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. 2012). 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 Havliček 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.

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

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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,
across women, positively covary with reproductive potential or cycle fertility. Levels of progesterone, by contrast, covary differently with within-cycle fertility status and between-women reproductive potential—in normally ovulating women, they negatively predict the former and, if at all, positively predict the latter. Roney and Simmons (2013)—not cited by HCBKR—found that women’s level of sexual interests covaried positively with women’s estradiol levels and negatively with progesterone levels within-cycle; levels of neither hormone predicted sexual interests across cycles or women. Important theoretical issues remain unresolved (e.g., do within-cycle variations pertain to levels of endogenous sexual motivation [Roney and Simmons 2013] or is “extended sexuality” during nonconceptive phases distinct in kind? [Grebe et al. 2013]). Regardless, Roney and Simmons convincingly document design for shifting sexual interests within-cycle, which HCBKR’s by-product hypothesis cannot explain.

Though Roney and Simmons explicitly examined reports of sexual desire, these may in turn reflect sexual interest evoked by male features—when concepitive, particular male features evoke women’s sexual interests, reported as desire. HCBKR’s claim that cycle shifts in preferences are weak is premature and likely wrong. Disattenuation for error of measurement of concepitive status and P-curve analysis imply that some shifts (e.g., regarding behavioral dominance or bodily attractiveness) are medium to large, especially when women evaluate men as sex partners, not long-term mates (Gangestad SW et al., unpublished data; cf. HCBKR and Dixson 2015).

Gangestad and Haselton (2015) list multiple possible explanations for women’s fertile-phase sexual interests, all of which deserve serious consideration.

**PHYLOGENETIC CONSIDERATIONS**

Nonhuman primate males in many species (with and without sexual swellings) possess adaptations for detecting within-cycle fertility using scent cues (see Thornhill and Gangestad 2008). And female primate sexual interests typically shift across the cycle adaptively (Dixson 2012). How does a species that has no hormone-dependent adaptations based on within-cycle variation (as HCBKR propose for humans) evolve from an ancestral species that does, yet retain these hormone-dependent shifts as “by-product”? Gould and Vrba (1982) emphasized that an adaptation’s function refers to benefits that led to the initial appearance of the trait, not current benefits. Hence, even if within-cycle shifts have no current adaptiveness, they remain adaptations for within-cycle variation if they were initially shaped by consequences pertaining to within-cycle variations. HCBKR offer no vision of an evolutionary process whereby within-cycle shifts changed from adaptations for within-cycle variation to by-products of between-woman variation. For example, were within-cycle variations lost at some point in humans, only to reappear as by-products? Such a phylogenetic scenario strikes us as even more “elaborate,” but less likely, than the scenarios HCBKR reject.

As illustrated above, research on cycle shifts has explicitly formulated, critically examined, and tested by-product hypotheses—in certain respects more deeply than HCBKR (see also Roney et al. 2015; Haselton 2015). The accusations embodied in their article’s title and introduction, then, are misplaced.

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**A new (or truly parsimonious) perspective? A comment on Havliček et al.**

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A surge of recent research has documented effects of reproductive hormones on human sexual behavior. And it now appears that human females—like their mammalian counterparts—experience estrous-like changes in sexual interests and attractiveness to males during the fertile phase of the ovulatory cycle.

Although not all purported effects may be robust (see Gildersleeve et al. 2014a), it is clear that some estrous-like shifts exist. But how do we understand these shifts theoretically? Havliček and colleagues claim that researchers have been hyperadapting to their approach and have neglected by-product explanations (Havliček et al. 2015; henceforth HCBKR). *Is this true?*

Recently, Gangestad and I outlined 10 theoretical proposals concerning women’s estrous sexual interests (see Table 1 in Gangestad and Haselton 2015). These include the notion that estrus is a vestigial holdover and therefore nonfunctional in ancestral (or modern) humans. We also describe a proposal close to that favored by HCBKR—that within-cycle shifts in sexual interests are by-products of adaptations for mate choice during fertile cycles.

We also outlined 3 proposals concerning estrous shifts in women’s attractiveness. One of these is that within-cycle shifts are a by-product of selection on women to display more general reproductive capacity (e.g., signaling overall estradiol level). These alternatives echo those described in earlier publications (Thornhill and Gangestad 2008; Haselton and Gildersleeve 2011).