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Ovulation, sex hormones, and women's mating psychology

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Keywords

menstrual cycle; mate preferences; mating; attractiveness; person perception

Abstract

The Dual Mating Strategy hypothesis proposes that women's preferences for uncommitted sexual relationships with men displaying putative fitness cues increase during the high-fertility phase of the menstrual cycle. Results consistent with this hypothesis are widely cited as evidence that sexual selection has shaped human mating psychology. However, the methods used in most of these studies have recently been extensively criticized. Here we discuss (1) new empirical studies that address these methodological problems and largely report null results and (2) an alternative model of hormonal regulation of women's mating psychology that can better accommodate these new data.

The Dual Mating Strategy hypothesis

Effects of fertility and hormonal status on women's mate preferences and sexual desire are widely cited as evidence that sexual selection (natural selection operating on the ability to obtain a mate) has shaped mating psychology in humans [1-8]. But do hormones regulate mating psychology in women? If so, how? And why? The last twenty years of research on this topic has been dominated by the Dual Mating Strategy hypothesis [1-8]. The Dual Mating Strategy hypothesis of ovulatory shifts in mating psychology proposes that heterosexual women show stronger preferences for uncommitted sexual relationships with men displaying putative cues of reproductive fitness (e.g., masculinized faces) during the high-fertility ovulatory phase of the menstrual cycle, while preferring long-term relationships with men displaying putative cues of prosociality, (e.g., feminized faces), at other points in the menstrual cycle [1-8]. In the most common version of this hypothesis these putative cyclic shifts in mate preferences and mating strategies (i.e., mating psychology) are predicted because they would, in theory, maximize the potential benefits of women's mate choices by seeing them secure prosocial, investing long-term partners while fathering healthy children via short-term relationships with men with heritable immunity to infectious illnesses. Controversially, obtaining good fitness genes for offspring via 'stealth' (i.e., cuckoldry) is an explicit feature of the Dual Mating Strategy hypothesis [1-8].

In this article, we will discuss evidence from new large-scale studies that strongly challenge this dominant and influential hypothesis. We also outline how the results of these new studies instead support an alternative framework in which women's general mating motivation increases during the fertile phase of the menstrual cycle, potentially reflecting fertility-linked change in motivational priorities [9].

Evidence for the Dual Mating Strategy hypothesis

Although the links are debated [see Box 1], some studies have reported that masculine characteristics in men's faces are positively associated with good physical health [10] and immunocompetence [11] and negatively associated with prosociality and willingness to invest effort in relationships [12,13]. Consequently, one of the most common tests of the Dual Mating Strategy hypothesis has been to compare preferences for masculine male faces when women are tested during the ovulatory phase of the menstrual cycle and during other phases [1]. Figure 1 shows examples of the type of stimuli (masculinized and feminized faces) typically used to test this hypothesis. One early, and particularly influential, study to have used such stimuli [2] found that women showed stronger preferences for masculine male faces when tested during the ovulatory phase of the menstrual cycle than when tested outside this high-fertility window. This cyclic shift in masculinity preference appeared to be most pronounced when partnered women (i.e., women in romantic relationships) assessed men's attractiveness for hypothetical short-term, rather than long-term, relationships. Many subsequent studies of women's preferences for facial masculinity reported similar results [4,14-21].

Similar patterns of results have also been reported by studies investigating changes in women's preferences for other putative fitness cues in men, such as body masculinity [22], vocal masculinity [23,24], facial symmetry [20,25], body odors of symmetric [26,27] or dominant [28] men, and behavioral displays of dominance [29,30]. Because the ovulatory phase of the menstrual cycle is characterized by high estradiol and low progesterone ([31] see Figure 2), cyclic shifts in women's mate preferences are generally thought to reflect the effects of estradiol and/or progesterone [17,19,21]. This being the case, the Dual Mating Strategy hypothesis also predicts that women's mate preferences will track changes in estradiol and/or progesterone, although some research has also implicated testosterone [16] and cortisol [21].

Findings consistent with the Dual Mating Strategy hypothesis, such as those described above, are influential and widely cited as evidence that sexual selection has shaped women's mate preferences [1-8]. However, there have recently been several prominent methodological criticisms of these studies.

Methodological problems with previous research

First, power analyses show that the majority of studies cited as evidence for the Dual Mating Strategy hypothesis are underpowered, many very badly so [34]. For example, to detect a medium effect with 80% power in a within-subject design when the timing and/or occurrence of ovulation was confirmed requires 55 to 71 participants, depending on whether participants were assigned to specific high- and low-fertility test sessions or a representative random sample of cycle days were tested [34]. To detect a medium effect with 80% power in a between-subject design would require 900 to 1000 participants [34]. Importantly, very few published studies reporting significant effects of cycle phase on mate preferences meet these criteria [34,35]. For example, the mean sample size in within-subject studies reporting significant effects of fertility on facial masculinity preferences published before 2018 is 40 and the median is 34 [35].

Second, most studies cited as evidence for the Dual Mating Strategy hypothesis relied on self-report data regarding the number of days since the onset of the last period of menstrual bleeding or expected number of days until the onset of the next period of menstrual bleeding to estimate women's position in the menstrual cycle [1,34,36]. Both empirical [37] and simulation [34] studies clearly demonstrate that such self-report methods do a poor job of reliably estimating women's position in the menstrual cycle. Nonetheless, a longitudinal study of over 26,000 diary entries from 1043 women [38], recently showed that robust effects of fertility on aspects of mating psychology can be obtained using self-report diary data in large longitudinal datasets.

Third, studies testing the Dual Mating Strategy hypothesis have often used cross-sectional (i.e., between-subject) designs [1,31]. These studies have reported mixed results, potentially because they were generally particularly badly underpowered [34] and/or because the substantial genetic variation in mate preferences [39] means between-subject designs are unsuitable for detecting what are presumably relatively subtle effects of sex hormones on preferences. Because of these issues, researchers have recently emphasized the importance of using longitudinal (i.e., within-subject) designs to test for changes in women's mate preferences during the menstrual cycle [1,31,35].

Do recent studies support the Dual Mating Strategy hypothesis?

There has recently been a concerted effort by many researchers to address these potentially important methodological limitations. For example, several recent large-scale, within-subject studies have investigated women's preferences for facial masculinity [40-42], beardedness [42,43], body masculinity [41,44], facial symmetry [41], or vocal masculinity [45] using luteinizing hormone (LH) tests and/or other hormone measures to confirm the timing and occurrence of ovulation. Notably, none of these studies observed significant effects of fertility on women's preferences for masculine or symmetric men. Those within-subject studies testing whether women's preferences for facial masculinity, facial symmetry, or body masculinity tracked changes in salivary estradiol and/or progesterone also typically found no evidence for hormonal regulation of women's mate preferences [35,46]. Although some longitudinal studies have reported positive effects of estradiol and/or negative effects of progesterone on women's masculinity preferences [42,47], the largely null results from these rigorous tests of the Dual Mating Strategy hypothesis suggest that the previously reported effects of cycle phase and steroid hormones on mate preferences are either not robust or are more complicated than has previously been claimed. Key features of recent longitudinal studies of women's mate preferences that challenge the Dual Mating Strategy hypothesis are summarized in Table 1.

Table 1. Mate-preference studies challenging the Dual Mating Strategy hypothesis.

Study	**N**	**Frequency of testing**	**Key outcome variables**	**Confirmed ovulation?**	**Evidence for within-women correlations with conception risk?**	**Evidence for within-women correlations with hormone levels?**
Marcinkowska et al. 2016 [40]	115	daily (over one cycle)	facial masculinity preference	yes	no	not tested
Marcinkowska et al. 2018 [41]	110	daily (over one cycle)	facial masculinity and symmetry preferences; body masculinity preference	yes	no	not tested
Dixson et al. 2018 [42]	68	twice (at high and low fertility)	facial masculinity preference	yes	no	yes (in sub-group of 36 women from whom saliva samples were collected)
Jünger et al. 2018 [44]	157	weekly (over two cycles)	body masculinity preference	yes	no	no
Marcinkowska et al. 2018 [46]	105	daily (over one cycle)	facial masculinity and symmetry preferences; body masculinity preference	yes	not tested	no
Jones et al. 2018 [35]	351	weekly (over one	facial masculinity	no	not tested	no

		to three cycles)	and symmetry preferences			
Jünger et al. 2018 Study 1 [45]	195	twice (at high and low fertility)	vocal masculinity	no	no	no
Jünger et al. 2018 Study 2 [45]	112	weekly (over one cycle)	vocal masculinity	yes	no	no

Some researchers have criticized the ecological validity of studies that manipulated the type of relationship women judged men's attractiveness for (short-term versus long-term) in research on hormonal regulation of women's mate preferences [48]. Might this methodological issue explain the null results in these studies? We suggest that this is unlikely. The studies described above that reported no significant effect of cycle phase or hormone levels on women's mate preferences and considered possible effects of relationship type typically observed significant effects of relationship type on mate preferences that did not interact with fertility and/or hormone levels [e.g., 35]. It is also clearly problematic to dismiss studies reporting null results that used this method, while accepting positive results from studies using the same method (e.g., [2]).

Two of the studies reporting null results for cyclic shifts in mate preferences used a relatively small number of stimuli in some of their preference tests [41,46]. Might this explain the null results in their studies? Again, we suggest that this is unlikely. While these studies observed no significant within-subject effects of fertility [41] or hormone levels [46] on women's preferences for body masculinity, these null results appear unlikely to be a consequence of the relatively small number of items (three) that they used to assess body preferences. In that data set, women's body preferences were correlated with their average hormone levels (i.e., between-women differences), but not daily hormone levels (i.e., within-woman changes) [46]. The potential function of such effects of average hormone levels is currently unclear, however.

Null results have also been reported in several studies testing the Dual Mating Strategy hypothesis using between-subject comparisons of women's masculinity preferences [39,40,42,49-52]. Given that between-subjects designs are likely to be ill equipped to test for hormonal regulation of mate preferences (see earlier discussion), these null results are more difficult to interpret, however [35]. Nonetheless, it is perhaps noteworthy that some of these studies reported negative (rather than null) effects in some of their analyses [39,50]. These negative effects would be particularly unlikely to occur if there was a robust positive effect of fertility on masculinity preferences [39,50].

The Dual Mating Strategy hypothesis and sexual desire

While most research on the Dual Mating Strategy hypothesis has investigated changes in women's mate preferences, other research has investigated how other aspects of women's sexual desire change over the menstrual cycle. Consistent with the Dual Mating Strategy hypothesis, one recent longitudinal study found that partnered women reported greater extra-pair sexual desire (i.e., greater desire for sex with men other than their primary partner) during the ovulatory phase of the menstrual cycle [53]. Another recent cross-sectional study with a large sample size found that women reported more openness to uncommitted sexual relationships during the high-fertility phase of the menstrual cycle than during low-fertility phases [46].

The results described above might initially appear consistent with the Dual Mating Strategy hypothesis's proposal that cyclic changes in mating psychology function to increase extra-pair sex during ovulation. However, other recent work suggests that that interpretation may be problematic. For example, longitudinal studies have reported similar patterns for cyclic shifts in both in-pair and extra-pair desire [38,54]. Indeed, while some early small-scale studies suggested that cyclic changes in extra-pair desire were moderated by individual differences in the physical attractiveness of women's romantic partners [e.g., 6,55] these results did not replicate reliably in a recent large-scale study [38] or in another recent study on a similar scale to the original work [53].

Other studies have reported hormone-linked changes in sexual desire that are not target-specific [54], including desire for sexual activity without a partner [56]. A large longitudinal study also found no evidence that openness to uncommitted sexual relationships was significantly related to changes in steroid hormone levels during the menstrual cycle [56]. Together, these results suggest a general change in sexual desire, rather than the specific change in extra-pair sexual desire proposed by the Dual Mating Strategy hypothesis. We also suggest here that these results indicating the existence of a general increase in sexual desire around ovulation are potentially problematic for the Extended Sexuality hypothesis, an alternative model of hormonal regulation of sexual desire that is more focused on fertility-linked change in *in*-pair sexual desire (see Box 2).

Do oral contraceptives alter mating psychology?

Most of the research testing the Dual Mating Strategy hypothesis has focused on fertility- and/or hormone-linked changes in mate preferences and sexual desire in women not using any form of hormonal contraceptive (i.e., women with 'natural' menstrual cycles). Other studies, however, tested for converging evidence for the Dual Mating Strategy hypothesis by investigating putative effects of oral contraceptive use on women's mate preferences, romantic relationships, and sexual desire, since oral contraceptives prevent the hormonal profile associated with the high-fertility ovulatory phase. The rationale for this approach is that oral contraceptive use suppresses ovulation and associated hormonal changes.

Several early studies reported that women using oral contraceptives showed weaker preferences for masculine men than did women not using oral contraceptives [57,58]. These results were interpreted as converging evidence for a positive association between fertility and women's masculinity preferences and preliminary evidence that oral contraceptives might alter women's mate preferences [57,58]. These results have not replicated well, however, with some studies reporting between-group differences in the opposite direction to those reported in the original studies [35,59].

Of course, women who use oral contraceptives and women who do not use oral contraceptives will likely differ in many ways other than their use of oral contraceptives, meaning that within-subject studies are necessary to establish whether oral contraceptive use does alter women's mate preferences [60,61]. The first of such studies reported that masculinity preferences weakened after women began using oral contraceptives [61]. However, a subsequent larger study did not replicate this effect and found no evidence that oral contraceptive use altered other aspects of women's mate preferences [35]. Furthermore, this latter study found no evidence that oral contraceptive users' mate preferences changed when they were on "placebo pills" (i.e., taking pills containing no exogenous hormones).

While the studies described above investigated the effects of oral contraceptive use on women's mate preferences directly, other research has investigated whether changes in oral contraceptive use after relationship formation disrupt women's relationship satisfaction.

Congruency in current and previous oral contraceptive use (but not use of oral contraceptives alone) predicted women's relationship satisfaction [62,63]. Again, however, a more recent high-powered study did not replicate these effects, suggesting that they are not robust [64]. Collectively, these results present little evidence for a reliable effect of oral contraceptive use on women's mate preferences or relationship satisfaction. Indeed, double-blind, randomized, placebo-controlled trials find little clear evidence that oral contraceptive use affects sexual functioning [65], but do find that oral contraceptive use decreases general wellbeing [66]. However, there was some preliminary evidence that specific sub-components of sexual functioning (e.g., desire) are affected by oral contraceptive use [65]. This latter preliminary evidence would be consistent with other recent work suggesting oral contraceptive use decreases some aspects of sexual functioning (e.g., decreases sexual behavior) in non-human primates, such as bonobos [67]. While there is then some preliminary (i.e., weak) evidence that oral contraceptive use might alter some aspects of women's mating psychology, the specific results of studies of the putative effects of oral contraceptives on women's mating psychology appear to provide little support for the Dual Mating Strategy hypothesis.

Our article focuses on empirical challenges to the Dual Mating Strategy hypothesis. However, there are also a variety of potential theoretical challenges to the Dual Mating Strategy hypothesis. Although such theoretical challenges are arguably more contentious than the empirical challenges, we briefly discuss them in Box 3.

An alternative to the Dual Mating Strategy hypothesis

As outlined above, data from recent studies of both mate preferences and aspects of sexual desire do not appear to straightforwardly support the Dual Mating Strategy hypothesis. Nonetheless, these studies do present compelling evidence for a general change in sexual desire over the menstrual cycle that occurs as a function of changes in hormone levels related to fertility. Is there an alternative model of hormonal regulation of women's mating psychology that is better able to accommodate these recent empirical challenges to the Dual Mating Strategy hypothesis? We suggest that there is.

The data described in this article can be accommodated in the 'estrous' model [68], which has recently been further developed [9]. This model proposes that the ovulatory phase of the menstrual cycle in women is characterized by increased sexual motivation, similar to that reported in other non-human primates during the fertile phase of their reproductive cycles (see [69] for a review of these studies). For example, estradiol positively and progesterone negatively predict sexual behavior in captive female macaques [70,71] and administering estradiol to female macaques increases both sexual receptivity and proceptivity [72,73]. Specific evidence for this model of hormonal regulation of mating psychology in humans comes from studies reporting an increase in women's general sexual desire [38,54,56,74], interest in sex with attractive men, including those they do not know well [75], and assertiveness [76] during the ovulatory phase of the menstrual cycle.

Importantly, this type of model makes no specific predictions about changes in the types of men that women are attracted to and does not emphasize the potential benefits of extra-pair sex. In fact, some versions of the model [68] explicitly propose that estrous may have evolved prior to pair-bonding and, in humans, need not necessarily confer any benefit to women in terms of reproductive success (i.e., fertility-linked change in sexual motivation might simply be vestigial). Alternatively, fertility-linked change in sexual motivation could function to free up resources (e.g., time, energy) for other priorities (e.g., obtaining food) when conception is unlikely to occur following intercourse [9]. Evidence for this latter type of fertility-linked change in general motivational priorities comes from recent work suggesting that increased sexual desire during the ovulatory phase of the menstrual cycle is accompanied by decreased food intake [77].

Concluding remarks and future directions

In conclusion, we suggest that the lack of clear evidence for fertility- or hormone-linked changes in women's mate preferences and extra-pair sexual desire in recent studies, including those conducted on a large scale, is problematic for the Dual Mating Strategy hypothesis. By contrast, alternative accounts, such as the 'estrous' and 'extended sexuality' models are better able to accommodate these new data.

Our overview of recent work on hormonal regulation of women's mating psychology highlights several important directions for future research. First, it is essential that researchers continue to rigorously test predictions from each of these theories, ideally focusing on testing competing predictions from each model. Such tests should include distinguishing between the two versions of the estrous model described in the previous section.

Second, research in this area must fully consider individual differences in the magnitude of cyclic changes in mating psychology. Large-scale studies suggest that the magnitude of cyclic shifts in mating psychology may vary substantially among women [35,38] and factors such as own and partner physical condition and/or market value were found to predict the magnitude of cyclic shifts in some small-scale studies [6,24,55,78; but see also 38 and 53]. Replicating and extending these findings in large-scale studies may yet provide insight into why results for cyclic changes in women's mate preferences vary across studies. Simply establishing whether individual differences in the magnitude of cyclic shifts in mating psychology are systematic or random would be an important step towards this goal.

Third, while most of the recent replication attempts for cyclic changes in mate preferences have focused on face and body preferences, there have been few attempts to replicate studies on preferences for male body odor [28] and behavioral displays [29,30]. Such replications are urgently needed because the existing studies on preferences in these domains have almost exclusively used between-subject designs and relatively small sample sizes.

Fourth, it is important that researchers continue to improve the methods used to assess hormonal status. For example, hormone measures from blood samples may be less susceptible to bias from individual differences in adiposity than the salivary assays typically used in this area. Mass spectroscopy also appears to be a considerable improvement on the immunoassay methods typically used to measure hormones in this field [79].

Finally, it is essential that researchers continue to develop new theoretical models of hormonal regulation of mating psychology that put forward new alternatives to the Dual Mating Strategy hypothesis and refine existing alternative models. Importantly, these refinements should include equivalence bounds [80] to define effect sizes that are too small to theoretically matter, facilitating equivalence tests that can provide evidence for the null, rather than only find or fail to find evidence against the null.

Text Box 1. Do men display genetic fitness cues? A critical aspect of the Dual Mating Strategy hypothesis is the proposal that women increase their reproductive fitness by mating with men displaying genetic fitness cues (i.e., cues that a man's offspring will have higher fitness). Many researchers have questioned the existence of such cues [e.g., 49,81] and evidence for their existence in men is arguably equivocal [10,82-89]. Moreover, some researchers have argued that an individual's typical or current physical condition need not necessarily be related to such cues [90,91], making it a difficult proposal to assess empirically in humans. Additionally, the strength of links between fitness and physical cues could differ according to ecological factors, such as environmental harshness [92,93]. The only study we are aware of to have directly tested whether women who mate with men displaying a putative genetic fitness cue (facial masculinity) actually do obtain fitness benefits found evidence that the daughters of masculine-faced men incur a potential fitness *cost* [81]. To date, the most reliable results suggesting the existence of genetic fitness cues in men comes from studies linking aspects of men's facial, bodily, and vocal appearance to their physical strength [92,93]. However, interpreting such results as evidence for the existence of genetic fitness cues rests on the assumption that physical strength is a genetic fitness cue [94].

Text Box 2. Considering the Extended Sexuality hypothesis. In our main text, we argue that results from recent large-scale studies of changes in sexual desire during the menstrual cycle present difficulties for the Dual Mating Strategy hypothesis. However, these results might also be problematic for at least one alternative theory of hormonal regulation of women's sexual desire. The Extended Sexuality hypothesis proposes that sex during nonconceptive phases of the menstrual cycle (e.g., during the luteal phase) functions, at least in part, to strengthen pairbonds and increase the male partner's investment in both the relationship and any existing children [95]. One recent study [96] reported a positive effect of progesterone on in-pair versus extra-pair desire. Since progesterone is higher during the luteal phase of the menstrual cycle than at other times (see Figure 2), this finding was interpreted as evidence for the Extended Sexuality hypothesis [96]. However, the results of studies [e.g., 38,54] finding that various aspects of sexual desire, including in-pair desire, actually increase during the *ovulatory* phase of the menstrual cycle (i.e., when progesterone is low) are difficult to reconcile with this Extended Sexuality hypothesis. It could be that in-pair desire increases during the luteal phase of the menstrual cycle in only a subgroup of women, such as those in particularly committed relationships [95]. However, such moderation effects would need to be substantial to reverse the direction of the seemingly robust overall positive effect of conception risk on in-pair desire reported in other studies.

Text Box 3. Theoretical challenges to the Dual Mating Strategy hypothesis. Putative benefits of extra-pair paternity (i.e., being fathered by a man other than the mother's primary romantic partner) for offspring reproductive fitness are a critical feature of the Dual Mating Shift hypothesis. However, if extra-pair paternity can be beneficial for offspring reproductive fitness, it is puzzling that genetic evidence suggests that rates of extra-pair paternity are generally relatively low. For example, recent genetic studies estimate extra-pair paternity rates in Western European (Netherlands, Italy, Spain) and African (South Africa, Mali) samples to be <2% per generation [97-101]. Although extra-pair paternity may be more common in some other human populations (e.g., Namibia's Himba), these higher rates appear to be driven almost entirely by women in arranged marriages [102], suggesting the higher extra-pair paternity rates are not due to cyclic changes in women's own mate preferences. Among the Himba, extra-pair paternity is uncommon in non-arranged (i.e., 'love') marriages [102]. These results suggest that the Dual Mating Strategy hypothesis might overestimate the importance of extra-pair mating.

It is also unclear whether the fertility-linked changes in behavior during the menstrual cycle predicted by the Dual Mating Strategy hypothesis would be of a sufficient magnitude to overcome the effects of stable individual differences in mating psychology on reproductive success. Studies of the contribution of genetic factors to women's mate preferences and mating strategies have typically reported that a substantial amount of the variation in both mate preferences and mating strategy [39,103-107] are explained by genetic factors. Given these large individual differences in preferences and behavior, the relatively small within-individual changes in behavior proposed by the Dual Mating Strategy hypothesis may not have an appreciable effect on women's reproductive fitness [108].

Another recent theoretical challenge to the Dual Mating Strategy comes from the proposal that within-women, fertility-linked changes in mating psychology might simply be low-cost functionless byproducts of processes that evolved because of between-women differences in mating psychology [48]. Although hotly debated [109,110], this hypothesis has received some preliminary support, at least in how it applies to mate preferences. For example, one recent study found that some aspects of women's mate preferences are predicted by between-women, but not within-woman, variation in hormone levels [46].

Figure Captions

Figure 1. Masculinized and feminized versions of a male prototype face. This type of stimuli is typically used to test for cyclic shifts in women’s masculinity preferences. Masculinized and feminized versions of male prototype faces are created by using computer graphic methods to shift their shape along a continuum defined by the average shape differences between a sample of male and a sample of female faces.

Figure 2. Typical changes in estradiol and progesterone during the menstrual cycle. Fertility is greatest on the two or three days preceding ovulation [32]. This high-fertility phase of the menstrual cycle is characterized by high estradiol and low progesterone. Hormone data are from a composite measure derived from actuarial tables [33]. On the x-axis, day zero is the day of ovulation.

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