Men's preferences for women's breast size and shape in four cultures

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21   ABSTRACT

22   The morphology of human female breasts typical for their permanent fat deposits

23   appears to be unique among primates. It has been previously suggested that female breast

24   morphology arose as a result of sexual selection. This is supported by evidence showing that

25   women with larger breasts tend to have higher estrogen levels; breast size may therefore serve

26   as an indicator of potential fertility. However, breasts become less firm with age and parity,

27   and breast shape could thus also serve as a marker of residual fertility. Therefore, cross-

28   culturally, males are hypothesized to prefer breast morphology that indicates both high

29   potential and residual fertility. To test this, we performed a survey on men´s preferences for

30   breast morphology in four different cultures (Brazil, Cameroon, the Czech Republic,

31   Namibia). As stimuli, we used two sets of images varying in breast size (marker of potential

32   fertility) and level of breast firmness (marker of residual fertility). Individual preferences for

33   breast size were variable, but the majority of raters preferred medium sized, followed by large

34   sized breasts. In contrast, we found systematic directional preferences for firm breasts across

35   all four samples. This pattern supports the idea that breast morphology may serve as a residual

36   fertility indicator, but offers more limited support for the potential fertility indicator

37   hypothesis. Future studies should focus on a potential interaction between the two parameters,

38   breast size and firmness, which, taken together, may help to explain the relatively large

39   variation in women's breast sizes.

40   Keywords: Permanent breasts, Mate preferences, Residual fertility, Nubility hypothesis,

41   Mammary gland, Human evolution

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1. Introduction

Women develop enlarged breasts during puberty, mainly due to the deposition of adipose tissue, and retain them through adulthood. This appears to be unique to humans, as in other primate species enlargement is restricted to periods of lactation. Although the proximate mechanisms involved in permanent breast development are relatively well understood (e.g., Anderson, 1983), the ultimate mechanisms involved in the evolution of permanent breasts are still debated. Hypotheses regarding their function can be classified into those that involve sexual selection and those that primarily rely on mechanisms of natural selection (Arieli, 2004; Barber, 1995). The latter suggests that adipose deposits may serve either as energy reserves for breast-fed infants during food scarcity or as thermo-insulation during cold nights (Pawlowski, 1999).

The sexual selection hypotheses propose that permanently enlarged breasts evolved via male choice. In this context, the specific morphology of women's breasts might be an honest signal of mate value if adipose deposits provide information on lactational capacity and/or fertility (Low, Alexander, & Noonan, 1987). This is supported by a study showing that breast size is positively associated with estrogen levels, which may, in turn, indicate higher potential fertility (Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004). Consequently, men are expected to be attracted to women with relatively large breasts. Nevertheless, research on attractiveness of women's breast size is inconclusive. Some studies show that men prefer larger breasts (Furnham, Dias, & McClelland, 1998; Zelazniewicz & Pawlowski, 2011) while others indicate preferences for medium (or medium to large) size (Dixson, Duncan, & Dixson, 2015; Dixson, Grimshaw, Linklater, & Dixson, 2011a) or even for small breasts (Furnham & Swami, 2007), and still others report no effect of size on attractiveness judgments (Dixson et al., 2011a; Horvath, 1979). Apart from methodological differences between studies, this mixed set of findings could be partly attributed either to cultural

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68   variation in the tested individuals (Dixson et al., 2011b) or temporal variation in preferences,

69   although a study testing several cohort samples across the 1990's did not support the latter

70   suggestion (Tantleff-Dunn, 2001). Alternatively, the variation in preferences might be due to

71   interactions with other parts of the body: large breasts are perceived to be more attractive in

72   women with low waist-to-hip ratios (Furnham et al., 1998; Singh & Young, 1995).

73   Furthermore, preferences for breast size may vary systematically across individuals.

74   Zelazniewicz & Pawlowski (2011) found that Polish men with high sociosexuality (i.e.,

75   tendency for sexual variety) prefer larger breasts. Similarly, a study from Malaysia found that

76   men of lower socio-economic status prefer larger breasts than their counterparts of higher

77   socio-economic status (Swami & Tovée, 2013b).

78   It has been further argued that breast symmetry may serve as a marker of

79   developmental stability. Indeed, there is some evidence showing that high breast asymmetry

80   is associated with lower fecundity (Manning, Scutt, Whitehouse, & Leinster, 1997; Moller,

81   Soler, & Thornhill, 1995; Scutt, Manning, Whitehouse, Leinster, & Massey, 1997) and with

82   higher risk of breast cancer (Scutt et al., 1997). In line with this, perceptual studies show that

83   symmetrical breasts are judged as more attractive (e.g., Dixson et al., 2011b).

84   Variation in breast morphology is, however, not restricted to size and symmetry—

85   breasts also vary greatly in shape. In general, breast shape changes with age and parity,

86   having a firmer appearance in younger adults (for brevity, we hereafter use the term "firm",

87   which is a tactile descriptor, even though we primarily refer to their visual appearance on

88   which our participants' preferences were based). Later in life, due to declining firmness of the

89   breasts' fibrous tissue, they become progressively more pendulous; this effect is amplified by

90   many factors, such as age, breast size, parity, weight loss, or smoking (Rinker, Veneracion, &

91   Walsh, 2010). The medical literature labels this phenomenon as breast ptosis, defined as a

92   sagging process where the breast falls onto the chest, flattens, and a nipple points downward

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93   (Rinker et al., 2010). Based on these changes, Marlowe (1998) proposed the nubility

94   hypothesis, suggesting that breast shape could be used as a reliable marker of residual

95   reproductive value, i.e., the expected future reproductive output of an individual, which is

96   negatively related to age. According to this hypothesis, men's perception of breast

97   attractiveness is expected to be primarily affected by their shape rather than size. Although

98   this hypothesis was formulated more than 15 years ago, to date its predictions have not, to our

99   knowledge, been directly tested.

100   The aim of this study was to test both preferences for breast size and breast shape. We

101   based our predictions about size preferences on the potential fertility hypothesis (Jasienska et

102   al., 2004) and about shape on the nubility hypothesis (Marlowe, 1998). As preferences may

103   vary across tested populations (Dixson et al., 2011b), we collected attractiveness ratings

104   across several populations varying in their cultural and socio-economic settings, including

105   two African communities (Cameroon, Namibia) and two industrialized urban populations (the

106   Czech Republic, Brazil). We expected to find preferences for firm breasts across the tested

107   countries. In contrast, we expected men to prefer larger breasts in countries with relatively

108   lower living standards and higher resource scarcity (here, Cameroon and Namibia) compared

109   with men in countries with relatively higher living standards (here, the Czech Republic and

110   Brazil). Resource scarcity is frequently associated with preferences for more corpulent bodies

111   (e.g., Wetsman & Marlowe, 1999). As breast size is to some extent positively associated with

112   body mass (Brown et al., 2012), preferences for larger breasts may simply reflect a

113   generalized preference for more corpulent women in communities that experience resource

114   scarcity.

115   To assess other factors that might be associated with breast preferences, we followed

116   findings from previous research (Dixson et al., 2011b; Zelazniewicz & Pawlowski, 2011).

117   Namely, we also tested effects of age, self-assessed attractiveness, relationship status, and

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118 sexual restrictiveness (here assessed in two ways, by self-reported number of sexual partners

119 and by using the Sociosexual Orientation Inventory, SOI-R: Penke & Asendorpf, 2008), each

120 of which has been found to be positively associated with preferences for larger breasts.

121

122 **2. Material and methods**

123

124 *2.1. Participants*

125   The data were collected as part of several larger projects investigating cross-cultural

126 predictors of physical attractiveness and intrasexual competition. The Brazilian sample

127 consisted of 44 male students of the University of São Paulo (mean age = 23.4ys; SD = 3.89;

128 range 18-34) approached on campus by local researchers (MACV and KJP). São Paulo is a

129 large urban agglomeration with a prevailing economic reliance on industrial production,

130 finance, and retail. Living standards range between moderate to rather high, with relatively

131 large social inequality. The population is highly culturally diverse, with most people being of

132 mixed descent, mainly of Amero-Indian, Portuguese, African, Japanese, and Middle Eastern

133 origin.

134   The sample from Cameroon consisted of 94 men (mean age = 22.8ys; SD = 4.15;

135 range 17-37); 49 students at the University of Buea (mean age = 22.9ys; SD = 3.69; range 17-

136 37) and 45 young men from the Big Babanki rural community (mean age = 22.7ys; SD =

137 4.63; range 18-37), located in the South and North West Regions, respectively. Students were

138 approached on campus by local (RA) and visiting (JV, KK and TK) researchers, while the

139 men from Big Babanki were recruited with the help of a local research assistant (EV) using

140 snowball sampling. The town Buea of the South West Region and the village Big Babanki of

141 the North West Region lie within the English speaking portion of Cameroon. The subsistence

142 is mainly agricultural, primarily based on production of yams, sweet potatoes, cassava, corn,

143 plantains, and palm oil. The community has a complex traditional governance system headed

144 by local chiefs, called 'Fons' in the North West Region and simply 'chiefs' in the South West

145 Region, all operating underneath a central governmental system.

146   In the Czech Republic, we collected data from 48 male students at Charles University

147 in Prague (mean age = 22.3ys; SD = 3.03; range 18-33), who were approached on campus or

148 in student dormitories by local researchers (JF, ZŠ and VT). Prague is capital of the country,

149 which can be characterized by a market economy based mainly on industrial production and

150 services. Living standards are relatively high, with low social inequality, and a relatively

151 culturally homogenous population.

152   The sample from Namibia consisted of 81 men (mean age = 22.7ys; SD = 3.97; range

153 18-36) from suburban sites (townships) of the Tseiblaagte and Karasburg communities of the

154 Karas region in southern Namibia. Both sites are characterized by a semi-arid environment

155 based on goat and cattle farming. In contrast to Cameroon, farms are typically larger and

156 commercially run; consequently, the majority of participants were landless, and of low socio-

157 economic status. Here, again, the participants were recruited by a local research assistant (RJ)

158 using snowball sampling. The samples from individual countries did not differ in their age (F

159 $(3,260) = 1.1$, $p = 0.35$).

160

161 *2.2. Stimuli and Procedure*

162   The stimuli on breast size were adopted from Dixson et al. (2011a) and consisted of 3

163 full frontal nude images (with the pubic area covered) digitally manipulated to vary only in

164 breast size (small, medium, large). The stimuli on breast shape variation were redrawn from

165 Rawson & Brooks (1984) and consisted of 4 profile drawings depicting gradually decreasing

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166 age-related firmness. The stimuli on breast size are shown in the Figure 1 and on breast shape

167 in Figure 2.

168   In both cases the stimuli were presented on laminated cards (4 x 9.5 cm) placed in

169 random order in front of the seated participant, who was asked to order the images from the

170 most to the least attractive. The researcher waited until the participants indicated they were

171 completely certain about their preferences before the order of the stimuli was recorded.

172 Participants also completed a questionnaire concerning their basic demographic data (e.g.,

173 age, education), self-rated facial and body attractiveness, relationship status, number of sexual

174 partners and SOI-R (Penke & Asendorpf, 2008).

175

176 *2.3 Statistical analysis*

177   To test for preferences in breast size or breast shape, we analysed data for the most

178 preferred stimuli. Under the null assumption of no systematic preferences, equal

179 representation of the individual stimuli was expected (i.e., we compared the frequency of the

180 most preferred against chance). A possible departure from the expected distribution was

181 tested by Chi-square tests together for all tested samples and separately for each sample,

182 respectively. In some cases, the frequency of the preferred stimuli was too low to allow for

183 statistical analysis and these data were therefore omitted. More specifically, only one Czech

184 participant showed preference for small breasts, and preferences for low firmness (stimuli #3

185 – low and #4 – very low) were represented with zero frequency in the Czech and Brazilian

186 samples. Note therefore that the degrees of freedom vary in different tests and so test statistics

187 may not be directly comparable across samples. We further compared the preferences across

188 the tested samples again using the Chi-square tests. Due to the low frequency of preferences

189 for the low firmness stimuli in the Brazilian and Czech samples as described above the breast

190 shape comparison across the samples is based only on the high and moderate firmness stimuli.

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191   The associations between preferences for breast size or shape with the modulating

192   factors of age, self-assessed facial and body attractiveness, SOI-R, and number of sexual

193   partners were explored using Kendall's Tau nonparametric correlations. The effect of

194   relationship status (single / coupled) on breast size and shape preferences was tested using

195   Chi-square tests or by the Fisher's Exact Test if the expected count in some cells was lower

196   than 5. To explore contribution of the modulating variables we build up the most

197   parsimonious model by employing backward stepwise multinomial regression model

198   separately for each sample. We set small breasts and firm breasts as the reference category

199   except in the sample from the Czech Republic where due to low frequency of small breast

200   preferences the medium breasts were set as the reference category. Similarly, due to the low

201   variation in breast firmness preferences in the Czech Republic (only 3 individuals selected

202   moderately firm stimuli) we were not able to perform meaningful logistic regression.

203

204   **3. Results**

205

206   *3.1. Breast size preferences*

207   Overall, preferences for breast size significantly varied across the four tested cultures

208   (Chi-square (6) = 23.9, p = 0.001). We thus tested preferences for breast size in each culture

209   separately. Medium sized breasts were most preferred in Brazil (52.3%, Chi-square (2) =

210   11.2, p = 0.004), the Czech Republic (70.2%, Chi-square (1) = 7.7, p = 0.006), and Namibia,

211   although here the effect only approached the formal level of significance (45.7%, Chi-square

212   (2) = 5.9, p = 0.054). In Cameroon, large sized breasts were the most frequently preferred, but

213   this effect was not formally significant (41.5%, Chi-square (2) = 4.7, p = 0.093). While

214   students from Cameroon most frequently preferred large sized breasts (55.1%), the young

215   men from the rural community most frequently preferred medium sized breasts (44.4%) and

216   the difference between these two groups was significant (Chi-square (2) = 7.8, p = 0.02).

217   Although the largest proportion of men (overall 47.4%; Chi-square (2) = 35.51, p < 0.001)

218   selected medium breast size (or large size in Cameroon) as the most attractive, in each

219   country there were also substantial proportions of men who selected otherwise. The only

220   exception was data from the Czech Republic, where only one of the participants preferred

221   small size (Figure 3).

222   To further explore this variability, we tested for individual differences in breast size

223   preferences. Descriptive data for candidate moderating variables are shown in Table 1. We

224   found no significant differences in preferences between men who reported being single and

225   those who were in a relationship; Brazil: Chi-square (1) = 1.94, p = 0.16; the Czech Republic:

226   Fisher's Exact Test: p = 0.182; Cameroon: Chi-square (2) = 0.39, p = 0.82; Namibia: Chi-

227   square (2) = 3.91, p = 0.14. There were also no significant associations with age, self-reported

228   facial attractiveness, number of sexual partners or participants' SOI-R scores, in any of the

229   tested countries (Table 2). In the Namibian sample, we found a significant positive correlation

230   between participants' body height and their preferences for large breast size, but no similar

231   association was observed in the three other samples. Finally, we found a significant positive

232   correlation between self-reported body attractiveness and preference for large breast size in

233   Namibia; a similar trend, though statistically non-significant, was found in Cameroon and the

234   Czech Republic, but not in Brazil (Table 2).

235   The Logistic regression model for the Brazilian sample included age and height and

236   was significantly better as compared to the baseline (Chi-square (4) = 13.476, p = 0.009, R^2

237   (Nagelkerke) = 0.321). However, neither age nor height alone significantly predicted breast

238   size preferences. In Cameroon, the final model included age, facial and body attractiveness

239   and number of sexual partners and was significant (Chi-square (8) = 22.261, p = 0.004, R^2

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240 (Nagelkerke) = 0.478). However, the only significant contributor was body attractiveness

241 which was positively associated with preferences for large breasts. In the Czech Republic, the

242 final model included body attractiveness and relationship status and was significant (Chi-

243 square (4) = 8.514, p = 0.014, R^2 (Nagelkerke) = 0.251). Single individuals and participants

244 who indicated higher body attractiveness significantly more frequently preferred larger

245 breasts. In Namibia, the final model included height and body attractiveness and was

246 significant (Chi-square (4) = 13.408, p = 0.009, R^2 (Nagelkerke) = 0.201). Body attractiveness

247 and marginally also height predicted preferences for large breasts. Estimated parameters for

248 the individual variables are shown in Table 3.

249

250 *3.2. Breast shape preferences*

251 As we did for breast size, we first examined overall breast shape preferences across

252 the four tested cultures. Due to low frequency of preferences for low breast firmness in Brazil

253 and the Czech Republic we restricted our analysis to the two categories represented the

254 firmest breast shape. Preferences for breast shape significantly varied across the tested

255 cultures (Chi-square (3) = 17.9, p < 0.001). The drawings of the firmest breasts were selected

256 as most preferred by the majority of the participants in all tested cultures; overall: 68.9%,

257 Brazil: 81.8% (Chi-square (1) = 18.69, p < 0.001), Cameroon: 51.0% (Chi-square (3) = 46.5,

258 p < 0.001, the Czech Republic: 93.8% (Chi-square (1) = 36.75, p < 0.001), and Namibia:

259 67.9% (Chi-square (2) = 48.3, p < 0.001) (Figure 4). Interestingly, preferences for the firmest

260 breasts were significantly (Chi-square (2) = 6.1, p = 0.046) more frequent in Cameroonian

261 students (63.3%) as compared to the young men from the rural community (37.8%).

262 We then tested for associations between preferences for breast firmness and the

263 selected individual characteristics. We found no significant associations between relationship

264 status in their preferences for breast shape; Brazil: Fisher's Exact Test: p = 0.431; Cameroon:

265   Chi-square (2) = 0.77, p = 0.68; the Czech Republic: Fisher's Exact Test: p = 1.0; Namibia:

266   Chi-square (1) = 2.24, p = 0.135. Similarly, no significant correlations with age, body height,

267   self-reported facial, and body attractiveness were found in any of the tested cultures. In the

268   Brazilian sample, we found a negative association between preferences for breast firmness

269   and both number of sexual partners and total SOI-R score. However, none of these

270   correlations were confirmed in the other three tested cultures (Table 4).

271   Subsequently we also tested for the contribution of the individual characteristics to the

272   variation in breast firmness preferences using backward stepwise multinomial logistic

273   regression. In Brazil, the final model included number of sexual partners and was

274   significantly better as compared to the baseline (Chi-square (1) = 6.042, p = 0.014, R^2

275   (Nagelkerke) = 0.215). Higher number of sexual partners significantly predicted preference

276   for lower breast firmness. In Cameroon, the final model included age and was significant

277   (Chi-square (2) = 6.999, p = 0.03, R^2 (Nagelkerke) = 0.178). Age marginally negatively

278   predicted preference for low breast firmness. In Namibia, the final model included number of

279   sexual partners, height and relationship status, but was not significantly better as compared to

280   the baseline (Chi-square (3) = 7.106, p = 0.069, R^2 (Nagelkerke) = 0.138). Estimated

281   parameters for the individual variables are shown in Table 5.

282

283   **4. Discussion**

284   The main aim of this study was to test preferences for female breast size and shape in

285   four different cultures. We found that, in three of the four tested cultures, medium size breasts

286   were judged as being the most attractive. However, a substantial portion of the participants

287   selected either large or small size as their most preferred, indicating considerable inter-

288   individual variation in breast size preferences. In contrast, the majority of raters showed

289   preferences for firm breasts, which are typical for women in late adolescence and young

290 adulthood. Our results thus support the idea that permanently enlarged breasts might be an

291 indicator of residual reproductive value.

292

293 *4.1. Preferences for breast size*

294   Our results show that medium sized breasts were most frequently preferred in Brazil,

295 the Czech Republic and Namibia. In contrast, large breasts were the most preferred in the

296 Cameroon sample. This inter-sample difference is consistent with the mixed picture that

297 emerges across other previous studies in different populations. For example, a study

298 conducted in Brazil (Bahia state) found preferences for relatively small breasts (Jones, 1996),

299 as did another in the UK (Furnham & Swami, 2007). Other studies found preferences for

300 large breasts (UK: Furnham, Dias, & McClelland, 1998; Poland: Zelazniewicz & Pawlowski,

301 2011) as we found in Cameroon, or for medium sized breasts (New Zealand: Dixson, Duncan,

302 & Dixson, 2015; Dixson et al., 2011a) as we found in the other 3 populations. This apparently

303 substantial variation in breast size preferences does not support the hypothesis that breast size

304 serves as a robust indicator of potential fertility, because if it did then we would expect large

305 breasts to be cross-culturally preferred (Jasienska et al., 2004). It should be noted, however,

306 that we tested only variation within the range of developed breasts. Highly underdeveloped

307 breasts may still indicate low potential fertility. Indeed, Dixson et al. (2015) reported that very

308 small breasts were systematically perceived as the least attractive, sexually mature and having

309 low nurturing abilities.

310   What, then, might preferences for breast size reflect? There is evidence that points

311 instead towards an association between preference for large breast size and scarcity (or

312 perhaps unpredictability) of resources in the environment. Dixson et al. (2011b) found that

313 men from Papua New Guinea, who are predominantly subsistence farmers, preferred large

314 breast size more frequently than men from New Zealand and Samoa. Furthermore, Malaysian

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315   men with low socioeconomic status tend to prefer larger breasts when compared to their

316   counterparts with higher socioeconomic status (Swami & Tovée, 2013b). As breast size is

317   associated with higher body mass (Brown et al., 2012) this preference may reflect a

318   generalized preference for women with plumper bodies, a tendency frequently found in

319   communities that experience resource scarcity (Sugiyama, 2004; Wetsman & Marlowe,

320   1999). This hypothesis was also partly supported by our data. According to the World Health

321   Organization (WHO, 2015), Cameroon has substantially lower gross national income per

322   capita and life expectancy at birth, higher maternal mortality ratio (per 100 000 live births),

323   and adult mortality rate, compared with the other sampled countries. Based on this, we might

324   therefore expect men in Cameroon to express preferences for larger breasts than men in the

325   other sampled countries, and this is what we found. However, the comparison of our two

326   Cameroonian subsamples presumably varying in socioeconomic status does not follow this

327   pattern. The university students were expected to prefer smaller breasts because they come

328   from more prosperous families, since in Cameroon a tuition fee is paid for university

329   education. The subsample of young men from the rural community (on mate preferences from

330   a similar community in Cameroon see Dixson et al., 2007), showed lower frequency of

331   preferences for large breasts as compared to the university students. Clearly, the findings at

332   within-country level do not necessarily need to follow the between-country comparisons.

333   Interestingly, we were unable to confirm a previously reported association between

334   high SOI and preference for large breasts (Zelazniewicz & Pawlowski, 2011). As the validity

335   of the SOI questionnaire might be limited in non-western cultures, we also used the number of

336   previous sexual partners as a proxy for behavioural sociosexuality, but even this variable was

337   not systematically associated with breast size preferences. This could possibly be attributed to

338   lower variation in breast size contained within our stimuli: we employed stimuli depicting

339   only three different breast sizes, whereas Zelazniewicz and Pawlowski (2011) used five

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340   different breast sizes and the differences between men with low and high SOI were observed

341   only in very large breast sizes. Thus, the robustness of this effect awaits further investigations

342   based on stimuli that better reflect natural variation in breast size within target populations.

343   We also found no systematic association between breast size preferences and age,

344   relationship status or body height; all indicators that we considered to be proxies for male

345   mate value. This is at odds with some previous findings. For instance, Dixson et al. (2011b)

346   reported that, in each of three tested cultures (New Zealand, Samoa, Papua New Guinea),

347   married men preferred larger breasts when compared to their unmarried counterparts. The

348   authors speculated that the preferences of husbands may have become adjusted after their

349   wives underwent physical changes resulting from pregnancy and breastfeeding. As we

350   expected that the majority of our participants would be unmarried, we instead asked them

351   about their relationship status. However, only in the sample from the Czech Republic did this

352   factor appear to be a predictor of breast size preferences — single men more frequently

353   reported preference for large breasts which is in the opposite direction to Dixson et al.

354   (2011b) findings Perhaps relationship status had no impact on breast size preferences in most

355   of our samples because the majority of the partners of our participants were relatively young

356   and had not yet had children. Although the correlation between breast size preferences and

357   body height in the Namibian sample reached a formal level of significance, these results

358   should be interpreted with caution due to the number of tests performed in total—the

359   association could be spurious and deserves replication. The only variable that showed

360   systematic association with breast size preferences was self-assessed body attractiveness (but

361   not facial attractiveness). Body attractiveness significantly predicted preferences for large

362   breasts in the Cameroonian, Czech, and Namibian samples (but not in Brazil). This indicates

363   that positive body image, which can be considered as contributing to self-perceived mate

364   value, may partly explain the relatively high inter-individual variation in breast size

365   preferences observed across all tested cultures. However, the effect sizes of these associations

366   are rather modest. The relatively high variation in breast size preferences thus remains to be

367   explained.

368   Perhaps there are other processes involved in breast size preferences. One possibility

369   would involve sexual imprinting-like mechanisms (for review see, Štěrbová & Valentová,

370   2012). If this is the case, one would, for instance, expect that men reared by women with

371   relatively small breasts would show preferences for small breasts. It has been found that men

372   attracted to lactating and pregnant women in adulthood are more likely to have a younger

373   sibling and presumably were more frequently exposed to maternal pregnancy and lactation

374   during their childhood (Enquist, Aronsson, Ghirlanda, Jansson, & Jannini, 2011). These

375   processes might not be adaptive *per se*, but could be considered an epiphenomenon of more

376   general sexual imprinting-like processes such as preference for facial appearance. Certainly,

377   these are speculative thoughts which should be tested empirically to assess their validity.

378   Finally, perceptions of breast attractiveness might be affected by the variation in breast

379   morphology in a given population, as breast size distribution may vary across different

380   populations. For instance, American women of Asian origin reported smaller breast size, on

381   average, compared with American women of European and African origin (Forbes &

382   Frederick, 2008). To our knowledge, similar data for sub-Saharan Africa are not available.

383   Nevertheless, if the prevalence of a studied trait affects preferences, and breasts in a given

384   population are, for instance, relatively large, then the men from this population may also show

385   preferences for relatively large breasts. Variation in breast size across individual countries

386   thus may potentially explain why in Cameroon, in contrast to the other study sites, we found

387   larger breasts to be most preferred.

388

389   *4.2. Preferences for breast shape*

390   As pointed out previously, women develop enlarged permanent breasts during puberty

391   mainly by depositing adipose tissue, while in other primate species mammary glands are

392   enlarged only during pregnancy and lactation. Women's breasts undergo further changes

393   related to age, breast size, number of pregnancies, and other factors such as changes in body

394   weight or smoking (Rinker et al., 2010). Interestingly, the effect of breastfeeding on breast

395   shape is currently debated: some studies report an adverse effect (Rauh et al., 2013) but others

396   do not (Rinker et al., 2010; Soltanian et al., 2012). On average, breasts become less firm with

397   age due to lower strength and elasticity of the skin and connective tissue. Based on this,

398   Marlowe (1998) proposed that breast shape (particularly how it is influenced by firmness)

399   may serve as an indicator of residual reproductive value. In other words, if the firmness of

400   women's breasts is a reliable marker of their nubility and nulliparity, men should show a

401   systematic and cross-cultural preference for it. Our results are fully in line with this

402   hypothesis.

403   Cross-culturally, we found systematic preferences for firm breast shape when

404   compared with more pendulous breast shapes. The relative strength of this preference was

405   most pronounced in the Czech Republic and Brazil, and least pronounced in Cameroon. We

406   suggest that this might be due to the higher frequency of male participants with children of

407   their own. Unfortunately, we did not collect data concerning number of children but the

408   World Health Organization (WHO) estimates the fertility rate to be 4.8 child per

409   Cameroonian woman in 2013 (compared to 3.1 in Namibia, 1.8 in Brazil, and 1.6 in the

410   Czech Republic). Having children could affect the shape of the participants' partner's breasts

411   and, as a consequence, also their preferences. Interestingly, we found no effect of relationship

412   status on breast shape preferences in Cameroon or in any of the other three tested cultures.

413   Numerous hypotheses have been proposed to explain permanent enlargement of

414   women's breasts. As discussed above, the hypotheses based on sexual selection focus either

415   on breast size as a marker of potential fertility (Jasienska et al., 2004) or on their shape (or

416   firmness) as a marker of age-related residual reproductive value (Marlowe, 1998). The other

417   set of hypotheses relies primarily on natural selection. It was, for instance, argued that

418   permanent breasts may serve as a storage organ for milk (Low, Alexander, & Noonan, 1987).

419   However, it is not clear why permanent enlargement should be unique to humans.

420   Furthermore, with the exception of deficient development of mammary tissue, there is little

421   evidence suggesting that breast size is related to lactational capacity (Anderson, 1983). Others

422   have proposed that adipose tissue in women's breasts and hips might harbour energy reserves

423   for the energetically expensive period of breastfeeding (Anderson, 1983). However, such

424   hypotheses do not easily account for the development of permanent breasts during puberty

425   and would rather predict their development shortly before or during pregnancy. Although

426   scenarios primarily based on sexual and natural selection appear, at face value, to be mutually

427   exclusive, they might in fact focus on two different facets of the evolution of permanent

428   breasts. The origin of a trait and its current function are two different processes and should

429   not be conflated (Gould & Vrba, 1982). Thus, permanent breasts, together with gynoid

430   deposits in hips and buttocks, might have evolved as energy deposits in early hominids as a

431   consequence of morphological changes related to bipedal locomotion. However, they might

432   have been subsequently shaped by sexual selection such that they then serve as a reliable

433   marker of residual reproductive value. Such a scenario could potentially explain the

434   development of permanent breasts during puberty, which appears to be enigmatic from points

435   of view that do not involve sexual selection.

436   Further, this alternative view is also in agreement with general principles involved in

437   the evolution of signals. Smith & Harper (1995) argued that most of the traits that evolved for

438   communicative purposes (i.e., signals) involve several evolutionary steps. First, perceivers are

439   selected to be sensitive to some morphological or behavioural traits of other individuals (e.g.,

440   of the opposite sex, in the case of mate selection processes) as such cues are reliable

441   indicators of future outcome (e.g., fertility potential). However, up to this point, the given trait

442   has served some other function and was not selected primarily for communication.

443   Nevertheless, if the trait affects perceivers' decisions, its appearance (together with

444   perceivers' cognitive apparatus) can become subsequently selected in a process known as

445   ritualization to form a distinct and reliable signal. Permanent breast morphology appears to be

446   specific to the human species and its peculiar morphology is in line with a possible signalling

447   function. Our results also indicate that breast shape systematically affects men's perception of

448   their attractiveness. This suggests that permanent breasts in humans may perhaps have

449   evolved as a true signal. However, we need more studies testing the robustness and specificity

450   of preferences for breast shape and tests of how reliably breast shape indicates residual

451   reproductive potential in comparison with other bodily features.

452   If breast shape does serve as an indicator of residual reproductive potential, one might

453   wonder why there is such a large variation in breast size. Marlowe (1998) has proposed that

454   an interaction between preferences for breast shape and size may help to explain the relatively

455   large variation in women's breast size. He hypothesised that men, in general, primarily prefer

456   breasts that appear to be firm and, to some extent, also large. This would give an advantage to

457   young women with large breasts. However, as large breasts compared to small ones tend to

458   become more pendulous with age (Rinker et al., 2010), this would give an advantage to older

459   women with small breasts as they might appear younger than their actual age. There is some

460   support for this claim, as it was reported that drawings of women with large breasts are

461   perceived older than the same drawings of women with small breasts (Furnham et al., 1998).

462   Here we tested the effect of breast shape and size using two different sets of stimuli and

463   therefore were not able to directly test Marlowe's prediction on the interaction between

464   preferences for shape and size. Future studies should therefore combine these two aspects of

465   breast morphology to test this prediction.

466

467   *4.3. Limitations*

468   The main limitation of our study is certainly the stimuli, which do not fully

469   incorporate natural variation in breast shape and size. However, a similar critique would apply

470   to the majority of the previous studies, as has already been highlighted by other researchers

471   (Dixson et al., 2015; Zelazniewicz & Pawlowski, 2011). Several earlier studies employed

472   drawings with two or three different breast sizes (Furnham et al., 1998; Furnham, Swami, &

473   Shah, 2006; Furnham, Hester, & Weir, 1990; Horvath, 1981). Schematic drawings and low

474   level of variation may at least partly account for the discrepancies across studies on breast size

475   preferences. However, this cannot be used to explain variation within our study, as all our

476   participants assessed the same set of stimuli.

477   More recently, some studies employed more realistic avatars, digitally manipulated in

478   five (Swami &Tovée, 2013a, 2013b) or even 14 (Swami et al., 2015) breast size steps.

479   However, in these studies, the avatars were presented in swimming suits, a fact that may again

480   have underestimated the actual effect size. Here we used full body topless stimuli with three

481   categories of breast size that were previously employed in studies by Dixson and colleagues

482   (2009, 2011a). Although digitally manipulated images are indisputably more realistic than

483   drawings, they still capture only a fraction of the natural variation in size and may also

484   introduce some artefacts. For instance, manipulations solely on breast size, while holding

485   constant BMI and other body dimensions and shapes, can lead to images with larger breasts

486   appearing somewhat unnatural. The manipulation of a single bodily characteristic is clearly

487   advantageous from the experimental design perspective. However, as most of body

488   characteristics are intercorrelated such an approach may lead to biased conclusions about the

489   contribution of the individual traits in real-life mate selection which is generally based on the

490   whole physique, among many other characteristics. To avoid this constrain, a possible

491   solution would be using stimuli that simultaneously manipulate inter-related traits, such as

492   both breast size and shape. Brooks et al. (2015), for example, used an alternative research

493   strategy by using avatars and 'virtual evolution' paradigm. The individual avatars varying in

494   numerous body measurements were assessed for their attractiveness and 50% of the most

495   attractive ones entered another generation of the ratings. The main changes appeared in the

496   area of waist, leg-length, and overall slenderness. The subsequent generations of the avatars

497   also increased their bust size, however, this appeared to be only after the above reported

498   characteristics showed lower variation.

499   For ratings of breast shape, we employed four profile drawings that were originally

500   used in forensic science (Rawson & Brooks, 1984) and which vary in level of perceived

501   firmness. However, as pointed out above, the breast firmness presumably interacts with breast

502   size. Unfortunately, there appear no available biometric data that would demonstrate age-

503   related changes in breast shape and their interaction with breast size. Further, breast shape is

504   not solely related to age but also to parity and we currently have rather limited knowledge

505   concerning what is the stronger predictor of breast shape: age, parity, the interaction between

506   them, or another factor such as body weight change (Rinker et al., 2010). In this respect,

507   studies from biological anthropology on changes in breast morphology would be appreciated

508   by evolutionary psychologists.

509   Interestingly, only very few studies have employed photographs of breasts from

510   individual women as stimuli; see Zelazniewicz and Pawlowski (2011) and Fink, Klappauf,

511   Brewer, & Shackelford (2014) for notable exceptions. Although this approach cannot control

512   for all possible confounding variables (e.g., effect of areola colour and size), it still provides

513   the most ecologically valid approach so far. It could be complemented by the use of

514   composite images or morphs naturally varying in a parameter of interest (e.g., size). If these

515   two approaches are used in a complementary fashion, they might provide us with a more

516   complex understanding of the perception of breast morphology. To explore preferences for

517   breast morphology in more detail, future studies might also consider using stimuli that more

518   completely cover the natural variability in breast morphology.

519

520   *4.4. Conclusions*

521   In conclusion, we provide the first evidence based on samples from several

522   populations for systematic male preferences for firm breast shape. Our results support the

523   view that breast shape may serve as an indicator of female residual reproductive value. In

524   contrast, we found relatively high variability in breast size preferences, with medium size

525   being the most frequently preferred across majority of the tested cultures. Future studies

526   should explore the interaction between preferences for shape and size, while employing more

527   realistic stimuli fully covering natural variation in breast morphology.

528

534   Fig 1: The stimuli used for testing preferences for breast size (small, medium, and

535 large). Redrawn from Dixson et al. (2011a).

536

537   Fig 2: The stimuli used for testing preferences for breast firmness (high, moderate,

538 rather low, and low). Redrawn from Rawson & Brooks 1984).

539

540   Fig. 3: Preferences for breast size (small, medium, large) in individual countries.

541 Frequency of the stimuli selected as the most attractive. The differences were significant at p

542 < 0.05 in Brazil and the Czech Republic, but not in Namibia (p = 0.054) and Cameroon (p =

543 0.093) (Chi-square test).

544

545   Fig. 4: Preferences for breast firmness in individual countries. Frequency of the stimuli

546 selected as the most attractive. All differences significant at $p < 0.001$ (Chi-square test).

547

548   Table 1: Descriptive statistics ($\overline{X} \pm$ SD) for the variables tested for their modulating effect on

549   breast preferences.

550

Sample	N	Age (SD)	Height (SD)	Facial Attractiveness (SD)	Body Attractiveness (SD)	# Sexual Partners (SD)	SOI (SD)	Partnered (%)
Brazil	44	23.7 (3.75)	175.6 (6.72)	4.5 (0.8)	4.1 (0.94)	10.6 (12.5)	45.1 (15.62)	42.9
Cameroon	94	22.8 (4.15)	171 (5.65)	4.3 (0.6)	4.3 (0.63)	4.5 (5.53)		72.3
The Czech Republic	48	22.3 (3.03)	182.5 (7.37)	2.6 (0.91)	2.5 (1.03)	3.5 (3.78)	33.2 (7.37)	30.8
Namibia	81	22.7 (3.97)	168.3 (6.69)	4.3 (0.82)	4.2 (1.02)	12.5 (11.84)	24.3 (6.84)	65.4

551

552

553   Table 2: Nonparametric correlations (Kendall's Tau) between breast size preference and

554   participants characteristics. * denotes correlations significant at the p < 0.05.

555

Sample	Age	Height	Facial Attractiveness	Body Attractiveness	# Sexual Partners	SOI
Brazil	0.175	0.159	0.006	-0.13	0.125	0.011
Cameroon	0.06	-0.123	0.00	0.19	0.23	-
The Czech Republic	-0.003	-0.005	0.111	0.25	-0.13	0.086
Namibia	0.113	0.206*	0.15	0.212*	0.089	0.128

556

557

558   Table 3: Parameter estimates of the final model based on the Backward stepwise multinomial

559   logistic regression separately for each country. Note that small breast size (medium size in the

560   Czech Republic) and the relationship status being single were set as the reference categories.

Brazil		B (SE)	Wald	p	Exp(B) (95% CI)
Medium	Intercept	15.728 (16.010)	0.965	0.326	
	Height	-0.049 (0.085)	0.334	0.563	0.952 (0.807-1.124)
	Age	-0.249 (0.163)	2.339	0.126	0.780 (0.567-1.072)
Large	Intercept	-16.572 (16.57)	1.000	0.317	
	Height	0.085 (0.087)	0.942	0.332	1.089 (0.917-1.292)
	Age	0.111 (0.150)	0.546	0.460	1.117 (0.833-1.497)
Cameroon					
Medium	Intercept	-1.663 (3.950)	0.177	0.674	
	# Sexual Partners	-0.293 (0.150)	3.807	0.051	0.746 (0.556-1.001)
	Age	-0.247 (0.136)	3.323	0.068	0.781 (0.599-1.019)
	Body Attractiveness	2.658 (1.280)	4.315	0.038	14.268 (1.162-175.190)
	Facial Attractiveness	-0.516 (1.237)	0.174	0.677	0.597 (0.053-6.739)
Large	Intercept	-3.815 (4.467)	0.729	0.393	
	# Sexual Partners	-0.025 (0.089)	0.080	0.777	0.975 (0.819-1.161)
	Age	0.069 (0.118)	0.338	0.561	1.071 (0.850-1.350)
	Body Attractiveness	3.699 (1.905)	3.769	0.052	40.390 (0.965-1690.258)
	Facial Attractiveness	-3.228 (1.712)	3.555	0.059	0.040 (0.001-1.136)
The Czech Republic					
Large	Intercept	-3.458 (1.228)	7.922	0.005	
	Body Attractiveness	0.858 (0.395)	4.733	0.030	2.359 (1.089-5.113)
	Relationship Status	1.597 (0.802)	3.966	0.046	4.939 (1.026-23.785)
Namibia					
Medium	Intercept	-19.433 (9.225)	4.437	0.035	
	Body Attractiveness	0.728 (0.327)	4.975	0.026	2.072 (1.092-3.929)
	Height	0.103 (0.054)	3.671	0.055	1.109 (0.998-1.232)
Large	Intercept	-27.999 (10.495)	7.117	0.008	
	Body Attractiveness	0.780 (0.385)	4.098	0.043	2.181 (1.025-4.641)
	Height	0.150 (0.060)	6.161	0.013	1.162 (1.032-1.308)

561

562   Table 4: Nonparametric correlations (Kendall's Tau) between breast shape preference and

563   participants characteristics. Note that due to low variability of preferences in the Czech

564   Republic correlations were not computed. * denotes correlations significant at the p < 0.05.

565

Sample	Age	Height	Facial Attractiveness	Body Attractiveness	# Sexual Partners	SOI
Brazil	0.215	0.103	0.061	013	0.263*	0.286*
Cameroon	-0.1	0.1	-0.107	-0.098	-0.021	
Namibia	0.133	-0.105	0.015	0.083	-0.112	-0.095

566

567

568 Table 5: Parameter estimates of the final model based on the Backward stepwise multinomial

569 logistic regression separately for each country. Note that firm breast shape and the

570 relationship status being single were set as the reference categories. The model based on the

571 data from the Czech Republic was omitted due to low data variation of the dependent

572 variable.

573

Brazil		B (SE)	Wald	p	Exp(B) (95% CI)
Moderate	Intercept	-2.453 (0.667)	13.541	0.000	
	# Sexual Partners	0.074 (0.032)	5.311	0.021	1.077 (1.011-1.011)
Cameroon					
Moderate	Intercept	0.292 (1.876)	0.024	0.876	
	Age	-0.004 (0.078)	0.003	0.958	0.996 (0.854-1.161)
Rather low	Intercept	7.604 (4.070)	3.490	0.062	
	Age	-0.374 (0.197)	3.594	0.058	0.688 (0.467-1.013)
Namibia					
Moderate	Intercept	11.247 (7.293)	2.378	0.123	
	# Sexual Partners	-0.046 (0.031)	2.190	0.139	0.955 (0.898-1.015)
	Height	-0.073 (0.044)	2.763	0.096	0.929 (0.852-1.013)
	Relationship Status	1.067 (0.652)	2.675	0.102	2.906 (0.809-10.433)

574

575

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Figure 1

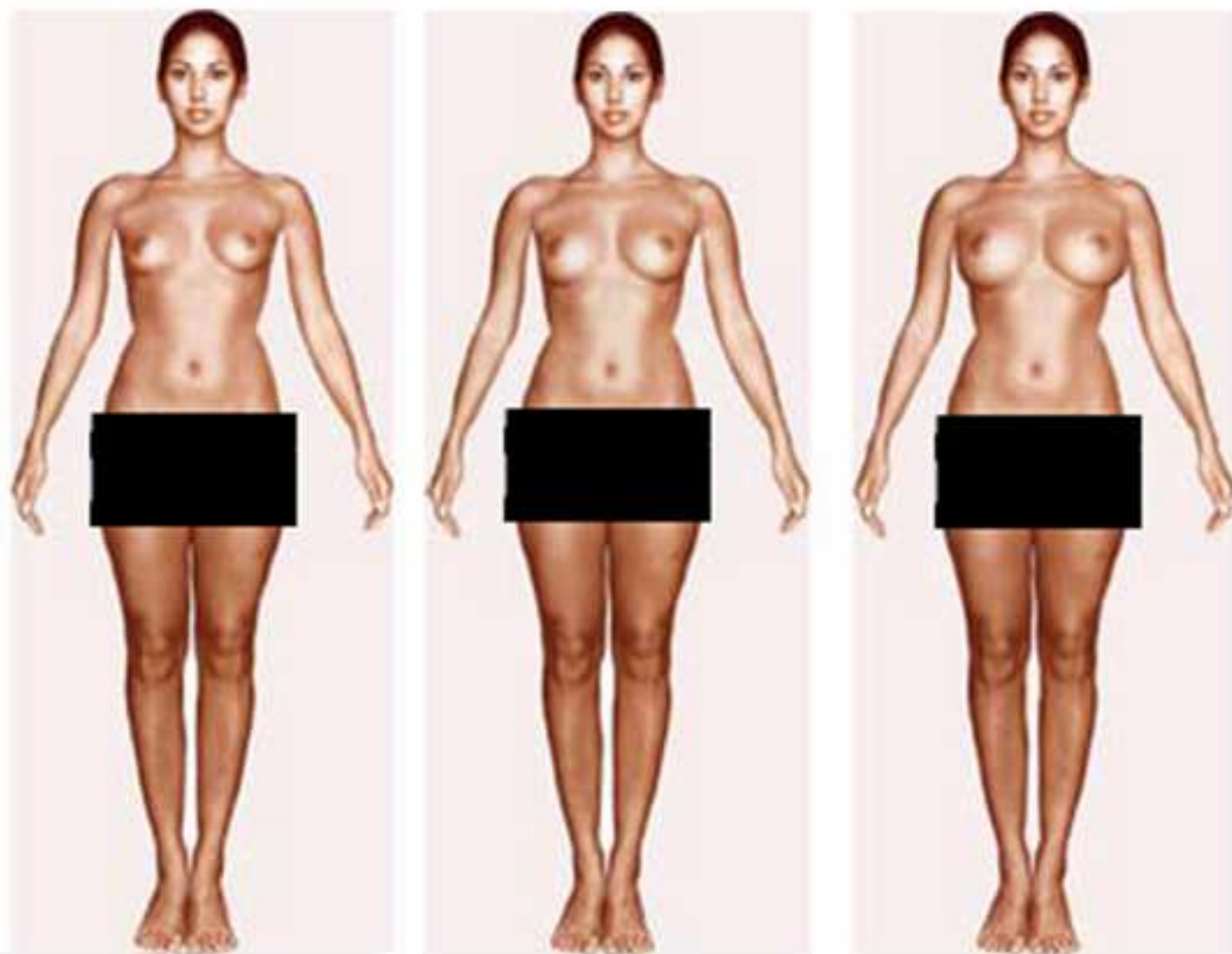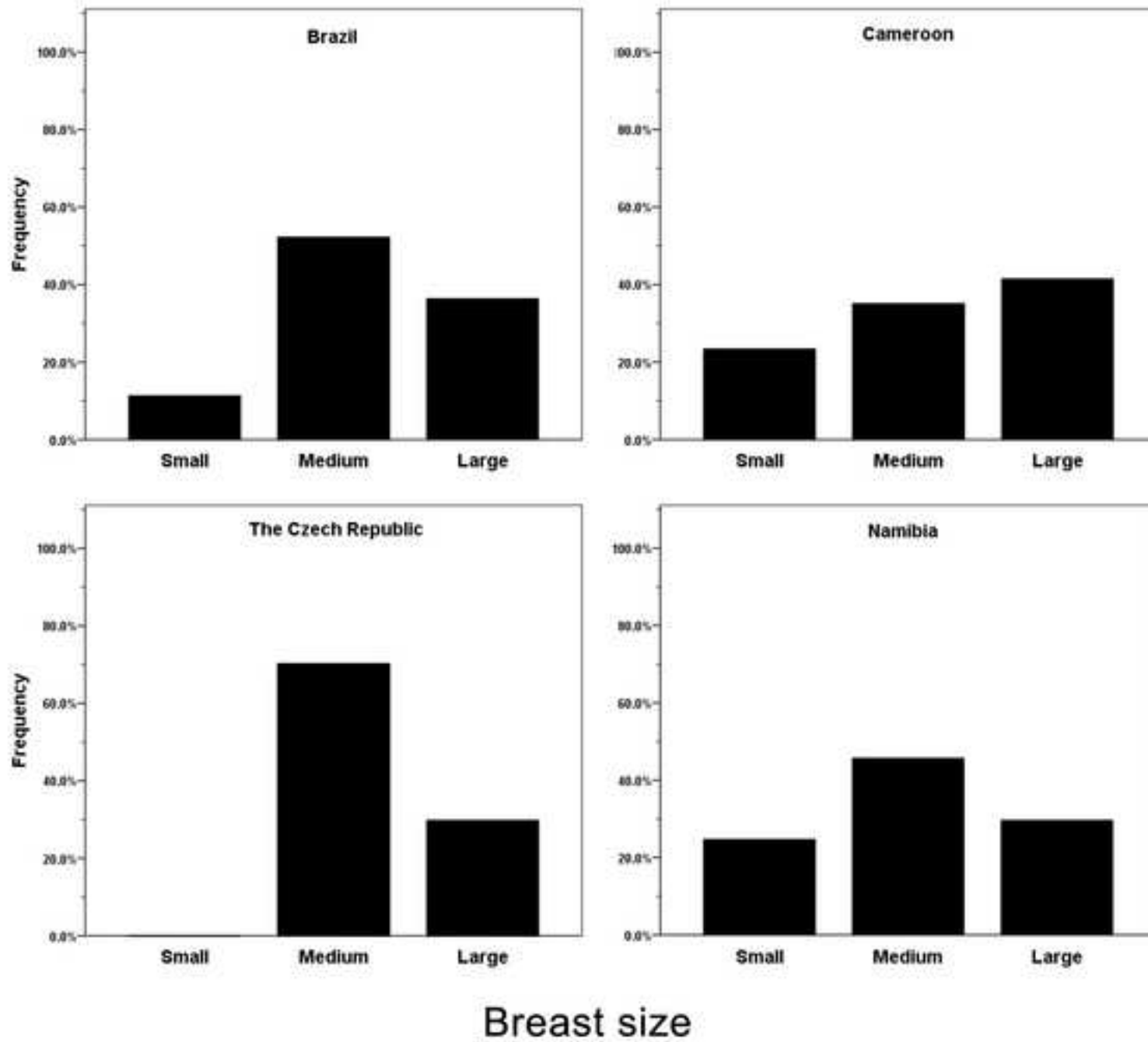**Figure 2**
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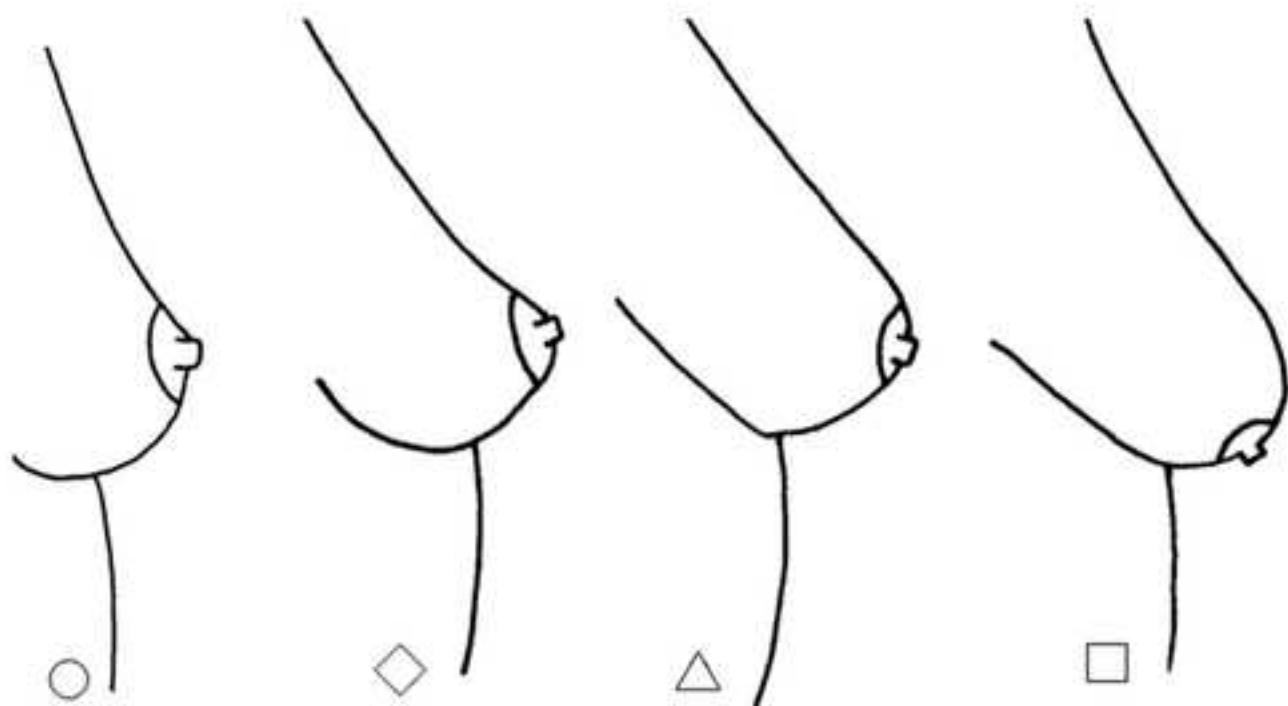
Breast size

Figure 4
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Breast firmness