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Rachel L. Grillot

Zachary L. Simmons
University of Portland, simmonsz@up.edu

Aaron W. Lukaszewski

James R. Roney

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2 Hormonal and morphological predictors of women's body attractiveness

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5 RACHEL L. GRILLOT^a, ZACHARY L. SIMMONS^a, AARON W. LUKASZEWSKI^a,
6 and JAMES R. RONEY^{a*}

7

8 ^a University of California, Santa Barbara

9

10

11

12 *corresponding author

13 e-mail: roney@psych.ucsb.edu

14 Phone: 805-893-4871

15 Fax: 805-893-2791

16 Department of Psychological and Brain Sciences

17 University of California, Santa Barbara

18 Santa Barbara, CA 93106-9660

19

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21

22 **Abstract**

23

24 Does women's body attractiveness predict indices of reproductive capacity? Prior
25 research has provided evidence that large breast size and low waist-to-hip ratio (WHR)
26 are positively associated with women's estrogen and progesterone concentrations, but no
27 previous studies appear to have directly tested whether ratings of women's body
28 attractiveness are predicted by higher concentrations of ovarian hormones measured
29 across broad regions of the menstrual cycle. Here, we collected daily saliva samples
30 across 1-2 menstrual cycles from a sample of young women; assayed the samples for
31 estradiol, progesterone, and testosterone; obtained anthropometric measurements of the
32 women's bodies; and also obtained attractiveness ratings of the women's bodies from
33 photographs of them taken in standardized clothing with faces obscured. Contrary to
34 previous research, mean hormone concentrations were uncorrelated with breast size and
35 WHR. Body mass index (BMI) was a very strong negative predictor of body
36 attractiveness ratings, similar to previous findings. Zero-order associations between
37 women's mean hormone concentrations and mean attractiveness ratings were not
38 significant; however, after controlling for BMI, attractiveness ratings were independently
39 and positively associated with both estradiol and testosterone concentrations. Discussion
40 focuses on the implications of these findings for whether attractiveness assessment
41 mechanisms are specialized for the detection of cues of differential fecundity in young
42 women's bodies.

43

44

45 **1. Introduction**

46

47 Functional approaches to understanding women's body attractiveness posit the
48 evolution of specialized mechanisms in perceivers that hone in on bodily features that
49 would have predicted reproductively valuable qualities in human ancestral environments,
50 such as health or fecundity (e.g., Gangestad & Scheyd, 2005; Symons, 1995). A low
51 waist-to-hip ratio (WHR), for instance, has been proposed to signal qualities such as
52 health, fecundity, and greater specialized fat stores for healthy fetal brain development
53 (Lassek & Gaulin, 2008; Singh, 1993b; Singh & Singh, 2011), and, as such, men's
54 preference for this trait in mating partners (e.g., Furnham et al., 1997; Singh, 1993a;
55 Streeter & McBurney, 2003) may provide an example of specialized preference
56 mechanisms honing in on reproductively valuable traits in others. Complicating this
57 issue, however, are findings from some non-Western cultures that suggest preferences for
58 larger body size and associated higher WHRs in women (Marlowe & Wetsman, 2001;
59 Wetsman & Marlowe, 1998; Yu & Shepard, 1998; c.f. Marlowe et al., 2005; Sugiyama,
60 2004; Swami & Tovee, 2007); some have argued from such findings that preferences for
61 traits such as low WHR are not products of specialized preference mechanisms but are
62 instead attributable to Western media influences (Yu & Shepard, 1998).

63

64 One strategy for testing whether attractiveness judgments are generated by
65 specialized preference mechanisms is to assess whether such judgments correlate with
66 biological markers of health or fecundity, since positive correlations would be difficult to

67 explain if attractiveness standards were culturally arbitrary. Women's concentrations of
68 estradiol and progesterone appear to act as biological markers of fecundity given
69 evidence that these concentrations are positively correlated with conception probabilities
70 (see Baird et al., 1999; Lipson & Ellison, 1996; Venners et al., 2006). Jasienska et al.
71 (2004) demonstrated that low WHR and large breast size predicted higher concentrations
72 of these ovarian hormones across broad regions of the menstrual cycle, suggesting that
73 these body shape characteristics may be valid cues of fecundity, at least within their
74 sample of well-nourished Polish women. These authors did not report associations
75 between hormone concentrations and ratings of the women's body attractiveness, but
76 such associations would more directly test whether preference mechanisms are attuned to
77 physical cues of fecundity. Law Smith et al. (2006) reported that ratings of women's
78 facial attractiveness were positively correlated with the women's late follicular estradiol
79 concentrations (see also Puts et al., 2013), whereas Rilling et al. (2009) failed to find a
80 significant correlation between ratings of women's body attractiveness and a single
81 measure of estradiol that did not control for cycle day. In summary, with respect to
82 hormonal correlates of women's body attractiveness, a single study has reported
83 significant correlations between ovarian hormone concentrations and both WHR and
84 breast size, but no previous study has tested for hormonal correlates of body
85 attractiveness ratings when hormones were measured across broad regions of the
86 menstrual cycle.

87

88 In the present research, we obtained salivary measurements of estradiol,
89 progesterone, and testosterone across 1-2 menstrual cycles from a sample of young

90 women; collected ratings of the women's body attractiveness from photos of them in
91 standardized clothing (with faces obscured); and also obtained measurements of body
92 mass index (BMI), breast size, and WHR. We hypothesized replication of higher
93 estradiol and progesterone among women with lower WHR and larger breast size
94 (Jasienska et al., 2004), and also predicted that concentrations of these hormones would
95 positively predict body attractiveness ratings. Although not a primary purpose of the
96 study, our data additionally allowed us to test for associations between body dimensions
97 and attractiveness ratings, and here we expected replication of negative correlations (in
98 Western cultures) between body attractiveness and both BMI and WHR (e.g., Rilling et
99 al., 2009; Singh & Singh, 2011; Streeter & McBurney, 2003; Tovee & Cornelissen,
100 2001).

101

102 **2. Methods**

103

104 *2.1. Body stimuli*

105

106 *2.1.1. Stimulus participants*

107

108 Body photographs were obtained from a sample of women who participated in a
109 larger study on the relationship between ovarian hormones and sexual psychology and
110 behavior within natural menstrual cycles (see Roney & Simmons, 2013). Women
111 participants provided daily saliva samples each morning across 1-2 menstrual cycles.
112 Although 52 total women participated in the study, saliva samples were not sent for assay

113 for women with many missing samples, and hormone data were ultimately obtained for
114 43 women; 41 of these women provided consent for use of their photographs in research.
115 Of those women, 33 were judged to have experienced at least one ovulatory menstrual
116 cycle (see below). These 33 women comprise the final stimulus sample (Mean age \pm SD
117 = 18.85 ± 1.28 years). Nineteen of the women self-identified as White, seven as Asian,
118 five as Hispanic, and two as mixed ethnicity; none of the hormone variables, body
119 dimensions, or attractiveness ratings differed significantly across ethnic categories.

120

121 *2.1.2. Anthropometry*

122

123 Participants attended four laboratory sessions per menstrual cycle; anthropometric
124 measurements were obtained in one of the sessions from the first cycle. Weight, muscle
125 mass, body fat, visceral fat, and water percentage were measured using a Tanita electrical
126 impedance scale (Tanita BC-573), and height was self-reported via questionnaire. The
127 values for height and weight were used to calculate body mass index (BMI). Women
128 research assistants used measuring tapes to measure breast size (the widest circumference
129 at the level of the chest) and underbreast circumference; following Jasienska et al. (2004),
130 the ratio of these two values was employed as a measure of relative breast size. WHR
131 was measured from photographs of the women using Adobe Photoshop Elements 3.0;
132 following a technique for photo measurements that was validated against direct body
133 measurements (Steve Gaulin, personal communication, September 2012), the waist was
134 defined as the narrowest point on the torso below the breasts, and the hips were defined
135 as the widest point below the waist. Two research assistants independently measured

136 these and computed the ratio of the two; the means of the two ratios ($r = 0.97$) were used
137 for data analyses.

138

139 *2.1.3. Hormone measures*

140

141 Morning saliva samples were first stored in women's home freezers and then
142 delivered weekly to our research lab, after which they were stored at -80 C until shipping
143 for assay (for full details of the collection procedure, see Roney & Simmons, 2013). We
144 initially estimated the day of ovulation as 15 days prior to the end of each cycle, and sent
145 for assay all samples in a nine day window centered on the estimated day of ovulation, as
146 well as samples from alternating days outside of this window. Samples were shipped on
147 dry ice to the Endocrine Core Laboratory at the California Regional Primate Research
148 Center, Davis, CA, where they were assayed for concentrations of estradiol, testosterone,
149 and progesterone. Full details of the assay procedures can be found in Roney & Simmons
150 (2013); intra- and inter-assay CVs were below 10 percent for each of the hormones.

151

152 Hormone data were used to re-estimate the day of ovulation based on the
153 conjunction of the mid-cycle estradiol drop and the initiation of the luteal phase
154 progesterone increase (for the specific algorithm, see Roney & Simmons, 2013).
155 Following Jasienska et al. (2004), we computed cycle mean estradiol as the mean
156 estradiol concentration for the 18 cycle days centered on the estimated day of ovulation,
157 whereas cycle mean progesterone was computed as the average concentration of
158 progesterone in the final 14 days of the cycle; although Jasienska et al. did not measure

159 testosterone, we computed cycle mean testosterone the same way as cycle mean estradiol
160 (i.e. an average of the 18 cycle days centered on ovulation), given similarities in the
161 secretion patterns of these hormones. Because identification of the day of ovulation was
162 not possible in anovulatory cycles, we restricted data analyses to ovulatory cycles in
163 order to ensure that similar cycle regions were being compared across women. Following
164 Ellison et al. (1987), we defined as anovulatory any cycle that did not achieve a
165 maximum progesterone value of at least 300 pmol/L.

166

167 Among the 41 women with both photo consent and hormone data, eight did not
168 experience an ovulatory cycle based on the above criterion. Among the remaining
169 women, 18 had hormone data for two ovulatory cycles, 10 women participated in both
170 cycles but only one of the two was judged ovulatory, and five women participated in a
171 single cycle that was also judged ovulatory; as such, the final sample included hormone
172 data from two cycles for 18 women and from one cycle for 15 women. Subject mean
173 hormone concentrations were computed from a single cycle mean (as defined above) for
174 the 15 women with one ovulatory cycle and as the average of the two cycle means for the
175 18 women with two ovulatory cycles (this procedure entailed that some women had more
176 reliable mean hormone values than others due to the larger number of sample days;
177 however, a set of mixed regression models that treated daily hormone concentrations as
178 dependent variables and body dimensions and attractiveness ratings as higher level
179 predictor variables – and thereby weighted women with more hormone data more heavily
180 due to the more reliable estimates of their hormone concentrations – produced identical
181 statistical conclusions to those presented below using subject mean hormone values).

182 Data analyses tested associations between these subject mean hormone values and both
183 body shape dimensions and mean body attractiveness ratings (see section 2.2.3).

184

185

186 *2.1.4. Stimulus photos*

187

188 During one of the four laboratory sessions, each woman was photographed in
189 standardized dress comprised of grey gym shorts and a blue tank top shirt. Photos were
190 taken with a digital camera at a standard distance in a windowless room with artificial
191 lighting. For each woman, photos were taken from front-facing, back-facing, and side-
192 facing perspectives; these three photos were placed together onto a single stimulus array
193 for each woman, with an opaque mask blocking the head area in each photo. An example
194 stimulus array appears in Fig. 1.

195

196 *2.2. Stimulus ratings*

197

198 *2.2.1. Rating participants*

199

200 Raters were UCSB students who participated in exchange for partial course credit.
201 The primary 39 raters were 23 men (Mean age \pm SD = 19.17 \pm 1.50 years) and 16 women
202 (Mean age \pm SD = 18.81 \pm 1.22 years), but an additional batch of 19 raters comprised of
203 11 women (Mean age \pm SD = 19.64 \pm 0.67 years) and 8 men (Mean age \pm SD = 19.38 \pm
204 1.30 years) was recruited in order to obtain ratings for five stimulus photos that were

205 previously omitted due to a clerical error. Participants provided written, informed consent
206 for their participation, and all procedures were approved by the UCSB Institutional
207 Review Board.

208

209 *2.2.2. Rating procedures*

210

211 Raters viewed the stimulus photos one at a time on a computer and were asked to
212 indicate how physically attractive each woman was, relative to other women of the same
213 age, on a 1-7 likert-type scale. After rating all of the stimuli for general attractiveness,
214 participants rated them for attractiveness “as a SHORT-TERM partner” and for
215 attractiveness “as a LONG-TERM partner,” with the order of these ratings
216 counterbalanced across raters; the order of photo presentation was randomized within
217 each rating dimension.

218

219 There was high between-rater agreement for each of the three rating dimensions
220 (all ICCs > 0.90); thus, ratings were aggregated across raters to give each woman a mean
221 rating for each rating dimension. The three rating dimensions also had high reliability (α
222 = 0.99 for the mean ratings) and were therefore averaged to create a composite
223 attractiveness variable that was used in subsequent data analyses. Male and female raters
224 were in high agreement regarding their perceptions of the women's attractiveness (ICC =
225 0.92 for the composite mean attractiveness ratings). The average attractiveness rating was
226 just below the midpoint of scale (composite attractiveness mean = 3.92, S.D. = 1.05).

227

228 2.2.3. *Data analyses*

229

230 Pearson correlation, partial correlation, and multiple regression were employed to
231 test relationships between women's mean hormone concentrations (as defined in 2.1.3),
232 body dimensions, and rated attractiveness. Following Jasienska et al. (2004), we also
233 constructed categorical body dimension groups (top vs. bottom quartile of WHR and
234 breast size, as well as combinations of above and below average WHR with above and
235 below average breast sizes) and *t*-tests and one-way ANOVAs were used to test whether
236 such groups differed in mean hormone concentrations. Bias-corrected, nonparametric
237 bootstrapping procedures (see Preacher & Hayes, 2008) were employed as tests of
238 whether specific body dimensions statistically mediated relationships between hormone
239 concentrations and attractiveness ratings. This analysis essentially tests whether a third
240 variable is related to both the hormones and attractiveness ratings such that its addition to
241 the model significantly diminishes the direct effect of hormones on attractiveness ratings;
242 mediation is established if the 95% confidence interval for the unstandardized indirect
243 effect does not include zero.

244

245 Measured variables more than three standard deviations from their respective
246 means were excluded to avoid undue influence of outliers; one subject mean testosterone
247 concentration and one BMI value were thus excluded (effect sizes for significant effects
248 were generally larger with the outliers included). After outlier removal, all mean hormone
249 and body dimension variables were approximately normally distributed by visual
250 inspection and the Shapiro-Wilk test.

251

252 **3. Results**

253

254 *3.1. Hormones*

255

256 Excluding the one woman whose mean testosterone concentration was an outlier,
257 the 32 women in the sample provided 798 saliva samples from the middle 18 days of
258 their respective cycles out of 900 eligible cycle days (89% compliance rate). After
259 selection of saliva samples from alternating days outside of the nine day window
260 surrounding the initial estimate of mid-cycle, measured hormone concentrations were
261 available for 565 and 577 of these days for estradiol and testosterone, respectively
262 (insufficient remaining quantity of saliva for assay accounted for the difference given that
263 testosterone was assayed first). With respect to the final 14 days of the cycle, 631 saliva
264 samples were collected out of 700 eligible cycle days (90% compliance rate);
265 progesterone assay values were obtained for 388 of these days. Mean hormone
266 concentrations aggregated across women and aligned against day of the cycle reproduced
267 prototypical hormone curves in this sample (see Fig. 1 in Roney & Simmons, 2013), thus
268 providing evidence for the validity of the hormone assays.

269

270 *3.2. Hormones and body dimensions*

271

272 Table 1 presents correlations between mean hormone concentrations, body
273 dimensions, and body attractiveness ratings. Contrary to previous findings (Jasienska et

274 al, 2004), there were null zero-order correlations between body dimensions and
275 hormones; neither WHR nor breast size was significantly associated with mean estradiol,
276 progesterone, or testosterone. Null results persisted in one-way ANOVAs that tested for
277 differences in mean hormone concentrations across the four body shape categories (large
278 and small WHR crossed with large and small breast size) defined by Jasienska et al.
279 (2004) (all $ps > 0.45$). Likewise, a series of t -tests found no differences in mean
280 hormones when comparing women in the top and bottom quartiles of breast size and
281 WHR, respectively (all $ps > 0.25$).

282

283 *3.3. Predictors of body attractiveness ratings*

284

285 *3.3.1. Morphological predictors*

286

287 Consistent with previous research, body attractiveness was significantly
288 negatively associated with both WHR and BMI (see Table 1). A multiple regression with
289 WHR and BMI entered together as predictors of body attractiveness ratings revealed a
290 strong independent effect of BMI ($\beta = -0.78, p < 0.001$) and a null effect of WHR ($\beta = -$
291 $0.03, p = 0.82$). BMI accounted for approximately 63% of the variance in women's body
292 attractiveness.

293

294 *3.3.2. Hormonal predictors*

295

296 As can be seen from Table 1, there were no significant zero-order correlations

297 between subject mean hormone concentrations and body attractiveness ratings, although
298 power limitations may have prevented detection of a small association between estradiol
299 and attractiveness ($r = 0.24$). The large association between BMI and attractiveness may
300 have obscured the influence of smaller predictor variables, however, and we therefore
301 tested whether hormone concentrations were correlated with attractiveness ratings after
302 controlling for the influence of BMI. Table 2 demonstrates that subject mean estradiol
303 and testosterone both exhibited significant partial correlations with body attractiveness
304 ratings after controlling for BMI. Progesterone was not a significant independent
305 predictor of the body attractiveness residuals from BMI, and neither WHR nor breast size
306 had residual variance from BMI that was significantly associated with any hormone. A
307 multiple regression analysis testing the partial effects of BMI, testosterone, and estradiol
308 revealed independent effects of BMI ($\beta = -0.83, p < 0.001$), mean estradiol ($\beta = 0.20, p =$
309 0.05), and mean testosterone ($\beta = 0.22, p = 0.04$); the two hormones jointly explained an
310 additional 10% of the variance in body attractiveness beyond that explained by BMI
311 alone (change in $R^2 F(2, 27) = 5.55, p = 0.01$).

312

313 Given that the estradiol and testosterone measurements represented subject means
314 for 18 days surrounding ovulation, it is possible that their associations with body
315 attractiveness could have been driven by effects in a narrow region of the cycle. To assess
316 this, Fig. 2 plots hormone concentrations against day of the cycle (aligned on the
317 estimated day of ovulation as day zero) with separate curves for women who were above
318 and below the mean residual attractiveness rating after controlling for BMI. It can be seen
319 that estradiol was consistently higher across the entire cycle among women who were

320 rated more attractive than predicted by their BMI alone (Fig. 2A); this pattern was less
321 consistent for testosterone, but still visible across broad regions of the cycle (Fig. 2B);
322 whereas the curves were very similar across the entire cycle for progesterone (Fig. 2C).

323

324 The patterns depicted in Fig. 2 suggest that, after controlling for BMI, other
325 observable cues in women's bodies both contribute to attractiveness judgments and
326 predict concentrations of estradiol and testosterone. In an exploratory attempt to identify
327 such cues, we employed nonparametric bootstrapping methods to first test whether scale
328 measures of women's muscle mass, visceral fat, body fat, or water percentage were
329 significant mediators between either estradiol or testosterone and women's body
330 attractiveness, controlling for BMI. None of these variables significantly mediated the
331 relationship between either of the hormones and attractiveness ratings, whether the
332 mediators were tested separately or jointly (all CIs for the indirect effects included zero).
333 Based on the subjective impression that women with higher residual attractiveness ratings
334 had waists that angled inward more sharply from their upper torsos, we also computed a
335 ratio of shoulder width (measured from front-facing photos) to waist width and tested it
336 as a mediator of the hormone effects. This shoulder-to-waist (SWR) ratio was in fact a
337 significant mediator between residual variance in women's body attractiveness from BMI
338 and both their estradiol (Indirect Effect = 0.117, SE = 0.078, 95% CI = 0.015 - 0.402) and
339 testosterone (Indirect Effect = 0.018, SE = 0.01, 95% CI = 0.004 – 0.05) concentrations,
340 with larger SWR associated with both higher hormone concentrations and greater
341 attractiveness. Neither shoulder width nor waist width on its own was a significant

342 mediator of the relationship between hormone concentrations and residual attractiveness
343 ratings (all CIs included 0).

344

345 **4. Discussion**

346

347 *4.1. Hormones, body dimensions, and body attractiveness*

348

349 The present research provided an initial, direct test of the possible relationship
350 between women's body attractiveness and their ovarian hormone production across broad
351 regions of the menstrual cycle. Contrary to our predictions, there were no significant
352 zero-order correlations between hormone concentrations and attractiveness ratings.
353 However, after controlling for BMI, which was strongly negatively associated with
354 attractiveness, women's concentrations of estradiol and testosterone were significantly
355 positively correlated with ratings of their body attractiveness. As can be seen from Fig. 2,
356 furthermore, these relationships held across broad regions of the menstrual cycle. These
357 patterns thus provide some evidence that perceivers' attractiveness judgments may in fact
358 hone in on cues of fecundity in young women's bodies, although interpretive questions
359 are raised by the necessity of holding BMI constant in order to demonstrate robust
360 relationships between hormones and attractiveness (see discussion of this issue in section
361 4.2 below).

362

363 Given previous research demonstrating higher estradiol and progesterone among
364 women with lower WHR and larger breast size (Jasienska et al., 2004), WHR and breast

365 size were expected to mediate any relationship between body attractiveness and hormone
366 concentrations. However, there was no evidence for this in our study. Neither breast size
367 nor WHR were associated with subject mean concentrations of estradiol, progesterone, or
368 testosterone; nor did they predict any hormone after controlling for variability in these
369 body shapes due to BMI. Thus, our results failed to replicate the pattern of associations
370 between body shapes and hormone concentrations demonstrated by Jasienska et al.
371 (2004).

372

373 Differences in the study samples may help account for inconsistencies between
374 results of the current study and that of Jasienska et al. (2004). Whereas Jasienska et al.
375 (2004) investigated over a hundred Polish women (mean age = 29 years), our sample was
376 younger (mean age = 18 years), more ethnically heterogeneous, and much smaller.
377 Menstrual cycles are notably less stable in young women (Metcalf & Mackenzie, 1980)
378 and may vary across cultural groups (Vitzthum, 2009), although ethnicity was not
379 associated with any variables examined in the present study and data were analyzed only
380 from cycles that were confirmed to be ovulatory. Nonetheless, age differences between
381 the samples still provide a plausible explanation for the different findings, and the current
382 results suggest that the hormone-body shape relationships reported by Jasienska et al.
383 (2004) may not generalize to younger samples of women. Although our sample size was
384 less than ideal, low power is unlikely to explain the null relationships between hormones,
385 WHR, and breast size given the absence of even trend-level effects in the relevant
386 analyses (see Table 1). Furthermore, our sample size was sufficient to detect relationships

387 between estradiol, testosterone, and residual variance in body attractiveness not
388 accounted for by BMI.

389

390 The lack of relationships between hormone concentrations and either WHR or
391 breast size suggested that at least one other physical cue was mediating the relationship
392 between both estradiol and testosterone and the body attractiveness residuals from BMI.
393 Exploratory analyses revealed the shoulder-to-waist ratio (SWR) as a statistical mediator
394 of the effects of both estradiol and testosterone on attractiveness ratings. These results
395 should be interpreted with caution, however, given both the number of potential
396 mediators tested (see section 3.3.2) and the fact that we had no way of testing whether
397 observers actually used this ratio as a perceptual cue that contributed to their
398 attractiveness judgments. SWR might correlate inversely with android fat depositions
399 (i.e. fat in the abdomen and upper torso) since such fat will cause the waist to spread out
400 toward the width of the shoulders and thus reduce this ratio (WHR may not capture quite
401 the same variable given cases of wide waists but even wider hips); android fat deposits, in
402 turn, have been shown to be strong negative predictors of body attractiveness ratings
403 (e.g., Faries & Bartholomew, 2012; Rilling et al., 2009). Ideally, android fat would be
404 measured more directly via tools such as dual-energy X-ray absorptiometry scans (see
405 Faries & Bartholomew, 2012; Sowers et al., 2001), and future research that combined
406 such measurements with hormone assays would allow for more precise tests of which
407 body dimensions may account for relationships between endocrine variables and body
408 attractiveness ratings.

409

410 *4.2. BMI, hormone concentrations, and specialized preference mechanisms*

411

412 Why was it necessary to control for BMI in order to see clear relationships
413 between ovarian hormone concentrations and body attractiveness ratings? If specialized
414 preference mechanisms track cues of fecundity as indexed by hormone concentrations,
415 then one might expect positive zero-order associations between hormones and
416 attractiveness without the need to control for other variables. We offer two conjectures
417 regarding this issue.

418

419 First, BMI may predict other fitness-relevant traits aside from fecundity that are
420 also relevant to attractiveness judgments. Higher BMI is strongly predictive of a wide
421 array of health problems in industrialized countries (e.g., Calle et al., 2003; Gilmore,
422 1999; Manson et al., 1995; Willett et al., 1995). Although many of those health problems
423 may not have been relevant to reproductive fitness in ancestral environments, higher BMI
424 has also been associated with greater fluctuating asymmetry (Hume & Montgomerie,
425 2001; Losken et al., 2005; Manning, 1995; Milne et al., 2003) and higher rates of
426 inflammation (e.g. Festa et al., 2001; Panagiotakos et al., 2005; Trayhurn & Wood,
427 2005), suggesting that greater BMI may predict greater developmental instability and
428 reduced immunocompetence, both of which likely entailed fitness costs to mates even
429 independent of any effects on fecundity. These inverse associations of BMI with health
430 and developmental stability – at least in industrialized nations – may lead cues of high
431 BMI to become associated with poor health, thus partly explaining the negative effect of
432 BMI on attractiveness. In addition, BMI is on average positively correlated with age in

433 the United States (Brown et al., 1992; Fryar et al., 2013; Lassek & Gaulin, 2006), such
434 that high BMI may become a cue associated with declining reproductive value (Wells,
435 2010). These associations of BMI with health and age appear to be reversed under
436 conditions of food shortage (e.g., women's BMI is known to decline with age in many
437 subsistence societies; see Jelliffe & Maddocks, 1964; Little et al., 1992; Shell-Duncan &
438 Yung, 2004; Tracer, 1991; also, BMI positively indexes health in societies where the
439 range of BMI is overall lower; see Hosegood & Campbell, 2003; Pierce et al., 2010), and
440 thus preference mechanisms that track cues of health and reproductive value may produce
441 opposite associations between BMI and attractiveness in regions with food surplus vs. in
442 regions with chronic nutritional stress (see Swami & Tovee, 2007; Wells, 2010). Whether
443 such BMI preferences reflect learned associations between cues of health or age and
444 BMI, or are the output of cognitive mechanisms that assess the reliability of food supply
445 over ontogeny and adjust BMI preferences accordingly, is unknown. Regardless, BMI
446 could act as a cue of health and age that has such large effects on attractiveness ratings
447 that it swamps the smaller effects on attractiveness of cues associated with ovarian
448 hormone production; once BMI is held constant, however, cues of hormone
449 concentrations emerge as significant predictors of attractiveness. On this account,
450 specialized perceptual mechanisms do in fact track cues of fecundity, but these cues have
451 smaller effects on attractiveness judgments than do cues associated with BMI.

452

453 Second, correlations between attractiveness ratings and salivary measures of
454 hormone concentrations may be partially obscured by associations between BMI and sex
455 hormone binding globulin (SHBG). SHBG binds to both estradiol and testosterone and

456 higher SHBG concentrations reduce the free, bioavailable concentrations of these
457 hormones that are measured in salivary assays (Ellison,1988). Higher BMI very strongly
458 and consistently predicts lower SHBG (e.g., Bruning et al., 1992; Dorgan et al., 1995;
459 Thomas et al., 1997; Turcato et al., 1997; Tworoger et al., 2006; for a review, see
460 Morisset et al., 2008), and experimentally induced weight loss can produce doubling of
461 SHBG concentrations (with associated drops in free but not total hormone
462 concentrations) in as little as two weeks (e.g., Kiddy et al., 1989, 1992; Turcato et al.,
463 1997; for a review, see Morisset et al., 2008). These patterns suggest that higher BMI is
464 likely to be associated with artificially inflated measures of salivary, free hormones
465 relative to the total ovarian hormone production; consistent with this, in a large study of
466 premenopausal women, BMI was significantly inversely correlated with total estradiol
467 but was uncorrelated with free estradiol (Tworoger et al., 2006). This in turn implies that
468 when two women have the same free hormone concentrations but differ in BMI, the
469 woman with lower BMI is likely to have greater ovarian hormone production since a
470 greater fraction of her hormones will be bound to SHBG. Likewise, when two women
471 have the same BMI but differ in free hormone concentrations, the woman with greater
472 free hormone concentrations should have higher ovarian production since the effect of
473 BMI on SHBG will be held constant. As such, if perceivers' attractiveness judgments
474 specifically track cues of ovarian hormone production, then BMI should negatively
475 predict attractiveness when free hormones are held constant and free hormones should
476 positively predict attractiveness when BMI is held constant, which is exactly the pattern
477 produced by the regression models in section 3.3.2. In short, controlling for BMI may
478 increase the size of correlations between free hormone concentrations and attractiveness

479 ratings by removing the variability in hormone concentrations that is associated with
480 binding proteins and is thus potentially unrelated to fecundity. This idea could be tested
481 more directly in future research that used blood samples in order to test associations
482 between body attractiveness and both total and free hormone concentrations.

483

484 *4.3. Independent effects of testosterone on attractiveness*

485

486 The positive effect of testosterone on attractiveness after controlling for BMI was
487 surprising given evidence that elevated testosterone in women may promote visceral fat
488 deposition (e.g., Evans et al., 1983; Sowers et al., 2001) and be associated with reduced
489 fecundity (e.g., Okon et al., 1998; Steinberger et al., 1979). Many of the negative effects
490 of testosterone on reproductive functioning are associated with obesity (Clark et al.,
491 1995; Kiddy et al., 1992; Pasquali et al., 1997) and associated reductions in SHBG (see
492 above), however, such that controlling for BMI may more uniquely capture follicle-
493 derived sources of testosterone that could in principle be associated with higher
494 fecundity. Testosterone acts a precursor to estradiol produced by the dominant follicle,
495 for instance, and peri-ovulatory peaks in estradiol are typically accompanied by
496 concomitant peaks in testosterone (e.g., Abraham, 1974; Campbell & Ellison, 1992;
497 Roney & Simmons, 2013) such that larger dominant follicles that produce higher
498 estradiol in more fertile cycles may likewise produce higher testosterone. As such, the
499 combination of estradiol and testosterone concentrations may better predict dominant
500 follicle production within ovulatory cycles than does the concentration of either hormone
501 alone, thus potentially explaining the independent effects of the two hormones on

502 attractiveness ratings. This is speculation, of course, and the unexpected association of
503 attractiveness with testosterone concentrations warrants replication before assigning
504 much confidence to the robustness of this finding.

505

506 *4.4. Conclusion*

507

508 The present study is to our knowledge the first to demonstrate a link between
509 women's body attractiveness and concentrations of ovarian hormones measured across
510 broad regions of the menstrual cycle. Both estradiol and testosterone independently
511 predicted body attractiveness ratings after controlling for the effects of BMI, which
512 suggests that preference mechanisms may indeed track cues of fecundity in young
513 women's bodies. The evidence for specialized attractiveness assessment mechanisms
514 could be substantially strengthened via cross-cultural demonstrations of relationships
515 between hormones and attractiveness across diverse ecological and social conditions,
516 however, and tests of such relationships therefore represent an important direction for
517 future research.

518

519

520

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522

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528

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729

730 **Figure Legends**

731

732 Figure 1. Sample stimulus photo.

733

734 Figure 2. Mean salivary estradiol (A), testosterone (B), and progesterone (C) aligned
735 against estimated day of cycle (day 0 represents the estimated day of ovulation) for below
736 and above average attractiveness residuals from BMI. Error bars represent SE.

737