

Women's preferences for men's beards show no relation to their ovarian cycle phase and sex hormone levels

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ABSTRACT

According to the ovulatory shift hypothesis, women's mate preferences for male morphology indicative of competitive ability, social dominance, and/or underlying health are strongest at the peri-ovulatory phase of the menstrual cycle. However, recent meta-analyses are divided on the robustness of such effects and the validity of the often-used indirect estimates of fertility and ovulation has been called into question in methodological studies. In the current study, we test whether women's preferences for men's beardedness, a cue of male sexual maturity, androgenic development and social dominance, are stronger at the peri-ovulatory phase of the menstrual cycle compared to during the early follicular or the luteal phase. We also tested whether levels of estradiol, progesterone, and the estradiol to progesterone ratio at each phase were associated with facial hair preferences. Fifty-two heterosexual women completed a two-alternative forced choice preference test for clean-shaven and bearded male faces during the follicular, peri-ovulatory (validated by the surge in luteinizing hormone or the drop in estradiol levels) and luteal phases. Participants also provided for one entire menstrual cycle daily saliva samples for subsequent assaying of estradiol and progesterone. Results showed an overall preference for bearded over clean-shaven faces at each phase of the menstrual cycle. However, preferences for facial hair were not significantly different over the phases of menstrual cycle and were not significantly associated with levels of reproductive hormones. We conclude that women's preferences for men's beardedness may not be related to changes in their likelihood of conception.

1. Introduction

Evolution by sexual selection occurs when morphological or behavioral characters result in variation in reproductive success among individuals (Andersson, 1994). Female choice has shaped the evolution of male ornaments and status signals in many species (Kokko et al., 2003), including humans (Dixon, 2009). Some sexually selected traits are physiologically costly to maintain and only sustainable by individuals of high genetic quality (Kokko et al., 2003). Female preferences for males bearing well developed secondary sexual traits can evolve via indirect sexual selection, wherein traits indirectly signal genetic quality (i.e. 'good genes') that enhance offspring fitness (Kokko et al., 2003). Ornaments can also evolve under direct selection, whereby secondary sexual characters are associated with competitive ability that enhance female and offspring fitness via material benefits (Wong and Candolin, 2005).

Women's preferences for exaggerated facial sexual dimorphism in men are argued to reflect sexual selection for both underlying genetic quality (Little et al., 2011) and direct benefits (Puts, 2010). Androgens play organizational roles in shaping masculine facial features, including a prominent jawline, brow ridge and midface in men (Whitehouse et al., 2015; Geniole et al., 2015). Facial masculinity is positively associated with male physical strength (Fink et al., 2007; Windhager et al., 2011), health at adolescence (Rhodes et al., 2003) and adulthood (Thornhill and Gangestad, 2006). However, androgens may impact on immune response (Muehlenbein and Bribiescas, 2005), so that only high quality males can maintain androgen-dependent traits and indirectly signal genetic qualities to mates (Foo et al., 2017). There is some evidence that testosterone is positively correlated with men's immune response and facial attractiveness (Rantala et al., 2012). However, not all studies have found that facial masculinity is associated with health (Boothroyd et al., 2013) and whether facial masculinity reflects

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immunocompetence remains controversial (Scott et al., 2013). Recently, Phalane et al. (2017) reported that facial masculinity and facial muscularity were associated with men's immunity and women's judgments of male health and attractiveness, highlighting a complex relationship between facial masculinity, immunity and male facial attractiveness.

In addition to facial masculinity, androgens promote facial hair growth in men (Randall, 2008). However, the androgenic processes underpinning beard growth differ from those for facial masculinity. Beard hair follicles are activated when testosterone is converted to dihydrotestosterone via 5 alpha reductase enzymes in the dermal papillae of hair follicles (Randall, 2008). Sexual dimorphism in facial hair first appears around 10 years of age (Trotter, 1922) and continues to develop in boys throughout adolescence, becoming fully developed at adulthood (Hamilton, 1958). The extent to which androgens exert their effects on facial hair are due to shared genetic background, so that beard pattern and density is identical in monozygotic twins, variable among dizygotic twins and highly variable among non-twin brothers (Hamilton, 1964). While facial hair appears to bear no cost to survival and is not related to proficiency in hunting or horticulture, beards enhance ratings of male sexual maturity and masculinity (Dixon, 2016). This suggests facial hair plays a role in intra-sexual signaling (Puts, 2010); accordingly, beards consistently enhance ratings of men's social status, dominance and aggressiveness (Dixon and Vasey, 2012; Muscarella and Cunningham, 1996; Neave and Shields, 2008; Saxton et al., 2016; Sherlock et al., 2017). Success in male-male competition can lead to higher status and signal resource holding potential and protection, so that beards likely signal direct rather than indirect benefits to women (Dixon et al., 2017a).

Given their associations with indirect and direct benefits, women may prefer masculine facial features and beards in partners. Although men's mating success is positively associated with facial masculinity (Hill et al., 2013; Rhodes et al., 2005) and beardedness (Barber, 2001), women's preferences for both traits are highly variable (Dixon et al., 2016). Some studies reported a greater preference for full beards among women (Pellegrini, 1973; Dixon et al., 2016; McIntosh et al., 2017), while others found that clean-shaven faces (Dixon and Vasey, 2012; Muscarella and Cunningham, 1996), or stubble (Dixon and Brooks, 2013; Dixon et al., 2013; Neave and Shields, 2008) were the most attractive. Similarly, mixed results are also reported for women's preference for craniofacial masculinity (Rhodes, 2006), and beards enhance ratings of male facial masculinity (Dixon et al., 2017a).

These inconsistencies in women's preferences are thought to reflect a paradoxical role of masculine traits in human mate choice decisions. On the one hand, phenotypic masculinity may reflect biological quality, while on the other hand, masculine traits are also associated with negative personality traits and potentially reduced paternal investment (Dixon, 2016). For instance, masculine men report stronger preferences for and engage more often in short-term than long-term relationships (Boothroyd et al., 2007, 2008; Rhodes et al., 2005), and women accurately judge male sexual infidelity using facial masculinity from photographs (Rhodes et al., 2013). Beardedness is positively associated with men's self-reported masculinity (Wood, 1986) and support of traditional masculine gender roles (Oldmeadow and Dixon, 2016a, 2016b), as well as their serum testosterone (Knussman and Christiansen, 1988), which is negatively associated with paternal investment (Gettler, 2014). Thus, women may face costs when choosing a masculine partner, which may explain why facial masculinity reduces paternal investment ratings (Kruger, 2006; Perrett et al., 1998).

Based on the possible trade-off between heritable biological quality and parental quality, women's preference for masculine traits could be greater in circumstances where these benefits are more likely to be realised (Gangestad and Simpson, 2000). Previous research reported women's preferences for masculine traits were strongest when judging short-term mates (Little et al., 2011), and particularly during the peri-ovulatory phase of the menstrual cycle (Gangestad and Thornhill,

2008). Ovulatory shifts have been found for masculine facial shape (Little et al., 2008; Penton-Voak et al., 1999; Penton-Voak and Perrett, 2000), deeper vocal pitch (Puts, 2005), and greater height (Pawlowski and Jasienska, 2005). However, this interpretation has recently been questioned (Dixon et al., 2017b; Scott et al., 2014), and is not supported by recent genetic evidence (Lee et al., 2014; Zietsch et al., 2015). Additionally, unsuccessful attempts to replicate ovulatory shift effects (Harris, 2011, 2013; Harris et al., 2013; Zietsch et al., 2015) and conflicting results from two separate meta-analyses (Gildersleeve et al., 2014a; Wood et al., 2014) has sparked debate regarding the robustness of ovulatory shift effects and highlighted issues of sampling techniques, statistical analyses, and methodologies (Gildersleeve et al., 2014b; Harris et al., 2014; Wood and Carden, 2014). One recurring methodological issue in tests of the ovulatory shift hypothesis concerns estimating fertility indirectly via questionnaires asking participants to recall the onset, length, and regularity of their menstrual cycles. These techniques are not only inaccurate owing to participant's memory and knowledge of their menstrual cycles (Jukic et al., 2008; Small et al., 2007), and variability in cycle physiology (Jasienska and Jasienski, 2008), but also result in unreliable estimates of current fertility (Blake et al., 2016; Gangestad et al., 2016). Further, studies often used small sample sizes and between-subject designs, which further reduce the likelihood of identifying robust effects (Gangestad et al., 2016). Thus, whether women's preferences for masculinity shift with ovulation remains contentious.

Women's menstrual cycles last, on average, 28 days (Popat et al., 2008) and the peri-ovulatory period is characterised by a surge in luteinizing hormone (LH) and an increase followed by a drop in estradiol levels (Lipson and Ellison, 1996). Studies using within-subject designs in concert with validating the peri-ovulatory phase via the LH surge and the drop in estradiol provide robust and statistically powerful tests of the ovulatory shift hypothesis (Blake et al., 2016; Gangestad et al., 2016). However, only a minority of studies have used these approaches. Peters et al. (2009) reported no significant within-subject differences in masculinity preferences from high and low fertility phases when the peri-ovulatory phase was validated via LH surges. Using within-subject designs, Feinberg et al. (2006) reported stronger preferences for vocal masculinity at the peri-ovulatory phase, particularly among women with low estradiol, while Roney et al. (2011) reported stronger facial masculinity preferences at the peri-ovulatory phase that were positively associated with estradiol. One cross-sectional study measuring women's reproductive hormones and their facial masculinity preferences reported positive associations between preferences and estradiol levels (Roney and Simmons, 2008) while two others did not (Escasa-Dorne et al., 2017; Marcinkowska et al., 2016). Previous studies investigating menstrual cycle shifts in women's preference for beards have found no evidence of a positive association (Dixon and Brooks, 2013; Dixon et al., 2013; Dixon and Rantala, 2016, 2017). However, these studies relied on inaccurate counting methods generated from self-report, using between-subject designs with small sample sizes. Therefore, it is unclear whether these null results are representative or reflect an inability to detect a true effect due to methodological issues.

The current study tests whether the attractiveness of men's beards shifts across the menstrual cycle where participant menstrual cycle phase was verified by daily measurements of sex hormone levels and LH tests. Preferences data were collected from 52 heterosexual women during the follicular, peri-ovulatory and luteal phases of their menstrual cycles. We also collected daily saliva samples for measurements of estradiol and progesterone at each phase of the cycle in order to test the hormonal associations underpinning potential cycle effects. Our sample size of 52 women and within-subject design at three targeted points of the menstrual cycle has 80% power to detect a medium effect size of $d = 0.5$ (Gangestad et al., 2016). Prior studies used natural facial stimuli to test women's preferences for men's facial hair that, although high in ecological validity, likely vary on several dimensions, including craniofacial masculinity, that influence women's preferences for beards

(Dixon et al., 2016, 2017a; Geniole and McCormick, 2015). Thus, we measured women's preferences for beards using controlled composite stimuli made from the same men with full beards and when clean-shaven. Finally, we used a two-alternative forced choice (2AFC) paradigm to measure preferences for beards rather than the Likert scales used in past studies (Dixon and Brooks, 2013; Dixon et al., 2013). 2AFC approaches were also validated in studies of women's facial masculinity preferences, which reported they are more accurate in detecting ideal and actual mate preferences than Likert scales (DeBruine, 2013; Lee and Zietsch, 2015). 2AFC have been used in repeated-measures designs to test whether women's preferences for masculine traits are stronger at the peri-ovulatory phase in many past studies (Little and Jones, 2012; Jones et al., 2017). We predicted that beards would be most attractive at the peri-ovulatory phase of the menstrual cycle and would be positively associated with women's estradiol levels.

2. Methods

2.1. Participants

Seventy-three women (Mean age = 28.08, SD = 4.33) were recruited from Malopolska region in Poland of whom 70 attended all the lab sessions. All participants reported having regular menstrual cycles (not more than ± 5 days of difference between consecutive cycles), no diagnosed health problems, were not pregnant, breast-feeding, or had not taken any form of hormonal contraception for at least 3 months prior to participation. We removed participants who did not complete the rating tasks or identified as homosexual, as sexual orientation influences facial hair preferences (Valentova et al., 2017). This left a final sample of 52 women.

2.2. Facial hair photographs

Thirty-seven men (mean age \pm SD = 27.9 \pm 5.75 years) of European ethnicity were photographed when clean-shaven and with 4–8 weeks of natural beard growth posing with a neutral facial expression. Photographs were taken using a digital camera (8.0 megapixels resolution) with subjects 150 cm from the photographer under controlled lighting (Dixon et al., 2017a). Composite stimuli were constructed using the Webmorph software package (DeBruine and Tiddeman, 2016) by identifying 189 facial landmarks on the images and averaging the shape and color information of the photographs. To create a composite bearded face and a composite clean-shaven face, we randomly selected five males from the total pool of 37. For each of the five males we used their bearded and clean-shaven versions to create a composite with a full beard and when clean-shaven. Thus, the pairs of composites represented the same five individuals when bearded and when clean-shaven (Fig. 1). This process was undertaken 10 times to create the 10 pairs of bearded and clean-shaven composite stimuli.

2.3. Procedure

Participants were given written instructions and were trained by a researcher in how to collect and store saliva samples, and received a set of 2 ml centrifuge tubes with minimum amount of required saliva marked and 10 LH Ovulation Kits with urine cups and written instructions. Participants collected saliva samples each morning from the onset of menstrual bleeding, until the last day of the cycle. Urinary tests were conducted between day 10 and 20 of the cycle or until obtaining a positive result. Participants attended three lab sessions. The first was scheduled before expected ovulation (before the 8th day of the cycle, early follicular phase), the second around ovulation (peri-ovulatory phase) and the third approximately one week after the ovulation (luteal phase).

During each meeting participants completed a two-alternative

forced choice (2AFC) experiment in which they were presented with 10 pairs of faces each containing clean-shaven and bearded composites and were asked to select the face they considered to be more sexually attractive. Stimulus pairs were presented in a randomized order and the position of the bearded and clean-shaven face (left or right-hand side) was randomized. Results obtained using 2AFC accurately predict actual and ideal mate preferences, while Likert scales are less effective (DeBruine, 2013). Moreover, 2AFC have been found to be more appropriate than Likert scales for studying context-dependent shifts in preferences for masculine face shape (Lee and Zietsch, 2015) and have been used in many past studies looking at changes in preferences over the menstrual cycle, some of which yielded significant effects of fertility (Little and Jones, 2012), while others have not (Jones et al., 2017).

2.4. Hormonal measurements

Luteinizing hormone (LH) was measured in urine samples by commercial kits. Levels of 17- β estradiol (E2) and progesterone (P) were measured in saliva samples. Daily levels of hormones throughout the cycle were measured: 15 days centered around ovulation (from late follicular phase to early luteal phase) for E2 and last 14 days of the cycle (luteal phase) for P. Daily values of both E2 and P from samples taken on days of each lab session were available for all women. Saliva samples were taken no earlier than 30 min after eating or drinking. Each sample was frozen in participant's home freezer immediately after collecting. All samples were transported in portable freezers from participants' homes to the laboratory where hormonal assays were conducted. Professional laboratory technicians conducted all measurements using commercially available hormonal assays of DRG International Incl. Elisa plates: SLV3140 for 17- α -hydroxy-progesterone (sensitivity: 2.5 pg/ml, standard range: 10–5000 pg/ml) and SLV4188 for 17- β estradiol (sensitivity: 0.4 pg/ml, standard range: 1–100 pg/ml). All hormonal assays were conducted in duplicates. The quality of hormonal analyses was monitored for each plate separately by including, also in duplicates, samples of known concentrations (i.e. “pools”) with low, medium and high P and E2 (in total 19 pools per plate dedicated for control measurements). For E2, inter-assay CV was 10.01%, and intra-assay was 7.5%. For P, inter-assay CV was 14.1%, and intra-assay was 4.9% (Schultheiss and Stanton, 2009).

2.5. Statistical analyses

We used repeated-measures ANOVAs and Bayesian repeated-measures ANOVAs to test the effect of fertility on bearded face preferences using JASP (Wagenmakers et al., 2017). We then used linear mixed regression models with maximum likelihood estimation to analyze the influence of hormones on bearded face preferences. Linear mixed regression models are appropriate for analyzing nested data with correlated error terms (Twisk, 2006). To prepare the hormone data for analysis, we first computed an E:P ratio term by dividing estradiol by progesterone values. We then computed averaged estradiol, progesterone, and E:P ratio values by averaging values across phases for each participant. All outliers for these hormone variables above ± 3 -SDs from the grand mean were winsorised to ± 3 -SD (a maximum of 3.4% of cases). After calculating means, we log-transformed all hormone variables due to significant positive skew and grand mean centered values for mixed model analysis.

We determined suitable error covariance matrices by comparing fit indices and choosing the matrix with the lowest -2 log likelihood ratio. We accounted for subject variation by including a random intercept in all models. We also inspected models for overly influential data points by examining and removing standardized residuals above ± 3 (a maximum of 1.2% of data points were removed). We further examined random slopes for the all fixed hormone predictors (Twisk, 2006). Our decision rule was to retain random slopes where $p < 0.05$, though no random slope was (all $p \leq 0.393$) and thus no



Fig. 1. Examples of the male stimuli used in this study. Images depict composites of the same five individuals when clean-shaven (left image) and with full beards (right image).

random slopes were included (many models also failed to converge when random slopes were included, thus supporting our decision to not retain the fully maximal model; Barr et al., 2013). We first tested the fixed effects of estradiol, progesterone, and menstrual cycle phase, using the peri-ovulatory phase as the reference category (Model 1). We then tested these same effects, plus all higher order interactions to account for interaction effects between estradiol, progesterone, and menstrual cycle phase (Sollberger and Ehlert, 2016; i.e., a full factorial design; Model 2). In Model 3, we tested the fixed effects of estradiol and progesterone without accounting for the fixed effect of menstrual cycle phase. In Model 4, we tested the fixed effects of estradiol, progesterone, and their interaction. In Model 5, we tested the fixed effects of the E:P ratio and menstrual cycle phase. In Model 6, we tested the same variables as Model 5, plus the higher order interaction. In Model 7, we tested the fixed effect of the E:P ratio without menstrual cycle phase.

3. Results

The proportion of bearded faces selected as most attractive was the dependent variable in repeated-measures ANOVAs where menstrual cycle phase (follicular, peri-ovulatory, luteal) was the within-subjects factor. We first analysed the full sample of participants without splitting analyses to account for whether ovulation was determined via LH surge or E2 drop. Women's facial hair preferences were greater than chance (0.50) in the early follicular ($t_{51} = 5.67$, $p < 0.001$), ovulatory ($t_{51} = 4.65$, $p < 0.001$), and luteal ($t_{51} = 4.81$, $p < 0.001$) phases (Fig. 2A). There was no significant effect of menstrual cycle phase on preferences ($F_{2,102} = 0.07$, $p = 0.935$; $\eta^2 = 0.001$). Bayesian analyses revealed that it is 15 times more likely to reflect a true null result than the hypothesised effect ($BF_M = 15.115$; see Table S1).

In the sample in which peri-ovulation was determined via E2 drop, facial hair preferences were greater than chance (0.50) in the early follicular ($t_{40} = 4.28$, $p < 0.001$), ovulatory ($t_{40} = 3.44$, $p < 0.001$), and luteal ($t_{40} = 3.84$, $p < 0.001$) phases (Fig. 2B). There was no significant effect of menstrual cycle phase on preferences ($F_{2,80} = 0.22$, $p = 0.803$; $\eta^2 = 0.005$). Bayesian analyses revealed that it is 11 times more likely to reflect a true null result than the hypothesised effect ($BF_M = 10.678$; see Table S2).

In the sample in which peri-ovulation was determined via an LH surge, facial hair preferences were greater than chance (0.50) in the early follicular ($t_{31} = 3.07$, $p = 0.004$), ovulatory ($t_{31} = 3.59$, $p < 0.001$), and luteal ($t_{31} = 3.84$, $p = 0.005$) phases (Fig. 2C). There

was no significant effect of menstrual cycle phase on preferences ($F_{2,62} = 0.40$, $p = 0.675$; $\eta^2 = 0.013$). Bayesian analyses revealed that it is 8 times more likely to reflect a true null result than the hypothesised effect ($BF_M = 7.807$; see Table S3).

As shown in Table 1, no main effect of menstrual cycle phase, estradiol, or progesterone was significant ($ps \geq 0.258$). No higher order interactions pertaining to estradiol, progesterone, or menstrual cycle phase were significant ($ps \geq 0.313$). No main effects of the E:P ratio were significant ($ps \geq 0.584$). No cycle phase \times E:P ratio interaction terms were significant ($ps \geq 0.233$). We then conducted sensitivity tests by restricting the sample only to women recording either a mid-cycle drop in estradiol in the same cycle, an LH surge, or those just recording an LH surge. No effect in these restricted analyses differed substantially from those reported here. No main effects for estradiol, menstrual cycle phase, and progesterone were significant ($ps \geq 0.196$). No higher order interactions pertaining to estradiol, progesterone, or menstrual cycle phase were significant ($ps \geq 0.294$). Main effects of the E:P ratio were not significant, $ps \geq 0.123$, and we note that the direction of the effect was negative. No cycle phase \times E:P ratio interaction terms were significant ($ps \geq 0.257$).

4. Discussion

We found that irrespective of their ovarian cycle phase and levels of reproductive hormones, women judged full beards as more attractive than clean-shaven faces. Preferences for facial hair were not stronger at the peri-ovulatory phase of the menstrual cycle nor among women with higher levels of estradiol. This pattern of results supports some previous studies that have not found ovulatory shifts in women's preferences for androgen dependent facial traits (Harris, 2011, 2013; Zietsch et al., 2015; Peters et al., 2009; Marcinkowska et al., 2016), including studies of women's preferences for facial hair (Dixon et al., 2013; Dixon and Brooks, 2013; Dixon and Rantala, 2016, 2017). Our results have implications for hypotheses linking women's fecundability with preferences for men's secondary sexual traits.

According to the ovulatory shift hypothesis, women's sexual receptivity and receptivity to men displaying well developed masculine secondary sexual traits become greater at the peri-ovulatory phase of the menstrual cycle when conception is most likely (Gangestad and Thornhill, 2008; Gangestad and Haselton, 2015). While initial studies provided compelling support for the ovulatory shift hypothesis (Gangestad and Thornhill, 2008), evidence from meta-analyses is

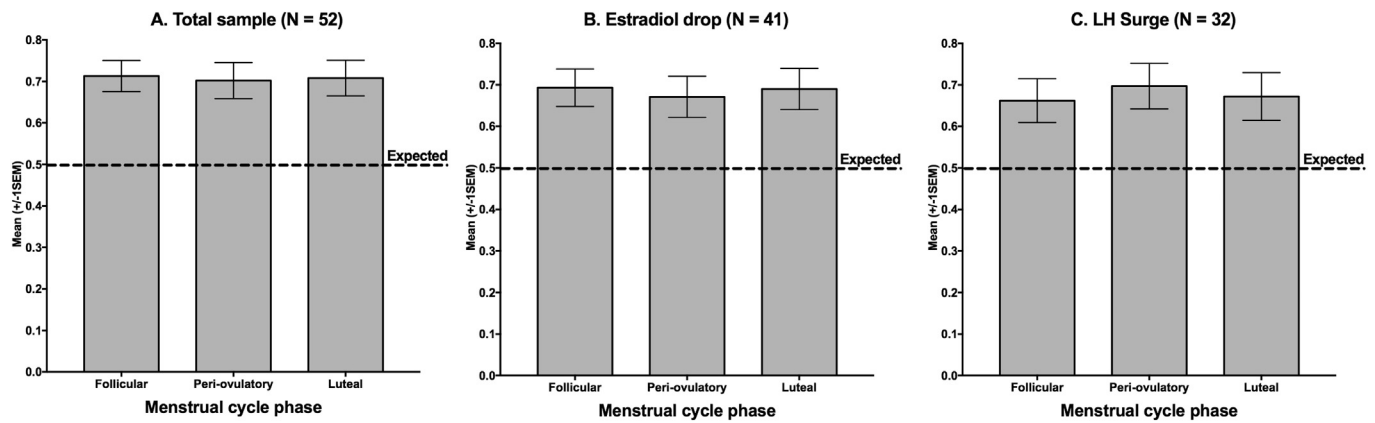


Fig. 2. Mean proportion of bearded faces selected as most attractive (± 1 SEM) among the same women during the follicular, peri-ovulatory and luteal phases of the menstrual cycle. Data are the total sample (A.), participants for whom the peri-ovulatory phase was characterised by the drop in estradiol (B.), and participants for whom the peri-ovulatory phase was characterised by the surge in luteinizing hormone (C.).

divided on whether ovulatory shifts occur and if so by how much (Gildersleeve et al., 2014a; Wood et al., 2014). Many of these studies used imprecise estimates of fertility generated from questionnaires that may have obscured effects of fertility on mate preferences (Blake et al., 2016; Gangestad et al., 2016). Attempts to determine cycle phase and ovulation based on self-reported dates of menstrual bleeding do not provide accurate estimations of events occurring during the cycle. This is due to high inter-individual variation that healthy, regularly menstruating women exhibit in cycle length, in chance of ovulation and sex hormone levels (Jasienska and Jasienski, 2008). This variation is a result of age (Lipson and Ellison, 1992), genetics (Jasienska et al., 2006a), anthropometric characteristics (Ziomkiewicz et al., 2008), prenatal environment (Jasienska et al., 2006b) and adult lifestyle (Jasienska, 2003). The current study determined the peri-ovulatory phase using hormonal measures and found no ovulatory shift in women's preferences for men's facial hair. Similarly, Peters et al. (2009) found no ovulatory shift in women's preferences for facial and bodily masculinity

when using a within-subjects design in which the peri-ovulatory phase was confirmed using LH surges. This suggests that women's preferences for masculine facial features and beardedness may not become stronger at the peri-ovulatory phase compared to other times during the menstrual cycle.

Estradiol has central neuroendocrine effects on female sexual receptivity among the anthropoid primates (Dixon, 2009) and may underpin aspects of women's sexual desires, attractiveness and assertiveness (Roney and Simmons, 2013; Puts et al., 2013; Blake et al., 2017a, 2017b). We also tested whether variation in women's estradiol and progesterone were associated with preferences for facial hair. We found no evidence that women's preferences for beardedness were associated with estradiol or progesterone, either independently or in concert. This finding contrasts with two studies that found elevated levels of estradiol at the peri-ovulatory phase were positively associated with women's preferences for facial masculinity (Ditzen et al., 2017; Roney et al., 2011), but supports another that reported no associations between

Table 1
Results of linear mixed models predicting beard preference from hormone values.

Predictor	Model							
	Model 1		Model 2		Model 3		Model 4	
	B	p	B	p	B	p	B	p
Follicular versus peri-ovulatory phase	0.02	0.474	0.04	0.225				
Luteal versus peri-ovulatory phase	0.03	0.258	0.03	0.385				
Estradiol	0.02	0.578	0.05	0.451	0.02	0.687	0.02	0.689
Progesterone	−0.02	0.510	−0.03	0.505	−0.02	0.535	−0.02	0.536
Estradiol × progesterone			−0.004	0.962			−0.0004	0.995
Estradiol × early follicular phase			−0.06	0.405				
Estradiol × luteal phase			−0.07	0.420				
Progesterone × early follicular phase			0.06	0.313				
Progesterone × luteal phase			−0.02	0.770				
Estradiol × progesterone × early follicular phase			−0.06	0.654				
Estradiol × progesterone × luteal phase			0.13	0.446				
	Model 5		Model 6		Model 7			
	B	p	B	p	B	p		
Follicular versus peri-ovulatory phase	0.02	0.468	0.03	0.309				
Luteal versus peri-ovulatory phase	0.03	0.283	0.03	0.264				
E:P ratio	0.02	0.584	0.03	0.447	0.02	0.613		
E:P ratio × early follicular phase			−0.07	0.233				
E:P ratio × luteal phase			−0.002	0.969				

Note. All models include a random intercept for subject. Random slopes for fixed hormone predictors were tested in separate models; In no case were any random slopes significant or retained ($ps \geq 0.393$).

salivary hormone levels and women's preferences for masculinity (Jones et al., 2017). Behavioral studies quantifying women's motivation to attend to facial stimuli using key tests found that ratios of estradiol relative to progesterone were positively associated with women's attention toward feminized and attractive female faces and masculinized, but not necessarily attractive, male faces (Wang et al., 2014). However, other studies that also used within-subject designs found positive associations between changes in testosterone but not estradiol or progesterone and preferences for facial masculinity (Bobst et al., 2014; Welling et al., 2007). Results of cross-sectional studies are also mixed, so that one study showed positive associations between women's estradiol and preferences for facial masculinity (Roney and Simmons, 2008), while others did not (Marcinkowska et al., 2016; Escasa-Dorne et al., 2017). Taken together, these mixed results suggest that relationships among reproductive hormones and women's mate preferences may not be generalizable.

To date, the current study provides the best test for menstrual cycle shifts in women's preferences for facial hair. Not only do we verify fertility and ovulation hormonally, which avoids the inaccuracies of counting methods based on self-report, but we also use highly controlled composite images as stimuli, removing idiosyncrasies in faces that would introduce additional variance (Dixon et al., 2017a). For example, past research has shown that subtle variation in beard quantity, patterning and distribution influences preferences for facial hair (Dixon and Brooks, 2013; Dixon and Rantala, 2016). Further, in natural stimuli craniofacial masculinity impacts subtly on the attractiveness of facial hair, so that women's preferences for beards were highest for men with intermediate levels of craniofacial masculinity (Dixon et al., 2017a). Experimentally manipulating the degree of masculinity in facial shape also increases women's preferences for beards in male faces with reduced rather than augmented facial masculinity (Dixon et al., 2016; Dixon et al., 2017a). The fact that we continue to find no shifts in preferences provides increased confidence that previous null results (Dixon et al., 2013; Dixon and Brooks, 2013; Dixon and Rantala, 2016, 2017) could reflect a true absence of an effect. However, there are some notable limitations in our study that should be highlighted. Thus, it could be argued that our use of composite stimuli which differed only on one dimension of facial masculinity, in concert with the use of a two-alternative forced choice design (2AFC) design, might artificially induce a facial hair preference when one may not occur using Likert scales and more natural stimuli presented singularly. However, studies have validated that the 2AFC test with composite faces manipulated to vary in singular dimensions of facial masculinity was a better predictor of women's ideal and actual masculinity preferences than rating scales (DeBruine, 2013). These approaches have been used in many past tests of women's preferences for male facial masculinity over the menstrual cycle, some of which reported positive (Little and Jones, 2012) while others reported null (Jones et al., 2017) results. It is also possible that the attractiveness levels of the facial composites influenced women's preferences for beards. Unfortunately, we did not control for facial attractiveness when constructing our composite stimuli and were unable to statistically control for the attractiveness of the composites during our analyses. We note that one of the methodological advantages in using composite facial stimuli in addition to reducing small differences among sets of natural faces, which allows for cleaner tests of the experimentally manipulated trait, is that homogeneity among the composite faces contained in the stimulus set in terms of shape, texture and attractiveness is increased. Nevertheless, further replication using more nuanced facial stimuli that controls for facial attractiveness, along with other methods for measuring preferences would be beneficial to ascertain the robustness of our results.

Although we used a powerful within-subjects repeated-measures design, participants were all recruited at the early follicular phase of the cycle, followed by the peri-ovulatory and the luteal phase. Viewing times toward sexual stimuli were longest among women at the peri-

ovulatory phase only when it was the first session in the cycle in which response times were quantified (Wallen and Rupp, 2010). Thus, we acknowledge that our study design may have induced carry-over effects and our findings should be interpreted cautiously. Further, although the peri-ovulatory phase was verified using the peak in LH, ovulatory shifts in mate preferences may be subtler and occur in concert with rising estradiol as women approach the peri-ovulatory phase, rather than at the peri-ovulatory period itself. We note that a cross-sectional study that used several different estimates of the fertile phase of the menstrual cycle found no relationship between the likelihood of conception and women's preferences for facial masculinity (Marcinkowska et al., 2016). Another possibility for our null finding is that menstrual cycle shifts in mate preferences occur among women currently in relationships and are contingent upon their partner's degree of masculinity (DeBruine et al., 2010; Gildersleeve et al., 2013). A study among romantically involved couples found that a stronger desire for extra-pair mates occurred at the fertile phase than the luteal phase among women with less facially attractive partners (Gangestad et al., 2010). We did not measure the characteristics of women's partners and past studies have reported that women's preferences for facial hair are positively associated with that of their partners (Dixon et al., 2013; Janif et al., 2014; Valentova et al., 2017). Finally, variation in women's willingness to engage in short-term relationships, as measured using the sociosexual inventory (SOI), may impact on mate preferences (Sacco et al., 2012) and might explain variation in preferences for facial hair. Thus, future research assessing whether women's partner's degree of beardedness and individual differences in sociosexuality interact with fertility to determine preferences for facial hair would be valuable.

The extent to which facial hair has been shaped by female choice is complex as, while fundamentally a biological characteristic, beardedness is culturally elaborated upon to varying degrees within and across societies (Robinson, 1976; Barber, 2001). It is possible that beards enhanced male attractiveness due to contemporary cultural trends in facial hair among our Polish participants. A recent cross-cultural study in which the frequencies of men's beardedness and women's preferences for beards were quantified found that beards were more attractive in populations where beardedness was more common (Dixon et al., 2017c). In that study, Polish men were the second most clean-shaven population in the sample, suggesting that current trends in beardedness may not be responsible for the preferences for beards in the current study. Instead, men's decisions to groom their facial hair may occur in response to social and economic factors in ways that are predicted by evolutionary theory. In addition to being positively associated with the frequency of beardedness, women's preferences for facial hair were also stronger in countries with lower average incomes (Dixon et al., 2017c). A longitudinal study spanning 1842–1972 among men from London, revealed that frequencies of moustaches, sideburns, mustache and sideburns in combination, clean-shavenness and full beards each had distinct periods in which they were most popular (Robinson, 1976). Using these data, Barber (2001) demonstrated that when sex-ratios were more male-biased and competition to attract mate was therefore stronger, men were more bearded. Facial hair unambiguously communicates age, sexual maturity (Dixon and Vasey, 2012; Neave and Shields, 2008), masculinity (Dixon and Brooks, 2013; Neave and Shields, 2008), dominance and aggressiveness (Dixon and Vasey, 2012; Dixon et al., 2017a; Geniole and McCormick, 2015; Muscarella and Cunningham, 1996; Neave and Shields, 2008; Sherlock et al., 2017; Saxton et al., 2016), suggesting a role of intra-sexual selection in shaping the evolution of beardedness (Dixon et al., 2017a, 2017c). Whether facial hair is associated with status acquisition and dominance in a manner that enhances male reproductive success remains a challenge for future research (Dixon et al., 2005; Grueter et al., 2015). For the present, our findings suggest that women's preferences for facial hair show no relation to their ovarian cycle phase and sex hormone levels.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.yhbeh.2017.11.006>.

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