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Human estrus: implications for relationship science

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Most mammalian females possess classic estrus, a discrete phase of the ovulatory cycle during which females engage in sex and undergo dramatic physical changes that make them attractive to males. By contrast, humans engage in sexual activity throughout the ovulatory cycle. But is it the case that humans possess *no* estrous-like changes across the cycle? Research over the past three decades has shown that, in fact, women's sexual desires change across the cycle, as do men's responses to women. Research over the last few years has sharpened scientific understanding of the precise nature of these changes. Nevertheless, many intriguing questions remain. We highlight recent work in this area and identify key opportunities for research in the future.

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Introduction

Mammalian females typically experience reproductive cycles lasting a few days up to several weeks. During the *follicular phase* of the cycle, ovarian follicles containing eggs compete for dominance. Under the influence of follicle stimulating hormone (FSH), they secrete the hormone *estrogen*, which in turn induces production of luteinizing hormone (LH) in the pituitary gland. A dominant follicle's rising estrogen secretion prompts an LH surge followed by a precipitous drop, leading one or more eggs to be released into the fallopian tubes and descend into the uterus, the phenomenon of *ovulation*. This event marks the beginning of the *luteal phase*. The empty follicle transforms into the corpus luteum, which produces the hormone *progesterone*, vital for preparation of the uterine lining for implantation. If the egg is fertilized and successfully implants, pregnancy ensues. If the egg remains unfertilized, the corpus luteum atrophies and, soon after, the blood-rich endometrial tissues are either absorbed by the uterus or, in rare cases including humans, shed through the reproductive tract. In humans, the follicular phase (onset of menstruation until ovulation) lasts, on average, just over two weeks, though duration can vary from 4 days to 4 weeks [1]. In the majority of cycles, the luteal phase (ovulation until menstrual onset) lasts two weeks, plus or minus a couple of days. See Figure 1.

In the vast majority of mammalian species, females experience classic *estrus* or heat: a discrete period of sexual receptivity — *welcoming* male advances — and proceptivity — actively *seeking* sex — confined to a few days just before ovulation, the *fertile window*. Only at this time, after all, do females require sex to conceive offspring. The primate order is exceptional. Although prosimians (e.g., lemurs, tarsiers) exhibit classic estrus, the vast majority of simian primates (monkeys and apes) are sexually active for at least several days outside of the fertile period [2]. Humans are an extreme case: Women may be sexually receptive or proceptive any time of the cycle, as well as other nonconceptive periods (e.g., pregnancy).

This remarkable feature of women has been of longstanding interest to biologists and anthropologists (e.g., [3,4]). Why did women evolve to seek sex throughout the cycle? What were the benefits of doing so, ancestrally? What do answers tell us about the nature of human reproduction and its larger biological and social context? And can they inform our understanding of romantic relationships today? Over the past two decades, these matters have been of keen interest to evolutionary psychologists. In this review, we emphasize major contributions published since mid-2012.

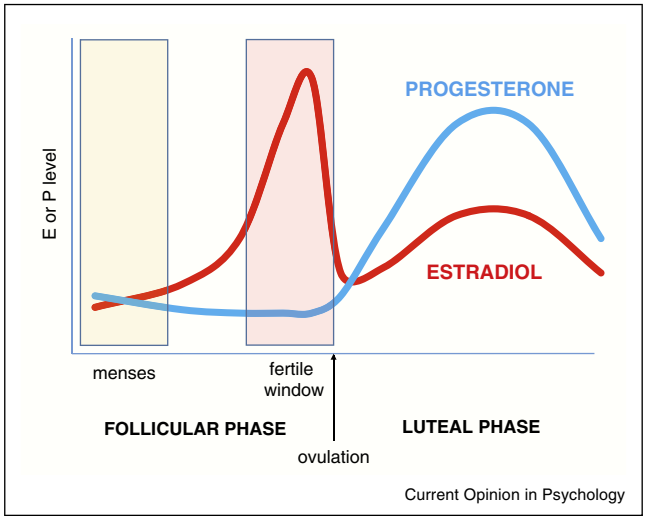
Do women retain a functionally distinct fertile phase?

Graded sexuality

Women's sexual activity is not confined to an estrous period. But are women's sexual interests truly constant across the cycle? Many female primates (e.g., rhesus macaques and marmosets) are often receptive to sexual advances by males outside of the fertile phase, but they initiate sex less [2].

In fact, women's sexual interests do appear to change across the cycle. Women exhibit greater genital arousal in response to erotica and sexually condition to stimuli more readily during the follicular phase [5–8]. A recent study identified hormonal correlates of these changes by tracking 43 women over time and performing salivary hormone assays [9•]. Women's sexual desire was greater during the

Figure 1



Changes in estradiol (the most prevalent form of estrogen produced by women) and progesterone levels across the cycle, based on data from [9•].

fertile window, and was positively related to estradiol levels (which peak just before ovulation), but negatively related to progesterone levels (which rise markedly during the luteal phase). These changes are probably subtle, as some studies using LH to verify timing of ovulation have not found them, despite 80% power to detect medium effect sizes (d = .5; e.g., [10]).

Changes in the male features that evoke sexual interest

Since the late 1990s, some researchers have argued that what changes most notably across the cycle is not sexual desire per se but, rather, the extent to which women's sexual interests are evoked by particular male features — specifically, male behavioral and physical features associated with dominance, assertiveness, and developmental robustness (see Box 1). Over 50 studies have examined changes across the cycle in women's attraction to these male features. Recently, the first meta-analyses of this literature appeared. Gildersleeve, Haselton, and Fales [11••] concluded that, on average, robust changes occur. Wood *et al.* [12], by contrast, argued that positive effects may be due to publication bias alone. A debate between these authors played out in commentary on Gildersleeve *et al.*'s paper and a reply in *Psychological Bulletin* [13••,14]. See Box 1, Meta-analyses of Cycle Shifts, for a summary.

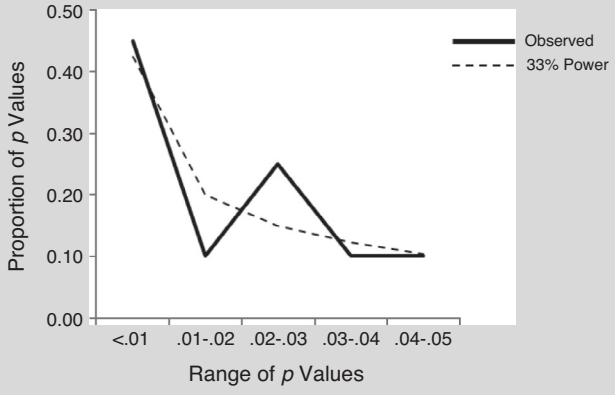
The importance of behavioral features?

Whereas preference shifts of major interest early on concerned male physical features (e.g., facial masculinity; scent), several recent studies have focused on women's reactions to men's behavior and dispositions. Previous research had found that women find male confidence, even a degree of arrogance, more sexually appealing during the fertile phase (e.g., [15,16]). Recent studies replicate and extend that work, finding not only that fertile-phase women are more sexually attracted to 'sexy cad' or behaviorally masculine men (relative to 'good dad' or less masculine men), but also that, during the fertile

Box 1 Meta-analyses of cycle shifts

The Ovulatory Shift Hypothesis posits that, at high fertility within the cycle, women experience increased sexual attraction to men possessing features hypothesized to have reflected genetic quality ancestrally (e.g., behavioral dominance; bodily, facial, and vocal masculinity; facial testosteronization; scents associated with symmetry; facial symmetry). A meta-analysis conducted by Gildersleeve *et al.* [11••] documented robust results consistent with this hypothesis. In commentaries, two sets of authors [14,41] claimed that apparent evidence in this literature instead may reflect publication bias or '*p*-hacking,' whereby researchers try out multiple analyses and report only those that 'worked' [42]. Are apparent cycle shifts merely *false positives*? A new technique allowed Gildersleeve *et al.* to address this question empirically. A *p*-curve is the frequency distribution of *p* values <.05. If no true effect exists, and findings are due to publication bias alone, the *p*-curve will be flat (~2.5% of studies will produce predicted significant effects, with equal numbers of *p* values between .00–.01, .01–.02, .02–.03, and so on). If apparent findings are due to *p*-hacking, the *p*-curve will be *left skewed*, with more *p*s close to .05 than .00. If real effects exist, the *p*-curve will be *right-skewed*, with more *p*-values close to 0 than just under .05 [43]. The figure below is the *p*-curve constructed from published studies included in Gildersleeve *et al.*'s meta-analysis and related studies [13••]. It and all others constructed by Gildersleeve *et al.* are significantly right-skewed, a signature of real effects. Wood *et al.* claimed to find little evidence of cycle shifts in their own meta-analysis [12]. But when Gildersleeve and colleagues reanalyzed the effects in aggregate, rather than in small subsets of effects, evidence was consistent with the ovulatory shift hypothesis [13••]. See this reply [13••] for additional concerns about Wood *et al.*'s meta-analysis. In sum, although we do not doubt that some apparent findings in the cycle shift literature could be false positives, the claim that cycle shifts in mate preferences are merely false positives is inconsistent with the evidence.

Figure. *p*-Curve of exact two-tailed *p* values evaluating the Cycle Shift Prediction, Context Moderation Prediction, and Partner Qualities Moderation Prediction.



Note: N = 20 *p*-values, total N across studies = 1644. *p*-Curve is significantly right skewed, $\chi^2(40) = 75.98$, $p = .0005$.

phase, women are more likely to flirt or engage with such men [17•,18].

Females of a variety of species, including primates [2], prefer dominant or high ranking males during the fertile phase of their cycles. These males may pass genetic benefits to offspring, as well as, potentially, offer material benefits (e.g., protect offspring). Women's fertile-phase sexual attraction to behavioral dominance appears to have deep evolutionary roots.

Is the preference shift for facial masculinity robust?

One early demonstration of a preference shift found that women during the fertile phase preferred facial masculinity (e.g., [19]). Two large recent studies have not replicated this effect [20,21•]. Whether this effect is variable across stimuli or simply absent is unclear at this point.

Dual sexuality

Within the *dual sexuality* framework, fertile-phase sexuality and non-fertile-phase sexuality have potentially overlapping but also distinct functions [22,23] (see Figure 2). In a number of primate species, extended sexuality — female receptivity and proceptivity at times other than the fertile phase — appears to function to confuse paternity by allowing non-dominant males sexual access (e.g., [24]). These males cannot rule out their own paternity, which might reduce their likelihood of harming a female's offspring. In humans, by contrast, extended sexuality may function to induce primary pair-bond partners to invest in women and offspring (e.g., [22]).

Some studies have found that women's sexual interests in men other than partners are strikingly rare during the luteal phase, relative to the fertile phase [25,26]. Other research has found moderating effects; for example, women who perceive their partners to lack sex appeal experience increased attraction to men other than partners, less satisfaction, and a more critical attitude toward partners, but only when fertile [27,28•]. Fertile-phase women in one study were more assertive and focused on their own, as opposed to their partner's, needs, especially when attracted to men other than partners during that phase [29•].

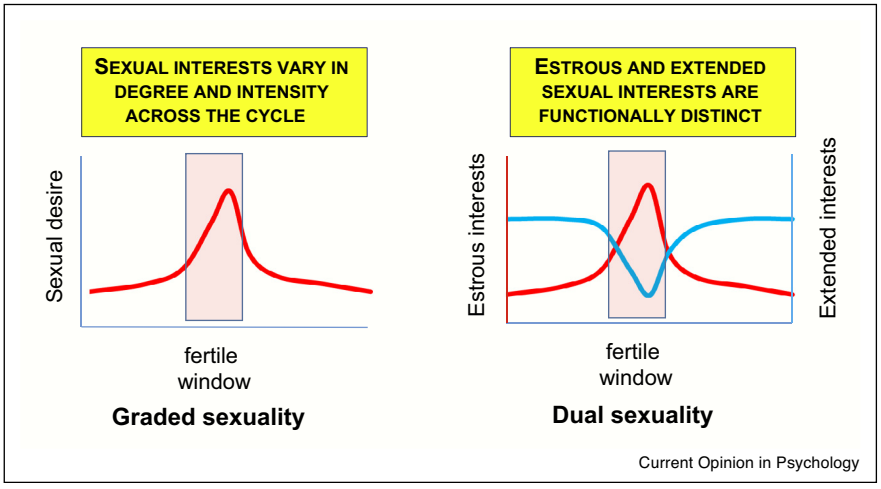
Most research on cycle shifts has been inspired by theory concerning women's distinctive sexual interests during the fertile phase. One study explicitly sought to understand factors influencing women's sexual interests during the luteal phase, finding that, at that time, but not during the fertile phase, women initiated sex more with primary partners when they were invested in their relationship more than were male partners [30••]. This pattern is consistent with the proposal that extended sexuality functions, in part, to encourage interest from valued male partners.

Others have proposed that women's estrous phase sexual interests have been modified by pair-bonding. See Table 1, Theoretical Issues and Proposals.

Cues of fertility status

Females across diverse species undergo physical and behavioral changes during estrus that males find

Figure 2



A simplified characterization of the distinction between the graded sexuality and dual sexuality models. In the *graded sexuality model*, a single form of sexual interests varies in intensity across the cycle. In the *dual sexuality model*, two functionally distinct forms of sexual interests have been selected — estrous (fertile-phase) sexual interests (in red) and extended (non-fertile-phase) sexual interests (in blue), which are prompted by *different* features, under *different* circumstances, in service of their distinct functions. In the graded sexuality model, estradiol fosters sexual interests; progesterone suppresses it. In the dual sexuality model, estradiol fosters estrous sexual interests; by contrast, progesterone fosters extended sexual interests.

attractive: changes in body scents in carnivores, rodents, and some primates; changes in appearance, such as sexual swellings, in baboons and chimpanzees; changes in solicitous behavior in rodents and many primates [2,31]. Because women lack obvious cyclic changes, it was widely assumed that cycle shifts in attractiveness were eliminated in humans, perhaps with the evolution of pair bonding [32].

In 1975, a pioneering study documented increased attractiveness of women's vaginal odors midcycle [33]. A quarter century later, research revealing other detectable fertile-phase changes began to accumulate, including increased attractiveness of women's upper torso odors, increased vocal pitch and attractiveness, and changes in women's style of dress and solicitous behaviors [34]. Meta-analysis of this literature confirms that changes across the cycle in women's attractiveness are often subtle, but robust (K. Gildersleeve, PhD dissertation, UCLA, 2014).

A notable recent study demonstrated that hormones implicated in attractiveness shifts in non-humans also predict attractiveness shifts in humans [35•]. Photos, audio clips, and salivary estrogen and progesterone were collected from 202 women at two cycle points. Men rated women's facial and vocal attractiveness highest when women's progesterone levels were low and estrogen levels high (characteristic of the follicular phase, and especially the fertile window).

Emerging evidence suggests that these changes affect interactions between males and females. During the fertile window, women report increased jealous behavior by male partners [25,29,36]. A possible mediator of such changes — testosterone — is higher in men after they smell t-shirts collected from women on high- than on low-fertility days of the cycle ([37]; cf. [38]). A recent study examined related phenomena in established relationships by bringing couples into the lab for a close interaction task (e.g., slow dancing) [39•]. Following the interaction, male partners viewed images of men who were attractive and described as competitive or unattractive and noncompetitive. Only men in the competitive condition showed increases in testosterone from baseline — and only when tested during their partner's fertile phase.

What remains less clear is how we can understand shifts in attractiveness from a theoretical perspective. It is unlikely

Table 1

Major Theoretical Issues and Proposals.

Theoretical issue	Theoretical position and illustrative references
The function of estrous sexual interests: What evolved functions have estrous sexual interests been shaped to serve?	1. Genetic benefits through sire choice (e.g., [13••,22,44]) 2. Direct benefits (e.g., protection) associated with social status [23] 3. Long-term mate choice [2] 4. None; estrous sexual interests are byproducts of selection on sexual interests during fertile cycles, which are associated with high estrogen levels [9•]
Modification of estrous sexual interests: Have estrous sexual interests been meaningfully modified since the evolution of pair-bonding in humans?	1. No, and these sexual interests have been functionally adaptive in the context of pair-bonding [23] 2. No, and these sexual interests have been maladaptive in the context of pair-bonding, but not fully selected out [23] 3. The *adaptive workaround* hypothesis: They have been modified to enhance the stability of strong pair-bonds; fertile-phase women seek sexual intimacy with strong pair-bond partners [45,46] 4. The *dual strategy* hypothesis: They have been modified to facilitate adaptive extra-pair mating [45]
Nature of cyclic shifts in sexual interests: Do fertile-phase and luteal-phase sexual interests differ in degree or been shaped to serve different functions?	1. The *graded sexuality* model: Fertile-phase and luteal-phase sexual desires differ only in degree (e.g., readiness to be evoked) [2,9•] 2. The *dual sexuality* model: Fertile-phase and luteal-phase sexual interests have been shaped to serve distinct (even if overlapping) functions [22,23]
The functions of extended sexual interests: What are the distinctive evolved functions of extended sexual interests?	1. To enhance investment by a pair-bond partner through extended sexual access, which maintains proximity and potentially fosters giving of direct benefits [3,22,23] 2. To enhance investment by a pair-bond partner through extended sexual access, which prevents monopolization by dominant males and increases paternity assurance of a non-dominant primary partner [23,47]
The evolutionary bases of fertile-phase attractiveness: Why does women's attractiveness vary across the cycle?	1. Women adaptively signal their fertility status and men have evolved to respond to these signals (e.g., [37]) 2. Women 'leak' incidental cues of their fertility status, including chemical cues, and men have evolved to respond to cues of the fertile phase [22,34] 3. Women adaptively signal overall reproductive capacity (e.g., through display of estradiol-linked traits), independent of phase [22]. Hormones associated with reproductive capacity (e.g., estradiol) vary across the cycle. This causes women to 'leak' incidental cues of their fertility status, and males have evolved to be attracted to these cues because they indicate overall reproductive capacity and/or fertility status

that women evolved to signal their fertility within the cycle to men [22,34]. In fact, the opposite may have occurred — active selection on women to conceal cues of ovulation, which could help to explain weak shifts in attractiveness relative to many species. Concealment might have promoted extended sexuality with its attendant benefits from investing males, or facilitated women's extra-pair mating (see Table 1). Possibly, the subtle physical changes that occur are merely 'leaky cues' that persist because fully concealing them suppresses hormone levels in ways that compromise fertility. Behavioral shifts, by contrast, may be tied to increases in women's sexual interests or motivation to compete with other women for desirable mates (e.g., [40•]).

Future directions

In closing, we see several key opportunities for advancing knowledge in this vibrant area of science.

First, the field has developed increasingly sophisticated alternative theoretical perspectives on cycle shifts. Further theory development requires that they be sufficiently tested. Table 1, Theoretical Issues and Proposals, offers a summary.

Second, many studies assess women's fertility through 'counting' methods involving women's reports of cycle characteristics, resulting in low precision and low power, and, potentially, inconsistent results (Gangestad *et al.*, unpublished). Within-subject studies using urinary LH tests are much more powerful. An analysis of the literature with these factors in mind and a set of methodological recommendations for future research are needed.

Third, studies examining the hormonal correlates of cycle shifts elucidate possible hormonal mechanisms, better unite human and non-human data, and provide some of the most compelling demonstrations of cycle effects (e.g., [9•,35•]). More are needed.

Fourth, in light of variable effect sizes [11••], future research should clarify which effects are robust.

Fifth, although recent studies have examined impact on phenomena core to relationship science [10,28•,29•,36], those impacts should be more fully explored. For instance, how do changes across the cycle affect relationship dynamics? How do estrous shifts or extended sexuality strengthen or interfere with bonding? And how do relationship features (e.g., the presence of children) moderate the nature and impact of these shifts?

The study of estrous-like phenomena in humans has become increasingly exciting and sophisticated, both empirically and theoretically. This work offers potentially profound insight into our deep ancestry through commonalities with our nonhuman cousins. At the same time, it reveals elements of human sexuality that are exceptional within the animal kingdom, providing a window onto the unique nature of human intimate relationships.

References and recommended reading

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Study of how estradiol, progesterone, and testosterone levels predict within-woman levels of sexual desire in 43 normally ovulating women over the course of 2 cycles. Levels of estradiol positively predicted within-women levels of sexual desire; levels of progesterone negatively predicted within-woman levels of sexual desire. Testosterone levels did not independently predict sexual desire.

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11. •• Gildersleeve K, Haselton MG, Fales M: **Do women's mate preferences change across the ovulatory cycle? A meta-analytic review**. *Psychol Bull* 2014, **140**:1205-1259.

Meta-analysis of published and unpublished studies evaluating the hypothesis that, at high relative to low-fertility within the ovulatory cycle, women experience increased sexual attraction to male features hypothesized to have indicated genetic quality ancestrally (e.g., scents associated with symmetry; facial, body, and vocal symmetry; features associated with testosterone). Analyses aggregating across male features provided strong support for the hypothesis, whereas results from analysis of individual features were mixed.

12. Wood W, Kressel L, Joshi PD, Louie B: **Meta-analysis of menstrual cycle effects on mate preferences**. *Emot Rev* 2014, **6**:229-249.
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Reply to critiques suggesting that cycle shifts documented in [11••] are due only to publication bias or are otherwise artifacts of research practices. Reply presents additional meta-analytic evidence (*p*-curves, see

Box 1) and analyzes another set of effects compiled by a different research team, with both sets of analyses providing evidence consistent with conclusions that cycle shifts documented in [11••] are robust and cannot explained by publication bias or researcher practices that increase type I errors.

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Normally ovulating women ($N = 31$) interacted with two men in fertile-phase and luteal-phase sessions: one a 'sexy cad' (charismatic, confident, socially dominant but unreliable) and one a 'good dad' (reliable, caring, and interested in a committed relationship, but neither confident nor charismatic). When fertile, women expressed greater attraction as a short-term date to the sexy cad, and engaged in greater levels of flirtatious behavior (coded from audio–video recordings) with the sexy cad.

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Study examined preferences for sexually dimorphic facial features in 12 different societies highly diverse with respect to economic development. In a subsample of 312 normally ovulating women, the authors detected no fertile phase increase in the preference for masculine male faces.

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Two studies examined women's feelings about their relationship and partner during high and low fertility phases of the cycle (LH tests verified ovulation). Women with partners high in sexual desirability felt closer to their partners and more satisfied with their relationships on high relative to low fertility within the cycle, whereas women with partners low in sexual desirability showed opposite patterns.

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In a sample of 66 romantically involved couples, study examined changes in women's and men's behavior toward each other along two dimensions: self-assertiveness and dependence. Both men and women were reported to engage in greater levels of self-assertiveness during the female partner's fertile phase. These fertile-phase increases were predicted by fertile-phase increases in women's sexual interests in men other than partners, but not by men's sexual interests in women other than partners.

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In a sample of 50 romantically involved and sexually active couples, study examined predictors of women's initiation of sex during the mid-luteal and fertile phases. Women initiated sex with their partners during the luteal phase especially when they were highly invested in their relationship but, relatively speaking, men lacked investment in their relationship, a pattern not characteristic of female-initiated sex during the fertile phase.

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Study collected photos, audio recordings, and salivary estradiol and progesterone from 202 women across two points in the cycle. Men rated photos and audio recordings as more attractive when women's progesterone levels were low (consistent with women being in the follicular phase) and when progesterone levels were low and estradiol levels high (a progesterone X estradiol interaction effect, consistent with women being in the high fertility window of the follicular phase).

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39. • Fales MR, Gildersleeve KA, Haselton MG: **Exposure to perceived male rivals raises men's testosterone on fertile relative to nonfertile days of their partner's ovulatory cycle**. *Horm Behav* 2014, **65**:454-460.

Thirty-four couples reported to the lab for a close interaction task (e.g., slow dancing) during high- and low-fertility phases of the female partner's ovulatory cycle. Following the interaction, male partners viewed images of men who were attractive and described as competitive or unattractive and noncompetitive. Only men in the competitive condition showed increases in testosterone from baseline, and only when tested during their partner's fertile phase — consistent with the challenge hypothesis.

40. • Durante KM, Griskevicius V, Cantú SM, Simpson JA: **Money, status, and the ovulatory cycle**. *J Market Res* 2014, **51**:27-39.

Reports three studies examining women's preferences for *positional goods* across the ovulatory cycle. Women at high fertility relative to low fertility chose options that maximized their advantage over another women (e.g., having more expensive jewellery), but not when options were framed as giving women advantages over men — consistent with

women having greater motivation to compete with other women when fertile within the cycle.

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