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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).

113
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.

130
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).

148
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 **2.2. Facial hair photographs**

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

268 **2.3. Procedure**

269 Participants were given written instructions and were trained by a researcher in how to
270 collect and store saliva samples, and received a set of 2 ml centrifuge tubes with minimum
271 amount of required saliva marked and 10 LH Ovulation Kits with urine cups and written
272 instructions. Participants collected saliva samples each morning from the onset of menstrual
273 bleeding, until the last day of the cycle. Urinary tests were conducted between day 10 and 20
274 of the cycle or until obtaining a positive result. Participants attended three lab sessions. The
275 first was scheduled before expected ovulation (before the 8th day of the cycle, early follicular
276 phase), the second around ovulation (peri-ovulatory phase) and the third approximately one
277 week after the ovulation (luteal phase).
278

279
280 During each meeting participants completed a two-alternative forced choice (2AFC)
281 experiment in which they were presented with 10 pairs of faces each containing clean-shaven
282 and bearded composites and were asked to select the face they considered to be more sexually
283 attractive. Stimulus pairs were presented in a randomized order and the position of the
284 bearded and clean-shaven face (left or right-hand side) was randomized. Results obtained
285 using 2AFC accurately predict actual and ideal mate preferences, while Likert scales are less
286 effective (DeBruine, 2013). Moreover, 2AFC have been found to be more appropriate than
287 Likert scales for studying context-dependent shifts in preferences for masculine face shape
288 (Lee & Zietsch, 2015) and have been used in many past studies looking at changes in
289 preferences over the menstrual cycle, some of which yielded significant effects of fertility
290 (Little & Jones, 2012), while others have not (Jones et al., 2017).
291

292 **2.4. Hormonal measurements**

293 Luteinizing hormone (LH) was measured in urine samples by commercial kits. Levels
294 of 17- β estradiol (E2) and progesterone (P) were measured in saliva samples. Daily levels of
295 hormones throughout the cycle were measured: 15 days centred around ovulation (from late
296 follicular phase to early luteal phase) for E2 and last 14 days of the cycle (luteal phase) for P.
297 Daily values of both E2 and P from samples taken on days of each lab session were available
298 for all women. Saliva samples were taken no earlier than 30 min after eating or drinking. Each
299 sample was frozen in participant's home freezer immediately after collecting. All samples
300 were transported in portable freezers from participants' homes to the laboratory where

301 hormonal assays were conducted. Professional laboratory technicians conducted all
302 measurements using commercially available hormonal assays of DRG International Incl. Elisa
303 plates: SLV3140 for 17- α -hydroxy-progesterone (sensitivity: 2.5 pg/ml, standard range: 10-
304 5000 pg/ml) and SLV4188 for 17- β estradiol (sensitivity: 0.4 pg/ml, standard range: 1-100
305 pg/ml). All hormonal assays were conducted in duplicates. The quality of hormonal analyses
306 was monitored for each plate separately by including, also in duplicates, samples of known
307 concentrations (i.e. “pools”) with low, medium and high P and E2 (in total 19 pools per plate
308 dedicated for control measurements). For E2, inter-assay CV was 10.01%, and intra-assay
309 was 7.5%. For P, inter-assay CV was 14.1 %, and intra-assay was 4.9% (Schultheiss and
310 Stanton 2009).

311

312 **2.5. Statistical analyses**

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

324

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

344

345 **3. Results**

346 The proportion of bearded faces selected as most attractive was the dependent variable
347 in repeated-measures ANOVAs where menstrual cycle phase (follicular, peri-ovulatory,
348 luteal) was the within-subjects factor. We first analysed the full sample of participants without
349 splitting analyses to account for whether ovulation was determined via LH surge or E2 drop.
350 Women’s facial hair preferences were greater than chance (0.50) in the early follicular ($t_{51} =$

351 5.67, $p < 0.001$), ovulatory ($t_{51} = 4.65$, $p < 0.001$), and luteal ($t_{51} = 4.81$, $p < 0.001$) phases
 352 (Figure 2A). There was no significant effect of menstrual cycle phase on preferences ($F_{2,102} =$
 353 0.07 , $p = 0.935$; $\eta^2 = 0.001$). Bayesian analyses revealed that it is 15 times more likely to
 354 reflect a true null result than the hypothesised effect ($BF_M = 15.115$; See Table S1).

355
 356 In the sample in which peri-ovulation was determined via E2 drop, facial hair
 357 preferences were greater than chance (0.50) in the early follicular ($t_{40} = 4.28$, $p < 0.001$),
 358 ovulatory ($t_{40} = 3.44$, $p < 0.001$), and luteal ($t_{40} = 3.84$, $p < 0.001$) phases (Figure 2B). There
 359 was no significant effect of menstrual cycle phase on preferences ($F_{2,80} = 0.22$, $P = 0.803$; η^2
 360 $= 0.005$). Bayesian analyses revealed that it is 11 times more likely to reflect a true null result
 361 than the hypothesised effect ($BF_M = 10.678$; See Table S2).

362
 363 In the sample in which peri-ovulation was determined via an LH surge, facial hair
 364 preferences were greater than chance (0.50) in the early follicular ($t_{31} = 3.07$, $p = 0.004$),
 365 ovulatory ($t_{31} = 3.59$, $p < 0.001$), and luteal ($t_{31} = 3.84$, $p = 0.005$) phases (Figure 2C). There
 366 was no significant effect of menstrual cycle phase on preferences ($F_{2,62} = 0.40$, $p = 0.675$; $\eta^2 =$
 367 0.013). Bayesian analyses revealed that it is 8 times more likely to reflect a true null result
 368 than the hypothesised effect ($BF_M = 7.807$; See Table S3).

369
 370 As shown in Table 1, no main effect of menstrual cycle phase, estradiol, or
 371 progesterone was significant ($ps \geq 0.258$). No higher order interactions pertaining to estradiol,
 372 progesterone, or menstrual cycle phase were significant ($ps \geq 0.313$). No main effects of the
 373 E:P ratio were significant ($ps \geq 0.584$). No cycle phase x E:P ratio interaction terms were
 374 significant ($ps \geq 0.233$). We then conducted sensitivity tests by restricting the sample only to
 375 women recording either a mid-cycle drop in estradiol in the same cycle, an LH surge, or those
 376 just recording an LH surge. No effect in these restricted analyses differed substantially from
 377 those reported here. No main effects for estradiol, menstrual cycle phase, and progesterone
 378 were significant ($ps \geq 0.196$). No higher order interactions pertaining to estradiol,
 379 progesterone, or menstrual cycle phase were significant ($ps \geq 0.294$). Main effects of the E:P
 380 ratio were not significant, $ps \geq 0.123$, and we note that the direction of the effect was negative.
 381 No cycle phase x E:P ratio interaction terms were significant ($ps \geq 0.257$).

382 383 4. Discussion

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

393
 394 According to the ovulatory shift hypothesis, women's sexual proceptivity and
 395 receptivity to men displaying well developed masculine secondary sexual traits become
 396 greater at the peri-ovulatory phase of the menstrual cycle when conception is most likely
 397 (Gangestad and Thornhill, 2008; Gangestad and Haselton, 2015). While initial studies
 398 provided compelling support for the ovulatory shift hypothesis (Gangestad and Thornhill,
 399 2008), evidence from meta-analyses is divided on whether ovulatory shifts occur and if so by
 400 how much (Gildersleeve et al., 2014a; Wood et al., 2014). Many of these studies used

401 imprecise estimates of fertility generated from questionnaires that may have obscured effects
402 of fertility on mate preferences (Blake et al., 2016; Gangestad et al., 2016). Attempts to
403 determine cycle phase and ovulation based on self-reported dates of menstrual bleeding do
404 not provide accurate estimations of events occurring during the cycle. This is due to high
405 inter-individual variation that healthy, regularly menstruating women exhibit in cycle length,
406 in chance of ovulation and sex hormone levels (Jasienska and Jasienski 2008). This variation
407 is a result of age (Lipson and Ellison 1992), genetics (Jasienska et al 2006a), anthropometric
408 characteristics (Ziomkiewicz et al 2008), prenatal environment (Jasienska et al 2006b) and
409 adult lifestyle (Jasienska 2003). The current study determined the peri-ovulatory phase using
410 hormonal measures and found no ovulatory shift in women's preferences for men's facial hair.
411 Similarly, Peters et al (2009) found no ovulatory shift in women's preferences for facial and
412 bodily masculinity when using a within-subjects design in which the peri-ovulatory phase was
413 confirmed using LH surges. This suggests that women's preferences for masculine facial
414 features and beardedness may not become stronger at the peri-ovulatory phase compared to
415 other times during the menstrual cycle.

417 Estradiol has central neuroendocrine effects on female sexual proceptivity among the
418 anthropoid primates (Dixson 2009) and may underpin aspects of women's sexual desires,
419 attractiveness and assertiveness (Roney and Simmons, 2013; Puts et al., 2013; Blake et al.,
420 2017a,b). We also tested whether variation in women's estradiol and progesterone were
421 associated with preferences for facial hair. We found no evidence that women's preferences
422 for beardedness were associated with estradiol or progesterone, either independently or in
423 concert. This finding contrasts with two studies that found elevated levels of estradiol at the
424 peri-ovulatory phase were positively associated with women's preferences for facial
425 masculinity (Ditzen et al., 2017; Roney et al., 2011), but supports another that reported no
426 associations between salivary hormone levels and women's preferences for masculinity (Jones
427 et al., 2017). Behavioral studies quantifying women's motivation to attend to facial stimuli
428 using key tests found that ratios of estradiol relative to progesterone were positively
429 associated with women's attention toward feminised and attractive female faces and
430 masculinised, but not necessarily attractive, male faces (Wang et al., 2014). However, other
431 studies that also used within-subject designs found positive associations between changes in
432 testosterone but not estradiol or progesterone and preferences for facial masculinity (Bobst et
433 al., 2014; Welling et al., 2007). Results of cross-sectional studies are also mixed, so that one
434 study showed positive associations between women's estradiol and preferences for facial
435 masculinity (Roney and Simmons, 2008), while others did not (Marcinkowska et al., 2016;
436 Escasa-Dorne et al., 2016). Taken together, these mixed results suggest that relationships
437 among reproductive hormones and women's mate preferences may not be generalizable.

439 To date, the current study provides the best test for menstrual cycle shifts in women's
440 preferences for facial hair. Not only do we verify fertility and ovulation hormonally, which
441 avoids the inaccuracies of counting methods based on self-report, but we also use highly
442 controlled composite images as stimuli, removing idiosyncrasies in faces that would introduce
443 additional variance (Dixson et al., 2017a). For example, past research has shown that subtle
444 variation in beard quantity, patterning and distribution influences preferences for facial hair
445 (Dixson & Brooks, 2013; Dixson & Rantala, 2016). Further, in natural stimuli craniofacial
446 masculinity impacts subtly on the attractiveness of facial hair, so that women's preferences
447 for beards were higher for men with intermediate levels of craniofacial masculinity (Dixson et
448 al., 2017a). Experimentally manipulating the degree of masculinity in facial shape also
449 increases women's preferences for beards in male faces with reduced rather than augmented
450 facial masculinity (Dixson et al., 2016; Dixson et al., 2017a). The fact that we continue to find

451 no shifts in preferences provides increased confidence that previous null results (Dixson et al.,
452 2013; Dixson and Brooks, 2013; Dixson and Rantala, 2016, 2017) could reflect a true absence
453 of an effect. However, there are some notable limitations in our study that should be
454 highlighted. Thus, it could be argued that our use of composite stimuli which differed only on
455 one dimension of facial masculinity, in concert with the use of a two-alternative forced choice
456 design (2AFC) design, might artificially induce a facial hair preference when one may not
457 occur using Likert scales and more natural stimuli presented singularly. However, studies
458 have validated that the 2AFC test with composite faces manipulated to vary in singular
459 dimensions of facial masculinity was a better predictor of women's ideal and actual
460 masculinity preferences than rating scales (DeBruine, 2013). These approaches have been
461 used in many past tests of women's preferences for male facial masculinity over the menstrual
462 cycle, some of which reported positive (Little & Jones, 2012) while others reported null
463 (Jones et al., 2017) results. It is also possible that the attractiveness levels of the facial
464 composites influenced women's preferences for beards. Unfortunately, we did not control for
465 facial attractiveness when constructing our composite stimuli and were unable to statistically
466 control for the attractiveness of the composites during our analyses. We note that one of the
467 methodological advantages in using composite facial stimuli in addition to reducing small
468 differences among sets of natural faces, which allows for cleaner tests of the experimentally
469 manipulated trait, is that homogeneity among the composite faces contained in the stimulus
470 set in terms of shape, texture and attractiveness is increased. Nevertheless, further replication
471 using more nuanced facial stimuli that controls for facial attractiveness, along with other
472 methods for measuring preferences would be beneficial to ascertain the robustness of our
473 results.

474
475 Although we used a powerful within-subjects repeated-measures design, participants
476 were all recruited at the early follicular phase of the cycle, followed by the peri-ovulatory and
477 the luteal phase. Viewing times towards sexual stimuli were longest among women at the
478 peri-ovulatory phase only when it was the first session in the cycle in which response times
479 were quantified (Wallen and Rupp 2010). Thus, we acknowledge that our study design may
480 have induced carry-over effects and our findings should be interpreted cautiously. Further,
481 although the peri-ovulatory phase was verified using the peak in LH, ovulatory shifts in mate
482 preferences may be subtler and occur in concert with rising estradiol as women approach the
483 peri-ovulatory phase, rather than at the peri-ovulatory period itself. We note that a cross-
484 sectional study that used several different estimates of the fertile phase of the menstrual cycle
485 found no relationship between the likelihood of conception and women's preferences for
486 facial masculinity (Marcinkowska et al., 2016). Another possibility for our null finding is that
487 menstrual cycle shifts in mate preferences occur among women currently in relationships and
488 are contingent upon their partner's degree of masculinity (DeBruine et al., 2010; Gildersleeve
489 et al., 2013). A study among romantically involved couples found that a stronger desire for
490 extra-pair mates occurred at the fertile phase than the luteal phase among women with less
491 facially attractive partners (Gangestad et al., 2010). We did not measure the characteristics of
492 women's partners and past studies have reported that women's preferences for facial hair are
493 positively associated with that of their partners (Dixson et al., 2013; Janif et al., 2014;
494 Valentova et al., 2017). Finally, variation in women's willingness to engage in short-term
495 relationships, as measured using the sociosexual inventory (SOI), may impact on mate
496 preferences (Sacco et al., 2012) and might explain variation in preferences for facial hair.
497 Thus, future research assessing whether women's partner's degree of beardedness and
498 individual differences in sociosexuality interact with fertility to determine preferences for
499 facial hair would be valuable.

500

501 The extent to which facial hair has been shaped by female choice is complex as, while
 502 fundamentally a biological characteristic, beardedness is culturally elaborated upon to varying
 503 degrees within and across societies (Robinson, 1976; Barber, 2001). It is possible that beards
 504 enhanced male attractiveness due to contemporary cultural trends in facial hair among our
 505 Polish participants. A recent cross-cultural study in which the frequencies of men's
 506 beardedness and women's preferences for beards were quantified found that beards were
 507 more attractive in populations where beardedness was more common (Dixson et al., 2017c).
 508 In that study, Polish men were the second most clean-shaven population in the sample,
 509 suggesting that current trends in beardedness may not be responsible for the preferences for
 510 beards in the current study. Instead, men's decisions to groom their facial hair may occur in
 511 response to social and economic factors in ways that are predicted by evolutionary theory. In
 512 addition to being positively associated with the frequency of beardedness, women's
 513 preferences for facial hair were also stronger in countries with lower average incomes
 514 (Dixson et al., 2017c). A longitudinal study spanning 1842-1972 among men from London,
 515 revealed that frequencies of moustaches, sideburns, moustache and sideburns in combination,
 516 clean-shavenness and full beards each had distinct periods in which they were most popular
 517 (Robinson, 1976). Using these data, Barber (2001) demonstrated that when sex-ratios were
 518 more male-biased and competition to attract mate was therefore stronger, men were more
 519 bearded. Facial hair unambiguously communicates age, sexual maturity (Dixson and Vasey,
 520 2012; Neave and Shields, 2008), masculinity (Dixson and Brooks, 2013; Neave and Shields,
 521 2008), dominance and aggressiveness (Dixson and Vasey, 2012; Dixson et al., 2017a;
 522 Geniole and McCormick, 2015; Muscarella and Cunningham, 1996; Neave and Shields,
 523 2008; Sherlock et al., 2016; Saxton et al., 2016), suggesting a role of intra-sexual selection in
 524 shaping the evolution of beardedness (Dixson et al., 2017a, 2017c). Whether facial hair is
 525 associated with status acquisition and dominance in a manner that enhances male reproductive
 526 success remains a challenge for future research (Dixson et al., 2005; Grueter et al., 2015). For
 527 the present, our findings suggest that women's preferences for facial hair show no relation to
 528 their ovarian cycle phase and sex hormone levels.

529

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537

538 **References**

- 539 Andersson, M. B. (1994). *Sexual selection*. Princeton University Press.
- 540 Baird, D.D., Weinberg, C.R., Wilcox, A.J., McConaughy, D.R., Musey, P.I., 1991. Using
 541 the ratio of urinary oestrogen and progesterone metabolites to estimate day of
 542 ovulation. *Stat. Med.* 10, 255–266.
- 543 Barber, N., 2001. Mustache fashion covaries with a good marriage market for women.
 544 *J. Nonverbal. Behav.* 25, 261-272.
- 545 Barr, D.J., Levy, R., Scheepers, C., Tily, H.J., 2013. Random effects structure for
 546 confirmatory hypothesis testing: Keep it maximal. *J. Mem. Lang.* 68, 255-278.
- 547 Blake, K.R., Bastian, B., O'Dean, S.M., Denson, T.F., 2017. High estradiol and low
 548 progesterone are associated with high assertiveness in women.
 549 *Psychoneuroendocrinology.* 75, 91-99.
- 550 Blake, K.R., Dixson, B.J.W., O'Dean, S.M., Denson, T.F., 2016. Standardized methodological

- 551 protocols for measuring the effects of fertility on women's behavior: A data-driven
 552 approach contrasting counting and hormonal methods. *Horm. Behav.* 81, 74-83.
- 553 Blake, K.R., Dixon, B.J.W., O'Dean, S.M., Denson, T. F., 2017. No compelling positive
 554 association between ovarian hormones and wearing red clothing when using
 555 multinomial analyses. *Horm. Behav.* 90, 129-135.
- 556 Bobst, C., Sauter, S., Foppa, A., Lobmaier, J.S., 2014. Early follicular testosterone level
 557 predicts preference for masculinity in male faces - but not for women taking hormonal
 558 contraception. *Psychoneuroendocrinology.* 41, 142–150.
- 559 Boothroyd, L. G., Jones, B. C., Burt, D. M., DeBruine, L. M., Perrett, D. I., 2008. Facial
 560 correlates of sociosexuality. *Evol. Hum. Behav.* 29, 211-218.
- 561 Boothroyd, L.G., Jones, B.C., Burt, D.M., Perrett, D.I. 2007. Partner characteristics
 562 associated with masculinity, health and maturity in male faces. *Pers. Individ. Diff.* 43,
 563 1161-1173.
- 564 Boothroyd, L. G., Scott, I., Gray, A. W., Coombes, C. I., Pound, N. 2013. Male facial
 565 masculinity as a cue to health outcomes. *Evol. Psychol.* 11, 147470491301100508.
- 566 DeBruine, L.M., 2013. Evidence versus speculation on the validity of methods for measuring
 567 masculinity preferences: comment on Scott et al. *Behav. Ecol.* 24, 591–593.
- 568 DeBruine, L., Jones, B.C., Frederick, D.A., Haselton, M.G., Penton-Voak, I.S., Perrett,
 569 D.I., 2010. Evidence for menstrual cycle shifts in women's preferences for
 570 masculinity: A response to Harris (in press) "Menstrual cycle and facial preferences
 571 reconsidered". *Evolut. Psychol.* 8, 147470491000800416.
- 572 DeBruine, L.M., Tiddeman, B.P., 2016. Webmorph. <http://webmorph.org>.
- 573 Ditzen, B., Palm-Fischbacher, S., Gossweiler, L., Stucky, L., Ehlert, U., 2017. Effects of
 574 stress on women's preference for male facial masculinity and their endocrine
 575 correlates. *Psychoneuroendocrinology.* 82, 67-74.
- 576 Dixon, A. F. (2009). *Sexual selection and the origins of human mating systems*. Oxford
 577 University Press.
- 578 Dixon, A.F, Dixon, B.J, Anderson, M., 2005. Sexual selection and the evolution of
 579 visually conspicuous sexually dimorphic traits in male monkeys, apes, and human
 580 beings. *Ann. Rev. Sex. Res.* 16, 1-19.
- 581 Dixon, B.J.W., 2016. Masculinity and femininity. In T. K. Shackelford & V. A. Weekes-
 582 Shackelford (Eds.), *Encyclopedia of Evolutionary Psychological Science*. Springer.
 583 DOI 10.1007/978-3-319-16999-6_3389-1.
- 584 Dixon, B. J., Brooks, R. C., 2013. The role of facial hair in women's perceptions of men's
 585 attractiveness, health, masculinity and parenting abilities. *Evol. Hum. Behav.* 34, 236-
 586 241.
- 587 Dixon, B. J. W, Lee, A. J., Sherlock, J. M., Talamas, S. N., 2017a. Beneath the beard:
 588 Do facial morphometrics influence the strength of judgments of men's beardedness?
 589 *Evol. Hum. Behav.* 38, 164-174.
- 590 Dixon, B. J. W, Little, A. C., Dixon, H. G., & Brooks, R. C., 2017b. Do prevailing
 591 environmental factors influence human preferences for facial morphology? *Behav.*
 592 *Ecol.* 28, 1217-1227.
- 593 Dixon, B. J.W, Rantala, M. J., 2016. The role of facial and body hair distribution in
 594 women's judgments of men's sexual attractiveness. *Arch. Sex. Behav.* 45, 877-889.
- 595 Dixon, B.J.W, Rantala, M.J., 2017. Further evidence using a continuous measure of
 596 conception probability that women's preferences for male facial and body hair may not
 597 change with fecundability. *Arch. Sex. Behav.* doi:10.1007/s10508-017-0973-x.
- 598 Dixon, B. J. W., Rantala, M. J., Melo, E. F., Brooks R. C., 2017c. Beards and the big city:
 599 Displays of masculinity may be amplified under crowded conditions. *Evol. Hum.*
 600 *Behav.* 38, 259-264.

- 601 Dixon, B. J.W., Sullikowski, D., Gouda-Vossos A., Rantala, M. J., Brooks R. C., 2016.
 602 The masculinity paradox: Facial masculinity and beardedness interact to determine
 603 women's ratings of men's facial attractiveness *J. Evol. Biol.* 29, 2311-2320.
- 604 Dixon, B. J., Tam, J. C., Awasthy, M., 2013. Do women's preferences for men's facial
 605 hair change with reproductive status? *Behav. Ecol.* 24, 708-716.
- 606 Dixon, B. J., Vasey, P. L., 2012. Beards augment perceptions of men's age, social status,
 607 and aggressiveness, but not attractiveness. *Behav. Ecol.* 23, 481-490.
- 608 Escasa-Dorne, M. J., Manlove, H., Gray, P. B., 2017. Women express a preference for
 609 feminized male faces after giving birth. *Adap. Hum. Behav. Physiol.* 1, 30-42.
- 610 Feinberg, D.R., Jones, B.C., Law Smith, M.J., Moore, F.R., DeBruine, L.M., Cornwell, R.E.,
 611 Hillier, S.G., Perrett, D.I., 2006. Menstrual cycle, trait estrogen level, and masculinity
 612 preferences in the human voice. *Horm. Behav.* 49, 215–222.
- 613 Fink, B., Neave, N., Seydel, H., 2007. Male facial appearance signals physical strength to
 614 women. *Am. J. Hum. Biol.* 19, 82-87.
- 615 Foo, Y. Z., Nakagawa, S., Rhodes, G., & Simmons, L. W., 2017. The effects of sex
 616 hormones on immune function: a meta-analysis. *Biol. Rev.* 92, 551-571.
- 617 Gangestad, S.W., Haselton, M.G., 2015. Human estrus: implications for relationship science.
 618 *Curr. Opin. Psychol.* 1, 45-51.
- 619 Gangestad, S. W., Haselton, M. G., Welling, L. L., Gildersleeve, K., Pillsworth, E. G.,
 620 Burriss, R. P., ... Puts, D. A., 2016. How valid are assessments of conception
 621 probability in ovulatory cycle research? Evaluations, recommendations, and
 622 theoretical implications. *Evol. Hum. Behav.* 37, 85-96.
- 623 Gangestad, S. W., Simpson, J. A., 2000. The evolution of human mating: Trade-offs and
 624 strategic pluralism. *Behav. Brain. Sci.* 23, 573-587.
- 625 Gangestad, S. W., Thornhill, R., 2008. Human oestrus. *Proc. R. Soc. Lond. B: Biol. Sci.* 275,
 626 991-1000.
- 627 Gangestad, S. W., Thornhill, R., Garver-Apgar, C. E., 2010. Men's facial masculinity
 628 predicts changes in their female partners' sexual interests across the ovulatory cycle,
 629 whereas men's intelligence does not. *Evol. Hum. Behav.* 31, 412-424.
- 630 Geniole, S. N., Denson T. F., Dixon B. J., Carré, J.M., McCormick, C. M., 2015. Evidence
 631 from meta analyses of the facial width-to-height ratio as an evolved cue of threat. *PloS*
 632 *ONE*, 10(7): e0132726. doi:10.1371/journal.pone.0132726.
- 633 Geniole, S. N., McCormick, C. M., 2015. Facing our ancestors: judgements of aggression
 634 are consistent and related to the facial width-to-height ratio in men irrespective of
 635 beards. *Evol. Hum. Behav.* 36, 279-285.
- 636 Gettler, L. T., 2014. Applying socioendocrinology to evolutionary models: fatherhood and
 637 physiology. *Evol. Anthropol.* 23, 146-160.
- 638 Gildersleeve, K., DeBruine, L., Haselton, M. G., Frederick, D. A., Penton-Voak, I. S., Jones,
 639 B. C., Perrett, D. I., 2013. Shifts in women's mate preferences across the ovulatory
 640 cycle: A critique of Harris (2011) and Harris (2012). *Sex Roles.* 69, 516-524.
- 641 Gildersleeve, K., Haselton, M.G., Fales, M.R., 2014a. Do women's mate preferences change
 642 across the ovulatory cycle? A meta-analytic review. *Psych. Bull.* 140, 1205–1259.
- 643 Gildersleeve, K., Haselton, M.G., Fales, M.R., 2014b. Meta-analyses and p-curves support
 644 robust cycle shifts in women's mate preferences: reply to Wood and Carden (2014)
 645 and Harris, Pashler, and Mickes (2014). *Psych. Bull.* 140, 1272–1280.
- 646 Grueter, C. C., Isler, K., & Dixon, B. J., 2015. Are badges of status adaptive in large
 647 complex primate groups? *Evol. Hum. Behav.* 36, 398-406.
- 648 Hamilton, J. B., 1964. Racial and genetic predisposition. *Clin. Obstet. Gynaecol.* 7,1075-1084.
- 649 Harris, C.R., 2011. Menstrual cycle and facial preferences reconsidered. *Sex Roles*, 64, 669-
 650 681.

- 651 Harris, C.R., 2013. Shifts in masculinity preferences across the menstrual cycle: Still not
652 there. *Sex Roles*. 69, 507-515.
- 653 Harris, C.R., Chabot, A., Mickes, L., 2013. Shifts in methodology and theory in menstrual
654 cycle research on attraction. *Sex Roles*. 69, 525-535.
- 655 Harris, C.R., Pashler, H., Mickes, L., 2014. Elastic analysis procedures: an incurable (but
656 preventable) problem in the fertility effect literature. Comment on Gildersleeve,
657 Haselton, and Fales (2014). *Psychol. Bull.* 140, 1260–1264.
- 658 Hill, A. K., Hunt, J., Welling, L. L., Cárdenas, R. A., Rotella, M. A., Wheatley, J. R., ...
659 Puts, D. A., 2013. Quantifying the strength and form of sexual selection on men's
660 traits. *Evol. Hum. Behav.* 34, 334-341.
- 661 Janif, Z. J., Brooks, R. C., Dixson, B. J., 2014. Negative frequency-dependent preferences
662 and variation in male facial hair. *Biol. Lett.* 10(4), 20130958.
- 663 Jasienska, G., 2003. Energy metabolism and the evolution of reproductive suppression in the
664 human female. *Acta. Biotheor.* 51, 1-18.
- 665 Jasienska, G., Kapiszewska, M., Ellison, P.T., et al., 2006. CYP17 genotypes differ in
666 salivary 17-beta estradiol levels: A study based on hormonal profiles from entire
667 menstrual cycles. *Cancer. Epidemiol. Biomarkers. Prevent.* 15, 2131-5.
- 668 Jasienska, G., Ziomkiewicz, A., Lipson, S.F., Thune, I., Ellison, P.T., 2006. High ponderal
669 index at birth predicts high estradiol levels in adult women. *Am. J. Hum. Biol.* 18,
670 133-40.
- 671 Jasienska, G., Jasienski, M., 2008. Interpopulation, interindividual, intercycle, and intracycle
672 natural variation in progesterone levels: A quantitative assessment and implications
673 for population studies. *Am. J. Hum. Biol.* 20, 35-42.
- 674 Jones, B. C., Hahn, A. C., Fisher, C. I., Wang, H., Kandrik, M., Han, C., Fasolt, V., Morrison,
675 D., Lee, A., Holzleitner, I., Roberts, S. C., Little, A., & DeBruine, L. (2017). Women's
676 preferences for facial masculinity are not related to their hormonal status. Doi:
677 <http://dx.doi.org/10.1101/136549>.
- 678 Jukic, A.M.Z., Weinberg, C.R., Wilcox, A.J., McConnaughey, D.R., Hornsby, P., Baird,
679 D.D., 2008. Accuracy of reporting of menstrual cycle length. *Am. J. Epidemiol.* 167,
680 25–33.
- 681 Knussman, R., Christiansen, K., 1988. Attributes of masculinity and androgen level. *Homo.*
682 39, 45-50.
- 683 Kokko, H., Brooks, R., Jennions, M. D., Morley, J., 2003. The evolution of mate choice and
684 mating biases. *Proc. R. Soc. Lond. B: Biol. Sci.* 270, 653-664.
- 685 Kruger, D. J., 2006. Male facial masculinity influences attributions of personality and
686 reproductive strategy. *Pers. Relat.* 13, 451-463.
- 687 Lee, A.J., Mitchem, D.G., Wright, M.J., Martin, N.G., Keller, M.C., Zietsch, B.P., 2014.
688 Genetic factors that increase male facial masculinity decrease facial attractiveness of
689 female relatives. *Psychol. Sci.* 25, 476–484.
- 690 Lee, A. J., Zietsch, B. P., 2015. Women's pathogen disgust predicting preference for facial
691 masculinity may be specific to age and study design. *Evol. Hum. Behav.* 36, 249-255.
- 692 Lipson, S.F., Ellison, P.T., 1992. Normative study of age variation in salivary progesterone
693 profiles. *J. Biosoc. Sci.* 24, 233-44.
- 694 Lipson, S.F., Ellison, P.T., 1996. Comparison of salivary steroid profiles in naturally
695 occurring conception and non-conception cycles. *Hum. Reprod.* 11, 2090–2096.
- 696 Little, A. C., Jones, B. C., 2012. Variation in facial masculinity and symmetry preferences
697 across the menstrual cycle is moderated by relationship context.
698 *Psychoneuroendocrinology*, 37, 999-1008.
- 699 Little, A.C., Jones, B.C., & DeBruine, L.M., 2008. Preferences for variation in masculinity

- 700 in real male faces change across the menstrual cycle: Women prefer more masculine
 701 faces when they are more fertile. *Pers. Individ. Diff.* 45, 478-482.
- 702 Little, A.C., Jones, B.C., DeBruine, L.M., 2011. Facial attractiveness: Evolutionary based
 703 research. *Phil. Trans. R. Soc. B: Biol. Sci.* 366, 1638-1659.
- 704 Marcinkowska, U.M., Ellison, P.T., Galbarczyk, A., Milkowska, K., Pawlowski, B., Thune,
 705 I., & Jasienska, G., 2016. Lack of support for relation between woman's masculinity
 706 preference, estradiol level and mating context. *Horm. Behav.* 78, 1-7.
- 707 McIntosh, T., Lee, A. J; Sidari, M., Stower, R., Sherlock, J. M., Dixson B. J. W., 2017.
 708 Microbes and masculinity: Does exposure to pathogenic cues alter women's
 709 preferences for male facial masculinity and beardedness? *PloS One*, 12(6), e0178206.
- 710 Muehlenbein MP, Bribiescas RG., 2005. Testosterone-mediated immune functions and male
 711 life histories. *Am. J. Hum. Biol.* 17, 527-58.
- 712 Muscarella, F., Cunningham, M.R., 1996. The evolutionary significance and social
 713 perception of male pattern baldness and facial hair. *Ethol. Sociobiol.* 17, 99-117.
- 714 Neave, N., Shields, K., 2008. The effects of facial hair manipulation on female perceptions of
 715 attractiveness, masculinity, and dominance in male faces. *Pers. Individ. Diff.* 45, 373-
 716 377.
- 717 Oldmeadow, J. A., Dixson, B. J., 2016a. The association between men's sexist attitudes
 718 and facial hair. *Arch. Sex. Behav.* 45, 891-899.
- 719 Oldmeadow, J. A., Dixson, B. J., 2016b. No contradictions, but directions for further
 720 research: A reply to Hellmer and Stenson. *Arch. Sex. Behav.* 45, 785-786.
- 721 Pawlowski, B., Jasienska, G., 2005. Women's preferences for sexual dimorphism in height
 722 depend on menstrual cycle phase and expected duration of relationship. *Biol. Psychol.*
 723 70, 38-43.
- 724 Pellegrini, R.J. 1973. Impressions of the male personality as a function of beardedness.
 725 *Psychology*, 10, 29-33.
- 726 Peters, M., Simmons, L.W., Rhodes, G., 2009. Preferences across the menstrual cycle for
 727 masculinity and symmetry in photographs of male faces and bodies. *PloS one*, 4(1),
 728 e4138.
- 729 Perrett, D.I., Lee, K.J., Penton-Voak, I., Rowland, D., Yoshikawa, S., Burt, D.M., . . .
 730 Akamatsu, S., 1998. Effects of sexual dimorphism on facial attractiveness. *Nature*.
 731 394, 884-887.
- 732 Penton-Voak, I.S., & Perrett, D.I., 2000. Female preference for male faces changes
 733 cyclically: Further evidence. *Evol. Hum. Behav.* 21, 39-48.
- 734 Penton-Voak, I.S., Perrett, D.I., Castles, D.L., Kobayashi, T., Burt, D.M., Murray, L.K.,
 735 Minamisawa, R., 1999. Menstrual cycle alters face preference. *Nature*, 399, 741-742.
- 736 Phalane, K. G., Tribe, C., Steel, H. C., Cholo, M. C., & Coetzee, V. (2017). Facial appearance
 737 reveals immunity in African men. *Scientific Reports*, 7.
- 738 Popat, V.B., Prodanov, T., Calis, K.A., & Nelson, L.M. 2008. The menstrual cycle.
 739 *Ann. N. Y. Acad. Sci.* 1135, 43-51.
- 740 Puts, D. A., 2005. Mating context and menstrual phase affect women's preferences for male
 741 voice pitch. *Evol. Hum. Behav.* 26, 388-397.
- 742 Puts, D. A., 2010. Beauty and the beast: mechanisms of sexual selection in humans. *Evol.*
 743 *Hum. Behav.* 31, 157-175.
- 744 Puts, D.A., Bailey, D.H., Cárdenas, R.A., Burriss, R.P., Welling, L.L., Wheatley, J.R.,
 745 Dawood, K., 2013. Women's attractiveness changes with estradiol and progesterone
 746 across the ovulatory cycle. *Horm. Behav.* 63,13-19.
- 747 Randall, V. A., 2008. Androgens and hair growth. *Dermatol. Ther.* 21, 314-328.
- 748 Rhodes, G., 2006. The evolutionary psychology of facial beauty *Ann. Rev. Psychol.* 57, 199-
 749 226.

- 750 Rhodes, G., Morley, G., Simmons, L.W., 2013. Women can judge sexual unfaithfulness
751 from unfamiliar men's faces. *Biol. Lett.* 9(1), 20120908.
- 752 Rhodes, G., Simmons, L.W., Peters, M., 2005. Attractiveness and sexual behavior: Does
753 attractiveness enhance mating success? *Evol. Hum. Behav.* 26, 186-201.
- 754 Rhodes, G., Chan, J., Zebrowitz, L.A., Simmons, L.W., 2003. Does sexual dimorphism
755 in human faces signal health? *Proc. R. Soc. Lond. B: Biol. Sci.* 270, S93-S95.
- 756 Robinson, D.E., 1976. Fashions in shaving and trimming of the beard: The men of the
757 *Illustrated London News*, 1842-1972. *Am. J. Sociol.* 81, 1133-1141.
- 758 Roney, J.R., Simmons, Z.L., 2008. Women's estradiol predicts preference for facial cues of
759 men's testosterone. *Horm. Behav.* 53, 14-19.
- 760 Roney, J. R., Simmons, Z. L., 2013. Hormonal predictors of sexual motivation in natural
761 menstrual cycles. *Horm. Behav.* 63, 636-645.
- 762 Roney, J.R., Simmons, Z.L., Gray, P.B., 2011. Changes in estradiol predict within women
763 shifts in attraction to facial cues of men's testosterone. *Psychoneuroendocrinology*, 36,
764 742-749.
- 765 Sacco, D. F., Jones, B. C., DeBruine, L. M., & Hugenberg, K. (2012). The roles of
766 sociosexual orientation and relationship status in women's face preferences. *Pers.*
767 *Indiv. Diff.* 53, 1044-1047.
- 768 Saxton, T.K., Mackey, L.L., McCarty, K., Neave, N., 2016. A lover or a fighter? Opposing
769 sexual selection pressures on men's vocal pitch and facial hair. *Behav. Ecol.* 27, 512–
770 519.
- 771 Schultheiss, O.C., Stanton, S.J., (2009). Assessment of salivary hormones. In: Harmon-Jones,
772 E., Beer, J.S., eds. *Methods in Social Neuroscience*. New York: Guilford Press.
- 773 Scott, I., Clark, A., Boothroyd, L., Penton-Voak, I., 2013. Do men's faces really signal
774 heritable immunocompetence? *Behav. Ecol.* 24, 579-589.
- 775 Scott, I.M., Clark, A.P., Josephson, S.C., Boyette, A.H., Cuthill, I.C., Fried, R.L., . . .
776 Jankowiak, W., 2014. Human preferences for sexually dimorphic faces may be
777 evolutionarily novel. *Proc. Nat. Acad. Sci. U.S.A.* 111, 14388-14393.
- 778 Sherlock, J.M., Tegg, B., Sulikowski, D., Dixon, B. J., 2017. Facial masculinity and
779 beardedness determine men's explicit, but not their implicit, responses to male
780 dominance. *Adapt. Hum. Behav. Physiol.* 3, 14–29.
- 781 Small, C.M., Manatunga, A.K., Marcus, M., 2007. Validity of self-reported menstrual cycle
782 length. *Ann. Epidemiol.* 17, 163–170.
- 783 Sollberger, S., Ehlert, U. 2016. How to use and interpret hormone ratios.
784 *Psychoneuroendocrinology*, 63, 385-397.
- 785 Thornhill, R., Gangestad, S.W. 2006. Facial sexual dimorphism, developmental stability,
786 and susceptibility to disease in men and women. *Evol. Hum. Behav.* 27. 131-144.
- 787 Trotter, M., (1922). A study of facial hair in the White and Negro races. *Wash. Univ. Stud.* 9,
788 273-289.
- 789 Twisk, J.W.R., 2006. *Applied multilevel analysis: A practical guide for medical researchers*
790 (6th edition). Cambridge, UK: Cambridge University Press.
- 791 Valentova, J.V., Varella, M., Bártová, K., Štěrbová, Z., & Dixon, B.J.W. 2017. Mate
792 preferences and choices for facial and body hair in heterosexual women and
793 homosexual men: Effects of sex, population, homogamy, and imprinting-like effects.
794 *Evol. Hum. Behav.* 38, 241-248.
- 795 Wagenmakers, E. J., Love, J., Marsman, M., Jamil, T., Ly, A., Verhagen, J., ... & Meerhoff,
796 F. (2017). Bayesian inference for psychology. Part II: example applications with
797 JASP. *Psychon. Bull. Rev.* 1-19.
- 798 Wallen, K., & Rupp, H. A. (2010). Women's interest in visual sexual stimuli varies with
799 menstrual cycle phase at first exposure and predicts later interest. *Horm. Behav.* 57,

- 800 263-268.
- 801 Wang, H., Hahn, A.C., Fisher, C.I., DeBruine, L.M., Jones, B.C. 2014. Women's hormone
802 levels modulate the motivational salience of facial attractiveness and sexual
803 dimorphism. *Psychoneuroendocrino.* 50, 246-251.
- 804 Welling, L.L., Jones, B.C., DeBruine, L.M., Conway, C.A., Law Smith, M.J., Little, A.C.,
805 Feinberg, D.R., Sharp, M.A., Al-Dujaili, E.A., 2007. Raised salivary testosterone in
806 women is associated with increased attraction to masculine faces. *Horm. Behav.* 52,
807 156–161.
- 808 Whitehouse, A. J., Gilani, S. Z., Shafait, F., Mian, A., Tan, D. W., Maybery, M. T., ... &
809 Eastwood, P. (2015). Prenatal testosterone exposure is related to sexually dimorphic
810 facial morphology in adulthood. In *Proc. R. Soc. B.* 282, 20151351.
- 811 Windhager, S., Schaefer, K., & Fink, B., 2011. Geometric morphometrics of male facial
812 shape in relation to physical strength and perceived attractiveness, dominance, and
813 masculinity. *Am. J. Hum. Biol.* 23, 805-814.
- 814 Wong, B. B., & Candolin, U. (2005). How is female mate choice affected by male
815 competition? *Biol. Rev.* 80, 559-571.
- 816 Wood, D.R. 1986. Self-perceived masculinity between bearded and non-bearded males.
817 *Percept. Mot. Skills.* 62, 769-770.
- 818 Wood, W., Carden, L., 2014. Elusiveness of menstrual cycle effects on mate preferences:
819 comment on Gildersleeve, Haselton, and Fales (2014). *Psychol. Bull.* 140, 1265–1271.
- 820 Wood, W., Kressel, L., Joshi, P.D., Louie. B., 2014. Meta-analysis of menstrual cycle effects
821 on women's mate preferences. *Emot. Rev.* 6, 229–249.
- 822 Zietsch, B.P., Lee, A.J., Sherlock, J.M., Jern, P. 2015. Variation in women's facial
823 masculinity preference is better explained by genetic differences than by previously
824 identified context-dependent effects. *Psychol. Sci.* 28, 1440-1448.
- 825 Ziomkiewicz, A., Ellison, P.T., Lipson, S.F., Thune, I., Jasienska, G., 2008. Body fat, energy
826 balance and estradiol levels: a study based on hormonal profiles from complete
827 menstrual cycles. *Hum. Reprod.* 23, 2555-63.

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 ($ps \geq .393$).