

The spandrels of Santa Barbara? A new perspective on the peri-ovulation paradigm

Running title: Evolution of menstrual cycle-related perception

Jan Havlíček^{1,2*}, Kelly D. Cobey^{3,4}, Louise Barrett⁵, Kateřina Klapilová^{1,2}, and S. Craig Roberts³

¹Charles University, Prague, Czech Republic

²National Institute of Mental Health, Klecany, Czech Republic

³School of Natural Sciences, University of Stirling, UK

⁴Laboratory of Experimental and Comparative Ethology (LEEC), University of Paris 13, France

⁵University of Lethbridge, Alberta, Canada

*Author for correspondence:

Jan Havlíček, Faculty of Science, Charles University; Viničná 7, 128 44 Prague 2, Czech Republic. Phone: +420 221 95 1853; E-mail jhavlicek@natur.cuni.cz

Abstract

Numerous recent studies document peri-ovulatory increases in women's physical attractiveness and in their preferences for certain male traits, which appear to be linked to cyclical fluctuation in levels of ovarian hormones. Changes in physical traits are subtle, leading to the widespread conclusion that cues of ovulation are adaptively concealed. It has been argued that concealment enables women to pursue a mixed-mating strategy characterized by pair-bonding with opportunistic extra-pair copulation with high quality mates when conception is possible. Men's preferences for peri-ovulatory cues and women's cyclical preference shifts are thus also argued to reflect distinct psychological adaptations. Here, we re-interpret the evidence for each of these putative adaptations and argue that cyclic changes need not result from incomplete concealment of ovulatory status. We also emphasize that ovarian hormone levels underpin between-individual differences in both women's attractiveness and their mate preferences, which influence the sexes' mate choice decisions. We contrast the salience and efficiency of these within- and between-individual effects, and suggest that, while both effects have the potential to influence mating behavior, the between-individual effects are stronger and more robust. This introduces the possibility that both men's increased attraction towards peri-ovulatory women and women's cyclical shifts in preference for certain male traits may not constitute adaptations *per se*, but are, instead, inevitable byproducts, or 'perceptual spandrels', of putative adaptations related to between-individual differences in reproductive potential. Our framework parsimoniously explains several observable phenomena, and potentially could transform the way evolutionary researchers interpret changes in behavior associated with the menstrual cycle.

Key words: menstrual cycle, fertility, ovarian hormones, mate preferences, attractiveness, adaptationism

Evolutionary psychologists use a Neo-Darwinian framework to provide answers to questions concerning the origin of specific psychological mechanisms. Central to this endeavor is the concept of *adaptation*. This term can be used in two senses. First, it is employed to characterize the process by which non-random or unequal reproduction, driven by specific heritable traits of an organism (i.e., the process of natural selection), results in organisms displaying some kind of fit to the environment. Second, it is used to describe the end-products of this process, i.e., traits that have evolved as a direct consequence of the fitness benefits they conferred on their bearers. In this paper, we refer only to the latter sense. Despite the centrality of adaptation in evolutionary thinking, there is a longstanding debate regarding the criteria by which a trait can be convincingly labeled as such, because traits that resemble adaptations may in fact originate via different evolutionary processes. For instance, Gould and Vrba (1982) introduced the concept of *exaptation*, which characterizes traits that evolved to fulfill one function but subsequently become beneficial for a different purpose.

In their (in)famous paper, Gould and Lewontin (1979) criticized researchers for concluding too readily that certain traits and behaviors were adaptations. An apparently adaptive trait is not always an adaptation, they argued, but may sometimes be a *spandrel*; an inevitable by-product of the development of another adaptive trait, without itself being a direct product of selection, perhaps due to gene pleiotropy, linkage disequilibrium, or developmental constraints. Note that spandrels may also be subsequently selected for new functions. Gould and Lewontin (1979) employed an analogy from architecture (a spandrel is the triangular area between supporting arches that are produced as an inevitable by-product of arch formation, but which thereby provides a surface that could then be exploited for decoration), specifically from the Basilica di San Marco in Venice (but see Houston 2009 for a critique of this architectural metaphor). They further argued that it is important to differentiate between adaptations, exaptations and spandrels if one is interested in explaining the origins of a trait, and how it may play a role in current behavior. In many cases this is a difficult task because it involves traits which are the end-products of past selection, hence we must infer the nature of previous selection pressures when attempting to reconstruct their origin.

In the case of psychological mechanisms, in particular, we face another disadvantage: these do not fossilize and we therefore cannot trace the temporal order of their origin. However, Andrews et al. (2002) provide a comprehensive analysis of approaches to identifying adaptations in the context of behavioral science, arguing that the main evidential burden is whether the trait displays features of special design: that is, it should be possible to demonstrate that the trait evolved to perform a specific function. Relevant criteria vary according to the nature of the trait under examination (e.g., morphological and cognitive traits may require different criteria), but include features like proficiency, efficiency, and specificity of the trait in question. Surprisingly, however, behavioral scientists have rarely employed this approach as a guideline for analysis of specific traits (for an exception, see Williams and Taylor 2006).

With the rise of evolutionary thinking in psychology, Gould and Lewontin's (1979) distinction between adaptations and spandrels, and the difficulty of identifying adaptation, have once again been brought to the fore. Although most researchers likely understand Gould and Lewontin's distinctions and recognise that, as Williams (1966) noted, adaptation is an onerous concept, it is apparent that empirical work too rarely pits competing hypotheses against each other in order to distinguish adaptationist explanations from by-products/spandrels. This statement applies to many evolutionary sub-disciplines, but arguably it is especially true of the strongly adaptationist research program pursued by evolutionary psychologists within the so-called "Santa Barbara school" (Bolhuis et al. 2011; Schulz 2011); here, in line with others, we use this term as a label for a particular way of reasoning, rather than a reference to a particular academic affiliation. The existence of a psychological adaptation is often inferred on the basis of a putative ancestral fitness benefit, and then tested by investigating whether particular behaviors that are elicited under various kinds of experimental (and less frequently, naturalistic) conditions are consistent with the existence of such an adaptation. Demonstrating the potential benefits of a trait is certainly an important and necessary step; however, as we have outlined, it may be insufficient evidence to conclude that a trait represents an adaptation, at least until it has been tested against alternative explanations for its evolutionary origin. To be clear, we do not wish to claim that

evolutionary psychologists have entirely failed to consider non-adaptationist interpretations; rather, we are simply stressing that byproduct explanations are not given quite the same level of empirical attention and are often not put to the test in the same systematic fashion (indeed, non-adaptationist explanations are frequently represented by a cursory note in a manuscript's discussion; for a notable exception, see Thornhill and Gangestad 2008). Here, we first briefly address the question of whether cyclical changes in women's appearance are consistent with the interpretation of an adaptation for concealment of ovulation. While many researchers conclude that subtle cyclical changes are byproducts of physiological changes associated with the menstrual cycle, we argue that this need not be explained by selection for concealment. We then address two intensively studied facets of human mating psychology that many researchers also consider to be psychological adaptations: (i) the proclivity for men to discriminate women's fertility status from physical and behavioral cues, and (ii) an increased preference in women for specific male traits around ovulation. In common with many researchers, we agree there might be selective benefits to both phenomena. However, we propose that, rather than being adaptations, both facets might be inevitable by-products (or perceptual spandrels) of more generalized hormone-dependent mate choice mechanisms.

Concealed ovulation as an adaptation

Based primarily on comparisons between humans and their closest extant relatives, chimpanzees, women historically have been considered to show concealed ovulation (e.g., Symons 1979). This is because, unlike humans, female chimpanzees undergo conspicuous cyclical changes in perineal morphology that index current fertility in a probabilistic manner and are attractive to males (Wallis 1992; Nunn 1999). Earlier hypotheses on this topic often assumed conspicuous cyclical changes to be the ancestral state for humans (e.g., Burt 1992). More recent phylogenetic analyses, however, suggest this may not be the case (Sillén-Tullberg and Møller 1993; Nunn 1999; Duda and Zrzavý 2013). Indeed, the last common ancestor of chimpanzees and humans may have been characterized by very moderate or even inconspicuous cyclical changes in morphology. Non-advertised ovulation might

therefore be due simply to differences in selective pressures acting on different primate lineages, a byproduct of bipedality (Pawłowski 1999) or perhaps something not obviously related to sexual behavior, such as the presence of large adrenal glands (reviewed in Thornhill and Gangestad 2008).

It remains the case, however, that many researchers see human ovulation as concealed. Functional hypotheses for concealed ovulation include the promotion of paternal care (Strasmann 1981) or paternity confusion (Hrdy 1979), and argue that concealment enables women to engage in extra-pair copulations with males of high genetic quality while retaining paternal investment of a primary bonded partner, and that this is especially likely to occur if the latter is of relatively low genetic quality (e.g., Thornhill and Gangestad 2008; Gangestad and Thornhill 2008; Gangestad and Haselton 2015; Haselton and Gildersleeve 2011).

Thornhill and Gangestad (2008) provide an extensive review of the evidence for concealed ovulation as an adaptation. They describe three key features that are thought to characterize concealment: (i) females should not alter their behavior in relation to their estrus/menstrual phase, (ii) sexual desire should be decoupled from the underlying hormonal changes governing the cycle, and (iii) physical and behavioral changes associated with ovulation should be greatly reduced or absent. Although they concede that none of these requirements appear to be strictly met in humans, they conclude that human ovulation is indeed concealed. They base this conclusion primarily on the third of these requirements, arguing that, because physical and behavioral cues are not easily detectable, this likely means that females have been under direct selection to suppress them. This reasoning leads to the concept of 'leaky cues', such that the ability to entirely suppress the hormone-dependent physical changes associated with ovulation are constrained by the necessity of maintaining reproductive function (see also Gangestad and Thornhill 2008; Gangestad and Haselton 2015; Haselton and Gildersleeve 2011).

Irrespective of whether there has been recent selection for concealment in the human lineage, or whether inconspicuous ovulation has been retained from the last chimpanzee-human common ancestor, most scholars agree that cyclical fluctuations in women's physical traits have not been

selected for specifically (i.e., they are not 'signals'; for an alternative view see Guéguen, 2012), but instead are byproducts of the hormonal changes that underpin ovulation (i.e., they are 'cues') (Pawlowski 1999; Thornhill and Gangestad 2008). With regard to these cues, the distinction between non-advertised ovulation (or 'undisclosed' ovulation: Thornhill and Gangestad 2008) and concealed ovulation rests critically on whether or not selection has acted to suppress ovulatory cues directly. Thus, if ovulation is simply non-advertised, then these physical and behavioral changes are just 'cues'. By contrast, if ovulation is concealed, these changes must be viewed as 'leaky cues'.

Which interpretation is correct? We do not necessarily wish to argue that ovulation is not concealed in humans; there is certainly evidence that could be used in favor of this hypothesis (see review in Thornhill and Gangestad 2008). However, we suggest that the subtlety of the physical and behavioral changes across women's menstrual cycles can plausibly be interpreted as simple byproducts of the underlying hormonal changes that occur *without* resorting to the claim of an adaptation in women to suppress these cues. This view is supported by the fact that the other two foundational features of the concealment hypothesis are not met. Furthermore, we think it is interesting to note that there is a growing body of literature showing that women behave in ways that attract more attention around ovulation, for example, by choice of more revealing or attractive clothing (Haselton et al. 2007; Beall and Tracy 2013). Is this a means of attracting the attention of potential extra-pair partners, as it has been interpreted, even if it also tends to increase jealousy and proprietary behavior in a partner? Or could it be that women simply choose their clothing in response to increased courtship motivation linked to their current hormonal profile? We do not know the answer, but this form of "advertisement" would appear to be directly at odds with the concept of adaptive concealment.

Is current fertility detection really an adaptation?

A separate question from how cyclical changes evolved is whether other people, particularly men, possess a specific adaptation to respond to cycle-related cues. We begin by briefly summarizing the evidence that has amassed over recent years.

Studies have shown that women's physical attractiveness, assessed in several sensory modalities, fluctuates across the menstrual cycle, with a peak in the late follicular phase, thus potentially providing cues to current fertility. For example, facial photographs taken during the follicular phase receive higher attractiveness ratings than those of the same women in the luteal phase (Roberts et al. 2004). Cue discrimination may be based on changes in soft facial tissue (Bobst and Lobmaier 2012) or a combination of shape and skin texture cues (Oberzaucher et al. 2012). Similarly, recordings of women's voices during the follicular phase are rated as more attractive than during the luteal phase (Fischer et al. 2011, Puts et al. 2013), likely due to elevated voice pitch (Fischer et al. 2011). Attractiveness of axillary (Havlíček et al. 2006; Gildersleeve et al. 2012) and vaginal (Doty et al. 1975) odors follows the same pattern. These changes may be underpinned by fluctuations in levels of ovarian hormones. For example, progesterone levels negatively predict facial attractiveness, and interactions between estradiol and progesterone predict voice attractiveness (Puts et al. 2013).

Cyclical variation in physical cues is mirrored by evidence from behavioral displays (Cantú et al. 2014), gait (Fink, Hugill and Lange 2012), and, as mentioned above, choice of clothing style (Haselton et al. 2007) and color (Beall and Tracy 2013). Together with physical changes, these behavioral cues may also influence men's attractiveness judgments of women (Miller, Tybur and Jordan 2007; Cobey et al. 2013), although clothing choices are dynamic, likely to be culturally dependent, and might be consciously deployed according to social context (Thornhill and Gangestad 2008).

Some researchers therefore argue that male attention to such cyclical fluctuations represents a psychological adaptation that (i) increases their chances of conceptive sex, and/or (ii) serves to intensify mate-guarding behaviors around ovulation and thus avoid the costs of cuckoldry (e.g., Gangestad and Thornhill 2008; Thornhill and Gangestad 2008; Haselton and Gildersleeve 2011).

The idea that men's ability to detect cues of current fertility represents a psychological adaptation has intuitive appeal because the potential benefits are clear. However, we can employ the approach of Andrews, Gangestad and Matthews (2002) to re-examine this claim more closely. For example, a defining characteristic of an adaptation is its efficiency in achieving the associated fitness-

related benefits. When considered from this perspective, it is immediately obvious that this putative adaptation is not particularly efficient. The physical changes in women's appearance around ovulation are almost beyond our capacity to measure, despite the aid of sophisticated technologies. For instance, a study examining changes in women's voices found that even detailed acoustic analysis of vocal parameters precluded unequivocal identification of the follicular phase (Fischer et al. 2011).

These low-amplitude fluctuations in the cycle-associated cues are matched by low proficiency in detection of ovulation by perceivers. In experimental tests using paired stimuli obtained under the same conditions from the same woman during the follicular and luteal phases (e.g., Figure 1), fertile stimuli were selected as most attractive only slightly above chance (~55% for faces: Roberts et al. 2004; 60% for clothing: Haselton et al. 2007). Although it has been argued that cyclical shifts in some modalities (e.g., body odor) are relatively large (Haselton and Gildersleeve 2011), effect sizes from any such experiment likely over-estimates the actual effect: simultaneous presentation of paired stimuli from the same woman never actually happens in real life. Actual cycle-related attractiveness judgments are, by definition, temporally distributed and, given low discrimination rates even in laboratory experiments, the extent to which they affect perception in real-world settings is questionable, even for long-term partners (Roberts et al. 2004). This might also explain why cross-sectional (in contrast to within-subject) studies frequently fail to find cyclical changes (e.g., Thornhill and Gangestad 1999).

To illustrate this point, consider the following thought experiment: imagine entering a room full of adult women and attempting to detect those near ovulation. We suspect that few people would consider themselves able to do this reliably, unless equipped with sophisticated devices such as hormone kits or transvaginal ultrasound equipment. If our sensitivity to detect leaking gas were as good as our ability to detect ovulation, the result would be a host of unwanted deaths.

As we have described, proponents of the concealment hypothesis argue that such cyclical changes are *expected* to be very subtle, because selection has directly acted on women to hide them. An alternative adaptive explanation is that their effects might be restricted to men who interact on a daily basis with particular women, such as their partners (e.g., Roberts et al. 2004). In this sense, the

mechanism allows men to assess variation in fertility once they are partnered, and does not function as a mechanism that assists in selecting potential mating partners in the first place. Although such effects are plausible (see e.g., Haselton and Gangestad 2006 for cyclic fluctuations in male mate guarding), to our knowledge, there are no studies available that explicitly compare ratings made by women's partners against those of men who are unfamiliar with a particular woman. Instead, studies on menstrual cycle-related attractiveness almost always involve men unknown to the women and make the assumption that they are testing realistic mate-choice (i.e., decision-making) processes.

This emphasis on decision-making has led to a focus on research that uses closely controlled experiments that test whether or not men can 'detect' signs of ovulation (for a review, see Haselton and Gildersleeve 2010). We have nothing against such studies in principle: they are both interesting and insightful, but they do not necessarily reflect real-world partner choice. Indeed, studies in other animals suggest that the limits of detection of variability in traits such as symmetry, assessed in laboratory-measured tests, renders such traits as ineffective for discriminating natural variation (e.g., Swaddle 1999; Swaddle et al. 2008).

Against this background of evidence, we acknowledge that a possible adaptation for concealment of ovulatory state, leading to 'leaky cues', might be the reason for relatively low efficiency of male preferences for current fertility cues, and that, as Thornhill and Gangestad (2008) suggest, in an evolutionary arms race between women's adaptive suppression of ovulatory cues and men's adaptations to detect them, women have the upper hand. Against this, however, we argue that an antagonistic coevolutionary race between these two adaptations is not the only plausible interpretation for the low efficiency of the male current fertility-related preferences. We now turn our attention to providing an alternative explanation for this phenomenon.

Cues of potential fertility

In contrast to our ability to detect cues of ovulation, we consider ourselves quite proficient at judging individual variation in attractiveness. The concept of beauty appears to be a human universal.

People readily agree on who is attractive and who is not (Langlois et al. 2000), and judgments are often consistent across people from different cultures and ethnicities (Jones 1995). Facial attractiveness is evident even to infants (Langlois et al. 1991). Put another way, neither men nor women would have much trouble dealing with the task of picking out attractive women within a busy room.

Proficiency in detecting attractiveness also implies efficiency in its communicative function. Factors underlying between-individual variation in attractiveness are well-documented. In the face, for example, attractiveness is mediated particularly by symmetry, sexual dimorphism, averageness and health (Gangestad and Scheyd 2005; Rhodes 2006). Most researchers agree that these traits are considered attractive because they reveal individual variation in mate quality leading to potential benefits in terms of reproductive success (Jokela 2009; Pflüger et al. 2012, but see Silva et al. 2012), and that preferences for these traits have been favored by selection. In terms of women's attractiveness to men, physical traits such as facial femininity (Smith, Specker and Korach 2010), gynoid fat distribution, waist-to-hip ratio (WHR) (Singh 2002), vocal characteristics (Brunings et al. 2013), and breast shape (Jasienska et al. 2004) are considered especially important, although their relative significance may vary across cultures. These traits develop during puberty under the influence of steroid hormones, particularly estrogen, and in adults they correlate with estrogen levels (Singh 2002; Law-Smith et al. 2006; Grillot et al. 2014). For example, individual variation in facial attractiveness is correlated with late-follicular estradiol levels (Durante and Li 2009; Bobst and Lobmaier 2012), women with larger breasts and smaller WHRs have higher sustained estradiol and progesterone levels across the cycle (Jasienska et al. 2004), and ratings of women's bodies (Grillot et al. 2014) or faces and bodies (Durante and Li 2009) are positively predicted by differences in their estradiol levels (Figure 2). Selection on preferences for these traits is likely to be strong, because hormone levels provide cues to a woman's future, or potential, fertility, at least over immediately forthcoming cycles (Lipson and Ellison 1996; Venners et al. 2006) and potentially over the lifespan. On this basis, the psychological mechanisms for discriminating attractiveness of potential partners are also considered to be adaptations (e.g., Thornhill and Gangestad 2008).

For balance, it should also be noted, however, that our understanding of associations between ovarian hormones and female physical attractiveness is currently far from settled (see e.g., Puts et al. 2013). This may partly be attributed to the methodology used. First, most studies correlate an individual body trait (e.g., WHR) with levels of a particular hormone (e.g., estradiol). However, because potential fertility is influenced by the concerted action of several hormones, it might be more appropriate to assess combined effects (e.g., progesterone to estrogen or estrogen to testosterone ratio) (Johnston and Franklin 1993). Second, for convenience, many studies use saliva samples, which provide measures of levels of free hormones. However, levels of free hormones might be obscured by body mass index (BMI) because fat tissue is negatively associated with sex hormone-binding proteins; studies employing blood samples to assess both free and bound hormone levels likely provide more valid data (for a full discussion see, Grillot et al. 2014). Finally, development of physical attractiveness-related characteristics may depend mainly on levels of hormones during puberty and subsequently become relatively stable. Although it is frequently assumed that pubertal levels of hormones and their adult levels are highly correlated (e.g., Law-Smith et al. 2006), this might only be partly true and cross-sectional studies with adults may thus underestimate this effect.

The perceptual spandrel hypothesis

Most scholars tend to view (i) current (i.e., whether a given woman is presently in the fertile phase of her menstrual cycle) and (ii) potential (i.e., a given woman's overall likelihood of being able to conceive) fertility-related contributions to attractiveness as two independent adaptations (e.g., Thornhill and Gangestad 2008). At first glance, this seems reasonable: one describes variation in attractiveness within individuals, while the other relates to between-individual variation. However, both sets of judgments hinge on the same underlying mechanism, namely levels of ovarian hormones, and could thus be expected to be strongly inter-linked (see Figure 3a). Understanding the evolution of preferences for such traits thus depends on an objective assessment of the relative selection pressures on the ability to discriminate current and potential fertility.

As described above, the low proficiency of males to detect current fertility indicates that selection on men's preferences for cues of high potential fertility may outweigh selection pressures on sensitivity to the physical changes related to current fertility. Further support for this contention comes from contrasting the levels of within-cycle and between-individual variation in studies of women's faces and axillary odor: between-individual variability in facial appearance is higher than within-cycle changes (Figure 1a, b). The same is true of variability in odor attractiveness (Havlíček et al., 2006; Fig.1c): although, on average, women's follicular phase odors were judged most attractive, the odor of many women during the menstrual and luteal phases was judged as more attractive than the odor of other women during the fertile phase.

Thus, even if ovulation detection is an adaptation, it appears to have a relatively small effect on men's behavior compared to their assessment of between-women variation in attractiveness. This, along with the similarities in underlying hormonal mechanism, raises the possibility that, rather than being an adaptation (again, defined by being a trait that evolved *as a direct consequence* of the benefits they confer), discrimination of ovulation-linked cues might arise as a by-product of a generalized preference among men for cues of high estrogen levels (or low progesterone to estrogen ratio) that discriminate between women in terms of potential fertility. The arguments presented by Gould and Lewontin (1979) with respect to by-products thus apply here. Although Gould and Lewontin focused on morphological traits, it is important to emphasize that such by-products are not restricted to morphology and their analogy can also be applied to psychological functioning (Gould 1991; Buss et al. 1998; Andrews et al. 2002). Thus, we suggest that perception of cyclical changes in physical attractiveness could be an example of a psychological, or more specifically, a perceptual spandrel. Note that this fulfills the criteria for an evolutionary by-product as recently discussed by Park (2007). In his critique of the loose use of this term, he proposed that, in order to avoid confusion, the term 'by-product' should not be used either to describe behavioral outcomes or effects of particular psychological mechanisms that arise as a consequence of novel inputs to the system, but should be applied only to the mechanisms themselves.

Although phrased somewhat differently, Roney (2009) reached a similar view. He argued that apparent preferences for female cues of ovulation are consistent with a general mechanism for cues of chronically high estradiol in women. He further suggests that this preference may be derived, in functional terms, from benefits gained through discrimination of differences in ovarian hormone levels between ovulatory and non-ovulatory cycles, rather than from the benefits gained through discriminating within-cycle variation. We think this is a persuasive and underappreciated point.

Indeed, we would go further: the argument can also be extended to between-individual differences in ovarian hormones levels. For instance, since estradiol levels vary between individuals, and these differences underpin between-individual differences in attractiveness (Figure 2), it is plausible that men's attention to estradiol-linked physical traits when making between-woman attractiveness judgments may also explain estradiol-linked within-individual attractiveness differences, regardless of whether these occur within or between cycles. Attention to ovarian hormone-linked markers of high potential fertility (e.g., facial femininity, body shape) could reap selective benefits in addition to targeting imminent ovulatory or conceptive cycles, because estradiol levels may reflect younger age (Mersereau et al. 2008) or relatively good nutritional status/condition (Venners et al. 2006; Ziolkiewicz et al. 2008), or be linked to traits like nulliparity and earlier onset of menarche (Windham et al. 2002). Indeed, between-individual differences in estradiol are robust and maintained across the cycle (Figure 3b), providing more stable and reliable cues of potential fertility than associations between estradiol concentration and ovulation (Figure 3). In contrast, one recent study found that within-individual changes in facial and vocal attractiveness were related to progesterone levels but between-individual differences were not (Puts et al. 2013). As these authors note, however, they collected hormonal samples at variable points of women's cycles, which could have the effect of underestimating any between-individual effects by a considerable margin. We clearly need more studies to disentangle these issues.

Cyclical shifts in women's mate preferences

The conceptual framework developed above could also conceivably be applied to the accumulating evidence for changes in women's mate preferences across the menstrual cycle. These preference shifts are characterized by an increased peri-ovulatory preference for traits that appear to be markers of male quality. Such shifts in preferences have been reported for a range of sexually dimorphic physical traits, including relatively masculine faces, bodies, and voices (Penton-Voak et al. 1999; Puts 2005; Little, Jones and Burriss 2007; Jones et al. 2008). Like changes in women's physical appearance, these changes are hormonally mediated. For example, preference changes for masculine male faces or vocal traits are mediated by changing levels of estradiol or its precursors such as testosterone (Feinberg et al. 2006; Welling et al. 2007; Bobst et al. 2014).

Currently, there are two main suggestions for why these shifts occur. The most influential and pervasive of these is the idea that psychological mechanisms are affected by cyclical hormonal fluctuations to increase attraction to markers of high genetic quality when conception is likely, providing a mechanism by which women maximize the quality of mating partners: the 'ovulatory shift hypothesis' (Thornhill and Gangestad 2008). Despite its prevalence and widespread acceptance within Evolutionary Psychology, this idea remains controversial and heavily contested outside this sphere (e.g., Gildersleeve et al. 2013; Harris 2013). Most recently, this has resulted in the publication of two meta-analyses aimed at establishing the robustness of the phenomenon. Far from reaching consensus, these papers produced widely contrasting results. While Gildersleeve et al. (2014a) found evidence for cycle-shifts mainly in short-term mating contexts, Wood et al. (2014) found no support for cycle-shifts influencing female mate preferences. Given that each research group was dealing with a largely overlapping body of literature, these results seem rather puzzling at first. On closer inspection, the differences are not, in fact, surprising.

First, although the sample for both meta-analyses did indeed overlap (32 published and 5 unpublished studies in common), their samples were not identical. Wood et al. (2014) presented data from 10 published and 8 unpublished studies unique to their sample, while Gildersleeve et al. (2014a) presented unique data from an additional 4 published and 6 unpublished studies. In addition, the two

studies used different inclusion criteria for the variables selected and structured their analyses differently. Most substantively, Gildersleeve et al. (2014a) conducted a two-tiered analysis, in which they first investigated whether there was an overall influence of cycle phase on preferences for a broad array of mate characteristics. This was followed by a more restrictive analysis that excluded those traits not widely accepted as cues of genetic quality, as well as excluding studies that either asked women to state their preferences (rather than directly rate stimuli for attractiveness) or which used stimuli that did not allow for any direct assessment of the trait in question (e.g., when vignettes describing visual characteristics were used, rather than using visual stimuli). By contrast, the analyses of Wood et al. (2014) consisted of testing for cycle-shifts for each mating characteristic separately, and did not combine effects across traits. Finally, Gildersleeve et al. (2014a) split their sample by relationship context (short-term, long-term and unspecified), whereas Wood et al. (2014) did not differentiate their sample in this way.

Given these differences in approach, the contrasting results are more easily explained. Indeed, the debate continues more or less unabated (Gildersleeve et al. 2014b; Harris et al. 2014; Wood 2014; Wood and Carden 2014). This is perhaps to be expected, however: as Ferguson (2014) points out in his commentary on this debate, meta-analyses rarely solve scientific disputes, because differences in theoretical outlook, along with the stance taken on a particular issue, inevitably influence the manner in which data are selected for inclusion in such analyses and how they are used to test a specific hypothesis. We feel this is a key point to make, but on slightly different terms. That is, in our view, part of the problem lies in characterizing within-individual preference shifts as adaptations when they should be considered as by-products of more general differences that exist between women. Theoretical reconceptualization along these lines may therefore pay dividends with respect to the design of future empirical work, rather than continued attempts to interrogate the existing data and establish some kind of consensus on the size and robustness of the effects.

To expand on this just a little, perhaps the most interesting aspect of the current meta-analyses, in our view, is the size of the effects found and the variability in these across different traits; it seems

that these do not just represent variability in the rigor of the methods and the definitions employed in such studies, but tell us something about the phenomenon itself. For example, Gildersleeve et al. (2014a) show that, although there was a significant overall effect of cycle phase on women's mate preferences, and a significant effect of short-term relationship context, the effect sizes were small to moderate (broad sample: overall, $g = 0.15$; short-term relationships, $g = 0.21$; narrow sample: overall, $g = 0.17$; short-term relationships, $g = 0.26$). Small effect sizes also characterize the analyses for individual traits, and there was also considerably more variability in the associations found (e.g., significant or marginally significant effects were found in the short-term context for body masculinity ($g = 0.35$) and behavioral dominance ($g = 0.19$), but not for facial symmetry ($g = 0.3$) or facial masculinity ($g = -0.02$)). In addition, Gildersleeve et al. (2014a) showed that, after controlling for relationship context, higher effect sizes were associated with a between-participant rather than a within-participant design. These authors point out that there are many potential unmeasured confounds and, as a result, it is difficult to know true effect sizes. In addition, the relationship between effect size and the presence of an adaptation is unlikely to be linear. We sympathize with this view and note that true effect sizes might be heterogeneous and, in different cases, either under- or over-estimated. Given the strong public interest in shifts in mating behavior across the menstrual cycle, it is important for scholars to provide context and convey what, if any, "real world" differences exist across the cycle. As we see it, however, the variable and elusive nature of the phenomenon is precisely what one would expect from a by-product explanation: that is, variability is not the consequence of experimental/measurement error and noise, but an inherent characteristic of the phenomenon under study. Thus, rather than speaking to a lack of methodological rigor within the current paradigm, as some suggest (Harris et al. 2014, Wood and Carden 2014), this variability and inconsistency might be more productively viewed as a mischaracterization of the nature of the effect: the effects of individual within-cycle shifts should, in fact, be small, statistically weak, and variable if they prove to be the by-products of more robust between-women differences.

The same point can be made for the finding that, in both sets of analyses, stronger effects were

found for those studies that specified a broad window of fertility (i.e., of around 9 days as opposed to 6) (Harris et al. 2014; Wood and Carden 2014). As Gildersleeve et al. (2014b) point out, this does not necessarily indicate less precision in the measurement of the fertile phase, as argued by Wood and Carden (2014) and Harris et al. (2014). Indeed, Gildersleeve et al. (2014b) argue that using 9-day window is a superior approach as it correctly captures fertile days of women with cycles longer than 28-days. Although this is correct, it is also true that the number of women having shorter cycles relative to those having longer cycles is relatively equal, which is why 28-days is usually chosen as an 'average cycle length' (Munster et al., 1992). Consequently, the use of a 9-day window may misclassify a similar number of women with shorter cycles as being fertile when they are not. In addition to issues of precision, however, stronger effects with a 9-day window might also suggest that shifts in preference are associated with levels of estrogen or other ovarian hormones (or their ratios), which fluctuate across the entire follicular phase of the cycle, rather than with the fertile window specifically; something that, again, would be in line with a by-product explanation, rather than one based on within-cycle shifts themselves being a target of selection.

The other explanation offered for why within-cycle shifts occur, proposed by Roney, is that shifts in preference are underpinned by differences in estrogen levels between different kinds of menstrual cycles, specifically between ovulatory/anovulatory or between conceptive/non-conceptive cycles (Roney and Simmons 2008; Roney 2009). Again, however, following a similar line of argument to the above, we suggest that any such *within-woman* changes in preference strength for male traits potentially could be explained by an even more general hormonal effect. That is, the attraction to phenotypic markers of male quality may be regulated by *between-woman* differences in ovarian hormone levels (for a similar argument see Dixon 2009, ch. 6). To understand our argument more fully with respect to reconceptualizing both the ovulatory shift hypothesis and Roney's variant on this theme, it is necessary to re-examine the underlying hormonal mechanisms.

Individual variation in women's preferences

A functional relationship between ovarian hormones and expression of preference for high-quality male traits (evidenced by studies of within-woman preferences) would also be expected to shape the level of demand for attractive characteristics among women who vary in baseline levels of ovarian hormones. Although direct evidence is currently lacking, there is persuasive indirect support for this prediction. For example, as estradiol levels predict between-individual differences in facial and body attractiveness (Figure 2), high-estradiol women have high 'mate value'. Such women may be relatively selective (Parker 1983), choosing and retaining male partners with the most attractive characteristics. For example, assortative mating for attractiveness is one of the most striking and robust findings in human mate choice (Berscheid et al. 1973). In terms of specific attractiveness components, women's self-rated attractiveness (which is strongly correlated with other-rated attractiveness) predicts stronger preference for male facial masculinity and symmetry (Little et al. 2001) and vocal masculinity (Feinberg et al. 2012). Women with more attractive bodies show stronger preferences for facial cues of male quality (Penton-Voak et al. 2002; Jones et al. 2005; Smith et al. 2009). These findings indicate a relationship between women's estrogen level and their preference for the same kind of characteristics that are also chosen when estrogen peaks in the cycle, around ovulation. They are also consistent with studies in animals demonstrating that female condition influences mate choice (Bakker, Künzler and Mazzi 1999; Cotton, Small and Pomiankowski 2006). Although we use the example of variation related to estrogen, links to attractiveness may also be dependent on between-individual variation in other hormones such as testosterone and progesterone or even combinations or interactions of several hormones (e.g., estrogen to testosterone ratio). The precise hormonal mechanisms associated with the preferences described remain a challenge for the future studies.

Importantly, differences in female condition also moderate the size of cycle-dependent changes in preferences and behavior. For example, although women express greater preference for masculine voices in the late follicular than the luteal phase, this effect is significantly less pronounced in women with relatively high estrogen levels (Feinberg et al. 2006). Attraction to male muscularity is similarly more phase-dependent among women of lower self-perceived mate value (Millar 2013). Sensitivity to

such changes in male muscularity is enhanced by greater self-evaluation of mate value during the fertile phase, thereby reducing costs of inappropriate partner choice (Beaulieu 2007). This may also influence relationship dynamics: women of lower mate value experience greater ovulatory shifts in mate-guarding (Haselton and Gangestad 2006). These effects were previously interpreted as part of a mixed mating strategy. More specifically, women of lower mate value are expected to experience difficulties in attracting partners of high genetic quality. As a consequence, it is argued that there should be activation of a contingent adaptation in which such women should be more likely to opportunistically pursue extra-pair sex with men of high genetic quality or current condition, while attempting to maintain strategic long-term relationships with the males who provide care and provision to the offspring. Such extra-pair sex can be functional only when pursued during the fertile window when conception is possible (e.g., Haselton and Gangestad 2006).

In contrast, we think that the observed patterns might be due to a ceiling effect on preferences among high-estrogen women. Such ceiling effects could lead to lower cyclical variation among high estrogen women compared to the change experienced by women with relatively lower mean estrogen levels. Future studies should specifically address these two competing interpretations. The mixed mating strategy hypothesis predicts that the cyclical changes in women of lower mate value will be more pronounced in coupled compared to single women, while these differences are not expected according to the perceptual spandrel hypothesis. Several previous studies touch partly on this issue, though they focus not on preferences but on actual behaviors. For example, Durante et al. (2008) found that single women, as compared to coupled women and those scoring high on a relationship satisfaction scale, revealed more skin during fertile periods of their cycle. A second study found no effect of relationship status on changes in sexiness of clothing style across the cycle and only single women showed cyclic increase in interest for going out (Schwarz and Hassebrauck 2008). None of these findings are predicted by the mixed mating strategy hypothesis, which would posit such effects in partnered women but not single women.

It has been further argued that the mid-cycle peak in preferences for cues of high quality

partners should be pronounced in short-term in contrast to long-term mating contexts or unspecified contexts. As shown above, the effect sizes of the cyclic fluctuations in the short-term context in the meta-analysis of Gildersleeve et al. (2014) varied greatly, being sometimes higher compared to studies in which relationship length was unspecified and sometimes not. We would, however, question the extent to which the concept of a “short vs. long term mating strategy” is primarily theory-driven rather than data-driven, and might have been imposed on participants by researchers. It is possible that such ideas only have salience and relevance in some cultures and not others, and this is an empirical issue that requires further exploration.

In summary, then, while one could postulate two independent adaptations – one for within-cycle variation in preferences and a second being sensitive to ovarian hormone-dependent individual quality – a more parsimonious explanation is that selection acting on between-individual expression also produces cyclical variation as an epiphenomenon. The evidence showing that these two processes are inter-linked is in complete agreement with this view.

Phylogenetic considerations

Our byproduct argument for both male preferences for cues of current fertility and cyclic variation in female preferences is inherently based on assumptions related to phylogenetic sequence. Though we have partly addressed these issues above, here we aim to summarize possible phylogenetic scenarios. The most elaborate scenario was proposed by Thornhill and Gangestad (2008). In brief, their argument was based on the notion that most mammals are only sexually active during a discrete fertile period (commonly coined estrus) and that this was perhaps true of the common ancestor of the anthropoid primates. In contrast, anthropoid primates are sexually active throughout the cycle, even when conception probability is extremely low. These authors argue that the functionality of estrus sexuality has nevertheless been retained in humans. Based on this, Thornhill and Gangestad propose the concept of dual sexuality, which argues that mate preferences when fertile and non-fertile are divergent. Specifically, this idea acknowledges that, although women are receptive to sex throughout the cycle

(termed 'extended sexuality'), preferences and sexual behavior during the fertile phase of the cycle reflect a suite of adaptations designed to sire offspring with males of high genetic quality (for details see Gangestad, Thornhill and Garver-Apgar 2005). Moreover, the ovulatory shift hypothesis argues that women's increased fertile phase preference for high-quality males should be specific to short-term, but not long-term, mating contexts. In this view, sexuality during the non-fertile phase of the cycle is thought to serve a different purpose, namely promoting long-term relationships and bonding (see e.g., Gangestad & Haselton 2015 for a recent argument of this kind) or paternity confusion. Several moderating factors to this hypothesis have been proposed, including that women coupled with low-quality partners should show relatively greater cyclical shifts in desire for extra-pair men or that there should be larger differences in cyclic shifts between single and coupled women (see above).

In contrast, we argue that the loss of a strict association between sexual behavior and estrus, occurring at the root of the anthropoid primate lineage (for discussion see Dixson 2009), enabled relatively independent evolution of mate preferences and sexual behavior, the latter of which may have been co-opted for other functions than conception. Due to various environmental, social and other factors, selection then led to variability in mating systems and preferences across anthropoid primate species (for review see Dixson 2012). Since (in contrast to the majority of anthropoid primates) humans form long-term pair-bonds or small and relatively stable polygynous groupings, mate preferences would reflect relatively stronger selection pressures on men to select among women based on cues of long-term fertility (Stewart-Williams and Thomas 2013; Roberts and Havlíček 2013). Putative adaptations to long-term pair-bonded relationships would involve adult attachment and romantic love (Fletcher et al. 2015), which have indeed been reported across various cultures (Jankowiak and Fischer 1992). In other words, we do not think that human sexuality need consist of two functionally distinct phases. This view does not preclude cyclic variation in sexual psychology and behavior as a byproduct of menstrual cycle physiology; however, we would posit that other non-sexual behaviours are expressed consistently throughout the cycle. Note that this scenario does not call for the relatively complex series of adaptations associated with the concept of dual sexuality, but only invokes variation in selection

pressure for males of different species to differentially value cues of current or potential fertility. Indeed, it could further be argued that the reproductive costs associated with extra-pair copulations (e.g., risk of being abandoned with a highly altricial offspring) might be sufficiently high so as to preclude adaptations for dual sexuality to evolve in any case (see Dixson 2009 for a similar critique). However, this issue would benefit from formal mathematical models, which would help to assess the circumstances under which we may expect such adaptations to evolve in our human ancestors.

Objections and counter-arguments

In the main body of this paper, we have proposed that discrimination of cues of ovulation by men and cyclical variation in women's mate preferences may both be byproducts of between-individual variation in cues and preferences, underpinned by similar hormonal mechanisms. Objections to our proposal could include the following: (i) We have misinterpreted the direction of causality. That is, selection has acted directly on perception of hormone-linked within-individual cues of current fertility and that perception for between-individual differences arose as a by-product. Indeed, it was recently argued that primate sexual swellings originally developed as signals of current fertility and were subsequently co-opted as signals of potential fertility signals (Huchard et al. 2009). (ii) Even if preferences relating to current fertility initially arose as a by-product of traits related to potential fertility, they have subsequently been the target of selection and formed new adaptations (secondary adaptations). (iii) Low efficiency in perception of current fertility cues might be a consequence of counter-selection in women to conceal ovulation. Finally, (iv) the ability to detect cues of current fertility among humans is not a by-product, nor is it adaptive; rather it is a vestige of the evolved ability to detect current cues of ovulation shown by our primate relatives.

Based on our comparison of features of special design, such as efficiency and proficiency, the first two objections appear unlikely. Furthermore, they are undermined by the fact that estradiol, the predominant and most potent estrogen in reproductively active women, is not in itself a reliable predictor of current fertility. Although it increases during the late follicular phase and triggers the luteinizing

hormone surge, it occurs at sustained levels during the luteal phase and even across menstruation, and varies considerably between different women and different cycles (Stricker et al. 2006) (Figure 3). This would result in a poor match between timing of ovulation and its associated effects on physical cues and women's preferences, if, as has been argued; these are directly regulated by estradiol. On the other hand, between-individual differences in estradiol are sustained across the cycle and average levels would thus provide relatively stable and reliable cues of potential fertility (Figures 2 and 3).

The third objection would necessitate that physical markers revealing a woman's current fertility were more obvious during our evolutionary history than they are today. There are two main versions of this argument. The first version often emphasizes the human – chimpanzee comparison and assumes (though often implicitly) chimpanzee-like cyclic fluctuations in appearance as an ancestral state (e.g., Symons 1979). However, as we previously outlined, recent phylogenetic analyses indicate that conspicuous markers of current fertility are an evolutionary novelty in the chimpanzee lineage, which makes this scenario unlikely (Nunn 1999; Duda and Zrzavý 2013; see also Pawlowski 1999). The second version concurs with phylogenetic reconstructions on the evolutionary novelty of the conspicuous cyclic fluctuations in morphology in the chimpanzee, and assumes that cyclic physical changes are byproducts of the menstrual cycle physiology in an ancestral species. However, it also requires that, somewhere in the evolutionary lineage of modern humans, selection favored females with less obvious cyclic changes because of the potential advantages for paternity confusion (e.g., Thornhill and Gangestad 2008). This might explain the low efficiency of current fertility-related preferences. Although there is robust evidence showing that ancestral females were unlikely to show conspicuous fluctuations, the phylogenetic studies are uncertain as to whether there was selection for concealment in the human lineage, but our byproduct hypothesis does not require such an evolutionary step. Furthermore, as argued above, it is at least possible that the altriciality of human offspring and the high costs of abandonment may have precluded selection for dual sexuality, which in turn makes selection for concealment less likely, though this is definitely a potential area of further research.

Finally, if the preferences for cues of current fertility are merely vestigial, but are not adaptive,

and have not been selected against in modern humans, they would not be expected to be linked to the preferences for cues of potential fertility, as proposed by the perceptual spandrel hypothesis. However, as reviewed above, this appears not to be the case.

Conclusions and implications

Whether and how men can detect women's current fertility status and how current fertility influences women's mate preferences have each generated enormous research interest. Within-individual change in hormone levels, particularly estrogen, is the putative mechanism underlying both research paradigms. As we have described, most researchers interpret changes in women's attractiveness or preferences in terms of their current fertility within a single menstrual cycle. Roney and co-workers argue that these changes may be by-products of variation in estrogen levels across different cycles (Roney and Simmons, 2008; Roney 2009). In contrast, we suggest that both kinds of effect might be explained by a general hormone-dependent mechanism based on between-individual differences in women's baseline estrogen levels. Women with relatively high estrogen levels are likely to have high potential fertility and selection will therefore strongly favor men to attend to estrogen-linked physical cues. Women with high baseline estrogen are also expected to exhibit higher demand for attractive male traits. The available evidence is consistent with this hypothesis. Furthermore, while Roney's hypothesis can account plausibly for most of the data and requires only a single mechanism to explain different observed effects, our idea additionally captures well-documented differences in attractiveness and preference between different individuals. According to our view, within-individual changes in women's attractiveness and preferences across or between cycles are most likely by-products, or perceptual spandrels, rather than specific and independent adaptations.

Based on this one may generate several specific predictions which could be tested in future studies. One clear prediction is that differences in reproductive hormone-related attractiveness among individual women should be considerably higher compared to cyclic fluctuations or differences between individual cycles. The same would apply to the differences in reproductive hormone-associated

preferences for cues of male quality among individual women compared to the cyclic shifts in these preferences. Further, we hypothesize that cyclical shifts show lower magnitude in women with high potential fertility. In contrast to the ovulatory shift hypothesis, we also predict that the cyclical fluctuations in preferences are not modulated by relationship status or are smaller in coupled women. To test these claims, data on hormones and preferences should be sampled repeatedly across several cycles to reliably capture all three levels of variability (i.e., within cycle, between individual cycles and between individuals).

In their defense of adaptationism, Buss *et al.* (1998) state "...we could not find a single example of an empirical discovery made about humans as a result of using the concepts of exaptations or spandrels". In contrast, we argue that, while between-individual cues of potential fertility and preferences are indeed suggestive of adaptations, the corresponding effects associated with current fertility may well be excellent examples of spandrels. We are aware that this suggestion is controversial and we hope it will provoke researchers to develop tests to confirm or refute it. As Houston (2009) points out, following his analysis of architectural adaptations, the lesson of Gould and Lewontin's (1979) paper is that adaptationist explanations can be dismissed even when there is evidence in their favor; an error we would certainly be at pains to avoid. Fruitful approaches might include direct tests of effect sizes for cyclical changes versus between-individual differences; more comparisons of the relative effects of ovarian hormone variability within/between cycles and between individuals; consideration of dose-dependent effects and interactions among different hormones; more attention to criteria of special design such as efficiency and proficiency; and consideration of the relative selection pressures that operate on markers of current and potential fertility in relation to socio-ecological conditions, including differences in individual motivation brought about by, for example, relationship status. Finally, we hope that our analytical approach will stimulate greater attention to alternative interpretations in other psychological domains.

Acknowledgements

We are grateful to Robin I. M. Dunbar, Benedict C. Jones, Karel Kleisner, and VítTřebický for their critical comments on previous versions of the manuscript. We also thank Steven W. Gangestad and two anonymous reviewers for their constructive comments that significantly improved the clarity and precision of our arguments. JH is supported by the Czech Science Foundation grant (14-02290S), SCR by a British Academy Mid-Career Fellowship, KDC by a Fyssen Fellowship, LB by NSERC Discovery Grant and Canada Research Chair Programs, and JH and KK by the Charles University Research Center (UNCE 204004).

Figure 1. Variation in women's attractiveness across the menstrual cycle.

(a) Face images are shown of the same woman in the follicular and luteal phase (from Roberts et al. 2004). In (b) the same image of one woman has been transformed to display specific shape and skin texture changes that occur across phases (from Bobst and Lobmaier 2012). Follicular images are judged more attractive, but within-cycle differences are subtle compared to between-individual variation (a versus b). (c) Mean ratings of axillary odor samples of twelve women. Follicular samples were assessed by male raters as smelling most pleasant, but there is greater between-individual variation in ratings (from Havlíček et al. 2006).

Figure 2. Between-individual variation in estrogen and attractiveness.

(a) Women whose bodies are judged more attractive have consistently higher mean salivary estradiol concentrations across the cycle (cycle day 0 represents estimated day of ovulation) (from Grillot et al. 2014). (b) Composite face images of ten women with highest (left) and lowest (right) levels of estrone-3-glucuronide, an estrogen metabolite. Images from Law-Smith et al. (2006).

Figure 3. Variation in estradiol levels across the menstrual cycle.

(a) Reference values for serum estradiol levels, from Stricker et al. (2006). Dashed lines represent reference levels for the mid-luteal phase (days +5 to +9 from the luteinizing hormone (LH) peak). In women with the highest estradiol levels, serum concentrations during the mid-luteal phase (red dashed line) are close to those found in women with median levels (black line) even at the estrogen peak, and far exceed those in women with low levels (blue line). (b) Putative estrogen-dependent mechanisms for temporal change in women's attractiveness and expressed mate preference. The schematic depicts typical variation in estradiol levels across two menstrual cycles in women with relatively high (H) or low (L) baseline estradiol. Most previous studies focus on within-cycle (WC) changes. Roney and Simmons (2008) refer to differences in mean estradiol between different cycles (BC; means for each cycle are represented by green dashed lines). Here, we depict cycle 2 in the low-estradiol example (L) as an exposed non-conceptive cycle with reduced estradiol levels (see (Grillot et al., 2014)). Mean estradiol levels between individuals (BI) are depicted with solid blue lines.

References

- Andrews PW, Gangestad SW, Matthews D. 2002. Adaptationism—how to carry out an exaptationist program. *Behav. Brain Sci.* 25: 489-504.
- Bakker TC, Künzler R, Mazzi D. 1999. Sexual selection: condition-related mate choice in sticklebacks. *Nature* 401: 234-234.
- Beall AT, Tracy JL. 2013. Women are more likely to wear red or pink at peak fertility. *Psychol. Sci.* 24: 1837-1841.
- Beaulieu DA. 2007. Avoiding costly mating mistakes: Ovulatory shifts in personal mate value assessment. *J. Soc. Pers. Relat.* 24: 441-455.
- Berscheid E, Dion K, Walster E, Walster GW. 1971. Physical attractiveness and dating choice: A test of the matching hypothesis. *J. Exp. Soc. Psychol.* 7: 173-189.
- Bobst C, Lobmaier JS. 2012. Men's preference for the ovulating female is triggered by subtle face shape differences. *Horm. Behav.* 62: 413-417.
- Bobst C, Sauter S, Foppa A, Lobmaier JS. 2014. Early follicular testosterone level predicts preference for masculinity in male faces—But not for women taking hormonal contraception. *Psychoneuroendocrinol.* 41: 142-150.
- Bolhuis JJ, Brown GR, Richardson RC, Laland KN. 2011. Darwin in mind: New opportunities for Evolutionary Psychology. *PLoS Biol.* 9:e1001109.
- Brunings JW, Schepens JJ, Peutz-Kootstra CJ, Kross KW. 2013. The expression of estrogen and progesterone receptors in the human larynx. *J. Voice* 27: 376-380.
- Burley N. 1979. Evolution of concealed ovulation. *Am. Nat.* 114: 835-858.
- Burt A. 1992. Concealed ovulation and sexual signals in primates. *Folia Primatol.* 58: 1-6
- Buss DM, Haselton MG, Shackelford TK, Bleske AL, Wakefield JC. 1998. Adaptations, exaptations, and spandrels. *Am. Psychol.* 53: 533-548.
- Cantú SM, Simpson JA, Griskevicius V, Weisberg YJ, Durante KM, Beal DJ. 2013. Fertile and selectively flirt. Women's behavior toward men changes across the ovulatory cycle. *Psychol. Sci.* 25:

431-438.

Cobey KD, Buunk AP, Pollet TV, Klipping C, Roberts SC. 2013. Men perceive their female partners, and themselves, as more attractive around ovulation. *Biol. Psychol.* 94: 513-516.

Cotton S, Small J, Pomiankowski A. 2006. Sexual selection and condition-dependent mate preferences. *Curr. Biol.* 16: R755-R765.

Dixson AF. 2009. *Sexual selection and the origins of human mating systems.* Oxford: Oxford University Press.

Dixson AF. 2012. *Primate sexuality: Comparative studies of the prosimians, monkeys, apes, and humans.* Oxford: Oxford University Press.

Doty RL, Ford M, Preti G, Huggins GR. 1975. Changes in the intensity and pleasantness of human vaginal odors during the menstrual cycle. *Science* 190: 1316-1318.

Duda P, Zrzavý J. 2013. Evolution of life history and behavior in Hominidae: Towards phylogenetic reconstruction of the chimpanzee–human last common ancestor. *J. Hum. Evol.* 65: 424-446.

Durante KM, Li NP. 2009. Oestradiol level and opportunistic mating in women. *Biol. Lett.* 5: 179-182.

Feinberg DR, DeBruine LM, Jones BC, Little AC, O'Connor JJ, Tigue CC. 2012. Women's self-perceived health and attractiveness predict their male vocal masculinity preferences in different directions across short- and long-term relationship contexts. *Behav. Ecol. Sociobiol.* 66: 413-418.

Feinberg DR, Jones BC, Law Smith MJ, Moore FR, DeBruine LM, Cornwell RE, Hillier SG, Perrett DI. 2006. Menstrual cycle, trait estrogen level, and masculinity preferences in the human voice. *Horm. Behav.* 49: 215-222.

Ferguson CJ. 2014. Comment: Why meta-analyses rarely resolve ideological debates. *Emot. Rev.* 6: 251-252.

Fink B, Hugill N, Lange BP. 2012. Women's body movements are a potential cue to ovulation. *Pers. Individ. Differ.* 53: 759-763.

Fischer J, Semple S, Fickenscher G, Jürgens R, Kruse E, Heistermann M, Amir O. 2011. Do women's voices provide cues of the likelihood of ovulation? The importance of sampling regime. *PLoS One* 6: e24490.

Fletcher GJ, Simpson JA, Campbell L, Overall NC. 2015. Pair-bonding, romantic love, and evolution. The curious case of *Homo sapiens*. *Perspect. Psychol. Sci.* 10: 20-36.

Gangestad SW, Thornhill R. 1998 Menstrual cycle variation in women's preferences for the scent of symmetrical men. *P. Roy. Soc. B-Biol. Sci.* 265: 927-933.

Gangestad SW, Scheyd GJ. 2005. The evolution of human physical attractiveness. *Annu. Rev. Anthropol.* 34: 523-548.

Gangestad SW, Thornhill R, Garver-Apgar CE. 2005. Adaptations to ovulation implications for sexual and social behavior. *Curr. Dir. Psychol. Sci.* 14: 312-316.

Gangestad SW, Thornhill R. 2008. Human oestrus. *P. Roy. Soc. B-Biol. Sci.* 275: 991-1000.

Gangestad SW, Haselton MG. 2015. Human estrus: Implications for relationship science. *Curr. Opin. Psychol.*

Gildersleeve KA, Haselton MG, Larson CM, Pillsworth EG. 2012. Body odor attractiveness as a cue of impending ovulation in women: Evidence from a study using hormone-confirmed ovulation. *Horm. Behav.* 61: 157-166.

Gildersleeve K, DeBruine L, Haselton MG, Frederick DA, Penton-Voak IS, Jones BC, Perrett DI. 2013. Shifts in women's mate preferences across the ovulatory cycle: A critique of Harris (2011) and Harris (2012). *Sex Roles* 69: 516-524.

Gildersleeve K, Haselton MG, Fales MR. 2014a. Do women's mate preferences change across the ovulatory cycle? A meta-analytic review. *Psychol. Bull.* 140: 1205-1259.

Gildersleeve K, Haselton MG, Fales MR. 2014b. Meta-analyses and P-curves support robust cycle shifts in women's mate preferences: Reply to Wood and Carden (2014) and Harris, Pashler, and Mickes (2014). *Psychol. Bull.* 140: 1272-1280.

Gould SJ. 1991. Exaptation: A crucial tool for an evolutionary psychology. *J. Soc. Issues.* 47: 43-

65.

Gould SJ, Lewontin RC. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *P. Roy. Soc. Lond. B-Biol. Sci.* 205: 581-598.

Gould SJ, Vrba ES. 1982. Exaptation—a missing term in the science of form. *Paleobiol.* 8: 4-15.

Grillot RL, Simmons ZL, Lukaszewski AW, Roney JR. 2014. Hormonal and morphological predictors of women's body attractiveness. *Evol. Hum. Behav.* 35: 176-183.

Guéguen N. 2012. Gait and menstrual cycle: Ovulating women use sexier gaits and walk slowly ahead of men. *Gait Posture* 35: 621-624.

Harris CR. 2013. Shifts in masculinity preferences across the menstrual cycle: Still not there. *Sex Roles* 69: 507-515.

Harris CR, Pashler H, Mickes L. 2014. Elastic analysis procedures: An incurable (but preventable) problem in the fertility effect literature. Comment on Gildersleeve, Haselton, and Fales (2014). *Psychol. Bull.* 140: 1260-1264.

Haselton MG, Gangestad SW. 2006. Conditional expression of women's desires and men's mate guarding across the ovulatory cycle. *Horm. Behav.* 49: 509-518.

Haselton MG, Gildersleeve K. 2011. Can men detect ovulation? *Curr. Dir. Psychol. Sci.* 20: 87-92.

Haselton MG, Mortezaie M, Pillsworth EG, Bleske-Rechek A, Frederick DA. 2007. Ovulatory shifts in human female ornamentation: Near ovulation, women dress to impress. *Horm. Behav.* 51: 40-45.

Havlíček J, Dvořáková R, Bartoš L, Flegr J. 2006. Non-advertized does not mean concealed: body odour changes across the human menstrual cycle. *Ethology* 112: 81-90.

Houston AI, 2009. San Marco and evolutionary biology. *Biol. Philos.* 24: 215-230.

Hrdy SB. 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethol. Sociobiol.* 1: 13-40.

Huchard E, Courtiol A, Benavides JA, Knapp LA, Raymond M, Cowlshaw G. 2009. Can fertility

signals lead to quality signals? Insights from the evolution of primate sexual swellings. *P. Roy. Soc. B-Biol. Sci.* 276: 1889-1897.

Jankowiak WR, Fischer EF. 1992. A cross-cultural perspective on romantic love. *Ethnology* 31:149-155.

Jasienska G, Ziomkiewicz A, Ellison TP, Lipson FS, Thune I. 2004. Large breasts and narrow waist indicate high reproductive potential in women. *P. Roy. Soc. B-Biol. Sci.* 271:1213 -1217.

Johnston VS, Franklin M. 1993. Is beauty in the eye of the beholder? *Ethol. Sociobiol.* 14: 183-199.

Jokela M. 2009. Physical attractiveness and reproductive success in humans: evidence from the late 20th century United States. *Evol. Hum. Behav.* 30: 342-350.

Jones D, Brace CL, Jankowiak W, Laland KN, Musselman LE, Langlois JH., Roggman LA, Pérusse D, Schweder B, Symons D. 1995. Sexual selection, physical attractiveness, and facial neoteny: cross-cultural evidence and implications. *Curr. Anthropol.* 36:723-748.

Jones BC, Little AC, Boothroyd L, Feinberg DR, Cornwell RE, DeBruine LM, Roberts SC, Penton-Voak IS, Law Smith MI, Moore FR, Davis HP, Perrett DI. 2005. Women's physical and psychological condition independently predict their preference for apparent health in faces. *Evol. Hum. Behav.* 26: 451-457.

Jones BC, DeBruine LM, Perrett DI, Little AC, Feinberg DR, Smith MJL. 2008. Effects of menstrual cycle phase on face preferences. *Arch. Sex. Behav.* 37: 78-84.

Langlois JH, Kalakanis L, Rubenstein AJ, Larson A, Hallam M, Smoot M. 2000. Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychol. Bull.* 126: 390-423.

Langlois JH, Ritter JM, Roggman LA, Vaughn LS. 1991. Facial diversity and infant preferences for attractive faces. *Dev. Psychol.* 27: 79-84.

Law Smith MLJ, Perrett DI, Jones BC, Cornwell RE, Moore FR, Feinberg DR, Boothroyd LG, Durrani SJ, Stirrat MR, Whiten S, Pitman RM, Hillier SG. 2006. Facial appearance is a cue to oestrogen levels in women. *P. Roy. Soc. B-Biol. Sci.* 273: 135-140.

Lipson SF, Ellison PT. 1996. Comparison of salivary steroid profiles in naturally occurring conception and non-conception cycles. *Hum. Reprod.* 11: 2090-2096.

Little AC, Burt DM, Penton-Voak IS, Perrett DI. 2001. Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *P. Roy. Soc. Lond. B-Biol. Sci.* 268: 39-44.

Little AC, Jones BC, Burriss RP. 2007. Preferences for masculinity in male bodies change across the menstrual cycle. *Horm. Behav.* 51: 633-639.

Mersereau JE, Evans ML, Moore DH, Liu JH, Thomas MA, Rebar RW, Pennington, E, Cedars MI. 2008. Luteal phase estrogen is decreased in regularly menstruating older women compared with a reference population of younger women. *Menopause* 15: 482-486.

Millar, M. 2013. Menstrual cycle changes in mate preferences for cues associated with genetic quality: the moderating role of mate value. *Evol. Psychol.* 11: 18-35.

Miller G, Tybur JM, Jordan BD. 2007. Ovulatory cycle effects on tip earnings by lap dancers: economic evidence for human estrus? *Evol. Hum. Behav.* 28: 375-381.

Munster K, Schmidt L, Helm P. 1992. Length and variation in the menstrual cycle—a cross-sectional study from a Danish county. *BJOG-Int. J. Obstet. Gy.* 99: 422-429.

Nunn CL. 1999. The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Anim. Behav.* 58: 229-246.

Oberzaucher E, Katina S, Schmehl SF, Holzleitner IJ, Mehu-Blantar I, Grammer K. 2012. The myth of hidden ovulation: Shape and texture changes in the face during the menstrual cycle. *J. Evol. Psychol.* 10: 163-175.

Park JH. 2007. Distinguishing byproducts from non-adaptive effects of algorithmic adaptations. *Evol. Psychol.* 5: 47-51.

Parker G. 1983. Mate quality and mating decisions. In: Bateson P, editor. *Mate choice*. Cambridge: Cambridge University Press. p. 141-166.

Pawlowski B. 1999. Loss of oestrus and concealed ovulation in human evolution: The case

against the sexual-selection hypothesis. *Curr. Anthropol.* 40: 257-276.

Penton-Voak IS, Little AC, Jones BC, Burt DM, Tiddeman BP, Perrett DI. 2003. Female condition influences preferences for sexual dimorphism in faces of male humans (*Homo sapiens*). *J. Comp. Psychol.* 117: 264-271.

Penton-Voak IS, Perrett DI, Castles DL, Kobayashi T, Burt DM, Murray LK, Minamisawa R. 1999. Menstrual cycle alters face preference. *Nature* 399: 741-742.

Pflüger LS, Oberzaucher E, Katina S, Holzleitner IJ, Grammer K. 2012. Cues to fertility: perceived attractiveness and facial shape predict reproductive success. *Evol. Hum. Behav.* 33: 708-714.

Pillsworth EG, Haselton MG. 2006. Male sexual attractiveness predicts differential ovulatory shifts in female extra-pair attraction and male mate retention. *Evol. Hum. Behav.* 27: 247-258.

Pipitone RN, Gallup GG. 2008. Women's voice attractiveness varies across the menstrual cycle. *Evol. Hum. Behav.* 29: 268-274.

Puts DA. 2005. Mating context and menstrual phase affect women's preferences for male voice pitch. *Evol. Hum. Behav.* 26: 388-397.

Puts DA, Bailey DH, Cárdenas RA, Burriss RP, Welling LL, Wheatley JR, Dawood K. 2013. Women's attractiveness changes with estradiol and progesterone across the ovulatory cycle. *Horm. Behav.* 63: 13-19.

Rhodes G. 2006. The evolutionary psychology of facial beauty. *Annu. Rev. Psychol.* 57: 199-226

Roberts SC, Havlicek J, Flegr J, Hruskova M, Little AC, Jones BC, Perrett DI, Petrie M. 2004. Female facial attractiveness increases during the fertile phase of the menstrual cycle. *P. Roy. Soc. Lond. B-Biol. Sci.* 271(Suppl 5): S270-S272.

Roberts SC, Havlíček J. 2013. Humans are dunnocks, not peacocks: On cause and consequence of variation in human mating strategies. *Psychol. Inq.* 24: 231-236.

Roney J. 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: 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.

Schulz AW. 2012. Heuristic evolutionary psychology. In: Plaisance KS, Reydon TAC, editors. *Philosophy of Behavioral Biology* Dordrecht, Netherlands: Springer. p. 217-234.

Sillén-Tullberg B, Møller AP. 1993. The relationship between concealed ovulation and mating system in anthropoid primates: A phylogenetic analysis. *Am. Nat.* 141:1-25.

Silva AS, Lummaa V, Muller U, Raymond M, Alvergne A. 2012. Facial attractiveness and fertility in populations with low levels of modern birth control. *Evol. Hum Behav.* 33 491-498.

Singh D. 2002. Female mate value at a glance: Relationship of waist-to-hip ratio to health, fecundity and attractiveness. *Neuroendocrinol. Lett.* 23(Suppl 4): 81-91.

Smith FG, Jones BC, Welling LL, Little AC, Vukovic J, Main JC, DeBruine LM. 2009. Waist-hip ratio predicts women's preferences for masculine male faces, but not perceptions of men's trustworthiness. *Pers. Individ. Differ.* 47: 476-480.

Smith EP, Specker B, Korach KS. 2010. Recent experimental and clinical findings in the skeleton associated with loss of estrogen hormone or estrogen receptor activity. *J. Steroid Biochem. Molec. Biol.* 118: 264-272.

Stewart-Williams S, Thomas A G. 2013. The ape that thought it was a peacock: Does evolutionary psychology exaggerate human sex differences?. *Psychol. Inq.* 24: 137-168.

Strassmann BI. 1981. Sexual selection, paternal care, and concealed ovulation in humans. *Ethol. Sociobiol.* 2: 31-40.

Stricker R, Eberhart R, Chevailler MC, Quinn FA, Bischof P, Stricker R. 2006. Establishment of detailed reference values for luteinizing hormone, follicle stimulating hormone, estradiol, and progesterone during different phases of the menstrual cycle on the Abbott ARCHITECT® analyzer. *Clin. Chemical Lab. Med.* 44: 883-887.

Swaddle JP. 1999. Limits to length asymmetry detection in starlings: implications for biological signalling. *P. Roy. Soc. B-Biol. Sci.* 266:1299-1303.

Swaddle JP, Ruff DA, Page LC, Frame AM, Long, VA. 2008. A test of receiver perceptual performance: European starlings' ability to detect asymmetry in a naturalistic trait. *Anim. Behav.* 76:487-495.

Symons D. 1979. *The evolution of human sexuality*. Oxford: Oxford University Press.

Thornhill R, Gangestad SW. 1999. The scent of symmetry: a human sex pheromone that signals fitness? *Evol. Hum. Behav.* 20: 175-201.

Thornhill R, Gangestad SW. 2008. *The evolutionary biology of human female sexuality*. Oxford: Oxford University Press.

Venners SA, Liu X, Perry MJ, Korrick SA, Li Z, Yang F, Yang J, Lasley BL, Xu X, Wang X. 2006. Urinary estrogen and progesterone metabolite concentrations in menstrual cycles of fertile women with non-conception, early pregnancy loss or clinical pregnancy. *Hum. Reprod.* 21: 2272-2280.

Wallis J. 1992. Chimpanzee genital swelling and its role in the pattern of sociosexual behavior. *Am. J. Primatol.* 28: 101-113.

Welling LL, Jones BC, DeBruine LM, Conway CA, Law Smith MJ, Little AC, Feinberg DR, Sharp MA, Al-Dujaili EA. 2007. Raised salivary testosterone in women is associated with increased attraction to masculine faces. *Horm. Behav.* 52: 156-161.

Williams GC. 1966. *Adaptation and natural selection: A critique of some current evolutionary thought*. Princeton: Princeton University Press.

Williams J, Taylor E. 2006. The evolution of hyperactivity, impulsivity and cognitive diversity. *J. Roy. Soc. Interface* 3: 399-413.

Windham GC, Elkin E, Fenster L, Waller K, Anderson M, Mitchell PR, Lasley B, Swan SH. 2002. Ovarian hormones in premenopausal women: variation by demographic, reproductive and menstrual cycle characteristics. *Epidemiology.* 13: 675-684.

Wood W. 2014. Author reply: Once again, menstrual cycles and mate preferences. *Emot. Rev.* 6: 258-260.

Wood W, Carden L. 2014. Elusiveness of menstrual cycle effects on mate preferences:

Comment on Gildersleeve, Haselton, and Fales (2014). *Psychol. Bull.* 140: 1265–1271.

Wood W, Kressel L, Joshi PD, Louie, B. 2014. Meta-analysis of menstrual cycle effects on women's mate preferences. *Emot. Rev.* 6: 229-249.

Ziomkiewicz A, Ellison PT, Lipson SF, Thune I, Jasienska G. 2008. Body fat, energy balance and estradiol levels: a study based on hormonal profiles from complete menstrual cycles. *Hum. Reprod.* 23: 2555-2563.