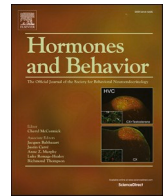




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Are women's sexual preferences for men's facial hair associated with their testosterone during the menstrual cycle?

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ABSTRACT

The ovulatory shift hypothesis proposes that women's mate preferences for androgen-dependent secondary sexual traits in men are most pronounced during the ovulatory phase of the menstrual cycle. Using an appropriately powered within-subjects design, we provide the first test of whether women's sexual preferences for male facial hair, which is reliably associated with male sexual maturity and masculinity, peak during the ovulatory phase among women with higher salivary testosterone. Sixty-five heterosexual women completed the study, which included a two-alternative forced choice preference test wherein participants selected the face they found most sexually attractive from pairs of composite images of the same men when fully bearded and when clean-shaven. The task was completed among the same participants during the follicular, ovulatory (validated by the surge in luteinizing hormone) and luteal phases. Participants also provided saliva samples for subsequent assaying of testosterone. We ran two models, both of which showed strong preferences among women for bearded over clean-shaven composite faces. In our first model, women's preferences for bearded faces were negatively associated with their salivary testosterone levels. In our second model, in which we included women's menstrual cycle phase, this negative association appeared to be driven by preferences among women in the ovulatory and follicular phases. However, the main effect of cycle phase and the interaction between testosterone and cycle phase were not statistically significant. Although further replication is required to confirm our findings, for the present we conclude that women's preferences for men's beardedness may not be related to changes in their salivary testosterone over the menstrual cycle in ways that support the ovulatory shift hypothesis.

1. Introduction

The last 30 years of research in human mate preferences suggests sexual selection has shaped the evolution of sexually dimorphic secondary sexual traits (Dixon, 2022). These studies have applied theories developed primarily in small animals, arachnids, and insects to the study of human morphology, concluding that variation in androgen-dependent traits in men may confer benefits to women that directly and indirectly enhance fecundability and offspring survival (Scott et al., 2013; Gangestad and Haselton, 2015).

One of the most extensively studied secondary sexual traits is male facial masculinity, which refers to a constellation of interrelated craniofacial metrics including jaw size, brow ridge prominence, and facial width, that broadly capture sex differences in shape and size

(Geniole et al., 2015; Little et al., 2011). Masculine facial features require testosterone for their expression, commencing in utero (Whitehouse et al., 2015), followed by androgenic surges in adolescence (Marečková et al., 2011), and reaching full development by adulthood (Roosenboom et al., 2018). While some studies reported facial masculinity was positively associated with circulating testosterone in men (Penton-Voak and Chen, 2004), more recent reports did not (Bird et al., 2016; Hodges-Simeon et al., 2016; Lefevre et al., 2013; Kordsmeyer et al., 2019). Likewise, some research has reported positive associations between male health, immune response, and facial masculinity (Foo et al., 2020; Rhodes et al., 2003; Rantala et al., 2012; Thornhill and Gangestad, 2006). However, others have not reported strong associations between facial masculinity and health (Boothroyd et al., 2013) or genetic immunity (Zaidi et al., 2019). Instead, links between facial

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masculinity and immune response may be influenced by facial adiposity (Rantala et al., 2013) and in combination with facial muscularity (Phalane et al., 2017). Thus, while it remains plausible that facial masculinity broadcasts information relating to underlying health that influences women's partner preferences, such associations require further empirical confirmation.

While the role of men's facial masculinity in communicating genetic quality to potential mates remains debatable, the evidence it reflects underlying social dominance and physical formidability appears more consistent. Thus, facial masculinity in men shares strong associations with underlying formidability, physical strength, and provisioning capabilities that potentially confer direct benefits and augment maternal fitness (Scott et al., 2013; Puts, 2010, 2016). Large-scale studies reported strong positive allometric associations between male facial masculinity and height (Zaidi et al., 2019), upper body strength (Caton and Dixon, 2022; Fink et al., 2007; Windhager et al., 2011; Butovskaya et al., 2022), and fighting ability (Caton et al., 2022a, 2022b, 2022c, 2004). Additionally, men with masculine faces may be more behaviourally dominant and assertive than men with less masculine faces (Geniole et al., 2015; Sell et al., 2012), which could result in resource acquisition via social coercion and establishing more beneficial positions within social hierarchies (Maner, 2017). These attributes may also be directly beneficial to mothers raising their offspring through the acquisition of tangible economic resources and protection (Scott et al., 2013; Puts, 2010, 2016).

In a similar vein to craniofacial masculinity, facial hair is highly sexually dimorphic (Trotter, 1922), and androgen-dependent (Randall, 2008), first appearing in early adolescence and is fully developed by young adulthood (Dixon and Rantala, 2016). In contrast to facial masculinity, which may rely primarily on testosterone for its development, facial hair grows following the conversion of testosterone to dihydrotestosterone via 5-alpha reductase II activity (Farthing et al., 1982; Imperato-McGinley and Zhu, 2002; Randall, 2008). Like facial masculinity, beards consistently enhance judgments of male age, masculinity, social status, dominance and aggressiveness (Dixon and Vasey, 2012; Dixon and Brooks, 2013; Geniole and McCormick, 2015; Gray et al., 2020; Muscarella and Cunningham, 1996; Neave and Shields, 2008), potentially by enhancing the size of the jaw (Dixon et al., 2017; Sherlock et al., 2016), masking less masculine facial traits (Mefodeva et al., 2020) and augmenting aggressive facial expressions (Craig et al., 2019; Dixon et al., 2021, 2022). Compared to clean-shaven men, bearded men report higher masculinity (Wood, 1986), greater dominance, assertiveness, and self-perceived facial masculinity (Mefodeva et al., 2020; Jach and Morón, 2020; Jach et al., 2023; Morón et al., 2024), stronger endorsement of traditionally masculine gender roles (Oldmeadow and Dixon, 2016) and have higher serum testosterone (Knussman and Christiansen, 1988). However, unlike facial masculinity there is no evidence that beardedness is associated with physical formidability (Dixon et al., 2018c), suggesting facial hair operates primarily as a badge of masculinity, social status, and biological maturity (Dixon et al., 2005; Grueter et al., 2015).

Although mating success may be higher among men with more masculine faces than men with less masculine faces (Hill et al., 2013; Kordsmeyer et al., 2018) and those with more facial hair (Štěrbová et al., 2019), women's explicit mate preferences for male facial dimorphism varies considerably across studies. Women's preferences for male facial masculinity vary within and between cultures (Borras-Guevara et al., 2017; DeBruine et al., 2010; Dixon et al., 2017b; Scott et al., 2014; Marcinkowska et al., 2019b). Likewise, women's mate preferences for male facial hair varies cross-culturally (Dixon et al., 2017, 2019b; Valentova et al., 2017), with some studies reporting beards augment male facial attractiveness (McIntosh et al., 2017; Stower et al., 2020), while others revealed clean-shaven faces were rated most attractive (Feinman and Gill, 1977; Wogalter and Hosie, 1991; Muscarella and Cunningham, 1996; Dixon and Vasey, 2012; Dixon et al., 2019a). Experiments wherein the facial stimulus included intermediate levels of

facial hair revealed that light distributions of facial hair (i.e. 'stubble') were most attractive (Dixon and Brooks, 2013; Dixon et al., 2013; Janif et al., 2014; Neave and Shields, 2008), possibly because it masks less attractive facial features like enlarged or reduced jaw size (Clarkson et al., 2020; Dixon et al., 2016, 2017b).

Some of this variation may also be attributable to negative social characteristics associated with physically masculine men. Thus, facially masculine men report more interest in short-term sexual partners than long-term relationships, more actual short-term than long-term sexual relationships, and higher rates of sexual infidelity than less masculine men (Arnocky et al., 2018; Polo et al., 2019; Rhodes et al., 2005, 2013). Furthermore, heterosexual women may accurately detect rates of male infidelity from their facial masculinity (Boothroyd et al., 2007, 2008; Rhodes et al., 2005, 2013) and facial masculinity may not be associated with women's perceptions of men's fathering abilities (Bartolome and Lee, 2023). As human mating systems reflect mutuality in selection of sexual partners (Dixon, 2009; Dixon, 2012), the higher number of short-term partners more masculine men report compared to less masculine men necessarily requires women to act upon preferences for masculine mates (Buss, 2003). As a result, trade-offs between possible direct and indirect benefits for offspring fitness may explain the maintenance of variation in women's mate preferences for facially masculine men, whereby less masculine partners are selected as more amenable and paternally investing within long-term than short-term relationships (Dixon et al., 2016; Kruger, 2006).

Over the last 30 years, notably after Gangestad and Simpson (2000) proposed mating strategies theory, a large literature has tested the social, ecological, and biological factors under which the costs of selecting more masculine and less paternally investing mates are potentially attenuated. Accordingly, the ovulatory shift hypothesis proposes that women's mate preferences for androgen dependent secondary sexual traits in men are strongest during the ovulatory phase of the menstrual cycle when the likelihood of conception is highest (Gangestad and Thornhill, 2008). Initial evidence revealed that women's preferences for masculine faces were indeed higher when conception was more likely (Gangestad and Thornhill, 2008). However, subsequent studies reported null results regarding fecundability and women's preferences for male facial masculinity (Harris, 2011, 2013; Zietsch et al., 2015) and facial hair (Dixon and Brooks, 2013; Dixon et al., 2013; Dixon and Rantala, 2016, 2017). Two meta-analyses also reported somewhat conflicting results. Wood et al. (2014) inferred from their analyses that women's potential fertility did not result in stronger preferences for facial masculinity. It is worth noting that shifts in the effect size (g) for women's preferences for masculinity in this meta-analysis was 0.08 and was based on a composite mate preference score including facial, bodily, and vocal masculinity. When ovulatory shifts in facial masculinity preferences were quantified, the effect size was over twice as large as the composite measure of masculinity ($g = 0.19$). When Gildersleeve et al. (2014) meta-analysed these effects, they reported that mate preferences for facial masculinity were significantly stronger at the more fertile phase of the menstrual cycle ($g = 0.13$), particularly when judging for short-term relationships ($g = 0.19$). Thus, taken together early studies may reflect small positive effects of facial masculinity on women's mate preferences when conception is more likely.

These meta-analyses also raised several methodological concerns among the studies they included. Notably, small sample sizes, the use of indirect measures of fertility employing questionnaires wherein participants recalled the details of their menstrual cycles, and variation across studies in characterising the fertile phase of the cycle (Harris et al., 2014; Wood and Carden, 2014). Self-reported menstrual cycles generate unreliable estimates of women's fecundability (Small et al., 2007), partly due to the differences in menstrual cycle length that occur within women without health complications who experience regular menstrual cycles (Jukic et al., 2008), and hormone levels (Jasienska and Jasienski, 2008; Marcinkowska, 2020). A complex combination of biosocial factors underpins this natural variation among women, beginning in utero

(Jasienska et al., 2006b), unfolding due to genetic differences during ontogeny (Jasienska et al., 2006a), variation in the distribution of body fat (Ziomkiewicz et al., 2008), lifestyle factors in adulthood (Jasienska, 2003), and natural changes in hormones with ageing (Lipson and Ellison, 1992). These individual differences are not accounted for when undertaking indirect measures of fecundability using questionnaires and statistical simulations highlighted that between-subject designs, indirect counting methods and low statistical power have contributed to mixed findings in this literature (Gangestad et al., 2016). Furthermore, indirect counting methods via surveys alone do not predict hormonally validated ovulatory periods with >30 % accuracy, whereas protocol employing counting methods in concert with LH tests predict ovulatory periods with >95 % accuracy (Blake et al., 2016). These methodological studies highlight the necessity to characterise the ovulatory phase and individual fluctuations in fecundability using hormonally validated methodologies.

Indeed, recent research where the ovulatory phase was validated hormonally did not report significant changes in women's preferences for male facial masculinity when employing between-participant (Marcinkowska et al., 2016; Escasa-Dorne et al., 2017) or within-participants designs (Bobst et al., 2014; Dixon et al., 2018b; Jones et al., 2018; Marcinkowska et al., 2018; Welling et al., 2007). Similarly, studies on women's preferences for male beardedness revealed no changes before and after the ovulatory phase when conception was validated using lutenizing hormone tests and when accounting for individual differences in salivary estradiol (E2) and progesterone (P) (Dixon et al., 2018a, 2018b). These studies suggest that individual variation in E2 and P levels over the menstrual cycle may not underpin women's preferences for androgen-dependent facial features in men (Jones et al., 2019).

Rather than changes in E2 and P, variation in women's testosterone (T) over the menstrual cycle may underpin shifts in sexual preferences for androgen-dependent facial traits in men. While T may not be positively associated with all aspects of women's sexual desires over the menstrual cycle (Jones et al., 2018; Roney and Simmons, 2013), some evidence suggests that T is positively associated with women's sexual drive (Riley, 2000), including longitudinal evidence reporting positive associations between T and LH with sexual drive (Salonia et al., 2008), and women reporting higher sexual drive had stronger preferences for male facial masculinity than women with lower sexual drive (Welling et al., 2008). Studies also reported positive associations between women's daily changes in salivary T and their preferences for masculine male faces (Welling et al., 2007), and in one study elevated preferences for facial masculinity at the early follicular stage of the menstrual cycle was positively correlated with women's salivary T (Bobst et al., 2014). While motivational salience towards attractive male faces, but not masculine male faces, was also higher among women with higher T (Wang et al., 2014), several studies have not reported that women's preferences for masculine male faces were positively associated with their salivary T (Ditzen et al., 2017; Marcinkowska et al., 2019a; Roney and Simmons, 2008; Roney et al., 2011). To our knowledge, research to date has not tested whether variation in women's salivary T over the menstrual cycle is associated with stronger sexual preferences for men's beardedness. To this end, this study tested whether individual differences in salivary T across the menstrual cycle positively predicted women's preferences for male beardedness. To this end, we tested the hypothesis that women's mate preferences for male beardedness are strongest during the ovulatory phase of the menstrual cycle, particularly among women with higher salivary T, compared to when measured at the follicular or luteal phases of the menstrual cycle.

2. Methods

2.1. Participants

Sixty-five women (Mean age = 27.87, SD = 4.30) were recruited

from the Malopolska region in Poland. 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. All participants completed the face preference task and all self-identified as heterosexual.

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 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., 2013, 2017a). Composite stimuli were constructed using the Webmorph software package (DeBruine, 2018) 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 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. We repeated this process to create 10 composite identities, resulting in 20 images. Thus, the pairs of composites represented the same five individuals when bearded and when clean-shaven (Fig. 1).

2.3. Procedure

Participants were given written instructions and were trained by a researcher in how to collect and store saliva samples. They each received a set of 2 ml centrifuge tubes with minimum amount of required saliva marked and 10 LH Ovulation Kits with urine cups with written instructions. Participants collected saliva samples each morning from the onset of menstrual bleeding, until the last day of their 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 (i.e., before the 8th day of the cycle, early follicular phase), the second around ovulation (ovulatory phase) and the third approximately one week after the ovulation (luteal phase). Testosterone (T) was measured from saliva samples collected daily. Participants were instructed to collect saliva samples immediately after waking up and at least 30 min after eating, drinking or smoking, and to freeze a sample immediately upon collection. During each meeting participants completed a two-alternative forced choice

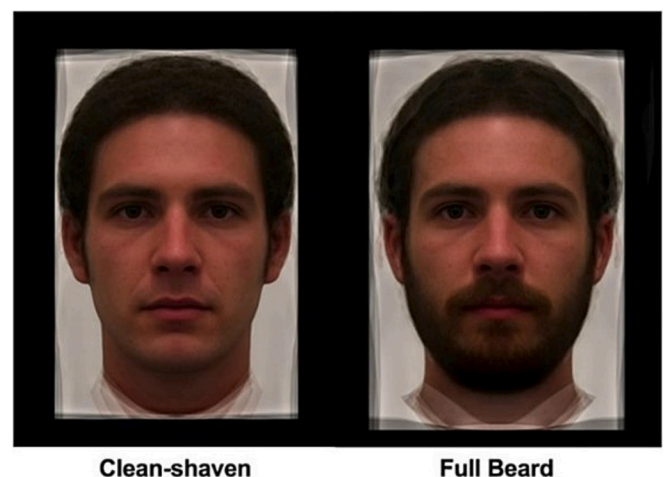


Fig. 1. An example of the stimuli employed in the current study. The faces reflect composites of the same five men photographed when clean-shaven (left image) and again with full beards (right image).

(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.

We validated the high fecundability phase using an LH test (Blake et al., 2016) and measured women's preferences for male facial hair and salivary T among 65 heterosexual women at three points of their menstrual cycles (follicular, ovulatory, and luteal). Gangestad et al. (2016) simulated over 58,000 menstrual cycles using published data on the lengths of ovulatory and luteal phases, which revealed that within-subjects study designs with 48 participants where ovulatory phases was determined using LH tests had 80 % statistical power to uncover medium effect sizes of $d = 0.5$, should they exist. Thus, our sample size of 65 women and our within-subjects design with the ovulatory phase defined via LH tests is appropriately powered (Gangestad et al., 2016). We also opted to use composite stimuli representing the same individuals photographed when clean-shaven and again with full beards, as previous research has reported that natural variation in male facial masculinity influences the strength of women's preferences for beardness (Dixon et al., 2016, 2017a; Geniole and McCormick, 2015).

2.4. Hormonal measurements

Hormonal measurements were conducted using commercially available hormonal assays from DRG International Incl. Elisa plates SLV3013 for testosterone (sensitivity: 1.9 pg/ml, standard range: 10–5000 pg/ml). To obtain the highest standard of the measurements, all hormonal assay samples were analysed in duplicates and the quality of hormonal measurements was controlled for each plate separately by including (in duplicates) samples of known concentrations (“pools”) of T (in total these control measurements consisted of, on average 18 pools per plate). Inter- and intraassay coefficients of variability (CVs) were computed and were at acceptable levels: the interassay CV was 15.32 %, and the intra-assay was 6.39 %. LH was measured in urine samples using commercially available LH tests that required participants to provide 30 mLU/ml of urine to ascertain whether an LH surge had occurred.

2.5. Statistical analyses

Stern and Casto (2024) recently reported that salivary testosterone significantly varied across cycle phases, such that higher levels of testosterone were reported mid-cycle during the fertile window compared to the luteal phase. To assess this in our sample, we conducted a linear mixed effects model, with subject-mean centered testosterone levels as the outcome variable, and cycle phase (with the luteal phase as the reference level) as a predictor and a random intercept of Participant ID. Outliers on testosterone were winsorised to 3SDs. These analyses were conducted using R statistical software (R Core Team, 2013).

To test causative effects of the menstrual cycle phase on women's preferences for male facial hair, we ran repeated-measures ANOVAs wherein the proportion of bearded faces chosen as most attractive was entered as the dependent variable and menstrual cycle phase (follicular, peri-ovulatory, luteal) was the within-subjects repeated-measures factor. In addition to traditional frequentist repeated-measures ANOVAs, we also conducted Bayesian repeated-measures ANOVAs using JASP (Van den Bergh et al., 2023; Wagenmakers et al., 2018). Bayesian analyses allow researchers to determine the strength of support for hypothesised and null effects using Bayes Factors (Van den Bergh et al., 2023; Wagenmakers et al., 2018). Finally, to determine whether women's preferences for facial hair were significantly stronger than that which would be expected by chance (i.e., 0.50) compared to clean-shaven faces, we used separate one sample within-subjects *t*-tests for each phase of the menstrual cycle, Cohen's *d* effect sizes are reported for the *t*-tests.

Finally, to analyze the association between hormones and

preferences for male facial hair, we used binomial mixed effects models with maximum likelihood estimation to analyze the association between circulating testosterone levels and women's preferences for beardness. Participant choice of face, either clean-shaven or bearded, was the outcome variable, coded as 0 and 1 respectively. In Model 1, we included testosterone level as the predictor, which was z-standardised, and outliers were winsorised to 3SDs. In Model 2, we added cycle phase (and its interaction with testosterone) to the model with the ovulatory phase as the reference category. Random intercepts were specified for grouping factors of Participant ID and Stimulus ID, following best practice (DeBruine and Barr, 2021). Random slopes were also specified maximally (Barr et al., 2013; Barr, 2013). The mixed effects models were conducted in R statistical software (R Core Team, 2013) using the lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2015) packages. Full model results, including the analysis code and estimated random effects, are provided in the supplementary materials (ESM1).

3. Results

3.1. Variation in testosterone levels across the menstrual cycle

Summary statistics on testosterone levels among our participants across the follicular, ovulatory, and luteal phases of the menstrual cycles are included in Table 1. Consistent with Stern and Casto (2024) we found that testosterone levels were higher during the ovulation phase compared to the luteal phase (Estimate = 2.86, Std. Error = 1.37, $t(182) = 2.09$, $p = 0.038$). There was no significant difference between the luteal and follicular phases (Estimate = 0.49, Std. Error = 1.37, $t(182) = 0.36$, $p = 0.722$). Results are shown in Fig. 2. Overall, the marginal $R^2 = 0.03$; for full model results, see the supplementary materials (ESM1).

3.2. The effect of menstrual cycle phase on preferences for bearded male faces

Repeated-measures ANOVA revealed no significant effect of menstrual cycle phase on preferences ($F_{2,108} = 0.88$, $p = 0.416$; $\eta^2 = 0.016$). Bayesian repeated-measures ANOVA analyses revealed that it is almost 18 times more likely to reflect a true null result than the hypothesised effect ($BF_{01} = 17.97$), while evidence in support of the alternative hypothesis was weak ($BF_{10} = 0.06$). Women's facial hair preferences were greater than chance (0.50) in the early follicular ($t_{64} = 5.93$, $p < 0.001$, $d = 0.74$), ovulatory ($t_{63} = 5.10$, $p < 0.001$, $d = 0.64$), and luteal ($t_{62} = 5.31$, $p < 0.001$; $d = 0.67$) phases (Fig. 3A-C).

3.3. The association between testosterone and preferences for bearded faces

We then analysed the association between testosterone and women's sexual preferences for male beardness using binomial mixed effects models that included testosterone level as the predictor (Model 1) and when adding menstrual cycle phase and its interaction with testosterone with the ovulatory phase as the reference category (Model 2). Across both models a significant intercept was found, indicating that overall women reported a greater preference for the bearded faces (Table 2). In Model 1, there was a negative, trending association between

Table 1

Testosterone levels measured in pg/ml among participants during the follicular, ovulatory, and luteal phases of their menstrual cycles.

Menstrual cycle phase	N	Mean	Std. Deviation	Minimum	Maximum
Follicular	64	27.816	12.542	5.333	69.965
Ovulation	64	30.450	14.369	2.461	71.727
Luteal	57	28.183	14.297	1.254	84.099
Average	65	28.304	10.509	6.051	55.634

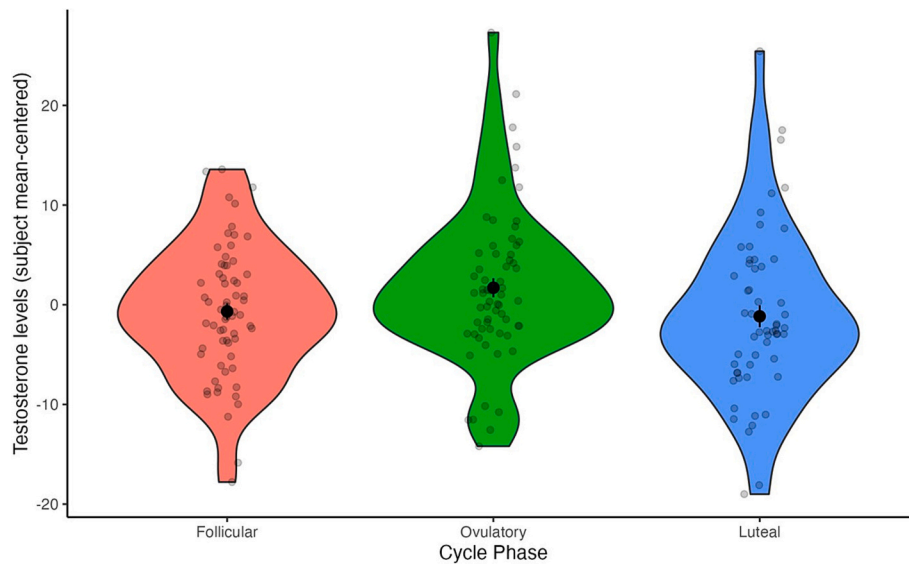


Fig. 2. Violin plot of subject mean-centred testosterone levels measured in pg/ml for each phase of the menstrual cycle.

testosterone and preference for beardedness, such that higher levels of testosterone were associated with a decreased preference for beardedness. However, this association was shy of significance ($p = 0.056$; Table 2). In Model 2, once cycle phase was included in the model, there was a statistically significant negative association between testosterone and women's preferences for male beardedness ($p = 0.036$; Table 2). Inspection of the data suggests that any negative association between testosterone levels and beard preferences was driven by selections made in the ovulatory and follicular phases (Fig. 4), though the interaction between testosterone and cycle phase was not statistically significant (Table 2).

4. Discussion

The current study reports the first test of whether women's sexual preferences for male beardedness are positively associated with fluctuations in salivary testosterone (T) over the menstrual cycle. Because T may be positively associated with women's sex drive and preferences for facial masculinity as women approach the ovulatory phase of the menstrual cycle, we hypothesised that preferences for facial hair would be strongest among women with higher T at the peri-ovulatory phase of the menstrual cycle than the follicular and luteal phases (Bobst et al., 2014). However, we found negative associations between women's preferences for male beardedness that were most pronounced, albeit not statistically significantly, among women when completing preference tests at the ovulatory and follicular phases of the cycle than the luteal phase. These findings have implications for understanding the role of hormonal variation across the menstrual cycle as predictors of women's mate preferences.

The ovulatory shift hypothesis proposes that women's sexual preferences for androgen-dependent masculine secondary sexual traits are strongest around the ovulatory period of the menstrual cycle (i.e., Gangestad and Thornhill, 2008). Although initial studies provided compelling support for this hypothesis (Gildersleeve et al., 2014), recent research employing hormonal measures to characterise fecundability have not reported that women's sexual preferences for male facial masculinity were stronger when potential fecundability was higher (Jones et al., 2019). In the current study, we found no support for the hypothesis that women's sexual preferences for male beardedness peaked at the ovulatory phase of the menstrual cycle. This result supports past research using appropriately powered sample sizes and hormonal validation of current fecundability that also reported that women's sexual preferences for male facial hair are not stronger at the

ovulatory phase of the menstrual cycle (Dixon et al., 2018a, 2018b). Furthermore, we note that our Bayesian analyses revealed that it is almost 18 times more likely that our data reflects a true null result, such that our findings that women's preferences for male facial hair do not show significant variation over the menstrual cycle may be accurate.

In a similar vein, previous studies measuring individual differences in estradiol and progesterone have not consistently reported women's preferences to be stronger at the more fertile phase of the menstrual cycle for either facial masculinity (Bobst et al., 2014; Dixon et al., 2018b; Jones et al., 2018; Marcinkowska et al., 2018; Welling et al., 2007) or beardedness (Dixon et al., 2018a, 2018b). Furthermore, variation in salivary T over the menstrual cycle is not consistently associated with women's preferences for masculine facial traits. In some cases, women's salivary T was positively associated with their preferences for male facial masculinity (Welling et al., 2007; Bobst et al., 2014), while in others it was not (Ditzen et al., 2017; Marcinkowska et al., 2019a; Roney and Simmons, 2008; Roney et al., 2011). As in Stern and Casto (2024), we found that testosterone levels were higher among participants during the peri-ovulatory phase than the luteal phase of the menstrual cycle. However, we found that T negatively predicted women's preferences for male beardedness and that this association may be driven by changes at the ovulatory and follicular phases of the cycle. Thus, our findings do not support models proposing that women's preferences for masculine partners increase alongside ovulatory shifts in hormone levels that are potentially associated with women's sexual proceptivity.

While our findings do not support trade-off models of human mating psychology proposing women bypass the potential costs of lower paternal investment to secure indirect genetic benefits from masculine partners, the biology of facial hair differs in important ways to craniofacial masculinity that may explain our results. Thus, both craniofacial morphology and facial hair are secondary sexual characteristics that are reliant for their development and full expression on androgens (Randall, 2008). However, the underlying androgenic pathways that govern their expression differ in ways that suggest differences in the role they play as sexual signals (Dixon and Rantala, 2016). Craniofacial masculinity develops under the actions of androgens beginning in utero (Whitehouse et al., 2015), becoming progressively more pronounced during late childhood and adolescence (Marečková et al., 2011), and is developed fully by adulthood (Penton-Voak and Chen, 2004). For facial hair to develop, testosterone must be converted to dihydrotestosterone within hair follicles via 5 alpha reductase II activity (Farthing et al., 1982; Randall, 2008). Although debate surrounds whether facial masculinity

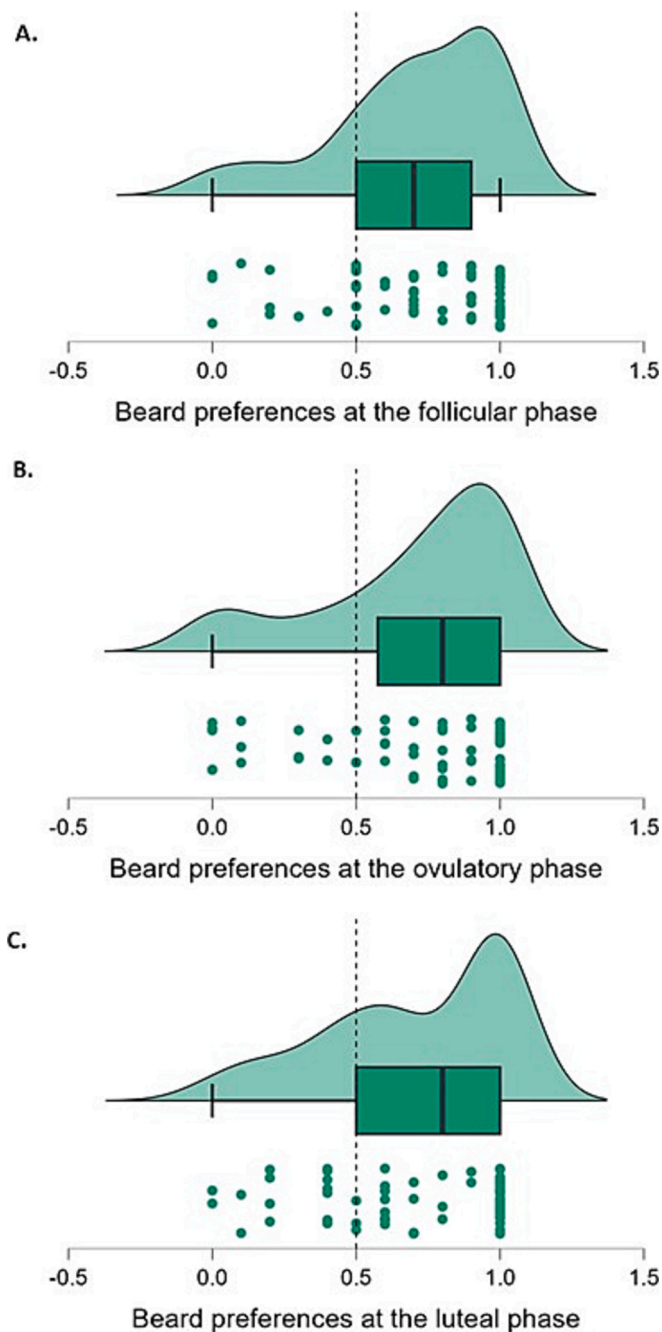


Fig. 3. Raincloud plots of the sexual preferences among women for men's beardedness at the follicular (A), ovulatory (B), and luteal (C) phases of the menstrual cycle. Data are mean distributions, medians, and individual proportions of bearded faces selected by participants.

Table 2

The fixed effects estimates from the binomial mixed effects models predicting preference for beardedness from testosterone levels.

	Model 1 (Marginal $R^2 = 0.01$)			Model 2 (Marginal $R^2 = 0.01$)		
	Estimate (Std. Error)	z-value	p-value	Estimate (Std. Error)	z-value	p-value
Intercept	1.60 (0.32)	4.97	< 0.001	1.58 (0.34)	4.60	< 0.001
T	-0.34 (0.18)	-1.91	0.056	-0.42 (0.20)	-2.10	0.036
F vs. P				0.02 (0.17)	0.10	0.919
L vs. P				0.06 (0.20)	0.31	0.754
T * F				-0.00 (0.24)	-0.02	0.984
T * L				0.22 (0.27)	0.84	0.403

reliably reflects underlying health and immunity (Dixon, 2022; Scott et al., 2013), recent evidence suggests it is positively associated with physical formidability (Caton and Dixon, 2022; Windhager et al., 2011), and social dominance (Mefodeva et al., 2020). In contrast, there is currently no evidence that facial hair is associated with underlying health, disease resistance (Dixon, 2022) or physical formidability (Dixon et al., 2018c; Kowal et al., 2021). Our findings that women's preferences for beardedness do not vary with hormonal changes over the menstrual cycle in a manner consistent with the ovulatory shift hypothesis may reflect that beards communicate aspects of mate value related to long-term paternal investment rather than genetic benefits that indirectly enhance maternal and offspring survival (Dixon et al., 2019a).

Women's mate preferences for sexually dimorphic traits in male faces vary cross-culturally (DeBruine et al., 2010; Marcinkowska et al., 2019b; Scott et al., 2014). In the current study, our sample was restricted to Polish women who judged beardedness to be more sexually attractive than clean-shaven faces. However, prior evidence that beards augment male facial attractiveness is mixed (Dixon, 2022), potentially because despite being biologically determined its presentation varies within and between populations due to prevailing cultural trends. Cross-cultural research suggests facial hair is judged as more attractive by heterosexual women living in lower socioeconomic urban settings, where more men were more bearded, and sex ratios were more male-biased (Dixon et al., 2017b, 2019b). Beards are also more common in countries with lower health, higher pathogens, and greater income disparity (Dixon and Lee, 2020; Pazhoohi and Kingstone, 2020). Although experimental evidence may not support the hypothesis that beards are more attractive to women when pathogens are primed or among women with higher pathogen disgust (Clarkson et al., 2020; Garza et al., 2024; McIntosh et al., 2017), facial hair consistently enhances ratings of intra-sexually relevant attributes in men including age, maturity, masculinity, social status, and dominance that may augment offspring fitness via tangible direct benefits (Dixon, 2022). For example, marriage announcements among high status men living in London from 1842 to 1972 revealed men were more bearded when sex ratios were male biased and the prevailing mating market reflected higher intra-sexual competition (Barber, 2001; Robinson, 1976). Several studies also report that beards augment ratings of attractiveness for long-term relationships and parenting abilities (Clarkson et al., 2020; Dixon and Brooks, 2013; Garza et al., 2023; Neave and Shields, 2008; Stower et al., 2020), notably among mothers with young infants (Dixon et al., 2019a). Finally, heterosexual women whose long-term partners had full beards reported greater reproductive success than women with clean-shaven long-term partners (Štěrbová et al., 2019). Future research exploring the mechanisms through which beardedness may operate in long-term mate choice may be more revealing than trade-off models of mate selection wherein androgen-dependent secondary sexual masculine traits may be preferred for short-term relationships characterised by low paternal investment.

Studies of face perceptions necessarily require researchers to make decisions regarding methodological approaches, such that the stimuli and the experimental design that are employed may have bearing on the generalizability of the results. We used composite faces created by

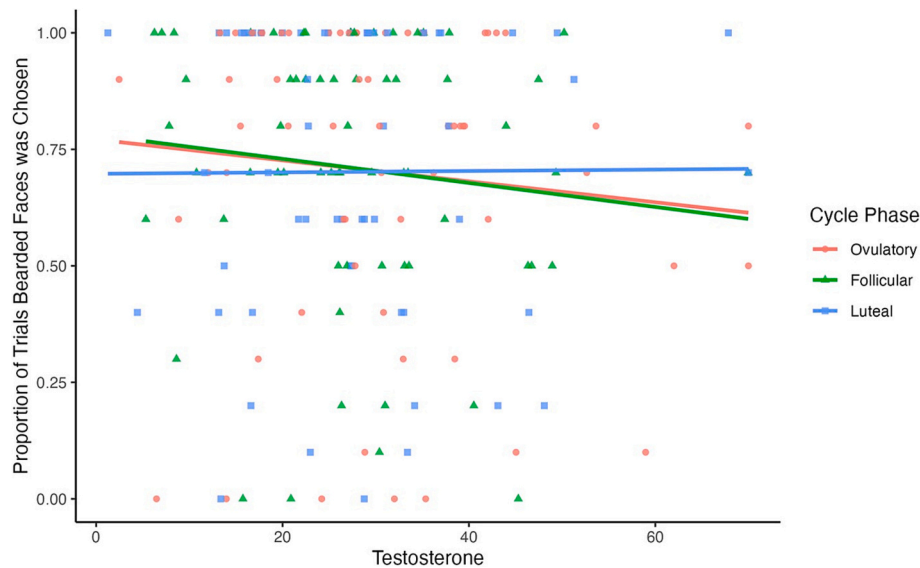


Fig. 4. The association between testosterone measured in pg/ml and preferences for beardedness across the menstrual cycle. Red dots represent preferences for facial hair at ovulatory phase; green triangles represent preferences during the follicular phase/menses, and blue squares represent preferences during the luteal phase.

blending randomly sampled subsets of five men photographed when clean-shaven and again with full beards from our total pool of 37. The composites were created using widely employed computer graphic techniques to present standardised bearded and clean-shaven faces (DeBruine, 2018). This approach is experimentally appealing as researchers can control idiosyncratic differences in craniofacial masculinity and femininity (Scott and Penton-Voak, 2011), which may influence perceptions of beardedness (Dixon et al., 2016, 2017a, 2024). However, we note that this may come at the expense of ecological validity, as during everyday life people are exposed to faces of many anonymous people that vary in numerous facial dimensions. Interestingly, data driven research models for attractiveness ratings of faces and bodies may be more revealing than theory driven models of the kind we used in our study (Brooks et al., 2015; Holzleitner et al., 2019). Our experimental approach has limitations that could be addressed in future research integrating data driven and theory driven models while employing natural facial stimuli. For the present, our study provides the first test of whether women's salivary T is positively associated with their preferences for male facial hair and contributes to a growing body of evidence suggesting women's sexual proceptivity towards men with well-developed androgen dependent facial traits may not be consistently positively associated with peri-ovulatory levels of T. More broadly speaking, our study contributes to a body of literature demonstrating that mating strategies theory and the ovulatory shift hypothesis may not explain variation in women's mate preferences for androgen-dependent secondary sexual facial traits in potential male partners.

CRediT authorship contribution statement

Barnaby J.W. Dixon: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Anthony J. Lee:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation. **Grazyna Jasienska:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization, Project administration. **Urszula M. Marcinkowska:** Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization.

Ethical statement

This research was approved by the Human Ethics Committee at Jagiellonian University, approval number: KBET/250/B/2014.

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Declaration of competing interest

All the authors associated with this manuscript declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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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.2025.105791>.

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