Ovulatory shifts in human female ornamentation: Near ovulation, women dress to impress

Martie G. Haselton [a,*], Mina Mortezaie [a], Elizabeth G. Pillsworth [b],
April Bleske-Rechek [c], David A. Frederick [d]

[a] Center for Behavior Evolution and Culture, Communication Studies and Department of Psychology, University of California, 2302 Rolfe Hall,
Los Angeles, CA, 90095, USA
[b] Center for Behavior Evolution and Culture and Department of Anthropology, University of California, Los Angeles, USA
[c] Department of Psychology, University of Wisconsin-Eau Claire, USA
[d] FPR-UCLA Center for Culture, Brain, and Development and Department of Psychology, University of California, Los Angeles, USA

Abstract

Humans differ from many other primates in the apparent absence of obvious advertisements of fertility within the ovulatory cycle. However, recent studies demonstrate increases in women's sexual motivation near ovulation, raising the question of whether human ovulation could be marked by observable changes in overt behavior. Using a sample of 30 partnered women photographed at high and low fertility cycle phases, we show that readily-observable behaviors – self-grooming and ornamentation through attractive choice of dress – increase during the fertile phase of the ovulatory cycle. At above-chance levels, 42 judges selected photographs of women in their fertile (59.5%) rather than luteal phase (40.5%) as "trying to look more attractive." Moreover, the closer women were to ovulation when photographed in the fertile window, the more frequently their fertile photograph was chosen. Although an emerging literature indicates a variety of changes in women across the cycle, the ornamentation effect is striking in both its magnitude and its status as an overt behavioral difference that can be easily observed by others. It may help explain the previously documented finding that men's mate retention efforts increase as their partners approach ovulation.
© 2006 Elsevier Inc. All rights reserved.

Keywords: Attractiveness; Clothing; Menstrual cycle; Ovulation; Sexual communication

One of the most noteworthy differences between humans and other closely related primates is the absence of clear advertisements of fertility within the ovulatory cycle (Dixson, 1998). Recent evidence has suggested, however, that there are subtle ovulatory cues in humans. Roberts et al. (2004) showed facial photographs of women taken during the follicular and luteal phases to male and female judges. On average, follicular phase images were judged more attractive approximately 54% of the time. Similarly, relative to those from other cycle phases, women's body scents near ovulation are judged as more attractive by men (Doty et al., 1975; Singh and Bronstad, 2001; Thornhill et al., 2003) and women's sexual desires vary across the cycle (Bullivant et al., 2004; Gangestad et al., 2002;

Haselton and Gangestad, 2006). Thus, human ovulation may not be completely concealed.

In the last decade, the literature on cyclic shifts in women's social motivations has grown rapidly. For ancestral women, the time required to collect food could have been considerable; thus, Fessler (2003) reasoned that there likely were tradeoffs across the cycle between feeding and other activities such as mating. Fessler (2003) compiled and reviewed evidence that women's appetites decrease near ovulation, and he hypothesized that this decrease in appetite at high fertility reflects an adaptation in women designed to decrease the motivational salience of goals that compete with efforts devoted to mating. As additional evidence supporting the hypothesis, Fessler reviewed studies showing that women's ranging activities, such as locomotion and volunteering for social activities, tend to increase near ovulation.

Other lines of evidence also indicate cyclic shifts in women's mating motivations. In a daily report study, Haselton and

---

Gangestad (2006) found that on high fertility days of the cycle women report a greater desire to go to clubs and parties where they might meet men. Macrae et al. (2002) found that women's ability to categorize male faces and male stereotypic words is faster near ovulation, suggesting increased attentiveness to "maleness" at high fertility. Other research shows that women's preferences for masculine features (e.g., masculine facial structure) increase near ovulation (reviewed in Gangestad et al., 2005a). Several rigorous within-subjects studies have found that women's attraction to and flirtation with men other than their primary partner is higher near ovulation than in other phases of the cycle (Gangestad et al., 2002; Haselton and Gangestad, 2006; also see Bullivant et al., 2004). Finally, Fisher (2004) found that women tested near midcycle, compared with those tested in other cycle phases, tend to give lower attractiveness ratings to photographs of female faces—an effect Fisher interpreted as evidence that women are more intra-sexually competitive near ovulation. In sum, a variety of data sources indicate that women's social motivations – in particular, their sexual motivations – increase near ovulation.

Hypothesis: ovulation and ornamentation

We hypothesize that changes in women's motivations manifest themselves in changes in *self-ornamentation* through attentive personal grooming and attractive choice of dress. Ornamentation in non-humans, including bright plumage, long tails, and large bodies, is generally presumed to be the product of sexual selection (Andersson, 1994). These traits are effective in attracting mates, either because they indicate fitness (e.g., due to costs of their maintenance) or due to pre-existing sensory biases (Daly and Wilson, 1983; Parsons, 1995; Zahavi, 1975). Although rare, animals occasionally employ behavioral orna-mentation, as opposed to morphological ornamentation, in the effort to attract mates. Male bowerbirds, for example, found in Australia and New Guinea, build elaborate structures ornamen-ted with brightly colored flowers and fruits in order to attract mates. Male bowerbirds will often also pick up a brightly colored object in their beaks while displaying to a female, thus effectively ornamenting themselves (Diamond, 1982; Gilliard, 1969). The purpose of these traits, both morphological and behavioral, is to attract reproductive partners, and animals do not expend energy producing these displays when mating is not likely. The bowerbird dismantles its bower and abandons its territory during the non-breeding months (Pruett-Jones and Pruett-Jones, 1982), and even birds that rely on morphological ornamentation, such as brightly colored feathers or bills, may exhibit sexual dimorphism only seasonally (Badyaev and Duckworth, 2003; Peters et al., 2004).

In humans too, ornamentation may serve the purpose of attracting mates, at least in part. In a recent study, Grammer et al. (2005) interviewed women at a discotheque; those who rated their clothing as "sexy" and "bold" also reported that their intention for the evening was to flirt or find a sex partner. Although the direction of causality is unclear, these findings suggest that women's clothing choices are linked with their motivations.

Prior research also has shown that men's behaviors toward their partners shift across the cycle. Three studies have shown that, in the fertile relative to the luteal phase of the cycle, men are more attentive and loving toward their partners (Gangestad et al., 2002; Haselton and Gangestad, 2006; Pillsworth and Haselton, 2006) and two have shown that men are more jealous and possessive (Gangestad et al., 2002; Haselton and Gang-estad, 2006). It is not yet known what cues drive these changes in men's behavior. One possibility is that men attend to differences in female behavior. For example, Haselton and Gangestad (2006) and Gangestad et al. (2002) found that women's reports of flirtatiousness with men other than their primary partner were higher when assessed during the late follicular as compared with the luteal phase of the cycle. In both studies, ovulatory increases in flirtatiousness statistically predicted ovulatory increases in male mate retention effort but did not fully account for them, leaving open the possibility that other ovulatory cues affect men's behavior—including the ornamentation effect we predict.

In this study, we measure an overt, readily observable behavior in women that we propose will be linked with ovulation. Specifically, we predict that women engage in self-ornamentation during the high fertility phase of the ovulatory cycle, thus placing themselves in the foreground of the social array.

Method

Procedure: photographic stimuli

Thirty women from the UCLA campus (mean age=21.07 years old; SD=2.35; range 18–37) posed for two standing full-body digital photographs with their hands placed at their sides (Canon PowerShot S410, 4.0 Megapixels). Women identified themselves as African American ($n=1$), Asian American ($n=10$), Caucasian ($n=6$), Hispanic/Latino ($n=7$), and mixed race or "other" ($n=6$). One photograph was taken on a high fertility day of the cycle (follicular phase) and one on a low fertility day of the cycle (luteal phase). Photographs were taken in the same location under standardized lighting conditions against a plain blue background. All women reported regular menstrual cycles (ranging between 26 and 35 days), were partnered (involved in a "committed romantic relationship" with a man), and none had used oral or other hormonal contraceptives within the last three months. Because previous studies have found stronger ovulatory effects in partnered than in non-partnered women (e.g., Havlicek et al., 2005; Pillsworth et al., 2004), we limited our investigation to partnered women.

Session scheduling and luteinizing hormone (LH) testing were conducted using the procedures described in Gangestad et al. (2002). There were three sessions—an initial session for cycle history assessment and scheduling and subsequent high and low fertility sessions. After initial sessions, women were scheduled to return for the next possible session (low or high) given their current cycle day. Low fertility sessions were scheduled to occur 4–10 days prior to the estimated day of next menstrual onset. Actual menstrual onset was reported by 66.7% of women after their low fertility session; for the balance of participants, menstrual onset was estimated using cycle length and the last date of menstrual onset. On average, based on these information sources, low fertility sessions took place 5.87 days prior to menses (SD=2.5; three women participated within 48 h of menstrual onset and possibly could have experienced premenstrual symptoms; therefore, days-to-menstrual-onset is included in the analyses presented below). High fertility sessions were scheduled to occur 15–17 days prior to the next estimated menstrual onset. Participants also reported to the laboratory to complete urine tests beginning two days prior to their high fertility session and continuing for three days after this session or until an LH surge was detected. Using an unmarked commercially available urinary stick ovulation test

(Clearblue™), all women were judged to have an LH surge between three days after and two days before their high fertility session. An LH surge typically proceeds ovulation by 24–48 h (Guermandi et al., 2001); thus, all women were likely to be near ovulation during their high fertility session. Within the fertile window of the cycle, conception risk increases as ovulation approaches (Wilcox et al., 1995). We therefore estimated days-to-ovulation (by adding two to days-to-LH surge; mean=3.03, SD=1.40) and included this estimate in the analyses reported below.

These 30 women were a subset of 58 originally recruited for the study. Women ineligible for inclusion in the study either showed no evidence of an LH surge (n=4), were rescheduled for low fertility sessions (due to their own time constraints) on days falling outside of the range of the luteal phase days (n=3), did not consent to having photos taken (n=7), consented to having their photos taken but did not consent to having their photos judged by people other than the researchers (n=7), or did not complete all sessions (n=7). There were no significant differences in relationship satisfaction, sociosexuality (Simpson and Gangestad, 1991), age, or relationship length between women retained in the study and those who were ineligible.

Participants were blind to the purpose of the study. They were told that the study examined health, personality, and sexuality, and that the urine tests examined "normal body chemistry." They were told that the photographs were being taken to assess attractiveness and the accuracy of independent raters' perceptions of their personality based on photographs alone; photographs were taken in each session ostensibly for reliability purposes. In the initial session, participants completed questionnaires that included information on sexuality and personality, thus justifying our description of the purposes of the study. In extensive debriefing, none guessed that the purpose of the study was to examine changes in clothing or attractiveness across the menstrual cycle.

To prevent any impact of variation in facial expression or facial appearance on ornamentation judgments, oval masks obscuring the entire face were applied to the photographs, leaving visible only hairstyle, jewelry, and clothing from head to toe.

Judges and experimental procedure

Judges were volunteers recruited by word of mouth (17 men and 25 women) from the UCLA and University of Wisconsin-Eau Claire campuses. Judges reported their ages by checking categories in a questionnaire: 28 were between 18 and 23 years old, seven were between 24 and 30, three were between 31 and 40, and two were 41 or older. All were blind to the fertility status of the photographs.

Image pairs were judged using a computer-based survey program (SurveyConsole™; http://www.surveyconsole.com/) that randomized the order of presentation of the 30 pairs and, within each pair, randomized the image (high vs. low fertility) presented on the left side of the screen. Judges were sent a unique Internet address link to the survey. Image sizes varied somewhat among judges depending on the size of the computer monitor used, with an approximate range of 4–6 in. high and 1.25–2 in. wide. For each set of images judges were asked, "In which photo is the person trying to look more attractive?" Judges mouse-clicked a box next to their choice. Judgments were made using this computer-based method to ensure that the fertility status of the photograph appearing on the right vs. the left side of the screen was random, thus ruling out the possibility that the lateral placement of high fertility images could not account for any effects we observed.

Results and discussion

We calculated scores for each woman by summing male and female judges' choices of her high fertility image and converting it to a percentage. Thus, a woman whose high fertility photo was chosen by all judges would receive a score of 100%. There was high inter-judge agreement about whether each woman's high or low fertility photograph was the one in which she was trying to look more attractive (agreement among male judges, $\alpha=0.86$; agreement among female judges, $\alpha=0.94$). We conducted a repeated measures analysis (General

Linear Models, SPSS 12.0) using photographed women as units of analysis (for information about judges as units of analysis, see below). To examine whether choices of high fertility images differed by sex of judge, sex of judge was a repeated factor (scores based on percent of male judges selecting the participant's high fertility photo vs. scores based on percent of female judges selecting a participant's high fertility photo). Days-to-ovulation (days from the date of a woman's high fertility photograph to ovulation) and days-to-menstrual-onset (days from the date of a woman's low fertility photograph to menstrual onset) were covariates.

This analysis includes a test of whether the overall marginal mean score (adjusted for covariates) differs from zero (a test of the intercept). We used this test to assess whether women's overall scores differed from chance (50% high fertility choices). To do this, we unit-transformed women's scores by subtracting 50% before conducting the analysis. The test of the intercept tells us whether the remainder is significantly above 0% (reflecting chance in the transformed scores). In the analysis, days-to-menstrual-onset was zero-centered, whereas days-to-ovulation was not transformed. Therefore, the effect of fertility status (testing whether a woman's score was above chance) was estimated at the average of days prior to menstrual onset (roughly a mid-luteal phase day of the cycle) and at the day of ovulation. Scores were above chance, $F(1, 27)=7.06$, $p=0.013$ (mean=59.5%; SEM=5%).

There also was an effect of days-to-ovulation, $F(1, 27)=4.25$, $p=0.049$, such that, within the fertile window, women who were photographed closer to the day of ovulation had higher scores (see Fig. 1). There was no effect of days-to-menstrual onset on women's scores, $F(1, 27)=0.01$, NS. Male and female judges' scores did not differ, nor did sex of judge interact with days-to-ovulation ($F[1, 27]=0.66$, NS; $F[1, 27]=2.59$, NS, respectively). There was an interaction of sex of judge and days-to-menstrual-onset, $F(1, 27)=5.97$, $p=0.021$; although neither simple effect was significant ($ps>0.50$), male judges tended to choose high fertility images more as women neared menses in their low fertility session, whereas the opposite was true for female judges.

In the facial attractiveness study noted in the introduction, Roberts et al. (2004) performed analyses treating judges as units of analysis rather than the photographed women as units of analysis as we have done. An analysis treating each judge as the unit of analysis would not permit generalization of an ovulatory cycle effect to the population from which our sample was drawn–the population of possible high vs. low fertility photographs–which is the primary population of interest. Rather, such an analysis examines whether results can be generalized to the population from which the judges were drawn. Nonetheless, analyses treating judges as units of analysis generated highly significant results.

The results support our prediction that women engage in active ornamentation, potentially in an attempt to appear more attractive, during the high fertility phase of the ovulatory cycle. Our inspection of the photographs suggested that this effect manifested itself in varied ways, some more obvious than others. For example, two women who dressed similarly in each session
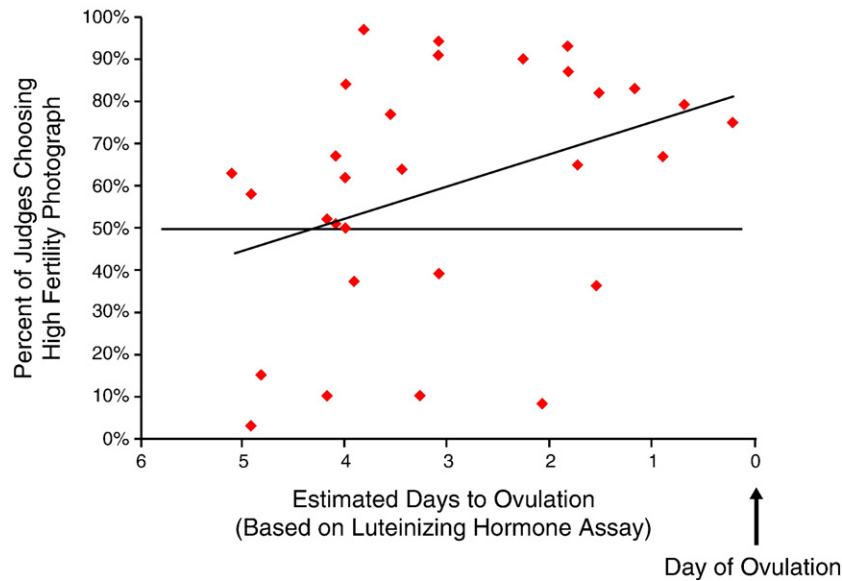
Fig. 1. Association between a woman's estimated number of days from ovulation when her high fertility photograph was taken and the percent of judges selecting it (controlling for the number of days between a woman's low fertility session and the date of next menstrual onset), partial $r(27)=0.37$, $p=0.049$.

wore tops with lace trim at high fertility; three wore skirts instead of pants; one woman added a fringy neck scarf; and several women simply showed more skin.

To systematically examine these ornamentation differences, three female research assistants coded the photographs by making eight qualitative assessments related to ornamentation (see Table 1). All coders were blind to the fertility status of the photographs. Two made initial assessments and the third resolved discrepancies. Coders were asked to indicate, for example, the photo in which the woman wore "more fashionable clothing" or "showed more skin" (possible responses: right photo, left photo, or no difference). Given low cell counts for some high versus low fertility comparisons (e.g., wearing a skirt in one session but not the other, high fertility = 3 women; low fertility = 0 women), and given that we had already conducted statistical comparisons of the high and low fertility photographs, we did not conduct statistical tests on

Table 1
Differences in women's clothing choices across high and low fertility photographs

Judgment (percent concordance of judges' codes)	High fertility	Low fertility
Wearing "more fashionable clothes" (70%)	18	8
Wearing "nicer clothes" (77%)	17	8
Showing more skin (upper body) (77%)	11	6
Showing more skin (lower body) (93%)	7	5
Wearing "sexier clothes" (70%)	6	7
Wearing more "accessories" (63%)	6	7
Wearing a skirt in one session but not other (100%)	3	0
Wearing a lacy top (80%)	3	1

Values represent counts within each category. High and low fertility values do not sum to 30 because judges did not perceive a difference between all photographs on each dimension (e.g., 4 out of 30 photo pairs were not judged to differ on wearing "more fashionable clothes"). Percent concordance is the agreement between two female judges before the third female judge resolved discrepancies.

these secondary codings. The results, however, are clear. High fertility clothing choices were coded as "more fashionable," "nicer," and showing more skin. Although women revealed more skin, clothing choices were not coded as "sexier" at high fertility, which could reflect norms of daytime student dress, in which sexually explicit clothing is not appropriate. Alternatively, the effect we have documented might reveal a general desire to look more attractive rather than to appear "sexy."

As shown in Fig. 1, women who were photographed closer to ovulation, as indicated by the LH assay, had their high fertility photo chosen more often by judges. This demonstrates that choices of fertile images are due to differences attributable to changes in body chemistry related to ovulation and not due to differences attributable to proximity to menses (where, although there was substantial variation in proximity to menses in the low fertility session, there was no hint of an association of days-to-menstrual onset with women's scores). Also as shown in Fig. 1, four fertile phase photos are notable because more than 90% of judges did *not* choose them. These data demonstrate that dress is influenced, of course, by more than cycle phase. A variety of external constraints (e.g., whether a woman rushed to campus for an exam or had a job interview on the day in question) affect clothing choices as well. Given these constraints, the relatively large difference between judges' choices of high and low fertility images (59.5% vs. 41.5%) is impressive.

Our results support a similar prediction made by Grammer et al. (2005) that women at a discotheque would display more skin when in the fertile phase of the cycle. Grammer et al. (2005) found that women's stated sexual motivation was linked to the revealingness of the clothing they wore to the discotheque but did not find compelling evidence of an ovulatory effect. In some analyses, Grammer et al. found evidence that estradiol was correlated with clothing revealingness. However, because estradiol varies more between women than within women (Gann et al., 2001; Ferrell et al., 2005), and shows a secondary

peak after ovulation (e.g., Alliende, 2002), estradiol levels cannot be used to assess cycle phase in cross-sectional studies (cf. DeBruine et al., 2005). Grammer's results may reflect trait-level estrogen effects, as estrogen is associated with factors relevant to female mating strategies, such as attractiveness (Fink and Penton-Voak, 2002; Law Smith et al., 2006) and age (Ferrell et al., 2005).

There are several competing explanations for the link between ovulation and clothing choices that we have documented. First, emerging evidence indicates that women become subtly more attractive near ovulation (e.g., Roberts et al., 2004; Singh and Bronstad, 2001; Thornhill et al., 2003). It is possible that women are sensitive to cyclic changes in their own physical attractiveness (Haselton and Gangestad, 2006), and they may choose to display their attributes through ornamentation that can result in any of a variety of attractiveness-related benefits, including esteem in the eyes of peers and increased attention from men (Langlois et al., 2000).

Second, as outlined in the introduction, women's mating motivations vary across the cycle (e.g., Bullivant et al., 2004; Fessler, 2003; Gangestad et al., 2002; Haselton and Gangestad, 2006). Thus, women may engage in ornamentation to attract mates. It is possible, in particular, that women may be aiming to attract mates *other than* their primary partners in order to gain access to good genes. Several rigorous within-subjects studies have found increases in women's desires for men other than their primary partner at high fertility (Gangestad et al., 2002, 2005b; Haselton and Gangestad, 2006; Pillsworth and Haselton, 2006), but no changes in desires for the primary partner (Gangestad et al., 2002, 2005b; Pillsworth and Haselton, 2006). Three studies show that increases in extra-pair attractions at high fertility are greatest for women who could, in theory, gain the most from extra-pair mating for genetic benefits, specifically women whose primary mates are relatively asymmetrical (Gangestad et al., 2005b) or lacking sexual attractiveness (Haselton and Gangestad, 2006; Pillsworth and Haselton, 2006). Preliminary evidence also suggests that women are intrasexually competitive near ovulation (Fisher, 2004), possibly because this is the time at which the costs and benefits of mating decisions are greatest (Fessler, 2003). Thus, near ovulation, women may also be competing with other women for the best mating opportunities.

In addition to these possibilities, changes in style of dress could reflect more general changes across the cycle, such as changes in mood. The evidence of cyclic changes in mood is mixed. Some studies show changes that are limited to or most prominent in women with premenstrual syndrome (Metcalf and Livesey, 1995; Sanders et al., 1983; also see Bäckström, 1983). Other studies fail to find any significant changes in mood across the cycle (e.g., Laessle et al., 1990; Van Goozen et al., 1997; Lahmeyer et al., 1982; Patkai et al., 1974). Several studies have shown that changes in mood across the cycle may be attributable to women's expectancies (leading to biased self-reporting) rather than genuine effects of the cycle on mood (e.g., Olasov and Jackson, 1987; Weidner and Helmig, 1990; also see Ruble, 1977). To the extent that mood effects are real, most evidence points to increases in negative affect as menstrual onset

approaches (e.g., Bäckström, 1983; Dennerstein and Burrows, 1979; Sanders et al., 1983; Van Goozen et al., 1997). If changes in mood are responsible for differences in women's style of dress from high to low fertility, one might naturally expect an increase in judges' choices of high fertility images for women whose low fertility photographs were taken closer to the day of menstrual onset, which we examined but did not find. Rather, the effects appear to be driven by proximity to ovulation.

Women also may become more sociable in general near ovulation. For example, although evidence is somewhat mixed (see Fessler, 2003) several studies suggest that women engage in more locomotor behavior near ovulation (measured using pedometers). If ovulation leads women to feel more sociable, they may also attend more to personal grooming and style of dress.

The ornamentation effect could be explained by some combination of the factors we have described. The mood and sociability effects, for example, could be the proximal psychological motives that underpin mating functions of attempting to appear more attractive. Indeed, Fessler (2003) proposed that evidence of periovulatory decreases in feeding behavior reflect adaptations for reducing the motivational salience of activities that compete directly or indirectly with mating, and periovulatory increases in social behavior reflect increased effort allocated to mating activities.

Each of the causal pathways we have outlined above can be tested in future research. For example, the proposal that ornamentation differences are directed toward extra-pair mates could be tested by examining whether partnered women show the effect more than unpartnered women and by examining whether the effect is attenuated among women whose long-term mates are attractive and symmetrical. The intrasexual competition function could be tested by subtly leading women to anticipate that their laboratory sessions will involve other female participants (intrasexual competitors) and will be run by highly attractive male experimenters.

Regardless of what underlying motivations or evolved functions are tied to the ornamentation effect, our results appear to provide strong objective evidence of changes in women's overt, observable behaviors associated with ovulation. In contrast to subtle changes in facial appearance (Roberts et al., 2004) and body scents (Doty et al., 1975; Singh and Bronstad, 2001; Thornhill et al., 2003), variation in women's self-grooming and ornamentation behaviors are perhaps the most readily available cues to ovulation and associated shifts in female motivation available to male partners. They may therefore be responsible, in part, for changes in relationship dynamics across the cycle, such as ovulatory increases in men's mate retention efforts (Gangestad et al., 2002; Haselton and Gangestad, 2006; Pillsworth and Haselton, 2006). The ornamentation effect is one of the most striking pieces of evidence that ovulation in humans is not fully concealed.

Acknowledgments

References

Alliende, M.E., 2002. Mean versus individual hormonal profiles in the menstrual cycle. Fertil. Steril. 78, 90–95.

Andersson, M.B., 1994. Sexual Selection. Princeton Univ. Press, Princeton.

Bäckström, T., 1983. Mood, sexuality, hormones, and the menstrual cycle: II. hormone levels and their relationship to the premenstrual syndrome. Psychosom. Med. 45, 503–507.

Badyaev, A.V., Duckworth, R.A., 2003. Context-dependent sexual advertisement: plasticity in development of sexual ornamentation throughout the lifetime of a passerine bird. J. Evol. Biol. 16, 1065–1076.

Bullivant, S.B., Sellergren, S.A., Stern, K., Spencer, N.A., Jacob, S., Mennella, J.A., McClintock, M.K., 2004. Women's sexual experience during the menstrual cycle: identification of the sexual phase by noninvasive measurement of luteinizing hormone. J. Sex Res. 41, 82–93.

Daly, M., Wilson, M., 1983. Sex, Evolution, and Behavior, 2nd ed. Willard Grant Press, Boston.

DeBruine, L.M., Jones, B.C., Perrett, D.I., 2005. Women's attractiveness judgments of self-resembling faces change across the menstrual cycle. Horm. Behav. 47, 379–383.

Dennerstein, L., Burrows, G.D., 1979. Affect and the menstrual cycle. J. Affective Disord. 1, 77–92.

Diamond, J.M., 1982. Evolution of bowerbirds' bowers: animal origins of the aesthetic sense. Nature 297, 99–102.

Dixson, A., 1998. Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes, and Human Beings. Oxford Univ. Press, New York.

Doty, R.L., Ford, M., Preti, G., Huggins, G.R., 1975. Changes in the intensity and pleasantness of human vaginal odors during the menstrual cycle. Science 190, 1316–1317.

Ferrell, R.J., O'connor, K.A., Rodriguez, G., Gorrindo, T., Holman, D.J., Brindle, E., Miller, R.C., Schechter, D.E., Korshalla, L., Simon, J.A., Mansfield, P.K., Wood, J.W., Weinstein, M., 2005. Monitoring reproductive aging in a 5-year prospective study: aggregate and individual changes in steroid hormones and menstrual cycle lengths with age. Menopause 12, 567–577.

Fessler, D.M.T., 2003. No time to eat: an adaptationist account of periovulatory behavioural changes. Q. Rev. Biol. 78, 3–21.

Fink, B., Penton-Voak, I.S., 2002. Evolutionary psychology of facial attractiveness. Curr. Dir. Psychol. Sci. 11, 154–158.

Fisher, M.L., 2004. Female intrasexual competition decreases female facial attractiveness. Proc. Biol. Sci. (Suppl.) 271, 283–285.

Gangestad, S.W., Thornhill, R., Garver, C., 2002. Changes in women's sexual interests and their partners' mate retention tactics across the menstrual cycle: evidence for shifting conflicts of interest. Proc. R. Soc. London, B 269, 975–982.

Gangestad, S.W., Thornhill, R., Garver-Apgar, C.E., 2005a. Adaptations to ovulation. In: Buss, D.M. (Ed.), The Handbook of Evolutionary Psychology. John Wiley and Sons, Hoboken, NJ, pp. 344–371.

Gangestad, S.W., Thornhill, R., Garver-Apgar, C.E., 2005b. Women's sexual interests across the ovulatory cycle depend on primary partner fluctuating asymmetry. Proc. R. Soc. London, B 272, 2023–2027.

Gann, P.H., Giovanazzi, S., Van Horn, L., Branning, A., Chatterton, R.T., 2001. Saliva as a medium for investigating intra- and interindividual differences in sex hormone levels in premenopausal women. Cancer Epidemiol., Biomarkers Prev. 1, 59–64.

Grammer, K., Renninger, L., Fischer, B., 2005. Disco clothing, female sexual motivation, and relationship status: is she dressed to impress? J. Sex Res. 41, 66–74.

Gilliard, E.T., 1969. Birds of Paradise and Bower Birds. Natural History Press, Garden City.

Guermandi, E., Vegetti, W., Bianchi, M.M., Uglietti, A., Ragni, G., Crosignani, P., 2001. Reliability of ovulation tests in infertile women. Obstet. Gynecol. 97, 92–96.

Haselton, M.G., Gangestad, S.W., 2006. Conditional expression of women's desires and men's mate guarding across the ovulatory cycle. Horm. Behav. 49, 509–518.

Havlicek, J., Roberts, S.C., Flegr, J., 2005. Women's preference for dominant male odour: effects of menstrual cycle and relationship status. Biol. Lett. 1, 256–259.

Laessle, R.G., Tuschl, R.J., Schweiger, U., Pirke, K.M., 1990. Mood changes and physical complaints during the normal menstrual cycle in healthy young women. Psychoneuroendocrinology 15, 131–138.

Lahmeyer, H.W., Miller, M., DeLeon-Jones, F., 1982. Anxiety and mood fluctuation during the normal menstrual cycle. Psychosom. Med. 44, 183–194.

Langlois, J.H., Kalakanis, L., Rubenstein, A.J., Larson, A., Hallam, M., Smoot, M., 2000. Maxims or myths of beauty? A meta-analytic and theoretical review. Psychol. Bull. 126, 390–423.

Law Smith, M.J., Perrett, D.I., Jones, B.C., Cornwell, R.E., Moore, F.R., Feinberg, D.R., Boothroyd, L.G., Stirrat, M.R., Whiten, S., Pitman, R.M., Hillier, S.G., 2006. Facial appearance is a cue to reproductive hormone levels in women. Proc. R. Soc. London, B 273 (1583), 135–140.

Macrae, C.N., Alnwick, K.A., Milne, A.B., Schloerscheidt, A.M., 2002. Person perception across the menstrual cycle: hormonal influences on social-cognitive functioning. Psychol. Sci. 13, 532–536.

Metcalf, M.G., Livesey, J.H., 1995. Distribution of positive moods in women with the premenstrual syndrome and in normal women. J. Psychosom. Res. 39, 609–618.

Olasov, B., Jackson, J., 1987. Effects of expectancies on women's reports of moods during the menstrual cycle. Psychosomatic Med. 49, 65–78.

Parsons, P.A., 1995. Stress and limits to adaptation: sexual ornaments. J. Evol. Biol. 8, 455–461.

Patkai, P., Johannson, G., Post, B., 1974. Mood, alertness and sympathetic-adrenal medullary activity during the menstrual cycle. Psychosomatic Med. 36, 503–512.

Peters, A., Denk, A.G., Delhey, K., Kempenaers, B., 2004. Carotenoid-based bill colour as an indicator of immunocompetence and sperm performance in male mallards. J. Evol. Biol. 17, 1111–1120.

Pillsworth, E.G., Haselton, M.G., 2006. Male sexual attractiveness predicts differential ovulatory shifts in female extra-pair attraction and male mate retention. Evol. Hum. Behav. 27, 247–258.

Pillsworth, E.G., Haselton, M.G., Buss, D.M., 2004. Ovulatory shifts in female sexual desire. J. Sex Res. 41, 55–65.

Pruett-Jones, M.A., Pruett-Jones, S.G., 1982. Spacing and distribution of bowers in Macgregor's bowerbird (*Amblyornis macgregoriae*). Behav. Ecol. Sociobiol. 11, 25–32.

Roberts, S.C., Havlicek, J., Flegr, J., Hruskova, M., Little, A.C., Jones, B.C., Perrett, D.I., Petrie, M., 2004. Female facial attractiveness increases during the fertile phase of the menstrual cycle. Proc. R. Soc. London, B (Suppl.) 271, S270–S272.

Ruble, D.N., 1977. Premenstrual symptoms: a reinterpretation. Science 197, 291–292.

Sanders, D., Warner, P., Bäckström, T., Bancroft, J., 1983. Mood, sexuality, hormones and the menstrual cycle: I. changes in mood and physical state: description of subjects and method. Psychosom. Med. 45, 487–501.

Simpson, J.A., Gangestad, S.W., 1991. Individual differences in sociosexuality: evidence for convergent and discriminant validity. J. Pers. Soc. Psy. 60, 870–883.

Singh, D., Bronstad, P.M., 2001. Female body odour is a potential cue to ovulation. Proc. R. Soc. London, B 268, 797–801.

Thornhill, R., Gangestad, S.W., Miller, R., Scheyd, G., McCollough, J.K., Franklin, M., 2003. Major histocompatibility complex genes, symmetry, and body scent attractiveness in men and women. Behav. Ecol. 14, 668–678.

Van Goozen, S.H.M., Wiegant, V.M., Endert, E., Helmond, F.A., 1997. Psychoendocrinological assessment of the menstrual cycle: the relationship between hormones, sexuality, and mood. Arch. Sex. Behav. 26, 359–382.

Weidner, G., Helmig, L., 1990. Cardiovascular stress reactivity and mood during the menstrual cycle. Women Health 16, 5–21.

Wilcox, A.J., Weinberg, C.R., Baird, D.D., 1995. Timing of sexual intercourse in relation to ovulation: effects of probability of conception, survival of pregnancy, and sex of the baby. N. Engl. J. Med. 333, 1517–1521.

Zahavi, A., 1975. Mate selection: a selection for a handicap. J. Theor. Biol. 53, 205–214.