ORIGINAL ARTICLE

Shifts in Women's Mate Preferences Across the Ovulatory Cycle: A Critique of Harris (2011) and Harris (2012)

Kelly Gildersleeve • Lisa DeBruine • Martie G. Haselton • David A. Frederick • Ian S. Penton-Voak • Benedict C. Jones • David I. Perrett

© Springer Science+Business Media New York 2013

Abstract Many studies have documented systematic shifts in women's mate preferences and sexual motivations across the ovulatory cycle. Harris (2012) presents a nonreplication of one particular finding in this literature—namely, that women's preference for masculinity in men's faces shifts across the cycle. Harris critiques the empirical and theoretical literature on cycle shifts and concludes that the cycle shift hypothesis should be abandoned. Here, we situate Harris's findings within the broader empirical literature and respond to several of the points in her critique. We conclude that the evidence for cycle shifts in women's mate preferences and sexual motivations is much stronger than

Introduction

basis of this work.

A rapidly growing literature in the evolutionary social sciences documents changes in women's motivations, desires, and behaviors across the ovulatory cycle (reviewed in Gangestad and Thornhill 2008; Haselton and Gildersleeve 2011; Thornhill and Gangestad 2008). Many of the studies in this literature aim to test the overarching hypothesis that, like females in most mammalian species—including species closely related to humans, such as chimpanzees (Stumpf and Boesch 2005), bonobos (Furuichi and Hashimoto 2002) and gorillas (Watts 1991)—women possess "a phase of female sexuality occurring near ovulation and distinct from other phases of the ovarian cycle in terms of female sexual motivations" (Gangestad and Thornhill 2008, p. 991).

Harris portrays and that she mischaracterizes the theoretical

Keywords Menstrual cycle · Ovulatory cycle · Ovulation ·

Facial masculinity · Mate preferences · Sexual motivations

Within this literature, dozens of studies aim to test the more specific hypothesis that women's preferences for certain characteristics in sex partners increase near ovulation, resulting in a shift in mate preferences across the cycle. This literature makes two major claims: one theoretical, and one empirical. These claims are independent—either, neither, or both could be true—and should be treated as such.

The theoretical claim is that women possess evolved psychological mechanisms that elevate preferences for characteristics that ancestrally reflected genetic quality—by which we mean the presence of genes with beneficial effects, absence of genes with harmful effects, or presence of a

K. Gildersleeve

Department of Psychology, UCLA, Los Angeles, CA, USA

L. DeBruine (☑) • B. C. Jones Institute of Neuroscience and Psychology, University of Glasgow, Glasgow, UK e-mail: lisa.debruine@glasgow.ac.uk

M. G. Haselton Departments of Communication Studies and Psychology, and Center for Behavior, Evolution, and Culture, UCLA, Los Angeles, CA, USA

D. A. Frederick Crean School of Health and Life Sciences, Chapman University, Orange, CA, USA

I. S. Penton-Voak School of Psychology, University of Bristol, Bristol, UK

D. I. Perrett School of Psychology, University of St. Andrews, St. Andrews, UK

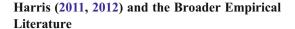
Published online: 11 April 2013



low overall number of mutated genes—in sex partners at high fertility. These mechanisms are thought to have increased ancestral females' likelihood of transmitting genetic benefits to offspring. A related claim is that masculinity, symmetry, and other sexually attractive characteristics reflected genetic quality in ancestral males (Gangestad and Thornhill 2008; Gangestad et al. 2007; Thornhill and Gangestad 2008).

The empirical claim is that women's preferences for a variety of characteristics in male partners change in systematic and nuanced ways across the ovulatory cycle. Studies have shown that, on high-fertility as compared with low-fertility days of the cycle, heterosexual women have an increased preference for masculine features (e.g., facial masculinity), correlates of bilateral symmetry (e.g., scent), and other characteristics correlated with sexual attractiveness in men (e.g., Gangestad et al. 2004; Gangestad and Thornhill 1998; participants recruited at a U.K. university, Little et al. 2007a, b; Puts 2005; participants recruited in Japan and the U.K., Penton-Voak et al. 1999). These preference shifts are often observed primarily when women evaluate men's desirability as short-term sex partners (a context in which preferences might historically have been particularly likely to impact immediate sexual decisions and behavior), rather than when women evaluate men's desirability as long-term relationship partners (e.g., Gangestad et al. 2004; Little et al. 2007b; Puts 2005; Penton-Voak et al. 1999, Study 2). The cycle shift hypothesis makes no predictions regarding cycle shifts in women's attractions to other women and has received the most empirical attention in the U.S. Thus, all of the findings described in this article are based on heterosexual participants. Furthermore, unless noted otherwise, participants were recruited at universities in the U.S.

Harris (2012) presents a reanalysis of data from a previously published study (Harris 2011) that examined cycle shifts in preferences for facial masculinity. Having found no evidence for a cycle shift in the original analysis or in the reanalysis, Harris concludes that the cycle shift hypothesis should be abandoned. Harris attempts to reinforce this claim in several ways. Harris cites an unpublished meta-analysis that purports to have found no robust cycle shift in preferences for masculinity or other characteristics hypothesized to have reflected genetic quality ancestrally. Harris also suggests that "researcher degrees of freedom" have contributed to the abundance of evidence for cycle shifts in mate preferences in the published literature. Lastly, Harris critiques a number of assumptions that she asserts are inherent in the cycle shift hypothesis. In this commentary, we situate Harris's findings within the broader empirical literature, briefly respond to Harris's claims about the unpublished meta-analysis, discuss Harris's speculations regarding "researcher degrees of freedom," and address several serious misconceptions present in Harris's discussion of the theoretical basis of the cycle shift hypothesis.



Harris's study (2011) aimed to test whether women prefer relatively more masculine male faces at high fertility as compared with low fertility. She conducted an Internet-based, between-participants study in which women (primarily from the US and Canada) completed a simple facial masculinity preference task in which they chose the most physically attractive face from two sets of five male faces varying in masculinity. Harris did not ask participants to consider a specific type of relationship (e.g., short-term sexual affair vs. long-term relationship) when evaluating the faces. Participants also recalled the date of their last menstrual onset. Harris counted forward from that date to the date of each woman's participation in the study and estimated fertility on that basis. In the original analyses, Harris (2011) found no evidence that women estimated to be on high-fertility days of the cycle preferred more masculine male faces than did women estimated to be on lowfertility days of the cycle.

DeBruine et al. (2010) questioned whether the null effect reported by Harris (2011) could be due to the age characteristics of the sample. Specifically, Harris's sample included a large number of women who were at an age associated with an elevated likelihood of experiencing anovulatory cycles (e.g., roughly a quarter of the sample was over the age of 40; Hale et al. 2007). In response, Harris (2012) conducted new analyses of the same dataset, limiting the sample to women under the age of 30. She again did not find the predicted cycle shift in preferences for facial masculinity.

Although we fully support Harris's decision to reanalyze her data, we have some concerns about the reanalysis and her interpretations of the results. The new analysis included 84 women in total, of whom only 19 were estimated to be in the high-fertility phase of the cycle (Harris, personal communication, Nov. 12, 2012). Past research has found that women's retrospectively recalled dates of menstrual onset are error-prone. For example, in one study, women were asked to report their last date of menstrual onset, which had also been prospectively collected within the past 30 days. Nearly one-fifth of the women reported a date that was off by at least 3 days (Wegienka and Day Baird 2005). Given that only a handful of days in the cycle are truly highfertility, error such as that associated with recalled dates of menstrual onset is particularly likely to result in low-fertility women being miscategorized as high-fertility. This problem can be minimized in Internet-based, between-participants studies with large samples or overcome in lab-based, within-participants studies that use hormone tests to verify ovulation (and ultimately, both are needed to achieve external and internal validity). However, the small sample of putatively high-fertility women in Harris' Internet-based study inspires little confidence in her results.



A broader issue is Harris' (2012) interpretation of her study's null result as evidence against the cycle shift hypothesis (the analysis section heading reads: "Further Evidence Against Cycle Preference Shifts"). This interpretation highlights an important misunderstanding—namely, that an absence of evidence of a cycle shift in facial masculinity preferences constitutes evidence of absence of this effect. We emphasize that even a null result from an extraordinarily well designed and rigorous study cannot prove the null hypothesis. Furthermore, a true null effect in this context would be consistent with several possible interpretations. For example, the overarching hypothesis that women experience a cycle shift in preferences for characteristics that reflected genetic quality ancestrally could simply be false. Another possibility is that the overarching hypothesis is correct, but facial masculinity did not reflect genetic quality ancestrally. A further possibility is that the study was underpowered or that methods for estimating women's cycle position or for measuring or manipulating facial masculinity were error-prone, in which case, additional replications—especially replications using more rigorous methods -are needed.

Along these lines and as we noted in our original response to the Harris (2011) paper (DeBruine et al 2010), despite the existence of a dozen or more papers on cycle shifts in preferences for masculine traits, Harris (2011) cited only the first two of these papers (Penton-Voak et al. 1999; Penton-Voak and Perrett 2000). This created a misleading impression of the relative weight of her nonreplication. Single studies that produce null effects, such as Harris's study, while informative, are not definitive (if they were, there would be no need for replications) and cannot overturn a literature containing many studies with statistically significant results. Although null results may be difficult to publish, leading to a "file drawer effect," exact replications of well-documented effects are also difficult to publish. Ultimately, meta-analyses (as discussed below) are needed to assess the influence of publication bias.

We also pointed out, more broadly, that many aspects of women's sexual motivations and related behaviors shift across the ovulatory cycle, including attractions to their own partners and other men, style of dress, and receptiveness to courtship invitations. Further evidence for these cycle shifts has been published subsequent to the publication of our response (DeBruine et al 2010) to Harris's (2011) paper (e.g., participants recruited in the U.K., Flowe et al. 2012; Gangestad et al. 2010a, b; Larson et al. 2012; participants recruited in the U.K., Little and Jones 2012; Millar 2013). As a collective, these converging lines of evidence provide strong support for cycle shifts in women's sexuality.

Relatedly, Harris (2012) correctly notes that studies examining shifts in women's attractions to men other than their primary partners are particularly relevant to the hypothesis

that women's mate preferences shift across the cycle. However, Harris incorrectly asserts that the cycle shift hypothesis predicts that women in general will experience a high-fertility increase in attractions to men other than their partners (i.e., a main effect of fertility on attractions to other men). This is puzzling because each of the seven articles that has reported a cycle shift in extra-pair attraction clearly outlines the prediction that these shifts will be moderated by primary partner characteristics. The logic is straightforward: all else equal, women whose primary partners are relatively lacking in the characteristics that they particularly prefer at high fertility (i.e., characteristics hypothesized to have reflected high underlying genetic quality ancestrally) will be, on average, more likely to experience an increase in attraction to certain other men at high fertility relative to low fertility. Thus, depending on the composition of a study's sample (e.g., a high proportion of women who happen to have partners relatively low in characteristics particularly preferred at high fertility), the main effect could emerge (and, indeed, Gangestad et al. 2002, found such an effect). However, the more precise prediction is that the high-fertility increase in women's extra-pair attractions will depend on their primary partner's characteristics.

Accordingly, each of the seven studies that has tested this idea has found evidence that women whose partners were lower in characteristics hypothesized to have reflected genetic quality ancestrally experienced greater attraction to other men at high fertility relative to low fertility (partner symmetry, Gangestad et al. 2005; partner sexual attractiveness, Pillsworth and Haselton 2006; partner sexual attractiveness relative to investment attractiveness, Haselton and Gangestad 2006; unshared MHC alleles with partner, Garver-Apgar et al. 2006; facial masculinity, Gangestad et al. 2010b; partner facial attractiveness, marginally significant at p=0.055, Gangestad et al. 2010b; composite partner face and body attractiveness, Larson et al. 2012). Although two of these studies reported additional non-significant interactions between fertility and partner characteristics (facial attractiveness, Gangestad et al. 2010b; sexual attractiveness, Larson et al. 2012), we are not aware of any cases in which a reversal of this pattern has been found. On balance, this is straightforward additional evidence that women's mate preferences and attractions shift in theoretically meaningful and nuanced ways across the cycle.

Meta-analyses of Cyclic Shifts in Women's Mate Preferences

We agree with Harris that meta-analyses ultimately are needed to address the question of whether there are robust effects in a given research literature and whether published statistically significant findings represent only the tip of an iceberg of



nonreplications. Harris cites an unpublished meta-analysis (Wood et al. 2012) that purports to show no robust shifts in women's mate preferences across the cycle. However, Harris does not acknowledge the existence of another unpublished meta-analysis on the same topic that was presented at one of the same conferences as the analysis by Wood and colleagues but that reached different conclusions (Haselton 2012; see also Gildersleeve et al. 2012, 2013). Harris's citation of one meta-analysis and not the other misleadingly implies that there is a final word on this issue. We decline to comment further on the results of either unpublished meta-analysis on the grounds that the works have not been properly vetted by peer review and are not available for public scrutiny. In our view, discussing such work, particularly in the context of a debate, challenges the scientific integrity of that debate.

Researcher Degrees of Freedom in the Cycle Shift Literature

Harris (2012) makes the very serious and unfounded claim that the abundance of evidence for cyclic shifts in women's mate preferences in the published literature reflects "researcher degrees of freedom" (i.e., researchers are selecting among methods or analyses to generate statistically significant results while 'invisibly' pushing up the familywise error rates, Simmons et al. 2011). To support this claim, Harris notes instances of methodological differences between studies and implies that such differences are arbitrary. To the contrary, we emphasize that differences between studies typically reflect constraints of study design and often reflect coherent progression in methodology.

For example, Harris expresses doubt in the results of Penton-Voak and Perrett (2000) and Penton-Voak et al. (1999) because Penton-Voak and Perrett (2000) used forward counting to estimate participants' position in the ovulatory cycle, but Penton-Voak et al. (1999) used backward counting. The forward counting method involves counting forward from a woman's last menstrual onset to estimate her current position in the cycle, whereas the backward counting method involves counting backward from a woman's next menstrual onset (following participation) to estimate her position in the cycle. Because there is greater variability in the length of the follicular phase (first half, from last menstrual onset to ovulation) than in the luteal phase (last half, from ovulation to next menstrual onset) of the menstrual cycle, the backward counting method is generally regarded as a more accurate method of estimating cycle position and fertility (Mikolajczyk and Stanford 2005). However, the backward counting method requires either following up with participants to prospectively verify next menstrual onset or collecting detailed information from participants to predict next menstrual onset (e.g., typical cycle length).

The lab-based, within-participants, relatively small-N design of Penton-Voak et al. (1999) facilitated using the backward counting method, whereas the single-shot, between-participants, large-N study design of Penton-Voak and Perrett (2000) precluded using this method.

Harris also criticizes Jones et al.'s (2005, Study 1 participants recruited in the UK; Study 2 participants recruited outside of the UK, predominantly in the US and Canada) findings linking progesterone levels to mate preferences because Study 1 used forward counting to estimate progesterone levels, but Study 2 used backward counting. However the cycle length data necessary to implement backward counting were not collected in Study 1 (as was stated in the methods section of Study 1), whereas these data were collected in Study 2. Furthermore, other studies have reported similar correlations between progesterone level estimated using the backward counting method and women's mate preferences, presenting converging evidence for the validity of this type of analysis (Garver-Apgar et al. 2008; Puts 2006). Indeed, in most of the studies cited by Harris (2012), researchers could not decide, post hoc, whether to use forward or backward counting to estimate fertility or hormone levels. Because study design typically dictates whether researchers are able to use forward vs. backward counting, there is no "researcher degrees of freedom" problem here.

Harris also criticizes studies examining cycle shifts in mate preferences for differing in how they have grouped and compared days of the ovulatory cycle. For example, Harris criticizes Jones et al. (2005, Study 2) for comparing follicular and midluteal phases, rather than comparing follicular and all nonfertile phases (following, e.g., Penton-Voak et al. 1999). However, the comparison of follicular and mid-luteal phases (Jones et al. 2005 Study 2) was motivated by contemporaneous work suggesting progesterone as a hormonal mediator of certain cyclic shifts in women's mate preferences (Puts 2006). The study was designed to test specific, a priori predictions about women's preferences on days of the menstrual cycle when progesterone level was high compared with days when progesterone level was low, and progesterone is typically elevated only during the mid-luteal phase in women who are not pregnant or using certain forms of hormonal contraceptives (Gilbert 2000). Relatedly, studies treating fertility as a continuous variable have replicated the positive association between fertility and women's preference for masculine traits (e.g., Gangestad et al. 2004, 2007). Findings like these suggest that the link between fertility and masculinity preferences is not simply an artifact of the use of slightly different high- and low-fertility groups across studies. In sum, differences between studies in high- and low-fertility groups often reflect specific theoretically and empirically motivated hypotheses, rather than "researcher degrees of freedom."

Harris also criticizes the use of tests of moderation in research on cycle shifts—for example, studies examining whether the extent to which women experience a high-



fertility increase in extra-pair attractions depends on their primary partner's qualities—as suggestive of "researcher degrees of freedom." However, as already noted above, these are precise tests (tests of specific interactions), and they show parallel results in the seven articles at issue. The probability that each of these studies shows results consistent with the others due to chance or due to researchers somehow capitalizing on chance is very low.

A related issue is Harris' claim (2012) that investigating other changes across the cycle, such as male partners' jealousy (which Harris refers to as "solicitousness") and women's interest in attending clubs and parties where they might meet men (Haselton and Gangestad 2006), is problematic because examining these effects multiplies the number of analyses in a paper. What Harris does not indicate, however, is that the findings involving these variables, as well as others she does not cite, are all logically consistent with the cycle shift hypothesis. For example, women reported that their male partners engaged in more jealous behavior on high-fertility than on low-fertility days of the cycle (Haselton and Gangestad 2006), a replication of a finding by Gangestad et al. (2002). If shifts in women's mate preferences and extra-pair attractions at high fertility have historically placed men at greater risk of non-paternity (raising a child to whom they were not genetically related), it is sensible to investigate whether men engage in behaviors that mitigate this risk, including behaving in a jealous fashion. It is misleading of Harris (2012) to suggest that multiple, logically consistent findings are more likely to be due to chance than a single finding. The reverse is true. In sum, we view the evidence as clearly indicating that cyclic shifts in preferences for various male traits are a genuine phenomenon in need of explanation. It is implausible that these findings are a mere artifact of "researcher degrees of freedom."

Misconceptions Involving the Theoretical Basis of the Cycle Shift Hypothesis

Harris (2012) critiques and discusses the evidence for a series of assumptions that she asserts are inherent to the hypothesis that women's mate preferences will shift in systematic ways across the ovulatory cycle. Her discussion contains ambiguities and serious inaccuracies that could spread detrimental misunderstandings of the cycle shift hypothesis and the current state of the evidence. Some of these issues have already been addressed in landmark writings in this literature (Gangestad and Thornhill 2008; Thornhill and Gangestad 2008); however, we briefly address several key additional issues here.

Misconception #1: The cycle shift hypothesis posits "hard-wired" psychological mechanisms.

According to Harris, the cycle shift hypothesis posits that women are "wired up" to engage in infidelity with particular types of men. We worry that the term "wired up" could imply that the cycle shift hypothesis posits the existence of psychological mechanisms that are lacking in plasticity or sensitivity to context. Hypothesizing the existence of psychological mechanisms that give rise to common patterns in cycling women's mate preferences does not imply invariability within or between women in these patterns. Indeed, scientists working in this area have already begun to examine how social and physical environments and individual differences contribute to theoretically meaningful variation across women in the nature and magnitude of the hypothesized cycle shifts (e.g., Feinberg et al. 2006; Millar 2013).

Misconception #2: The cycle shift hypothesis posits that these mechanisms evolved in and are currently fitness-enhancing in humans.

We emphasize that the cycle shift hypothesis is agnostic as to whether the posited psychological mechanisms initially evolved in humans or in an ancestral species. The hypothesis is also agnostic as to whether these mechanisms, if present in modern women, are vestigial, have been maintained by selection, or have been modified by selection to serve some other function (see Thornhill and Gangestad 2008, chapter 8; Haselton and Gangestad 2012). Thus, far from Harris's (2012) assertion that the cycle shift hypothesis implies that "women should pair-bond with more femininefaced men and thus reap the benefits of having them as permanent partners, but should seek to mate with masculine-faced men when conception is likely in order to obtain the best genes for their offspring," the hypothesis in fact makes no claims regarding how various mating patterns would impact women's fitness in modern environments, nor does it make recommendations for what women should do.

Misconception #3: The cycle shift hypothesis is only about female infidelity.

Harris claims that the cycle shift hypothesis is, at its core, about female infidelity. We fully acknowledge that writings in this literature have often emphasized female extra-pair sex (sexual infidelity) as one route through which selection could have favored the evolution of psychological mechanisms that produce cycle shifts in mate preferences. However, selection could have favored the evolution of these psychological mechanisms in the absence of female extra-pair sex. For instance, we noted above that cycle shifts in mate preferences might be vestigial in modern women. One possibility is that psychological mechanisms that produce cycle shifts evolved in ancestral species that did not typically pair-bond because these shifts increased females' probability of conceiving with males of relatively high genetic quality (e.g., see Stumpf et al. 2005, on sire choice



in chimpanzees). These cycle shifts might not confer any reproductive benefits in the context of pair-bonding but nonetheless persist in modern humans (see Thornhill and Gangestad 2008 for a detailed discussion).

Misconception #4: The cycle shift hypothesis requires that female infidelity occurred primarily at high fertility and more frequently than sex with the primary partner.

Harris asserts that the posited psychological mechanisms could only have evolved if females engaged in extra-pair sex primarily within the high-fertility window and at a rate that exceeded their rate of sex with their primary partner. As just noted, the cycle shift hypothesis does not require any female extra-pair sex. Nonetheless, if the posited psychological mechanisms did evolve as a result of female extra-pair sex, these mechanisms could have evolved as long as extra-pair sex occurred at a higher rate within the fertile window than outside of the fertile window, regardless of the overall rate of extra-pair sex or rate of sex with a primary partner. Any high-fertility increase in extra-pair sex would have increased the probability of conceiving with the extra-pair partner.

Misconception #5: The cycle shift hypothesis requires that female infidelity occurred at a high rate.

Harris also claims that the cycle shift hypothesis requires that women engaged in high rates of infidelity in the ancestral past. Again, the cycle shift hypothesis does not require any female extra-pair sex. Nonetheless, researchers in this area have argued explicitly against the idea that rates of female extra-pair sex would have to have been high for selection to favor cycle shifts in mate preferences (Gangestad and Thornhill 2008, pp. 995-996). These researchers note that extra-pair paternity rates (female conceptions with extra-pair sex partners) might have occurred at relatively low rates ancestrally, partly because of costs associated with a primary partner detecting infidelity (e.g., loss of paternal care; Buss and Shackelford 1997). Indeed, rates of extra-pair paternity in modern humans have been estimated at around 3 % in one cross-cultural study (Anderson 2006; though as high as 18 % in a particular population of semi-nomadic pastoralists; Scelza 2011). Although generally low, there is no reason to believe that rates such as these would have been insufficient for the posited psychological mechanisms to evolve. As has been noted in this literature, raptors (e.g., eagles, harriers, hawks) tend to have very low rates of extra-pair paternity (less than 5 % and often close to 1 %), and yet researchers have documented tactics among males that appear to reflect adaptations for reducing the risk of extra-pair paternity (see Thornhill and Gangestad 2008).

Misconception #6: There is very little evidence of costs associated with choosing more masculine men as long-term mates.



As Harris correctly notes, an implication of the cycle shift hypothesis is that women who select long-term mates who are relatively low in characteristics particularly desired at high fertility might be somewhat more likely to engage in extra-pair sex at this time. Some researchers have suggested that this pattern is made more probable by a tendency among women to prefer long-term mates who are relatively low in characteristics particularly desired at high fertility, due to certain costs associated with selecting long-term mates relatively high in these characteristics in the ancestral past (discussed in more detail below). First, we emphasize that, as long as characteristics particularly desired at high fertility (e.g., masculinity) were reliable indicators of genetic quality in the ancestral past, the posited cycle shifts could have evolved. This holds true even if males relatively high or low in these characteristics were otherwise equally desirable as long-term mates.

Setting that issue aside, Harris (2012) suggests that the only evidence of costs associated with choosing more masculine men as long-term mates comes from studies showing that more masculine men (i.e., men displaying exaggerated sex-typical physical characteristics) are perceived to have more antisocial personality traits (participants recruited in the UK, Perrett et al. 1998). However, studies have also found that more facially masculine men report stronger preferences for uncommitted sexual relationships (e.g., participants recruited in the U.K. for both studies, Boothroyd et al. 2008, 2011), report having had more short-term sexual relationships (e.g., Frederick and Haselton 2007; participants recruited in Australia; Rhodes et al. 2005), report more incidences of extra-pair sex while in committed relationships, and report more incidences of attracting mates away from other relationships (participants recruited in Australia, Rhodes et al. 2013) than do more facially feminine men. These findings suggest that women who chose more masculine men as long-term mates in the ancestral past might have received less investment, partly as a result of their partner allocating time and resources to the pursuit of other mates. Findings such as these show that there is more evidence than Harris acknowledges supporting the notion that ancestral females who chose relatively masculine longterm mates incurred certain costs.

Misconception #7: The cycle shift hypothesis requires that the immunocompetence handicap hypothesis is true.

Harris claims that the immunocompetence handicap hypothesis (ICHH, Folstad and Karter 1992) is a critical component of the cycle shift hypothesis and notes that evidence for the ICHH in humans is weak. First, the ICHH is not a critical component of the cycle shift hypothesis (see Thornhill and Gangestad 2008, Chapter 7, for an outline of viable alternative hypotheses). As noted above, evidence from modern men suggests that masculinity would have been associated

with higher reproductive success ancestrally, perhaps by increasing males' ability to attract sex partners. In turn, females who preferred more masculine males as high-fertility sex partners might have produced children who themselves attracted a larger number of sex partners (thereby creating selective pressure favoring cycle shifts in women's preferences for masculinity). Furthermore, noting that evidence for the ICHH in humans is weak is not a novel contribution; indeed, many evolutionary psychologists would agree (e.g., Scott et al 2012; Thornhill and Gangestad 2008). Moreover, the ICHH outlines only one possible mechanism underlying associations between masculine traits and physical condition (i.e., good health). That recent work has, by and large, not supported this particular mechanism does not necessarily mean that researchers should disregard evidence for positive correlations between masculinity and measures of men's health (Gangestad et al. 2010c; participants recruited in Australia, Rhodes et al. 2003; Thornhill and Gangestad 2006) or between masculinity and other characteristics thought to have enhanced offspring survival and reproductive success in ancestral environments (e.g., physical strength, participants recruited in Germany, Fink et al. 2007; Sell et al. 2009). Indeed, very recent work has reported a positive correlation between men's facial masculinity and an objective measure of their immune function (participants recruited in Latvia, Rantala et al. 2013). In sum, even if evidence for the ICHH is weak, other mechanisms involving the transmission of health benefits to offspring remain viable.

Final Remarks

We reiterate here the position that we advanced in our initial response (DeBruine et al. 2010): null findings for cycle shifts in women's mate preferences, such as those presented by Harris (2011, 2012), must be viewed in the context of the larger relevant research literature. As the science on a topic as complex as links between hormones and social behavior grows and matures, ideas will naturally become refined to reflect this complexity by, for example, investigating the causes of variation among women in the magnitude of cyclic shifts (e.g., Feinberg et al. 2006; Larson et al. 2012; Millar 2013). Methods for studying these complex phenomena will also grow in precision, and the theoretical models underlying them will change in the face of new empirical findings. The fact that these progressions have occurred in this literature is a sign of its health.

In summary, since our initial commentary in 2010, cycle effects have received increasing theoretical and empirical attention (e.g., participants recruited in the U.K., Flowe et al. 2012; Gangestad et al. 2010a, b; Larson et al. 2012; Little and Jones 2012; Millar 2013), generating increasingly nuanced predictions and a large number of studies providing

evidence that women's sexual motivations and mate preferences shift systematically across the ovulatory cycle. A substantial number of studies and converging lines of evidence support the conclusion that women's sexual attraction to certain characteristics in men—including facial masculinity—is elevated at high fertility. Harris (2012) misrepresents the cycle shift hypothesis and supporting evidence, concluding that "the evidence (or lack thereof) should be enough to lay to rest the theory of menstrual cycle preference shifts for masculinity." Having carefully reviewed this literature, we disagree with Harris's conclusion and instead anticipate that this area of research will continue to thrive, ultimately contributing to a more sophisticated and complete understanding of human sexuality.

References

- Anderson, K. G. (2006). How well does paternity confidence match actual paternity? Evidence from worldwide nonpaternity rates. *Current Anthropology*, 47, 435–461. doi:10.1086/504167.
- Boothroyd, L. G., Jones, B. C., Burt, D. M., DeBruine, L. M., & Perrett, D. I. (2008). Facial correlates of sociosexuality. *Evolution and Human Behavior*, 29, 211–218. doi:10.1016/j.evolhumbehav. 2007.12.009.
- Boothroyd, L. G., Cross, C. P., Gray, A. W., Coombes, C., & Gregson-Curtis, K. (2011). Perceiving the facial correlates of sociosexuality: Further evidence. *Personality and Individual Differences*, 50, 422–425. doi:10.1016/j.paid.2010.10.017.
- Buss, D. M., & Shackelford, T. K. (1997). From vigilance to violence: Mate retention tactics in married couples. *Journal of Personality and Social Psychology*, 72, 346–361. doi:10.1037// 0022-3514.72.2.346.
- DeBruine, L., Jones, B. C., Frederick, D. A., Haselton, M. G., Penton-Voak, I. S., & Perrett, D. I. (2010). Evidence for menstrual cycle shifts in women's preferences for masculinity. *Evolutionary Psychology*, 8, 768–775.
- Feinberg, D. R., Jones, B. C., Law Smith, M. J., Moore, F. R., DeBruine, L. M., Cornwell, R. E., . . . Perrett, D. I. (2006). Menstrual cycle, trait estrogen level and masculinity preferences in the human voice. *Hormones and Behavior*, 49, 215–222. doi:10.1016/j.yhbeh.2005.07.004
- Fink, B., Neave, N., & Seydel, H. (2007). Male facial appearance signals physical strength to women. *American Journal of Human Biology*, 19, 82–87. doi:10.1002/ajhb.20583.
- Flowe, H. D., Swords, E., & Rockey, J. C. (2012). Women's behavioural engagement with a masculine male heightens during the fertile window: Evidence for the cycle shift hypothesis. *Evolution and Human Behavior*, 33, 285–290. doi:10.1016/j.evolhumbehav. 2011.10.006.
- Folstad, I., & Karter, A. J. (1992). Parasites, bright males, and the immunocompetence handicap. *American Naturalist*, 139, 603– 622. doi:10.1086/285346.
- Frederick, D. A., & Haselton, M. G. (2007). Why is muscularity sexy? Tests of the fitness indicator hypothesis. *Personality and Social Psychology Bulletin, 33*, 1167–1183. doi:10.1177/0146167207303022.
- Furuichi, T., & Hashimoto, C. (2002). Why female bonobos have a lower copulation rate during estrus than chimpanzees. In C. Boesch, G. Hohmann, & L. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 156–167). Cambridge:



- Cambridge University Press. doi:10.1017/CBO9780511 606397.016.
- Gangestad, S. W., & Thornhill, R. (1998). Menstrual cycle variation in women's preference for the scent of symmetrical men. Proceedings of the Royal Society of London B, 265, 927–933. doi:10.1098/rspb.1998.0380.
- Gangestad, S. W., & Thornhill, R. (2008). Human oestrus. *Proceedings of the Royal Society B*, 275, 991–100. doi:10.1111/j.0956-7976.2004.01503010.x.
- Gangestad, S. W., Thornhill, R., & Garver, C. E. (2002). Changes in women's sexual interests and their partners' mate-retention tactics across the menstrual cycle: Evidence for shifting conflicts of interest. *Proceedings of the Royal Society of London B*, 269, 975–982. doi:10.1098/rspb.2001.1952.
- Gangestad, S. W., Simpson, J. A., Cousins, A. J., Garver-Apgar, C. E., & Christensen, P. N. (2004). Women's preferences for male behavioral displays change across the menstrual cycle. *Psychological Science*, 15, 203–207. doi:10.1111/j.0956-7976.2004.01503010.x.
- Gangestad, S. W., Thornhill, R., & Garver-Apgar, C. E. (2005). Women's sexual interests across the ovulatory cycle depend on primary partner developmental instability. *Proceedings of the Royal Society of London B, 272*, 2023–2027. doi:10.1098/ rspb.2005.3112.
- Gangestad, S. W., Garver-Apgar, C. E., Simpson, J. A., & Cousins, A. J. (2007). Changes in women's mate preferences across the ovulatory cycle. *Journal of Personality and Social Psychology*, 92, 151–163. doi:10.1037/0022-3514.92.1.151.
- Gangestad, S. W., Thornhill, R., & Garver-Apgar, C. E. (2010a). Fertility in the cycle predicts women's interest in sexual opportunism. *Evolution and Human Behavior*, 31, 400–411. doi:10.1016/j.evolhumbehav.2010.05.003.
- Gangestad, S. W., Thornhill, R., & Garver-Apgar, C. E. (2010b). Men's facial masculinity predicts changes in their female partners' sexual interests across the ovulatory cycle, whereas men's intelligence does not. *Evolution and Human Behavior*, 31, 412–424. doi:10.1016/j.evolhumbehav.2010.06.001.
- Gangestad, S. W., Merriman, L. A., & Emery Thompson, M. (2010). Men's oxidative stress, fluctuating asymmetry and physical attractiveness. *Animal Behaviour*, 80, 1005–1013. doi:10.1016/j.evolhumbehav.2010.05.003.
- Garver-Apgar, C. E., Gangestad, S. W., Thornhill, R., Miller, R. D., & Olp, J. J. (2006). Major Histocompatibility Complex alleles, sexual responsivity, and unfaithfulness in romantic couples. *Psychological Science*, 17, 830–835. doi:10.1016/j.evolhumbehav.2007.12.007.
- Garver-Apgar, C. E., Gangestad, S. W., & Thornhill, R. (2008). Hormonal correlates of women's mid-cycle preference for the scent of symmetry. *Evolution and Human Behavior*, 29, 223–232. doi:10.1016/j.evolhumbehav.2007.12.007.
- Gilbert, S. F. (2000). *Developmental biology*. Sunderland: Sinauer. doi:10.1006/dbio.1996.0032.
- Gildersleeve, K., Haselton, M. G., & Fales, M. (2012). Do women's mate preferences change across the ovulatory cycle? A metaanalytic review. Paper presented at the conference of the Human Behavior and Evolution Society, Albuquerque, NM.
- Gildersleeve, K., Haselton, M. G., & Fales, M. (2013). Do women's mate preferences change across the ovulatory cycle? A metaanalytic review. Poster presented at the conference of the Society for Personality and Social Psychology, New Orleans, LA.
- Hale, G. E., Zhao, X., Hughes, C. L., Burger, H. G., Robertson, D. M., & Fraser, I. S. (2007). Endocrine features of menstrual cycles in middle and late reproductive age and the menopausal transition classified according to the staging of reproductive aging (STRAW) staging system. *The Journal of Clinical Endocriniology & Metabolism*, 92, 3060–3067. doi:10.1210/jc.2007-0066.

- Harris, C. R. (2011). Menstrual cycle and facial preferences reconsidered. Sex Roles, 64, 669–681. doi:10.1007/s11199-010-9772-8
- Harris, C. R. (2012). Shifts in masculinity preferences across the menstrual cycle: Still not there. Sex Roles. doi:10.1007/s11199-012-0229-0.
- Haselton, M. G. (2012). Fertile minds: Changes in human social behavior across the ovulatory cycle. Paper presented at the conference of the Association for Psychological Science, Chicago, IL.
- Haselton, M. G., & Gangestad, S. W. (2006). Conditional expression of women's desires and men's mate guarding across the ovulatory cycle. *Hormones and Behavior*, 49, 509–518. doi:10.1016/ j.yhbeh.2005.10.006.
- Haselton, M. G., & Gangestad, S. W. (2012). Human estrus and pairbonding. Talk presented at the Human Behavior and Evolution Society Annual Conference, Albuquerque, New Mexico.
- Haselton, M. G., & Gildersleeve, K. (2011). Can men detect ovulation? Current Directions in Psychological Science, 20, 87–92. doi:10.1177/0963721411402668.
- Jones, B.C., Perrett, D.I., Little, A.C., Boothroyd, L.G., Cornwell, R.E., Feinberg, D.R., . . . Moore, F.R. (2005). Menstrual cycle, pregnancy and oral contraceptive use alter attraction to apparent health in faces. *Proceedings of the Royal Society of London B*, 272, 347-354. doi:10.1098/rspb.2004.2962
- Larson, C. M., Pillsworth, E. G., & Haselton, M. G. (2012). Ovulatory shifts in women's attractions to primary partners and other men: Further evidence of the importance of primary partner sexual attractiveness. *PLoS One*, 7, e44456. doi:10.1371/journal.pone.0044456.
- Little, A. C., & Jones, B. C. (2012). Variation in facial masculinity and symmetry preferences across the menstrual cycle is moderated by relationship context. *Psychoneuroendocrinology*, 37, 999–10008. doi:10.1016/j.psyneuen.2011.11.007.
- Little, A. C., Jones, B. C., & Burriss, R. P. (2007). Preferences for masculinity in male bodies change across the menstrual cycle. *Hormones and Behavior*, 31, 633–639. doi:10.1016/j.yhbeh.2007.03.006.
- Little, A. C., Jones, B. C., Burt, D. M., & Perrett, D. I. (2007). Preferences for symmetry in faces change across the menstrual cycle. *Biological Psychology*, 76, 209–216. doi:10.1016/ j.biopsycho.2007.08.003.
- Mikolajczyk, R. T., & Stanford, J. B. (2005). A new method for estimating the effectiveness of emergency contraception that accounts for variation in timing of ovulation and previous cycle length. *Fertility and Sterility*, 83, 1764–1770. doi:10.1016/ j.fertnstert.2005.01.097.
- Millar, M. (2013). Menstrual cycle changes in mate preferences for cues associated with genetic quality: The moderating role of mate value. *Evolutionary Psychology*, 11, 18–35.
- Penton-Voak, I. S., & Perrett, D. I. (2000). Female preference for male faces changes cyclically: Further evidence. *Evolution and Human Behavior*, 21, 39–48. doi:10.1016/S1090-5138(99)00033-1.
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K., et al. (1999). Menstrual cycle alters face preference. *Nature*, 399, 741–742. doi:10.1038/21557.
- Perrett, D. I., Lee, K., Penton-Voak, I. S., Rowland, D. A., Yoshikawa, S., Burt, D. M., . . . Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature*, 394, 884–887. doi:10.1038/29772
- Pillsworth, E. G., & Haselton, M. G. (2006). Male sexual attractiveness predicts differential ovulatory shifts in female extra-pair attraction and male mate retention. *Evolution and Human Behavior*, 27, 247–258. doi:10.1016/j.evolhumbehav.2005.10.002.
- Puts, D. A. (2005). Mating context and menstrual phase affect women's preferences for male voice pitch. *Evolution and Human Behavior*, 26, 388–397. doi:10.1016/j.evolhumbehav.2005.03.001.
- Puts, D. A. (2006). Cyclic variation in women's preferences for masculine traits: Potential hormonal causes. *Human Nature*, 17, 114– 127. doi:10.1007/s12110-006-1023-x.



- Rantala, M. J., Coetzee, V., Moore, F. R., Skrinda, I., Kecko, S., Krama, T., . . . Krams, I. (2013). Adiposity, compared with masculinity, serves as a more valid cue to immunocompetence in human mate choice. *Proceedings of the Royal Society B*, 280 (1751). doi:10.1098/rspb.2012.2495
- Rhodes, G., Chan, J., Zebrowitz, L. A., & Simmons, L. W. (2003). Does sexual dimorphism in human faces signal health? *Proceedings of the Royal Society B*, 270, S93–S95. doi:10.1098/rsbl.2003.0023.
- Rhodes, G., Simmons, L. W., & Peters, M. (2005). Attractiveness and sexual behavior: Does attractiveness enhance mating success? *Evolution and Human Behavior*, 26, 186–201. doi:10.1016/j.evolhumbehav.2004.08.014.
- Rhodes, G., Morley, G., & Simmons, L. W. (2013). Women can judge sexual unfaithfulness from unfamiliar men's faces. *Biology Let*ters, 9(1). doi:10.1098/rsbl.2012.0908.
- Scelza, B. A. (2011). Female choice and extra-pair paternity in a traditional human population. *Biology Letters*, 7, 889–891. doi:10.1098/rsbl.2011.0478.
- Scott, I. M. L., Clark, A. P., Boothroyd, L. G. & Penton-Voak, I. S. (2012). Do men's faces really signal heritable immunocompetence? *Behavioral Ecology*. Advance online publication. doi:10.1093/beheco/ars092
- Sell, A., Cosmides, L., Tooby, J., Sznycer, D., von Rueden, C., & Gurven, M. (2009). Human adaptations for the visual assessment of strength and fighting ability from the body and face.

- *Proceedings of the Royal Society B, 276*, 575–584. doi:10.1098/rspb.2008.1177.
- Simmons, J. P., Nelson, L. D., & Simonsohn, U. (2011). False-positive psychology: Undisclosed flexibility in data collection and analysis allows presenting anything as significant. *Psychological Science*, 22, 1359–1366. doi:10.1177/0956797611417632.
- Stumpf, R. M., & Boesch, C. (2005). Does promiscuous mating preclude female choice? Female sexual strategies in chimpanzees (Pan troglodytes verus) of the Tai National Park, Cote d'Ivoire. Behavioral Ecology and Sociobiology, 57, 511–524. doi:10.1007/ s00265-004-0868-4.
- Thornhill, R., & Gangestad, S. W. (2006). Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. *Evolution and Human Behavior*, 27, 131–144. doi:10.1016/j.evolhumbehav.2005.06.001.
- Thornhill, R., & Gangestad, S. W. (2008). The evolutionary biology of human female sexuality. Oxford: Oxford University Press.
- Watts, D. P. (1991). Mountain gorilla reproduction and sexual behavior. *American Journal of Primatology*, 24, 211–225. doi:10.1002/ajp.1350240307.
- Wegienka, G., & Day Baird, D. (2005). A comparison of recalled date of last menstrual period with prospectively recorded dates. *Journal of Women's Health*, 14, 248–252. doi:10.1089/jwh.2005.14.248.
- Wood, W., Kressel, L., Joshi, P., & Louie, B. (2012). Women's mate preferences: A meta-analysis of menstrual cycle effects. Manuscript Submitted for Publication.

