

Fertile women evaluate male bodies as more attractive, regardless of masculinity

Julia Jünger ^{*}, Tobias L. Kordsmeyer, Tanja M. Gerlach, Lars Penke

Department of Psychology & Leibniz ScienceCampus Primate Cognition, University of Goettingen, Gosslerstrasse 14, 37073 Goettingen, Germany



ARTICLE INFO

Article history:

Initial receipt 15 January 2018

Final revision received 17 March 2018

Keywords:

Ovulatory cycle
Mate preferences
Body masculinity
Steroid hormones
Fertility
Attractiveness

ABSTRACT

Ovulatory cycle shifts in women's mate preferences have been documented for several physical and behavioral traits. Research suggests that, at peak fertility, women tend to prefer men with characteristics that reflect good genes for short-term sexual relationships. However, existing findings have been criticized for methodological flexibility and failing attempts to replicate core results. In a large ($N = 157$), pre-registered, within-subject study spanning two ovulatory cycles, we investigated cycle shifts in women's mate preferences for masculine bodies. Using a large set of natural stimuli, we found that when fertile, women's ratings of male bodies increased for sexual as well as for long-term attractiveness. Both effects were partially mediated by the estradiol-to-progesterone-ratio. Furthermore, moderation analyses revealed that both shifts were only evident in women in relationships, but not in singles. Contrary to previous findings, male masculine traits did not interact with cycle phase to predict attraction, indicating that women's preferential priorities do not shift. Taken together, our results do not support women's mate preference shifts, as assumed by the good genes ovulatory shift hypothesis, but are consistent with shifting motivational priorities throughout the cycle. Implications of these results for female estrus theories and methodological recommendations for future research are discussed.

© 2018 Elsevier Inc. All rights reserved.

1. Introduction

The existence of systematic changes in women's mate preferences across the ovulatory cycle has been discussed widely in the evolutionary sciences. There is evidence that naturally cycling women in their fertile phase, compared to their luteal phase, evaluate masculine stimuli as more attractive for short-term relationships (Gangestad, Garver-Apgar, Simpson, & Cousins, 2007; Gildersleeve, Haselton, & Fales, 2014a). However, recent research casts doubts on these results (Gangestad et al., 2016; Wood, Kressel, Joshi, & Louie, 2014). Whereas there are already some researchers debating if ovulatory shifts in women's preferences for masculine faces, voices or odor exist (e.g. Feinberg et al., 2006; Harris, 2011, 2013; Peters, Simmons, & Rhodes, 2009; Thornhill, Chapman, & Gangestad, 2013), surprisingly little research focused on possible preference changes for masculine bodies. Therefore, the present study aims to clarify whether women experience such systematic shifts across the ovulatory cycle and whether these shifts are regulated by changes in steroid hormones or moderated by women's relationship status or self-reported stress levels.

Many non-human mammals show estrus behavior during ovulation, and their fertile phase is the only time when they are sexually receptive or proceptive. In rats, cats, cattle, and sheep, female behavioral changes

and sexual activity is mediated by changes in ovarian hormones (Dixson, 2012; Feder, 1981). Moreover, females of many non-human primate species change their mate preferences across the ovulatory cycle: When fertile, they mate more selectively, choosing high-quality males, likely to enhance their own and their offspring's survival and fitness (Matsumoto-Oda, 1999; Pieta, 2008; Stumpf & Boesch, 2005).

Unlike other primates, human females appear equally sexually receptive throughout the whole ovulatory cycle. However, they experience similar changes in ovarian hormones and their sexual interests vary across the cycle (Arslan, Schilling, Gerlach, & Penke, 2017; Gangestad, Thornhill, & Garver, 2002; Gangestad, Thornhill, & Garver-Apgar, 2005; Haselton & Gangestad, 2006; Roney & Simmons, 2013, 2016). This raises the question if women may also, homologous to some non-human primate species, experience ovulatory cycle shifts regarding their mate preferences. Whether human estrus exists and what its implications for women's mate choice are is still controversially debated in the literature. The most popular hypothesis regarding changes in women's mate preferences across the ovulatory cycle is the good genes ovulatory shift hypothesis (Arslan et al., 2017; Gangestad et al., 2005). It states that human females change their mate preferences systematically across the ovulatory cycle and this may have evolved to facilitate a flexible mixed mating strategy in order to increase females' reproductive fitness. Accordingly, on fertile days, women should be sexually attracted to characteristics in men that reflect high genetic quality, compared to their none-fertile days (Gildersleeve et al., 2014a). These

^{*} Corresponding author.

E-mail address: julia.juenger@psych.uni-goettingen.de (J. Jünger).

preference shifts should only be present in the context of short-term sexual relationships. For long-term relationships, women should put higher value on mates with a high potential and willingness to provide parental effort and these long-term preferences should not vary across the ovulatory cycle (Gildersleeve et al., 2014a; Thornhill & Gangestad, 2015).

There are some masculine traits in men that are particularly assumed to reflect men's genetic quality. Masculine men have sometimes been found to show higher circulating testosterone levels (Penton-Voak & Chen, 2004, but see Kandrik et al., 2017; Scott et al., 2014 for contradictory evidence), which might make them an indicator of superior immune functioning in line with the immunocompetence handicap hypothesis (Hamilton & Zuk, 1982). Moreover, taller men have higher reproductive success (Mueller & Mazur, 2001; Nettle, 2002; Pawlowski, Dunbar, & Lipowicz, 2000, but see Stulp & Barrett, 2016) and indicators of physical strength could attract mates (Sell, Lukaszewski, & Townsley, 2017) because strength increases success in competing with other men and might therefore be a cue of male protection abilities (Hill et al., 2013; Kordsmeyer, Hunt, Puts, Ostner, & Penke, 2017; Sell, Hone, & Pound, 2012). Furthermore, masculine characteristics in general have been linked to men's success in attracting mates (Gildersleeve et al., 2014a). Therefore, masculinity is argued to be a good indicator for genetic quality in men and should be a good variable to investigate possible cycle shifts in women's mate preferences. Previous studies have already found evidence for cycle shifts for masculine faces (Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000), voices (Feinberg et al., 2006; Puts, 2005) and odor (Gangestad & Thornhill, 1998; Havlíček, Roberts, & Flegr, 2005; Thornhill et al., 2013), apparently supporting the good genes ovulatory shift hypothesis. However, recent research casts doubt on this evidence, particularly because of several studies reporting null effects (e.g., Gangestad et al., 2016; Peters et al., 2009) and diverging conclusions from two recent meta-analyses on ovulatory cycle shifts (Gildersleeve et al., 2014a; Wood et al., 2014) lead to a considerable debate (Gangestad & Haselton, 2015; Gildersleeve, Haselton, & Fales, 2014b; Harris, Pashler, & Mickes, 2014; Hyde & Salk, 2014; Jones, 2014; Wood & Carden, 2014; Wood et al., 2014; Wood, 2014). In particular, cycle shifts in preferences for masculine faces could not be replicated in recent studies (Harris, 2011, 2013; Jones et al., 2018a; Marcinkowska, Galbarczyk, & Jasienska, 2018; Muñoz-Reyes et al., 2014; Peters et al., 2009; Scott et al., 2014).

The difficulty to replicate previous findings on cycle shifts in mate preferences could at least in part be ascribed to three issues evident in many earlier studies: low statistical power, methodological flexibility, and lack of hormone assessments. In many previous studies, sample sizes have likely been too small and interindividual (instead of intraindividual) comparisons have made it even more difficult to achieve appropriate statistical power (Gangestad et al., 2016). Moreover, across those studies, women's cycle phase was estimated with varying methods (Harris, 2011). Urine tests, which measure the luteinizing hormone (LH) to pinpoint ovulation, have often been missing (Gangestad et al., 2016). Finally, while changes in women's mate preferences should be regulated by changes in steroid hormones, almost all of the above referenced studies lacked direct assessments of these hormones (but see Marcinkowska et al., 2018; Jones et al., 2018a). In sum, the exact association between ovulatory cycle shifts in women's mate preferences and changes in steroid hormones remains unclear. Additional evidence that clarifies the current scientific discourse with multiple hormone assessments throughout the cycle is needed.

Only few studies so far have focused on masculine *bodies*, which is surprising, since human bodies are highly sexually dimorphic. Masculinity, as a purported indicator of good genes, is probably best identifiable in body characteristics. In particular, only three studies have demonstrated that women's preferences for men's masculine body traits may change across the ovulatory cycle: during their fertile phase, women showed an increase in mate preferences for tall men (Pawlowski & Jasienska, 2005), masculine body shape (Little, Jones, & Burriss, 2007), and rated muscularity (Gangestad et al., 2007). In

contrast, two studies did not find evidence for ovulatory cycle shifts in preferences for body masculinity (Marcinkowska et al., 2018; Peters et al., 2009). Notably, all these studies used artificial stimuli (e.g., drawn or morphed), which might not mirror real world instantiations of body masculinity and its range (but see Gangestad et al., 2007). In addition, these studies either had relatively small sample sizes for both female participants (but see Gangestad et al., 2007) and male stimuli, conducted interindividual (instead of intraindividual) comparisons (but see Marcinkowska et al., 2018; Peters et al., 2009), or did not measure hormones (but see Marcinkowska et al., 2018). Measuring hormones, however, is crucial to pinpoint the mechanisms potentially underlying ovulatory cycle shifts. If preference shifts are indeed regulated by changes in steroid hormones, they should be mediated by changes in estradiol and progesterone (Jones et al., 2005; Jones et al., 2018a; Puts, 2006; Roney & Simmons, 2008; Roney, Simmons, & Gray, 2011), as the fertile phase of the cycle prior to ovulation is characterized by higher levels of estradiol and lower levels of progesterone (Gangestad & Haselton, 2015; Puts et al., 2013). In contrast, levels of estradiol are lower and levels of progesterone are higher during the luteal phase, when conception risk is low. However, the analysis of estradiol, progesterone and the estradiol-to-progesterone-ratio (E/P ratio) might not be sufficient. Recent research suggests that psychological stress and the hormone cortisol should also be measured. Stress was found to induce higher cortisol levels (Herrera, Nielsen, & Mather, 2016), sometimes inhibiting estradiol emission in young women (Roney & Simmons, 2015) and decrease women's preferences for male facial masculinity (Ditzen, Palm-Fischbacher, Gossweiler, Stucky, & Ehlert, 2017 but see Jones et al., 2018a). Therefore, women's stress level might affect their mate preferences across the ovulatory cycle and should be investigated as a possible moderator. Furthermore, another hormone that might influence ovulatory cycle shifts is testosterone, which varies slightly but systematically across the cycle (e.g. Puts, 2006; Roney & Simmons, 2013). In recent studies, it was shown that women's preferences for masculine faces are strongest when testosterone levels are relatively high (Welling et al., 2007) and that early follicular testosterone correlates positively with preferences for men's facial masculinity (Bobst, Sauter, Foppa, & Lobmaier, 2014). These results indicate that testosterone may potentially also play a role in masculinity preference shifts across the cycle.

While steroid hormones may be the underlying physiological mechanism, to get a more complete picture of the processes underlying ovulatory cycle shifts, other variables should be taken into account. One such variable might be women's relationship status. According to the dual mating strategy hypothesis (Pillsworth & Haselton, 2006) based on the strategic pluralism model (Gangestad & Simpson, 2000), women may receive fitness benefits when forming a relationship with a reliable investing man, while seeking good genes from another man through extra-pair sexual encounters. Studies found that at peak fertility women are more likely to have sexual fantasies about men other than their primary partner (Gangestad et al., 2002), while reporting more commitment to their primary partner in the luteal phase compared to the late follicular phase (Jones et al., 2005). There is also evidence for cycle shifts in general sexual desire among partnered women that did not occur for singles (Roney & Simmons, 2016). In addition, normally cycling women in committed relationships have been found to report stronger masculinity preferences than singles (Jones et al., 2018a) and to rate the odor of dominant men as sexy, whereas singles did not (Havlíček et al., 2005). Therefore, women's relationship status could be a moderator of cycle shifts in mate preferences and should be investigated in greater detail.

1.1. Overview of the current study

In the current study, we aim to clarify a) whether there are mate preference shifts for masculine male body characteristics across the ovulatory cycle, b) which hormonal changes might underlie these shifts and c) which moderators influence these shifts. By employing a pre-registered study design with a large sample size and multiple assessment of

steroid hormones across two ovulatory cycles, we directly addressed criticism of cycle effect studies recently raised in the literature. In particular, in our study, women's fertile phase was not only estimated via forward- and backward counting methods, but was also validated with the use of urine tests measuring the luteinizing hormone. In addition, instead of just estimating the levels of ovarian hormones according to the calculated conception risk, they were directly assessed in women's saliva. Hormones such as cortisol and testosterone, which have only infrequently been investigated in previous research, were analyzed as possible mediator variables in an exploratory manner. To increase ecological validity in the assessment of women's masculinity preferences, we used natural, unmanipulated 3D stimuli, which avoid potentially unnatural characteristics or exaggerating effects in artificially manipulated stimuli. A large set of stimuli were presented to increase reliability. Masculinity indicators were measured directly from the stimulus men in order to test if cycle shifts lead to stronger preferences for natural body masculinity and to explore which aspects of body masculinity are most important in that regard. Finally, possible moderating influences of women's relationship status and self-reported stress were investigated.

1.2. Hypotheses and research questions

All hypotheses tested in the current manuscript are part of a pre-registration.¹ Following previous findings on ovulatory cycle shifts in mate preferences, we hypothesized that women in the fertile phase, as compared to their luteal phase, evaluate masculine bodies as more attractive for short-term relationships (Hypothesis 1). This effect should be mediated by increases in estradiol and decreases in progesterone (Hypothesis 2). Following the good genes ovulatory shift hypothesis, women in their fertile phase should be more sexually attracted to men with indicators of high genetic quality, compared to low-fertility days of their cycle (Gangestad et al., 2005; Gildersleeve et al., 2014a). Therefore we also pre-registered the hypothesis that shifts in short-term mate preferences are shown for men with the visual cues of upper-body strength (shoulder-chest ratio, shoulder-hip ratio, upper-torso volume relative to lower-torso volume, upper arm circumference) and taller body height. Additionally, shifts in short-term mate preferences could also be shown for men with higher testosterone levels (which has been assumed to coordinate all kinds of visible masculinity cues) and higher physical strength (Hypothesis 3a). It should be noted that, contrary to the other body characteristics measured directly from the body scans, testosterone and strength do not constitute directly visible cues. Still, both can be assumed to be linked to morphological cues visible in the body stimuli (e.g. Bhasin, 2003; Pound, Penton-Voak, & Surridge, 2009), but potentially not captured by the other measures. Therefore, we included them here as indirect cues. We predict our findings to be robust when controlling for the possible confounding variables age and body mass index (BMI). Because of the ongoing debate about whether or not cycle shifts in preferences for masculine characteristics exist, we also pre-registered the alternative hypothesis that naturally cycling women in their fertile phase, compared to their luteal phase, do not differ in their evaluations of masculine stimuli's attractiveness for short-term relationships (Hypothesis 3b). One possible moderator for these cycle shifts might be women's relationship status. Since it remains unclear if single and partnered women both pursue different mating strategies across the cycle, we state two alternative hypotheses: Cycle phase shifts in preferences for short-term mates are larger for partnered women than for single women (as predicted by the strategic pluralism model, Gangestad & Simpson, 2000; Hypothesis 4a), or, alternatively, relationship status does not affect the strength of cycle shifts in preferences for short-term mates (Hypothesis 4b). Because recent research suggests that psychological stress inhibits estradiol concentrations in young women (Roney & Simmons, 2015), we hypothesize self-reported stress as a moderator for occurring cycle shifts: Cycle shifts

should be attenuated when self-reported stress is high (Hypothesis 5). In accordance with the good genes ovulatory shift hypothesis, we also hypothesized that preference shifts should be absent or only weakly present when it comes to long-term mate preferences (Hypothesis 6; Gildersleeve et al., 2014a).

2. Material and methods

Our hypotheses, the study design, the sampling and the analysis plan had been pre-registered online at the Open Science Framework (<https://osf.io/egjwv/>) before any data have been collected or analyzed. All participants signed a written consent and the ethics committee of the Institute of Psychology at the University of Goettingen approved the protocol (no. 144).

2.1. Participants and recruitment

Out of 180 recruited participants, 157 heterosexual female participants (aged 18–35, $M = 23.3$, $SD = 3.4$) finished all sessions and were therefore included in further analyses. Seventeen women who only attended the introductory session of the study dropped out before participation (six fulfilled one of the exclusion criteria below, four quit the study without further reasons, four did not respond to emails, three had scheduling problems). Another six dropped out during the study because they only completed the first testing session (four had scheduling problems, two did not respond to emails after the first session). Based on the inclusion criteria of other ovulatory cycle studies, our participants had to fit to the following preregistered criteria: female, between 18 and 30 years old², naturally cycling (no hormonal contraception for at least three months, no expected switch to hormonal contraception during the study, no current pregnancy or breastfeeding, no birth-giving or breast-feeding during the previous three months, not taking hormone-based medication or anti-depressants). Additionally, they had to report that their ovulatory cycles had a regular length between 25 and 35 days during the last 3 months. At the beginning of the study, 75 of the participants reported to be in a relationship, 82 reported to be single. By completion of all sessions, participants received a payment of 80€ or course credit, and a 3D printed figure of themselves.

2.2. Procedure

All participants took part in five individually scheduled sessions. In the first introductory session the participants received detailed information about the general procedure, duration of the study and compensation. Furthermore, the experimenter explained the ovulation tests and checked the inclusion criteria. To count the days to the next ovulation and to plan the dates of the experimental sessions, cycle length as well as the dates of the last and the next menstrual onset were assessed. Finally, demographic data was collected.

Sessions two to five, the computer-based testing sessions, took place across two ovulatory cycles per participant, once per cycle during the fertile and once during the luteal phase. To control for possible effects of diurnal changes in hormone levels (Bao et al., 2003; Veldhuis et al., 1988), all sessions took place in the second half of the day (mainly between 11.30 am and 6 pm). When arriving at the lab, participants first completed a screening questionnaire, assessing their eligibility and some control variables for the saliva samples (Schultheiss & Stanton, 2009). Next, the saliva samples were collected via passive drool before the participants started their first rating task.³ In their first testing

² One of the participants reported to be 35 years old. We included her data because she met all other including criteria and had positive LH-tests. Excluding her data did not change the results.

³ The described study on ovulatory cycle shifts for body masculinity was one part of a larger study (see pre-registration). Participants also had to complete other rating tasks and anthropometric data was collected between these tasks. The duration of one testing session was approximately 2–2.5 h.

¹ This pre-registration also contained further hypotheses that are not part of the present paper.

session, all participants then saw a short preview video, presenting all male bodies they were about to evaluate for 1 s each, to avoid biased ratings resulting from not being familiar with the attractiveness range of all bodies. Furthermore, they were instructed to evaluate the men's attractiveness as they perceived it in that moment, independent of their current relationship status or general interest in other men.

Participants were then presented with the stimuli in a randomized order. The bodies were displayed rotating around their vertical axis, allowing them to be inspected from every side. To avoid the influence of confounding variables like facial attractiveness or skin color, the bodies were consistently colored in grey, without texture or head (see Fig. 1). Thereby the stimuli contained information on body morphology only. Participants rated each stimulus after at least one full rotation, but were able to inspect them for as long as they preferred. Every stimulus was rated separately for sexual attractiveness (assessing short-term attraction) and for attractiveness as a long-term relationship partner on an eleven-point Likert scale from -5 (extremely unattractive) to $+5$ (extremely attractive), including zero as a neutral point. Definitions of sexual attractiveness and attractiveness for a long-term relationship were provided prior to the ratings and read as follows:

- a) *Sexually attractive*: Men that score high would be very attractive for a sexual relationship that can be short-lived and must not contain any other commitment. Men scoring low would be very unattractive for a sexual relationship.
- b) *Attractive for a long-term partnership*: Men that score high would be very attractive for a committed relationship with a long-term perspective. Men that score low would be very unattractive as a long-term partner.

After each session, the appointment for the next session was arranged individually based on participant's ovulatory cycle.

Furthermore, all participants of the current study were asked to participate in a separate daily online diary study (Arslan, Jünger, Gerlach, Ostner, & Penke, 2016) that was conducted in parallel to the described lab study. Within this diary study, participants had to fill out a questionnaire about daily feelings and behavior across 70 days. We used the stress ratings from this study for further analyses (see below for more details).

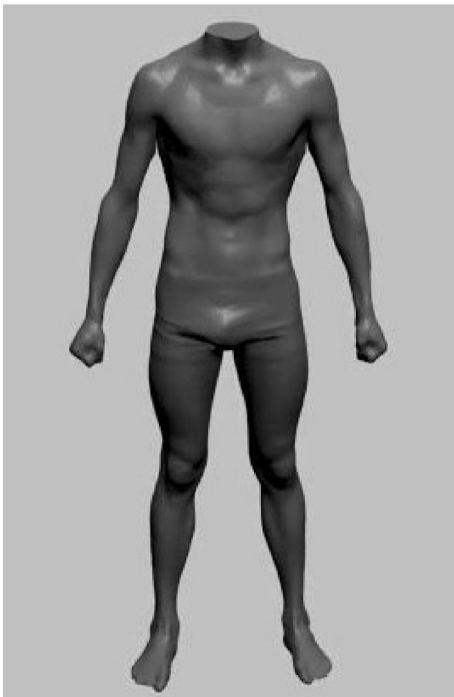


Fig. 1. Static example of a 3D male body stimulus.

3. Measures

3.1. Ovulatory cycle phase

Women's cycle phase was determined by the reverse cycle day method, based on the estimated day of the next menstrual onset (Gildersleeve, Haselton, Larson, & Pillsworth, 2012) and confirmed by highly sensitive (10 mIU/ml) urine ovulation test strips from purbay®, which measure the luteinizing hormone (LH). These LH-tests had to be done at home at the estimated day of ovulation and the four days prior to that and results were self-reported by the participants. The study investigated two ovulatory cycles in which every participant reported to the lab twice: Once while being fertile (at the days prior to ovulation, usually reverse cycle day 16–18, with reverse cycle day 16 as the most ideal date) and once when not fertile (during the luteal phase, after ovulation and prior to the next menstrual onset, usually reverse cycle day 4–11, with reverse cycle days 6 to 8 as the most ideal dates). An Excel sheet was used to compute the acceptable days for the testing sessions and to track whether a participant started in her fertile or luteal phase. Of all participants who finished all sessions, 66 participants started with the first session in their luteal phase, 91 started in the fertile phase.

3.2. Stimuli and masculinity measures

Eighty male bodies, collected in an independent study (Kordsmeyer et al., 2017; Kordsmeyer & Penke, 2017), were presented. All stimuli were natural male bodies of men in standardized underwear (tight shorts), captured with a high-resolution 3D body scanner (Vitus Smart XXL by Human Solutions). Men were instructed to stand upright with legs hip-width apart, arms extended and held slightly away from the body, making a fist with thumbs showing forward, the head positioned in accordance with the Frankfurt Horizontal, and to breathe normally during the scanning process. Body models were scaled so that they retained original height differences. Since we did not find any differences in attractiveness ratings between presenting the bodies life-sized via beamer on a white wall or on a computer screen in a pretest,⁴ we decided to present the stimuli on computer screens. Out of the 165 available bodies, we preselected stimuli based on adequate scan quality (12) and avoided missing values on target men's data (40). Among the remaining ones, selection of 80 suitable stimuli occurred at random. Visual cues of upper body strength were directly measured from the body scans using the automatic measures of the software Anthroscan (all according to ISO 20685:2005), including the following parameters relevant to this study: bust-chest girth (Anthroscan measure 4510), hip girth (7520), upper arm girth (8520). In addition to automatic measurements, biacromial shoulder width was measured manually (on screen) as the direct distance between the left and right acromion processes. The volume (in liters) of upper torso and lower torso was also measured from scans. We calculated shoulder-chest ratio, shoulder-hip ratio and the relative volume of upper torso to lower torso. Physical strength was operationalized as the aggregated mean of men's dominant hand grip (88.2% used their right hand) and upper body strength, measured with a hand dynamometer (Saehan SH5001), following the procedure described in Sell et al. (2009). The maximum strength of three trials for each measurement was used. Height was measured with a stadiometer. To measure men's testosterone levels, saliva samples

⁴ Between-subject design. Stimuli were divided in two sets (76 bodies per set) to avoid raters' tiredness, resulting in 15 rater per condition per set. All bodies were rated on eleven point Likert scales from -5 ("extremely unattractive") to $+5$ ("extremely attractive"). Comparisons between the ratings of all bodies revealed no significant differences between both conditions (presenting the stimuli on a computer screen vs. life-sized via beamer; $N = 60$, $M_{\text{Computer}} = -0.15$, $SD_{\text{Computer}} = 0.59$, $M_{\text{Beamer}} = 0.05$, $SD_{\text{Beamer}} = 0.66$, $t(58) = -1.25$, $p = 0.22$). Moreover, the attractiveness ratings in both conditions correlated highly ($r = 0.94$, $p \leq 0.001$).

were taken across two afternoon testing sessions under resting conditions and analyzed via immunoassays (see Kordsmeyer et al., 2017). The values were averaged and log transformed.

Descriptive statistics for attractiveness ratings and masculinity measures of all men used as stimuli are shown in Table 1. To investigate the validity of the chosen stimuli, we analyzed attractiveness ratings from an independent sample of participants (60 female raters) in a pretest (interrater agreement was high, $\alpha = 0.92$). Pretest ratings correlated negatively with stimuli men's BMI ($r = -0.30, p = 0.01$) and waist-to-hip-ratio ($r = -0.46, p < 0.001$). They correlated positively with chest-to-waist-ratio ($r = 0.58, p < 0.001$), as well as facial attractiveness ($r = 0.26, p = 0.02$), rated by another independent sample of 12 female raters from standardized photographs. The latter correlation confirms the one ornament hypothesis, which proposes correlated attractiveness of faces and bodies (Thornhill & Grammer, 1999).

3.3. Hormone measures

For hormone assays, we collected four saliva samples from each participant (one per testing session). Contamination of saliva samples was minimized by asking participants to abstain from eating, drinking (except plain water), smoking, chewing gum or brushing teeth for at least 1 h before each session. The samples were stored at $-80\text{ }^{\circ}\text{C}$ directly after collection until shipment on dry ice to the Kirschbaum Lab at Technical University of Dresden, Germany, where estradiol, progesterone, testosterone and cortisol was assessed via liquid chromatography mass spectrometry (LCMS; Gao, Stalder, & Kirschbaum, 2015). Since the LCMS analysis of the estradiol levels did only detect 22% of all possible values, the samples were reanalyzed using the highly sensitive 17β -estradiol enzyme immunoassay kit (IBL International, Hamburg, Germany). These latter estradiol values were used in subsequent analyses. We centered all hormone values on their subject-specific means and scaled them afterwards (i.e. divided them by a constant), so that the majority of the distribution for each hormone varied from -0.5 to 0.5 to facilitate calculations in the linear mixed models (as in Jones et al., 2018a, b, c). This is a common procedure to isolate effects of within-subject changes in hormones, avoiding the influence of outliers on results and dealing with the non-normal distribution of hormone levels. Hormone levels were nearly normally distributed afterwards, a figure showing the distribution of hormone levels after this procedure can be found in the supplement (Fig. S1). Importantly, this procedure did not change any findings compared to analyses with untransformed hormone values. The R code for this procedure can be found in the open script.

3.4. Stress ratings

Self-reported stress was measured via one item ("Today I was stressed out") on a five point Likert-scale (from "less than usual" to

Table 1
Descriptive statistics of male stimuli characteristics and the ratings for short-term sexual attractiveness (ST) and long-term attractiveness (LT).

	<i>M</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
Age	24.09	3.33	18.00	34.00
Height (cm)	180.11	7.38	160.50	202.00
Weight (kg)	75.21	11.49	52.70	109.80
BMI	23.19	2.53	17.06	33.49
Strength (kg)	48.48	7.85	31.00	69.00
SCR	0.39	0.02	0.35	0.46
SHR	0.40	0.02	0.34	0.44
Attractiveness rating ST	-0.36	2.78	-5.00	5.00
Attractiveness rating LT	-0.32	2.77	-5.00	5.00

Note. BMI = Body mass index, SCR = shoulder chest ratio, SHR = shoulder hip ratio, ST = short-term sexual attractiveness, LT = long-term attractiveness. Attractiveness rating scales ranged from -5 to $+5$.

"more than usual") on a daily basis within the accompanying online diary study (see above) with planned missings.⁵ For the analysis, the respective stress value of the same day of the lab testing session was taken. If there was no existing value for that day, we averaged the values of the two days before and after the testing day, if available. In total, 54 of the 157 participants were excluded from analyses, 26 because they did not take part in the diary study at all, 20 because they did not fill out enough days to get at least data for one fertile and one luteal session, eight because they took part in the study at another time window (not parallel to the lab study). Sixty-two participants filled out enough days for at least one fertile and one luteal session, 41 filled out enough days to analyze both fertile and both luteal sessions, resulting in an available dataset of 160 cycles (out of 314 possible cycles) in total.

3.5. Statistical analyses

All analyses were calculated with the statistic software R 3.4.0 (R Core Team, 2016). The following packages were used: lme4 1.1-13 (Bates, Maechler, Bolker, & Walker, 2014), lmerTest 2.0-33 (Kuznetsova, Brockhoff, & Christensen, 2015), ggplot2 2.2.1 (Wickham, 2009), psych 1.7.5 (Revelle, 2016), dplyr (Wickham, 2011).

4. Results

4.1. Preliminary analyses

First, we counted how many cycles were reported as being irregular (more than three days deviation between testing session and a-priori defined windows of appropriate testing days; see section "ovulatory cycle phase"). Even though all participants reported to have regular ovulatory cycles in the introductory session, eight women reported irregularity in both investigated cycles, 32 reported one cycle being irregular, resulting in 48 out of 314 (15.3%) cycles being irregular. Next we checked how many of the participants' ovulatory cycles had positive LH tests (indicating a LH surge) in the calculated fertile phase to detect non-ovulatory cycles. Twelve participants reported negative LH test results for both investigated cycles, nine reported negative LH tests results for one cycle. In total, the LH tests in 33 of all 314 cycles (10.5%) were negative. Additionally, we checked the temporal relationship between the reported day of LH surge and the date of scheduled testing session. Because ovulation usually occurs within 24–36 h after the observed LH surge, testing sessions that were scheduled more than two days after the surge might have already been in the early luteal phase. Out of the 281 cycles for which an LH surge was observed, thirteen (4.63%) purportedly fertile phase sessions were scheduled three or four days after the LH surge. Therefore, 268 (95.37%) were scheduled within an appropriate range of three days before to two days after the LH surge (in total: $M = -0.12, SD = 1.39$ days in relation to the day of the observed LH surge). A histogram showing the distribution of days of fertile phase testing sessions relative to the observed LH surge can be found in the supplement (Fig. S2). Participants with irregular cycles, negative LH-tests or the risk of early luteal phase instead of fertile phase testing session were still included in the main analyses, but excluded in robustness checks.

4.2. Ovulatory cycle shifts in women's mate preferences for body masculinity

First we tested whether there were ovulatory cycle shifts in women's attractiveness ratings for male bodies, independent from

⁵ The participants had to fill out >100 items per day. Therefore, we decided to reduce the daily items by planned missings to avoid too much dropouts, but still get enough data for every item. The relevant stress item was shown on about 40% of all days.

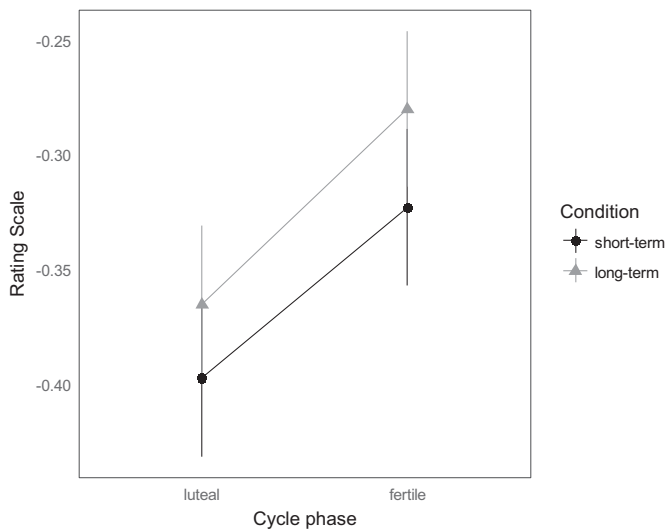


Fig. 2. Averaged attractiveness ratings for short-term (measured as sexual attractiveness) and long-term relationships in function of women's cycle phase. Rating scale ranged from -5 to $+5$, the Y-axis is truncated. Error bars represent 95% confidence intervals.

men's masculinity characteristics (Hypotheses 1 and 6). For multilevel analyses, we included attractiveness ratings as dependent variable (Model 1 with sexual attractiveness, Model 2 with long-term attractiveness), a random intercept per female rater as well as for male stimulus, and women's cycle phase (0 = luteal phase, 1 = fertile phase) as a fixed effect. This analysis showed a significant cycle shift in women's attraction: When fertile, ratings for sexual attractiveness were higher than in the luteal phase of the ovulatory cycle ($\gamma = 0.07$, $SE = 0.02$, $t = 4.44$, $p < 0.001$, $95\%CI = [0.04; 0.11]$), supporting Hypothesis 1. Similar results were found for the long-term attractiveness ratings ($\gamma = 0.09$, $SE = 0.02$, $t = 4.83$, $p < 0.001$, $95\%CI = [0.05; 0.12]$), contrary to Hypothesis 3. Fig. 2 shows how women's attraction changes as a function of cycle phase. These results indicate the existence of ovulatory cycle shifts on women's mate attraction to male bodies, independent of the relationship condition (sexual- vs. long-term), such that, in general, fertile women rated males' bodies as being more attractive.

Second, we tested if participants showed preference shifts across the ovulatory cycle for specific body characteristics that reflect masculinity (Hypotheses 3a, 3b and 6). Again, female raters as well as the male stimuli were treated as random effects. Women's cycle phase and men's masculine characteristics were treated as fixed effects.⁶ Men's baseline testosterone levels, body height, physical strength, shoulder-chest ratio (SCR), shoulder-hip ratio (SHR), upper torso volume relative to lower torso volume and upper arm circumference were analyzed as masculine traits. Two separate analyses were run for a) sexual attractiveness and b) long-term attractiveness as dependent variables. The values of all men's masculine traits were z-standardized in order to place all on the same scale and to ease interpretation of regression coefficients (γ). Multilevel within-subjects comparisons across two ovulatory cycles again showed significant cycle shifts for women's attraction in sexual as well as long-term attractiveness. In their fertile phase, women rated male bodies as more attractive for both relationship conditions, but none of the masculine traits interacted with cycle phase. Table 2 reports the results of the multilevel analyses of cycle phase and men's masculine traits for sexual attractiveness ratings. For ratings of long-term attractiveness, the results were similar (Table 3). Significant effects were found for cycle phase and physical strength,

whereas all interactions between cycle phase and masculine characteristics remained non-significant. These results again support Hypothesis 1 and contradict Hypothesis 6. All effects for cycle phase and strength remained significant when controlling for men's age and BMI. However, there were significant main effects of men's BMI when including the control variables in the mixed effect model (sexual: $\gamma = -1.11$, $SE = 0.31$, $t = -3.59$, $p < 0.001$, $95\%CI = [-1.68; -0.54]$; long-term: $\gamma = -1.03$, $SE = 0.28$, $t = -3.71$, $p < 0.001$, $95\%CI = [-1.55; -0.51]$), as well as for men's age (sexual: $\gamma = -0.14$, $SE = 0.06$, $t = -2.38$, $p = 0.02$, $95\%CI = [-0.25; -0.03]$; long-term: $\gamma = -0.13$, $SE = 0.05$, $t = -2.44$, $p = 0.02$, $95\%CI = [-0.23; -0.03]$). These results indicate an absence of ovulatory cycle shifts in preferences for any masculine characteristic, contradicting Hypothesis 3a, but supporting Hypothesis 3b. Women rated men's attractiveness as higher in their fertile phase, compared to their luteal phase, regardless of masculinity. However, women showed preferences for strong men, younger men, and men with a lower BMI, but independent of cycle phase. All results were comparable across both attraction outcomes (sexual and long-term attractiveness).

As cycle shift in women's attraction were not driven by shifts towards stronger preferences for men with more masculine bodies, we further analyzed rating differences between fertile and luteal phase ratings. A very high Spearman rank correlation between sexual attractiveness ratings of the fertile and the luteal phase ($r = 0.998$, $p < 0.001$) indicated that the rank order of the most attractive to the most unattractive body was virtually identical in fertile and luteal phases. When looking at the differences in ratings between the fertile and the luteal phase, we found that most of the bodies (82.5%) received slightly better ratings in the fertile phase ($M_{fertile} = -0.32$, $SD = 1.77$; $M_{luteal} = -0.4$, $SD = 1.8$; $d = 0.04$), even the least attractive ones. Long-term attractiveness ratings showed similar results: The Spearman-rank correlation between fertile and luteal phase ($r = 0.997$, $p < 0.001$) indicated hardly any rank order changes from the most attractive to the least attractive bodies. Again, most of the bodies (78.8%) received a better rating in the fertile phase compared to the luteal phase ($M_{fertile} = -0.28$, $SD = 1.57$; $M_{luteal} = -0.37$, $SD = 1.62$; $d = 0.06$). These results show that women consistently evaluate all men's bodies as more attractive when they are in their fertile phase, leaving virtually no room for differential effects of masculinity cues.

4.3. Steroid hormones as possible mediators

In order to analyze whether steroid hormones mediate effects of cycle phase (Hypothesis 2), estradiol, progesterone, testosterone, cortisol and estradiol-to-progesterone ratio (E/P ratio) were entered in the multilevel model. Results depicted in Table 4 demonstrate that for both attractiveness ratings, the E/P ratio partially mediated the effect of cycle phase on attractiveness ratings. Ratings were higher when the E/P ratio was high (i.e., in the fertile phase of the ovulatory cycle), the effect for cycle phase decreased, but stayed significant, partially supporting Hypothesis 2. We found additional partial mediator effects for estradiol, progesterone and cortisol, in that sexual attractiveness ratings were higher when estradiol and cortisol levels were lower, while long-term attractiveness ratings were higher when progesterone was high. Again the effect for cycle phase decreased in both cases, but stayed significant. All other measured hormones did not have any significant effects on the attractiveness ratings. However, our decision to include the E/P ratio in the same model with estradiol and progesterone might have caused collinearity problems. Therefore, we additionally calculated separate models with estradiol, progesterone, testosterone and cortisol as fixed effects, but excluding E/P ratio, for sexual as well as long-term attractiveness ratings. Results remained virtually identical, besides the former negative effect of cortisol on sexual- and the positive effect of progesterone on long-term attractiveness ratings that slightly failed to reach significance (Table 5). However, the effect sizes for all effects did not change noticeably.

⁶ Separate models for all cues revealed comparable results.

Table 2
Results of multilevel regression analyses of sexual attractiveness ratings as a function of cycle phase and men's masculinity cues.

	γ	SE	t	p	95% CI
Women's cycle phase	0.07	0.02	4.44	<0.001	[0.04, 0.11]
Men's baseline testosterone level	-0.02	0.22	-0.10	0.92	[-0.44, 0.39]
Men's body height	-0.11	0.25	-0.43	0.67	[-0.57, 0.36]
Men's physical strength	0.60	0.26	2.34	0.02	[0.12, 1.09]
Men's SCR	-0.03	0.28	-0.11	0.91	[-0.57, 0.50]
Men's SHR	0.34	0.30	1.12	0.26	[-0.23, 0.91]
Men's upper-torso volume (relative to lower-torso volume)	-0.16	0.23	-0.73	0.47	[-0.59, 0.26]
Men's upper arm circumference	-0.33	0.27	-1.12	0.22	[-0.83, 0.18]
Cycle phase \times men's baseline testosterone level	0.02	0.02	0.81	0.42	[-0.02, 0.05]
Cycle phase \times men's body height	0.03	0.02	1.31	0.19	[-0.01, 0.07]
Cycle phase \times men's physical strength	-0.00	0.02	-0.11	0.91	[-0.05, 0.04]
Cycle phase \times men's SCR	-0.00	0.02	-0.10	0.92	[-0.05, 0.04]
Cycle phase \times men's SHR	0.00	0.03	0.11	0.91	[-0.05, 0.05]
Cycle phase \times men's upper torso volume	0.01	0.02	0.75	0.46	[-0.02, 0.05]
Cycle phase \times men's upper arm circumference	-0.02	0.02	-0.72	0.47	[-0.06, 0.03]

Note. Women's cycle phase, men's masculine traits and their interactions as predictors for sexual attractiveness ratings. All variables had 50,240 observations (157 participants \times 4 test sessions \times 80 stimuli). We dummy-coded the variable cycle phase with 0 = luteal, 1 = fertile. All values were z-standardized.

Table 3
Results of multilevel regression analyses of long-term attractiveness ratings as a function of cycle phase and men's masculinity cues.

	γ	SE	t	p	95% CI
Women's cycle phase	0.09	0.02	4.83	<0.001	[0.05, 0.12]
Men's baseline testosterone level	-0.03	0.20	-0.13	0.90	[-0.40, 0.35]
Men's body height	-0.04	0.22	-0.20	0.84	[-0.47, 0.38]
Men's physical strength	0.47	0.23	2.00	<0.05	[0.03, 0.90]
Men's SCR	0.01	0.26	0.03	0.98	[-0.48, 0.49]
Men's SHR	0.28	0.27	1.01	0.32	[-0.24, 0.79]
Men's upper-torso volume (relative to lower-torso volume)	-0.21	0.20	-1.02	0.31	[-0.59, 0.18]
Men's upper arm circumference	-0.30	0.24	-1.25	0.22	[-0.76, 0.15]
Cycle phase \times men's baseline testosterone level	0.02	0.02	0.84	0.40	[-0.02, 0.05]
Cycle phase \times men's body height	0.02	0.02	0.97	0.33	[-0.02, 0.06]
Cycle phase \times men's physical strength	-0.00	0.02	-0.03	0.97	[-0.05, 0.04]
Cycle phase \times men's SCR	0.02	0.03	0.64	0.52	[-0.03, 0.07]
Cycle phase \times men's SHR	-0.01	0.03	-0.53	0.60	[-0.07, 0.04]
Cycle phase \times men's upper torso volume	0.01	0.02	0.58	0.56	[-0.03, 0.05]
Cycle phase \times men's upper arm circumference	-0.02	0.02	-0.70	0.49	[-0.06, 0.03]

Note. Women's cycle phase, men's masculine traits and their interactions as predictors for long-term attractiveness ratings. All variables had 50,240 observations (157 participants \times 4 test sessions \times 80 stimuli). We dummy-coded the variable cycle phase with 0 = luteal, 1 = fertile. All values were z-standardized.

4.4. Relationship status

To test if women's current relationship status moderated the ovulatory cycle shifts in their mate attraction (Hypothesis 4a and 4b), we first classified all women who reported to be in an open relationship,⁷ in a committed relationship, engaged, or married as in a relationship. During the study, the relationship status changed for 13 participants. Their data was categorized in accordance with their relationship status on the particular testing day. We again calculated a multilevel mixed regression model with female rater and male stimuli as random effects, women's cycle phase and their relationship status were treated as fixed effects. As shown in Table 6, there was a significant interaction between cycle phase and relationship status, but no significant main effects. To closer investigate this interaction effect, we analyzed ratings from partnered women vs. singles separately. Results displayed in Table 7 indicate that only partnered women showed cycle shifts and rated men's bodies as more attractive when they were fertile. The results were similar for sexual- and for long-term relationships and support Hypothesis 4a, but not 4b.

4.5. Self-reported stress

Furthermore, we analyzed whether self-reported stress moderated the relationship between cycle phase and attractiveness ratings

⁷ We additionally analyzed the data by classifying women who reported to be in an open relationship as singles, which did not change any results notably.

(Hypothesis 5). We calculated two further multilevel models (Model 1 for sexual-, Model 2 for long-term attractiveness ratings). Again, female raters as well as the male stimuli were treated as random effects. Women's cycle phase and self-reported stress ratings were treated as fixed effects. Since many women did not fill out the self-reported stress item for every testing day due to the planned missings design (see Methods), data for only about half of the sample (25,600 observations, $n = 103$ who completed minimum one cycle) was available. For sexual attractiveness ratings as outcome, we found a main effect of self-reported stress ($\gamma = -0.06$, $SE = 0.02$, $t = -2.97$, $p < 0.01$, $95\%CI = [-0.10; -0.02]$), revealing that sexual attractiveness ratings were higher when self-reported stress was lower. The main effect of cycle phase ($\gamma = 0.03$, $SE = 0.06$, $t = 0.55$, $p = 0.58$, $95\%CI = [-0.08; 0.14]$) and the interaction between cycle phase and self-reported stress were not significant ($\gamma = 0.03$, $SE = 0.03$, $t = 1.18$, $p = 0.24$, $95\%CI = [-0.02; 0.08]$). For long-term ratings as outcomes, we found a main effect of cycle phase ($\gamma = 0.14$, $SE = 0.06$, $t = 2.44$, $p = 0.01$, $95\%CI = [0.03; 0.26]$), showing that attractiveness ratings were higher in the fertile phase. The main effect of self-reported stress ($\gamma = -0.03$, $SE = 0.02$, $t = -1.44$, $p = 0.15$, $95\%CI = [-0.07; 0.01]$) and the interaction between cycle phase and self-reported stress were not significant ($\gamma = -0.02$, $SE = 0.03$, $t = -0.76$, $p = 0.45$, $95\%CI = [-0.07; 0.03]$). For both sexual- and long-term attractiveness, cycle phase and self-reported stress did not interact, indicating that there was no moderation effect of self-reported stress on cycle effects. These results contradict Hypothesis 5, but suggest that high stress overrides any cycle effects on sexual attraction.

Table 4
Multilevel regression analyses of attractiveness ratings as a function of cycle phase and hormone levels as possible mediator variables.

	γ	SE	t	p	95% CI
Sexual					
Cycle phase	0.07	0.02	3.26	<0.01	[0.03; 0.12]
Estradiol	-0.10	0.03	-3.14	<0.01	[-0.17; -0.04]
Progesterone	0.03	0.03	1.05	0.30	[-0.03; 0.08]
E/P	0.05	0.02	2.39	0.02	[0.01; 0.09]
Testosterone	0.01	0.01	0.90	0.37	[-0.01; 0.04]
Cortisol	-0.06	0.03	-2.07	0.04	[-0.11; -0.00]
Long-term					
Cycle phase	0.10	0.02	4.13	<0.001	[0.05; 0.15]
Estradiol	-0.05	0.03	-1.40	0.16	[-0.12; 0.02]
Progesterone	0.07	0.03	2.20	0.03	[0.01; 0.12]
E/P	0.05	0.02	2.48	0.01	[0.01; 0.10]
Testosterone	0.02	0.01	1.24	0.21	[-0.01; 0.04]
Cortisol	-0.02	0.03	-0.73	0.47	[-0.08; 0.04]

Note. All variables had 42,720 observations (157 participants × 4 test sessions × 80 stimuli – missing values). We dummy-coded the variable cycle phase with 0 = luteal, 1 = fertile. All hormone values were centered to their subject-specific means and then scaled.

Table 5
Multilevel regression analyses of attractiveness ratings as a function of cycle phase and hormone levels as possible mediator variables, excluding the E/P-ratio.

	γ	SE	t	p	95% CI
Sexual					
Cycle phase	0.09	0.02	4.08	<0.001	[0.05; 0.13]
Estradiol	-0.08	0.03	-2.59	<0.01	[-0.14; -0.02]
Progesterone	0.02	0.03	0.77	0.44	[-0.03; 0.08]
Testosterone	0.01	0.01	0.78	0.44	[-0.02; 0.04]
Cortisol	-0.05	0.03	-1.80	0.07	[-0.10; 0.00]
Long-term					
Cycle phase	0.12	0.02	5.01	<0.001	[0.07; 0.16]
Estradiol	-0.03	0.03	-0.76	0.45	[-0.09; 0.04]
Progesterone	0.06	0.03	1.92	0.06	[-0.00; 0.11]
Testosterone	0.02	0.01	1.12	0.26	[-0.01; 0.04]
Cortisol	-0.01	0.03	-0.43	0.67	[-0.07; 0.04]

Note. All variables had 42,720 observations (157 participants × 4 test sessions × 80 stimuli – missing values). We dummy-coded the variable cycle phase with 0 = luteal, 1 = fertile. All hormone values were centered to their subject-specific means and then scaled.

4.6. Robustness checks

We conducted further analyses to test the robustness of our effects. To rule out that our results might have been caused by order effects of testing sessions (in particular participating in the first session when fertile; Suschinsky, Bossio, & Chivers, 2014), we controlled for type of first phase in our analyses. For both sexual- and long-term attraction the effect of cycle phase remained stable (sexual: $\gamma = 0.07, SE = 0.02, t = 4.44, p < 0.001, 95\%CI = [0.04; 0.11]$; long-term: $\gamma = 0.09, SE = 0.02, t = 4.83, p < 0.001, 95\%CI = [0.05; 0.12]$). Starting fertile vs. luteal did not affect the attractiveness ratings (sexual: $\gamma = -0.04, SE = 0.13, t = -0.33, p = 0.74, 95\%CI = [-0.30; 0.21]$; long-term: $\gamma = -0.17, SE = 0.14, t = -1.19, p = 0.24, 95\%CI = [-0.44; 0.11]$). Next, we added a variable for values of the first vs. the second tested ovulatory cycle as fixed effect to our basic model with cycle phase as another fixed effect, female raters and male stimuli as random slopes, to see if there were differences in ratings. For sexual- as well as for long-term relationships, the effects of cycle phase remained stable (sexual: $\gamma = 0.07, SE = 0.02, t = 4.45, p < 0.001, 95\%CI = [0.04; 0.11]$; long-term: $\gamma = 0.09, SE = 0.02, t = 4.85, p < 0.001, 95\%CI = [0.05; 0.12]$), but the attractiveness ratings were significantly higher in the first cycle across all participants (sexual: $\gamma = -0.31, SE = 0.02, t = -18.62, p < 0.001, 95\%CI = [-0.34; -0.28]$; long-term: $\gamma = -0.38, SE = 0.02, t = -21.32, p < 0.001, 95\%CI = [-0.41; -0.34]$). Next we conducted all our analyses only with women who perfectly met all inclusion

Table 6
Multilevel regression analyses of attractiveness ratings as a function of cycle phase and women's relationship status.

	γ	SE	t	p	95% CI
Sexual					
Cycle phase	0.01	0.02	0.56	0.57	[-0.03; 0.06]
Relationship status	0.09	0.06	1.37	0.17	[-0.04; 0.21]
Cycle phase × relationship status	0.12	0.03	3.68	<0.001	[0.06; 0.19]
Long-term					
Cycle phase	0.03	0.02	1.26	0.21	[-0.02; 0.08]
Relationship status	-0.06	0.07	-0.97	0.33	[-0.19; 0.07]
Cycle phase × relationship status	0.11	0.04	3.20	0.001	[0.04; 0.18]

Note. All variables had 50,240 observations (157 participants × 4 test sessions × 80 stimuli). We dummy-coded the variable cycle phase with 0 = luteal, 1 = fertile, and relationship status with 0 = single, 1 = in a relationship.

Table 7
Multilevel regression analyses of attractiveness ratings as a function of cycle phase with separate analyses for partnered vs. single women.

	γ	SE	t	p	95% CI
Sexual: partnered women					
Cycle phase	0.14	0.02	5.77	<0.001	[0.09; 0.19]
Sexual: single women					
Cycle phase	0.01	0.02	0.62	0.54	[-0.03; 0.06]
Long-term: partnered women					
Cycle phase	0.14	0.03	5.56	<0.001	[0.09; 0.19]
Long-term: single women					
Cycle phase	0.03	0.02	1.28	0.20	[-0.02; 0.08]

Note. Models for partnered women had 24,000 observations, models for single women had 26,240 observations. We dummy-coded the variable cycle phase with 0 = luteal, 1 = fertile.

criteria ($N = 112$ who reported positive LH-tests in their fertile phase and a regular cycle length in both investigated cycles⁸). Results remained virtually identical and can be found in the supplement. In summary, the results remained robust across all checks.

5. Discussion

In the current study, we sought to clarify whether women experience mate preference shifts for male body masculinity across the ovulatory cycle and, further, investigated potential mediators and moderators of these effects. We conducted a large, pre-registered within-subjects study including assessment of salivary hormones and luteinizing hormone tests. Multilevel intraindividual comparisons across two ovulatory cycles showed significant cycle shifts in women's attraction: When fertile, women's ratings of men's bodies increased for sexual- as well as for long-term attractiveness. Cycle effects were partially mediated by the E/P ratio as well as by lower estradiol and cortisol (sexual attractiveness ratings) and higher progesterone levels (long-term ratings). However, the effects of cortisol and progesterone did not remain significant when excluding the E/P ratio because of possible collinearity problems. Shifts in attraction were only found for women in relationships and were not moderated by self-reported stress, though cycle shifts in sexual attraction disappeared when stress was high. Contrary to previously reported findings, men's masculine body characteristics did not interact with cycle phase to predict sexual attractiveness, indicating no shifts in preferences for specific traits. The same was true for long-term attractiveness.

⁸ We pre-registered as part of our sampling size determination strategy that we will also report when effect sizes are notably different within the sample of the first $N = 120$. As these 112 women met all inclusion criteria exactly as pre-registered and do not exceed the number of 120, the reported results for these participants could be seen as the pre-registered sample.

5.1. Cycle effects: preference vs. motivational priority shifts

Our results support the existence of a human female estrus, because we found differences in women's attraction to men's bodies between the fertile and the luteal phase of the ovulatory cycle. Importantly, these results are in contrast to many prior findings. The most widespread perspective in the existing cycle effects literature, derived from the strategic pluralism model, is that women's mate preferences will only shift for men's characteristics that reflect good genes and only when men are evaluated for short-term sexual attractiveness (Gildersleeve et al., 2014a). Contrary to our predictions based on this perspective, but in line with recent literature on ovulatory cycle shifts for masculine faces (Harris, 2011, 2013; Jones et al., 2018a; Muñoz-Reyes et al., 2014; Peters et al., 2009; Scott et al., 2014) and morphed bodies (Marcinkowska et al., 2018), we did not find evidence for preferences shifts for masculine bodies that could be interpreted as stronger sexual selection for good genes when fertile. Women did not prefer male body masculinity, presumably reflecting good genes, more when they were fertile, compared to their luteal days. In fact, they evaluated exactly the same bodies as more or less attractive, no matter if they rated them in their fertile or their luteal phase. Our findings can rather be interpreted as in line with a motivational priority shift account (Roney & Simmons, 2017). This account entails a shift in motivational priorities towards mating behavior in the fertile phase of the ovulatory cycle, when conception provides a fitness benefit that outweighs the costs of sex, resulting in increased sexual motivation. A fertile phase increase in sexual motivation has repeatedly been found in sexual desire research (e.g., Arslan et al., 2017; Bullivant et al., 2004; Gangestad et al., 2002, 2005; Natale, Albertazzi, & Cangini, 2003; Roney & Simmons, 2013): When fertile, women more frequently initiate sexual behavior, and experience stronger sexual desire and more sexual fantasies. This increase in sexual motivation could probably explain the general increase in attractiveness ratings of masculine bodies in the fertile phase of the ovulatory cycle. However, we have not tested sexual desire in our study. To ascertain that an increase in sexual desire or, more specifically, motivational priority shifts explain our effects, further research should directly test sexual desire as a mediator of cycle shifts in women's attraction.

5.2. Relationship status and stress as moderators

In the current study, increasing attractiveness ratings in the fertile phase were significant in the full sample, but further analyses indicated that they held only for women in relationships, not for singles. This effect is also in line with prior research on sexual desire: In a diary study, Roney and Simmons (2016) recently found that only women in relationships, but not singles, experience higher sexual desire in their fertile phase. Similarly, in a small between-subjects study, Havlíček et al. (2005) found that only fertile women in relationships rated the smell of dominant men as being particularly sexy, whereas single women did not. The findings of this study were interpreted as indication for a mixed mating strategy in line with the strategic pluralism model (i.e., women preferring men with characteristics of good genes for short-term extra-pair relationships, while seeking men willing to invest in their offspring for long-term relationships). However, since we did neither find differences between sexual- and long-term preferences nor increased attraction to masculinity cues that have been argued to reflect good genes, we suggest a motivational priority shifts as a more parsimonious explanation. If motivational priority shifts occur when fitness benefits of conception outweighs the costs of sex, this might particularly be the case for women in relationships. Single women have more often changing partnerships and might therefore expect higher risks of sexual behavior like infection or injury that are possibly not outbalanced by the benefits of conception in the fertile phase. Furthermore, for women in relationships, a partner who potentially cares for their offspring is available, in contrast to single women, for whom it might be too costly to risk that the offspring's father

might not show any paternal effort at all. However, to learn more about the cost/benefit ratio of sex related to relationship status, further research should focus on differences between partnered and single women regarding motivational priority shifts.

Another possible moderator of ovulatory cycle shifts in women's mate preferences in recent research was self-reported stress. Prior studies indicated that stress suppresses an increase in women's masculinity preferences (Ditzen et al., 2017, but see Jones et al., 2018a) and decreases estradiol levels (Roney & Simmons, 2015). Nevertheless, we did not find a moderator effect of self-reported stress on cycle shifts in mate attraction, even though cycle shifts in sexual attraction to male bodies disappeared when stress accounted for. However, self-reported stress values are subjective and might not always reflect the physiological stress level. For a clarification of the relationship between stress, cycle shifts and mate preferences, more research is needed.

5.3. Hormonal changes as mediating mechanisms

Previous research has found that estradiol positively and progesterone negatively predicts fluctuations in sexual desire (Roney & Simmons, 2013, 2016). Other cycle studies found that women's estradiol level is a predictor of preferences for masculine voices (Pisanski et al., 2014), and higher estimated estradiol levels increased attraction for dominance in long-term mates (Lukaszewski & Roney, 2009). Our results do not entirely support these findings. The increase in sexual- as well as long-term attractiveness ratings for men's bodies were partially mediated by the E/P ratio, validating that the found effect is due to women's fertility status. The effects of cortisol (sexual attractiveness) and progesterone (long-term attractiveness) were not robust in further analyses. Measured salivary estradiol levels were a predictor for sexual attraction only, but in the opposite direction as expected: ratings were higher when estradiol levels were lower. This effect was independent of the effect of the E/P ratio, which is more directly associated with fertility, and might be due to the fact that there is a second, somewhat smaller estradiol peak in the luteal phase (Goodman, 2009) which overlaps with the timing of many luteal phase sessions. However, these results, especially the counter intuitive effect of estradiol, should be replicated before being interpreted further. Furthermore, hormone levels should ideally be measured daily to see if testing sessions in the luteal phase really overlap with the secondary estradiol peak.

5.4. Methodological considerations and future research

Many previous studies have reported shifts across the cycle in preferences for masculine cues and other presumed indicators of good genes. Our results on body preferences clearly diverge in this regard, which raises the question of why this might be. One possibility is that we were the first to use natural bodies as stimuli, yielding a higher ecological validity than artificially drawn or morphed stimuli. So far, other published ovulatory cycle effects for body masculinity cues may be contingent on the use of computer-generated bodies, morphed to an artificial, potentially supranatural level of masculinity. We also deviated from earlier studies by not using 2D images or drawings, but rotating 3D models. These models capture natural variation in morphology, the focus of our study, and display it more fully than 2D images or drawings can (compare Marlowe, Apicella, & Reed, 2005). However, since the 3D models were devoid of texture (incl. body hair) and standardized for color, they might also have looked less natural. Therefore our results might have been different if subjects had rated actual photos of bodies rather than 3D representations. Future studies should investigate if our results replicate with different stimulus materials.

Besides the nature of stimuli, there are also other considerable differences between our and prior studies, especially in how to determine women's fertile days. A substantial fraction of published studies used various calendar-based counting methods (forward or backward counting, or combinations thereof) to estimate the day of ovulation. In

addition, some studies used broader (8–9 days in length), others more narrow (6–7 days) fertile windows, or calculated fertility continuously based on different fertility estimates. Many did not use LH tests to validate fertility, although these tests can be seen as the gold standard (Gangestad et al., 2016). Our study did not only use LH tests for validating women's fertile phase, but additionally followed up on all participants to verify their date of the next menstrual onset to be able to backward count to their fertile days. These methods correspond to the state of the art to pinpoint ovulation. Another reason might be that there is huge variation in previous studies in sample sizes and within- vs. between-subjects designs. Many studies only investigated 25 to 50 participants (e.g. Feinberg et al., 2006; Peters et al., 2009), or used between-subject designs (e.g. Havlíček et al., 2005; Little et al., 2007; Pawlowski & Jasienska, 2005). Between-subject ovulatory cycle studies require very large sample sizes to achieve acceptable levels of statistical power (Gangestad et al., 2016), hence within-subject designs should be the designs of choice. The cycle shifts that we found had very small effect sizes. Previous studies worked with relatively small sample sizes. Therefore, they would not have been able to show such small effects. Hence, previously reported effects might have been false positives or due to publication bias. Nevertheless, some of the published studies found evidence for preference shifts in line with the good genes ovulatory shift hypothesis (e.g., Gangestad et al., 2007; Little et al., 2007). Since we had a rather large sample size, used a large number of stimuli and tested all participants four times across two ovulatory cycles, our study had comparatively large power to detect shifts in preferences for masculinity cues. Additionally, in a recent study Marcinkowska et al. (2018) also could not replicate cycle shifts in women's preferences for masculinized bodies. However, finding null results running more powerful tests with better methods is not unique to the mate preference literature, but also to other important parts of evolutionary sciences and beyond. For example, Jones et al. (2018c) found no evidence that disgust sensitivity tracked changes in hormone levels, contradicting the Compensatory Prophylaxis Hypothesis of pathogen disgust, underlining the importance of high powered study designs. Still, single studies cannot resolve the diverse range of findings in the literature, and more highly powered replication studies will be necessary. Future research should reduce methodological flexibility by agreeing on design and analytic standards and base studies on large sample sizes in order to find out under which circumstances cycle shifts in female mate preferences as well as other previously reported popular effects can be found, and for which characteristics they are robust.

6. Conclusions

In sum, our findings show that cycle shifts in women's attraction to male bodies exist, but they do not seem to alter preferences for body characteristics at all, leaving no room for cycle shifts in mate preferences for masculine characteristics or any other assumed indicators of good genes. They are rather in line with a motivational priority shift towards mating effort for women in their fertile phase, resulting in a more favorable evaluation of all male bodies (on average) in terms of sexual- and long-term attractiveness. These shifts appear to be exclusive for women in romantic relationships. Our results contradict some prominent previous findings and indicate that future research is indispensable for clarifying under which conditions cycle shifts can be found and for investigating which findings of previous ovulatory cycle research (e.g., shifts for voices or social dominant behavior; cues to fertility) are robust. Therefore, more and preferably pre-registered studies with a high statistical power and good methodological standards are necessary for finding out the exact relationship between women's ovulatory cycles, steroid hormones, and their mate preferences.

Declaration of interest

The authors declare that they have no conflict of interest.

Acknowledgments

This research was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – Project number 254142454/GRK 2070. We thank Ben Jones and an anonymous reviewer for valuable comments and insightful feedback on an earlier version of this article. Furthermore, we thank Ruben C. Arslan for valuable statistical advice, Christian Treffenstädt for assistance in the programming process, Kelly Gildersleeve for kindly providing a blueprint of an Excel sheet to calculate fertile windows, Alex Stern for helpful comments on prior versions of this manuscript and our research assistants Laura Botzet, Silvia Bradatsch, Paulina Lauer and Laura Specker-Mattißen, without whom this large data collection would not have been possible.

Open practices statement

The study reported in this article was preregistered. The data and instruction material has been made available at the Open Science Framework. We did not post, however, the stimuli videos to protect the privacy of our male participants.

Appendix A. Supplementary data

Supplementary information are available at <https://osf.io/n4hj6/>. Supplementary data to this article can be found online at <https://doi.org/10.1016/j.evolhumbehav.2018.03.007>.

References

- Arslan, R. C., Jünger, J., Gerlach, T. M., Ostner, J., & Penke, L. (2016). *Pre-registration. Online diary study of ovulatory cycle shifts on sexual desire, sexual activity, and mating behavior.* (Retrieved from osf.io/d3avf/).
- Arslan, R. C., Schilling, K. M., Gerlach, T. M., & Penke, L. (2017). Using 26 thousand diary entries to show ovulatory changes in sexual desire and behaviour. Retrieved from psyarxiv.com/jp2ym.
- Bao, A. M., Liu, R. Y., Van Someren, E. J., Hofman, M. A., Cao, Y. X., & Zhou, J. N. (2003). Diurnal rhythm of free estradiol during the menstrual cycle. *Eur. J. Endocrinol.*, *148*, 227–232. <https://doi.org/10.1530/eje.0.1480227>.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). *lme4: Linear mixed-effects models using Eigen and S4. R package version 1.* (pp. 1–13).
- Bhasin, S. (2003). Regulation of body composition by androgens. *J. Endocrinol. Investig.*, *26*, 814–822. <https://doi.org/10.1007/BF03345230>.
- Bobst, C., Sauter, S., Foppa, A., & Lobmaier, J. S. (2014). Early follicular testosterone level predicts preference for masculinity in male faces, but not for women taking hormonal contraception. *Psychoneuroendocrinology*, *41*, 142–150. <https://doi.org/10.1016/j.psyneuen.2013.12.012>.
- Bullivant, S. B., Sellergren, S. A., Stern, K., Spencer, N. A., Jacob, S., Mennella, J. A., & McClintock, M. K. (2004). Women's sexual experience during the menstrual cycle: Identification of the sexual phase by noninvasive measurement of luteinizing hormone. *The Journal of Sex Research*, *41*, 82–93. <https://doi.org/10.1080/00224490409552216>.
- Ditzen, B., Palm-Fischbacher, S., Gossweiler, L., Stucky, L., & Ehler, U. (2017). Effects of stress on women's preference for male facial masculinity and their endocrine correlates. *Psychoneuroendocrinology*, *82*, 67–74. <https://doi.org/10.1016/j.psyneuen.2017.05.006>.
- Dixon, A. F. (2012). *Primate sexuality.* Oxford, UK: Oxford University Press.
- Feder, H. H. (1981). Estrous cyclicity in mammals. In N. T. Adler (Ed.), *Neuroendocrinology of reproduction* (pp. 279–384). New York: Plenum Press.
- Feinberg, D. R., Jones, B. C., Smith, M. L., 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. *Horm. Behav.*, *49*, 215–222. <https://doi.org/10.1016/j.yhbeh.2005.07.004>.
- Gangestad, S. W., Garver-Appar, C. E., Simpson, J. A., & Cousins, A. J. (2007). Changes in women's mate preferences across the ovulatory cycle. *J. Pers. Soc. Psychol.*, *92*, 151.
- Gangestad, S. W., & Haselton, M. G. (2015). Human estrus: Implications for relationship science. *Current Opinion in Psychology*, *1*, 45–51. <https://doi.org/10.1016/j.copsyc.2014.12.007>.
- Gangestad, S. W., Haselton, M. G., Welling, L. L., Gildersleeve, K., Pillsworth, E. G., Burriss, R. P., ... Puts, D. A. (2016). How valid are assessments of conception probability in ovulatory cycle research? Evaluations, recommendations, and theoretical implications. *Evol. Hum. Behav.*, *37*, 85–96. <https://doi.org/10.1016/j.evolhumbehav.2015.09.001>.
- Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behav. Brain Sci.*, *23*, 573–587. <https://doi.org/10.1017/S0140525X0000337X>.
- Gangestad, S. W., & Thornhill, R. (1998). Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proc. R. Soc. B*, *265*, 927–933. <https://doi.org/10.1098/rspb.1998.0380>.

- Gangestad, S. W., Thornhill, R., & Garver, C. E. (2002). Changes in women's sexual interests and their partner's mate-retention tactics across the menstrual cycle: Evidence for shifting conflicts of interest. *Proc. R. Soc. B*, 269, 975–982. <https://doi.org/10.1098/rspb.2001.1952>.
- Gangestad, S. W., Thornhill, R., & Garver-Appar, C. E. (2005). Adaptations to ovulation: Implications for sexual and social behavior. *Curr. Dir. Psychol. Sci.*, 14, 312–316. <https://doi.org/10.1111/j.0963-7214.2005.00388.x>.
- Gao, W., Stalder, T., & Kirschbaum, C. (2015). Quantitative analysis of estradiol and six other steroid hormones in human saliva using a high throughput liquid chromatography–tandem mass spectrometry assay. *Talanta*, 143, 353–358.
- Gildersleeve, K., Haselton, M. G., & Fales, M. R. (2014a). Do women's mate preferences change across the ovulatory cycle? A meta-analytic review. *Psychol. Bull.*, 140, 1205–1259. <https://doi.org/10.1037/a0035438>.
- Gildersleeve, K., Haselton, M. G., & Fales, M. R. (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. <https://doi.org/10.1037/a0037714>.
- Gildersleeve, K. A., Haselton, M. G., Larson, C. M., & Pillsworth, E. G. (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. <https://doi.org/10.1016/j.yhbeh.2011.11.005>.
- Goodman, H. M. (2009). *Basic medical endocrinology* (4th ed.). Amsterdam: Elsevier Academic Press.
- Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science*, 218, 384–387. <https://doi.org/10.1126/science.7123238>.
- Harris, C. R. (2011). Menstrual cycle and facial preferences reconsidered. *Sex Roles*, 64, 669–681. <https://doi.org/10.1007/s11199-010-9772-8>.
- Harris, C. R. (2013). Shifts in masculinity preferences across the menstrual cycle: Still not there. *Sex Roles*, 69, 507–515. <https://doi.org/10.1007/s11199-012-0229-0>.
- Harris, C. R., 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. <https://doi.org/10.1037/a0036478>.
- Haselton, M. G., & Gangestad, S. W. (2006). Conditional expression of women's desires and men's mate guarding across the ovulatory cycle. *Horm. Behav.*, 49, 509–518. <https://doi.org/10.1016/j.yhbeh.2005.10.006>.
- Havlíček, J., Roberts, S. C., & Flegr, J. (2005). Women's preference for dominant male odour: Effects of menstrual cycle and relationship status. *Biol. Lett.*, 1, 256–259. <https://doi.org/10.1098/rsbl.2005.0332>.
- Herrera, A. Y., Nielsen, S. E., & Mather, M. (2016). Stress-induced increases in progesterone and cortisol in naturally cycling women. *Neurobiology of Stress*, 3, 96–104. <https://doi.org/10.1016/j.yynstr.2016.02.006>.
- Hill, A. K., Hunt, J., Welling, L. L., Cárdenas, R. A., Rotella, M. A., Wheatley, J. R., & Puts, D. A. (2013). Quantifying the strength and form of sexual selection on men's traits. *Evol. Hum. Behav.*, 34, 334–341. <https://doi.org/10.1016/j.evolhumbehav.2013.05.004>.
- Hyde, J. S., & Salk, R. H. (2014). Comment: Menstrual cycle fluctuations in women's mate preferences. *Emot. Rev.*, 6, 253–254. <https://doi.org/10.1177/1754073914523049>.
- Jones, B. C. (2014). Comment: Alternatives to Wood et al.'s conclusions. *Emot. Rev.*, 6, 254–256. <https://doi.org/10.1177/1754073914523048>.
- Jones, B. C., Hahn, A. C., Fisher, C. I., Wang, H., Kandrik, M., & DeBruine, L. M. (2018a). General sexual desire, but not desire for uncommitted sexual relationships, tracks changes in women's hormonal status. *Psychoneuroendocrinology*. <https://doi.org/10.1101/155788>.
- Jones, B. C., Hahn, A. C., Fisher, C. I., Wang, H., Kandrik, M., Han, C., & DeBruine, L. M. (2018b). No compelling evidence that preferences for facial masculinity track changes in women's hormonal status. *Psychol. Sci.* <https://doi.org/10.1101/136549>.
- Jones, B. C., Hahn, A. C., Fisher, C. I., Wang, H., Kandrik, M., Lee, A. J., ... DeBruine, L. M. (2018c). Hormonal correlates of pathogen disgust: Testing the compensatory prophylaxis hypothesis. *Evol. Hum. Behav.* <https://doi.org/10.1101/156430>.
- Jones, B. C., Little, A. C., Boothroyd, L., DeBruine, L. M., Feinberg, D. R., Smith, M. L., ... Perrett, D. I. (2005). Commitment to relationships and preferences for femininity and apparent health in faces are strongest on days of the menstrual cycle when progesterone level is high. *Horm. Behav.*, 48, 283–290. <https://doi.org/10.1016/j.yhbeh.2005.03.010>.
- Kandrik, M., Hahn, A. C., Han, C., Wincenciak, J., Fisher, C. I., DeBruine, L. M., & Jones, B. C. (2017). Does the interaction between cortisol and testosterone predict men's facial attractiveness? *Adaptive Human Behavior and Physiology*, 3, 275–281. <https://doi.org/10.1007/s40750-017-0064-1>.
- Kordsmeyer, T., Hunt, J., Puts, D. A., Ostner, J., & Penke, L. (2017). The relative importance of intra- and intersexual selection on human male sexually dimorphic traits. Retrieved from [psyarxiv.com/edw4f](https://arxiv.org/abs/1705.04444).
- Kordsmeyer, T., & Penke, L. (2017). Effects of male testosterone and its interaction with cortisol on self- and observer-rated personality states in a competitive mating context. Retrieved from [psyarxiv.com/wv5dc](https://arxiv.org/abs/1705.04444).
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2015). *Package 'lmerTest': R package version, 2.0-33*.
- Little, A. C., Jones, B. C., & Burriss, R. P. (2007). Preferences for masculinity in male bodies change across the menstrual cycle. *Horm. Behav.*, 51, 633–639. <https://doi.org/10.1016/j.yhbeh.2007.03.006>.
- Lukaszewski, A. W., & Roney, J. R. (2009). Estimated hormones predict women's mate preferences for dominant personality traits. *Personal Individ. Differ.*, 47, 191–196. <https://doi.org/10.1016/j.paid.2009.02.019>.
- Marcinkowska, U. M., Galbarczyk, A., & Jasienska, G. (2018). La donna è mobile? Lack of cyclical shifts in facial symmetry, and facial and body masculinity preferences – A hormone based study. *Psychoneuroendocrinology*, 88, 47–53. <https://doi.org/10.1016/j.psyneuen.2017.11.007>.
- Marlowe, F., Apicella, C., & Reed, D. (2005). Men's preferences for women's profile waist-to-hip ratio in two societies. *Evol. Hum. Behav.*, 26, 458–468. <https://doi.org/10.1016/j.evolhumbehav.2005.07.005>.
- Matsumoto-Oda, A. (1999). Female choice in the opportunistic mating of wild chimpanzees (*Pan troglodytes schweinfurthii*) at Mahale. *Behav. Ecol. Sociobiol.*, 46, 258–266. <https://doi.org/10.1007/s002650050618>.
- Mueller, U., & Mazur, A. (2001). Evidence of unconstrained directional selection for male tallness. *Behav. Ecol. Sociobiol.*, 50, 302–311. <https://doi.org/10.1007/s002650100370>.
- Muñoz-Reyes, J. A., Iglesias-Julios, M., Martín-Elola, C., Losada-Pérez, M., Monedero, I., Pita, M., & Turiegano, E. (2014). Changes in preference for male faces during the menstrual cycle in a Spanish population. *Anales de Psicología/Annals of Psychol.*, 30, 667–675. <https://doi.org/10.6018/analesps.30.2.145221>.
- Natale, V., Albertazzi, P., & Cangini, A. (2003). The effects of menstrual cycle on dreaming. *Biol. Rhythm. Res.*, 34, 295–303. <https://doi.org/10.1076/brhm.34.3.295.18808>.
- Nettle, D. (2002). Height and reproductive success in a cohort of British men. *Hum. Nat.*, 13, 473–491. <https://doi.org/10.1007/s12110-002-1004-7>.
- Pawlowski, B., Dunbar, R. I., & Lipowicz, A. (2000). Evolutionary fitness: Tall men have more reproductive success. *Nature*, 403, 156. <https://doi.org/10.1038/35003107>.
- Pawlowski, B., & Jasienska, G. (2005). Women's preferences for sexual dimorphism in height depend on menstrual cycle phase and expected duration of relationship. *Biol. Psychol.*, 70, 38–43. <https://doi.org/10.1016/j.biopsycho.2005.02.002>.
- Penton-Voak, I. S., & Chen, J. Y. (2004). High salivary testosterone is linked to masculine male facial appearance in humans. *Evol. Hum. Behav.*, 25, 229–241. <https://doi.org/10.1016/j.evolhumbehav.2004.04.003>.
- Penton-Voak, I. S., & Perrett, D. I. (2000). Female preference for male faces changes cyclically: Further evidence. *Evol. Hum. Behav.*, 21, 39–48. [https://doi.org/10.1016/S1090-5138\(99\)00033-1](https://doi.org/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., & Minamisawa, R. (1999). Menstrual cycle alters face preference. *Nature*, 399, 741–742. <https://doi.org/10.1038/21557>.
- Peters, M., Simmons, L. W., & Rhodes, G. (2009). Preferences across the menstrual cycle for masculinity and symmetry in photographs of male faces and bodies. *PLoS One*, 4, e4138. <https://doi.org/10.1371/journal.pone.0004138>.
- Pieta, K. (2008). Female mate preferences among Pan troglodytes schweinfurthii of Kanyawara, Kibale National Park, Uganda. *Int. J. Primatol.*, 29, 845. <https://doi.org/10.1007/s10764-008-9282-5>.
- Pillsworth, E. G., & Haselton, M. G. (2006). Women's sexual strategies: The evolution of long-term bonds and extrapair sex. *Annual Review of Sex Research*, 17, 59–100. <https://doi.org/10.1080/10532528.2006.10559837>.
- Pisanski, K., Hahn, A. C., Fisher, C. I., DeBruine, L. M., Feinberg, D. R., & Jones, B. C. (2014). Changes in salivary estradiol predict changes in women's preferences for vocal masculinity. *Horm. Behav.*, 66, 493–497. <https://doi.org/10.1016/j.yhbeh.2014.07.006>.
- Pound, N., Penton-Voak, I. S., & Surrige, A. K. (2009). Testosterone responses to competition in men are related to facial masculinity. *Proc. R. Soc. B*, 276, 153–159. <https://doi.org/10.1098/rspb.2008.0990>.
- Puts, D. A. (2005). Mating context and menstrual phase affect women's preferences for male voice pitch. *Evol. Hum. Behav.*, 26, 388–397. <https://doi.org/10.1016/j.evolhumbehav.2005.03.001>.
- Puts, D. A. (2006). Cyclic variation in women's preferences for masculine traits. *Hum. Nat.*, 17, 114. <https://doi.org/10.1007/s12110-006-1023-x>.
- Puts, D. A., Bailey, D. H., Cárdenas, R. A., Burriss, R. P., Welling, L. L., Wheatley, J. R., & Dawood, K. (2013). Women's attractiveness changes with estradiol and progesterone across the ovulatory cycle. *Horm. Behav.*, 63, 13–19. <https://doi.org/10.1016/j.yhbeh.2012.11.007>.
- R Core Team (2016). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*. Retrieved from <http://www.R-project.org/>.
- Revelle, W. (2016). *Psych: Procedures for personality and psychological research (Version 1.6.12)*. ([Computer software]. Retrieved from Error! Hyperlink reference not valid).
- Roney, J. R., & Simmons, Z. L. (2008). Women's estradiol predicts preference for facial cues of men's testosterone. *Horm. Behav.*, 53, 14–19. <https://doi.org/10.1016/j.yhbeh.2007.09.008>.
- Roney, J. R., & Simmons, Z. L. (2013). Hormonal predictors of sexual motivation in natural menstrual cycles. *Horm. Behav.*, 63, 636–645. <https://doi.org/10.1016/j.yhbeh.2013.02.013>.
- Roney, J. R., & Simmons, Z. L. (2015). Elevated psychological stress predicts reduced estradiol concentrations in young women. *Adaptive Human Behavior and Physiology*, 1, 30–40. <https://doi.org/10.1007/s40750-014-0004-2>.
- Roney, J. R., & Simmons, Z. L. (2016). Within-cycle fluctuations in progesterone negatively predict changes in both in-pair and extra-pair desire among partnered women. *Horm. Behav.*, 81, 45–52. <https://doi.org/10.1016/j.yhbeh.2016.03.008>.
- Roney, J. R., & Simmons, Z. L. (2017). Ovarian hormone fluctuations predict within-cycle shifts in women's food intake. *Horm. Behav.*, 90, 8–14. <https://doi.org/10.1016/j.yhbeh.2017.01.009>.
- Roney, J. R., Simmons, Z. L., & Gray, P. B. (2011). Changes in estradiol predict within-women shifts in attraction to facial cues of men's testosterone. *Psychoneuroendocrinology*, 36, 742–749. <https://doi.org/10.1016/j.psyneuen.2010.10.010>.
- Schultheiss, O. C., & Stanton, S. J. (2009). Assessment of salivary hormones. In E. Harmon-Jones, & J. S. Beer (Eds.), *Methods in social neuroscience* (pp. 17–44). New York, NY: Guilford Press.
- Scott, I. M., Clark, A. P., Josephson, S. C., Boyette, A. H., Cuthill, I. C., Fried, R. L., ... Honey, P. L. (2014). Human preferences for sexually dimorphic faces may be evolutionarily novel. *Proc. Natl. Acad. Sci.*, 111, 14388–14393. <https://doi.org/10.1073/pnas.1409643111>.
- 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. *Proc. R. Soc. B*, 276, 575–584. <https://doi.org/10.1098/rspb.2008.1177>.

- Sell, A., Hone, L. S., & Pound, N. (2012). The importance of physical strength to human males. *Hum. Nat.*, 23, 30–44. <https://doi.org/10.1007/s12110-012-9131-2>.
- Sell, A., Lukaszewski, A. W., & Townsley, M. (2017). Cues of upper body strength account for most of the variance in men's bodily attractiveness. *Proc. R. Soc. B*, 284, 20171819. <https://doi.org/10.1098/rspb.2017.1819>.
- Stulp, G., & Barrett, L. (2016). Evolutionary perspectives on human height variation. *Biol. Rev.*, 91, 206–234. <https://doi.org/10.1111/brv.12165>.
- 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, Côte d'Ivoire. *Behav. Ecol. Sociobiol.*, 57, 511–524. <https://doi.org/10.1007/s00265-004-0868-4>.
- Suschinsky, K. D., Bossio, J. A., & Chivers, M. L. (2014). Women's genital sexual arousal to oral versus penetrative heterosexual sex varies with menstrual cycle phase at first exposure. *Horm. Behav.*, 65, 319–327. <https://doi.org/10.1016/j.yhbeh.2014.01.006>.
- Thornhill, R., Chapman, J. F., & Gangestad, S. W. (2013). Women's preferences for men's scents associated with testosterone and cortisol levels: Patterns across the ovulatory cycle. *Evol. Hum. Behav.*, 34, 216–221. <https://doi.org/10.1016/j.evolhumbehav.2013.01.003>.
- Thornhill, R., & Gangestad, S. W. (2015). The functional design and phylogeny of women's sexuality. In T. K. Shackelford, & R. D. Hansen (Eds.), *The evolution of sexuality* (pp. 149–184). Switzerland: Springer International Publishing.
- Thornhill, R., & Grammer, K. (1999). The body and face of woman: One ornament that signals quality? *Evol. Hum. Behav.*, 20, 105–120. [https://doi.org/10.1016/S1090-5138\(98\)00044-0](https://doi.org/10.1016/S1090-5138(98)00044-0).
- Veldhuis, J. D., Christiansen, E., Evans, W. S., Kolp, L. A., Rogol, A. D., & Johnson, M. L. (1988). Physiological profiles of episodic progesterone release during the midluteal phase of the human menstrual cycle: Analysis of circadian and ultradian rhythms, discrete pulse properties, and correlations with simultaneous luteinizing hormone release. *The Journal of Clinical Endocrinology & Metabolism*, 66, 414–421. <https://doi.org/10.1210/jcem-66-2-414>.
- Welling, L. L., Jones, B. C., DeBruine, L. M., Conway, C. A., Smith, M. L., Little, A. C., ... Al-Dujaili, E. A. (2007). Raised salivary testosterone in women is associated with increased attraction to masculine faces. *Horm. Behav.*, 52, 156–161. <https://doi.org/10.1016/j.yhbeh.2007.01.010>.
- Wickham, H. (2009). *Ggplot2: Elegant graphics for data analysis*. <https://doi.org/10.1007/978-0-387-98141-3>.
- Wickham, H. (2011). The split-apply-combine strategy for data analysis. *J. Stat. Softw.*, 40, 1–29. <https://doi.org/10.18637/jss.v040.i01>.
- Wood, W. (2014). Author reply: Once again, menstrual cycles and mate preferences. *Emot. Rev.*, 6, 258–260. <https://doi.org/10.1177/1754073914523053>.
- 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. <https://doi.org/10.1037/a0036722>.
- Wood, W., Kressel, L., Joshi, P. D., & Louie, B. (2014). Meta-analysis of menstrual cycle effects on women's mate preferences. *Emot. Rev.*, 6, 229–249. <https://doi.org/10.1177/1754073914523073>.