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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.

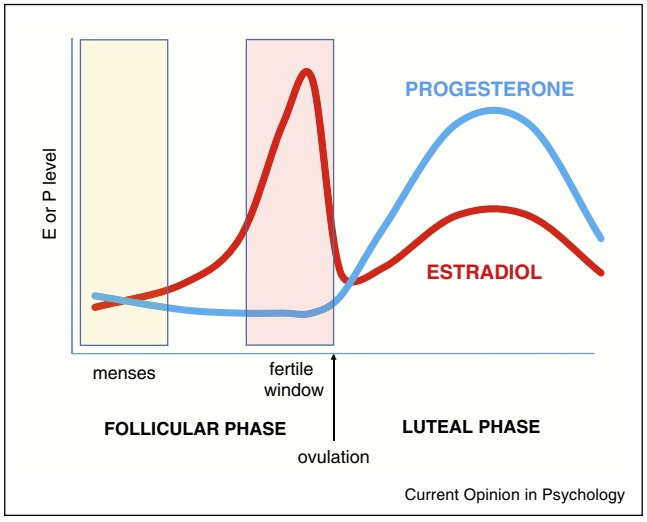
## Do women retain a functionally distinct fertile phase?

### 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.

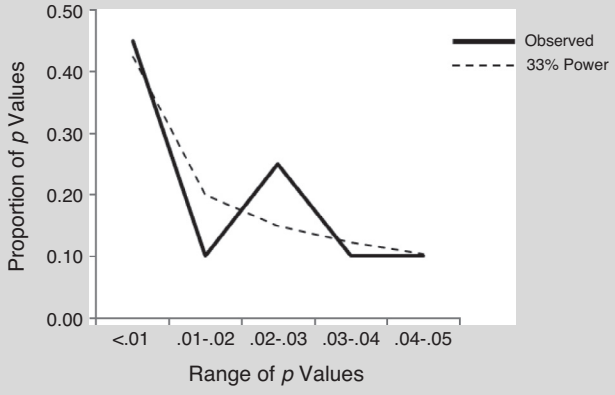
## The importance of behavioral features?

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, $\chi^2(40) = 75.98$, $p = .0005$.