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Body odor attractiveness as a cue of impending ovulation in women: Evidence from a study using hormone-confirmed ovulation

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ABSTRACT

Scent communication plays a central role in the mating behavior of many nonhuman mammals but has often been overlooked in the study of human mating. However, a growing body of evidence suggests that men may perceive women's high-fertility body scents (collected near ovulation) as more attractive than their low-fertility body scents. The present study provides a methodologically rigorous replication of this finding, while also examining several novel questions. Women collected samples of their natural body scent twice — once on a low-fertility day and once on a high-fertility day of the ovulatory cycle. Tests of luteinizing hormone confirmed that women experienced ovulation within two days of their high-fertility session. Men smelled each woman's high- and low-fertility scent samples and completed discrimination and preference tasks. At above-chance levels, men accurately discriminated between women's high- and low-fertility scent samples (61%) and chose women's high-fertility scent samples as more attractive than their low-fertility scent samples (56%). Men also rated each scent sample on sexiness, pleasantness, and intensity, and estimated the physical attractiveness of the woman who had provided the sample. Multilevel modeling revealed that, when high- and low-fertility scent samples were easier to discriminate from each other, high-fertility scent samples received even more favorable ratings compared with low-fertility scent samples. This study builds on a growing body of evidence indicating that men are attracted to cues of impending ovulation in women and raises the intriguing question of whether women's cycling hormones influence men's attraction and sexual approach behavior.

Introduction

The importance of scent communication in mammalian mating behavior is well established. Studies dating back to the 1930s have shown that female body scents produced on high-fertility days of the ovulatory cycle (just preceding and including the day of ovulation) can serve as powerful attractants for males. These scents appear to capture male interest and elicit hormonal and behavioral responses that set the stage for mating. Among rats, mice, hamsters, lemmings, dogs, and many other mammals, males prefer the scents of high-fertility, or *estrous*, females to the scents of low-fertility, or *non-estrous*, females (e.g., Bronson, 1974; Carr, 1974; Doty and Dunbar, 1974; Hayashi and Kimura, 1974; Huck and Banks, 1984; Johnston, 1974; Le Magnen, 1952; Lydell and Doty, 1972). Male hamsters respond to isolated estrous female scents with increased circulating androgen levels (e.g., Pfeiffer and Johnston, 1994), and male rats respond to these scents with a variety of stereotypic mating behaviors (e.g., Sachs, 1997). Moreover, male hamsters, dogs, cattle, sheep, and rhesus macaques have been shown to attempt to copulate with non-estrous and pregnant females, males, and dummies that have been rubbed with estrous female scents. Males do not typically attempt to copulate with these partners in the absence of these added estrous scents (Goodwin et al., 1979; Kelley, 1937; Michael et al., 1971; O'Connell and Meredith, 1984; Paleologou, 1977; Singer et al., 1976). Importantly, male rats and rhesus macaques that have been experimentally rendered incapable of smelling do not exhibit these responses to estrous female scents (e.g., Lumia et al., 1987; Michael and Keverne, 1968). This set of findings is consistent with the notion that natural selection has acted on males to respond favorably to scent cues associated with female fertility and the potential reproductive opportunities these cues reveal.

The human capacity for scent communication has historically been considered weak relative to most other mammal species, resulting in a tendency to overlook the potential role of scent in human mating. However, a growing body of evidence now suggests that men may perceive samples of women's natural body scents collected on high-fertility days of the ovulatory cycle as more pleasant and sexually attractive than samples collected on low-fertility days of the cycle (Doty et al.,

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1975; Havlíček et al., 2006; Kuukasjärvi et al., 2004; Poran, 1994; Singh and Bronstad, 2001; Thornhill et al., 2003; but see Thornhill and Gangestad, 1999). These studies have helped to reinvigorate scientific interest in human scent communication by raising the intriguing question of whether men can, at some level, detect ovulation through women's body odors (for a review of evidence for cues of ovulation across scent and other modalities, see Haselton and Gildersleeve, 2011).

No study to date has provided a definitive answer to this question. Of those studies that have examined men's attraction to women's high- versus low-fertility body scents, none has included a hormonal verification of ovulation. Instead, previous studies have relied on women's self-reported cycle dates (e.g., retrospectively recalled date of last menstrual onset) to estimate ovulatory cycle position. Other work has shown that these self-report methods tend to introduce error into cycle position estimates, as evidenced by a high percentage of participants failing to show hormonal evidence of ovulation within their expected high-fertility window (e.g., 28%, Durante et al., 2008; 39%, Gangestad et al., 2002).

In addition, several previous studies in this line of work are limited by small samples of women ($N=4$, Doty et al., 1975; $N=12$, Havlíček et al., 2006; $N=17$ in Study 1 and $N=4$ in Study 2, Singh and Bronstad, 2001). And as a consequence, two of these studies performed statistical analyses that treated men (raters), rather than women (scent donors), as units of analysis (Doty et al., 1975; Singh and Bronstad, 2001). When raters are treated as units of analysis, any observed differences between attractiveness ratings of high- versus low-fertility scent samples can be assumed to generalize to other potential raters but cannot be assumed to generalize to other potential scent donors. In other words, these statistical analyses do not test the null hypothesis of central interest—namely, that any observed differences between attractiveness ratings of high- versus low-fertility scent samples can be accounted for by sampling error associated with the women included in the study (in other words, by chance alone and for reasons unrelated to fertility, some women will smell better on high-fertility than on low-fertility days). A statistically powerful test of this hypothesis, treating women as units of analysis, requires a substantial sample of women.

Lastly, three previous studies in this line of work are limited by their use of a "between-women" design, rather than a more powerful "within-woman" design (e.g., Kuukasjärvi et al., 2004; Thornhill and Gangestad, 1999; Thornhill et al., 2003). In between-women designs, each woman provides either a high- or a low-fertility scent sample, whereas in within-woman designs, each woman provides both a high- and a low-fertility scent sample. In between-women designs, noise due to random variation between women in scent attractiveness can influence estimates of the effect of fertility on scent attractiveness. This is not the case in within-woman designs. Thus, between-women designs may yield relatively less precise estimates of the true magnitude of the effect.

The contribution of the present study to this line of work is twofold. First, this study was designed to address the methodological limitations of previous work. Specifically, we included tests of luteinizing hormone to verify that the women in our study ovulated within two days of their high-fertility session (and excluded from analyses those women who did not meet this criterion), used a within-woman design, included a larger sample of women as scent donors than has been included in previous within-women studies of these effects ($n=41$), and performed statistical analyses treating scent raters and scent donors as units of analysis, which allowed us to assess the generalizability of our findings to other potential raters and scent donors.

A second goal of this study was to examine two related research questions. First, one might conduct a study examining men's attraction to women's high- versus low-fertility body scents and find that scent attractiveness ratings did not significantly differ between high and low fertility. This apparent null effect would be consistent with two interpretations: either (a) women's scents are truly no more attractive to men at high fertility than they are at low fertility, or (b) some women's high- and low-fertility scent samples were difficult to discriminate from one another (perhaps as a result of random variation in those women's activities across the two sampling points), and this prevented or obscured any true effect of fertility on scent attractiveness. If (a) is correct, then women should receive similar high- and low-fertility scent attractiveness ratings regardless of how easy it is to discriminate between their high- and low-fertility scent samples. If (b) is correct, then women should receive the most discrepant high- vs. low-fertility scent attractiveness ratings—with high-fertility scent samples rated as more attractive than low-fertility samples—when their body odor samples are easiest for men to discriminate. To proactively address this problem of interpretation, we included a discrimination task that has not been used in previous studies of this kind. We then used multilevel modeling to examine the magnitude of the difference between high- and low-fertility scent attractiveness ratings as a function of the ease with which men could discriminate between women's high- and low-fertility scent samples.

Second, of those studies showing that men are more attracted to high- than to low-fertility female stimuli, few have tested whether the observed effect was indeed driven by proximity to ovulation within the high-fertility phase, rather than proximity to events within the low-fertility phase of the cycle (e.g., the approach of menstrual onset; reviewed in Haselton and Gildersleeve, 2011). This test is critical for establishing the validity of the interpretation that these effects reflect a male adaptation for detecting female fertility. If this interpretation is correct, then women should receive more discrepant high- vs. low-fertility scent attractiveness ratings—with high-fertility scent samples rated as more attractive than low-fertility samples—the closer to ovulation they provide their high-fertility scent samples. To test this prediction, we included luteinizing hormone tests to verify ovulation, which enabled us to pinpoint the probable day of ovulation for all of the women included in our final sample. We also obtained self-reported dates of next menstrual onset for the majority of women in our sample. We then used multilevel modeling to examine the magnitude of the difference between high- and low-fertility scent attractiveness ratings as a function of the proximity of women's high-fertility session to ovulation and of the proximity of their low-fertility session to menses. In sum, this study was designed to provide a more rigorous and nuanced test of the effect of fertility on men's attraction to women's body scents.

Methods

Participants

Scent donors

Forty-one women ($M=20.23$ years, $SD=3.76$), the majority of whom were university students, participated as scent donors. These women reported regular menstrual cycles and had not used any form of hormonal contraception (e.g., birth control pills, Norplant, vaginal ring, birth control patch, Depo-Provera, Mirena IUD) in the three months prior to their participation. Because we were concerned about possible contamination of samples by the scent of smoke, we included only self-identified nonsmokers in the sample. Women received credit in a research course or $45 for their participation.

Scent raters

One hundred twelve men ($M=20.70$ years, $SD=4.35$), the majority of whom were university students, participated as scent raters. Because smokers are twice as likely to demonstrate olfactory deficits as nonsmokers (Frye et al., 1990), we included only self-identified nonsmokers in the sample. Men received credit in a research course or $20 for their participation.

Scheduling procedures

Prior to their enrollment in the study, women completed a brief telephone interview that included questions about their average menstrual cycle length, regularity, and past two dates of menstrual onset. We used this information to schedule each woman to collect samples of her natural body scent on two occasions — once on an estimated high-fertility day of her cycle and once on an estimated low-fertility day of her cycle. We used the reverse cycle day method to identify high- and low-fertility target days for scheduling these sessions (e.g., see Gangestad et al., 2002; Haselton and Gangestad, 2006). We assumed that ovulation occurs, on average, approximately 15 days prior to next menstrual onset (Dixon et al., 1980; Weinberg et al., 1994; Wilcox et al., 2000; but see Cole et al., 2009, for evidence suggesting that ovulation occurs slightly later in the cycle). Accordingly, we scheduled women to collect their high-fertility scent samples 16 to 18 days prior to their predicted date of next menstrual onset (one to three days prior to their predicted ovulation) and their low-fertility scent samples three to 10 days prior to their predicted date of next menstrual onset. Actuarial data indicate that these windows fall within the high- and low-fertility phases of the menstrual cycle, respectively, for most women (Wilcox et al., 2001).

We took two additional measures to ensure that high- and low-fertility sessions were scheduled accurately. First, we verified that high-fertility scent collection took place near ovulation by having participants complete a series of five Clearblue ovulation tests in their predicted high-fertility window (from two days before to two days after their high-fertility scent collection). These tests measure luteinizing hormone (LH) in urine, which rises approximately 24–48 h prior to ovulation (Testart and Frydman, 1982). LH tests are 97% accurate in verifying ovulation as detected by ultrasound (Guermandi et al., 2001). These tests were unmarked, and when asked during debriefing, no participant guessed that they were designed to measure luteinizing hormone or detect ovulation. Second, we verified that low-fertility scent collection took place within the low-fertility phase of the menstrual cycle by having participants report the date of their next menstrual onset following completion of the study by calling, emailing, or sending a prepaid postcard to the lab. Thirty-six women reported their date of next menstrual onset in this way. For the remaining five women, we predicted their date of next menstrual onset using their self-reported date of last menstrual onset and average cycle length.

Of a larger sample initially participating in the study ($N=71$), 19 women did not show evidence of an LH surge within two days of their high-fertility scent collection, and, based on their verified date of next menstrual onset, 11 women completed sessions outside of their predetermined high- and/or low-fertility windows. These 30 women were excluded from all analyses. This exclusion rate (42%) is comparable to that reported in previous studies with similar methods (e.g., 39% in Gangestad et al., 2002, and 28% in Durante et al., 2008).

The final sample of scent donors consisted of 41 women with hormonally verified ovulation. Participants collected their high-fertility scent samples an average of 16.20 days ($SD=1.72$) prior to next menstrual onset and showed evidence of an LH surge that same day ($M=0.17$ days before high-fertility scent collection, $SD=1.48$). Participants collected their low-fertility scent samples an average of 5.88 days ($SD=2.99$) prior to next menstrual onset. Twenty-three women collected their high-fertility scent samples first, and 18 collected their low-fertility scent samples first (as we report below, there were no statistically significant effects of order on the results).

Scent collection procedures

Approximately three days before each of their scheduled scent collections, women came to the lab to receive instructions and materials for collecting their scent samples. Women were asked to wear 100% cotton gauze pads in both underarms for a period of 24 h. Researchers showed the women how to position the pads in direct contact with their underarm skin and apply first aid tape to hold the pads in place. To eliminate residual odors and to minimize differences between participants in hygienic and other practices that could affect body odor, participants were asked to complete a “wash-out” phase prior to putting on their pads and to follow strict behavioral guidelines while wearing their pads over the next 24 h. The wash-out phase involved washing their bed sheets and the clothes they would be wearing over the pads with fragrance-free laundry detergent and showering with fragrance-free bath products (e.g., shampoo, conditioner, soap). Participants were asked to refrain from the following while wearing their pads: using perfumes, deodorants, or antiperspirants; eating pungent foods (e.g., garlic, asparagus, pepperoni); drinking alcohol; using tobacco products or recreational drugs; spending time in rooms with strong odors (e.g., smoke, incense); engaging in sexual activities with another person; and sharing their bed with another person or a pet. After this 24 h period, participants removed their pads, placed them in ziplock bags (pre-marked with the participant's ID number and “left” or “right”), and returned them to the lab. The pads were frozen at −17 °C for an average of 21 days ($SD=13.09$) until the rating session. Freezing has been shown to preserve samples of human body odor without altering perceptions of these odors (Lenochova et al., 2009; Roberts et al., 2008).

Compliance interview

Both times a participant returned her scent samples to the lab, she was asked to respond to a brief series of questions assessing how long she had worn her gauze pads, whether she had completed each step of the wash-out phase prior to applying the pads, and whether she had followed each of the behavioral guidelines for remaining odor-neutral while wearing the pads. In addition, participants were asked to report whether they had engaged in any strenuous physical activities (e.g., working out) or taken vitamins while wearing the gauze pads, since these behaviors might also influence body scent. These interviews were conducted by female research assistants who had been trained to encourage participants to honestly report their involvement in potentially scent-influencing behaviors by emphasizing that there would be absolutely *no penalties* for failures to follow the guidelines and that it was crucial to our research to know whether the pads might be contaminated with non-human odors.

Scent rating procedures

Because scent samples were collected over the course of three academic terms separated by campus closures, three separate rating sessions were held (one at the end of each term). Men rated the scent samples of all of the women who had participated in that term, regardless of whether those women showed evidence of ovulation and were included in the analyses reported below. Thus, in the first session, 37 men rated samples provided by a total of 18 women, of whom 13 were included in the analyses reported below. In the second session, 26 men rated samples provided by a total of 21 women, of whom 11 were included in the analyses reported below. In the third session, 49 men rated samples provided by a total of 32 women, of whom 17 were included in the analyses reported below. We collected ratings of women who did not show evidence of ovulation for other research purposes and do not include the data from these women in the analyses below.

Prior to each rating session, we transferred the scent samples (gauze pads) into open-top, 2 oz cylindrical plastic bottles (similar to travel size shampoo bottles) and allowed them to warm to room temperature for approximately 2 h. We then set up a series of scent rating stations in a large classroom. At each station, we placed three bottles (marked A, B, and C) containing scent samples from the same woman. Bottles A and B were randomly assigned to contain either the woman's high- or low-fertility right underarm sample. Therefore, if Bottle A contained the woman's high-fertility sample, Bottle B contained her low-fertility sample. Bottle C was randomly assigned to contain the matching (left underarm) sample of either Bottle A or Bottle B. Scent rating stations were spaced apart by at least a few feet and were surrounded by cardboard carrels to create privacy.

Raters were told only that they would be rating gauze pads that had been worn by women. They filed into the classroom and were directed to the scent rating stations in a pre-randomized order. They were not informed that the same woman had provided all three samples at a given station. At each station, raters completed three tasks: a) a matching task designed to measure ability to discriminate between high- and low-fertility scent samples from the same woman, b) a forced-choice task designed to measure preference for high- versus low-fertility scent samples, and c) scale ratings of each scent sample. For the matching (high-low discrimination) task, men were asked to smell the samples in Bottles A, B, and C and then indicate on their rating form which sample — A or B — smelled most similar to sample C. For the forced-choice (high-fertility preference) task, men were asked to take a "hearty sniff" of the samples in Bottles A and B and indicate which sample — A or B — smelled more attractive to them. For the scale ratings, raters were asked to evaluate the contents of Bottles A and B individually on pleasantness, sexiness, and intensity and to guess how physically attractive the woman was who had provided each scent sample. Ratings were made on a scale from 1 to 10, where 1 = very un-[sexy/pleasant/intense/physically attractive] and 10 = very [sexy/pleasant/intense/physically attractive].

Raters typically completed scent rating tasks in 30 to 60 min. They were allowed to take short breaks in between tasks as they moved from one scent rating station to the next. Because multiple men were completing these tasks at the same time, men occasionally approached scent rating stations that were occupied by another rater. In such instances (which were rare), a research assistant directed these men to move on to the next station on their list and to then return to the occupied station once they had completed their next set of ratings (and once the other rater had moved on). This measure was taken to ensure that breaks between scent rating stations were of approximately equal length and were relatively constant across rating sessions (e.g., men in relatively well-attended rating sessions did not spend more time waiting between scent rating stations than did men in relatively less well-attended rating sessions). Research assistants carefully recorded any deviations from pre-randomized scent rating station orders.

Results

Compliance with scent collection guidelines

Women reported wearing their gauze pads for an average of 21.75 h ($SD = 3.23$) per session and for slightly longer at low fertility ($M = 22.96$, $SD = 3.18$) than at high fertility ($M = 20.53$, $SD = 5.17$, $t(40) = -2.75$, $p = .01$). However, looking across all 82 scent samples (one high- and one-low fertility sample from each of 41 women), correlations between wear-time and ratings of pleasantness, sexiness, intensity, and inferred physical attractiveness were not significant (all $|r|$s $\leq .16$, all ps $\geq .16$), and as we report below, there were no statistically significant effects of wear-time on the results. Participants reported engaging in an average of 0.68 potentially scent-influencing behaviors at high fertility ($SD = 0.72$) and at low fertility ($SD = 0.85$) (rate was identical across sessions). At high fertility, failure to wash bedding and clothing with the provided fragrance-free detergent was the most commonly reported scent-influencing behavior ($n = 12$), followed by taking vitamins ($n = 10$), spending time in rooms with strong odors ($n = 5$), eating pungent foods ($n = 4$), sharing their bed with another person ($n = 2$), washing their bedding and/or clothing with a scented detergent ($n = 2$), wearing deodorant ($n = 1$), smoking ($n = 1$), and engaging in sexual activity ($n = 1$). At low fertility, failure to wash bedding and clothing with the provided fragrance-free detergent was again the most commonly reported scent-influencing behavior ($n = 13$), followed by taking vitamins ($n = 6$), sharing their bed with another person ($n = 5$), eating pungent foods ($n = 4$), spending time in rooms with strong odors ($n = 3$), working out ($n = 2$), washing their bedding and/or clothing with a scented detergent ($n = 1$), using scented hairspray ($n = 1$), and smoking ($n = 1$).

In order to provide a tightly controlled test of fertility effects on scent attractiveness without sacrificing the external validity afforded by a larger sample of participants, we ran two sets of analyses: in the first set of analyses, we included all scent donors, whereas in the second set of analyses, we included "ideal" scent donors only. Ideal scent donors were defined as those women who had worn their gauze pads for approximately the same amount of time at high and low fertility (no more than four hours difference in wear-time) and did not report spending time in rooms with strong odors, eating pungent foods, sharing their bed with another person, washing their bedding and/or clothing with a scented detergent, wearing deodorant, using perfumes or scented cosmetic products, smoking, engaging in sexual activity, taking vitamins, or working out during either of their sessions. Because a large number of participants failed to wash their clothing and bedding with the provided fragrance-free laundry detergent, we were able to test whether failure to do so was associated with scent ratings. Looking across all 82 scent samples, failure to use the provided detergent was not correlated with ratings of pleasantness, sexiness, intensity, or inferred physical attractiveness (all $|r|$s $\leq .02$, all ps $\geq .83$). Therefore, we chose to include as ideal scent donors those women who reported as their only guideline violation a failure to use the provided detergent. Looking across these women's 30 scent samples, failure to use the provided detergent remained unassociated with ratings of pleasantness, sexiness, intensity, or inferred physical attractiveness (all $|r|$s $\leq .11$, all ps $\geq .55$). The resulting sample of 15 ideal scent donors reported wearing their gauze pads for an average of 22.1 h at high fertility ($SD = 4.18$) and at low fertility ($SD = 3.36$).

Notes on data analyses

For analyses for which we had a strong a priori hypothesis, we used directed tests, as recommended by Rice and Gaines (1994). These tests increase power to identify anticipated effects by partitioning the Type-I error rate (α) into two asymmetrical segments (critical regions), with the larger segment associated with effects in the expected direction or "tail" of the sampling distribution. In the following analyses, we used an α of 0.05 and allocated $4/5*\alpha$, or 0.04, to the expected tail and $1/5*\alpha$, or 0.01, to the unexpected tail. For all other analyses, we used traditional two-tailed tests, which allocate $1/2*\alpha$, or 0.025, to both tails. When directed p values are reported, they are marked as "p_{dir}."

For each man and woman, we computed two scores — a "high-low discrimination score" and a "high-fertility preference score." This allowed us to run analyses treating men (raters) and women (scent donors) as units of analysis. A rater's high-low discrimination score was computed as the percentage of matching task trials on which he correctly matched scent sample C with scent sample A or B, indicating an ability to accurately discriminate high- and low-fertility samples provided by the same woman. A rater's high-fertility preference score was computed as the percentage of trials on which, given a forced choice between scent samples A and B, he chose a woman's high-fertility sample as more attractive than her low-fertility sample. A scent donor's high-low discrimination score was computed as the percentage of matching task trials on which her scent sample C was correctly matched with her scent sample A or B, indicating that her high- and low-fertility samples could be accurately discriminated from each other. A scent donor's high-fertility preference score was computed as the percentage of trials on which, in a forced choice between scent samples A and B, her high-fertility sample was chosen as more attractive than her low-fertility sample.

Matching task: Are high- and low-fertility scents discriminable?

For all scent donors ($n=41$), high- and low-fertility scent samples were correctly discriminated from each other on 61% of the trials. This rate was significantly above chance (50%) treating raters as units of analysis ($t(111)=9.94$, $p_{dir}<.001$, $d=0.94$) and treating donors as units of analysis ($t(40)=3.82$, $p_{dir}<.001$, $d=0.60$). For the reduced sample of ideal scent donors ($n=15$), high- and low-fertility scent samples were correctly discriminated from each other on 64% of the trials. This rate was significantly above chance (50%) treating raters as units of analysis ($t(111)=6.93$, $p_{dir}<.001$, $d=0.66$) and treating donors as units of analysis ($t(14)=3.38$, $p_{dir}=.004$, $d=0.89$).

Forced choice task: Are high-fertility scents preferred over low-fertility scents?

Three raters failed to complete the forced choice section of their rating forms. Therefore, this analysis is based on the remaining 109 raters' responses. For all scent donors, high-fertility scent samples were chosen as more attractive than low-fertility scent samples provided by the same woman on 56% of the forced choice trials. This rate was significantly above chance (50%) treating raters as units of analysis ($t(108)=4.49$, $p_{dir}<.001$, $d=0.43$) but was only marginally above chance treating donors as units of analysis ($t(40)=1.53$, $p_{dir}=.08$, $d=0.24$). For the reduced sample of ideal scent donors, high-fertility scent samples were chosen as more attractive than low-fertility scent samples provided by the same woman on 55% of the forced choice trials. This rate was significantly above chance (50%) treating raters as units of analysis ($t(108)=3.03$, $p_{dir}=.002$, $d=0.29$) but was not significant treating donors as units of analysis ($t(14)=0.89$, $p_{dir}=.24$, $d=0.23$).

Importantly, high-fertility preference scores were correlated with high-low discrimination scores for all scent donors ($r=.37$, $p=.02$) and for the reduced sample of ideal donors ($r=.68$, $p=.005$), meaning that a woman's high-fertility scent sample was even more likely to be chosen as more attractive than her low-fertility scent sample if her samples were relatively easy to discriminate from each other. We examined high-low discrimination as a potential moderator of the fertility effects on scent attractiveness ratings in the next set of analyses.

Scale ratings: What factors moderate the association between fertility and scent attractiveness ratings?

As shown in Table 1, for all scent donors and for ideal scent donors, high-fertility scent samples received higher ratings of pleasantness and sexiness and were judged to have come from more physically attractive women than were low-fertility scent samples (all $p_{dir}s \le .05$). These effects were consistently stronger in the reduced sample of ideal scent donors than in the full sample of scent donors. Additionally, for all scent donors and for ideal scent donors, high-fertility scent samples received slightly lower ratings of scent intensity than did low-fertility scent samples; however, this effect was not statistically significant in the full or reduced sample.

Our design involved scent samples nested within donors and raters, who were crossed with each other. In other words, each scent sample was associated with one donor (the woman who provided that sample) and multiple raters (the raters who rated that sample), but not all samples were associated with the same donor or raters. Thus, one can think of each scent sample as nested within a donor(column)-by-rater(row) cell. Accordingly, any given scent sample's ratings could reflect the contribution of variables associated with that particular sample, the donor who provided it, and the raters who rated it, as well as interactions among sample, donor, and rater variables. With this in mind, we ran a series of cross-classified multilevel models with scent samples as Level 1 units and donors and raters (crossed) as Level 2 units (i.e. a 2-level model with a 2-way cross-classification at Level 2; Raudenbush and Bryk, 2002). Analyses were carried out using the HCM2 module for cross-classified models in HLM 6.08 (Raudenbush et al., 2009).

Ratings of pleasantness, sexiness, and inferred physical attractiveness were highly intercorrelated (for the full set of 82 scent samples, all

Table 1
Descriptive statistics, *t* test results, and effect sizes (Cohen's *d*) comparing high-fertility with low-fertility scent ratings among all scent donors and ideal scent donors.

	Mean (*SD*)		*d*	*t*	*p*	p_{dir} (predicted effects)
All scent donors (n = 41)						
High-low discrimination score	61% (0.18)		0.60	3.82	<.001	<.001
High-fertility preference score	56% (0.25)		0.24	1.53	.133	.083
	High-fertility	*Low-fertility*				
Pleasantness	5.02 (1.02)	4.66 (1.20)	0.32	1.84	.074	.046
Sexiness	4.60 (1.01)	4.25 (1.17)	0.32	1.92	.062	.038
Inferred physical attractiveness	5.07 (0.91)	4.72 (1.06)	0.35	2.02	.05	.031
Attractivenes composite	4.90 (0.98)	4.55 (1.14)	0.33	1.93	.06	.038
Intensity	4.50 (1.14)	4.76 (1.31)	−0.22	−1.31	.199	
Ideal scent donors (n = 15)						
High-low discrimination score	64% (0.16)		0.89	3.38	.004	.003
High-fertility preference score	55% (0.23)		0.23	0.89	.391	.244
	High-fertility	*Low-fertility*				
Pleasantness	5.08 (1.07)	4.50 (1.38)	0.46	1.85	.086	.054
Sexiness	4.64 (1.04)	4.08 (1.33)	0.47	1.87	.082	.051
Inferred physical attractiveness	5.13 (0.92)	4.58 (1.17)	0.52	1.90	.078	.049
Attractivenes composite	4.95 (1.01)	4.38 (1.28)	0.48	1.89	.08	.05
Intensity	4.57 (1.07)	5.11 (1.50)	−0.41	−1.44	.173	

Note. For high-low discrimination and high-fertility preference scores, Cohen's *d* represents the standardized difference between chance (50%) and the percentage of trials on which high- and low-fertility samples were correctly discriminated from each other and high-fertility samples were chosen over low-fertility samples, respectively. For pleasantness, sexiness, inferred physical attractiveness, attractiveness composite, and intensity, Cohen's *d* represents the standardized difference between high- and low-fertility scent ratings, adjusting for the correlation between high- and low-fertility ratings. By psychological standards, effect sizes (*d*s) of 0.2, 0.5, and 0.8 are considered small, medium, and large, respectively (Cohen, 1988).

rs ≥ .81, all ps < .001, Cronbach's alpha = .99; for the ideal set of 30 scent samples, all rs ≥ .98, all ps < .001, Cronbach's alpha = .99). Therefore, we averaged these three ratings to create a scent attractiveness composite variable (ATTR). We used this variable as the outcome in all multilevel models. In order to estimate the main effect of fertility on scent attractiveness, we first specified a fully random model that included a single, Level-1 predictor — fertility (FERT), a dummy variable taking on a value of one for high-fertility samples and zero for low-fertility samples. We ran this model twice, once for all scent donors and once for ideal scent donors.

As shown in Table 2, for all scent donors and for ideal scent donors, fertility had a significant positive effect on scent attractiveness ($p_{dir} = .04$ and $p_{dir} = .03$, respectively). Indeed, fertility accounted for a sizable proportion of the sample-level variance in scent attractiveness — 17% for all scent donors and for ideal scent donors. In addition, both analyses revealed significant unexplained variance associated with scent donors in the effect of fertility on scent attractiveness, suggesting that donor variables might moderate this effect. In contrast, neither analysis revealed significant unexplained variance associated with raters in the effect of fertility on scent attractiveness. Therefore, our next set of analyses sought to identify donor variables that predicted the magnitude of the positive effect of fertility on scent attractiveness.

Because the previous analyses showed that a non-significant portion of unexplained variance in the effect of fertility on scent attractiveness was associated with raters, we eliminated this variance component from the model. At Level 1, we entered fertility (FERT from the previous analysis) and potential covariates, including intensity (INTENS), a continuous variable representing a given scent sample's mean intensity rating; days in freezer, a continuous variable representing the number of days a given scent sample had remained in the freezer prior to the rating session; hours worn, a continuous variable representing the number of hours a given sample had been worn; and for the analysis involving all scent donors, scent-influencing behaviors (BEHAV), a continuous variable representing the number of potentially scent-influencing behaviors (including working out and taking vitamins) that a scent donor reported engaging in while wearing a given sample. In order to test for cross-level interactions between donor variables and fertility on scent attractiveness, we entered all of the following predictors into the Level 2 slope equation associated with fertility: session order, a dummy variable taking on a value of one for women who completed their high-fertility session first and zero for women who completed their low-fertility session first; donor high-low discrimination score (DONOR_DISC), a continuous variable representing the percentage of trials on which a given scent donor's high- and low-fertility scent samples had been accurately discriminated (mean-centered); days to menses, a continuous variable representing the number of days that a given scent donor collected her low-fertility scent samples prior to her next menstrual onset; and days to ovulation (DAYS_OV), a continuous variable representing the number of days that a given scent donor collected her high-fertility scent samples prior to her predicted ovulation. Days to ovulation was computed as the number of days from the high-fertility session to the day of luteinizing hormone surge, plus two days to account for the approximate time between the rise in luteinizing hormone and ovulation (Testart and Frydman, 1982). As before, we ran this model twice, once for all scent donors and once for ideal scent donors.

In both analyses, all of the following variables had non-significant effects and were eliminated from the model: days in freezer (all women, $p = 0.87$; ideal women, $p = 0.86$), hours worn (all women, $p = 0.15$; ideal women, $p = 0.58$), session order (all women, $p = 0.11$; ideal women, $p = 0.90$), and days to menstrual onset (all women, $p = 0.97$; ideal women, $p = 0.87$). In both analyses, intensity (INTENS) had a small but significant positive effect on scent attractiveness and was therefore retained as a covariate ($p < .001$). For the analysis including all scent donors, scent-influencing behaviors (BEHAV) had a significant negative effect on scent attractiveness and was retained as a covariate ($p < .01$).

As shown in Table 3, both analyses revealed a significant cross-level interaction between donor high-low discrimination score (DONOR_DISC) and fertility (FERT), meaning that women whose high- and low-fertility scent samples were relatively easier to discriminate from each other tended to receive even higher scent attractiveness ratings at high fertility compared to low fertility (both p_{dir}s ≤ .001). This interaction is presented for all scent donors in Fig. 1. The analysis including all scent donors did not reveal any other significant cross-level interactions. In comparison, the analysis including only ideal scent donors yielded an additional significant cross-level interaction between days to ovulation (DAYS_OV) and fertility (FERT), meaning that women who completed their high-

Table 2
Results from fully random cross-classified model predicting scent attractiveness from fertility.

Mixed model: $ATTR_{ijk} = \theta_0 + \theta_1 FERT_{ijk} + b_{00j} + b_{10j} FERT_{ijk} + c_{00k} + c_{10k} FERT_{ijk} + e_{ijk}$

All scent donors ($n = 41$)

Fixed effect	Coefficient	*SE*	*t* ratio	*p*	p_{dir} (predicted effects)
θ_0	4.55	0.19	24.53	<.001	
θ_1 (fertility)	0.34	0.18	1.91	.056	.035
Random effect	Variance	*df*	X^2	*p*	
b_{00j} (unexplained rater effect on intercept)	0.52	111	550.75	<.001	
b_{10j} (unexplained rater effect on fertility slope)	0.004	111	77.11	>.5	
c_{00k} (unexplained donor effect on intercept)	1.17	40	998.91	<.001	
c_{10k} (unexplained donor effect on fertility slope)	1.24	40	625.33	<.001	
e_{ijk} (residual error)	1.79				
Deviance = 11385.88					

Ideal scent donors ($n = 15$)

Fixed effect	Coefficient	*SE*	*t* ratio	*p*	p_{dir} (predicted effects)
θ_0	4.38	0.32	13.49	<.001	
θ_1 (fertility)	0.56	0.29	1.95	.05	.031
Random effect	Variance	*df*	X^2	*p*	
b_{00j} (unexplained rater effect on intercept)	0.5	111	273.89	<.001	
b_{10j} (unexplained rater effect on fertility slope)	0.005	111	110.46	>.5	
c_{00k} (unexplained donor effect on intercept)	1.47	14	448.18	<.001	
c_{10k} (unexplained donor effect on fertility slope)	1.14	14	190.63	<.001	
e_{ijk} (residual error)	1.85				
Deviance = 4400.94					

Table 3
Results from cross-classified model predicting scent attractiveness from sample and donor variables.

All scent donors ($n=41$)

Mixed model: $ATTR_{ijk}=\theta_0+\theta_1 FERT_{ijk}+\theta_2 INTENS_{ijk}+\theta_3 BEHAV_{ijk}+\beta_{11} DONOR\_DISC_k{}^{*}FERT_{ijk}+b_{00j}+c_{00k}+c_{10k}FERT_{ijk}+e_{ijk}$

Fixed effect	Coefficient	*SE*	*t* ratio	*p*	p_{dir} (predicted effects)
θ_0	4.64	0.22	20.33	<.001	
θ_1 (fertility)	0.36	0.16	2.25	.024	.015
θ_2 (intensity)	0.04	0.013	3.32	.001	
θ_3 (scent-influencing Behaviors)	−0.32	0.12	−2.64	.009	
β_{11} (donor discrimination∗fertility)	2.28	0.72	3.18	.002	.001
Random effect	Variance	*df*	X^2	*p*	
b_{00j} (unexplained rater effect on intercept)	0.54	111	1078.86	<.001	
c_{00k} (unexplained donor effect on intercept)	1.23	40	1058.46	<.001	
c_{10k} (unexplained donor effect on fertility slope)	0.95	39	480.76	<.001	
e_{ijk} (residual error)	1.78				
Deviance = 11363.68					

Ideal scent donors ($n=15$)

Mixed model: $ATTR_{ijk}=\theta_0+\theta_1 FERT_{ijk}+\theta_2 INTENS_{ijk}+\beta_{11} DONOR\_DISC_k{}^{*}FERT_{ijk}+\beta_{12} DAYS\_OV_k{}^{*}FERT_{ijk}+b_{00j}+c_{00k}+c_{10k}FERT_{ijk}+e_{ijk}$

Fixed effect	Coefficient	*SE*	*t* ratio	*p*	p_{dir} (predicted effects)
θ_0	3.86	0.37	10.4	<.001	
θ_1 (fertility)	1.05	0.29	3.63	.001	<.001
θ_2 (intensity)	0.1	0.02	4.9	<.001	
β_{11} (donor discrimination∗fertility)	4.34	0.98	4.43	<.001	<.001
β_{12} (days to ovulation∗fertility)	−0.22	0.11	−2.06	.039	.024
Random effect	Variance	*df*	X^2	*p*	
b_{00j} (unexplained rater effect on intercept)	0.46	111	413.86	<.001	
c_{00k} (unexplained donor effect on intercept)	1.79	14	573.51	<.001	
c_{10k} (unexplained donor effect on fertility slope)	0.47	12	90.34	<.001	
e_{ijk} (residual error)	1.82				
Deviance = 4367.75					

fertility session nearer to their predicted day of ovulation tended to receive even higher scent attractiveness ratings at high fertility compared with low fertility ($p_{dir}=.02$) than did women who completed their high-fertility session farther from ovulation. That this cross-level interaction was significant but the cross-level interaction between days to menstrual onset and fertility was not indicates that the effect of fertility on scent attractiveness is driven by changes related to the approach of ovulation rather than changes related to the approach of menses.

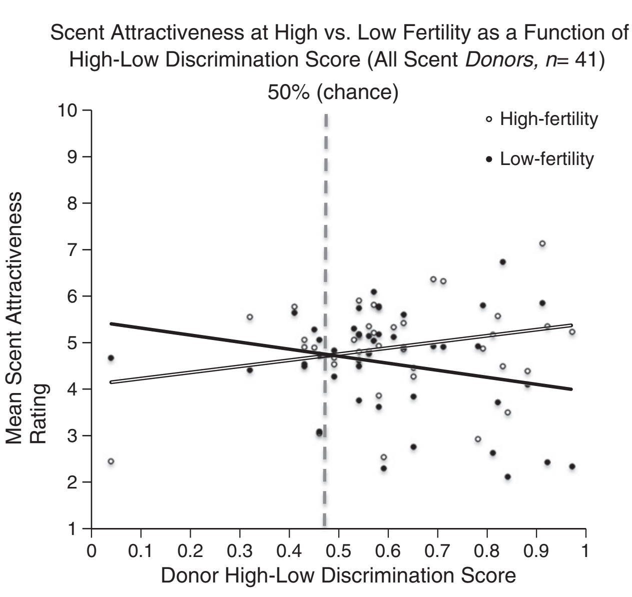

Fig. 1. Difference between high- and low-fertility scent attractiveness ratings (high-fertility minus low-fertility) as a function of donor high-low discrimination score. Women whose high- and low-fertility scent samples were more easily discriminated received more favorable ratings of high- relative to low-fertility scent samples.

Exploratory analyses

As shown in Table 3, after adding key donor-level moderators, there remained a significant amount of unexplained variance across donors in the effect of fertility on scent attractiveness. We performed several follow-up exploratory analyses on the full sample of scent donors to identify possible donor-level predictors of this variability. None of the following donor-level variables was found to moderate the effect of fertility on scent attractiveness: age ($\beta=-0.05$, $p=0.12$, $n=40$), facial attractiveness ($\beta=0.05$, $p=0.74$, $n=38$), body attractiveness (clothed) ($\beta=0.06$, $p=0.73$, $n=38$), lifetime number of relationships ($\beta=-0.10$, $p=0.19$, $n=41$), and lifetime number of sex partners ($\beta=-0.14$, $p=0.13$, $n=34$) (sample size varies across measures because some women chose not to have their photograph taken or to respond to all questionnaire items). Information concerning photo rating procedures is available from the authors. One donor-level variable was found to significantly moderate the effect of fertility on scent attractiveness: relationship status ($\beta=0.52$, $p=0.04$, $n=41$). Women who were involved in a romantic relationship at the time of their participation received higher ratings of their high-fertility scent samples relative to their low-fertility scent samples than did women who were not involved in a romantic relationship at the time of their participation. This effect was not predicted a priori and should be interpreted with appropriate caution given the number of associations tested.

Rater habituation and fatigue

Scent rating sessions were long and demanding. Therefore, a reasonable concern is that habituation and fatigue may have influenced men's evaluations of scent attractiveness, possibly resulting in a decline across the rating sessions in accuracy at discriminating between high-and low-fertility scent samples or in preference for high-fertility over low-fertility scent samples. Thus, habituation and fatigue effects may have downwardly biased effect size estimates and produced an artifactual association between high-low discrimination and high-fertility preference. Because each rater proceeded to the scent rating stations in a pre-randomized order (and any deviations from this order were carefully recorded), we were able to directly examine associations between trial number (whether a rater evaluated a set of scent samples first, second, third, etc. within the rating session), high-low discrimination, and high-fertility preference. Trial number was weakly *positively* associated with high-low discrimination ($r = 0.09$ over a total of 1541 matching task trials) and not meaningfully associated with high-fertility preference ($r = -0.009$ over a total of 1495 forced-choice trials). Therefore, habituation and fatigue appear not to have markedly influenced the effect sizes reported above, nor to have produced the observed association between high-low discrimination and high-fertility preference.

Discussion

Across many species of mammals, males are strongly attracted to female scent cues associated with the fertile period of the ovulatory cycle. This study tested and found evidence supporting a parallel effect in humans — namely, that men can detect and are attracted to women's body scents associated with the fertile period of the ovulatory cycle. This is not the first study to demonstrate this effect; however, it is perhaps the most definitive, using tight controls on odor collection and storage, hormone tests to confirm ovulation, a within-woman design to control for between-women variation in scent attractiveness, and multilevel modeling to appropriately analyze the complex, nested data that resulted from this research design.

In this study, men demonstrated an above-chance ability to discriminate between samples of natural body odor collected from the same women on high- versus low-fertility days of the ovulatory cycle. Men also showed an above-chance preference for women's high-fertility over their low-fertility scent samples. Several factors contributed to the magnitude of this preference. First, women who provided scent samples that were the least likely to be contaminated by non-human odors tended to receive higher attractiveness ratings at high relative to low fertility. In addition, women whose high- and low-fertility samples were relatively easy to discriminate from each other tended to receive higher attractiveness ratings at high relative to low fertility. And lastly, among women whose scent samples were least likely to be contaminated by non-human odors, the proximity of women's high-fertility session to ovulation predicted the magnitude of the positive effect of fertility on scent attractiveness. In other words, women who collected their high-fertility scent samples closest to the day of ovulation tended to receive the highest attractiveness ratings at high relative to low fertility. In contrast, the proximity of these women's low-fertility sessions to menses did not predict the magnitude of this effect.

These nuanced patterns are consistent with the hypothesis that women's body scents contain information relevant to assessing their current fertility status and that men are sensitive to these fertility cues. The specificity of these patterns also helps to rule out a variety of mundane alternative explanations. For example, we found that the positive effect of fertility on men's evaluations of women's body scent attractiveness was strongest when men rated high- and low-fertility scent samples that were most easily discriminated. Importantly, greater discriminability was not associated with a randomly-patterned increase in preference discrepancy (i.e. sometimes favoring the high-fertility scent sample and sometimes favoring the low-fertility scent sample), which would be expected if increased preference discrepancy were simply a byproduct of raters being better able to differentiate between the two different scents for reasons unrelated to fertility. Rather, more discriminable high- and low-fertility scent sample pairs received more discrepant attractiveness ratings *favoring the high-fertility scent sample*. This observation is consistent with the notion that, when men can detect differences between high- and low-fertility scents, they prefer high-fertility scents.

In addition, we found that the positive effect of fertility on men's evaluations of women's body scent attractiveness was strongest among women whose samples were least likely to contain non-human odor contaminants. This indicates that differences in ratings received by high- versus low-fertility scent samples resulted from natural changes in women's body scents across the cycle, rather than chance effects or experimental artifacts. Likewise, we found that, among women whose samples were least likely to be contaminated by non-human odors, differences in ratings received by high- versus low-fertility scent samples were driven by proximity to ovulation and not proximity to menstrual onset. This indicates that these differences resulted from hormonal events accompanying ovulation rather than from hormonal events occurring outside of the fertile window. In other words, this finding indicates that the high-fertility increase in women's scent attractiveness observed in this study reflects genuine fertility cues rather than artifacts of other changes in hormones across the cycle. Taken together, this set of findings provides strong support for the notion that men are attracted to cues of impending ovulation in women's body scents, possibly reflecting a male adaptation for female fertility detection.

How might changes in the attractiveness of women's body odors to men across the ovulatory cycle affect men's behavior? As noted earlier, research on nonhuman mammals has shown that exposure to fertile female scents can bring about dramatic changes in males, including increased attraction to females and the immediate enactment of certain mating behaviors. These behavioral responses appear to be mediated by elevated levels of sex hormones in response to fertile female scents. Is there evidence for similar effects among men?

Several studies have shown that women in heterosexual relationships report that their partners are more loving and attentive, jealous and proprietary, vigilant of their activities, and monopolizing of their time near ovulation as compared with less fertile days of the ovulatory cycle (Gangestad et al., 2002; Haselton and Gangestad, 2006; Pillsworth and Haselton, 2006b). Also, in a naturalistic study, exotic dancers recorded their tip earnings every night for approximately two ovulatory cycles. The normally-ovulating dancers reported considerably greater tip earnings near ovulation than on less fertile days of the cycle ($335 per shift at high fertility, compared with only $260 at low fertility), whereas dancers using hormonal contraception did not show this pattern. Lastly, in a lab study, men who interacted with a naturally-cycling female confederate (with whom they were not previously acquainted) on high-fertility days of her ovulatory cycle mimicked her behavior more (indicating liking) and subsequently made riskier decisions in a "blackjack" task than did men who interacted with the same female confederate on low-fertility days of her cycle (Miller and Maner, 2010b). This set of studies suggests that men's behaviors with their relationship partners—and possibly with other female acquaintances—may vary across these women's ovulatory cycles. If this is indeed the case, then an important question for future research is whether these patterns are mediated, at least in part, by men's responses to fertility cues in these women.

A growing body of research suggests that fertility cues are present across a number of modalities (reviewed in Haselton and Gildersleeve, 2011). However, it is yet unknown whether men's responses to these cues contribute to changes in men's behavior directed toward those women. Nonetheless, having documented that men evaluate the attractiveness of women's high- and low-fertility body scents quite differently, this study hints at the possibility that some changes in men's behavior across women's ovulatory cycles could be mediated by exposure to scent cues of fertility. Consistent with this possibility—and paralleling some effects in nonhuman mammals—emerging evidence suggests that men experience changes in sex hormone levels and mating-related cognitions following exposure to scent stimuli from high-fertility women. Across two studies, men who smelled T-shirts worn by women on high-fertility days of the ovulatory cycle showed higher testosterone levels at post-test than did men who smelled T-shirts worn by those women on low-fertility days of the cycle (Miller and Maner, 2010a). In a separate study, men who smelled T-shirts worn by women on high-fertility days of the ovulatory cycle exhibited marginally greater implicit activation of sexual concepts than did men who smelled T-shirts worn by those women on low-fertility days of the cycle (Miller and Maner, 2010b). Lastly, in a study using similar methods, men who smelled women's high-fertility T-shirts inferred significantly greater sexual arousal (but not other emotions) on behalf of the women who had provided the T-shirts than did men who smelled those women's low-fertility T-shirts (Miller and Maner, 2010b). This last effect was observed only among men who reported a high sensitivity to odors. Taken together, these findings suggest that exposure to women's high-fertility body scents may increase men's testosterone levels and prime certain mating-related cognitions, potentially leading men to direct greater mating effort toward women at high fertility.

This study and the related research reviewed in this paper highlight opportunities for future research examining the potential role of scent cues of fertility in heterosexual relationship dynamics. For example, one next step for future research will be to document changes across the ovulatory cycle in men's behaviors with their female romantic partners, as well as changes in the attractiveness of those women's body scents, in order to examine whether there is correspondence between the two. In addition, although it is likely that there are many kinds of fertility cues, another interesting possibility hinted at by this work is that men who are regularly exposed to their female romantic partners' natural body odors might show different patterns of behavior across their partners' ovulatory cycles than men who are not. For example, men who regularly have sex or cosleep with their female romantic partners or whose partners do not engage in practices that mask their natural body scents may experience greater exposure to and hence more opportunities to detect and respond to scent cues of fertility than do other men. This idea is supported, in part, by the finding in this study that the positive effect of fertility on men's evaluations of women's body scents was more pronounced when women's natural body scents had not been contaminated or masked by artificial fragrances.

In sum, this study adds to a growing body of work suggesting that scent communication may serve an important, yet still largely overlooked, role in human mating behavior. Men exhibit greater attraction to scents associated with impending ovulation than to scents associated with less fertile days of the ovulatory cycle, and emerging evidence suggests that men may experience a suite of adaptive endocrine, psychological, and behavioral changes in response to changes accompanying ovulation in women. Many of these effects parallel effects previously observed only in nonhuman mammals. Given the increasing availability of state-of-the-art menstrual cycle study methods and the many fascinating questions that still remain, researchers are now poised to make significant contributions toward a more nuanced and fundamental scientific understanding of scent communication, relationship dynamics, and the role of scent in human nature.

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