

1 **Ovulation, sex hormones, and women’s mating psychology**

2

3

Benedict C Jones¹, Amanda C Hahn², Lisa M DeBruine¹

4

5 1. Institute of Neuroscience & Psychology, University of Glasgow, Scotland, UK

6

2. Department of Psychology, Humboldt State University, California, USA

7

8 Corresponding author

9 Benedict Jones (ben.jones@glasgow.ac.uk), Institute of Neuroscience & Psychology,

10 University of Glasgow, Scotland, UK.

11

12 **Acknowledgments**

13 This work was supported by ERC grants awarded to BCJ (OCMATE) and LMD (KINSHIP). We

14 thank Ruben Arslan, Julia Jünger, Steve Gangestad, Tanja Gerlach, Anthony Lee, Lars Penke,

15 James Roney, and Brendan Zietsch for discussions.

16

17 **Keywords**

18 menstrual cycle; mate preferences; mating; attractiveness; person perception

19

20

21 Abstract

22 The Dual Mating Strategy hypothesis proposes that women's preferences for uncommitted
23 sexual relationships with men displaying putative fitness cues increase during the high-fertility
24 phase of the menstrual cycle. Results consistent with this hypothesis are widely cited as
25 evidence that sexual selection has shaped human mating psychology. However, the methods
26 used in most of these studies have recently been extensively criticized. Here we discuss (1)
27 new empirical studies that address these methodological problems and largely report null
28 results and (2) an alternative model of hormonal regulation of women's mating psychology
29 that can better accommodate these new data.

30

31

32

33

34

35

36

37

38

39

40

41

42

43

44

45

46

47

48

49

50

51

52

53

54 The Dual Mating Strategy hypothesis

55 Effects of fertility and hormonal status on women's mate preferences and sexual desire are
56 widely cited as evidence that sexual selection (natural selection operating on the ability to
57 obtain a mate) has shaped mating psychology in humans [1-8]. But do hormones regulate
58 mating psychology in women? If so, how? And why? The last twenty years of research on this
59 topic has been dominated by the Dual Mating Strategy hypothesis [1-8]. The Dual Mating
60 Strategy hypothesis of ovulatory shifts in mating psychology proposes that heterosexual
61 women show stronger preferences for uncommitted sexual relationships with men displaying
62 putative cues of reproductive fitness (e.g., masculinized faces) during the high-fertility
63 ovulatory phase of the menstrual cycle, while preferring long-term relationships with men
64 displaying putative cues of prosociality, (e.g., feminized faces), at other points in the
65 menstrual cycle [1-8]. In the most common version of this hypothesis these putative cyclic
66 shifts in mate preferences and mating strategies (i.e., mating psychology) are predicted
67 because they would, in theory, maximize the potential benefits of women's mate choices by
68 seeing them secure prosocial, investing long-term partners while fathering healthy children
69 via short-term relationships with men with heritable immunity to infectious illnesses.
70 Controversially, obtaining good fitness genes for offspring via 'stealth' (i.e., cuckoldry) is an
71 explicit feature of the Dual Mating Strategy hypothesis [1-8].

72

73 In this article, we will discuss evidence from new large-scale studies that strongly challenge
74 this dominant and influential hypothesis. We also outline how the results of these new
75 studies instead support an alternative framework in which women's general mating
76 motivation increases during the fertile phase of the menstrual cycle, potentially reflecting
77 fertility-linked change in motivational priorities [9].

78

79

80 **Evidence for the Dual Mating Strategy hypothesis**

81 Although the links are debated [see Box 1], some studies have reported that masculine
82 characteristics in men's faces are positively associated with good physical health [10] and
83 immunocompetence [11] and negatively associated with prosociality and willingness to invest
84 effort in relationships [12,13]. Consequently, one of the most common tests of the Dual
85 Mating Strategy hypothesis has been to compare preferences for masculine male faces when
86 women are tested during the ovulatory phase of the menstrual cycle and during other phases
87 [1]. Figure 1 shows examples of the type of stimuli (masculinized and feminized faces)
88 typically used to test this hypothesis. One early, and particularly influential, study to have

89 used such stimuli [2] found that women showed stronger preferences for masculine male
90 faces when tested during the ovulatory phase of the menstrual cycle than when tested
91 outside this high-fertility window. This cyclic shift in masculinity preference appeared to be
92 most pronounced when partnered women (i.e., women in romantic relationships) assessed
93 men's attractiveness for hypothetical short-term, rather than long-term, relationships. Many
94 subsequent studies of women's preferences for facial masculinity reported similar results
95 [4,14-21].

96
97 Similar patterns of results have also been reported by studies investigating changes in
98 women's preferences for other putative fitness cues in men, such as body masculinity [22],
99 vocal masculinity [23,24], facial symmetry [20,25], body odors of symmetric [26,27] or
100 dominant [28] men, and behavioral displays of dominance [29,30]. Because the ovulatory
101 phase of the menstrual cycle is characterized by high estradiol and low progesterone ([31] see
102 Figure 2), cyclic shifts in women's mate preferences are generally thought to reflect the
103 effects of estradiol and/or progesterone [17,19,21]. This being the case, the Dual Mating
104 Strategy hypothesis also predicts that women's mate preferences will track changes in
105 estradiol and/or progesterone, although some research has also implicated testosterone [16]
106 and cortisol [21].

107
108 Findings consistent with the Dual Mating Strategy hypothesis, such as those described above,
109 are influential and widely cited as evidence that sexual selection has shaped women's mate
110 preferences [1-8]. However, there have recently been several prominent methodological
111 criticisms of these studies.

112

113 **Methodological problems with previous research**

114 First, power analyses show that the majority of studies cited as evidence for the Dual Mating
115 Strategy hypothesis are underpowered, many very badly so [34]. For example, to detect a
116 medium effect with 80% power in a within-subject design when the timing and/or occurrence
117 of ovulation was confirmed requires 55 to 71 participants, depending on whether participants
118 were assigned to specific high- and low-fertility test sessions or a representative random
119 sample of cycle days were tested [34]. To detect a medium effect with 80% power in a
120 between-subject design would require 900 to 1000 participants [34]. Importantly, very few
121 published studies reporting significant effects of cycle phase on mate preferences meet these
122 criteria [34,35]. For example, the mean sample size in within-subject studies reporting

123 significant effects of fertility on facial masculinity preferences published before 2018 is 40 and
124 the median is 34 [35].

125

126 Second, most studies cited as evidence for the Dual Mating Strategy hypothesis relied on self-
127 report data regarding the number of days since the onset of the last period of menstrual
128 bleeding or expected number of days until the onset of the next period of menstrual bleeding
129 to estimate women's position in the menstrual cycle [1,34,36]. Both empirical [37] and
130 simulation [34] studies clearly demonstrate that such self-report methods do a poor job of
131 reliably estimating women's position in the menstrual cycle. Nonetheless, a longitudinal study
132 of over 26,000 diary entries from 1043 women [38], recently showed that robust effects of
133 fertility on aspects of mating psychology can be obtained using self-report diary data in large
134 longitudinal datasets.

135

136 Third, studies testing the Dual Mating Strategy hypothesis have often used cross-sectional
137 (i.e., between-subject) designs [1,31]. These studies have reported mixed results, potentially
138 because they were generally particularly badly underpowered [34] and/or because the
139 substantial genetic variation in mate preferences [39] means between-subject designs are
140 unsuitable for detecting what are presumably relatively subtle effects of sex hormones on
141 preferences. Because of these issues, researchers have recently emphasized the importance
142 of using longitudinal (i.e., within-subject) designs to test for changes in women's mate
143 preferences during the menstrual cycle [1,31,35].

144

145 **Do recent studies support the Dual Mating Strategy hypothesis?**

146 There has recently been a concerted effort by many researchers to address these potentially
147 important methodological limitations. For example, several recent large-scale, within-subject
148 studies have investigated women's preferences for facial masculinity [40-42], beardedness
149 [42,43], body masculinity [41,44], facial symmetry [41], or vocal masculinity [45] using
150 luteinizing hormone (LH) tests and/or other hormone measures to confirm the timing and
151 occurrence of ovulation. Notably, none of these studies observed significant effects of fertility
152 on women's preferences for masculine or symmetric men. Those within-subject studies
153 testing whether women's preferences for facial masculinity, facial symmetry, or body
154 masculinity tracked changes in salivary estradiol and/or progesterone also typically found no
155 evidence for hormonal regulation of women's mate preferences [35,46]. Although some
156 longitudinal studies have reported positive effects of estradiol and/or negative effects of

157 progesterone on women's masculinity preferences [42,47], the largely null results from these
 158 rigorous tests of the Dual Mating Strategy hypothesis suggest that the previously reported
 159 effects of cycle phase and steroid hormones on mate preferences are either not robust or are
 160 more complicated than has previously been claimed. Key features of recent longitudinal
 161 studies of women's mate preferences that challenge the Dual Mating Strategy hypothesis are
 162 summarized in Table 1.

163

164 **Table 1.** Mate-preference studies challenging the Dual Mating Strategy hypothesis.

165

Study	N	Frequency of testing	Key outcome variables	Confirmed ovulation?	Evidence for within-women correlations with conception risk?	Evidence for within-women correlations with hormone levels?
Marcinkowska et al. 2016 [40]	115	daily (over one cycle)	facial masculinity preference	yes	no	not tested
Marcinkowska et al. 2018 [41]	110	daily (over one cycle)	facial masculinity and symmetry preferences; body masculinity preference	yes	no	not tested
Dixon et al. 2018 [42]	68	twice (at high and low fertility)	facial masculinity preference	yes	no	yes (in sub-group of 36 women from whom saliva samples were collected)
Jünger et al. 2018 [44]	157	weekly (over two cycles)	body masculinity preference	yes	no	no
Marcinkowska et al. 2018 [46]	105	daily (over one cycle)	facial masculinity and symmetry preferences; body masculinity preference	yes	not tested	no
Jones et al. 2018 [35]	351	weekly (over one)	facial masculinity	no	not tested	no

		to three cycles)	and symmetry preferences			
Jünger et al. 2018 Study 1 [45]	195	twice (at high and low fertility)	vocal masculinity	no	no	no
Jünger et al. 2018 Study 2 [45]	112	weekly (over one cycle)	vocal masculinity	yes	no	no

166

167 Some researchers have criticized the ecological validity of studies that manipulated the type
 168 of relationship women judged men's attractiveness for (short-term versus long-term) in
 169 research on hormonal regulation of women's mate preferences [48]. Might this
 170 methodological issue explain the null results in these studies? We suggest that this is unlikely.

171 The studies described above that reported no significant effect of cycle phase or hormone
 172 levels on women's mate preferences and considered possible effects of relationship type
 173 typically observed significant effects of relationship type on mate preferences that did not
 174 interact with fertility and/or hormone levels [e.g., 35]. It is also clearly problematic to dismiss
 175 studies reporting null results that used this method, while accepting positive results from
 176 studies using the same method (e.g., [2]).

177

178 Two of the studies reporting null results for cyclic shifts in mate preferences used a relatively
 179 small number of stimuli in some of their preference tests [41,46]. Might this explain the null
 180 results in their studies? Again, we suggest that this is unlikely. While these studies observed
 181 no significant within-subject effects of fertility [41] or hormone levels [46] on women's
 182 preferences for body masculinity, these null results appear unlikely to be a consequence of
 183 the relatively small number of items (three) that they used to assess body preferences. In that
 184 data set, women's body preferences were correlated with their average hormone levels (i.e.,
 185 between-women differences), but not daily hormone levels (i.e., within-woman changes)
 186 [46]. The potential function of such effects of average hormone levels is currently unclear,
 187 however.

188

189 Null results have also been reported in several studies testing the Dual Mating Strategy
 190 hypothesis using between-subject comparisons of women's masculinity preferences
 191 [39,40,42,49-52]. Given that between-subjects designs are likely to be ill equipped to test for
 192 hormonal regulation of mate preferences (see earlier discussion), these null results are more
 193 difficult to interpret, however [35]. Nonetheless, it is perhaps noteworthy that some of these

194 studies reported negative (rather than null) effects in some of their analyses [39,50]. These
195 negative effects would be particularly unlikely to occur if there was a robust positive effect of
196 fertility on masculinity preferences [39,50].

197

198 **The Dual Mating Strategy hypothesis and sexual desire**

199 While most research on the Dual Mating Strategy hypothesis has investigated changes in
200 women's mate preferences, other research has investigated how other aspects of women's
201 sexual desire change over the menstrual cycle. Consistent with the Dual Mating Strategy
202 hypothesis, one recent longitudinal study found that partnered women reported greater
203 extra-pair sexual desire (i.e., greater desire for sex with men other than their primary partner)
204 during the ovulatory phase of the menstrual cycle [53]. Another recent cross-sectional study
205 with a large sample size found that women reported more openness to uncommitted sexual
206 relationships during the high-fertility phase of the menstrual cycle than during low-fertility
207 phases [46].

208

209 The results described above might initially appear consistent with the Dual Mating Strategy
210 hypothesis's proposal that cyclic changes in mating psychology function to increase extra-pair
211 sex during ovulation. However, other recent work suggests that that interpretation may be
212 problematic. For example, longitudinal studies have reported similar patterns for cyclic shifts
213 in both in-pair and extra-pair desire [38,54]. Indeed, while some early small-scale studies
214 suggested that cyclic changes in extra-pair desire were moderated by individual differences in
215 the physical attractiveness of women's romantic partners [e.g., 6,55] these results did not
216 replicate reliably in a recent large-scale study [38] or in another recent study on a similar
217 scale to the original work [53].

218

219 Other studies have reported hormone-linked changes in sexual desire that are not target-
220 specific [54], including desire for sexual activity without a partner [56]. A large longitudinal
221 study also found no evidence that openness to uncommitted sexual relationships was
222 significantly related to changes in steroid hormone levels during the menstrual cycle [56].
223 Together, these results suggest a general change in sexual desire, rather than the specific
224 change in extra-pair sexual desire proposed by the Dual Mating Strategy hypothesis. We also
225 suggest here that these results indicating the existence of a general increase in sexual desire
226 around ovulation are potentially problematic for the Extended Sexuality hypothesis, an

227 alternative model of hormonal regulation of sexual desire that is more focused on fertility-
228 linked change in *in*-pair sexual desire (see Box 2).

229

230 **Do oral contraceptives alter mating psychology?**

231 Most of the research testing the Dual Mating Strategy hypothesis has focused on fertility-
232 and/or hormone-linked changes in mate preferences and sexual desire in women not using
233 any form of hormonal contraceptive (i.e., women with ‘natural’ menstrual cycles). Other
234 studies, however, tested for converging evidence for the Dual Mating Strategy hypothesis by
235 investigating putative effects of oral contraceptive use on women’s mate preferences,
236 romantic relationships, and sexual desire, since oral contraceptives prevent the hormonal
237 profile associated with the high-fertility ovulatory phase. The rationale for this approach is
238 that oral contraceptive use suppresses ovulation and associated hormonal changes.

239

240 Several early studies reported that women using oral contraceptives showed weaker
241 preferences for masculine men than did women not using oral contraceptives [57,58]. These
242 results were interpreted as converging evidence for a positive association between fertility
243 and women’s masculinity preferences and preliminary evidence that oral contraceptives
244 might alter women’s mate preferences [57,58]. These results have not replicated well,
245 however, with some studies reporting between-group differences in the opposite direction to
246 those reported in the original studies [35,59].

247

248 Of course, women who use oral contraceptives and women who do not use oral
249 contraceptives will likely differ in many ways other than their use of oral contraceptives,
250 meaning that within-subject studies are necessary to establish whether oral contraceptive use
251 does alter women’s mate preferences [60,61]. The first of such studies reported that
252 masculinity preferences weakened after women began using oral contraceptives [61].
253 However, a subsequent larger study did not replicate this effect and found no evidence that
254 oral contraceptive use altered other aspects of women’s mate preferences [35]. Furthermore,
255 this latter study found no evidence that oral contraceptive users’ mate preferences changed
256 when they were on “placebo pills” (i.e., taking pills containing no exogenous hormones).

257

258 While the studies described above investigated the effects of oral contraceptive use on
259 women’s mate preferences directly, other research has investigated whether changes in oral
260 contraceptive use after relationship formation disrupt women’s relationship satisfaction.

261 Congruency in current and previous oral contraceptive use (but not use of oral contraceptives
262 alone) predicted women's relationship satisfaction [62,63]. Again, however, a more recent
263 high-powered study did not replicate these effects, suggesting that they are not robust [64].
264 Collectively, these results present little evidence for a reliable effect of oral contraceptive use
265 on women's mate preferences or relationship satisfaction. Indeed, double-blind, randomized,
266 placebo-controlled trials find little clear evidence that oral contraceptive use affects sexual
267 functioning [65], but do find that oral contraceptive use decreases general wellbeing [66].
268 However, there was some preliminary evidence that specific sub-components of sexual
269 functioning (e.g., desire) are affected by oral contraceptive use [65]. This latter preliminary
270 evidence would be consistent with other recent work suggesting oral contraceptive use
271 decreases some aspects of sexual functioning (e.g., decreases sexual behavior) in non-human
272 primates, such as bonobos [67]. While there is then some preliminary (i.e., weak) evidence
273 that oral contraceptive use might alter some aspects of women's mating psychology, the
274 specific results of studies of the putative effects of oral contraceptives on women's mating
275 psychology appear to provide little support for the Dual Mating Strategy hypothesis.

276

277 Our article focuses on empirical challenges to the Dual Mating Strategy hypothesis. However,
278 there are also a variety of potential theoretical challenges to the Dual Mating Strategy
279 hypothesis. Although such theoretical challenges are arguably more contentious than the
280 empirical challenges, we briefly discuss them in Box 3.

281

282 **An alternative to the Dual Mating Strategy hypothesis**

283 As outlined above, data from recent studies of both mate preferences and aspects of sexual
284 desire do not appear to straightforwardly support the Dual Mating Strategy hypothesis.
285 Nonetheless, these studies do present compelling evidence for a general change in sexual
286 desire over the menstrual cycle that occurs as a function of changes in hormone levels related
287 to fertility. Is there an alternative model of hormonal regulation of women's mating
288 psychology that is better able to accommodate these recent empirical challenges to the Dual
289 Mating Strategy hypothesis? We suggest that there is.

290

291 The data described in this article can be accommodated in the 'estrous' model [68], which has
292 recently been further developed [9]. This model proposes that the ovulatory phase of the
293 menstrual cycle in women is characterized by increased sexual motivation, similar to that
294 reported in other non-human primates during the fertile phase of their reproductive cycles

295 (see [69] for a review of these studies). For example, estradiol positively and progesterone
296 negatively predict sexual behavior in captive female macaques [70,71] and administering
297 estradiol to female macaques increases both sexual receptivity and proceptivity [72,73].
298 Specific evidence for this model of hormonal regulation of mating psychology in humans
299 comes from studies reporting an increase in women's general sexual desire [38,54,56,74],
300 interest in sex with attractive men, including those they do not know well [75], and
301 assertiveness [76] during the ovulatory phase of the menstrual cycle.

302

303 Importantly, this type of model makes no specific predictions about changes in the types of
304 men that women are attracted to and does not emphasize the potential benefits of extra-pair
305 sex. In fact, some versions of the model [68] explicitly propose that estrous may have evolved
306 prior to pair-bonding and, in humans, need not necessarily confer any benefit to women in
307 terms of reproductive success (i.e., fertility-linked change in sexual motivation might simply
308 be vestigial). Alternatively, fertility-linked change in sexual motivation could function to free
309 up resources (e.g., time, energy) for other priorities (e.g., obtaining food) when conception is
310 unlikely to occur following intercourse [9]. Evidence for this latter type of fertility-linked
311 change in general motivational priorities comes from recent work suggesting that increased
312 sexual desire during the ovulatory phase of the menstrual cycle is accompanied by decreased
313 food intake [77].

314

315 **Concluding remarks and future directions**

316 In conclusion, we suggest that the lack of clear evidence for fertility- or hormone-linked
317 changes in women's mate preferences and extra-pair sexual desire in recent studies,
318 including those conducted on a large scale, is problematic for the Dual Mating Strategy
319 hypothesis. By contrast, alternative accounts, such as the 'estrous' and 'extended sexuality'
320 models are better able to accommodate these new data.

321

322 Our overview of recent work on hormonal regulation of women's mating psychology
323 highlights several important directions for future research. First, it is essential that
324 researchers continue to rigorously test predictions from each of these theories, ideally
325 focusing on testing competing predictions from each model. Such tests should include
326 distinguishing between the two versions of the estrous model described in the previous
327 section.

328

329 Second, research in this area must fully consider individual differences in the magnitude of
330 cyclic changes in mating psychology. Large-scale studies suggest that the magnitude of cyclic
331 shifts in mating psychology may vary substantially among women [35,38] and factors such as
332 own and partner physical condition and/or market value were found to predict the magnitude
333 of cyclic shifts in some small-scale studies [6,24,55,78; but see also 38 and 53]. Replicating
334 and extending these findings in large-scale studies may yet provide insight into why results for
335 cyclic changes in women's mate preferences vary across studies. Simply establishing whether
336 individual differences in the magnitude of cyclic shifts in mating psychology are systematic or
337 random would be an important step towards this goal.

338

339 Third, while most of the recent replication attempts for cyclic changes in mate preferences
340 have focused on face and body preferences, there have been few attempts to replicate
341 studies on preferences for male body odor [28] and behavioral displays [29,30]. Such
342 replications are urgently needed because the existing studies on preferences in these
343 domains have almost exclusively used between-subject designs and relatively small sample
344 sizes.

345

346 Fourth, it is important that researchers continue to improve the methods used to assess
347 hormonal status. For example, hormone measures from blood samples may be less
348 susceptible to bias from individual differences in adiposity than the salivary assays typically
349 used in this area. Mass spectroscopy also appears to be a considerable improvement on the
350 immunoassay methods typically used to measure hormones in this field [79].

351

352 Finally, it is essential that researchers continue to develop new theoretical models of
353 hormonal regulation of mating psychology that put forward new alternatives to the Dual
354 Mating Strategy hypothesis and refine existing alternative models. Importantly, these
355 refinements should include equivalence bounds [80] to define effect sizes that are too small
356 to theoretically matter, facilitating equivalence tests that can provide evidence for the null,
357 rather than only find or fail to find evidence against the null.

358

359

360 **Text Box 1. Do men display genetic fitness cues?** A critical aspect of the Dual Mating Strategy
361 hypothesis is the proposal that women increase their reproductive fitness by mating with
362 men displaying genetic fitness cues (i.e., cues that a man's offspring will have higher fitness).
363 Many researchers have questioned the existence of such cues [e.g., 49,81] and evidence for
364 their existence in men is arguably equivocal [10,82-89]. Moreover, some researchers have
365 argued that an individual's typical or current physical condition need not necessarily be
366 related to such cues [90,91], making it a difficult proposal to assess empirically in humans.
367 Additionally, the strength of links between fitness and physical cues could differ according to
368 ecological factors, such as environmental harshness [92,93]. The only study we are aware of
369 to have directly tested whether women who mate with men displaying a putative genetic
370 fitness cue (facial masculinity) actually do obtain fitness benefits found evidence that the
371 daughters of masculine-faced men incur a potential fitness cost [81]. To date, the most
372 reliable results suggesting the existence of genetic fitness cues in men comes from studies
373 linking aspects of men's facial, bodily, and vocal appearance to their physical strength [92,93].
374 However, interpreting such results as evidence for the existence of genetic fitness cues rests
375 on the assumption that physical strength is a genetic fitness cue [94].

376

377 **Text Box 2. Considering the Extended Sexuality hypothesis.** In our main text, we argue that
378 results from recent large-scale studies of changes in sexual desire during the menstrual cycle
379 present difficulties for the Dual Mating Strategy hypothesis. However, these results might also
380 be problematic for at least one alternative theory of hormonal regulation of women's sexual
381 desire. The Extended Sexuality hypothesis proposes that sex during nonconceptive phases of
382 the menstrual cycle (e.g., during the luteal phase) functions, at least in part, to strengthen
383 pairbonds and increase the male partner's investment in both the relationship and any
384 existing children [95]. One recent study [96] reported a positive effect of progesterone on in-
385 pair versus extra-pair desire. Since progesterone is higher during the luteal phase of the
386 menstrual cycle than at other times (see Figure 2), this finding was interpreted as evidence
387 for the Extended Sexuality hypothesis [96]. However, the results of studies [e.g., 38,54]
388 finding that various aspects of sexual desire, including in-pair desire, actually increase during
389 the *ovulatory* phase of the menstrual cycle (i.e., when progesterone is low) are difficult to
390 reconcile with this Extended Sexuality hypothesis. It could be that in-pair desire increases
391 during the luteal phase of the menstrual cycle in only a subgroup of women, such as those in
392 particularly committed relationships [95]. However, such moderation effects would need to
393 be substantial to reverse the direction of the seemingly robust overall positive effect of

394 conception risk on in-pair desire reported in other studies.

395

396 **Text Box 3. Theoretical challenges to the Dual Mating Strategy hypothesis.** Putative benefits of
397 extra-pair paternity (i.e., being fathered by a man other than the mother's primary romantic
398 partner) for offspring reproductive fitness are a critical feature of the Dual Mating Shift
399 hypothesis. However, if extra-pair paternity can be beneficial for offspring reproductive
400 fitness, it is puzzling that genetic evidence suggests that rates of extra-pair paternity are
401 generally relatively low. For example, recent genetic studies estimate extra-pair paternity
402 rates in Western European (Netherlands, Italy, Spain) and African (South Africa, Mali) samples
403 to be <2% per generation [97-101]. Although extra-pair paternity may be more common in
404 some other human populations (e.g., Namibia's Himba), these higher rates appear to be
405 driven almost entirely by women in arranged marriages [102], suggesting the higher extra-
406 pair paternity rates are not due to cyclic changes in women's own mate preferences. Among
407 the Himba, extra-pair paternity is uncommon in non-arranged (i.e., 'love') marriages [102].
408 These results suggest that the Dual Mating Strategy hypothesis might overestimate the
409 importance of extra-pair mating.

410

411 It is also unclear whether the fertility-linked changes in behavior during the menstrual cycle
412 predicted by the Dual Mating Strategy hypothesis would be of a sufficient magnitude to
413 overcome the effects of stable individual differences in mating psychology on reproductive
414 success. Studies of the contribution of genetic factors to women's mate preferences and
415 mating strategies have typically reported that a substantial amount of the variation in both
416 mate preferences and mating strategy [39,103-107] are explained by genetic factors. Given
417 these large individual differences in preferences and behavior, the relatively small within-
418 individual changes in behavior proposed by the Dual Mating Strategy hypothesis may not
419 have an appreciable effect on women's reproductive fitness [108].

420

421 Another recent theoretical challenge to the Dual Mating Strategy comes from the proposal
422 that within-women, fertility-linked changes in mating psychology might simply be low-cost
423 functionless byproducts of processes that evolved because of between-women differences in
424 mating psychology [48]. Although hotly debated [109,110], this hypothesis has received some
425 preliminary support, at least in how it applies to mate preferences. For example, one recent
426 study found that some aspects of women's mate preferences are predicted by between-
427 women, but not within-woman, variation in hormone levels [46].

428

429

430 **Figure Captions**

431

432 **Figure 1. Masculinized and feminized versions of a male prototype face.** This type of stimuli is
433 typically used to test for cyclic shifts in women's masculinity preferences. Masculinized and
434 feminized versions of male prototype faces are created by using computer graphic methods
435 to shift their shape along a continuum defined by the average shape differences between a
436 sample of male and a sample of female faces.

437

438 **Figure 2. Typical changes in estradiol and progesterone during the menstrual cycle.** Fertility is
439 greatest on the two or three days preceding ovulation [32]. This high-fertility phase of the
440 menstrual cycle is characterized by high estradiol and low progesterone. Hormone data are
441 from a composite measure derived from actuarial tables [33]. On the x-axis, day zero is the
442 day of ovulation.

443

444 **References**

- 445 1. Gildersleeve, K., Haselton, M. G., & Fales, M. R. (2014). Do women's mate preferences
446 change across the ovulatory cycle? A meta-analytic review. *Psychological Bulletin*,
447 140, 1205.
- 448 2. Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K., &
449 Minamisawa, R. (1999). Menstrual cycle alters face preference. *Nature*, 399, 741.
- 450 3. Little, A. C., Jones, B. C., & DeBruine, L. M. (2011). Facial attractiveness: evolutionary based
451 research. *Philosophical Transactions of the Royal Society B*, 366, 1638-1659.
- 452 4. Johnston, V. S., Hagel, R., Franklin, M., Fink, B., & Grammer, K. (2001). Male facial
453 attractiveness: Evidence for hormone-mediated adaptive design. *Evolution and*
454 *Human Behavior*, 22, 251-267.
- 455 5. Grammer, K., Fink, B., Møller, A. P., & Thornhill, R. (2003). Darwinian aesthetics: sexual
456 selection and the biology of beauty. *Biological Reviews*, 78, 385-407.
- 457 6. Pillsworth, E. G., & Haselton, M. G. (2006). Male sexual attractiveness predicts differential
458 ovulatory shifts in female extra-pair attraction and male mate retention. *Evolution*
459 *and Human Behavior*, 27(4), 247-258.
- 460 7. Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: Trade-offs and
461 strategic pluralism. *Behavioral and Brain Sciences*, 23, 573-587.

- 462 8. Jones, B. C., DeBruine, L. M., Perrett, D. I., Little, A. C., Feinberg, D. R., & Smith, M. J. L.
463 (2008). Effects of menstrual cycle phase on face preferences. *Archives of Sexual*
464 *Behavior*, 37, 78-84.
- 465 9. Roney, J. R. (in press). Functional roles of gonadal hormones in human pair bonding and
466 sexuality. In O. C. Schultheiss & P. H. Mehta (Eds.), *Routledge International Handbook*
467 *of Social Neuroendocrinology*. Abingdon, UK: Routledge.
- 468 10. Thornhill, R., & Gangestad, S. W. (2006). Facial sexual dimorphism, developmental
469 stability, and susceptibility to disease in men and women. *Evolution and Human*
470 *Behavior*, 27, 131-144.
- 471 11. Rantala, M. J., Moore, F. R., Skrinda, I., Krama, T., Kivleniece, I., Kecko, S., & Krams, I.
472 (2012). Evidence for the stress-linked immunocompetence handicap hypothesis in
473 humans. *Nature Communications*, 3, 694.
- 474 12. Perrett, D. I., Lee, K. J., Penton-Voak, I., Rowland, D., Yoshikawa, S., Burt, D. M., ... &
475 Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature*,
476 394, 884.
- 477 13. Boothroyd, L. G., Jones, B. C., Burt, D. M., & Perrett, D. I. (2007). Partner characteristics
478 associated with masculinity, health and maturity in male faces. *Personality and*
479 *Individual Differences*, 43, 1161-1173.
- 480 14. Frost, P. (1994). Preference for darker faces in photographs at different phases of the
481 menstrual cycle: preliminary assessment of evidence for a hormonal relationship.
482 *Perceptual and Motor Skills*, 79(1), 507-514.
- 483 15. Penton-Voak, I. S., & Perrett, D. I. (2000). Female preference for male faces changes
484 cyclically: Further evidence. *Evolution and Human Behavior*, 21, 39-48.
- 485 16. Welling, L. L., Jones, B. C., DeBruine, L. M., Conway, C. A., Smith, M. L., Little, A. C., ... & Al-
486 Dujaili, E. A. (2007). Raised salivary testosterone in women is associated with
487 increased attraction to masculine faces. *Hormones and Behavior*, 52, 156-161.
- 488 17. Roney, J. R., & Simmons, Z. L. (2008). Women's estradiol predicts preference for facial
489 cues of men's testosterone. *Hormones and Behavior*, 53(1), 14-19.
- 490 18. Vaughn, J. E., Bradley, K. I., Byrd-Craven, J., & Kennison, S. M. (2010). The effect of
491 mortality salience on women's judgments of male faces. *Evolutionary Psychology*, 8,
492 147470491000800313.
- 493 19. Roney, J. R., Simmons, Z. L., & Gray, P. B. (2011). Changes in estradiol predict within-
494 women shifts in attraction to facial cues of men's testosterone.
495 *Psychoneuroendocrinology*, 36, 742-749.

- 496 20. Little, A. C., & Jones, B. C. (2012). Variation in facial masculinity and symmetry preferences
497 across the menstrual cycle is moderated by relationship context.
498 *Psychoneuroendocrinology*, 37, 999-1008.
- 499 21. Ditzen, B., Palm-Fischbacher, S., Gossweiler, L., Stucky, L., & Ehlert, U. (2017). Effects of
500 stress on women's preference for male facial masculinity and their endocrine
501 correlates. *Psychoneuroendocrinology*, 82, 67-74.
- 502 22. Little, A. C., Jones, B. C., & Burriss, R. P. (2007). Preferences for masculinity in male bodies
503 change across the menstrual cycle. *Hormones and Behavior*, 51, 633-639.
- 504 23. Puts, D. A. (2006). Cyclic variation in women's preferences for masculine traits. *Human*
505 *Nature*, 17, 114-127.
- 506 24. Feinberg, D. R., Jones, B. C., Smith, M. L., Moore, F. R., DeBruine, L. M., Cornwell, R. E., ...
507 & Perrett, D. I. (2006). Menstrual cycle, trait estrogen level, and masculinity
508 preferences in the human voice. *Hormones and Behavior*, 49, 215-222.
- 509 25. Little, A. C., Jones, B. C., Burt, D. M., & Perrett, D. I. (2007). Preferences for symmetry in
510 faces change across the menstrual cycle. *Biological Psychology*, 76, 209-216.
- 511 26. Gangestad, S. W., & Thornhill, R. (1998). Menstrual cycle variation in women's preferences
512 for the scent of symmetrical men. *Proceedings of the Royal Society of London B*, 265,
513 927-933.
- 514 27. Thornhill, R., & Gangestad, S. W. (1999). The scent of symmetry: a human sex pheromone
515 that signals fitness?. *Evolution and Human Behavior*, 20, 175-201.
- 516 28. Havlicek, J., Roberts, S. C., & Flegr, J. (2005). Women's preference for dominant male
517 odour: effects of menstrual cycle and relationship status. *Biology Letters*, 1, 256-259.
- 518 29. Gangestad, S. W., Garver-Apgar, C. E., Simpson, J. A., & Cousins, A. J. (2007). Changes in
519 women's mate preferences across the ovulatory cycle. *Journal of Personality and*
520 *Social Psychology*, 92, 151.
- 521 30. Gangestad, S. W., Simpson, J. A., Cousins, A. J., Garver-Apgar, C. E., & Christensen, P. N.
522 (2004). Women's preferences for male behavioral displays change across the
523 menstrual cycle. *Psychological Science*, 15, 203-207.
- 524 31. Gangestad, S. W., & Haselton, M. G. (2015). Human estrus: Implications for relationship
525 science. *Current Opinion in Psychology*, 1, 45-51.
- 526 32. Wilcox, A. J., Dunson, D. B., Weinberg, C. R., Trussell, J., & Baird, D. D. (2001). Likelihood of
527 conception with a single act of intercourse: providing benchmark rates for
528 assessment of post-coital contraceptives. *Contraception*, 63, 211-215.

- 529 33. Garver-Apgar, C. E., Gangestad, S. W., & Thornhill, R. (2008). Hormonal correlates of
530 women's mid-cycle preference for the scent of symmetry. *Evolution and Human*
531 *Behavior*, 29, 223-232.
- 532 34. Gangestad, S. W., Haselton, M. G., Welling, L. L., Gildersleeve, K., Pillsworth, E. G., Burriss,
533 R. P., ... & Puts, D. A. (2016). How valid are assessments of conception probability in
534 ovulatory cycle research? Evaluations, recommendations, and theoretical
535 implications. *Evolution and Human Behavior*, 37, 85-96.
- 536 35. Jones, B. C., Hahn, A. C., Fisher, C. I., Wang, H., Kandrik, M., Han, C., ... & Roberts, C.
537 (2018). No compelling evidence that preferences for facial masculinity track changes
538 in women's hormonal status. *Psychological Science*. in press.
- 539 36. Roney, J. R. (2018). Hormonal mechanisms and the optimal use of luteinizing hormone
540 tests in human menstrual cycle research. *Hormones and Behavior*.
- 541 37. Blake, K. R., Dixon, B. J., O'dean, S. M., & Denson, T. F. (2016). Standardized protocols for
542 characterizing women's fertility: A data-driven approach. *Hormones and Behavior*, 81,
543 74-83.
- 544 38. Arslan, R. C., Schilling, K. M., Gerlach, T. M., & Penke, L. (2018). Using 26 thousand diary
545 entries to show ovulatory changes in sexual desire and behaviour. *Journal of*
546 *Personality and Social Psychology*, in press.
- 547 39. Zietsch, B. P., Lee, A. J., Sherlock, J. M., & Jern, P. (2015). Variation in women's
548 preferences regarding male facial masculinity is better explained by genetic
549 differences than by previously identified context-dependent effects. *Psychological*
550 *Science*, 26, 1440-1448.
- 551 40. Marcinkowska, U. M., Ellison, P. T., Galbarczyk, A., Milkowska, K., Pawlowski, B., Thune, I.,
552 & Jasienska, G. (2016). Lack of support for relation between woman's masculinity
553 preference, estradiol level and mating context. *Hormones and Behavior*, 78, 1-7.
- 554 41. Marcinkowska, U. M., Galbarczyk, A., & Jasienska, G. (2018). La donna è mobile? Lack of
555 cyclical shifts in facial symmetry, and facial and body masculinity preferences-A
556 hormone based study. *Psychoneuroendocrinology*, 88, 47-53.
- 557 42. Dixon B., Blake, K. R., Denson, T. F., Gooda-Vossos, A., Sulikowski, D., Rantala, M. J., &
558 Brooks, R. C. (2018). The role of mating context and fecundability in women's
559 preferences for men's facial masculinity and beardedness.
560 *Psychoneuroendocrinology*. in press.

- 561 43. Dixson, B. J., Lee, A. J., Blake, K. R., Jasienska, G., & Marcinkowska, U. M. (2018). Women's
562 preferences for men's beards show no relation to their ovarian cycle phase and sex
563 hormone levels. *Hormones and Behavior*, 97, 137-144.
- 564 44. Jünger, J., Kordsmeyer, T. L., Gerlach, T. M., & Penke, L. (2018). Fertile women evaluate
565 male bodies as more attractive, regardless of masculinity. *Evolution and Human*
566 *Behavior*. in press.
- 567 45. Jünger, J., Motta-Mena, N. V., Cardenas, R., Bailey, D., Rosenfield, K. A., Schild, C., Penke,
568 L., & Puts, D. A. (2018). Do women's preferences for masculine voices shift across the
569 ovulatory cycle? *Hormones and Behavior*, 106, 122-134.
- 570 46. Marcinkowska, U. M., Kaminski, G., Little, A. C., & Jasienska, G. (2018). Average ovarian
571 hormone levels, rather than daily values and their fluctuations, are related to facial
572 preferences among women. *Hormones and Behavior*, 102, 114-119.
- 573 47. Pisanski, K., Hahn, A. C., Fisher, C. I., DeBruine, L. M., Feinberg, D. R., & Jones, B. C. (2014).
574 Changes in salivary estradiol predict changes in women's preferences for vocal
575 masculinity. *Hormones and Behavior*, 66(3), 493-497.
- 576 48. Havli_ek, J., Cobey, K. D., Barrett, L., Klapilová, K., & Roberts, S. C. (2015). The spandrels of
577 Santa Barbara? A new perspective on the peri-ovulation paradigm. *Behavioral*
578 *Ecology*, 26(5), 1249-1260.
- 579 49. Scott, I. M., Clark, A. P., Josephson, S. C., Boyette, A. H., Cuthill, I. C., Fried, R. L., ... &
580 Honey, P. L. (2014). Human preferences for sexually dimorphic faces may be
581 evolutionarily novel. *Proceedings of the National Academy of Sciences*, 111, 14388-
582 14393.
- 583 50. Harris, C. R. (2013). Shifts in masculinity preferences across the menstrual cycle: Still not
584 there. *Sex Roles*, 69, 507-515.
- 585 51. Muñoz-Reyes, J. A., Iglesias-Julios, M., Martín-Elola, C., Losada-Pérez, M., Monedero, I.,
586 Pita, M., & Turiégano, E. (2014). Changes in preference for male faces during the
587 menstrual cycle in a Spanish population. *Anales de Psicología/Annals of Psychology*,
588 30, 667-675.
- 589 52. Marcinkowska, U. M., Jasienska, G., & Prokop, P. (2018). A comparison of masculinity
590 facial preference among naturally cycling, pregnant, lactating, and post-menopausal
591 women. *Archives of Sexual Behavior*, 47(5), 1367-1374.
- 592 53. Shimoda, R., Campbell, A., & Barton, R. A. (2017). Women's emotional and sexual
593 attraction to men across the menstrual cycle. *Behavioral Ecology*, 29, 51-59.

- 594 54. Roney, J. R., & Simmons, Z. L. (2016). Within-cycle fluctuations in progesterone negatively
595 predict changes in both in-pair and extra-pair desire among partnered women.
596 *Hormones and Behavior*, 81, 45-52.
- 597 55. Haselton, M. G., & Gangestad, S. W. (2006). Conditional expression of women's desires
598 and men's mate guarding across the ovulatory cycle. *Hormones and behavior*, 49(4),
599 509-518.
- 600 56. Jones, B. C., Hahn, A. C., Fisher, C. I., Wang, H., Kandrik, M., & DeBruine, L. M. (2018).
601 General sexual desire, but not desire for uncommitted sexual relationships, tracks
602 changes in women's hormonal status. *Psychoneuroendocrinology*, 88, 153-157.
- 603 57. Little, A. C., Jones, B. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2002). Partnership
604 status and the temporal context of relationships influence human female preferences
605 for sexual dimorphism in male face shape. *Proceedings of the Royal Society of London*
606 *B*, 269, 1095-1100.
- 607 58. Feinberg, D. R., DeBruine, L. M., Jones, B. C., & Little, A. C. (2008). Correlated preferences
608 for men's facial and vocal masculinity. *Evolution and Human Behavior*, 29, 233-241.
- 609 59. Cobey, K. D., Little, A. C., & Roberts, S. C. (2015). Hormonal effects on women's facial
610 masculinity preferences: The influence of pregnancy, post-partum, and hormonal
611 contraceptive use. *Biological Psychology*, 104, 35-40.
- 612 60. Alvergne, A., & Lummaa, V. (2010). Does the contraceptive pill alter mate choice in
613 humans?. *Trends in Ecology & Evolution*, 25, 171-179.
- 614 61. Little, A. C., Burriss, R. P., Petrie, M., Jones, B. C., & Roberts, S. C. (2013). Oral
615 contraceptive use in women changes preferences for male facial masculinity and is
616 associated with partner facial masculinity. *Psychoneuroendocrinology*, 38, 1777-
617 1785.
- 618 62. Roberts, S. C., Little, A. C., Burriss, R. P., Cobey, K. D., Klapilová, K., Havlíček, J., ... & Petrie,
619 M. (2014). Partner choice, relationship satisfaction, and oral contraception: The
620 congruency hypothesis. *Psychological Science*, 25, 1497-1503.
- 621 63. Russell, V. M., McNulty, J. K., Baker, L. R., & Meltzer, A. L. (2014). The association between
622 discontinuing hormonal contraceptives and wives' marital satisfaction depends on
623 husbands' facial attractiveness. *Proceedings of the National Academy of Sciences*,
624 111, 17081-17086.
- 625 64. Jern, P., Kärnä, A., Hujanen, J., Erlin, T., Gunst, A., Rautaheimo, H., ... & Zietsch, B. P.
626 (2018). A high-powered replication study finds no effect of starting or stopping

- 627 hormonal contraceptive use on relationship quality. *Evolution and Human Behavior*.
628 in press.
- 629 65. Zethraeus, N., Dreber, A., Ranehill, E., Blomberg, L., Labrie, F., von Schoultz, B., ... &
630 Hirschberg, A. L. (2016). Combined oral contraceptives and sexual function in women-
631 a double-blind, randomized, placebo-controlled trial. *The Journal of Clinical*
632 *Endocrinology & Metabolism*, 101(11), 4046-4053.
- 633 66. Zethraeus, N., Dreber, A., Ranehill, E., Blomberg, L., Labrie, F., von Schoultz, B., ... &
634 Hirschberg, A. L. (2017). A first-choice combined oral contraceptive influences general
635 well-being in healthy women: a double-blind, randomized, placebo-controlled trial.
636 *Fertility and Sterility*, 107(5), 1238-1245.
- 637 67. Agnew, M. K., Asa, C. S., Clyde, V. L., Keller, D. L., & Meinelt, A. (2016). A survey of bonobo
638 (*Pan paniscus*) oral contraceptive pill use in North American zoos. *Zoo biology*, 35(5),
639 444-453.
- 640 68. Gangestad, S. W., & Thornhill, R. (2008). Human oestrus. *Proceedings of the Royal Society*
641 *of London B*, 275, 991-1000.
- 642 69. Roney, James R. "An evolutionary functional analysis of the hormonal predictors of
643 women's sexual motivation." In *The evolution of sexuality*, pp. 99-121. Springer,
644 Cham, 2015.
- 645 70. Michael, R. P., Richter, M. C., Cain, J. A., Zumpe, D., & Bosnall, R. W. (1978). Artificial
646 menstrual cycles, behavior and the role of androgens in female rhesus monkeys.
647 *Nature*, 275, 439-440.
- 648 71. Wallen, K., Winston, L. A., Gaventa, S., Davis-DaSilva, M., & Collins, D. C. (1984).
649 Periovulatory changes in female sexual behavior and patterns of ovarian steroid
650 secretion in group-living rhesus monkeys. *Hormones and Behavior*, 18, 431-450.
- 651 72. Zumpe, D., Bosnall, R. W., & Michael, R. P. (1983). Behavior of rhesus monkeys during 28-
652 day cycles of estrogen treatment. *Behavioral Neuroscience*, 97, 615-623.
- 653 73. Zehr, J. L., Maestripieri, D., & Wallen, K. (1998). Estradiol increases female sexual initiation
654 independent of male responsiveness in rhesus monkeys. *Hormones and Behavior*, 33,
655 95-103.
- 656 74. Roney, J. R., & Simmons, Z. L. (2013). Hormonal predictors of sexual motivation in natural
657 menstrual cycles. *Hormones and Behavior*, 63, 636-645.
- 658 75. Gangestad, S. W., Thornhill, R., & Garver-Apgar, C. E. (2010). Fertility in the cycle predicts
659 women's interest in sexual opportunism. *Evolution and Human Behavior*, 31(6), 400-
660 411.

- 661 76. Blake, K. R., Bastian, B., O'Dean, S. M., & Denson, T. F. (2017). High estradiol and low
662 progesterone are associated with high assertiveness in women.
663 *Psychoneuroendocrinology*, 75, 91-99.
- 664 77. Roney, J. R., & Simmons, Z. L. (2017). Ovarian hormone fluctuations predict within-cycle
665 shifts in women's food intake. *Hormones and Behavior*, 90, 8-14.
- 666 78. Millar, M. (2013). Menstrual cycle changes in mate preferences for cues associated with
667 genetic quality: The moderating role of mate value. *Evolutionary Psychology*, 11(1),
668 147470491301100103.
- 669 79. Schultheiss, O. C., Dlugash, G., & Mehta, P. H. (in press). Hormone measurement in social
670 neuroendocrinology: A comparison of immunoassay and mass spectroscopy methods.
671 In O. C. Schultheiss & P. H. Mehta (Eds.), *Routledge international handbook of social*
672 *neuroendocrinology*. Abingdon, UK: Routledge.
- 673 80. Lakens, D. (2017). Equivalence tests: a practical primer for t tests, correlations, and meta-
674 analyses. *Social Psychological and Personality Science*, 8(4), 355-362.
- 675 81. Lee, A. J., Mitchem, D. G., Wright, M. J., Martin, N. G., Keller, M. C., & Zietsch, B. P. (2014).
676 Genetic factors that increase male facial masculinity decrease facial attractiveness of
677 female relatives. *Psychological Science*, 25, 476-484.
- 678 82. Arnocky, S., Hodges-Simeon, C., Ouellette, D., & Albert, G. (2018). Do men with more
679 masculine voices have better immunocompetence?. *Evolution and Human Behavior*.
- 680 83. Kandrik, M., Hahn, A. C., Han, C., Wincenciak, J., Fisher, C. I., DeBruine, L. M., & Jones, B. C.
681 (2017). Does the Interaction Between Cortisol and Testosterone Predict Men's Facial
682 Attractiveness?. *Adaptive Human Behavior and Physiology*, 3, 275-281.
- 683 84. Kordsmeyer, T. L., Lohöfener, M., & Penke, L. (2018). Male Facial Attractiveness,
684 Dominance, and Health and the Interaction between Cortisol and Testosterone.
685 *Adaptive Human Behavior and Physiology*, 1-12.
- 686 85. Paw_owski, B., Nowak, J., Borkowska, B., Augustyniak, D., & Drulis-Kawa, Z. (2017). Body
687 height and immune efficacy: testing body stature as a signal of biological quality.
688 *Proc. R. Soc. B*, 284, 20171372.
- 689 86. Rhodes, G., Chan, J., Zebrowitz, L. A., & Simmons, L. W. (2003). Does sexual dimorphism in
690 human faces signal health?. *Proceedings of the Royal Society of London B: Biological*
691 *Sciences*, 270(Suppl 1), S93-S95.
- 692 87. Kalick, S. M., Zebrowitz, L. A., Langlois, J. H., & Johnson, R. M. (1998). Does human facial
693 attractiveness honestly advertise health? Longitudinal data on an evolutionary
694 question. *Psychological science*, 9(1), 8-13.

- 695 88. Krams, I. A., Skrinda, I., Kecko, S., Moore, F. R., Krama, T., Kaasik, A., ... & Rantala, M. J.
696 (2014). Body height affects the strength of immune response in young men, but not
697 young women. *Scientific reports*, 4, 6223.
- 698 89. Skrinda, I., Krama, T., Kecko, S., Moore, F. R., Kaasik, A., Meija, L., ... & Krams, I. (2014).
699 Body height, immunity, facial and vocal attractiveness in young men.
700 *Naturwissenschaften*, 101, 1017-1025.
- 701 90. Getty, T. (2002). Signaling health versus parasites. *The American Naturalist*, 159(4), 363-
702 371.
- 703 91. Kokko, H., Brooks, R., Jennions, M. D., & Morley, J. (2003). The evolution of mate choice
704 and mating biases. *Proceedings of the Royal Society of London B: Biological Sciences*,
705 270(1515), 653-664.
- 706 92. Sell, A., Cosmides, L., Tooby, J., Sznycer, D., Von Rueden, C., & Gurven, M. (2009). Human
707 adaptations for the visual assessment of strength and fighting ability from the body
708 and face. *Proceedings of the Royal Society of London B: Biological Sciences*,
709 276(1656), 575-584.
- 710 93. Sell, A., Bryant, G. A., Cosmides, L., Tooby, J., Sznycer, D., Von Rueden, C., ... & Gurven, M.
711 (2010). Adaptations in humans for assessing physical strength from the voice.
712 *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20100769.
- 713 94. Gallup, A. C., & Fink, B. (2018). Handgrip strength as a Darwinian fitness indicator in men.
714 *Frontiers in psychology*, 9, 439.
- 715 95. Grebe, N. M., Gangestad, S. W., Garver-Apgar, C. E., & Thornhill, R. (2013). Women's
716 luteal-phase sexual proceptivity and the functions of extended sexuality.
717 *Psychological Science*, 24(10), 2106-2110.
- 718 96. Grebe, N. M., Thompson, M. E., & Gangestad, S. W. (2016). Hormonal predictors of
719 women's extra-pair vs. in-pair sexual attraction in natural cycles: Implications for
720 extended sexuality. *Hormones and Behavior*, 78, 211-219.
- 721 97. Larmuseau, M. H., Matthijs, K., & Wenseleers, T. (2016). Cuckolded fathers rare in human
722 populations. *Trends in ecology & evolution*, 31(5), 327-329.
- 723 98. Boattini, A., Sarno, S., Pedrini, P., Medoro, C., Carta, M., Tucci, S., ... & Pettener, D. (2015).
724 Traces of medieval migrations in a socially stratified population from Northern Italy.
725 Evidence from uniparental markers and deep-rooted pedigrees. *Heredity*, 114, 155.
- 726 99. Solé-Morata, N., Bertranpetit, J., Comas, D., & Calafell, F. (2015). Y-chromosome diversity
727 in Catalan surname samples: insights into surname origin and frequency. *European*
728 *Journal of Human Genetics*, 23, 1549.

- 729 100. Greeff, J. M., & Erasmus, J. C. (2015). Three hundred years of low non-paternity in a
730 human population. *Heredity*, 115, 396.
- 731 101. Larmuseau, M. H. D., Vanoverbeke, J., Van Geystelen, A., Defraene, G., Vanderheyden,
732 N., Matthys, K., ... & Decorte, R. (2013). Low historical rates of cuckoldry in a Western
733 European human population traced by Y-chromosome and genealogical data.
734 *Proceedings of the Royal Society of London B*, 280, 20132400.
- 735 102. Scelza, B. A. (2011). Female choice and extra-pair paternity in a traditional human
736 population. *Biology Letters*, rsbl20110478.
- 737 103. Zietsch, Brendan P., Karin JH Verweij, Andrew C. Heath, and Nicholas G. Martin. (2011).
738 Variation in human mate choice: simultaneously investigating heritability, parental
739 influence, sexual imprinting, and assortative mating. *American Naturalist*, 177, 605-
740 616.
- 741 104. Bailey, J. M., Kirk, K. M., Zhu, G., Dunne, M. P., & Martin, N. G. (2000). Do individual
742 differences in sociosexuality represent genetic or environmentally contingent
743 strategies? Evidence from the Australian twin registry. *Journal of Personality and*
744 *Social Psychology*, 78, 537.
- 745 105. Cherkas, L. F., Oelsner, E. C., Mak, Y. T., Valdes, A., & Spector, T. D. (2004). Genetic
746 influences on female infidelity and number of sexual partners in humans: a linkage
747 and association study of the role of the vasopressin receptor gene (AVPR1A). *Twin*
748 *Research and Human Genetics*, 7, 649-658.
- 749 106. Zietsch, B. P., Westberg, L., Santtila, P., & Jern, P. (2015). Genetic analysis of human
750 extrapair mating: heritability, between-sex correlation, and receptor genes for
751 vasopressin and oxytocin. *Evolution and Human Behavior*, 36, 130-136.
- 752 107. Zietsch, B. P., Morley, K. I., Shekar, S. N., Verweij, K. J., Keller, M. C., Macgregor, S., ... &
753 Martin, N. G. (2008). Genetic factors predisposing to homosexuality may increase
754 mating success in heterosexuals. *Evolution and Human Behavior*, 29, 424-433.
- 755 108. Zietsch, B. P. (2016). Individual differences as the output of evolved calibration
756 mechanisms: Does the theory make sense in view of empirical observations?. *Current*
757 *Opinion in Psychology*, 7, 71-75.
- 758 109. Gangestad, S. W., & Grebe, N. M. (2015). Are within-cycle variations in women's sexual
759 interests mere by-products? A comment on Havli_ek et al. *Behavioral Ecology*, 26(5),
760 1262-1263.
- 761 110. Haselton, M. G. (2015). Comment on Havlicek et al. (2015): Is their perspective really
762 new (or truly parsimonious)?. *Behavioral Ecology*.