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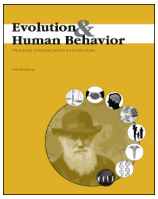

Original Article

Attunement to the fertility status of same-sex rivals: women's testosterone responses to olfactory ovulation cues

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ABSTRACT

Evolutionary theories of mating suggest that changes in fertility across the menstrual cycle play an important role in sexual selection. In line with this framework, the current research examined whether olfactory cues to the fertility of a same-sex rival would prompt hormonal signs of intrasexual competition in women. Women exposed to the scent of another woman close to ovulation subsequently displayed higher levels of testosterone than women exposed to the scent of a woman far from ovulation. Whereas women exposed to the scent of a woman in the mid-luteal phase displayed sizable decreases in testosterone over time, no such decline was observed among women exposed to the scent of a woman near ovulation. Thus, olfactory cues signaling a rival's heightened level of fertility were associated with endocrinological responses in women that could be linked to intrasexual competition.

During the course of their menstrual cycle, women undergo dramatic shifts in their level of fertility, and those shifts are linked to a variety of important mating-related processes. Dozens of studies inspired by an evolutionary perspective have demonstrated that during peak fertility when conception risk is highest, women experience a shift in their mating strategy, such that they focus relatively greater effort on attracting men displaying signs of good genes (Penton-Voak et al., 1999; Gangestad, Thornhill, & Garver-Apgar, 2005; Haselton & Gangestad, 2006; Gangestad, Garver-Apgar, Simpson, & Cousins, 2007; Little, Jones, & Burriss, 2007). Changes in female fertility have also been linked to mating-related responses in men: evidence suggests that men are attuned to cues of heightened female fertility and, when exposed to those cues, men display physiological, psychological, and behavioral signs of heightened sexual interest (Haselton & Gildersleeve, 2011; Miller & Maner, 2010, 2011; Miller, Tybur, & Jordan, 2007; Pipotone & Gallup, 2008; Roberts et al., 2004; however, see also Roney & Simmons, 2012).

Although the consequences of female fertility have been explored in the context of intersexual selection, fewer studies have examined the consequences of female fertility for intrasexual competition. Although there are exceptions (Fisher, 2004; Durante, Griskevicius, Hill, Perlloux, & Li, 2011; Lucas & Koff, 2013), such studies have focused on competitive responses among women who are themselves highly fertile. Very little is known about how women respond to heightened fertility levels in a same-sex rival. The current research helps fill this gap in the literature by examining how cues of female fertility affect physiological processes associated with intrasexual competition in other women. We test the hypothesis that the scent of female fertility affects other women's levels of testosterone—a hormone closely linked to intrasexual competition.

1. Intrasexual competition and female fertility

In humans and many other species, individuals frequently compete with members of their own sex in order to gain reproductive access to opposite-sex partners (Buss, 1988). Although Darwin (1871) originally thought of intrasexual competition as a primarily male phenomenon, recent evolutionary perspectives suggest that intrasexual competition is common among females, as well (Hrdy, 1981; Walters & Crawford, 1994; Fisher, 2004; Li, Smith, Griskevicius, Cason, & Bryan, 2010). In species in which both sexes invest in parental care, such as humans, both sexes discriminate in their choice of mates and compete over access to high-quality mates (Trivers, 1972).

The degree to which people perceive a same-sex individual as a threatening rival depends on whether that individual displays characteristics valued by the opposite sex. For example, men are attracted to cues of youth, fertility, and sexual accessibility in women (Symons, 1979; Buss & Schmitt, 1993) and, consequently, women are particularly vigilant of other women who display cues of youth, fertility, and sexual accessibility (e.g., Maner et al., 2003, Maner, Miller, Rouby, & Gailliot, 2009). Further, women frequently derogate and indirectly aggress against attractive women who display an interest in short-term sexual encounters (Leenaars, Dane, & Marini, 2008; Vaillancourt & Sharma, 2011). Behaviors such as derogation and aggression reflect strategies used to reduce the mate value of same-sex rivals (Buss & Dedden, 1990; Fisher, 2004). Thus, women displaying

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desirable characteristics—including youth, fertility, and sexual accessibility—serve as potent rivals for other women and, consequently, they elicit responses associated with intrasexual competition.

Combining these findings with research on menstrual cycle effects helps generate novel predictions about how women will react to other women who are highly fertile. Around the time of ovulation when fertility levels peak, women display increased interest in short-term mating with high-quality mates (those with good genes; Gangestad et al., 2007). For example, around the time of ovulation, women in relationships have strong desires for extra-pair sex and are more likely to flirt with other men, particularly when their current partner is low in attractiveness (Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006). Moreover, men are attuned to women's shifts in fertility and find women near ovulation to be particularly attractive (Haselton & Gildersleeve, 2011; also Roberts et al., 2004). Thus, around the time of ovulation, women display the very characteristics (sexual accessibility and desirability) that other women find most threatening in an intrasexual rival. Consequently, women may respond to highly fertile women in a competitive fashion. Indeed, females of many mammalian species are particularly vigilant of other females high in fertility (Ziegler et al., 1993; Palagi, Telara, & Tarli, 2004; Scordato & Drea, 2007). In yellow baboons, for example, females tend to monopolize the attention of males when other females are likely to conceive (Wasser, 1983).

2. The role of scent

For many sexually reproducing species, female fertility is detected via olfactory processes. Males are sensitive to chemosensory signals released by females during estrous (Ziegler et al., 1993, Ziegler, Schultz-Darken, Scott, Snowdon, & Ferris, 2005). Similar findings have been observed in humans, as men are attracted to the scent of women close to ovulation (Singh & Bronstad, 2001; Thornhill et al., 2003; Havlíček, Dvořáková, Bartoš, & Flegr, 2006; Miller & Maner, 2010; Gildersleeve, Haselton, Larson, & Pillsworth, 2012).

Sensitivity to olfactory fertility cues is not restricted to males. Females of a variety of species are sensitive to chemosensory signals left by same-sex rivals high in fertility (e.g., Scordato & Drea, 2007). For example, female cotton-top tamarins are more vigilant to scent marks left by high-fertility rivals (females in the periovulatory phase) than low-fertility rivals (Ziegler et al., 2005). Moreover, non-human females display competitive responses to the scent of a high-fertility rival. For example, during breeding seasons when same-sex rivals are high in fertility, female ring-tailed lemurs display increased countermarking of other females' genital marks—a behavior that reduces the value of the rival's original scent mark (Palagi et al., 2004).

In the current paper, we suggest that vigilance to rivals' olfactory fertility cues may occur in human females, and that this vigilance will be reflected in basic physiological processes. In particular, we test the hypothesis that, in response to olfactory cues of other women's high fertility, women will display heightened levels of testosterone—a physiological response associated with intrasexual competition.

3. Testosterone and intrasexual competition

Testosterone is a key hormone involved in intrasexual competition (Mazur & Booth, 1998; Archer, 2006). According to the challenge hypothesis (Wingfield, Hegner, Dufty, & Ball, 1990), during periods of social instability or when reproductive challenges arise, testosterone levels rise to facilitate intrasexual competition (e.g., fights for territory, dominance, resources, or access to a potential reproductive opportunity). This hypothesis has been applied primarily to males because they are typically the less "choosy" of the two sexes and thus are more likely to compete over potential mates (Trivers, 1972). However, as mentioned earlier, human females also engage in intrasexual competition and, consequently, the challenge hypothesis may also apply to women. Consistent with this perspective, evidence indicates that anticipation of a competition leads to increases in testosterone among women, as well as men (Booth, Shelley, Mazur, Tharp, & Kittok, 1989; Bateup, Booth, Shirtcliff, & Granger, 2002; Oliveira, Gouveia, & Oliveira, 2009; Edwards & Kurlander, 2010). Moreover, taking hormonal contraceptives, which suppress testosterone levels, decreases intrasexual competition in pair-bonded women (Cobey, Klipping, & Buunk, 2013). Thus, to facilitate intrasexual competition, women exposed to olfactory fertility cues may display heightened levels of testosterone.

4. Overview

The current research examines whether olfactory cues signaling the presence of a highly fertile female influence other women's testosterone levels. Women were exposed to the scent of women high versus low in fertility status. Salivary testosterone levels were then assessed. We hypothesized that women exposed to the scent of another woman high in fertility would display higher levels of testosterone than women exposed to the scent of a woman low in fertility.

5. Methods

5.1. Participants

Twenty-five undergraduate women (ages 18–21; 56% using oral contraceptives) participated for course credit. To prepare for the experiment, participants refrained from activities known to affect hormone levels: eating food or drinking caffeinated beverages or alcohol for 2 hours prior to testing; exercising for 12 hours prior to testing; smoking for 6 hours prior to testing. To reduce diurnal variability in testosterone levels, all participants reported to the lab between the hours of 12 pm and 4 pm.

5.2. Odor collection

Four normally cycling women with menstrual cycles lasting approximately 28 days were given two plain white t-shirts to be used as odor stimuli. The t-shirts were the same as those used in Experiment 1 of Miller and Maner (2010) and Experiment 2 of Miller and Maner (2011). One t-shirt was worn during the nights of days 13, 14, 15 of the menstrual cycle (late follicular phase—high fertility); the other was worn during the nights of days 20, 21, and 22 (luteal phase—low fertility). To reduce extraneous odors, women were asked to shower with unscented soap and shampoo and refrain from (1) using perfumes, deodorants, and antiperspirants; (2) eating odor producing food (e.g., chili, garlic, pepper, vinegar, asparagus); (3) smoking cigarettes, drinking alcohol, and using drugs; and (4) engaging in sexual activity and sleeping in the same bed as someone else. All women indicated that they adhered to these instructions. A research assistant smelled each t-shirt and confirmed that none smelled of extraneous odors (e.g., perfume, smoke). Shirts were kept in sealed plastic bags in a freezer between experimental sessions. All shirts were used within 6 days of being worn. Studies have demonstrated that freezing has little effect on subsequent odors after thawing (Roberts, Gosling, Carter, & Petrie, 2008; Lenochova, Roberts, & Havlicek, 2009).

5.3. Odor smelling

Participants were told that "the study investigates how much we can tell about another person without even meeting them. We are interested in how much people can tell about a person from their smell. Today we will be investigating this by having you smell a shirt that was worn earlier in the day by a female student. We're also interested in the role that hormones play in this process, so we'll be collecting some saliva from you throughout the experiment which will later be examined for hormones." No mention was made of ovulation, fertility, testosterone, competition, or the hypotheses of the study.

After rinsing their mouth out with water and providing a baseline saliva sample, participants were randomly assigned to smell a particular t-shirt with the constraint that, for each t-shirt supplier, a similar number of participants smelled both t-shirts worn by that woman. $N = 4$ and $N = 5$ were assigned to smell t-shirt supplier A's low- and high-fertility shirts, respectively. $N = 2$ and $N = 3$ smelled t-shirt supplier B's low- and high-fertility shirts, respectively. $N = 4$ smelled t-shirt supplier C's low- and high-fertility shirts. $N = 2$ and $N = 1$ smelled t-shirt supplier D's low- and high-fertility shirts, respectively. Thus, 13 participants were assigned to smell a t-shirt worn during high fertility (days 13–15); 12 participants were assigned to smell a t-shirt worn during low fertility (days 20–22).

Participants smelled the t-shirt three times with approximately 5 minutes between each time point (i.e., 0 minutes, 5 minutes, 10 minutes). Each time, participants put their nose to the opening of a plastic bag containing the t-shirt and took several large inhalations. These inhalations took place in a small laboratory room with the door shut and in the presence of one female experimenter. After each inhalation, the experimenter closed the bag to preserve the smell. Experimenters were blind to the phase of the shirt supplier's menstrual cycle[1].

5.4. Testosterone measurement

Participants provided three saliva samples via passive drool (approximately 4 ml per sample). The samples were collected immediately prior to initial odor exposure, approximately 7 minutes post-odor exposure (thus soon after the second inhalation), and approximately 15 minutes post-initial odor exposure (thus soon after the third inhalation). At the outset of the study, participants were provided a small bottle of water to facilitate salivation if needed. Saliva samples were frozen at −20 °C. To precipitate mucins, samples were thawed and centrifuged at 3000 rpm for 10 minutes. Supernatant was stored at −20 °C until assayed. Commercially available solid-phase Coat-A-Count^{125}I radioimmunoassay kits provided by Siemens Medical Solutions Diagnostics (Los Angeles, CA) were used to measure concentrations of testosterone (pg/ml). Standards were diluted with distilled water. Tubes were incubated overnight after adding radio-labeled tracer. All samples were processed in duplicate using a high-throughput, automated gamma counter. The intra- and inter-assay CVs were 12.1% and 5.0%, respectively, commensurate with other salivary testosterone assays including female samples (Liening, Stanton, Saini, & Schultheiss, 2010; Stanton, Liening, & Schultheiss, 2011).

6. Results

The testosterone data violated the independence assumptions of ordinary least squares procedures; testosterone observations were nested within fertility status, which was nested within donors. Thus, we tested whether smelling fertile versus non-fertile women's t-shirts predicted changes in testosterone using the following three-level growth curve model:

$$\begin{aligned} Y_{tid}(\text{Testosterone Level}) = {} & b_0 + b_{1id}(\text{Time}) + b_{2id}(\text{Fertility Status}_\text{P}) \\ & + b_{3d}(\text{Mean Fertility Status}_\text{G}) \\ & + b_{4id}(\text{Fertility Status}_\text{P} \times \text{Time}) \\ & + b_{4id}(\text{Fertility Status}_\text{G} \times \text{Time}) + r_{0id} \\ & + r_{1id} + u_{0d} + u_{1d} + e_{tid}, \end{aligned} \tag{1}$$

where t indexes time, i indexes individuals, d indexes donors, P indicates that a variable was person centered and G indicates that a variable was grand mean centered. Thus, testosterone levels were regressed onto time of testosterone assessment in the first level of the model; the intercept and slope terms of that model were regressed onto fertility status in the second level of the model. Time was coded such that Time 1 = 0, Time 2 = 1, and Time 3 = 2 (so that the intercept represented baseline testosterone levels). Mean fertility status (i.e., the proportion of donors' t-shirt's worn while she was fertile) was controlled to isolate the purely within-donor effects of fertility status (see Raudenbush & Bryk, 2002, pp. 141–143; removing this control did not meaningfully alter the results). The cross-level Fertility Status$_\text{P}$ × Time interaction thus estimates the extent to which testosterone changed differentially across participants exposed to a donor's t-shirt when she was fertile versus not fertile.

The main effect of fertility status was not significant, $t(23) = .25$, $p = .807$, indicating that baseline testosterone did not differ across the two conditions. Consistent with predictions, the Fertility × Time interaction was significant, $t(23) = 2.56$, $p = .018$, $d = 1.07$, indicating that testosterone changed differentially across the two fertility conditions. The testosterone trajectories of participants in each condition are depicted in Fig. 1. Whereas testosterone decreased over the course of the experimental session among participants exposed to the odor of a woman when she was low in fertility ($\pi = -3.36$, SE $= 1.24$, $t(2) = 2.70$, $p = .088$), testosterone remained stable (and actually increased over time, though not to a statistically significant degree) among participants exposed to the odor of a woman high in fertility ($\pi = 1.10$, SE $= 1.25$, $t(2) = 0.88$, $p = .473$). A separate analysis in which Time was recoded so that the intercept represented testosterone levels at the final assessment (Time 1 = −2, Time 2 = −1, Time 3 = 0; see Bryk & Raudenbush, 1987) indicated that, despite having similar levels of testosterone at the beginning of the study, female participants exposed to the odor of a woman when she was high in fertility had higher levels of

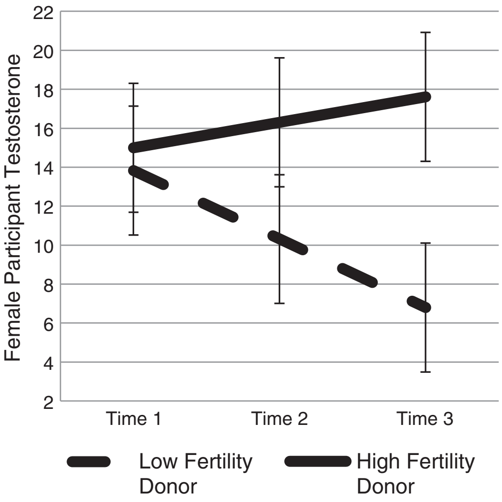

Fig. 1. Change in women's testosterone (pg/ml) varied as a function of the t-shirt wearer's fertility status. Women smelling low-fertility shirts (but not high-fertility shirts) displayed decreases in testosterone over time, such that those in the high-fertility condition displayed significantly higher testosterone levels at post-test.

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[1] As reported in Miller and Maner (2010, 2011), after the third and final saliva sample was collected, participants again smelled their assigned t-shirt and rated the odor in terms of how intense, pleasant, and attractive it smelled. Participants were also told that the t-shirt wearer had been asked to relive an emotionally arousing event; they then rated the t-shirt wearer on how angry, happy, scared, and sexually aroused she seemed. No effects of fertility status were found for these measures in the current sample. At the end of the session participants completed a battery of personality scales including the social phobia scale (Mattick & Clarke, 1998), the sociosexual orientation inventory (Simpson & Gangestad, 1991), the narcissistic personality inventory (Raskin & Terry, 1988), and the chemical sensitivity scale (Nordin, Millqvist, Löwhagen, & Bende, 2003), but data from those measures were not analyzed in the current study.

testosterone at the final assessment ($M = 17.19$, SE $= 3.13$) than female participants exposed to the odor of a women when she was low in fertility ($M = 7.20$, SE $= 3.11$), $t(23) = 2.23$, $p = .031$, $d = .93$.

We conducted supplemental analyses to examine the robustness of the predicted effect. Given the small number of t-shirt donors, we examined whether the effect was due to one or two of the donors, or whether participants' testosterone levels were similarly responsive across donors. We compared the model summarized by Eq. (1), in which all t-shirt donors were constrained to have the same effect on changes in participants' testosterone levels, to a model that allowed this effect to vary randomly across t-shirt donors. The less restrictive model that allowed donor effects to vary did not provide a better fit to the data, $\chi^2(4) = 0.12$, $p > .50$, indicating that statistically equivalent effects were observed across the four donors.

We also conducted analyses to examine whether the predicted effect was robust to several moderators known to affect fertility and testosterone responses. First, given some evidence that whether or not women are in a committed relationship moderates effects of their own fertility status on their behavior (e.g., Durante, Li, & Haselton, 2008) we examined whether the relationship status (0 = not committed, 1 = committed) of participants interacted with donor's fertility status to predict changes in testosterone. We entered the fertility status dummy code, a relationship status dummy code, the Fertility Status × Relationship Status interaction, and the Fertility Status × Relationship Status × Time interaction into Eq. (1). Neither interaction was significant (for the Fertility Status × Relationship Status interaction, $t(21) = -1.052$, $p = .305$; for the Fertility Status × Relationship Status × Time interaction, $t(21) = 1.312$, $p = .204$), suggesting that the donor's fertility status had similar effects on committed versus uncommitted women's testosterone responses. Nevertheless, given the low power of this test, we also repeated the primary analysis summarized by Eq. (1) two more times, once using only women in a committed relationship and once using only women not in a committed relationship. Despite the low power of these analyses, fertility status remained significantly predictive of changes in testosterone among committed women, $t(5) = 2.69$, $p = .043$, $d = 2.41$, and marginally predictive of changes in testosterone among uncommitted women, $t(16) = 1.88$, $p = .083$, $d = 0.94$.

Second, given some previous evidence for differential testosterone responses among women on versus not on hormonal birth control (Lopez, Hay, & Conklin, 2009), we also examined whether the birth control status (0 = no birth control, 1 = birth control) of participants interacted with donor's fertility status to predict changes in testosterone. We entered the fertility status dummy code, a birth control dummy code, the Fertility Status × Birth Control interaction, and the Fertility Status × Birth Control × Time interaction into Eq. (1). Although female participants on hormonal birth control trended toward having lower levels of testosterone than naturally cycling women at baseline, $t(21) = -1.10$, $p = .283$, the key interactive effect of contraception status and fertility status on changes in testosterone did not approach significance, $t(21) = 0.36$, $p = .721$. Nevertheless, because of the low power of this test, we also repeated the primary analysis summarized by Eq. (1) two more times, once using only women taking a form of hormonal contraception and once using only naturally cycling women. Despite the low power of these analyses, fertility status remained marginally predictive of changes in testosterone among naturally cycling women, $t(9) = 1.83$, $p = .100$, $d = 1.23$, and significantly predictive of changes in testosterone among women on hormonal contraception, $t(12) = 2.42$, $p = .032$, $d = 1.39$.

7. Discussion

Across a range of species, intrasexual competition among females is influenced by the fertility status of those females. The current research provides new evidence that a similar process may occur in humans, by demonstrating that women's testosterone levels are responsive to olfactory cues to another woman's fertility. Research in other species has documented links between female testosterone levels and intrasexual competition and aggression (Beehner, Philips-Conroy, & Whitten, 2005; Sandell, 2007). Thus, the current findings indicate not only that women are sensitive to other women's fertility status, but also that this sensitivity affects an endocrinological response known to promote female intrasexual competition.

7.1. Implications of this research

Several previous studies have shown that fertility plays a role in competition among women, but those studies have focused mainly on the possibility that women who are in their fertile phase become especially competitive with other women (Lucas & Koff, 2013). Durante et al. (2011), for example, found that when close to ovulation, women were more motivated to enhance their physical appearance in order to outcompete attractive rivals. Fisher (2004) found that on days close to ovulation, women were especially likely to derogate other women's facial appearance. The current study, in contrast, demonstrates that women exposed to fertility cues from other women display responses that are consistent with intrasexual competition. Testosterone levels themselves are not the only factor that contributes to competitive behavior; for example, androgen receptor functioning also plays a central role (Simmons & Roney, 2011). Nevertheless, the current work suggests that the fertility status of rivals might have consequences for female intrasexual competition. Indeed, in other primate species, females display the most vigilance to a rival's scent when both females are likely to conceive (Scordato & Drea, 2007).

The current findings fit with endocrinological theories of intrasexual competition. Across several species including humans, testosterone rises in anticipation of intrasexual competition as a way of motivating competitive behavior (Booth et al., 1989). Although we did not observe increases in testosterone in these studies, the relatively higher testosterone levels arising from exposure to scents of fertility suggest that those scents might lead women to respond with greater competitive behavior than they would otherwise. Indeed, in his seminal review on the association between testosterone and competition, Archer (2004) suggested that high testosterone levels among women may be associated with an assertive personality style that hinders the formation of female–female alliances and instead promotes subtle forms of female–female competition such as indirect aggression. Future research would benefit from testing whether women's testosterone responses to cues of a rival's fertility are associated with indirect aggression targeted at that rival.

The current findings also have implications for evolutionary theories of sex differences. Adaptationist theories linking testosterone with intrasexual competition have typically been applied to males. However, there is reason to suspect similar associations between testosterone and intrasexual competition among females, particularly in species in which males engage in parental care. Wingfield et al. (2000) noted that female testosterone levels (relative to testosterone levels of males) in monogamous and less sexually dimorphic species tend to be higher than in other species. They suggested that for such species, testosterone may play an important role in female competition. Indeed, for several mammalian species, androgens play an important role in competition, dominance, and aggression among females, as well as males (Gray, Whitsett, & Ziesenis, 1978; Albert, Jonik, Walsh, & Petrovic, 1989; Frank, Glickman, & Licht, 1991; Miller, Maner, & McNulty, 2012). The current findings extend those prior findings and suggest that cues to potential mating-related challenges (such as the presence of a threatening rival) may influence testosterone levels among women. Thus, although the links between intrasexual competition and testosterone have typically been applied to males, in humans they may apply to both sexes.

7.2. Limitations and future directions

Limitations of the current study provide valuable opportunities for further research. First, we can only speculate as to the specific physiological structures underlying the testosterone responses observed in the current research. Nevertheless, the extent literature could implicate the hypothalamic-pituitary-adrenal (HPA) axis. Although testosterone in women is produced in both the adrenal glands and ovaries, it is produced primarily by the adrenal glands (Jones & Lopez, 2006). Additionally, aggression has been linked to the production of adrenal androgens in females (Pajer et al., 2006) and males (Ramirez, 2003; Scotti, Belen, Jackson, & Demas, 2008). Moreover, oral contraceptives are known to suppress the production of testosterone by the ovaries (Aden, Jung-Hofman, & Kuhl, 1998); we saw no differential effects in women who were on oral contraceptives, suggesting that ovarian androgens may have accounted less for the observable variability in testosterone than androgens produced by the adrenal glands.

Second, it is important to note that scent cues of high fertility did not increase testosterone in women. Rather, they prevented the decrease in testosterone observed among participants exposed to scents of a woman low in fertility. One possible interpretation is that exposure to the scent of women at low fertility suppresses the release of testosterone. However, the pattern we observed is also consistent with that observed in male samples: Although men exposed to control scents (i.e., scents from a shirt not worn by anyone or scents from a shirt worn by a woman low in fertility) displayed a decrease in testosterone over time, men exposed to scents of women high in fertility displayed no change in testosterone levels (Miller & Maner, 2010). These findings suggest that scent cues of fertility offset a general decrease in testosterone typically observed over the course of an experimental session (e.g., Mazur, Susman, & Edelbrock, 1997; Schultheiss, Wirth, & Stanton, 2004, Schultheiss et al., 2005). Those general decreases may result from a variety of factors, including diurnal variation (testosterone levels tend to decrease across the day) and the way in which samples are collected and processed (Dabbs, 1990; Granger, Shirtcliff, Booth, Kivlighan, & Schwartz, 2004). Nevertheless, because methodological factors influencing change in testosterone apply equally across conditions, comparisons of relative changes in testosterone across conditions provide a useful picture of stimulus-driven endocrinological effects. Thus, the cross-condition comparisons in the current study reveal a pattern by which cues of high fertility led to higher testosterone levels in women than cues of low fertility.

Third, participants in the current study were explicitly told that the t-shirts they smelled had been worn by other women, which precludes a test of whether the chemical scent on its own is enough to elicit the testosterone response. Many biologists have argued that the vomeronasal organ, which is largely responsible for chemosensory communication in other species, is no longer present and functioning in humans (e.g., Johnson, Josephson, & Hawke, 1985). In addition, some studies have demonstrated null effects of female fertility on men's testosterone responses (e.g., Strom, Ingberg, Druvefors, Theodorsson, & Theodorsson, 2012). Roney and Simmons (2012) found no effects of fertile female scents on men's testosterone and argued that conscious knowledge of the scent's source may be a necessary eliciting condition for testosterone reactivity (cf. Miller & Maner, 2011). The current results do not preclude this possibility. Future research would benefit from assessing directly whether chemical scents alone are enough to affect perceiver testosterone levels in humans.

Fourth, the current study was not adequately powered to test moderating variables. Although we found no moderating effects of relationship status or hormonal contraceptive status, for instance, future research should continue to assess the potential role of those variables. In addition, participants' own phase of menstrual cycle could moderate the effects we observed, as women may be most strongly oriented toward short-term mating (and thus intrasexual competition) around ovulation (Haselton & Gangestad, 2006; Durante et al., 2011). We did not assess phase of the participants' menstrual cycle in this research, but future research would benefit from investigating potential moderating effects of this variable.

Fifth, this paper reports only a single study with a relatively small sample. Although providing suggestive evidence, the study would benefit from replication using a larger sample.

Sixth, the current research operationalized female fertility in terms of the day of a woman's menstrual cycle. Other methods (e.g., directly assessing the LH surge) provide a more precise means of identifying the timing of female ovulation, and studies would benefit from using the most precise methods available for assessing female fertility.

Finally, although the current findings are consistent with our hypothesis that women's testosterone responses reflect an orientation toward intrasexual rivalry, there is another possibility worth considering. It is possible that women's responses to female ovulation cues could partially reflect an orientation toward mating. That is, these findings could potentially reflect a component of same-sex sexuality. Some research in other mammalian species demonstrates that female fertility induces mating behaviors in both males and females. For example, Japanese macaque females are mounted by both males and females during periods of high fertility (O'Neill, Fedigan, & Ziegler, 2004). Other research in humans may suggest a similar attraction to women high in fertility: Kuukasjärvi et al. (2004) found a marginally significant effect such that women, as well as men, perceived scents of other women close to ovulation as more sexually attractive than scents of women far from ovulation. However, at least one other study found null effects of fertility scents on women's explicit ratings of sexual attractiveness (Trouton, Guitar, Carmen, Geher, & Grandis, 2012), suggesting that women's responses to the scent of other females may involve subtle or non-conscious processes. Nevertheless, women could experience some level of sexual attraction to fertile females—perhaps reflecting a byproduct of a male adaptation designed to help men identify fertility shifts in women. If women are in fact attracted to cues of fertility, heightened testosterone levels could reflect that attraction. Future studies are needed to examine more closely the extent to which cues of female fertility influence women's motives for mating versus intrasexual competition.

In closing, the current research provides evidence that women are capable of detecting a rival's ovulatory scent cues and, moreover, that those cues are linked with functionally relevant endocrinological responses. Thus, the current findings provide new information about the ways in which women's physiology may have evolved to respond to a rival's heightened fertility. Exploring the more downstream consequences of those endocrinological responses provides several intriguing directions for future research.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2013.07.005.

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