

1 **TITLE:** Women's preferences for men's beards show no relation to their ovarian cycle phase
2 and sex hormone levels

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5 **SHORT TITLE:** Women's fertility and preferences for beards.

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51 **ABSTRACT**

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

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73 **Key words:** Facial attractiveness; menstrual cycle; facial hair; sexual selection.

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101 **1. Introduction**

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

114 Women’s preferences for exaggerated facial sexual dimorphism in men are argued to
115 reflect sexual selection for both underlying genetic quality (Little et al., 2011) and direct
116 benefits (Puts, 2010). Androgens play organizational roles in shaping masculine facial
117 features, including a prominent jawline, brow ridge and midface in men (Whitehouse et al.,
118 2015). Facial masculinity is positively associated with male physical strength (Fink et al.,
119 2007; Windhager et al., 2011), health at adolescence (Rhodes et al., 2003) and adulthood
120 (Thornhill and Gangestad, 2006). However, androgens may impact on immune response
121 (Muehlenbein and Bribiescas, 2005), so that only high quality males can maintain androgen-
122 dependent traits and indirectly signal genetic qualities to mates (Foo et al., 2017). There is
123 some evidence that testosterone is positively correlated with men’s immune response and
124 facial attractiveness (Rantala et al., 2012). However, not all studies have found that facial
125 masculinity is associated with health (Boothroyd et al., 2013) and facial masculinity reflects
126 immunocompetence remains controversial (Scott et al., 2013). Recently, Phalane et al (2017)
127 reported that facial masculinity and facial muscularity were associated with men’s immunity
128 and women’s judgments of male health and attractiveness, highlighting a complex
129 relationship between facial masculinity, immunity and male facial attractiveness.

131 In addition to facial masculinity, androgens promote facial hair growth in men
132 (Randall, 2008). However, the androgenic processes underpinning beard growth differ from
133 those for facial masculinity. Beard hair follicles are activated when testosterone is converted
134 to dihydrotestosterone via 5 alpha reductase enzymes in the dermal papillae of hair follicles
135 (Randall, 2008). Sexual dimorphism in facial hair first appears around 10 years of age (Trotter,
136 1922) and continues to develop in boys throughout adolescence, becoming fully developed at
137 adulthood (Hamilton 1958). The extent to which androgens exert their effects on facial hair
138 are due to shared genetic background, so that beard pattern and density is identical in
139 monozygotic twins, variable among dizygotic twins and highly variable among non-twin
140 brothers (Hamilton, 1964). While facial hair appears to bear no cost to survival and is not
141 related to proficiency in hunting or horticulture, beards enhance ratings of male sexual
142 maturity and masculinity (Dixson, 2016). This suggests facial hair plays a role in intra-sexual
143 signaling (Puts, 2010); accordingly, beards consistently enhance ratings of men’s social status,
144 dominance and aggressiveness (Dixson and Vasey, 2012; Muscarella and Cunningham, 1996;
145 Neave and Shields, 2008; Saxton et al., 2016; Sherlock et al., 2017). Success in male-male
146 competition can lead to higher status and signal resource holding potential and protection, so
147 that beards likely signal direct rather than indirect benefits to women (Dixson et a., 2017a).

149 Given their associations with indirect and direct benefits, women may prefer
150 masculine facial features and beards in partners. Although men’s mating success is positively

151 associated with facial masculinity (Hill et al., 2013; Rhodes et al., 2005) and beardedness
152 (Barber, 2001), women's preferences for both traits are highly variable (Dixson et al., 2016).
153 Some studies reported a greater preference for full beards among women (Pellegrini, 1973;
154 Dixson et al., 2016; McIntosh et al., 2017), while others found that clean-shaven faces
155 (Dixson and Vasey, 2012; Muscarella and Cunningham, 1996), or stubble (Dixson and
156 Brooks, 2013; Dixson et al., 2013; Neave and Shields, 2008) were the most attractive.
157 Similarly, mixed results are also reported for women's preference for craniofacial masculinity
158 (Rhodes, 2006), and beards enhance ratings of male facial masculinity (Dixson et al., 2017a).
159

160 These inconsistencies in women's preferences are thought to reflect a paradoxical role
161 of masculine traits in human mate choice decisions. On the one hand, phenotypic masculinity
162 may reflect biological quality, while on the other hand, masculine traits are also associated
163 with negative personality traits and potentially reduced paternal investment (Dixson, 2016).
164 For instance, masculine men report stronger preferences for and engage more often in short-
165 term than long-term relationships (Boothroyd et al., 2007, 2008; Rhodes et al., 2005), and
166 women accurately judge male sexual infidelity using facial masculinity from photographs
167 (Rhodes et al., 2013). Beardedness is positively associated with men's self-reported
168 masculinity (Wood, 1986) and support of traditional masculine gender roles (Oldmeadow and
169 Dixson, 2016a, 2016b), as well as their serum testosterone (Knussman and Christiansen,
170 1988), which is negatively associated with paternal investment (Gettler, 2014). Thus, women
171 may face costs when choosing a masculine partner, which may explain why facial masculinity
172 reduces paternal investment ratings (Kruger, 2006; Perrett et al., 1998).
173

174 Based on the possible trade-off between heritable biological quality and parental
175 quality, women's preference for masculine traits could be greater in circumstances where
176 these benefits are more likely to be realised (Gangestad and Simpson, 2000). Previous
177 research reported women's preferences for masculine traits were strongest when judging
178 short-term mates (Little et al., 2011), and particularly during the peri-ovulatory phase of the
179 menstrual cycle (Gangestad and Thornhill, 2008). Ovulatory shifts have been found for
180 masculine facial shape (Little et al., 2008; Penton-Voak et al., 1999; Penton-Voak and Perrett,
181 2000), deeper vocal pitch (Puts, 2005), and greater height (Pawlowski and Jasienska, 2005).
182 However, this interpretation has recently been questioned (Dixson et al., 2017b; Scott et al.,
183 2014), and is not supported by recent genetic evidence (Lee et al., 2014; Zietsch et al., 2015).
184 Additionally, unsuccessful attempts to replicate ovulatory shift effects (Harris, 2011, 2013;
185 Harris et al., 2013; Zietsch et al., 2015) and conflicting results from two separate meta-
186 analyses (Gildersleeve et al., 2014a; Wood et al., 2014) has sparked debate regarding the
187 robustness of ovulatory shift effects and highlighted issues of sampling techniques, statistical
188 analyses, and methodologies (Gildersleeve et al. 2014b; Harris et al. 2014; Wood and Carden
189 2014). One recurring methodological issue in tests of the ovulatory shift hypothesis concerns
190 estimating fertility indirectly via questionnaires asking participants to recall the onset, length,
191 and regularity of their menstrual cycles. These techniques are not only inaccurate owing to
192 participant's memory and knowledge of their menstrual cycles (Jukic et al., 2008; Small et al.,
193 2007), and variability in cycle physiology (Jasienska and Jasienski, 2008), but also result in
194 unreliable estimates of current fertility (Blake et al., 2016; Gangestad et al., 2016). Further,
195 studies often used small sample sizes and between-subject designs, which further reduces the
196 likelihood of identifying robust effects (Gangestad et al., 2016). Thus, whether women's
197 preferences for masculinity shift with ovulation remains contentious.
198

199 Women's menstrual cycles last, on average, 28 days (Popat et al., 2008) and the peri-
200 ovulatory period is characterized by a surge in luteinizing hormone (LH) and an increase

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

220
221 The current study tests whether the attractiveness of men's beards shifts across the
222 menstrual cycle where participant menstrual cycle phase was verified by daily measurements
223 of sex hormone levels and LH tests. Preferences data were collected from 52 heterosexual
224 women during the follicular, peri-ovulatory and luteal phases of their menstrual cycles. We
225 also collected daily saliva samples for measurements of estradiol and progesterone at each
226 phase of the cycle in order to test the hormonal associations underpinning potential cycle
227 effects. Our sample size of 52 women and within-subject design at three targeted points of the
228 menstrual cycle has 80% power to detect a medium effect size of $d = 0.5$ (Gangestad et al.,
229 2016). Prior studies used natural facial stimuli to test women's preferences for men's facial
230 hair that, although high in ecological validity, likely vary on several dimensions, including
231 craniofacial masculinity, that influence women's preferences for beards (Dixson et al., 2016,
232 2017a; Geniole and McCormick, 2015). Thus, we measured women's preferences for beards
233 using controlled composite stimuli made from the same men with full beards and when clean-
234 shaven. Finally, we used a two-alternative forced choice (2AFC) paradigm to measure
235 preferences for beards rather than the Likert scales used in past studies (Dixson & Brooks,
236 2013; Dixson et al., 2013). 2AFC approaches were also validated in studies of women's facial
237 masculinity preferences, which reported they are more accurate in detecting ideal and actual
238 mate preferences than Likert scales (DeBruine, 2013; Lee & Zietsch, 2015). 2AFC have been
239 used in repeated-measures designs to test whether women's preferences for masculine traits
240 are stronger at the peri-ovulatory phase in many past studies (Little & Jones, 2012; Jones et
241 al., 2017). We predicted that beards would be most attractive at the peri-ovulatory phase of
242 the menstrual cycle and would be positively associated with women's estradiol levels.

243 244 **2. Methods**

245 **2.1. Participants**

246 Seventy-three women (Mean age = 28.08, SD = 4.33) were recruited from Malopolska
247 region in Poland of whom 70 attended all the lab sessions. All participants reported having
248 regular menstrual cycles (not more than +/- 5 days of difference between consecutive cycles),
249 no diagnosed health problems, were not pregnant, breast-feeding, or had not taken any form
250 of hormonal contraception for at least 3 months prior to participation. We removed

251 participants who did not complete the rating tasks or identified as homosexual, as sexual
 252 orientation influences facial hair preferences (Valentova et al., 2017). This left a final sample
 253 of 52 women.
 254

255 **2.2. Facial hair photographs**

256 Thirty-seven men (mean age \pm SD = 27.9 \pm 5.75 years) of European ethnicity were
 257 photographed when clean-shaven and with 4-8 weeks of natural beard growth posing with a
 258 neutral facial expression. Photographs were taken using a digital camera (8.0 megapixels
 259 resolution) with subjects 150 cm from the photographer under controlled lighting (Dixson et
 260 al., 2017a). Composite stimuli were constructed using the Webmorph software package
 261 (DeBruine and Tiddeman, 2016) by identifying 189 facial landmarks on the images and
 262 averaging the shape and color information of the photographs. To create a composite bearded
 263 face and a composite clean-shaven face, we randomly selected five males from the total pool
 264 of 37. For each of the five males we used their bearded and clean-shaven versions to create a
 265 composite with a full beard and when clean-shaven. Thus, the pairs of composites represented
 266 the same five individuals when bearded and when clean-shaven (Figure 1). This process was
 267 undertaken 10 times to create the 10 pairs of bearded and clean-shaven composite stimuli.
 268



269 Figure 1. Examples of the male stimuli used in this study. Images depict composites of the
 270 same five individuals when clean-shaven (left image) and with full beards (right image).
 271
 272

273 **2.3. Procedure**

274 Participants were given written instructions and were trained by a researcher in how to
 275 collect and store saliva samples, and received a set of 2 ml centrifuge tubes with minimum
 276 amount of required saliva marked and 10 LH Ovulation Kits with urine cups and written
 277 instructions. Participants collected saliva samples each morning from the onset of menstrual

278 bleeding, until the last day of the cycle. Urinary tests were conducted between day 10 and 20
 279 of the cycle or until obtaining a positive result. Participants attended three lab sessions. The
 280 first was scheduled before expected ovulation (before the 8th day of the cycle, early follicular
 281 phase), the second around ovulation (peri-ovulatory phase) and the third approximately one
 282 week after the ovulation (luteal phase).
 283

284 During each meeting participants completed a two-alternative forced choice (2AFC)
 285 experiment in which they were presented with 10 pairs of faces each containing clean-shaven
 286 and bearded composites and were asked to select the face they considered to be more sexually
 287 attractive. Stimulus pairs were presented in a randomized order and the position of the
 288 bearded and clean-shaven face (left or right-hand side) was randomized. Results obtained
 289 using 2AFC accurately predict actual and ideal mate preferences, while Likert scales are less
 290 effective (DeBruine, 2013). Moreover, 2AFC have been found to be more appropriate than
 291 Likert scales for studying context-dependent shifts in preferences for masculine face shape
 292 (Lee & Zietsch, 2015) and have been used in many past studies looking at changes in
 293 preferences over the menstrual cycle, some of which yielded significant effects of fertility
 294 (Little & Jones, 2012), while others have not (Jones et al., 2017).
 295

296 **2.4. Hormonal measurements**

297 Luteinizing hormone (LH) was measured in urine samples by commercial kits. Levels
 298 of 17- β estradiol (E2) and progesterone (P) were measured in saliva samples. Daily levels of
 299 hormones throughout the cycle were measured: 15 days centred around ovulation (from late
 300 follicular phase to early luteal phase) for E2 and last 14 days of the cycle (luteal phase) for P.
 301 Daily values of both E2 and P from samples taken on days of each lab session were available
 302 for all women. Saliva samples were taken no earlier than 30 min after eating or drinking. Each
 303 sample was frozen in participant's home freezer immediately after collecting. All samples
 304 were transported in portable freezers from participants' homes to the laboratory where
 305 hormonal assays were conducted. Professional laboratory technicians conducted all
 306 measurements using commercially available hormonal assays of DRG International Incl. Elisa
 307 plates: SLV3140 for 17- α -hydroxy-progesterone (sensitivity: 2.5 pg/ml, standard range: 10-
 308 5000 pg/ml) and SLV4188 for 17- β estradiol (sensitivity: 0.4 pg/ml, standard range: 1-100
 309 pg/ml). All hormonal assays were conducted in duplicates. The quality of hormonal analyses
 310 was monitored for each plate separately by including, also in duplicates, samples of known
 311 concentrations (i.e. "pools") with low, medium and high P and E2 (in total 19 pools per plate
 312 dedicated for control measurements). For E2, inter-assay CV was 10.01%, and intra-assay
 313 was 7.5%. For P, inter-assay CV was 14.1 %, and intra-assay was 4.9% (Schultheiss and
 314 Stanton 2009).
 315

316 **2.5. Statistical analyses**

317 We used repeated-measures ANOVAs and Bayesian repeated-measures ANOVAs to
 318 test the effect of fertility on bearded face preferences using JASP (Wagenmakers et al., 2017).
 319 We then used linear mixed regression models with maximum likelihood estimation to analyze
 320 the influence of hormones on bearded face preferences. Linear mixed regression models are
 321 appropriate for analyzing nested data with correlated error terms (Twisk, 2006). To prepare
 322 the hormone data for analysis, we first computed an E:P ratio term by dividing estradiol by
 323 progesterone values. We then computed averaged estradiol, progesterone, and E:P ratio values
 324 by averaging values across phases for each participant. All outliers for these hormone
 325 variables above ± 3 -SDs from the grand mean were winsorised to ± 3 -SD (a maximum of
 326 3.4% of cases). After calculating means, we log-transformed all hormone variables due to
 327 significant positive skew and grand mean centered values for mixed model analysis.

328
 329 We determined suitable error covariance matrices by comparing fit indices and
 330 choosing the matrix with the lowest -2 log likelihood ratio. We accounted for subject
 331 variation by including a random intercept in all models. We also inspected models for overly
 332 influential data points by examining and removing standardized residuals above ± 3 (a
 333 maximum of 1.2% of data points were removed). We further examined random slopes for the
 334 all fixed hormone predictors (Twisk, 2006). Our decision rule was to retain random slopes
 335 where $p < .05$, though no random slope was (all $p \leq .393$) and thus no random slopes were
 336 included (many models also failed to converge when random slopes were included, thus
 337 supporting our decision to not retain the fully maximal model; Barr, Levy, Scheepers, and
 338 Tily, 2013). We first tested the fixed effects of estradiol, progesterone, and menstrual cycle
 339 phase, using the peri-ovulatory phase as the reference category (Model 1). We then tested
 340 these same effects, plus all higher order interactions to account for interaction effects between
 341 estradiol, progesterone, and menstrual cycle phase (Sollberger and Ehlert, 2016; i.e., a full
 342 factorial design; Model 2). In Model 3, we tested the fixed effects of estradiol and
 343 progesterone without accounting for the fixed effect of menstrual cycle phase. In Model 4, we
 344 tested the fixed effects of estradiol, progesterone, and their interaction. In Model 5, we tested
 345 the fixed effects of the E:P ratio and menstrual cycle phase. In Model 6, we tested the same
 346 variables as Model 5, plus the higher order interaction. In Model 7, we tested the fixed effect
 347 of the E:P ratio without menstrual cycle phase.

349 3. Results

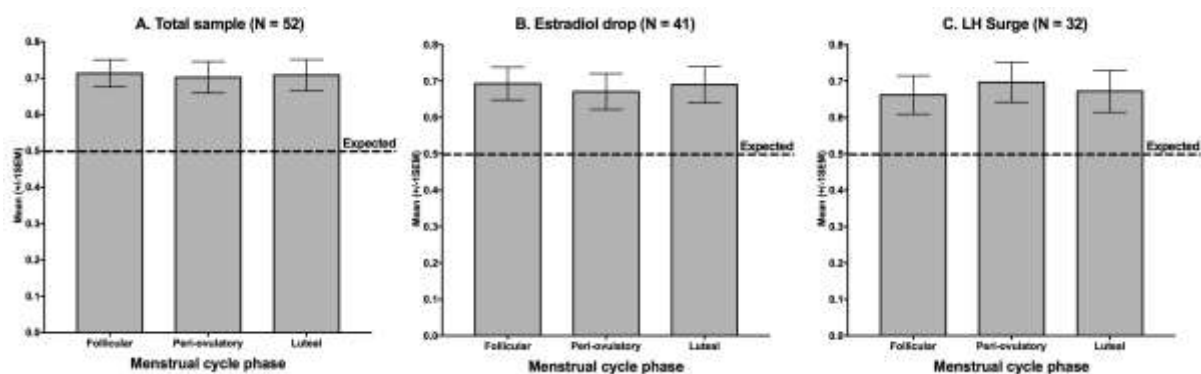
350 The proportion of bearded faces selected as most attractive was the dependent variable
 351 in repeated-measures ANOVAs where menstrual cycle phase (follicular, peri-ovulatory,
 352 luteal) was the within-subjects factor. We first analysed the full sample of participants without
 353 splitting analyses to account for whether ovulation was determined via LH surge or E2 drop.
 354 Women's facial hair preferences were greater than chance (0.50) in the early follicular ($t_{51} =$
 355 $5.67, p < 0.001$), ovulatory ($t_{51} = 4.65, p < 0.001$), and luteal ($t_{51} = 4.81, p < 0.001$) phases
 356 (Figure 2A). There was no significant effect of menstrual cycle phase on preferences ($F_{2,102} =$
 357 $0.07, p = 0.935; \eta^2 = 0.001$). Bayesian analyses revealed that it is 15 times more likely to
 358 reflect a true null result than the hypothesised effect ($BF_M = 15.115$; See Table S1).

360 In the sample in which peri-ovulation was determined via E2 drop, facial hair
 361 preferences were greater than chance (0.50) in the early follicular ($t_{40} = 4.28, p < 0.001$),
 362 ovulatory ($t_{40} = 3.44, p < 0.001$), and luteal ($t_{40} = 3.84, p < 0.001$) phases (Figure 2B). There
 363 was no significant effect of menstrual cycle phase on preferences ($F_{2,80} = 0.22, P = 0.803; \eta^2 =$
 364 0.005). Bayesian analyses revealed that it is 11 times more likely to reflect a true null result
 365 than the hypothesised effect ($BF_M = 10.678$; See Table S2).

367 In the sample in which peri-ovulation was determined via an LH surge, facial hair
 368 preferences were greater than chance (0.50) in the early follicular ($t_{31} = 3.07, p = 0.004$),
 369 ovulatory ($t_{31} = 3.59, p < 0.001$), and luteal ($t_{31} = 3.84, p = 0.005$) phases (Figure 2C). There
 370 was no significant effect of menstrual cycle phase on preferences ($F_{2,62} = 0.40, p = 0.675; \eta^2 =$
 371 0.013). Bayesian analyses revealed that it is 8 times more likely to reflect a true null result
 372 than the hypothesised effect ($BF_M = 7.807$; See Table S3).

374 As shown in Table 1, no main effect of menstrual cycle phase, estradiol, or
 375 progesterone was significant ($ps \geq 0.258$). No higher order interactions pertaining to estradiol,
 376 progesterone, or menstrual cycle phase were significant ($ps \geq 0.313$). No main effects of the
 377 E:P ratio were significant ($ps \geq 0.584$). No cycle phase x E:P ratio interaction terms were

378 significant ($ps \geq 0.233$). We then conducted sensitivity tests by restricting the sample only to
 379 women recording either a mid-cycle drop in estradiol in the same cycle, an LH surge, or those
 380 just recording an LH surge. No effect in these restricted analyses differed substantially from
 381 those reported here. No main effects for estradiol, menstrual cycle phase, and progesterone
 382 were significant ($ps \geq 0.196$). No higher order interactions pertaining to estradiol,
 383 progesterone, or menstrual cycle phase were significant ($ps \geq 0.294$). Main effects of the E:P
 384 ratio were not significant, $ps \geq 0.123$, and we note that the direction of the effect was negative.
 385 No cycle phase x E:P ratio interaction terms were significant ($ps \geq 0.257$).
 386



387
 388 Figure 2. Mean proportion of bearded faces selected as most attractive (± 1 SEM) among the
 389 same women during the follicular, peri-ovulatory and luteal phases of the menstrual cycle.
 390 Data are the total sample (A.), participants for whom the peri-ovulatory phases as
 391 characterised by the drop in estradiol (B.), and participants for whom the peri-ovulatory
 392 phase was characterised by the surge in lutenizing hormone (C.).

393 394 4. Discussion

395 We found that irrespective of their ovarian cycle phase and levels of reproductive
 396 hormones, women judged full beards as more attractive than clean-shaven faces. Preferences
 397 for facial hair were not stronger at the peri-ovulatory phase of the menstrual cycle nor among
 398 women with higher levels of estradiol. This pattern of results supports some previous studies
 399 that have not found ovulatory shifts in women's preferences for androgen dependent facial
 400 traits (Harris, 2011, 2013; Zietsch et al., 2015; Peters et al., 2009, Marcinkowska et al. 2016),
 401 including studies of women's preferences for facial hair (Dixson et al., 2013; Dixson and
 402 Brooks, 2013; Dixson and Rantala, 2016, 2017). Our results have implications for hypotheses
 403 linking women's fecundability with preferences for men's secondary sexual traits.
 404

405 According to the ovulatory shift hypothesis, women's sexual proceptivity and
 406 receptivity to men displaying well developed masculine secondary sexual traits become
 407 greater at the peri-ovulatory phase of the menstrual cycle when conception is most likely
 408 (Gangestad and Thornhill, 2008; Gangestad and Haselton, 2015). While initial studies
 409 provided compelling support for the ovulatory shift hypothesis (Gangestad and Thornhill,
 410 2008), evidence from meta-analyses is divided on whether ovulatory shifts occur and if so by
 411 how much (Gildersleeve et al., 2014a; Wood et al., 2014). Many of these studies used
 412 imprecise estimates of fertility generated from questionnaires that may have obscured effects
 413 of fertility on mate preferences (Blake et al., 2016; Gangestad et al., 2016). Attempts to
 414 determine cycle phase and ovulation based on self-reported dates of menstrual bleeding do
 415 not provide accurate estimations of events occurring during the cycle. This is due to high
 416 inter-individual variation that healthy, regularly menstruating women exhibit in cycle length,
 417 in chance of ovulation and sex hormone levels (Jasienska and Jasienski 2008). This variation

418 is a result of age (Lipson and Ellison 1992), genetics (Jasienska et al 2006a), anthropometric
419 characteristics (Ziomkiewicz et al 2008), prenatal environment (Jasienska et al 2006b) and
420 adult lifestyle (Jasienska 2003). The current study determined the peri-ovulatory phase using
421 hormonal measures and found no ovulatory shift in women's preferences for men's facial hair.
422 Similarly, Peters et al (2009) found no ovulatory shift in women's preferences for facial and
423 bodily masculinity when using a within-subjects design in which the peri-ovulatory phase was
424 confirmed using LH surges. This suggests that women's preferences for masculine facial
425 features and beardedness may not become stronger at the peri-ovulatory phase compared to
426 other times during the menstrual cycle.

427
428 Estradiol has central neuroendocrine effects on female sexual proceptivity among the
429 anthropoid primates (Dixson 2009) and may underpin aspects of women's sexual desires,
430 attractiveness and assertiveness (Roney and Simmons, 2013; Puts et al., 2013; Blake et al.,
431 2017a,b). We also tested whether variation in women's estradiol and progesterone were
432 associated with preferences for facial hair. We found no evidence that women's preferences
433 for beardedness were associated with estradiol or progesterone, either independently or in
434 concert. This finding contrasts with two studies that found elevated levels of estradiol at the
435 peri-ovulatory phase were positively associated with women's preferences for facial
436 masculinity (Ditzen et al., 2017; Roney et al., 2011), but supports another that reported no
437 associations between salivary hormone levels and women's preferences for masculinity (Jones
438 et al., 2017). Behavioral studies quantifying women's motivation to attend to facial stimuli
439 using key tests found that ratios of estradiol relative to progesterone were positively
440 associated with women's attention toward feminised and attractive female faces and
441 masculinised, but not necessarily attractive, male faces (Wang et al., 2014). However, other
442 studies that also used within-subject designs found positive associations between changes in
443 testosterone but not estradiol or progesterone and preferences for facial masculinity (Bobst et
444 al., 2014; Welling et al., 2007). Results of cross-sectional studies are also mixed, so that one
445 study showed positive associations between women's estradiol and preferences for facial
446 masculinity (Roney and Simmons, 2008), while others did not (Marcinkowska et al., 2016;
447 Escasa-Dorne et al., 2016). Taken together, these mixed results suggest that relationships
448 among reproductive hormones and women's mate preferences may not be generalizable.

449
450 To date, the current study provides the best test for menstrual cycle shifts in women's
451 preferences for facial hair. Not only do we verify fertility and ovulation hormonally, which
452 avoids the inaccuracies of counting methods based on self-report, but we also use highly
453 controlled composite images as stimuli, removing idiosyncrasies in faces that would introduce
454 additional variance (Dixson et al., 2017a). For example, past research has shown that subtle
455 variation in beard quantity, patterning and distribution influences preferences for facial hair
456 (Dixson & Brooks, 2013; Dixson & Rantala, 2016). Further, in natural stimuli craniofacial
457 masculinity impacts subtly on the attractiveness of facial hair, so that women's preferences
458 for beards were higher for men with intermediate levels of craniofacial masculinity (Dixson et
459 al., 2017a). Experimentally manipulating the degree of masculinity in facial shape also
460 increases women's preferences for beards in male faces with reduced rather than augmented
461 facial masculinity (Dixson et al., 2016; Dixson et al., 2017a). The fact that we continue to find
462 no shifts in preferences provides increased confidence that previous null results (Dixson et al.,
463 2013; Dixson and Brooks, 2013; Dixson and Rantala, 2016, 2017) could reflect a true absence
464 of an effect. However, there are some notable limitations in our study that should be
465 highlighted. Thus, it could be argued that our use of composite stimuli which differed only on
466 one dimension of facial masculinity, in concert with the use of a two-alternative forced choice
467 design (2AFC) design, might artificially induce a facial hair preference when one may not

468 occur using Likert scales and more natural stimuli presented singularly. However, studies
469 have validated that the 2AFC test with composite faces manipulated to vary in singular
470 dimensions of facial masculinity was a better predictor of women's ideal and actual
471 masculinity preferences than rating scales (DeBruine, 2013). These approaches have been
472 used in many past tests of women's preferences for male facial masculinity over the menstrual
473 cycle, some of which reported positive (Little & Jones, 2012) while others reported null
474 (Jones et al., 2017) results. It is also possible that the attractiveness levels of the facial
475 composites influenced women's preferences for beards. Unfortunately, we did not control for
476 facial attractiveness when constructing our composite stimuli and were unable to statistically
477 control for the attractiveness of the composites during our analyses. We note that one of the
478 methodological advantages in using composite facial stimuli in addition to reducing small
479 differences among sets of natural faces, which allows for cleaner tests of the experimentally
480 manipulated trait, is that homogeneity among the composite faces contained in the stimulus
481 set in terms of shape, texture and attractiveness is increased. Nevertheless, further replication
482 using more nuanced facial stimuli that controls for facial attractiveness, along with other
483 methods for measuring preferences would be beneficial to ascertain the robustness of our
484 results.

485
486 Although we used a powerful within-subjects repeated-measures design, participants
487 were all recruited at the early follicular phase of the cycle, followed by the peri-ovulatory and
488 the luteal phase. Viewing times towards sexual stimuli were longest among women at the
489 peri-ovulatory phase only when it was the first session in the cycle in which response times
490 were quantified (Wallen and Rupp 2010). Thus, we acknowledge that our study design may
491 have induced carry-over effects and our findings should be interpreted cautiously. Further,
492 although the peri-ovulatory phase was verified using the peak in LH, ovulatory shifts in mate
493 preferences may be subtler and occur in concert with rising estradiol as women approach the
494 peri-ovulatory phase, rather than at the peri-ovulatory period itself. We note that a cross-
495 sectional study that used several different estimates of the fertile phase of the menstrual cycle
496 found no relationship between the likelihood of conception and women's preferences for
497 facial masculinity (Marcinkowska et al., 2016). Another possibility for our null finding is that
498 menstrual cycle shifts in mate preferences occur among women currently in relationships and
499 are contingent upon their partner's degree of masculinity (DeBruine et al., 2010; Gildersleeve
500 et al., 2013). A study among romantically involved couples found that a stronger desire for
501 extra-pair mates occurred at the fertile phase than the luteal phase among women with less
502 facially attractive partners (Gangestad et al., 2010). We did not measure the characteristics of
503 women's partners and past studies have reported that women's preferences for facial hair are
504 positively associated with that of their partners (Dixson et al., 2013; Janif et al., 2014;
505 Valentova et al., 2017). Finally, variation in women's willingness to engage in short-term
506 relationships, as measured using the sociosexual inventory (SOI), may impact on mate
507 preferences (Sacco et al., 2012) and might explain variation in preferences for facial hair.
508 Thus, future research assessing whether women's partner's degree of beardedness and
509 individual differences in sociosexuality interact with fertility to determine preferences for
510 facial hair would be valuable.

511
512 The extent to which facial hair has been shaped by female choice is complex as, while
513 fundamentally a biological characteristic, beardedness is culturally elaborated upon to varying
514 degrees within and across societies (Robinson, 1976; Barber, 2001). It is possible that beards
515 enhanced male attractiveness due to contemporary cultural trends in facial hair among our
516 Polish participants. A recent cross-cultural study in which the frequencies of men's
517 beardedness and women's preferences for beards were quantified found that beards were

518 more attractive in populations where beardedness was more common (Dixson et al., 2017c).
 519 In that study, Polish men were the second most clean-shaven population in the sample,
 520 suggesting that current trends in beardedness may not be responsible for the preferences for
 521 beards in the current study. Instead, men's decisions to groom their facial hair may occur in
 522 response to social and economic factors in ways that are predicted by evolutionary theory. In
 523 addition to being positively associated with the frequency of beardedness, women's
 524 preferences for facial hair were also stronger in countries with lower average incomes
 525 (Dixson et al., 2017c). A longitudinal study spanning 1842-1972 among men from London,
 526 revealed that frequencies of moustaches, sideburns, moustache and sideburns in combination,
 527 clean-shavenness and full beards each had distinct periods in which they were most popular
 528 (Robinson, 1976). Using these data, Barber (2001) demonstrated that when sex-ratios were
 529 more male-biased and competition to attract mate was therefore stronger, men were more
 530 bearded. Facial hair unambiguously communicates age, sexual maturity (Dixson and Vasey,
 531 2012; Neave and Shields, 2008), masculinity (Dixson and Brooks, 2013; Neave and Shields,
 532 2008), dominance and aggressiveness (Dixson and Vasey, 2012; Dixson et al., 2017a;
 533 Geniole and McCormick, 2015; Muscarella and Cunningham, 1996; Neave and Shields,
 534 2008; Sherlock et al., 2016; Saxton et al., 2016), suggesting a role of intra-sexual selection in
 535 shaping the evolution of beardedness (Dixson et al., 2017a, 2017c). Whether facial hair is
 536 associated with status acquisition and dominance in a manner that enhances male reproductive
 537 success remains a challenge for future research (Dixson et al., 2005; Grueter et al., 2015). For
 538 the present, our findings suggest that women's preferences for facial hair show no relation to
 539 their ovarian cycle phase and sex hormone levels.

540

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548

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

Predictor	Model							
	Model 1		Model 2		Model 3		Model 4	
	<i>B</i>	<i>p</i>	<i>B</i>	<i>p</i>	<i>B</i>	<i>p</i>	<i>B</i>	<i>p</i>
Follicular versus peri-ovulatory phase	0.02	.474	0.04	.225				
Luteal versus peri-ovulatory phase	0.03	.258	0.03	.385				
Estradiol	0.02	.578	0.05	.451	0.02	.687	0.02	.689
Progesterone	-0.02	.510	-0.03	.505	-0.02	.535	-0.02	.536
Estradiol x Progesterone			-0.004	.962			-0.0004	.995
Estradiol x early follicular phase			-0.06	.405				
Estradiol x luteal phase			-0.07	.420				
Progesterone x early follicular phase			0.06	.313				
Progesterone x luteal phase			-0.02	.770				
Estradiol x progesterone x early follicular phase			-0.06	.654				
Estradiol x progesterone x luteal phase			0.13	.446				
	Model 5		Model 6		Model 7			
	<i>B</i>	<i>p</i>	<i>B</i>	<i>p</i>	<i>B</i>	<i>p</i>		
Follicular versus peri-ovulatory phase	0.02	.468	0.03	.309				
Luteal versus peri-ovulatory phase	0.03	.283	0.03	.264				
E:P ratio	0.02	.584	0.03	.447	0.02	.613		
E:P ratio x early follicular phase			-0.07	.233				
E:P ratio x luteal phase			-0.002	.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 ($ps \geq .393$).