Greater precision, not parsimony, is the key to testing the peri-ovulation spandrel hypothesis

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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 sceptical 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 re-examined 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 to other relevant papers (e.g., Jasienska et al. 2004) and ultimately concluding that "perceivers' attractiveness judgements 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, while 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 characterised by estradiol alone, but results from concerted hormonal action. There is need to conduct analysis using a broader array of hormones influencing reproductive functioning and perceptions of attractiveness (even including cortisol, testosterone, oxytocine LH, FSH and GnRH), 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 Gerbe (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. Since 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 Gerbe (2015) argued that our hypothesis is not phylogenetically parsimonious. They assume that, among non-human 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 cycle likely varies across species. In our view, the crucial evolutionary change that took place at the root of anthropoid primates is the decoupling sexual activity from *strict dependence* on sex hormones (by no means do we claim that sex hormones play no role in female primate 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 behaviour in relation to social context and not simply their own hormone levels (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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