

The scent of attractiveness: Levels of reproductive hormones explain individual differences in women's body odour

Janek S. Lobmaier¹, Urs Fischbacher^{2,3}, Urs Wirthmüller⁴, Daria Knoch¹

¹ Department of Social Psychology and Social Neuroscience, Institute of Psychology,
University of Bern, Bern, Switzerland

² Department of Economics, University of Konstanz, Konstanz, Germany

³ Thurgau Institute of Economics, Kreuzlingen, Switzerland

⁴ Universitätsinstitut für Klinische Chemie, University of Bern, Bern, Switzerland

Authors for correspondence :

Janek Lobmaier : janek.lobmaier@psy.unibe.ch

Daria Knoch : daria.knoch@psy.unibe.ch

Abstract

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37 Individuals are thought to have their own distinctive body odour which reportedly plays an
38 important role in mate choice. In the present study we investigated individual differences in
39 body odours of women and examined whether some women generally smell more attractive
40 than others or whether odour preferences are a matter of individual taste. We then explored
41 whether levels of reproductive hormones explain women's body odour attractiveness, to test
42 the idea that body odour attractiveness may act as a chemosensory marker of reproductive
43 fitness. Fifty-seven men rated body odours of 28 healthy, naturally cycling women of
44 reproductive age. We collected all odours at peak fertility to control for menstrual cycle
45 effects on body odour attractiveness. Women's salivary estradiol, progesterone, testosterone
46 and cortisol levels were assessed at the time of odour collection to test whether hormone
47 levels explain body odour attractiveness. We found that the men highly agreed on how
48 attractive they found women's body odours. Interestingly, women's body odour attractiveness
49 was predicted by their estradiol and progesterone levels: The higher a woman's levels of
50 estradiol and the lower her levels of progesterone, the more attractive her body odour was
51 rated. In showing that women's body odour attractiveness is explained by levels of female
52 reproductive hormones, but not by levels of cortisol or testosterone, we provide evidence that
53 body odour acts as a valid cue to potential fertility.

54
55 *Keywords:* olfaction, estradiol, progesterone, odour preference, human leucocyte
56 antigen, HLA, major histocompatibility complex, MHC

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1. Introduction

59 Olfaction allegedly plays an important role in mate choice of both human and non-human
60 species [cf., 1, 2, 3]. It is widely thought that every individual has her own unique body
61 odour, much like a fingerprint [4]. Here we collected women's body odours to examine
62 whether some women generally smell more attractive than others or whether odour
63 attractiveness lies "in the nose of the smeller". And if some women generally smell more
64 attractive than others, can a woman's body odour attractiveness be explained by her
65 individual levels of reproductive hormones (e.g., estradiol and progesterone)?

66 Studies on physical attractiveness of women's faces and bodies have found that men
67 show remarkable agreement on who is seen as attractive and who not [e.g., 5, 6]. An
68 evolutionary approach to female attractiveness proposes that men should generally prefer
69 women who signal high reproductive health and fertility [e.g., 7, 8, 9]. In women,
70 reproductive health can be indexed by levels of reproductive hormones: Elevated levels of
71 female reproductive hormones increase the likelihood of conception [e.g., 10, 11]. Female
72 reproductive hormones, in particular estradiol and progesterone, have been shown to be
73 positively related to women's facial and body attractiveness. For example, higher levels of
74 estradiol and progesterone lead to larger breasts and curvier waists, resulting in the hourglass
75 figure that is typically preferred by men [12, 13; but see 14, 15]. Similarly, faces of women
76 with higher estradiol levels are judged as being more attractive than faces of women with low
77 estradiol levels [e.g., 16; but see 15, 17].

78 The present study investigates for the first time whether the same is true for women's
79 body odours. Given that attractiveness is thought to signal various desirable qualities of a
80 potential partner (e.g., health, reproductive success) and assuming that body odours play an
81 important role in human mate choice [e.g., 2], it is likely that body odour attractiveness acts as
82 a chemosensory signal of reproductive fitness. We hence expect individual levels in

83 reproductive hormones (e.g., estradiol and progesterone) to be related to women's body odour
84 attractiveness.

85 Although no study has yet directly tested whether reproductive hormones are related to
86 body odour attractiveness in women, there is some indirect evidence for a link between
87 hormones and odour attractiveness. For example, in naturally cycling women body odour
88 varies significantly across the menstrual cycle. An increasing number of studies report that
89 women's body odour is rated as more attractive if gathered during the late follicular phase
90 (near ovulation) compared to odour that was collected in other cycle phases [18-21]. The late
91 follicular phase coincides with high estradiol and low progesterone levels. While within-
92 woman variation in hormone levels may explain within-woman variance in body odour
93 attractiveness, no study has yet directly investigated whether individual hormone levels are
94 associated with between-women variation in body odour attractiveness.

95 The main source of human body odour are the apocrine sweat glands [cf. 22]. An
96 individual's characteristic body odour results from various bacteria operating upon the
97 viscous secretions of these glands, producing a complex mixture of volatile organic
98 compounds [23-27]. Other candidates that contribute to body odour are odorous steroids and
99 unsaturated fatty acids, such as 3M2H [e.g., 28]. Given that odorous steroids are related to
100 reproductive hormones it is conceivable that levels of endogenous reproductive hormones are
101 related to body odour. Men and women differ substantially in the structure and flora of the
102 axillary scent glands [29-31] and in the odorous steroids contained in their sweat [32, 33].
103 These sex differences and the fact that they become active after puberty suggest that they play
104 a role in sexual communication [34].

105 A further factor reported to influence body odour and body odour preferences are the
106 genes at the major histocompatibility complex [MHC, or human leukocyte antigen system,
107 HLA, in humans, see 35 for a review]. Some studies have suggested that men prefer body
108 odours of HLA-dissimilar or HLA-heterozygous women [e.g., 36]. Studies looking at HLA-

109 mediated odour preferences imply that, rather than showing universal preferences for certain
110 body odours, men have individual preferences for women's body odours, depending on the
111 woman's and their own genetic make-up.

112 The present study sets out to investigate whether men agree when judging the
113 attractiveness of women's body odours and if so, whether this can be explained by women's
114 individual levels of reproductive hormones (estradiol, and progesterone). Because women's
115 body odour has been reported to vary across the menstrual cycle [e.g., 18, 19], we controlled
116 for cycle effects of body odour by collecting women's body odours during the late follicular
117 phase (LH-peak). Hence, we not only controlled for menstrual cycle phase, but in fact also
118 targeted odour collection to take place at peak fertility which, from a biological perspective, is
119 the most relevant period of the menstrual cycle, since only then women can conceive. To
120 control for HLA-associated odour preferences, we typed raters and donors at five HLA loci
121 and calculated the HLA similarity between each rater and donor. We also calculated a
122 measure of donor heterozygosity by adding up for each donor the number of alleles that were
123 heterozygous. We collected axillary odour samples using cotton pads.

124 We first calculated the intraclass correlation coefficient (ICC) to quantify the inter-rater
125 reliability. We then used multilevel linear regressions to test whether women's estradiol and
126 progesterone levels predict the attractiveness of their body odour. Our analyses also
127 considered potential effects of testosterone and HLA on body odour preferences. Levels of the
128 stress hormone cortisol were also included, since stress and anxiety are known to have an
129 impact on body odour [e.g., 37, 38]. The advantage of using multilevel regressions is that we
130 can enter participants as level-2 variable with hormone levels and ratings nested within
131 participants, enabling us to analyse the data without aggregating scores. Paralleling studies on
132 facial and body attractiveness, we expect women's estradiol and progesterone levels to be
133 positively associated with women's body odour attractiveness, since lifetime estradiol and
134 progesterone are positively related to a woman's reproductive potential [e.g., 10, 12].

135

136 **2. Methods**

137 **(a) Participants**

138 Forty-two women (odour donors, mean age = 20.8, *SD* = 6.6) and 57 men (odour raters,
139 mean age = 23, *SD* = 2.8) initially took part in this study. All participants reported being
140 Caucasian and of European descent (at least back to their grandparents) and being
141 heterosexual. The study was conducted according to the principles expressed in the
142 Declaration of Helsinki. All participants provided written informed consent to take part in this
143 study and were treated in accordance with the ethical protocol approved by the Faculty of
144 Human Sciences of the University of Bern and by the Ethics Committee of the Canton of
145 Bern. Odour donors received 140 CHF and odour raters received 45 CHF as compensation.

146

147 **(b) Odour collection procedure**

148 Odour donors (all female) were initially screened in a telephone interview for the
149 required inclusion criteria: (a) aged between 17 and 40 years, (b) medication-free (including
150 hormonal contraception for at least 3 previous months), (c) regular menstrual cycle (average
151 length of between 25 and 35 days), (d) not pregnant or breastfeeding and (e) non-smoker. In
152 the same telephone interview we also collected demographic information and information
153 about their menstrual cycle (regularity, length and onset of last menstrual bleeding).

154 Using OvaCUE© fertility monitors, we predicted high fertility days during which odour
155 collection was to take place (see electronic supplementary material, ESM1, Section A). One
156 day before the date of predicted peak fertility, participants started collecting body odour using
157 cotton axillary pads.

158 The odour donors were requested to follow a strict schedule of dietary and behavioural
159 restrictions while collecting their body odour (see electronic supplementary material, ESM1
160 Section B, for details). On the evenings of the sampling, before applying the cotton axillary

161 pads to their left and right armpits, odour donors were instructed to take a shower with the
162 non-perfumed soap supplied in the material package. Then donors fixed cotton pads (Ebelin
163 cosmetic pads, DM-drogerie markt, www.dm-drogeriemarkt.de) to both armpits using 3M
164 Micropore surgical tape. Donors collected body odour on three consecutive nights. To
165 determine time of highest fertility, participants completed a series of urine tests measuring the
166 luteinizing hormone (LH) using one-step urine ovulation tests with a reported LH sensitivity
167 of 10mIU/ml (David One Step Ovulation Tests, Runbio Biotech, China, <http://www.runbio->
168 [bio.com](http://www.runbio.com)). Women were instructed to perform urine tests twice a day (morning and evening)
169 starting one day before the date of predicted peak fertility. After a positive test result,
170 participants continued performing the tests until the results became negative for two
171 subsequent days. Participants photographed each test using their smart phones and sent the
172 picture to the study manager, who verified whether the test was positive or not.

173 In the evenings before body odour collection, each donor collected a saliva sample from
174 which steroid hormone levels (testosterone, estradiol, progesterone, and cortisol) were
175 determined. Participants were instructed to refrain from eating and to abstain from caffeine
176 for at least 30 minutes prior to saliva collection. Participants were asked to rinse their mouth
177 with fresh water and to wait approximately 5 min before providing saliva. Samples were
178 collected by passive drool using a commercially available sampling device (SaliCaps, IBL,
179 International, Hamburg, Germany). The saliva samples were stored at -28°C and were later
180 analyzed by an independent laboratory (Dresden Lab Service GmbH, Dresden, Germany)
181 using liquid chromatography with coupled tandem mass spectrometry (LC-MS/MS). LC-
182 MS/MS has become the method of choice for steroid analysis because of its high sensitivity,
183 better reproducibility, greater specificity, and ability to analyse multiple steroids
184 simultaneously.

185 After odour collection, the pads were stored in separate sealable plastic bags and were
186 frozen at -30°C until use. Previous studies have shown that freezing has no significant effect
187 on attractiveness ratings [39].

188 When returning their body odour samples to the lab, donors were asked a series of
189 questions in a structured face-to-face interview, adapted from Gildersleeve and colleagues
190 [40]. In this interview, we assessed how long the women had worn their axillary pads and
191 whether they had complied with the dietary and behavioural restrictions (see electronic
192 supplementary material, ESM1, Section C, for details).

193 **(c) Donor dropouts**

194 Only pads from the night closest to the LH peak were included in the study. Of the 42
195 women, nine did not show an LH peak during odour collection and five had violated the
196 dietary and behavioural restrictions, resulting in a total of 28 donors who provided pads for
197 the present study (age range: 18 - 36 years; mean = 26.9; SD= 3.6). We note that this range
198 was rather skewed; there was only one woman who was 36, all the rest were between 18 and
199 28 years of age. Excluding the 36 year old woman from the analyses did not change the
200 results (see electronic supplementary material, ESM3).

201 **(d) Odour rating procedure**

202 Every rater rated the body odours of all 28 women that were available for this study.
203 Ratings took place on four afternoons. Each rater appeared on two of these afternoons,
204 separated by one week. On each afternoon, raters evaluated the odours of 14 women. Half of
205 the participants rated left-arm pads, the other half rated right-arm pads. Left and right arm
206 pads were rated on separate afternoons. Each pad was hence defrosted only once for this study
207 and was destroyed and disposed of after use. The pads were thawed three hours before the
208 respective rating session started and were placed in separate 500ml opaque glass jars [cf. 41,
209 42, 43]. Three research assistants smelled the pads and confirmed that none was contaminated
210 with extraneous odours (e.g., perfume, smoke).

211 To assess the odour preferences we closely followed the procedures reported in [41, 42].
212 To prepare for the rating session, odour raters (all male) were asked not to eat and to refrain
213 from drinking caffeinated or alcoholic beverages for 1 h prior to testing, as these activities are
214 known to affect smelling ability. After giving informed consent, the participants underwent
215 two practice trials. Participants were asked to smell and rate the body odours of two women
216 who were not included in the experiment proper. After the practice trials a male experimenter
217 gave them a tube (SaliCaps, IBL, International, Hamburg, Germany) to collect their saliva
218 sample from which we assessed testosterone levels. The saliva samples were stored at -28°C
219 and were later analyzed together with the donors' saliva samples by an independent laboratory
220 (Dresden Lab Service GmbH, Dresden, Germany) using LC-MS/MS.

221 In each session, odour raters rated the body odours of 14 different women. The jars
222 containing the pads of these women were placed in separate visually shielded booths. Order
223 of pads was randomized for each rater. Odour raters were asked to rate the women's body
224 odour samples on a visual analogue scale (0-100) for attractiveness. If a rater found any of the
225 samples too weak to assess, he was asked to select "I cannot smell the sample" instead of
226 using the rating scales; these samples were not included in further analysis. Sniffing time was
227 not restricted (see electronic supplementary material, ESM2, for details).

228 At the very end of the second session, participants were given 12 Sniffin' Sticks
229 (Screening 12 Test, Burghart Messtechnik GmbH, www.burghart-mt.de), to evaluate their
230 general smelling abilities.

231 All data collection was conducted using Qualtrics (www.qualtrics.com), running on
232 individual portable tablet computers.

233

234 **(e) Rater dropouts**

235 One rater did not return for the second test session, and another scored low on the
236 Sniffin' Sticks (score of 3 out of 12). These two raters were excluded from further analyses.

237 The final sample hence consisted of 55 raters ranging in age between 20 and 37 years (mean =
238 23; SD = 2.9). Of these, four did not provide blood samples for HLA analyses.

239 (f) HLA typing procedure

240 All participants (28 women, 57 men) were invited to the laboratory for venous blood
241 sampling. Before blood sampling, participants read the study information and gave written
242 informed consent. The participants' blood samples (10 ml) were genotyped for HLA-class I
243 (HLA-A, HLA-B and HLA-C) and class II (HLA-DRB1, HLA-DQB1) using LinkS \dot{e} q™ test
244 kits (Linkage Biosystems™). These test kits are based on real-time polymerase chain reaction
245 (PCR) using allele-specific exponential amplification (sequence-specific primers). The
246 resulting amplimers were subjected at end-point to a melting curve analysis to identify
247 specific DNA based on melting temperature using SYBR® Green. Attribution of HLA-
248 genotypes was done using SureTyper™ software. Ambiguities were resolved using
249 alternative typing methods via routine HLA-typing.

250

251 3. Statistical analysis

252 Statistical analyses were performed using SPSS 24.0 and level of significance was set at
253 $p < .05$. We first calculated the intraclass correlation coefficient (ICC) to quantify how much
254 the raters agree on the attractiveness of women's odours. We then ran multilevel linear
255 regressions with attractiveness ratings as dependent variables. The first model included
256 estradiol and progesterone levels as Level-1 predictors of body odour judgements. Raters
257 were entered at Level 2. We then repeated the analysis after adding the estradiol x
258 progesterone interaction as additional Level 1 predictor. In a second model, we included
259 testosterone and cortisol together with estradiol and progesterone levels at Level 1. In a third
260 model, we included rater testosterone levels together with donor estradiol and progesterone at
261 Level 1 to examine whether testosterone influences body odour perception. This analysis was

262 repeated after adding the donor estradiol x rater testosterone and donor progesterone x rater
263 testosterone interactions as additional Level 1 predictor. In a final model, we controlled for
264 the influence of HLA similarity between raters and donors. To do so, we calculated an HLA-
265 Similarity-Index for each rater-donor pair. We also calculated a continuous measure of HLA-
266 heterozygosity by adding up for each donor the number of alleles that were heterozygous.
267 These HLA indices were then entered as covariates, together with donor estradiol and
268 progesterone levels.

269 The reported estimates in the multilevel models are unstandardised regression
270 coefficients. Because examination of hormonal data revealed that the distributions were
271 skewed, we log transformed the hormone values to achieve normal distributions. We report
272 analyses performed with log-transformed data, but whether we used raw or normalised data
273 did not change the results.

274 **4. Results**

275 A total of 1540 (28 x 55) ratings were completed. Of these, 101 (6.5 %) were rated as not
276 perceivable. We note that the non-perceivable trials were not always from the same pad (i.e.,
277 woman). In other words, there was no pad that was not perceivable in all cases: the non-
278 perceivable pads did not come from specific women, but were randomly distributed over
279 different donors. Ratings of left and right pads correlated with $R = .668$, $p < .001$, and there
280 was no significant difference between the attractiveness of left and right pads ($p = .886$),
281 therefore they were pooled for all subsequent analyses.

282 *Hormone data:* For donors, estradiol levels ranged from 3.2 pg/ml to 15.6 pg/ml (mean =
283 7.1, $SD = 3.1$), progesterone levels ranged from 2.5 pg/ml to 87.7 pg/ml (mean = 21.3, $SD =$
284 22.0), testosterone levels ranged from 3.2 pg/ml to 15.8 pg/ml (mean = 7.7, $SD = 3.5$), and
285 cortisol levels from 0.3 nmol/L to 10.6 nmol/L (mean = 2.1, $SD = 2.3$). For raters, we

286 measured only testosterone levels, ranging from 37.15 pg/ml to 118.3 pg/ml (mean = 70.02,
287 $SD = 19.18$).

288 *Interrater-reliability:* Intraclass correlation was high ($ICC = .983$), indicating excellent
289 reliability. This suggests that raters agreed highly on which odours they found more and
290 which ones they found less attractive.

291 *Body odour attractiveness:* The model including donor estradiol and progesterone levels
292 as covariates revealed that a woman's estradiol and progesterone levels both significantly
293 predicted her body odour attractiveness. For estradiol, the relationship was positive
294 (*Unstandardised Regression Coefficient (Estimate)* = 9.62; *standard error (SE)* = 3.225;
295 95%CI [3.29, 15.95]; $t = 2.982$, $df = 1376.042$; $p = .003$) and for progesterone the relationship
296 was negative (*Estimate* = -10.83; $SE = 1.295$; 95%CI [-13.371, -8.290]; $t = -8.362$; $df =$
297 1378.216; $p < .001$). The estradiol x progesterone interaction did not reach statistical
298 significance (*Estimate* = 10.52; $SE = 6.809$; 95%CI [-2.832, 23.880]; $t = 1.546$; $df =$
299 1375.512; $p = .122$). Figure 1 depicts the positive relationship between estradiol and body
300 odour attractiveness ratings (left panel) and the negative relationship between progesterone
301 and attractiveness ratings (right panel).

302 --- Figure 1 about here ---

303 When additionally entering donor testosterone and cortisol levels into the model, the
304 effects for estradiol (*Estimate* = 11.73; $SE = 3.536$; 95%CI [4.794, 18.667]; $t = 3.318$; $df =$
305 1374.949; $p = .001$) and progesterone (*Estimate* = -10.28; $SE = 1.357$; 95%CI [-12.938, -
306 7.614]; $t = -7.573$; $df = 1375.700$; $p < .001$) remained significant, the effects of testosterone
307 (*Estimate* = -.265; $SE = 3.210$; 95%CI [-6.562, 6.032]; $t = -.083$; $df = 1374.558$; $p = .934$) and
308 cortisol (*Estimate* = -2.040; $SE = 1.656$; 95%CI [-5.288, 1.209]; $t = -1.232$; $df = 1376.047$; $p =$
309 .218) were not significant.

310 The third model, where we tested for influences of men's testosterone levels on their
311 ratings of women's body odour attractiveness, we again found effects of donor estradiol

312 (*Estimate* = 9.590; *SE* = 3.228; 95%CI [3.258, 15.921]; *t* = 2.971; *df* = 1374.445; *p* = .003)
313 and progesterone (*Estimate* = -10.829; *SE* = 1.296; 95% CI [-13.371, -8.286]; *t* = -8.356; *df* =
314 1376.452; *p* < .001) but no effect of rater testosterone (*Estimate* = 4.272; *SE* = 5.025; 95% CI
315 [-5.637, 14.180]; *t* = .850; *df* = 1199.656; *p* = .396). Also, neither the rater testosterone x
316 donor estradiol interaction (*Estimate* = -21.425; *SE* = 21.531; 95%CI [-63.663, 20.812]; *t* = --
317 .995; *df* = 1388.165; *p* = .320) nor the rater testosterone x donor progesterone interaction
318 (*Estimate* = -12.056; *SE* = 8.361; 95%CI [-28.458, 4.347]; *t* = -1.442; *df* = 1376.426; *p* =
319 .150) were significant.

320 The final model, where we additionally included HLA-similarity between donor and rater
321 and donor HLA-heterozygosity as covariates, again showed significant effects of estradiol
322 (*Estimate* = 8.634; *SE* = 3.421; 95%CI [1.921, 15.347]; *t* = 2.523; *df* = 1273.149; *p* = .012)
323 and progesterone (*Estimate* = -11.027; *SE* = 1.347; 95%CI [-13.669, -8.385]; *t* = -8.189; *df* =
324 1275.034; *p* < .001), but no effect of HLA similarity (*Estimate* = .34; *SE* = 0.351; 95%CI [-
325 .344, 1.034]; *t* = .983; *df* = 1323.910; *p* = .326) or HLA heterozygosity (*Estimate* = 64.65; *SE*
326 = .434; 95%CI [-1.494, .209]; *t* = 1.480; *df* = 1275.174; *p* = .139).

327

328 **5. Discussion**

329 We tested whether women's individual levels of reproductive hormones (e.g., estradiol
330 and progesterone) are associated with how attractive they smell and to what extent men agree
331 when judging the attractiveness of different women's body odours. We found that men highly
332 agreed on which odours they found attractive and which ones they liked less. Most
333 interestingly, we found that women's levels of endogenous estradiol and progesterone
334 predicted their body odour attractiveness. Specifically, women's body odours were rated as
335 being more attractive the higher their estradiol levels and the lower their progesterone levels
336 were. Cortisol and testosterone levels were not associated with how attractive women's body
337 odours were rated.

338 From an evolutionary point of view female attractiveness is thought to provide cues to
339 various desirable qualities that males may seek for in mates. Having high estradiol levels is
340 one of the desirable traits that men may seek in a woman, since estradiol is positively related
341 to a woman's reproductive potential [e.g., 10]. Hence, selection on preferences for cues
342 potentially signalling high estradiol levels is likely to be strong, because they provide
343 information about a woman's future, or potential, fertility [11, 44]. The present study provides
344 evidence that estradiol is positively related to women's body odour attractiveness, suggesting
345 that body odour acts as a reliable cue to potential fertility.

346 Interestingly, we found a negative relation between women's progesterone levels and their
347 body odour attractiveness. This may seem surprising because lifetime progesterone levels are
348 thought to be positively related to a woman's reproductive potential [e.g., 10, 12]. We note
349 however that we collected all body odours at peak fertility, when women naturally smell their
350 best [cf., 18, 19, 21, 40]. At peak fertility, women typically have high estradiol and low
351 progesterone levels, and the estradiol-to-progesterone ratio is highly correlated with women's
352 fertility across the menstrual cycle [45, 46]. Even though all the odour samples in the present
353 study came from currently fertile women, raters chose those odours to be most attractive that
354 came from women who were most fertile at that moment (i.e., who had highest estradiol
355 levels and lowest progesterone levels). This supports the notion that body odour is a cue to
356 fertility: the higher a woman's fertility, the more attractive her body odour was to men.

357 The biochemical mechanism underlying the relationship between sex steroids and
358 women's body odour is not clear. One possibility is that sex hormones act indirectly on body
359 odour via body temperature regulation. It has been shown that the control of skin blood flow
360 and sweating are modified by estradiol and progesterone, whereby estradiol promotes heat
361 dissipation (i.e., augmented cutaneous vasodilation and higher propensity of sweating, [47])
362 and progesterone is reported to promote heat conservation [for reviews see 48, 49]. Increased
363 skin blood flow and sweating may lead to the excretion of certain odorous volatiles which on

364 their part might function as a cue to higher estradiol levels. A more direct explanation for the
365 effect of hormones on body odour might be that the axillary region secretes odorous
366 compounds resembling estradiol and progesterone. Transferred to our findings, this means
367 that an attractive body odour is a particularly female odour. Alternatively, estradiol and
368 progesterone may act directly on the volatile compounds or on the bacteria operating upon the
369 viscous secretions of various sweat glands. These hypotheses, while speculative in nature,
370 may help explain the interrelation between levels of female sex steroids and body odour
371 attractiveness, but will have to be specifically tested in future studies.

372 Because some studies have found that body odour preferences are mediated by the human
373 leukocyte antigen, [HLA, see 35 for a review] we controlled for HLA-mediated effects of
374 body odour preferences by including HLA-similarity between donor and rater at five HLA
375 loci and donor HLA-heterozygosity as covariates. Neither of these genetic measures predicted
376 woman's body odour attractiveness. These results add to the growing body of literature that
377 questions HLA-mediated odour preferences in men [e.g., 42, 50, 51; for a meta-analysis, see
378 52].

379 Together our findings suggest that some women generally smell nicer than others and
380 that the attractiveness of women's body odour is influenced by their estradiol and
381 progesterone levels rather than by individual preferences of the rater or by human leucocyte
382 antigens (HLA). Chemical communication of sex and reproductive stage are ubiquitous in the
383 animal kingdom, facilitating sexual selection that arises through competition over mates [53].
384 Our results provide strong evidence that humans also use chemical signals to communicate
385 their reproductive potential. Since estradiol and progesterone levels can be seen as indices of
386 reproductive health and fertility, we propose that body odours serve as reliable cues to
387 women's reproductive fitness.

388

389 **Ethics**

390 The study was approved by the Ethics Committees of the Faculty of Human Sciences of the
391 University of Bern (Nr.: 2016-11-00004) and of the Canton of Bern (KEK-Nr.: 242/ 15) and
392 was conducted according to the principles expressed in the Declaration of Helsinki.

393

394 **Data accessibility**

395 The dataset used for this manuscript is available at datadryad.org.

396 <https://doi.org/10.5061/dryad.g5n1785>

397

398 **Author contributions**

399 JL, UF & DK designed the study, UW performed HLA typing, JL & UF analysed the data, JL
400 & DK wrote the manuscript, UF und UW provided helpful input on manuscript drafts.

401

402 **Competing interests**

403 All authors gave final approval for publication and have no competing interests.

404

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415

416 **References:**

- 417 1. Roberts S.C., Gosling L.M., Carter V., Petrie M. 2008 MHC-correlated odour
418 preferences in humans and the use of oral contraceptives. *Proc Biol Sci* **275**(1652),
419 2715-2722. (doi:F542428772R96X64 [pii]
420 10.1098/rspb.2008.0825).
- 421 2. Lubke K.T., Pause B.M. 2015 Always follow your nose: The functional significance
422 of social chemosignals in human reproduction and survival. *Hormones and Behavior* **68**,
423 134-144. (doi:10.1016/j.yhbeh.2014.10.001).
- 424 3. Gosling L.M., Roberts S.C. 2001 Scent-marking by male mammals: Cheat-proof
425 signals to competitors and mates. *Adv Stud Behav* **30**, 169-217. (doi:Doi 10.1016/S0065-
426 3454(01)80007-3).
- 427 4. Penn D.J., Oberzaucher E., Grammer K., Fischer G., Soini H.A., Wiesler D., Novotny
428 M.V., Dixon S.J., Xu Y., Brereton R.G. 2007 Individual and gender fingerprints in human
429 body odour. *J R Soc Interface* **4**(13), 331-340. (doi:C14291T735824274 [pii]
430 10.1098/rsif.2006.0182).
- 431 5. Langlois J.H., Kalakanis L., Rubenstein A.J., Larson A., Hallam M., Smoot M. 2000
432 Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychological*
433 *Bulletin* **126**(3), 390-423. (doi:10.1037/0033-2909.126.3.390).
- 434 6. Cunningham M.R., Roberts A.R., Wu C.H., Barbee A.P., Druen P.B. 1995 Their Ideas
435 of Beauty Are, on the Whole, the Same as Ours - Consistency and Variability in the Cross-
436 Cultural Perception of Female Physical Attractiveness. *Journal of Personality and Social*
437 *Psychology* **68**(2), 261-279. (doi:Doi 10.1037//0022-3514.68.2.261).
- 438 7. Symons D. 1979 *The evolution of human sexuality*. Oxford, Oxford University
439 Press.
- 440 8. Thornhill R., Grammer K. 1999 The body and face of woman: One ornament that
441 signals quality? *Evolution and Human Behavior* **20**(2), 105-120. (doi:10.1016/s1090-
442 5138(98)00044-0).
- 443 9. Thornhill R., Gangestad S.W. 1999 Facial attractiveness. *Trends Cogn Sci* **3**(12),
444 452-460. (doi:S1364-6613(99)01403-5 [pii]).
- 445 10. Jasienska G. 2013 *The fragile wisdom: an evolutionary view on women's biology*
446 *and health*. Cambridge MA, Harvard University Press.
- 447 11. Lipson S.F., Ellison P.T. 1996 Comparison of salivary steroid profiles in naturally
448 occurring conception and non-conception cycles. *Hum Reprod* **11**(10), 2090-2096.
- 449 12. Jasienska G., Ziomkiewicz A., Ellison P.T., Lipson S.F., Thune I. 2004 Large breasts
450 and narrow waists indicate high reproductive potential in women. *Proceedings of the*
451 *Royal Society B-Biological Sciences* **271**(1545), 1213-1217.
452 (doi:10.1098/rspb.2004.2712).

- 453 13. Singh D. 1993 Adaptive Significance of Female Physical Attractiveness - Role of
454 Waist-to-Hip Ratio. *Journal of Personality and Social Psychology* **65**(2), 293-307. (doi:Doi
455 10.1037/0022-3514.65.2.293).
- 456 14. Grillo R.L., Simmons Z.L., Lukaszewski A.W., Roney J.R. 2014 Hormonal and
457 morphological predictors of women's body attractiveness. *Evolution and Human
458 Behavior* **35**(3), 176-183.
- 459 15. Jones B.C., Hahn A.C., Fisher C.I., Wang H., Kandrik M., Lao J., Han C., Lee A.J.,
460 Holzleitner I.J., DeBruine L.M. 2018 No compelling evidence that more physically
461 attractive young adult women have higher estradiol or progesterone. *bioRxiv*.
462 (doi:10.1101/136515).
- 463 16. Law Smith M.J., Perrett D.I., Jones B.C., Cornwell R.E., Moore F.R., Feinberg D.R.,
464 Boothroyd L.G., Durrani S.J., Stirrat M.R., Whiten S., et al. 2006 Facial appearance is a cue
465 to oestrogen levels in women. *Proceedings of the Royal Society B-Biological Sciences*
466 **273**(1583), 135-140. (doi:10.1098/rspb.2005.3296).
- 467 17. Puts D.A., Bailey D.H., Cardenas R.A., Burriss R.P., Welling L.L.M., Wheatley J.R.,
468 Dawood K. 2013 Women's attractiveness changes with estradiol and progesterone
469 across the ovulatory cycle. *Hormones and Behavior* **63**(1), 13-19.
470 (doi:10.1016/j.yhbeh.2012.11.007).
- 471 18. Singh D., Bronstad P.M. 2001 Female body odour is a potential cue to ovulation.
472 *Proceedings of the Royal Society B* **268**, 797-801.
- 473 19. Gildersleeve K.A., Haselton M.G., Larson C.M., Pillsworth E.G. 2012 Body odor
474 attractiveness as a cue of impending ovulation in women: evidence from a study using
475 hormone-confirmed ovulation. *Horm Behav* **61**(2), 157-166.
476 (doi:10.1016/j.yhbeh.2011.11.005).
- 477 20. Havlicek J., Dvorakova R., Bartos L., Flegr J. 2006 Non-advertised does not mean
478 concealed: Body odour changes across the human menstrual cycle. *Ethology* **112**, 81-90.
- 479 21. Cerda-Molina A.L., Hernandez-Lopez L., de la O C.E., Chavira-Ramirez R.,
480 Mondragon-Ceballos R. 2013 Changes in Men's Salivary Testosterone and Cortisol
481 Levels, and in Sexual Desire after Smelling Female Axillary and Vulvar Scents. *Frontiers
482 in endocrinology* **4**, 159. (doi:10.3389/fendo.2013.00159).
- 483 22. Doty R.L. 1981 Olfactory Communication in Humans. *Chem Senses* **6**(4), 351-376.
484 (doi:DOI 10.1093/chemse/6.4.351).
- 485 23. Albone E.S., Gosden P.E., Ware G.C., Macdonald D.W., Hough N. 1977 Bacterial
486 Action and Chemical Signaling in Red Fox and Other Mammals. *Abstr Pap Am Chem S*
487 **174**(Sep), 22-22.
- 488 24. Leyden J.J., McGinley K.J., Holzle E., Labows J.N., Kligman A.M. 1981 The
489 microbiology of the human axilla and its relationship to axillary odor. *J Invest Dermatol*
490 **77**(5), 413-416.
- 491 25. Stoddart D.M. 1990 *The scented ape: the biology and culture of human odor*.
492 Cambridge, UK, Cambridge University Press.
- 493 26. Taylor D., Daulby A., Grimshaw S., James G., Mercer J., Vaziri S. 2003
494 Characterization of the microflora of the human axilla. *Int J Cosmet Sci* **25**(3), 137-145.
495 (doi:10.1046/j.1467-2494.2003.00181.x).
- 496 27. James A.G., Hyliands D., Johnston H. 2004 Generation of volatile fatty acids by
497 axillary bacteria. *Int J Cosmet Sci* **26**(3), 149-156. (doi:10.1111/j.1467-
498 2494.2004.00214.x).
- 499 28. Martin A., Saathoff M., Kuhn F., Max H., Terstegen L., Natsch A. 2010 A functional
500 ABCC11 allele is essential in the biochemical formation of human axillary odor. *J Invest
501 Dermatol* **130**(2), 529-540. (doi:10.1038/jid.2009.254).

- 502 29. Doty R.L., Orndorff M.M., Leyden J., Kligman A. 1978 Communication of gender
503 from human axillary odors: relationship to perceived intensity and hedonicity. *Behav*
504 *Biol* **23**(3), 373-380.
- 505 30. Jackman P.J., Noble W.C. 1983 Normal axillary skin microflora in various
506 populations. *Clin Exp Dermatol* **8**(3), 259-268.
- 507 31. Brody B. 1975 The sexual significance of the axillae. *Psychiatry* **38**(3), 278-289.
- 508 32. Gower D.B., Ruparelia B.A. 1993 Olfaction in humans with special reference to
509 odorous 16-androstenes: their occurrence, perception and possible social, psychological
510 and sexual impact. *J Endocrinol* **137**(2), 167-187.
- 511 33. Gower D.B., Bird S., Sharma P., House F.R. 1985 Axillary 5 alpha-androst-16-en-3-
512 one in men and women: relationships with olfactory acuity to odorous 16-androstenes.
513 *Experientia* **41**(9), 1134-1136.
- 514 34. Hays W.S.T. 2003 Human pheromones: have they been demonstrated? *Behav Ecol*
515 *Sociobiol* **54**(2), 89-97. (doi:10.1007/s00265-003-0613-4).
- 516 35. Havlicek J., Roberts S.C. 2009 MHC-correlated mate choice in humans: a review.
517 *Psychoneuroendocrinology* **34**(4), 497-512. (doi:S0306-4530(08)00266-7 [pii]
518 10.1016/j.psyneuen.2008.10.007).
- 519 36. Thornhill R., Gangestad S.W., Miller R., Scheyd G., McCollough J.K., Franklin M.
520 2003 Major histocompatibility complex genes, symmetry, and body scent attractiveness
521 in men and women. *Behavioral Ecology* **14**(5), 668-678. (doi:10.1093/beheco/arg043).
- 522 37. Prehn A., Ohrt A., Sojka B., Ferstl R., Pause B.M. 2006 Chemosensory anxiety
523 signals augment the startle reflex in humans. *Neuroscience Letters* **394**(2), 127-130.
524 (doi:10.1016/j.neulet.2005.10.012).
- 525 38. Mujica-Parodi L.R., Strey H.H., Frederick B., Savoy R., Cox D., Botanov Y., Tolkunov
526 D., Rubin D., Weber J. 2009 Chemosensory Cues to Conspecific Emotional Stress Activate
527 Amygdala in Humans. *Plos One* **4**(7). (doi:ARTN e6415
528 10.1371/journal.pone.0006415).
- 529 39. Lenochova P., Roberts S.C., Havlicek J. 2009 Methods of Human Body Odor
530 Sampling: The Effect of Freezing. *Chem Senses* **34**(2), 127-138.
531 (doi:10.1093/chemse/bjn067).
- 532 40. Gildersleeve K.A., Fales M.R., Haselton M.G. 2017 Women's evaluations of other
533 women's natural body odor depend on target's fertility status. *Evol Hum Behav* **38**(2),
534 155-163.
- 535 41. Roberts S.C., Gosling L.M., Carter V., Petrie M. 2008 MHC-correlated odour
536 preferences in humans and the use of oral contraceptives. *Proceedings of the Royal*
537 *Society B-Biological Sciences* **275**(1652), 2715-2722. (doi:10.1098/rspb.2008.0825).
- 538 42. Probst F., Fischbacher U., Lobmaier J.S., Wirthmuller U., Knoch D. 2017 Men's
539 preferences for women's body odours are not associated with human leucocyte antigen.
540 *Proc Biol Sci* **284**(1864). (doi:10.1098/rspb.2017.1830).
- 541 43. Fialova J., Roberts S.C., Havlicek J. 2016 Consumption of garlic positively affects
542 hedonic perception of axillary body odour. *Appetite* **97**, 8-15.
543 (doi:10.1016/j.appet.2015.11.001).
- 544 44. Venners S.A., Liu X., Perry M.J., Korricks S.A., Li Z., Yang F., Yang J., Lasley B.L., Xu X.,
545 Wang X. 2006 Urinary estrogen and progesterone metabolite concentrations in
546 menstrual cycles of fertile women with non-conception, early pregnancy loss or clinical
547 pregnancy. *Hum Reprod* **21**(9), 2272-2280. (doi:10.1093/humrep/del187).
- 548 45. Landgren B.M., Uden A.L., Diczfalusy E. 1980 Hormonal profile of the cycle in 68
549 normally menstruating women. *Acta Endocrinol (Copenh)* **94**(1), 89-98.

- 550 46. Baird D.D., Weinberg C.R., Wilcox A.J., McConaughey D.R., Musey P.I. 1991 Using
551 the ratio of urinary oestrogen and progesterone metabolites to estimate day of
552 ovulation. *Stat Med* **10**(2), 255-266.
- 553 47. Stephenson L.A., Kolka M.A. 1999 Esophageal temperature threshold for sweating
554 decreases before ovulation in premenopausal women. *J Appl Physiol (1985)* **86**(1), 22-
555 28. (doi:10.1152/jappl.1999.86.1.22).
- 556 48. Charkoudian N., Hart E.C.J., Barnes J.N., Joyner M.J. 2017 Autonomic control of
557 body temperature and blood pressure: influences of female sex hormones. *Clin Auton*
558 *Res* **27**(3), 149-155. (doi:10.1007/s10286-017-0420-z).
- 559 49. Charkoudian N., Stachenfeld N. 2016 Sex hormone effects on autonomic
560 mechanisms of thermoregulation in humans. *Auton Neurosci* **196**, 75-80.
561 (doi:10.1016/j.autneu.2015.11.004).
- 562 50. Kromer J., Hummel T., Pietrowski D., Giani A.S., Sauter J., Ehninger G., Schmidt
563 A.H., Croy I. 2016 Influence of HLA on human partnership and sexual satisfaction.
564 *Scientific Reports* **6**, 32550. (doi:10.1038/srep32550).
- 565 51. Santos P.S.C., Schinemann J.A., Gabardo J., Bicalho M.D. 2005 New evidence that
566 the MHC influences odor perception in humans: a study with 58 Southern Brazilian
567 students. *Hormones and Behavior* **47**(4), 384-388. (doi:10.1016/j.yhbeh.2004.11.005).
- 568 52. Winternitz J., Abbate J.L., Huchard E., Havlicek J., Garamszegi L.Z. 2017 Patterns of
569 MHC-dependent mate selection in humans and nonhuman primates: a meta-analysis.
570 *Mol Ecol* **26**(2), 668-688. (doi:10.1111/mec.13920).
- 571 53. Wyatt T.D. 2003 *Pheromones and animal behavior: communication by smell and*
572 *taste*. London, Cambridge University Press.
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Figure Captions:

577 *Figure 1.* Relationship between mean odour attractiveness ratings and estradiol levels (left
578 panel) and progesterone levels (right panel), including regression lines and confidence
579 intervals (95%).
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