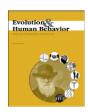
Section 1

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Original Articles

Women's evaluations of other women's natural body odor depend on target's fertility status



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ABSTRACT

A large research literature indicates that men perceive women as more attractive when they are at high fertility than at low fertility within the ovulatory cycle. However, it remains unclear whether women also perceive women as more attractive at high fertility. This study examined women's ratings of samples of natural body odor collected from naturally-cycling women at high and low fertility within the cycle and from hormonal contraceptive-using women at mid-cycle. Like men, women rated naturally-cycling women's high-fertility scent samples as more attractive than their low-fertility samples. Women rated hormonal contraceptive (HC) users' scent samples as more attractive than naturally-cycling women's high- and low-fertility samples, though the difference between HC and high-fertility samples was statistically significant only when raters were treated as the unit of analysis. These findings reveal a potentially important role for scent communication in women's perceptions of other women and are consistent with the notion that the ovulatory cycle could influence women's interactions with one another. The findings also highlight the need for rigorous investigations of the possible impacts of hormonal contraception on women's attractiveness and social relationships with other women.

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1. Introduction

A large research literature indicates that men evaluate women's faces, voices, and natural body odors as subtly more attractive on the handful of high-fertility days leading up to ovulation, as compared with the low-fertility days comprising the remainder of the cycle (reviewed in Haselton & Gildersleeve, 2011, 2016; meta-analyzed in Gildersleeve & Haselton, 2015). Findings concerning men's evaluations of the attractiveness of women's high- versus low-fertility body scents appear to be robust, with many studies reporting evidence that men perceive women's high-fertility scents as more pleasant and sexier (e.g., Cerda-Molina, Hernández-López, de la O, Chavira-Ramírez, & Mondragón-Ceballos, 2013; Doty, Ford, Preti, & Huggins, 1975; Gildersleeve, Haselton, Larson, & Pillsworth, 2012; Havlíček, Dvorakova, Bartos, & Flegr, 2006; Singh & Bronstad, 2001; Thornhill et al., 2003; but see Thornhill & Gangestad, 1999). Moreover, preliminary evidence suggests that men respond to women's high-fertility scents with greater levels of testosterone, as well as motivations and behaviors thought to facilitate courtship behavior (reviewed in Makhanova & Miller, 2013). For example, in a recent study, men who inhaled underarm or vulvar scents collected from women at high fertility subsequently experienced increases in testosterone and sexual interest, whereas men who inhaled

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scents collected from women at low fertility experienced a decrease in testosterone and no change in sexual interest (Cerda-Molina et al., 2013; also see Miller & Maner, 2010a, 2010b; but see Roney & Simmons, 2012, for a null effect of high-fertility scents versus water on men's testosterone).

Parallel patterns have been extensively documented in nonhuman mammals. Across diverse species, it is typical for females to experience physical changes, including changes in scent, during the brief high-fertility period approaching ovulation. Males typically respond to these fertility cues with enhanced sexual interest and, in some cases, increases in hormones that facilitate mating and intrasexual competition (e.g., Amstislavskaya & Popova, 2004; Bronson & Desjardins, 1982; Elvira, Herndon, & Wilson, 1982; Gordon, Bernstein, & Rose, 1978; Kavaliers, Choleris, & Colwell, 2001; Perret & Schilling, 1995; Rose, Gordon, & Bernstein, 1972; Ziegler, Schultz-Darken, Scott, Snowdon, & Ferris, 2005). Thus, in both humans and nonhuman mammals, cues of fertility within the ovulatory cycle appear to play a role in regulating male–female and, possibly, male–male social interactions.

But what about female–female social interactions? A recent study of chacma baboons suggests that sensitivity to cues of female fertility within the ovulatory cycle is not unique to males. In the study, female baboons were more aggressive toward females in the high-fertility period of the ovulatory cycle than toward females in other reproductive states (i.e. in the low-fertility period of the cycle, pregnant, or lactating; Huchard & Cowlishaw, 2011). Female aggressors therefore appeared to detect cues of fertility in potential targets and increase aggression

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toward the females who were likely to be most attractive to prospective mates and therefore posed the greatest competitive threat. Given strong evidence that men are sensitive to subtle cues of women's fertility within the cycle, this finding in baboons raises the question of whether women are also sensitive to cues of fertility in other women.

To date, only four studies have produced data relevant to addressing this question. Although these studies provide valuable preliminary evidence, their findings have been mixed, and their methods have been limited. Three of these studies examined possible ovulatory cycle effects on women's evaluations of other women's natural body scent. In one study, women (n = 12) rated T-shirts worn by female stimulus donors estimated to be closer to ovulation within the cycle as smelling more attractive than T-shirts worn by stimulus donors estimated to be farther from ovulation (i.e. a "between-donors" design; donor n = 41; Kuukasjärvi et al., 2004). Likewise, in a recent study using a more powerful "within-donors" design, women (n = 58) rated T-shirts worn by women at high fertility as smelling more pleasant than T-shirts worn by the same women at low fertility (donor n = 13, though two donors provided only low-fertility T-shirts; Woodward, Thompson, & Gangestad, 2015). However, in another study using a within-donors design, neither heterosexual women (n = 12) nor non-heterosexual women (n = 8) rated T-shirts worn by women at high fertility as smelling more attractive than T-shirts worn at low fertility (donor n = 17; Trouton, Guitar, Carmen, Geher, & Grandis, 2012). Lastly, one study used a within-donors design to examine possible ovulatory cycle effects on women's evaluations of other women's facial attractiveness. Women (n = 131) judged photographs of women taken at high fertility as more attractive than photographs of the same women at low fertility (donor n = 48; Roberts et al., 2004).

A limitation of all of these studies is that estimations of stimulus donors' positions in the cycle (and of their current fertility) were based on methods that involve counting forward from a self-reported date of last menstrual onset to the day of participation. In comparison with methods that involve counting backward from a prospectively verified date of next menstrual onset or repeat assessments of luteinizing hormone within the expected fertile window, such "forward counting" methods are low in validity (they are relatively poor at estimating women's true fertility within the cycle) and offer low statistical power to detect true cycle effects (see Gangestad et al., 2015; Gonzales & Ferrer, 2015). Forward counting methods perform poorly largely because they are vulnerable to error in women's recollections of their date of last menstrual onset. Recall error can be substantial; for example, one study compared women's retrospective reports of their date of last menstrual onset to the date they had prospectively reported (see Wegienka & Baird, 2005) and found that, although 56% of the women retrospectively reported the correct date, 19% were off by three or more days (and note that the fertile window itself lasts only approximately 6 days; Wilcox, Weinberg, & Baird, 1995).

In addition, all but one of these past studies (Kuukasjärvi et al., 2004) presented analyses treating *raters* as the statistical "unit of analysis" and did not present analyses treating *stimulus donors* as the unit of analysis. Statistically significant fertility effects based on analyses treating raters as the unit of analysis justify the inference that other samples of raters from the population also will probably evaluate those particular high-fertility stimuli as more attractive than those particular low-fertility stimuli. However, such analyses cannot rule out the possibility that differences between high- and low-fertility stimuli that are idiosyncratic to a particular stimulus set have produced the illusion of a fertility effect.

For example, if a scent study similar to those described above used a stimulus set that included one low-fertility scent sample that smelled particularly unpleasant, analyses that collapsed across donors in order to examine variation among raters in their evaluations of high- versus low-fertility scent samples – in other words, that treated *raters* as the unit of analysis – might well detect an apparent fertility effect. However, this effect could be driven entirely

by the single unpleasant smelling low-fertility sample, which might have smelled unpleasant for any number of reasons not necessarily related to fertility (e.g., the stimulus donor ate garlic that day but did not report it to the researcher).

In contrast, analyses that collapsed across raters in order to examine variation among donors in the evaluations they received for their high-versus low-fertility samples – in other words, that treated *donors* as the unit of analysis – would be less likely to detect this potentially spurious fertility effect against the background of between-donor variation in high- versus low-fertility scent attractiveness. We emphasize that *only donors-as-unit analyses* provide a test of the key hypothesis of interest – namely, that women generally are more attractive at high than at low fertility within the ovulatory cycle. Once a fertility effect has been compellingly demonstrated by conducting donors-as-unit analyses, raters-as-unit analyses are useful for establishing the generalizability of the finding to other possible samples of raters.

Finally, whereas previous studies examining men's evaluations of women's high- versus low-fertility attractiveness have typically proposed that men's preference for high-fertility stimuli reflects psychological adaptations for detecting cues of women's current fertility within the cycle (e.g., see Singh & Bronstad, 2001), studies examining women's evaluations of other women's high- and low-fertility attractiveness have tended to frame such analyses as exploratory or did not explicate a clear rationale for why we should expect women to be sensitive to cues of fertility in other women. In fact, there are several reasons to expect that women, like men, will perceive women as more attractive at high fertility within the ovulatory cycle. First, given evidence that females of related primate species likely possess psychological mechanisms that enable them to detect cues of fertility in other females (e.g., see Huchard & Cowlishaw, 2011), it is plausible that such mechanisms could appear in human females as a vestigial trait passed down from a shared ancestor in which such mechanisms were functional. Alternatively, given that human males appear to possess psychological mechanisms that enable them to detect cues of fertility in women, it is plausible that such mechanisms could appear in women as a mere byproduct of their shared physiology with men (e.g., arising due to developmental constraints).

However, we think it is more likely that selection pressures encountered by ancestral human females actively favored the psychological mechanisms that now enable women to perceive cues of high fertility in other women as attractive. These mechanisms may not necessarily have been selected de novo in humans; rather, they may have been passed down from ancestral species and maintained in human females because of their reproductive benefits. For example, three non-mutually exclusive possibilities are that (a) selection favored a sensitivity among women to cues of overall reproductive quality in other women (i.e. between-women variation in reproductive potential), (b) selection favored sensitivity to cues of current cycle fertility in other women (i.e. within-women, between-cycle variation in fertility), and (c) selection favored sensitivity to cues of fertility within the cycle in other women (i.e. within-women, within-cycle variation in fertility). Detecting cues of any of these three types of variation might have reproductively benefitted women in a variety of ways, including enabling them to direct increased aggression at female rivals who posed a heightened competitive threat in general (relative to other women), in their current cycle (relative to other cycles), or at this point within their current cycle (relative to other points within their cycle).

Notably, some factors – such as estradiol levels – are thought to correlate with overall reproductive quality, current cycle fertility, and fertility within the cycle (see Law Smith et al., 2006; Puts et al., 2014). Therefore, if female sensitivity to cues of estradiol initially evolved to enable women to detect between-women variation in overall reproductive quality, it might also incidentally confer an ability to detect withinwomen variation in current cycle fertility or fertility within the cycle (or vice versa. For an extended discussion of similar evolutionary explanations for men's sensitivity to cues of fertility in women, see Havlíček,

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