

argue that between-women calibrations better account for the available data. The between-cycle theory (see [Lukaszewski and Roney 2009](#); [Roney 2009](#); [Roney and Simmons 2008, 2013](#)) proposes hormonal mechanisms that calibrate attention away from markers of men's genetic quality during periods of low fecundity—as during lactational amenorrhea or other causes of energetic stress—in order to shift attention and motivation toward more pressing adaptive problems. The theory hypothesizes estradiol as an efficient signal to regulate these calibrations given its association with cycle fecundity (see [Ellison 2001](#)); however, because estradiol also peaks near ovulation within-cycles, this mechanism may also generate small ovulatory shifts in some measures of women's mate preferences.

[Havlíček et al. \(2015\)](#) incorporate the idea that estradiol may regulate cycle-phase shifts in mate preferences but argue that such shifts arise as by-products of linkages between estradiol, reproductive potential, and mate preferences across different women. The general argument seems to be that it is functional for more attractive women to have stronger preferences for more masculine traits in men (though this is never defended), estradiol is an internal signal of women's attractiveness that calibrates such mate preferences, and thus any within-women shifts in preferences—whether within- or between-cycles—are by-products of between-women linkages between attractiveness and preferences as mediated by estradiol (at least, we think this is the argument; [Havlíček et al. 2015](#) are quite vague).

This between-women argument is unlikely to be correct. The main problem is that estradiol is a poor internal signal of women's long-term attractiveness relative to other women. First, even within ovulatory cycles, correlations between average estradiol and physical attractiveness are small (e.g., [Grillot et al. 2014](#)). More importantly, women in natural fertility populations thought to be similar to human ancestral environments have spent most of their lives under anovulatory conditions with very low estradiol and have only rarely experienced high fertility cycles between births (see [Strassmann 1997](#)). As such, at most times, estradiol would not have reliably differentiated between women who differed in long-term reproductive value due to differences in age or health. (Note also that reproductive value peaks just after puberty during a period of adolescent subfertility that is associated with *lower* ovarian hormones than found in the ovulatory cycles of older women with lower reproductive value; see [Ellison 2001](#).) [Havlíček et al. \(2015\)](#) argue that between-women differences in estradiol are larger than within- or between-cycle differences (see their Figure 3), but they focused on comparisons of ovulatory cycles in modern environments and failed to accurately account for conditions in natural fertility populations.

The lack of temporally stable relationships between estradiol and attractiveness under ancestral conditions challenges the position that within-cycle shifts in preferences arise as by-products of between-women links between attractiveness and estradiol. If [Havlíček et al. \(2015\)](#) argue that women's preferences are designed to change with the large changes in estradiol associated with transitions between ovulatory and anovulatory time periods, then their position reduces to a variant of between-cycle theory and cycle-phase shifts can no longer be explained as by-products of stable differences between women. Alternatively, if they argue that preferences do not track changes in estradiol across ovulatory and anovulatory time periods (and instead track more stable individual differences in physical attractiveness), then they lose the linkages between estradiol and preferences that are necessary to explain within-cycle preference shifts. Either way, their theory faces serious challenges.

Finally, we would like to comment briefly on [Havlíček et al.'s \(2015\)](#) claim that “empirical work too rarely pits competing hypotheses against each other” and that this is “especially true” of

evolutionary psychologists within the “Santa Barbara school.” This unsupported assertion is false. In fact, our colleagues John Tooby and Leda Cosmides—who probably exemplify any such “Santa Barbara school” better than anyone (indeed, the articles cited by [Havlíček et al. 2015](#) identify them with this approach by name)—have produced remarkably detailed empirical tests between adaptationist and by-product accounts of many phenomena (for review of a research program dedicated to such tests, see [Cosmides and Tooby 2005](#)). Furthermore, given how vaguely [Havlíček et al. \(2015\)](#) specified both the logic of their proposed between-women adaptation and the empirical means of distinguishing it from other positions, their criticisms of evolutionary psychologists seem somewhat ironic.

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REFERENCES

- Cosmides L, Tooby J. 2005. Neurocognitive adaptations designed for social exchange. In Buss DM, editor. *The handbook of evolutionary psychology*. Hoboken (NJ): Wiley. p. 584–627.
- Ellison PT. 2001. *On fertile ground*. Cambridge (MA): Harvard University Press.
- Grillot RL, Simmons ZL, Lukaszewski AW, Roney JR. 2014. Hormonal and morphological predictors of women's body attractiveness. *Evol Hum Behav.* 35:176–183.
- Havlíček J, Cobey KD, Barrett L, Klapilová K, Roberts SC. 2015. The spandrels of Santa Barbara: a new perspective on the peri-ovulation paradigm. *Behav Ecol.*
- Lukaszewski AW, Roney JR. 2009. Estimated hormones predict women's mate preferences for dominant personality traits. *Pers Ind Diff.* 47:191–196.
- Roney JR. 2009. The role of sex hormones in the initiation of human mating relationships. In: Ellison P, Gray P, editors. *The endocrinology of social relationships*. Cambridge (MA): Harvard University Press. p. 246–269.
- Roney JR, Simmons ZL. 2008. Women's estradiol predicts preference for facial cues of men's testosterone. *Horm Behav.* 53:14–19.
- Roney JR, Simmons ZL. 2013. Hormonal predictors of sexual motivation in natural menstrual cycles. *Horm Behav.* 63:636–645.
- Strassmann BI. 1997. The biology of menstruation in *Homo sapiens*: total lifetime menses, fecundity, and nonsynchrony in a natural-fertility population. *Curr Anthropol.* 38:123–129.

Greater precision, not parsimony, is the key to testing the peri-ovulation spandrel hypothesis: a response to comments on Havlíček et al. 2015

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We welcome the wide range of comments provoked by the introduction of our alternative theoretical perspective on the

peri-ovulation paradigm (Havlíček et al. 2015)—some positive and some very critical—and here we address briefly some of the key objections.

First, a key assumption of our “peri-ovulation spandrel” hypothesis is that the formation of long-term relationships is critical to understanding human mate preferences. Echoing Dixson (2015), we are skeptical about the ecological validity of distinguishing between short-term and long-term mating preferences. Researchers frequently ask participants to describe their preferences in each context and, as Haselton (2015) describes, effects are often stronger in short-term contexts. In reality, little is known about how these categories are interpreted and distinguished by participants. Moreover, if such a distinction does exist, the extent to which meaningful change in mating strategy can be elicited by brief instructions on a questionnaire is likely to be, at best, individually variable. We suspect that many participants, especially in non-western communities, do not easily conceptualize the distinction, and its validity should be theoretically and methodologically reexamined and validated before robust claims are made about its utility.

Second, our hypothesis relies on the presence of shared hormonal mechanisms that underpin both between-individual differences and cyclic shifts in attractiveness and preferences. For illustrative purposes, we mainly employed examples related to estradiol. This emphasis might have confused some commentators or led to the view that our hypothesis is based solely on estradiol-related effects. Indeed, we did caution that other hormones, or combinations and interactions between different hormones, could be important. Leaving this aside, Roney et al. (2015) argue that our hypothesis is likely incorrect as the association between adult levels of estradiol and attractiveness is small—citing their own work (Grillot et al. 2014)—despite, in that paper, both noting methodological weaknesses compared with other relevant papers (e.g., Jasienska et al. 2004) and ultimately concluding that “perceivers’ attractiveness judgments may in fact hone in on cues of fecundity in young women’s bodies.” They also contend that there was an absence of stable associations between hormone levels and attractiveness in ancestral populations. Of course, data to support the latter statement do not exist. It is also worth noting that, although average levels of ovarian hormones in women from nonindustrial societies, with relatively infrequent ovulatory cycles, are certainly lower than in western countries (Jasienska 2013), these populations still contain substantial individual variation in hormonal levels, irrespective of the absolute mean value. It is not unreasonable, therefore, to imagine that this variation could be associated with attractiveness, as it is in other populations. Similarly, an informed interpretation of between-individual stability in association between attractiveness and hormonal levels would allow for age-dependent trajectories in both variables: the relevant comparison to be made, then, is not between adolescents and older women, as they seem to suggest, but among individuals within a cohort. In any case, with regard to the actual strength of association between hormone levels and attractiveness, our point is not that the between-individual association is remarkably strong (it is of course influenced by individual differences in diet, stress, infections, etc.), but rather that it appears to be stronger than the association within (or between) cycles in the same woman.

It is worth reiterating here a general methodological concern regarding hormone measurement. Hormone measurement via blood samples is more reliable than salivary assays as the former accounts for both free and bound hormone levels and is less confounded by adiposity and diet. Furthermore, individual women vary in their sensitivity to sex hormones as a consequence of variability in genes coding for linked receptors (Westberg et al. 2001). There

is a genuine absence of good evidence for how hormones affect mate preferences. For example, although Lobmaier et al. (2015) note that cyclical shifts in facial attractiveness were not associated with salivary estradiol levels, reproductive capacity (or potential fertility) is not characterized by estradiol alone, but results from concerted hormonal action. There is a need to conduct analysis using a broader array of hormones influencing reproductive functioning and perceptions of attractiveness (even including cortisol, testosterone, oxytocin luteinizing hormone, follicle-stimulating hormone, and gonadotropin-releasing hormone), and perhaps also receptor level activity, before we can expect to develop a fine-grained understanding of links between hormonal levels and physical attractiveness/mate preferences.

Third, Gangestad and Grebe (2015) and Haselton (2015) state that effect sizes in cyclic preference shifts might be underestimated by imprecise assessment of ovulation (e.g., by using counting methods instead of ovulation kits). However, it is equally plausible that more precise assessment might lead to lower effect sizes. Because lengths of menstrual cycles are roughly equally distributed around a 28-day mean, imprecise measurement of cycle phase might underestimate the effect sizes in short cycles, but overestimate them in longer cycles. Nonetheless, whatever estimate we eventually place on the actual effect sizes of cycle shifts, they will be far smaller than between-individual effects, and our interpretation of their relative salience remains unaffected.

Finally, Gangestad and Grebe (2015) argued that our hypothesis is not phylogenetically parsimonious. They assume that, among nonhuman primates, males are able to detect ovulation-related cues and “female primate sexual interests typically shift across the cycle adaptively.” They ask: “how could within cycle changes in humans evolve as a byproduct if ancestral species had these within cycle adaptations?” This argument relies on accepting the premise that female primate sexuality is tightly linked to cycle (and thus to ovarian hormones), but if this premise is incorrect, then the question of parsimony becomes less relevant (note also that evolutionary processes are not always parsimonious). In fact, the strength of the link between sexuality and the ovarian cycle likely varies across species. In our view, the crucial evolutionary change that took place at the root of anthropoid primates is the decoupling of sexual activity from *strict dependence* on sex hormones (by no means do we claim that sex hormones play no role in female primate of sexuality). Such decoupling allowed sexuality to be co-opted for other functions (e.g., paternity confusion, appeasement, etc.). Importantly, this also allowed relatively independent evolution of mate preferences, which is a distinct process from, and should not be conflated with, expressions of sexual desire. Thus, males of different anthropoid species would be expected to differentially evaluate cues of current or potential fertility (or both) based on their socioecology (e.g., mating system), though there might be some phylogenetic constraints in individual lineages (and these are hotly debated). For instance, in male baboons, the ability to assess conceptive cycles increases with tenure length in the troop. But males are not “helpless” in the face of fertile females (e.g., alpha males may concede conceptions to subordinates to increase the number of males with a reproductive stake in the group, so helping defend the alpha’s offspring) and females vary in their sexual behavior in relation to social context and not simply their own hormone levels (Clarke et al. 2009; Henzi et al. 2009). Thus, the pattern we see in humans (i.e., focus of male mate preferences on potential fertility) is not an evolutionary novelty but a variation on a common theme seen across anthropoid primate taxa, despite the relative rarity among anthropoid primates of long-term bonded relationships.

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REFERENCES

- Clarke PMR, Henzi SP, Barrett L. 2009. Sexual conflict in chacma baboons, *Papio hamadryas ursinus*: absent males select for proactive females. *Anim Behav*. 77:1217–1225.
- Dixon A. 2015. Human sexuality and the menstrual cycle: comment on Havlíček et al. *Behav Ecol*. 26:1261.
- Gangestad SW, Grebe NM. 2015. Within-cycle variations in women's sexual interests: mere byproducts?: a comment on Havlíček et al. *Behav Ecol*. 26:1262–1263.
- Grillot RL, Simmons ZL, Lukaszewski AW, Roney JR. 2014. Hormonal and morphological predictors of women's body attractiveness. *Evol Hum Behav*. 35:176–183.
- Haselton MG. 2015. Is the perspective of Havlíček et al. really new (or truly parsimonious)?: a comment on Havlíček et al. *Behav Ecol*.
- Havlíček J, Cobey KD, Barrett L, Klapilová K, Roberts SC. 2015. The spandrels of Santa Barbara? A new perspective on the peri-ovulation paradigm. *Behav Ecol*. 26:1249–1260.
- Henzi SP, Clarke PMR, van Schaik CP, Pradhan, GR, Barrett L. 2009. Infanticide and reproductive restraint in a polygynous social mammal. *Proc Natl Acad Sci USA*. 107:2130–2135.
- Jasienska G. 2013. *The Fragile Wisdom*. Cambridge (MA): Harvard University Press.
- Jasienska G, Ziolkiewicz A, Ellison PT, Lipson SF, Thune I. 2004. Large breasts and narrow waists indicate high reproductive potential in women. *Proc Biol Sci*. 271:1213–1217.
- Lobmaier JS, Klatt WK, Lory V, Probst F. 2015. The many sides of the peri-ovulatory coin: comment on Havlíček et al. *Behav Ecol*. 26:1261–1262.
- Roney JR, Lukaszewski AW, Simmons ZL, Eisenbruch AB, Grillot RL. 2015. A between-women account of cycle phase shifts is probably wrong: comment on Havlíček et al. *Behav Ecol*. 26:1264–1265.
- Westberg L, Baghaei F, Rosmond R, Hellstrand M, Landén M, Jansson M, Holm G, Björntorp P, Eriksson E. 2001. Polymorphisms of the androgen receptor gene and the estrogen receptor beta gene are associated with androgen levels in women. *J Clin Endocrinol Metab*. 86:2562–2568.