

Chapter 15: Female adaptations to ovulation

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Abstract

Particularly when compared to many other primates, human females appear to have lost any cues to their ovulatory status at some point during our evolutionary past. Until recently, it was assumed that the timing of peak fertility was hidden from both men and women.

However, current evidence suggests that subtle changes in women's behavior and preferences that correspond with the periovulatory period of a woman's menstrual cycle persist and may function to promote conception, particularly with higher quality males. Women appear more sexually motivated, are rated as more attractive, and may be better able to attract a mate around ovulation compared to other points in the cycle. Moreover, women report higher attraction to putative indicators of underlying genetic health in men when conception is most likely, which may allow offspring to reap associated genetic benefits. Critically, men seem capable of detecting subtle cues to ovulation, increasing their ratings of the attractiveness of periovulatory women and, according to their romantic partners, engaging in more mate guarding behavior. Altogether, the current research suggests that female ovulation is not entirely concealed.

Keywords: Estrus, ovulation, adaptation, menstrual cycle, attractiveness, preferences.

1 Introduction

Cues to ovulation status in nonhuman primates are varied and numerous, including exaggerated sexual swellings (Nunn, 1999), changes in proceptive and receptive behavior (Baum et al., 1977), and changes in body odor (Clarke et al., 2009). Anthropoid primates (those comprising apes, Old World monkeys, and New World monkeys) differ from the general mammalian pattern of a precise estrous period (Heistermann et al., 2001; Hrdy and Whitten, 1987). Catarrhines (apes and Old World monkeys), in particular, demonstrate ovarian cycles characterized by long follicular phases and extended periods of mating, resulting in alterations or an end to the usual harmonization between ovulation and sexual activity (Heistermann et al., 2001; Hrdy and Whitten, 1987; Nunn, 1999; van Schaik et al., 2000). Certainly, humans are not the only primate species where the female is sexually receptive throughout her cycle. For example, both chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) practice nonconceptive sexual behavior (sexual activity that cannot result in conception), but female bonobos are especially known for mating with multiple males throughout the cycle (reviewed in Wrangham, 1993).

Some female primates, such as vervet monkeys (Andelman, 1987) and Hanuman langurs (Heistermann et al., 2001), have apparently evolved the capacity to conceal ovulation from males. This may function to confuse paternity among males, possibly leading to a reduction in infanticide (Heistermann et al., 2001; Hrdy, 1979; Hrdy and Whitten, 1987; van Schaik et al., 2000). Infanticide by males is common among primates when a new male takes over breeding in a single-male group or rises to breeding status in a multi-male group. Although this behavior benefits the infanticidal male by returning nursing females to estrus, it represents a substantial reproductive loss for the females (reviewed in van Schaik et al., 2000), who invest heavily in their offspring. Therefore, an extended period of sexual activity coupled with a

polyandrous mating strategy would make assessing paternity difficult (van Schaik et al., 1999, 2000), which may affect males' propensity to commit infanticide (Borries et al., 1999; Heistermann et al., 2001; Hrdy, 1979; Robbins, 1995; Soltis et al., 2000; Schaik et al., 1999). Concealing ovulation would thus not only confuse paternity, but could also potentially allow more room for female choice by preventing dominant males from knowing when to monopolize fertile females.

2 Concealed ovulation in humans

Several scholars have suggested that human females lack estrous, a sharp increase in sexual interest and activity that typically occurs at or near ovulation, and have also evolved to conceal ovulation from males (Benshoof and Thornhill, 1979; Burley, 1979; Daniels, 1983; Manson, 1986; Marlowe, 2004; Pawłowski, 1999; Sillen-Tullberg and Møller, 1993; Strassmann, 1981; Turke, 1984). Certainly, women are continuously receptive to sexual advances throughout their menstrual cycles and ovulation is not generally consciously perceived by men or even by the ovulating women themselves (Burley, 1979). Menstruation is the only overt sign of a woman's ovulatory cycle, although there may be other, more subtle cues to a woman's fertility status (discussed later). In fact, scientists did not determine the timing of ovulation until 1930 (Burley, 1979; Campbell, 1966), prior to which some believed a woman could conceive throughout her cycle (Latz, 1939) or were most fertile near or during menstruation (Campbell, 1960). That the timing of peak fertility was unknown by medical professionals and scholars for so long demonstrates how well ovulation is concealed from both men and women. Moreover, while the Hadza, a hunter-gatherer society in Tanzania, know that sex causes conception, most wrongly believe that conception occurs immediately after menstruation ends (Marlowe, 2004). That the timing of conception is unknown in

traditional societies similar to those in which humans evolved reinforces the idea that ovulation is not consciously perceived.

Because ovulation appears to be concealed from the women experiencing it, as well as the men around them (Alexander and Noonan, 1979; Burley, 1979; Daniels, 1983; Marlowe, 2004), it may be concealed for more than one purpose. Concealed ovulation may enable women to better deceive their mates (Alexander and Noonan, 1979; Daniels, 1983) and may have evolved as a way of preventing women from avoiding conception through abstinence from intercourse near ovulation (Burley, 1979). If women had knowledge of ovulation, they would be able to exercise considerable control over their reproductive status, perhaps having fewer children or possibly none at all. Clearly, these practices are nonadaptive as they limit reproductive potential, thus physiological changes that lessened female awareness of ovulation may have been selected because women who were less aware of ovulation would have left more descendants (Burley, 1979). However, it is plausible that human females evolved the capacity to conceal ovulation, and human males lost the ability to detect ovulation, for several other related reasons. Like scholars have suggested for other primates (van Schaik et al., 1999, 2000), our extended periods of mating would make assessing paternity difficult if mating were polyandrous. Confusing paternity may have the added benefits of improving male behavior towards potential offspring (Sillen-Tullberg and Møller, 1993) and reducing rates of males committing infanticide (Borries et al., 1999; Heistermann et al., 2001; Hrdy, 1979; Robbins, 1995; Soltis et al., 2000; van Schaik et al., 1999), as they may be less likely to deduce non-paternity. Indeed, men favor children who resemble them (Burch and Gallup, 2000; DeBruine, 2004; Platek et al., 2002, 2003; Volk and Quinsey, 2002; Welling et al., 2011) and are more likely to abuse step-children or adopted children than biological children (Daly and Wilson, 1984, 1985; Wilson and Daly, 1987, 2002), indicating

that doubts surrounding paternity may increase risks to an infant and that these risks may be abated if the timing of peak fertility is unknown.

In line with the above reasoning, Alexander and Noonan (1979) argued that the lack of cues to ovulation evolved to increase paternal certainty and force males into pair bonds. In other words, they suggest that women have evolved the capacity to conceal ovulation to, in essence, trick men into long-term relationships because men will not know when or how often to copulate to ensure conception and will therefore be less tempted to leave the female to look for others to impregnate (see also Strassman, 1981; Turke, 1984). Extended receptivity, ovulatory asynchrony across women, and concealed ovulation would thus pressure men to engage in extended courtships and behave increasingly paternally (Alexander and Noonan, 1979; Turke, 1984). Furthermore, men mated to women who do not advertise their fertility status would be less victimized by mate-poaching rivals. This would increase paternity certainty and, by extension, male investment in offspring (Alexander and Noonan, 1979; Symons, 1979; Turke, 1984), which would benefit the woman. Burley (1979), however, pointed out that these arguments (Alexander and Noonan, 1979; Symons, 1979; Turke, 1984) are somewhat flawed because they imply that women obtained mates ancestrally by getting pregnant and that men's explicit purpose in seeking out females is to get them pregnant. First, because women invest more in offspring care (e.g., via gestation and lactation), it would make more sense for women to be relatively certain of male investment prior to becoming pregnant because conceiving before attaining male investment would likely promote, rather than discourage, male abandonment. Burley asserted that "[the] establishment of a pair bond prior to having offspring is a norm found in many, if not most, human cultures, and is certainly found throughout the animal kingdom when biparental care is present" (Burley, 1979, p.839). Also, because of the extended period of offspring dependency in humans, males may also

benefit from forming pair bonds as the increased paternal investment likely increased offspring survival (Alexander and Noonan, 1979; Burley, 1979; Sillen-Tullberg and Møller, 1993; Strassman, 1981), particularly in the mobile hunter-gatherer groups that predominated the ancestral past of humans (Lee and DeVore, 1968). It therefore seems unlikely that concealed ovulation evolved for the purposes of female deception used to force males into pair bonds.

However, Burley's (1979) assertion that concealed ovulation functions to prevent women from avoiding pregnancy is likely incorrect because it assumes that women's receptivity and initiation of sexual activity is not increased as a function of ovulation, which may not be the case. Indeed, women may initiate more sexual activity during the fertile period of their menstrual cycles than at other times (Adams et al., 1978; Matteo and Rissman, 1984; but see Brewis and Meyer, 2005). Others have supposed that concealed ovulation allows women greater flexibility in choosing a mate (Benshoof and Thornhill, 1979; Strassman, 1981; Symons, 1979). Concealing ovulation could facilitate cuckoldry by limiting males' perceived need to guard their partners during peak fertility and could allow women to choose genetically superior men to sire their offspring (Benshoof and Thornhill, 1979). In other words, concealed ovulation might facilitate successful deception by women seeking extra-pair copulations. Also, concealing ovulation may limit indiscriminate attention from males, thereby reducing potentially dangerous attention from unwanted suitors (Provost et al., 2008). Strassman (1981) suggests that low status males, in particular, would benefit from monogamy and investment (rather than lots of mating effort) if only they could be confident in their paternity. Concealing ovulation from males could offer this confidence by reducing the perceived risk of cuckoldry. As discussed by Marlowe (2004), ovulation would be easy to detect by men if it were in the interest of women for men to be able to detect it.

Relatively recently, evidence that cues to fertility status have not been totally lost has been accumulating (Gangestad and Thornhill, 2008). Women lack the overt cues (e.g., exaggerated sexual swellings) to fertility status that are demonstrated by many fertile nonhuman primate females (Wallen and Zehr, 2004). However, selection pressures favoring complete concealment of ovulation by women, combined with mechanisms to detect fertility status by men, may have resulted in partial concealment of ovulation. Similarly, perhaps complete concealment of ovulation would be maladaptive because women would not be better able to attract high quality men around ovulation, when conception is more likely, than during infertile phases of the menstrual cycle. Regardless of the possible reasons, it seems that, in contrast to earlier assertions, women may demonstrate semi-concealed ovulation.

3 Cues to ovulation in human females

Increasing research on physical and behavioral cues to women's fertility status has surfaced over the last decade (Gangestad and Thornhill, 2008). For example, women decrease their food consumption and increase their motor activity around ovulation (Fessler, 2003a; Gong et al., 1989), possibly to focus on other important behaviors, such as mating effort (Fessler, 2003a). Among women with premenstrual syndrome, the pre-ovulatory increase in estradiol is associated with an increase in positive mood (Bäckström et al., 1983). Women also experience improved creativity during the pre-ovulatory phase relative to the mid-luteal phase and menses (Krug et al., 1994, 1996) and improvement in some cognitive tasks around ovulation (Becker et al., 1982; Broverman et al., 1981). Overall, these studies underline the possibility that hormonal variation across the ovulatory cycle may alter female behavior. Such variations could have implications for women's reproductive status if they influence female or male mating behavior or perceptions of female attractiveness.

The variety and volume of studies investigating human sexual behavior as a function of cycle status are substantial and indicate that the fertile period of the menstrual cycle may be accompanied by an increase in physical attractiveness (e.g., Roberts et al., 2004), sexual motivation (e.g., Grammer et al., 1997), and sexual activity (e.g., Adams et al., 1978; Wilcox et al., 2004; but see Brewis and Meyer, 2005). Ovulatory cues may even be perceived by men to some extent (Haselton and Gildersleeve, 2011) and may be accompanied by other adaptive behaviors, such as shifts in preferences toward cues to genetic fitness when conception is most likely (Gangestad and Thornhill, 2008; Jones et al., 2008). These subtle physical and behavioral signs of conception risk indicate that the previously accepted conclusion that women have evolved to conceal ovulation does not fully represent reality.

3.1 Changes in attractiveness

The long-held assumptions that physical cues to human female fertility status and that changes in female attractiveness as a function of fertility status have disappeared over time have been challenged by recent findings. Women are rated as more attractive in terms of facial appearance (Puts et al., in press; Roberts et al., 2004), vocal characteristics (Bryant and Haselton, 2009; Pipitone and Gallup, 2008; Puts et al., in press), and body fat distribution (i.e., have a more attractive waist-to-hip ratio, Kirchengast and Gartner, 2002) around ovulation than at other, nonfertile times in their menstrual cycles. Peak fertility is associated with greater breast symmetry (Manning et al., 1996; Scutt and Manning, 1996), with symmetric breasts possibly signaling underlying phenotypic quality and fertility in women (Manning et al., 1997). Finally, one study found that naturally-cycling (i.e., not using hormonal contraceptives) exotic dancers receive more tips during peak fertility versus other points in the menstrual cycle (Miller et al., 2007). While it remains unclear whether changes in physical or

behavioral characteristics (or both) in women at ovulation are driving this change in male spending patterns, it is nonetheless striking.

Women, similar to females of several other primate species (e.g., Cerda-Molina et al., 2006; Crawford et al., 2011; Smith and Abbott, 1998), appear to have a more appealing body odor around peak fertility (Doty et al., 1975; Gildersleeve et al., 2012; Havlíček et al., 2006; Kuukasjärvi et al., 2004; Miller and Maner, 2010; Singh and Bronstad, 2001; Thornhill et al., 2003). Doty et al. (1975) found that male judges rated the scent of vaginal secretions sampled at high fertility as more pleasant than vaginal secretion samples taken from the same women at low fertility. Sampling body odor using cotton pads worn in the armpit for 24 hours in 3 different menstrual cycle phases, Havlíček et al. (2006) found that men rated the odor of women in the fertile follicular phase of their menstrual cycles as more attractive than the odor of women in the menstrual or luteal phases. Together with the evidence of increased physical and vocal attractiveness at ovulation, these studies suggest that a woman's attractiveness and, by extension, her ability to attract a mate are highest on the fertile days of her cycle, which would not be expected if ovulation was truly no longer detectable in women. Thus, it appears that men are maximally attracted to ovulating women.

Women also use strategies to augment their physical attractiveness around ovulation, with several studies finding that women modulate their appearance and clothing to enhance their attractiveness when they are most fertile (Durante et al., 2008; Haselton et al., 2007; Hill and Durante, 2009; Röder et al., 2009; Schwarz and Hassebrauck, 2008), possibly as a reaction to a periovulatory decrease in self-esteem (Hill and Durante, 2009). Using diary data from 40 naturally-cycling women and male ratings of photographs, Schwarz and Hassebrauck (2008) found that women dressed more provocatively and were rated as more attractive during high-

fertility days compared to low-fertility days (Durante et al., 2008; Haselton et al., 2007).

Women also report feeling more attractive and desirable (Röder et al., 2009; but see Schwarz and Hassebrauck, 2008), and draw more revealing, sexier clothing when asked to illustrate an outfit they would wear to a social function (Durante et al., 2008) near ovulation. Lastly, Hill and Durante (2009) found that women's self-esteem decreases near ovulation, when they are most attractive to men, which may function to increase motivation to enhance attractiveness. Collectively, these studies suggest an increase in women's sexual motivation and desire to attract a mate while fertile.

3.2 Sexual behavior and motivation

Peak fertility is accompanied by an increase in motor (Morris and Udry, 1970) and sexual activities (Morris and Udry, 1982), with some evidence indicating that sexual encounters increase (Wilcox et al., 2004; but see Brewis and Meyer, 2005) and are more likely to be female-initiated around ovulation (Adams et al., 1978; Matteo and Rissman, 1984). Ovulation is also associated with an increase in sexual desire (Stanislaw and Rice, 1988) and fantasy (Regan, 1996), attention to attractive men (Anderson et al., 2010), sexual self-stimulation (Harvey, 1987), and arousal in response to sexually explicit material (Slob et al., 1996; Zillmann et al., 1994). Furthermore, women describe an increased desire for orgasm at peak fertility compared to other points in the menstrual cycle (Regan, 1996), which may have important implications if, as some research suggests (Baker and Bellis, 1993; Wildt et al., 1998; Zervomanolakis et al., 2009), orgasm increases the likelihood of conception. Therefore, contrary to the idea that women have evolved the capacity to conceal ovulation from themselves and others, the signs of peak fertility may simply be less overt than they are in some other primates. Additionally, attitudes towards risk-taking, which are correlated with the probability of victimization (Fetchenhauer and Rohde, 2002), may decrease at ovulation

(Bröder and Hohmann, 2003; Chavanne and Gallup, 1998), which suggests that women alter their behavior to avoid rape and possible impregnation by unwanted males, although one study has found that rape is no less frequent during the ovulatory phase of the menstrual cycle (Fessler, 2003b). Similarly, ratings of disgust toward incest increase around mid-cycle (Fessler and Navarrete, 2003). Taken together, these findings intimate an increase in sexual motivation associated with peak fertility that is accompanied by a decrease in behaviors that may lead to a detrimental pairing.

The apparent changes in female sexual psychology associated with conception risk appear to elevate competition with same-sex competitors over potential mates. Women derogate same-sex competitors by downplaying their physical attractiveness (Fisher, 2004; Jones et al., 2011; Vukovic et al., 2009; Welling et al., 2007), which causes men to lower their attractiveness ratings of the derogated rivals (Fisher and Cox, 2009). Fisher (2004) found that competition and derogation, meaning any act intended to decrease the perceived value of a rival, increased during periods of the menstrual cycle characterized by high estrogen, such as ovulation. While presumed estrogen level was negatively related to women's ratings of the facial attractiveness of other women, there was no relationship between estrogen and women's ratings of the attractiveness of male faces (Fisher, 2004). Correspondingly, Vukovic et al. (2009) found that post-menopausal women rated photographs of feminine-faced (i.e., attractive, O'Toole et al., 1998) women as more attractive than pre-menopausal women, but there was no difference in ratings of male faces (see also Jones et al., 2011). This effect was independent of possible effects of participant age and suggests that dislike of attractive same-sex competitors decreases as fertility decreases (Jones et al., 2011; Vukovic et al., 2009). Women also feel more attractive (Röder et al., 2009; Schwarz and Hassebrauck, 2008) and are more willing to spend money on sexy, rather than functional, clothing (Hill and Durante,

2009) around ovulation than at other times, though they do not spend money at an increased rate more generally at ovulation (Röder et al., 2009).

There is some evidence, as indicated by pupil dilation, that women have a greater interest in their primary partners during the fertile phase of the menstrual cycle, but this pattern is also observed in response to attractive opposite-sex celebrities (Laeng and Falkenberg, 2007), suggesting a general response not directed specifically at long-term partners. Additionally, although Brewis and Meyer's (2005) large-scale cross-cultural study on sexual intercourse over the menstrual cycle found no increase in sexual intercourse around ovulation, this study only looked at coitus rates among married couples. It is possible that ovulation-related changes in sexual behavior would be more evident in short-term mating contexts and/or extra-pair copulations (see Gangestad and Simpson, 2000). Certainly, a significant amount of research suggests that women increase their interest in extra-pair, versus in-pair, men surrounding ovulation. Women are less motivated toward sex for the purposes of intimacy (Sheldon et al., 2006) and are more sexually opportunistic (Gangestad et al., 2010) near ovulation than at other times. They demonstrate a greater interest in attending social gatherings (Haselton and Gangestad, 2006), visiting singles nightclubs without their romantic partner (Grammer et al., 1997), extra-pair men (Gangestad et al., 2002), extra-pair sexual activity (Baker and Bellis, 1995; Bellis and Baker, 1990), and extra-pair sexual fantasies (Gangestad et al., 2002) around ovulation. Women also report less commitment to, and relationship satisfaction with, their current primary partner, and feel and are perceived by others to be more desirable and physically attractive around ovulation, possibly because of increases in estradiol levels (Durante and Li, 2009). Certainly, high estradiol, which first peaks around ovulation in humans (Baird and Fraser, 1974), appears to play a role in female

receptivity to copulatory solicitation across several species (Beach, 1948; Kendrick and Dixson, 1985).

That ovulation is associated with increased attractiveness (Bryant and Haselton, 2009; Havlíček et al., 2006; Kirchengast and Gartner, 2002; Kuukasjärvi et al., 2004; Miller et al., 2007; Pipitone and Gallup, 2008; Puts et al., in press; Roberts et al., 2004; Singh and Bronstad, 2001) and increases in possible sexually-motivated behavior (Durante et al., 2008; Grammer et al., 1997; Haselton et al., 2007; Hill and Durante, 2009; Röder et al., 2009; Schwarz and Hassebrauck, 2008) contradicts the supposition that humans have lost estrus. However, it is worth underlining that cues to human fertility over the menstrual cycle are very subtle, indicating that obvious fertility signals that would attract indiscriminate attention, potentially cause dominant males to monopolize fertile women, and constrain or eliminate female choice would be detrimental. Nonetheless, ovulation is associated with several within-subject changes, including a greater interest in extra-pair men among women with partners who carry less complementary MHC alleles (Garver-Apgar et al., 2006), among women with less attractive partners (Haselton and Gangestad, 2006; Pillsworth and Haselton, 2006), and among women with less symmetrical partners (Gangestad et al., 2005). These latter findings may reflect a tendency to seek out men of better genetic quality when conception is likely. Therefore, it is possible that women engage in a dual-mating strategy, whereby they seek out men of high genetic quality when conception is likely in order to secure good genes for potential offspring and seek out caring, investing mates during other times (Gangestad and Simpson, 2000).

3.3 Cyclic variation in preferences for male traits

According to the ovulatory shift hypothesis, systematic changes in female mating-related behavior and preferences should be expected over the course of the menstrual cycle (Gangestad and Thornhill, 1998; Grammer, 1993; Thornhill and Gangestad, 1999). Women who procreate with genetically fit men may reap reproductive benefits if those genes are passed on to offspring because it could increase the likelihood that the offspring will survive and eventually reproduce themselves. Using this reasoning, preferences should not necessarily remain constant because men who possess good genes may not offer other benefits to the mother and child, such as caring or investing behaviors (Perrett et al., 1998). However, preferences for good genes should be maximal at peak conception (Gangestad and Thornhill, 1998). In fact, there is evidence that men who possess good genes invest less in their mates and offspring (Penton-Voak and Perrett, 2001; Perrett et al., 1998), explaining why preference shifts for putative cues to good genes are most pronounced when women judge men's attractiveness for a short-term (i.e., sexual) relationship versus a long-term (i.e., committed) one (Gangestad et al., 2004; Little et al., 2002, 2007a; Little and Jones, 2011; Penton-Voak et al., 1999; Puts, 2005).

Several researchers have hypothesized that attractiveness judgments reflect evolved preferences that identify aspects of underlying mate quality and heritable immunity to multiple forms of genetic and environmental stress (e.g., DeBruine et al., 2010, 2011; Fink and Penton-Voak, 2002; Langlois et al., 1994; Miller and Todd, 1998; Møller and Thornhill, 1998; Thornhill and Gangestad, 1993). Consistent with this view, male facial attractiveness has been found to be positively related to a genetic profile associated with immunity to infectious diseases (Lie et al., 2008; Roberts et al., 2005), good semen quality (Soler et al., 2003; but see Peters et al., 2008), reproductive success (Jokela, 2009), and longevity (Henderson and Anglin, 2003). More specifically, traits such as symmetry and masculinity

affect male attractiveness and are thought to signal genetic quality (reviewed in Gangestad and Thornhill, 2008), with symmetric (Miller and Todd, 1998; Thornhill and Møller, 1997; Waynforth, 1998) and masculine (Apicella et al., 2007; Rhodes et al., 2003, 2005; Thornhill and Gangestad, 2006) traits positively related to long-term health and reproductive success in men.

In line with the ovulatory shift hypothesis, several studies report increases in women's preferences for putative cues to male mate quality, including preferences for the odor of men who are more dominant, symmetrical, and heterozygous at the MHC (Gangestad and Thornhill, 1998; Havlíček et al., 2005; Rikowski and Grammer, 1999; Thornhill and Gangestad, 1999; Thornhill et al., 2003). Women also demonstrate a stronger preference for male facial symmetry (Little et al., 2007b; but see Cárdenas and Harris, 2007; Koehler et al., 2006), the faces of men with symmetrical bodies (Thornhill and Gangestad, 2003), masculine male faces (Johnston et al., 2001; Jones et al., 2005a; Little et al., 2008; Penton-Voak and Perrett, 2000; Penton-Voak et al., 1999; Welling et al., 2007), masculine male body shape (Little et al., 2007c), masculine vocal characteristics in men's voices (Feinberg et al., 2006; Puts, 2005), and height (Pawlowski and Jasienska, 2005) around ovulation than at other times in the menstrual cycle. These shifts in preferences are likely driven by hormonal variation across the menstrual cycle, although debate still surrounds whether menstrual cycle preference shifts are driven by estradiol (Feinberg et al., 2006; Garver-Apgar et al., 2008; Roney and Simmons, 2008; Rosen and López, 2009; Rupp et al., 2009), progesterone (Garver-Apgar et al., 2008; Jones et al., 2005a; Puts, 2006; Rupp et al., 2009), prolactin (Puts, 2006), testosterone (Welling et al., 2007), cortisol (López et al., 2009), or some hormonal combination (Frost, 1994; Garver-Apgar et al., 2008; Lukaszewski and Roney, 2009; Puts, 2006; Welling et al., 2007). Furthermore, women's accuracy at classifying faces as male is

greatest at peak fertility (Macrae et al., 2002), particularly when those faces are more sex-typical (i.e., masculine, Johnston et al., 2008). Notably, lesbian women categorize female, not male, faces more accurately around ovulation (Brinsmead-Stockham et al., 2008), which suggests that these findings are dependent on the mate choice relevance of the target faces.

In line with the above findings for physical traits, preferences for non-physical traits, such as male dominant and competitive behavioral displays (Gangestad et al., 2007; Gangestad et al., 2004; Lukaszewski and Roney, 2009) and courtship language (Rosen and López, 2009) are also highest around ovulation in women. Using video clips of men competing for a lunch date, Gangestad et al. (2004) found that women rated men who displayed social presence and direct intrasexual competitiveness as more attractive on high-fertility days of the menstrual cycle than on low-fertility days, although this association was only evident when judging men's attractiveness for a short-term (versus long-term) relationship. More recently, Guéguen (2009a, 2009b) found that women are more likely to agree to a man's request to exchange phone numbers or dance if they are in the late-follicular phase of the menstrual cycle (the fertile phase immediately preceding ovulation) compared to the luteal phase of the menstrual cycle (the non-fertile phase following ovulation), indicating that women may be most receptive to courtship at peak fertility. Therefore, changes in women's preferences for male traits generalize to behavioral ones and are not limited to physical characteristics.

4 Male detection of ovulation

In addition to assuming that ovulation is concealed from women's conscious detection (e.g., Burley, 1979; Daniels, 1983), those who argue that ovulation is concealed also stipulate that it is imperceptible to men (e.g., Marlowe, 2004; Pawłowski, 1999; Strassmann, 1981). That women are rated as more attractive near ovulation (Bryant and Haselton, 2009; Doty et al.,

1975; Havlíček et al., 2006; Kirchengast and Gartner, 2002; Kuukasjärvi et al., 2004; Miller and Maner, 2010; Pipitone and Gallup, 2008; Puts et al., in press; Roberts et al., 2004; Singh and Bronstad, 2001; Thornhill et al., 2003) suggests that physical cues to ovulation can be perceived by others. Moreover, as mentioned earlier, Miller et al. (2007) found that naturally-cycling lap dancers earn significantly more money in tips at high fertility (\$335 per shift) than at low fertility (\$260 per shift) across the menstrual cycle. This result effectively demonstrates that women are not only more attractive at ovulation, but that this change in attractiveness can also have a direct impact on male behavior.

Attractive women have particularly high mating standards (Buss and Shackelford, 2008), receive more male attention (Buss and Barnes, 1986), and are more likely to be poached by a rival (Schmitt and Buss, 2001). Given that women appear to be more attractive and sexually motivated around mid-cycle, and also show more interest in extra-pair copulations, increased attention from long-term partners would be expected in order for men to decrease the likelihood that their partner will stray or be poached by a rival. In fact, three studies have shown a relationship between female conception risk and female perceptions of attentive, jealous, and proprietary behaviors from their male partners (Gangestad et al., 2002; Haselton and Gangestad, 2006; Pillsworth and Haselton, 2006). Jealousy and other mate guarding behaviors are hypothesized to function to reduce the likelihood of a partner straying or being poached (e.g., Buss, 1988; Daly et al., 1982; Shackelford et al., 2005, 2008; Welling et al., 2011), which, given that the potential reproductive costs of infidelity would be highest around ovulation, would make an increase in these behaviors at peak fertility a potentially adaptive tactic. Gangestad et al. (2002) asked women about their sexual interests and the behavior of their partners twice: once within 5 days before a luteinizing hormone surge (i.e., at high fertility) and once during the luteal phase (i.e., at low fertility). They found that women

reported greater interest in, and fantasy about, extra-pair men during the high-fertility test session compared to the low-fertility test session. There was no effect of fertility status on women's interest in or fantasy about their primary partners. Interestingly, women also reported that their primary partners were more attentive and proprietary towards them near ovulation than during the luteal phase, suggesting that men engage in more mate retention tactics when their partners are more likely to get pregnant (Gangestad et al., 2002).

Haselton and Gangestad (2006) expanded on the above work, finding that partnered women reported more extra-pair flirtations and an increase in mate guarding tactics by their partners near ovulation. The increase in mate retention tactics was modulated by female attractiveness, whereby the mid-cycle shift in mate guarding behaviors by primary partners was higher for less attractive women versus attractive women (who experience relatively high levels of mate guarding throughout the cycle). Also, this male increase in proprietary behaviors during their partner's fertile phase is strongest in men with partners demonstrating a stronger desire to engage in extra-pair mating (Gangestad et al., 2002; Haselton and Gangestad, 2006), suggesting either that women's attention to extra-pair men may drive this increased attention or that men are sensitive to other fertility-associated cues and become more responsive to the threat of extra-pair men as a result. Men do indeed increase their ratings of the dominance of other men when their partners are fertile (Burriss and Little, 2006), which supports the notion that men are able to detect the increased risk of cuckoldry, at least to some extent.

Importantly, these findings demonstrate that partner ovulation-dependent shifts in male behavior may be sensitive to possible fitness rewards (Haselton and Gangestad, 2006).

Similarly, women with less sexually attractive partners report receiving more love and attention from their male partners around ovulation than women who rated their partners as more sexually attractive (Pillsworth and Haselton, 2006). While these reported increases in

mate retention tactics may be reactionary to women's increased attractiveness (e.g., Miller et al., 2007) and interest in extra-pair males (e.g., Gangestad et al., 2002), these findings contrast with the concept that ovulation is fully concealed. However, converging evidence from the male partners themselves is needed because, at present, it is not clear whether these female perceptions reflect an actual increase in male behavior, or whether women simply notice these behaviors more when their interest in extra-pair men is highest.

A recent double-blind study provides additional evidence that men both perceive subtle cues to ovulation and that those cues affect their mating behaviors. Miller and Maner (2010) investigated how the scents of women at peak fertility influence male endocrinological responses by having men smell T-shirts worn by women near ovulation or T-shirts worn by the same women during the luteal (nonfertile) phase of the menstrual cycle. Prior to smelling the T-shirt randomly assigned to them, men provided a baseline saliva sample that was used to measure testosterone level. Next, participants smelled the T-shirt three times over a 15-minute interval and then provided another saliva sample. They found that, when controlling for baseline testosterone levels, testosterone was substantially higher in men exposed to the odor of a woman close to ovulation than in men exposed to the odor of a woman in the luteal phase of her cycle (Miller and Maner, 2010; but see Roney and Simmons, 2012). This is the first research to provide direct evidence that olfactory cues to female fertility across the menstrual cycle can influence male hormonal responses. Testosterone levels in men are associated with competitiveness and dominance (Mazur and Booth, 1998; Zitzmann and Nieschlag, 2001), which are behavioral cues that women find particularly attractive at ovulation (Gangestad et al., 2004). Significantly, some evidence suggests that men's testosterone levels respond to mating-relevant cues, such as interacting with a woman (Ronay and von Hippel, 2010; Roney et al., 2007; Roney et al., 2003) or viewing erotic films (Hellhammer et al., 1985; Rubin et al.,

1979), suggesting that testosterone may be related to an increase in men's mating motivation. In line with this hypothesis, male exposure to the scent of a woman near ovulation leads to increased implicit accessibility of sexual concepts and heightened perceptions of women's sexual arousal (Miller and Maner, 2011). Men are also more likely to mimic a woman (a behavior that reflects attraction between people) and make risky decisions (a decision-making strategy men use to display desirable traits to women) when face to face with a fertile-phase female confederate than when interacting with a confederate during other, nonfertile menstrual cycle phases (Miller and Maner, 2011). These findings thus imply that men not only perceive cues to female conception risk, but also that these cues may have a direct influence on their behavior.

5 Hormonal contraceptives

It is highly probable that the various changes that occur over the ovulatory cycle are driven by natural changes in hormone levels (e.g., Garver-Apgar et al., 2008; Jones et al., 2005a, 2008; Little et al., 2006, 2008; Puts, 2006; Puts et al., in press; Welling et al., 2007). Given this relationship, it is perhaps predictable that these hormone-mediated changes in women's appearance, behavior, and preferences are largely absent in women using hormonal contraceptives (e.g., Gangestad et al., 2007; Guéguen, 2009b; Jones et al., 2005b; Krug et al., 1994; Laeng and Falkenberg, 2007; Little et al., 2007c; Pawlowski and Jasienska, 2005; Penton-Voak et al., 1999; Puts, 2005, 2006; Rosen and López, 2009). For example, changes in gross electrical activity in the brain over the menstrual cycle, and the corresponding increase in scores on certain performance tasks during the periovulatory period, are not present in women using hormonal contraceptives (Becker et al., 1982). Also, the rise in female-initiated sexual activity around peak fertility is eliminated in hormonal contraceptive users (Adams et al., 1978).

Hormonal contraceptives may interfere with the cyclic nature of women's attractiveness. As mentioned, women are rated as more attractive around ovulation compared to other points in the cycle (e.g., Bryant and Haselton, 2009; Miller et al., 2007; Pipitone and Gallup, 2008; Puts et al., in press; Roberts et al., 2004), but studies have found no such variation in attractiveness in women using contraceptives (Kuukasjärvi et al., 2004; Miller et al., 2007; Pipitone and Gallup, 2008). In contrast to naturally-cycling women, hormonally-contracepting lap dancers showed no earnings peak associated with cycle phase (Miller et al., 2007). Pill users also show no peak in odor (Kuukasjärvi et al., 2004) or vocal (Pipitone and Gallup, 2008) attractiveness. This may limit women's overall ability to attract a high-quality mate. Additionally, women's potentially adaptive shifts in preferences over the menstrual cycle, such as increases in preferences for masculinity (Penton-Voak et al., 1999; Puts, 2006) and male scent (Thornhill and Gangestad, 2003), and shifts in attention toward courtship language (Rosen and López, 2009), are not present in hormonal contraceptive users. These findings have led some researchers to speculate that the hormonal contraceptive pill may detrimentally influence mate preferences and mate choice (Alvergne and Lummaa, 2009; Havlíček and Roberts, 2009; Roberts et al., 2008; Wedekind and Füre, 1997; Welling, in press). Regardless, the absence of menstrual cycle shifts in attractiveness, behavior, and preferences in hormonal contraceptive users emphasizes the importance of underlying hormonal mechanisms on human mating behavior and psychology.

6 Conclusions

Previously, it has been argued that women would not benefit from advertising their fertility status for several reasons, such as the possibility that advertising high conception risk may lead to unwanted male attention that could constrain female choice (Gangestad and Thornhill,

2008; Thornhill and Gangestad, 2008). However, because women are more attractive, appear more sexually motivated, and increase their preferences for putative cues to male genetic quality around ovulation, and because men appear capable of detecting these subtle cues to ovulation, it is evident that ovulation is not entirely concealed. This has led some to speculate that women have evolved to conceal cues to ovulation, but that men have simultaneously evolved to detect ovulation (Gangestad and Thornhill, 2008; Haselton and Gildersleeve, 2011; Thornhill and Gangestad, 2008). This view stipulates that the existing signs of approaching ovulation are not shaped by selection, but leak out despite female selection to conceal them. Alternatively, it is possible that selection favored cues that are subtle enough to allow women to avoid unwanted male attention, but that also allow them to attract attention from desired mates at opportune times. Behavioral cues could be especially easily directed toward desired mates. This would provide women with clear reproductive advantages and may also benefit male partners, who may be more likely than other men to detect these fertility-related changes in their partners (Haselton and Gildersleeve, 2011) and may engage in tactics designed to reduce the risk of cuckoldry (Gangestad et al., 2002; Haselton and Gangestad, 2006; Pillsworth and Haselton, 2006).

As mentioned, the specific endocrine mechanisms behind women's changes in attractiveness, behavior, and preferences are still under debate. In many species, including nonhuman primates (Wallen and Zehr, 2004), estrogen seems to facilitate estrus behaviors (Giraldi et al., 2004). In human females, although some researchers have found associations with estradiol and periovulatory changes (Feinberg et al., 2006; Garver-Apgar et al., 2008; Roney and Simmons, 2008; Rosen and López, 2009; Rupp et al., 2009), other work has found independent effects of progesterone (Jones et al., 2005a), prolactin (Puts, 2006), testosterone (Welling et al., 2007), cortisol (López et al., 2009), or a combination of various hormones

(Frost, 1994; Garver-Apgar et al., 2008; Lukaszewski and Roney, 2009; Puts, 2006; Welling et al., 2007). For instance, Puts et al. (in press) found that progesterone and its interaction with estradiol negatively predicted vocal attractiveness and overall (facial plus vocal) attractiveness to men across the cycle, but that progesterone alone negatively predicts ratings of facial attractiveness. Therefore, it is possible that the causes of estrus-like behaviors in women are less straight forward than similar behaviors in other primates, indicating that more work on the hormonal mechanisms underpinning women's cyclic shifts is clearly needed.

Contrary to earlier assertions, current research suggests that women's ovulatory status is not entirely hidden. Although overt signals that indicate impending ovulation, like those present in some other primates (Baum et al., 1977; Clarke et al., 2009; Nunn, 1999), are absent or reduced in human females, subtle indicators of peak fertility remain. Indeed, observable cues to ovulation and associated shifts in behavior and preferences are becoming increasingly well-documented. Continued investigation of these cyclic shifts promises to further illuminate important design features of human mating psychology and elucidate the mating dynamics of ancestral human populations.

7 References

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