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Invited Commentaries

Human sexuality and the menstrual cycle: a comment on Havlíček et al.

Alan Dixson

School of Biological Sciences, Victoria University of Wellington, BP 600, Wellington 5024, New Zealand

Havlíček et al. (2015) have provided an excellent critique of the current status of the "ovulatory shift" hypothesis of women's sexual attractiveness, and the "human estrus" hypothesis of female mate choice. The first of these hypotheses posits that women become significantly more sexually attractive (e.g., due to changes in visual or vocal traits) during the periovulatory phase of the menstrual cycle. The second hypothesis proposes that women are significantly more attracted to certain masculine traits (e.g., masculinized faces) during the fertile phase of the cycle and that female mate choices are significantly affected on this basis. Yet, as Havlíček et al. point out, "physical changes in women's appearance around ovulation are almost beyond our capacity to measure." Likewise, "even detailed acoustic analysis precludes unequivocal identification of the follicular phase." Such facts confirm that men are unable to determine when women are likely to ovulate, and that "shifts" in attractiveness around ovulation are biologically trivial, if they exist at all. As for increased responsiveness to masculine traits during the fertile phase of the cycle, these are likewise very small, if they exist at all (e.g., see Peters et al. 2009; Harris 2011, 2013), and probably have no relevance to human sexual behavior in the real world (Dixson 2009, 2012).

Havlíček et al. rightly emphasize that hormones influence human sexual attractiveness via effects that are expressed over the long term, rather than during individual menstrual cycles. Thus, women who have consistently higher levels of estradiol have more attractive faces (Law Smith et al. 2006). Women who have a healthy distribution of body fat, and an "hourglass" body shape, have higher circulating levels of estrogen and are more fertile (Jasieñska et al. 2004; Singh et al. 2010). The reason why cues relating to underlying reproductive health and fertility do not fluctuate significantly during menstrual cycles, relates to the long-term nature of reproductive processes and mate-choice decisions that have characterized the course of human evolution. Long-term monogamous or polygynous relationships between women and men occur in the majority of recent human cultures around the world, and would likely have been present in our African ancestors (Dixson 2009). We reproduce slowly, and human offspring are dependent on their parents for many years. Where masculine mate choices are concerned, cues that advertise long-term female health and fertility are thus adaptive; likewise, female mate choice is focused on long-term reproductive outcomes, rather than on periovulatory, extrapair copulations in quest of "better genes."

Perhaps, as Havlíček et al. suggest, women who exhibit generally higher levels of circulating estradiol might also show some greater propensity to display small changes in attractiveness (and behavior) during the menstrual cycle. These small changes, if they exist, would constitute side effects, and epiphenomena, rather than being reproductive adaptations. In which case, surely it is time to acknowledge that the "ovulatory shift" and "human estrus" hypotheses are flawed, and to accept that they should be discarded.

Address correspondence to A. Dixson. E-mail: alan.dixson@vuw.ac.nz.

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The many sides of the periovulational coin: a comment on Havlíček et al.

Janek S. Lobmaier,[a,b] Wilhelm K. Klatt,[a,b] Vanda Lory,[a,b] and Fabian Probst[a,b]
[a]Institute of Psychology, University of Bern, Fabrikstrasse 8, 3012 Bern, Switzerland and [b]Center for Cognition Learning and Memory, University of Bern, Fabrikstrasse 8, 3012 Bern, Switzerland

Havlíček et al. (2015) discuss the possibility that men's increased attraction to periovulatory women and women's cyclic shifts in

preference for certain male traits may not constitute adaptations per se, but might instead be inevitable by-products of putative adaptations related to between-individual differences in reproductive potential. This is an interesting approach and has prompted us to reflect on aspects of our own studies. In the following, we outline some thoughts that have emerged from our reflections, which call for a more differentiated view on what may be spandrels and what may be adaptations. We then propose an alternative explanation for why women might appear to look more attractive during the periovulatory phase of their menstrual cycle.

The periovulatory paradigm is a 2-sided coin: any observable change between 2 specific cycle phases could be driven by the one or the other phase (baseline problem). If, for example, women report to be more convivial during the periovulatory phase compared with the luteal phase, this could be because women are more outgoing around ovulation. Alternatively, women might be more reserved and safety seeking during the luteal phase. Given that during the luteal phase a woman's body prepares for potential pregnancy, any risk-avoiding behavior would seem adaptive while there might be no direct advantage in being more sociable around ovulation. What might seem a spandrel when looking at one phase might make perfect adaptational sense when looking at the other.

Furthermore, we see the need to differentiate between what may or may not be adaptations for men versus what may or may not be adaptations for women. From a man's perspective, a healthy and feminine (i.e., attractive) appearance will always be important because cues to health and femininity putatively signal reproductive potential. Insofar we agree with the authors that most men will readily pick out attractive women in a busy room. We also agree that the task would be much more difficult when asked to pick out ovulating women in the same busy room. While it is highly adaptive for men to recognize cues to potential fertility (irrespective of cycle phase), there is arguably no need for an adaptation that enables men to discriminate ovulating from nonovulating women in a group of women they meet for the first time. It may however be of adaptive value for men to be able to track the fertility window of their own (long term) partner (minimize cuckoldry risk, maximize reproduction). But such ability may rest on behavioral rather than on purely physical cues, as we will suggest below. For women on the other hand, it is not always of equal importance to be attracted to the most masculine men. It may instead be advantageous to be attracted to healthy and strong men while fertile and to seek more feminine traits in a partner during the luteal phase. Such opportunistic mating strategies afford that a woman adjusts her behavior to the situational circumstances. Behavioral adjustments in turn require that a woman is (unconsciously) aware of her menstrual cycle.

In a series of studies from our own lab (e.g., Bobst and Lobmaier 2012, 2014), we found that men preferred the ovulatory woman over women in their luteal phase in a forced-choice paradigm (very similar to Roberts et al. 2004). Notwithstanding the justified criticism that forced-choice paradigms in no way resemble situations in the real world, we note that we found no evidence that differences in estradiol may explain why ovulatory women appear to be more attractive. This is in conflict with Havlíček et al.'s suggestion that men's preference for portraits of ovulatory women may be a by-product of a general preference of women with high estradiol levels. Shifts in apparent attractiveness may instead result from subtle behavioral changes: during ovulation, women may have been flirting with the camera more, resulting in more charismatic portraits. We suggest that women's changes in attractiveness, preferences, and behavior across the menstrual cycle are not necessarily spandrels, but instead

may originate in subtle appetitive changes in the woman. Because a woman can reproduce only during the fertile window of her cycle, it is conceivable that her appetite for sex may increase subtly around ovulation, and this increased appetite may indeed be an adaptation.

Address correspondence to J.S. Lobmaier. E-mail: janek.lobmaier@psy.unibe.ch.

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Are within-cycle variations in women's sexual interests mere by-products? A comment on Havlíček et al.

Steven W. Gangestad and Nicholas M. Grebe
Department of Psychology, University of New Mexico, MSC 03-2220, 1 University of New Mexico, Albuquerque, NM 87131, USA

Havlíček et al. (2015) (hereafter, HCBKR) propose that cyclic shifts in women's mate preferences are by-products of adaptations that adjust preferences to individual reproductive potential, as reflected by hormone levels. Similarly, men prefer hormone-related cues because they discriminate between individual women's reproductive potential, generating as by-product cyclic variation in women's attractiveness. In their view, then, adaptations that drive cyclic variation were *not* shaped by benefits pertaining to cyclic variation.

These proposals may fruitfully inspire new theory, critical analysis, and research designed to test alternative conceptualizations of cycle shifts. Nonetheless, HCBKR vastly overstate the case that researchers have neglected particular kinds of explanations (e.g., by-product hypotheses) and insufficiently acknowledge substantial empirical and theoretical challenges their proposals face. We focus on two (see also Roney et al. 2015).

We largely attend to HCBKR's claims regarding women's mate preferences and sexual interests. Indeed, in our view, selection has led to suppression of incidental cues of the fertile phase and men's abilities to detect these cues *are* very poor. Moreover, men *should* value women for long-term reproductive potential, which we agree men discriminate better than fertile phases (though we do not see that men's discrimination of women's fertile phase is *solely* by-product of the latter; e.g., Puts et al. 2013). See Thornhill and Gangestad (2008).

THE ROLE OF PROGESTERONE

Estradiol levels peak just prior to ovulation and, hence, predict within-cycle fertility status. But as HCBKR note, mean levels also,