturbation, and Infidelity.* London: Chapman and Hall, 1995.

Beauchamp, G.K., Doty, R.L., Moulton, D.G., and Mugford, R.A. The pheromone concept in mammalian chemical communication: a critique. In *Mammalian Olfaction, Reproductive Processes, and Behavior.* R.L. Doty (Ed.). New York: Academic Press, 1976, pp. 143–160.

Beckerman, S., Lizarralde, R., Ballew, C., Schroeder, S., Fingelton, C., Garrison, A., and Smith, H. The Barí partible paternity project: preliminary results. *Current Anthropology* 39:164–167, 1998.

Benshoof, L., and Thornhill, R. The evolution of monogamy and loss of estrus in humans. *Journal of Social and Biological Structures* 2:95–106, 1979.

Brooksbank, B.W.L. Urinary excretion of androst-16-en-3 alpha-ol in human male axillary sweat. *Experientia* 30:864–865, 1962.

Brooksbank, B.W.L., and Haslewood, G.A.D. The estimation of androst-16-en-3 alpha-ol in human urine. Partial synthesis of androstenol and its β-glucosiduronic acid. *Biochemistry Journal* 80:488–496, 1961.

Burt, A. Perspective: the evolution of fitness. *Evolution* 49:1–8, 1996.

Buss, D.M. *The Evolution of Desire: Strategies of Human Mating.* New York: Basic Books, 1994.

Cohen, J., and Cohen, P. *Applied Multiple Regression/Correlation Analysis for the Behavioral Sciences.* Hillsdale, NJ: Erlbaum, 1975.

Doty, R.L. Olfactory communication in humans. *Chemical Senses* 6:351–376, 1981.

Eisner, T., and Meinwald, J. The chemistry of sexual selection. *Proceedings of the National Academy of Sciences* 92:50–55, 1995.

Folstad, I., and Karter, A.J. Parasites, bright males, and the immunocompetence handicap. *American Naturalist* 139:603–622, 1992.

Franzoi, S.L., and Herzog, M.E. Judging physical attractiveness: what body aspects do we use? *Personality and Social Psychology Bulletin* 13:19–33, 1987.

Furlow, B.F., Armijo-Prewitt, T., Gangestad, S.W., and Thornhill, R. Fluctuating asymmetry and psychometric intelligence. *Proceedings Royal Society of London B* 264:823–829, 1997.

Furlow, B., Gangestad, S.W., and Armijo-Prewitt, T. Developmental stability and human violence. *Proceedings Royal Society of London B* 266:1–6, 1998.

Gangestad, S.W. Sexual selection and physical attractiveness: implications for mating dynamics. *Human Nature* 4:205–236, 1993.

Gangestad, S.W. Evolutionary psychology and genetic variation: non-adaptive, fitness-related and adaptive. In *Characterizing Human Psychological Adaptations. Ciba Foundation Symposium 208.* G.R. Bock and G. Cardew (Eds.). New York: John Wiley and Sons, 1997, pp. 212–223.

Gangestad, S.W., and Simpson, J.A. Toward an evolutionary history of female sociosexual variation. *Journal of Personality* 58:69–96, 1990.

Gangestad, S.W., and Thornhill, R. Human sexual selection and developmental stability. In *Evolutionary Social Psychology.* J.A. Simpson and D.T. Kenrick (Eds.). Mahwah, NJ: Lawrence Erlbaum Associates, 1997a, pp. 169–195.

Gangestad, S.W., and Thornhill, R. The evolutionary psychology of extrapair sex: the role of fluctuating asymmetry. *Evolution and Human Behavior* 18:69–88, 1997b.

Gangestad, S.W., and Thornhill, R. Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proceedings Royal Society of London B* 265:927–933, 1998a.

Gangestad, S.W., and Thornhill, R. The analysis of fluctuating asymmetry redux: the robustness of parametric statistics. *Animal Behaviour* 55:497–501, 1998b.

Gangestad, S.W., and Thornhill, R. Individual differences in developmental precision and fluctuating asymmetry: a model and its implications. *Journal of Evolutionary Biology* 12:402–416, 1999.

Gangestad, S.W., Thornhill, R., and Yeo, R.A. Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology* 15:73–85, 1994.

Gower, D.B., and Ruperelia, B.A. Olfaction in humans with special reference to odorous 16-androstenes: their occurrence, perception and possible social, psychological and sexual impact. *Journal of Endocrinology* 137:167–187, 1993.

Grafen, A. Biological signals as handicaps. *Journal of Theoretical Biology* 144:517–546, 1990.

Grammer, K. 5-alpha-androst-16en-3 alpha-on: a male pheromone? A brief report. *Ethology and Sociobiology* 14:201–214, 1993.

Grammer, K., and Jutte, A. The war of odors: importance of pheromones for human reproduction. *Gynakologisch-geburtshilfliche Rundschau* 37:150–153, 1997.

Grammer, K., Jutte, A., and Fischmann, B. Der Kampf der Geschlechter und der Krieg der Signale. In *Liebe, Lust und Leidenschaft. Sexualäty im Spiegelder Wissenschaft.* B. Kanitscheider (Ed.). Stuttgart: Herzel, 1997, pp. 91–120.

Herz, R.S., and Cahill, E.D. Differential use of sensory information in sexual behavior as a function of gender. *Human Nature* 8:275–286, 1997.

Hill, K., and Hurtado, A.M. *Ache Life History.* New York: Aldine de Gruyter, 1996.

Hrdy, S.B. *The Woman that Never Evolved.* Cambridge: Harvard University Press, 1981.

Jöchle, W. Coitus induced ovulation. *Contraception* 7:523–564, 1973.

Kirkpatrick, M. Good genes and direct selection in the evolution of mating preferences. *Evolution* 50: 2125–2140, 1996.

Kohl, J.V., and Francoeur, R.T. *The Scent of Eros.* New York: Continuum, 1995.

Leung, B., and Forbes, M.R. Fluctuating asymmetry in relation to stress and fitness: effects of trait type as revealed by meta-analysis. *Ecoscience* 3:400–413, 1996.

Livshits, G., and Kobyliansky, E. Fluctuating asymmetry as a possible measure of developmental homeostasis in humans: a review. *Human Biology* 63:441–466, 1991.

Manning, J.T. Fluctuating asymmetry and body weight in men and women: implications for sexual selection. *Ethology and Sociobiology* 16:145–155, 1995.

Manning, J.T., Koukourakis, K., and Brodie, D.A. Fluctuating asymmetry, metabolic rate and sexual selection in human males. *Evolution and Human Behavior* 18:15–21, 1997.

Manning, J.T., Scutt, D., and Lewis-Jones, D.I. Developmental stability, ejaculate size and sperm quality in men. *Evolution and Human Behavior* 19:273–282, 1998.

Møller, A.P. Developmental stability and fitness: a review. *American Naturalist* 149:916–942, 1997.

Møller, A.P. Developmental stability is related to fitness. *Ecology Letters* (in press).

Møller, A.P. Sperm competition and sexual selection. In *Sperm Competition and Sexual Selection.* T.R. Birkhead and A.P. Møller (Eds.). London: Academic Press, 1998, pp. 55–90.

Møller, A.P., and Alatalo, R.V. Good genes effects in sexual selection. *Proceedings of the Royal Society of London B* 266:85–91, 1999.

Møller, A.P., and Pagel, M. Developmental stability and signaling among cells. *Journal of Theoretical Biology* 193:497–506, 1998.

Møller, A.P., and Swaddle, J.P. *Asymmetry, Developmental Stability and Evolution.* Oxford: Oxford University Press, 1997.

Møller, A.P., and Thornhill, R. A meta-analysis of the heritability of developmental stability. *Journal of Evolutionary Biology* 10:1–16, 1997a.

Møller, A.P., and Thornhill, R. Developmental stability is heritable. *Journal of Evolutionary Biology* 10: 69–76, 1997b.

Møller, A.P., and Thornhill, R. Male parental care, differential parental investment by females, and sexual selection. *Animal Behaviour* 55:1507–1515, 1998a.

Møller, A.P., and Thornhill, R. Bilateral symmetry and sexual selection: a meta-analysis. *American Naturalist* 151:174–192, 1998b.

Ober, C., Weitkamp, L.R., Cox, N., Dytch, H., Kostyu, D., and Elias, S. HLA and mate choice in humans. *American Journal of Human Genetics* 61:497–504, 1997.

Pagel, M. Honest signalling among gametes. *Nature* 363:539–541, 1993.

Pause, B.M., Sojka, B., Krauel, K., Fehmwolfsdorf, G., and Ferstl, R. Olfactory information-processing during the course of the menstrual cycle. *Biological Psychology* 44:31–54, 1996.

Penn, D., and Potts, W.K. Chemical signals and parasite-mediated sexual selection. *Trends in Ecology and Evolution* 13:391–396, 1998.

Petrie, M., Doums, C., and Møller, A.P. The degree of extra-pair paternity increases with genetic variance. *Proceedings National Academy of Sciences* 95:9390–9395, 1998.

Petrie, M., and Kempenaers, B. Extra-pair paternity in birds: explaining variation between species and populations. *Trends in Ecology and Evolution* 13:52–58, 1998.

Pomiankowski, A., and Møller, A.P. A resolution of the lek paradox. *Proceedings Royal Society of London B* 260:21–29, 1995.

Regan, P.C. Rhythms of desire: the association between menstrual cycle phases and female sexual desire. *Canadian Journal of Human Sexuality* 5:145–156, 1996.

Regan, P.C., and Berscheid, E. Gender differences in beliefs about the causes of male and female sexual desire. *Personal Relations* 2:345–358, 1995.

Rice, W.R., and Gaines, S.D. "Heads I win, tails you lose": testing directional alternative hypotheses in ecological and evolutionary research. *Trends in Ecology and Evolution* 9:235–237, 1994.

Rikowski, A., and Grammer, K. Human body odour, symmetry, and attractiveness. Abstract of paper presented at 14th Biennial Conference of the International Society of Human Ethology, Vancouver, B.C., August 19–23, 1998.

Schaal, B., and Porter, R.H. "Microsmatic humans" revisited: the generation and perception of chemical signals. *Advances in the Study of Behavior* 20:135–199, 1991.

Shackelford, T.K., and Larsen, R.J. Facial asymmetry as indicator of psychological, emotional, and physiological distress. *Journal of Personality and Social Psychology* 72:456–466, 1997.

Smuts, B.B., and Smuts, R.W. Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior* 22:1–63, 1993.

Stern, K., and McClintock, M.K. Regulation of ovulation by human pheromones. *Nature* 392:177–179, 1998.

Swaddle, J.P., Witter, M.S., and Cuthill, I.C. The analysis of fluctuating asymmetry. *Animal Behaviour* 48:986–989, 1994.

Symons, D. *The Evolution of Human Sexuality.* Oxford: Oxford University Press, 1979.

Thornhill, R. Alternative hypotheses for traits believed to have evolved by sperm competition. In *Sperm Competition and the Evolution of Animal Mating Systems.* R.L. Smith (Ed.). New York: Academic Press, 1984, pp. 151–178.

Thornhill, R. Female preference for the pheromone of males with low fluctuating asymmetry in the Japanese scorpionfly (Panorpa japonica: Mecoptera). *Behavioral Ecology* 3:277–283, 1992.

Thornhill, R., and Alcock, J. *The Evolution of Insect Mating Systems.* Cambridge, MA: Harvard University Press, 1983.

Thornhill, R., and Gangestad, S.W. Human facial beauty: averageness, symmetry, and parasite resistance. *Human Nature* 4:237–270, 1993.

Thornhill, R., and Gangestad, S.W. Fluctuating asymmetry and human sexual behavior. *Psychological Science* 5:297–302, 1994.

Thornhill, R., and Møller, A.P. Developmental stability, disease and medicine. *Biological Reviews* 72: 497–548, 1997.

Thornhill, R., and Møller, A.P. The relative importance of size and asymmetry in sexual selection. *Behavioral Ecology* 9:546–551, 1998.

Thornhill, R., Gangestad, S.W., and Comer, R. Human female orgasm and mate fluctuating asymmetry. *Animal Behaviour* 50:1601–1615, 1995.

Trivers, R.L. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man.* B. Campbell (Ed.). Chicago: Aldine Publishing Company, 1972, pp. 136–179.

Vierling, J.S., and Rock, J. Variations in olfactory sensitivity to exaltolide during the menstrual cycle. *Journal of Applied Physiology* 22:311–315, 1967.

Vroon, P. *Smell: The Secret Seducer.* English Translation of 1994 Dutch edition. New York: Farrar, Straus and Giroux, 1997.

Wedekind, C. Detailed information about parasites as revealed by sexual ornamentation. *Proceedings Royal Society of London B* 247:169–174, 1992.

Wedekind, C., and Füri, S. Body odor preference in men and women: do they aim for specific MHC combinations or simply heterozygosity? *Proceedings of the Royal Society of London B* 264:1471–1479, 1997.

Wedekind, C., Seebeck, T., Bettens, F., and Paepke, A.J. MHC-dependent mate preferences in humans. *Proceedings Royal Society of London B* 260:245–249, 1995.

Wilkinson, G.S., Presgraves, D.C., and Crymes, L. Male eye span in stalk-eyed flies indicates genetic quality by meiotic drive suppression. *Nature* 391:276–279, 1998.

Williams, G.C. *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought.* Princeton: Princeton University Press, 1966.

Wilson, M., and Daly, M. The man who mistook his wife for a chattel. In *The Adapted Mind: Evolutionary Psychology and the Generation of Culture.* J.H. Barkow, L. Cosmides, and J. Tooby (Eds.). Oxford, UK: Oxford University Press, 1992, pp. 289–326.

Zahavi, A. Mate selection—a selection for a handicap. *Journal of Theoretical Biology* 53:205–214, 1975.

Zahavi, A., and Zahavi, A. *The Handicap Principle.* Oxford: Oxford University Press, 1997.