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

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ABSTRACT

The morphology of human female breasts typical for their permanent fat deposits appears to be unique among primates. It has been previously suggested that female breast morphology arose as a result of sexual selection. This is supported by evidence showing that women with larger breasts tend to have higher estrogen levels; breast size may therefore serve as an indicator of potential fertility. However, breasts become less firm with age and parity, and breast shape could thus also serve as a marker of residual fertility. Therefore, cross-culturally, males are hypothesized to prefer breast morphology that indicates both high potential and residual fertility. To test this, we performed a survey on men´s preferences for breast morphology in four different cultures (Brazil, Cameroon, the Czech Republic, Namibia). As stimuli, we used two sets of images varying in breast size (marker of potential fertility) and level of breast firmness (marker of residual fertility). Individual preferences for breast size were variable, but the majority of raters preferred medium sized, followed by large sized breasts. In contrast, we found systematic directional preferences for firm breasts across all four samples. This pattern supports the idea that breast morphology may serve as a residual fertility indicator, but offers more limited support for the potential fertility indicator hypothesis. Future studies should focus on a potential interaction between the two parameters, breast size and firmness, which, taken together, may help to explain the relatively large variation in women's breast sizes.

Keywords: Permanent breasts, Mate preferences, Residual fertility, Nubility hypothesis, Mammary gland, Human evolution

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

variation in the tested individuals (Dixson et al., 2011b) or temporal variation in preferences, although a study testing several cohort samples across the 1990's did not support the latter suggestion (Tantleff-Dunn, 2001). Alternatively, the variation in preferences might be due to interactions with other parts of the body: large breasts are perceived to be more attractive in women with low waist-to-hip ratios (Furnham et al., 1998; Singh & Young, 1995). Furthermore, preferences for breast size may vary systematically across individuals. Zelazniewicz & Pawlowski (2011) found that Polish men with high sociosexuality (i.e., tendency for sexual variety) prefer larger breasts. Similarly, a study from Malaysia found that men of lower socio-economic status prefer larger breasts than their counterparts of higher socio-economic status (Swami & Tovée, 2013b).

It has been further argued that breast symmetry may serve as a marker of developmental stability. Indeed, there is some evidence showing that high breast asymmetry is associated with lower fecundity (Manning, Scutt, Whitehouse, & Leinster, 1997; Moller, Soler, & Thornhill, 1995; Scutt, Manning, Whitehouse, Leinster, & Massey, 1997) and with higher risk of breast cancer (Scutt et al., 1997). In line with this, perceptual studies show that symmetrical breasts are judged as more attractive (e.g., Dixson et al., 2011b).

Variation in breast morphology is, however, not restricted to size and symmetry—breasts also vary greatly in shape. In general, breast shape changes with age and parity, having a firmer appearance in younger adults (for brevity, we hereafter use the term "firm", which is a tactile descriptor, even though we primarily refer to their visual appearance on which our participants' preferences were based). Later in life, due to declining firmness of the breasts' fibrous tissue, they become progressively more pendulous; this effect is amplified by many factors, such as age, breast size, parity, weight loss, or smoking (Rinker, Veneracion, & Walsh, 2010). The medical literature labels this phenomenon as breast ptosis, defined as a sagging process where the breast falls onto the chest, flattens, and a nipple points downward

(Rinker et al., 2010). Based on these changes, Marlowe (1998) proposed the nubility hypothesis, suggesting that breast shape could be used as a reliable marker of residual reproductive value, i.e., the expected future reproductive output of an individual, which is negatively related to age. According to this hypothesis, men's perception of breast attractiveness is expected to be primarily affected by their shape rather than size. Although this hypothesis was formulated more than 15 years ago, to date its predictions have not, to our knowledge, been directly tested.

The aim of this study was to test both preferences for breast size and breast shape. We based our predictions about size preferences on the potential fertility hypothesis (Jasienska et al., 2004) and about shape on the nubility hypothesis (Marlowe, 1998). As preferences may vary across tested populations (Dixson et al., 2011b), we collected attractiveness ratings across several populations varying in their cultural and socio-economic settings, including two African communities (Cameroon, Namibia) and two industrialized urban populations (the Czech Republic, Brazil). We expected to find preferences for firm breasts across the tested countries. In contrast, we expected men to prefer larger breasts in countries with relatively lower living standards and higher resource scarcity (here, Cameroon and Namibia) compared with men in countries with relatively higher living standards (here, the Czech Republic and Brazil). Resource scarcity is frequently associated with preferences for more corpulent bodies (e.g., Wetsman & Marlowe, 1999). As breast size is to some extent positively associated with body mass (Brown et al., 2012), preferences for larger breasts may simply reflect a generalized preference for more corpulent women in communities that experience resource scarcity.

To assess other factors that might be associated with breast preferences, we followed findings from previous research (Dixson et al., 2011b; Zelazniewicz & Pawlowski, 2011). Namely, we also tested effects of age, self-assessed attractiveness, relationship status, and

sexual restrictiveness (here assessed in two ways, by self-reported number of sexual partners and by using the Sociosexual Orientation Inventory, SOI-R: Penke & Asendorpf, 2008), each of which has been found to be positively associated with preferences for larger breasts.

2. Material and methods

2.1. Participants

The data were collected as part of several larger projects investigating cross-cultural predictors of physical attractiveness and intrasexual competition. The Brazilian sample consisted of 44 male students of the University of São Paulo (mean age = 23.4ys; SD = 3.89; range 18-34) approached on campus by local researchers (MACV and KJP). São Paulo is a large urban agglomeration with a prevailing economic reliance on industrial production, finance, and retail. Living standards range between moderate to rather high, with relatively large social inequality. The population is highly culturally diverse, with most people being of mixed descent, mainly of Amero-Indian, Portuguese, African, Japanese, and Middle Eastern origin.

The sample from Cameroon consisted of 94 men (mean age = 22.8ys; SD = 4.15; range 17-37); 49 students at the University of Buea (mean age = 22.9ys; SD = 3.69; range 17-37) and 45 young men from the Big Babanki rural community (mean age = 22.7ys; SD = 4.63; range 18-37), located in the South and North West Regions, respectively. Students were approached on campus by local (RA) and visiting (JV, KK and TK) researchers, while the men from Big Babanki were recruited with the help of a local research assistant (EV) using snowball sampling. The town Buea of the South West Region and the village Big Babanki of 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 ($F_{(3,260)} = 1.1$, $p = 0.35$).

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

age-related firmness. The stimuli on breast size are shown in the Figure 1 and on breast shape in Figure 2.

In both cases the stimuli were presented on laminated cards (4 x 9.5 cm) placed in random order in front of the seated participant, who was asked to order the images from the most to the least attractive. The researcher waited until the participants indicated they were completely certain about their preferences before the order of the stimuli was recorded. Participants also completed a questionnaire concerning their basic demographic data (e.g., age, education), self-rated facial and body attractiveness, relationship status, number of sexual partners and SOI-R (Penke & Asendorpf, 2008).

2.3 Statistical analysis

To test for preferences in breast size or breast shape, we analysed data for the most preferred stimuli. Under the null assumption of no systematic preferences, equal representation of the individual stimuli was expected (i.e., we compared the frequency of the most preferred against chance). A possible departure from the expected distribution was tested by Chi-square tests together for all tested samples and separately for each sample, respectively. In some cases, the frequency of the preferred stimuli was too low to allow for statistical analysis and these data were therefore omitted. More specifically, only one Czech participant showed preference for small breasts, and preferences for low firmness (stimuli #3 – low and #4 – very low) were represented with zero frequency in the Czech and Brazilian samples. Note therefore that the degrees of freedom vary in different tests and so test statistics may not be directly comparable across samples. We further compared the preferences across the tested samples again using the Chi-square tests. Due to the low frequency of preferences for the low firmness stimuli in the Brazilian and Czech samples as described above the breast shape comparison across the samples is based only on the high and moderate firmness stimuli.

The associations between preferences for breast size or shape with the modulating factors of age, self-assessed facial and body attractiveness, SOI-R, and number of sexual partners were explored using Kendall's Tau nonparametric correlations. The effect of relationship status (single / coupled) on breast size and shape preferences was tested using Chi-square tests or by the Fisher's Exact Test if the expected count in some cells was lower than 5. To explore contribution of the modulating variables we build up the most parsimonious model by employing backward stepwise multinomial regression model separately for each sample. We set small breasts and firm breasts as the reference category except in the sample from the Czech Republic where due to low frequency of small breast preferences the medium breasts were set as the reference category. Similarly, due to the low variation in breast firmness preferences in the Czech Republic (only 3 individuals selected moderately firm stimuli) we were not able to perform meaningful logistic regression.

3. Results

3.1. Breast size preferences

Overall, preferences for breast size significantly varied across the four tested cultures (Chi-square (6) = 23.9, p = 0.001). We thus tested preferences for breast size in each culture separately. Medium sized breasts were most preferred in Brazil (52.3%, Chi-square (2) = 11.2, p = 0.004), the Czech Republic (70.2%, Chi-square (1) = 7.7, p = 0.006), and Namibia, although here the effect only approached the formal level of significance (45.7%, Chi-square (2) = 5.9, p = 0.054). In Cameroon, large sized breasts were the most frequently preferred, but this effect was not formally significant (41.5%, Chi-square (2) = 4.7, p = 0.093). While students from Cameroon most frequently preferred large sized breasts (55.1%), the young

men from the rural community most frequently preferred medium sized breasts (44.4%) and the difference between these two groups was significant (Chi-square (2) = 7.8, p = 0.02). Although the largest proportion of men (overall 47.4%; Chi-square (2) = 35.51, p < 0.001) selected medium breast size (or large size in Cameroon) as the most attractive, in each country there were also substantial proportions of men who selected otherwise. The only exception was data from the Czech Republic, where only one of the participants preferred small size (Figure 3).

To further explore this variability, we tested for individual differences in breast size preferences. Descriptive data for candidate moderating variables are shown in Table 1. We found no significant differences in preferences between men who reported being single and those who were in a relationship; Brazil: Chi-square (1) = 1.94, p = 0.16; the Czech Republic: Fisher's Exact Test: p = 0.182; Cameroon: Chi-square (2) = 0.39, p = 0.82; Namibia: Chi-square (2) = 3.91, p = 0.14. There were also no significant associations with age, self-reported facial attractiveness, number of sexual partners or participants' SOI-R scores, in any of the tested countries (Table 2). In the Namibian sample, we found a significant positive correlation between participants' body height and their preferences for large breast size, but no similar association was observed in the three other samples. Finally, we found a significant positive correlation between self-reported body attractiveness and preference for large breast size in Namibia; a similar trend, though statistically non-significant, was found in Cameroon and the Czech Republic, but not in Brazil (Table 2).

The Logistic regression model for the Brazilian sample included age and height and was significantly better as compared to the baseline (Chi-square (4) = 13.476, p = 0.009, R^2 (Nagelkerke) = 0.321). However, neither age nor height alone significantly predicted breast size preferences. In Cameroon, the final model included age, facial and body attractiveness and number of sexual partners and was significant (Chi-square (8) = 22.261, p = 0.004, R^2

(Nagelkerke) = 0.478). However, the only significant contributor was body attractiveness which was positively associated with preferences for large breasts. In the Czech Republic, the final model included body attractiveness and relationship status and was significant (Chi-square (4) = 8.514, p = 0.014, R^2 (Nagelkerke) = 0.251). Single individuals and participants who indicated higher body attractiveness significantly more frequently preferred larger breasts. In Namibia, the final model included height and body attractiveness and was significant (Chi-square (4) = 13.408, p = 0.009, R^2 (Nagelkerke) = 0.201). Body attractiveness and marginally also height predicted preferences for large breasts. Estimated parameters for the individual variables are shown in Table 3.

3.2. Breast shape preferences

As we did for breast size, we first examined overall breast shape preferences across the four tested cultures. Due to low frequency of preferences for low breast firmness in Brazil and the Czech Republic we restricted our analysis to the two categories represented the firmest breast shape. Preferences for breast shape significantly varied across the tested cultures (Chi-square (3) = 17.9, p < 0.001). The drawings of the firmest breasts were selected as most preferred by the majority of the participants in all tested cultures; overall: 68.9%, Brazil: 81.8% (Chi-square (1) = 18.69, p < 0.001), Cameroon: 51.0% (Chi-square (3) = 46.5, p < 0.001, the Czech Republic: 93.8% (Chi-square (1) = 36.75, p < 0.001), and Namibia: 67.9% (Chi-square (2) = 48.3, p < 0.001) (Figure 4). Interestingly, preferences for the firmest breasts were significantly (Chi-square (2) = 6.1, p = 0.046) more frequent in Cameroonian students (63.3%) as compared to the young men from the rural community (37.8%).

We then tested for associations between preferences for breast firmness and the selected individual characteristics. We found no significant associations between relationship status in their preferences for breast shape; Brazil: Fisher's Exact Test: p = 0.431; Cameroon:

Chi-square (2) = 0.77, p = 0.68; the Czech Republic: Fisher's Exact Test: p = 1.0; Namibia: Chi-square (1) = 2.24, p = 0.135. Similarly, no significant correlations with age, body height, self-reported facial, and body attractiveness were found in any of the tested cultures. In the Brazilian sample, we found a negative association between preferences for breast firmness and both number of sexual partners and total SOI-R score. However, none of these correlations were confirmed in the other three tested cultures (Table 4).

Subsequently we also tested for the contribution of the individual characteristics to the variation in breast firmness preferences using backward stepwise multinomial logistic regression. In Brazil, the final model included number of sexual partners and was significantly better as compared to the baseline (Chi-square (1) = 6.042, p = 0.014, R^2 (Nagelkerke) = 0.215). Higher number of sexual partners significantly predicted preference for lower breast firmness. In Cameroon, the final model included age and was significant (Chi-square (2) = 6.999, p = 0.03, R^2 (Nagelkerke) = 0.178). Age marginally negatively predicted preference for low breast firmness. In Namibia, the final model included number of sexual partners, height and relationship status, but was not significantly better as compared to the baseline (Chi-square (3) = 7.106, p = 0.069, R^2 (Nagelkerke) = 0.138). Estimated parameters for the individual variables are shown in Table 5.

4. Discussion

The main aim of this study was to test preferences for female breast size and shape in four different cultures. We found that, in three of the four tested cultures, medium size breasts were judged as being the most attractive. However, a substantial portion of the participants selected either large or small size as their most preferred, indicating considerable inter-individual variation in breast size preferences. In contrast, the majority of raters showed preferences for firm breasts, which are typical for women in late adolescence and young

adulthood. Our results thus support the idea that permanently enlarged breasts might be an indicator of residual reproductive value.

4.1. Preferences for breast size

Our results show that medium sized breasts were most frequently preferred in Brazil, the Czech Republic and Namibia. In contrast, large breasts were the most preferred in the Cameroon sample. This inter-sample difference is consistent with the mixed picture that emerges across other previous studies in different populations. For example, a study conducted in Brazil (Bahia state) found preferences for relatively small breasts (Jones, 1996), as did another in the UK (Furnham & Swami, 2007). Other studies found preferences for large breasts (UK: Furnham, Dias, & McClelland, 1998; Poland: Zelazniewicz & Pawlowski, 2011) as we found in Cameroon, or for medium sized breasts (New Zealand: Dixson, Duncan, & Dixson, 2015; Dixson et al., 2011a) as we found in the other 3 populations. This apparently substantial variation in breast size preferences does not support the hypothesis that breast size serves as a robust indicator of potential fertility, because if it did then we would expect large breasts to be cross-culturally preferred (Jasienska et al., 2004). It should be noted, however, that we tested only variation within the range of developed breasts. Highly underdeveloped breasts may still indicate low potential fertility. Indeed, Dixson et al. (2015) reported that very small breasts were systematically perceived as the least attractive, sexually mature and having low nurturing abilities.

What, then, might preferences for breast size reflect? There is evidence that points instead towards an association between preference for large breast size and scarcity (or perhaps unpredictability) of resources in the environment. Dixson et al. (2011b) found that men from Papua New Guinea, who are predominantly subsistence farmers, preferred large breast size more frequently than men from New Zealand and Samoa. Furthermore, Malaysian

men with low socioeconomic status tend to prefer larger breasts when compared to their counterparts with higher socioeconomic status (Swami & Tovée, 2013b). As breast size is associated with higher body mass (Brown et al., 2012) this preference may reflect a generalized preference for women with plumper bodies, a tendency frequently found in communities that experience resource scarcity (Sugiyama, 2004; Wetsman & Marlowe, 1999). This hypothesis was also partly supported by our data. According to the World Health Organization (WHO, 2015), Cameroon has substantially lower gross national income per capita and life expectancy at birth, higher maternal mortality ratio (per 100 000 live births), and adult mortality rate, compared with the other sampled countries. Based on this, we might therefore expect men in Cameroon to express preferences for larger breasts than men in the other sampled countries, and this is what we found. However, the comparison of our two Cameroonian subsamples presumably varying in socioeconomic status does not follow this pattern. The university students were expected to prefer smaller breasts because they come from more prosperous families, since in Cameroon a tuition fee is paid for university education. The subsample of young men from the rural community (on mate preferences from a similar community in Cameroon see Dixson et al., 2007), showed lower frequency of preferences for large breasts as compared to the university students. Clearly, the findings at within-country level do not necessarily need to follow the between-country comparisons.

Interestingly, we were unable to confirm a previously reported association between high SOI and preference for large breasts (Zelazniewicz & Pawlowski, 2011). As the validity of the SOI questionnaire might be limited in non-western cultures, we also used the number of previous sexual partners as a proxy for behavioural sociosexuality, but even this variable was not systematically associated with breast size preferences. This could possibly be attributed to lower variation in breast size contained within our stimuli: we employed stimuli depicting only three different breast sizes, whereas Zelazniewicz and Pawlowski (2011) used five

different breast sizes and the differences between men with low and high SOI were observed only in very large breast sizes. Thus, the robustness of this effect awaits further investigations based on stimuli that better reflect natural variation in breast size within target populations.

We also found no systematic association between breast size preferences and age, relationship status or body height; all indicators that we considered to be proxies for male mate value. This is at odds with some previous findings. For instance, Dixson et al. (2011b) reported that, in each of three tested cultures (New Zealand, Samoa, Papua New Guinea), married men preferred larger breasts when compared to their unmarried counterparts. The authors speculated that the preferences of husbands may have become adjusted after their wives underwent physical changes resulting from pregnancy and breastfeeding. As we expected that the majority of our participants would be unmarried, we instead asked them about their relationship status. However, only in the sample from the Czech Republic did this factor appear to be a predictor of breast size preferences — single men more frequently reported preference for large breasts which is in the opposite direction to Dixson et al. (2011b) findings Perhaps relationship status had no impact on breast size preferences in most of our samples because the majority of the partners of our participants were relatively young and had not yet had children. Although the correlation between breast size preferences and body height in the Namibian sample reached a formal level of significance, these results should be interpreted with caution due to the number of tests performed in total—the association could be spurious and deserves replication. The only variable that showed systematic association with breast size preferences was self-assessed body attractiveness (but not facial attractiveness). Body attractiveness significantly predicted preferences for large breasts in the Cameroonian, Czech, and Namibian samples (but not in Brazil). This indicates that positive body image, which can be considered as contributing to self-perceived mate value, may partly explain the relatively high inter-individual variation in breast size

preferences observed across all tested cultures. However, the effect sizes of these associations are rather modest. The relatively high variation in breast size preferences thus remains to be explained.

Perhaps there are other processes involved in breast size preferences. One possibility would involve sexual imprinting-like mechanisms (for review see, Štěrbová & Valentová, 2012). If this is the case, one would, for instance, expect that men reared by women with relatively small breasts would show preferences for small breasts. It has been found that men attracted to lactating and pregnant women in adulthood are more likely to have a younger sibling and presumably were more frequently exposed to maternal pregnancy and lactation during their childhood (Enquist, Aronsson, Ghirlanda, Jansson, & Jannini, 2011). These processes might not be adaptive *per se*, but could be considered an epiphenomenon of more general sexual imprinting-like processes such as preference for facial appearance. Certainly, these are speculative thoughts which should be tested empirically to assess their validity.

Finally, perceptions of breast attractiveness might be affected by the variation in breast morphology in a given population, as breast size distribution may vary across different populations. For instance, American women of Asian origin reported smaller breast size, on average, compared with American women of European and African origin (Forbes & Frederick, 2008). To our knowledge, similar data for sub-Saharan Africa are not available. Nevertheless, if the prevalence of a studied trait affects preferences, and breasts in a given population are, for instance, relatively large, then the men from this population may also show preferences for relatively large breasts. Variation in breast size across individual countries thus may potentially explain why in Cameroon, in contrast to the other study sites, we found larger breasts to be most preferred.

4.2. Preferences for breast shape

As pointed out previously, women develop enlarged permanent breasts during puberty mainly by depositing adipose tissue, while in other primate species mammary glands are enlarged only during pregnancy and lactation. Women's breasts undergo further changes related to age, breast size, number of pregnancies, and other factors such as changes in body weight or smoking (Rinker et al., 2010). Interestingly, the effect of breastfeeding on breast shape is currently debated: some studies report an adverse effect (Rauh et al., 2013) but others do not (Rinker et al., 2010; Soltanian et al., 2012). On average, breasts become less firm with age due to lower strength and elasticity of the skin and connective tissue. Based on this, Marlowe (1998) proposed that breast shape (particularly how it is influenced by firmness) may serve as an indicator of residual reproductive value. In other words, if the firmness of women's breasts is a reliable marker of their nubility and nulliparity, men should show a systematic and cross-cultural preference for it. Our results are fully in line with this hypothesis.

Cross-culturally, we found systematic preferences for firm breast shape when compared with more pendulous breast shapes. The relative strength of this preference was most pronounced in the Czech Republic and Brazil, and least pronounced in Cameroon. We suggest that this might be due to the higher frequency of male participants with children of their own. Unfortunately, we did not collect data concerning number of children but the World Health Organization (WHO) estimates the fertility rate to be 4.8 child per Cameroonian woman in 2013 (compared to 3.1 in Namibia, 1.8 in Brazil, and 1.6 in the Czech Republic). Having children could affect the shape of the participants' partner's breasts and, as a consequence, also their preferences. Interestingly, we found no effect of relationship status on breast shape preferences in Cameroon or in any of the other three tested cultures.

Numerous hypotheses have been proposed to explain permanent enlargement of women's breasts. As discussed above, the hypotheses based on sexual selection focus either

on breast size as a marker of potential fertility (Jasienska et al., 2004) or on their shape (or firmness) as a marker of age-related residual reproductive value (Marlowe, 1998). The other set of hypotheses relies primarily on natural selection. It was, for instance, argued that permanent breasts may serve as a storage organ for milk (Low, Alexander, & Noonan, 1987). However, it is not clear why permanent enlargement should be unique to humans. Furthermore, with the exception of deficient development of mammary tissue, there is little evidence suggesting that breast size is related to lactational capacity (Anderson, 1983). Others have proposed that adipose tissue in women's breasts and hips might harbour energy reserves for the energetically expensive period of breastfeeding (Anderson, 1983). However, such hypotheses do not easily account for the development of permanent breasts during puberty and would rather predict their development shortly before or during pregnancy. Although scenarios primarily based on sexual and natural selection appear, at face value, to be mutually exclusive, they might in fact focus on two different facets of the evolution of permanent breasts. The origin of a trait and its current function are two different processes and should not be conflated (Gould & Vrba, 1982). Thus, permanent breasts, together with gynoid deposits in hips and buttocks, might have evolved as energy deposits in early hominids as a consequence of morphological changes related to bipedal locomotion. However, they might have been subsequently shaped by sexual selection such that they then serve as a reliable marker of residual reproductive value. Such a scenario could potentially explain the development of permanent breasts during puberty, which appears to be enigmatic from points of view that do not involve sexual selection.

Further, this alternative view is also in agreement with general principles involved in the evolution of signals. Smith & Harper (1995) argued that most of the traits that evolved for communicative purposes (i.e., signals) involve several evolutionary steps. First, perceivers are selected to be sensitive to some morphological or behavioural traits of other individuals (e.g.,

of the opposite sex, in the case of mate selection processes) as such cues are reliable indicators of future outcome (e.g., fertility potential). However, up to this point, the given trait has served some other function and was not selected primarily for communication. Nevertheless, if the trait affects perceivers' decisions, its appearance (together with perceivers' cognitive apparatus) can become subsequently selected in a process known as ritualization to form a distinct and reliable signal. Permanent breast morphology appears to be specific to the human species and its peculiar morphology is in line with a possible signalling function. Our results also indicate that breast shape systematically affects men's perception of their attractiveness. This suggests that permanent breasts in humans may perhaps have evolved as a true signal. However, we need more studies testing the robustness and specificity of preferences for breast shape and tests of how reliably breast shape indicates residual reproductive potential in comparison with other bodily features.

If breast shape does serve as an indicator of residual reproductive potential, one might wonder why there is such a large variation in breast size. Marlowe (1998) has proposed that an interaction between preferences for breast shape and size may help to explain the relatively large variation in women's breast size. He hypothesised that men, in general, primarily prefer breasts that appear to be firm and, to some extent, also large. This would give an advantage to young women with large breasts. However, as large breasts compared to small ones tend to become more pendulous with age (Rinker et al., 2010), this would give an advantage to older women with small breasts as they might appear younger than their actual age. There is some support for this claim, as it was reported that drawings of women with large breasts are perceived older than the same drawings of women with small breasts (Furnham et al., 1998). Here we tested the effect of breast shape and size using two different sets of stimuli and therefore were not able to directly test Marlowe's prediction on the interaction between

preferences for shape and size. Future studies should therefore combine these two aspects of breast morphology to test this prediction.

4.3. Limitations

The main limitation of our study is certainly the stimuli, which do not fully incorporate natural variation in breast shape and size. However, a similar critique would apply to the majority of the previous studies, as has already been highlighted by other researchers (Dixson et al., 2015; Zelazniewicz & Pawlowski, 2011). Several earlier studies employed drawings with two or three different breast sizes (Furnham et al., 1998; Furnham, Swami, & Shah, 2006; Furnham, Hester, & Weir, 1990; Horvath, 1981). Schematic drawings and low level of variation may at least partly account for the discrepancies across studies on breast size preferences. However, this cannot be used to explain variation within our study, as all our participants assessed the same set of stimuli.

More recently, some studies employed more realistic avatars, digitally manipulated in five (Swami &Tovée, 2013a, 2013b) or even 14 (Swami et al., 2015) breast size steps. However, in these studies, the avatars were presented in swimming suits, a fact that may again have underestimated the actual effect size. Here we used full body topless stimuli with three categories of breast size that were previously employed in studies by Dixson and colleagues (2009, 2011a). Although digitally manipulated images are indisputably more realistic than drawings, they still capture only a fraction of the natural variation in size and may also introduce some artefacts. For instance, manipulations solely on breast size, while holding constant BMI and other body dimensions and shapes, can lead to images with larger breasts appearing somewhat unnatural. The manipulation of a single bodily characteristic is clearly advantageous from the experimental design perspective. However, as most of body characteristics are intercorrelated such an approach may lead to biased conclusions about the

contribution of the individual traits in real-life mate selection which is generally based on the whole physique, among many other characteristics. To avoid this constrain, a possible solution would be using stimuli that simultaneously manipulate inter-related traits, such as both breast size and shape. Brooks et al. (2015), for example, used an alternative research strategy by using avatars and 'virtual evolution' paradigm. The individual avatars varying in numerous body measurements were assessed for their attractiveness and 50% of the most attractive ones entered another generation of the ratings. The main changes appeared in the area of waist, leg-length, and overall slenderness. The subsequent generations of the avatars also increased their bust size, however, this appeared to be only after the above reported characteristics showed lower variation.

For ratings of breast shape, we employed four profile drawings that were originally used in forensic science (Rawson & Brooks, 1984) and which vary in level of perceived firmness. However, as pointed out above, the breast firmness presumably interacts with breast size. Unfortunately, there appear no available biometric data that would demonstrate age-related changes in breast shape and their interaction with breast size. Further, breast shape is not solely related to age but also to parity and we currently have rather limited knowledge concerning what is the stronger predictor of breast shape: age, parity, the interaction between them, or another factor such as body weight change (Rinker et al., 2010). In this respect, studies from biological anthropology on changes in breast morphology would be appreciated by evolutionary psychologists.

Interestingly, only very few studies have employed photographs of breasts from individual women as stimuli; see Zelazniewicz and Pawlowski (2011) and Fink, Klappauf, Brewer, & Shackelford (2014) for notable exceptions. Although this approach cannot control for all possible confounding variables (e.g., effect of areola colour and size), it still provides the most ecologically valid approach so far. It could be complemented by the use of

composite images or morphs naturally varying in a parameter of interest (e.g., size). If these two approaches are used in a complementary fashion, they might provide us with a more complex understanding of the perception of breast morphology. To explore preferences for breast morphology in more detail, future studies might also consider using stimuli that more completely cover the natural variability in breast morphology.

4.4. Conclusions

In conclusion, we provide the first evidence based on samples from several populations for systematic male preferences for firm breast shape. Our results support the view that breast shape may serve as an indicator of female residual reproductive value. In contrast, we found relatively high variability in breast size preferences, with medium size being the most frequently preferred across majority of the tested cultures. Future studies should explore the interaction between preferences for shape and size, while employing more realistic stimuli fully covering natural variation in breast morphology.

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Fig 1: The stimuli used for testing preferences for breast size (small, medium, and large). Redrawn from Dixson et al. (2011a).

Fig 2: The stimuli used for testing preferences for breast firmness (high, moderate, rather low, and low). Redrawn from Rawson & Brooks 1984).

Fig. 3: Preferences for breast size (small, medium, large) in individual countries. Frequency of the stimuli selected as the most attractive. The differences were significant at $p < 0.05$ in Brazil and the Czech Republic, but not in Namibia ($p = 0.054$) and Cameroon ($p = 0.093$) (Chi-square test).

Fig. 4: Preferences for breast firmness in individual countries. Frequency of the stimuli selected as the most attractive. All differences significant at $p < 0.001$ (Chi-square test).

548 Table 1: Descriptive statistics ($\overline{X}$ ± 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

Table 5: Parameter estimates of the final model based on the Backward stepwise multinomial logistic regression separately for each country. Note that firm breast shape and the relationship status being single were set as the reference categories. The model based on the data from the Czech Republic was omitted due to low data variation of the dependent variable.

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)

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Figure 1

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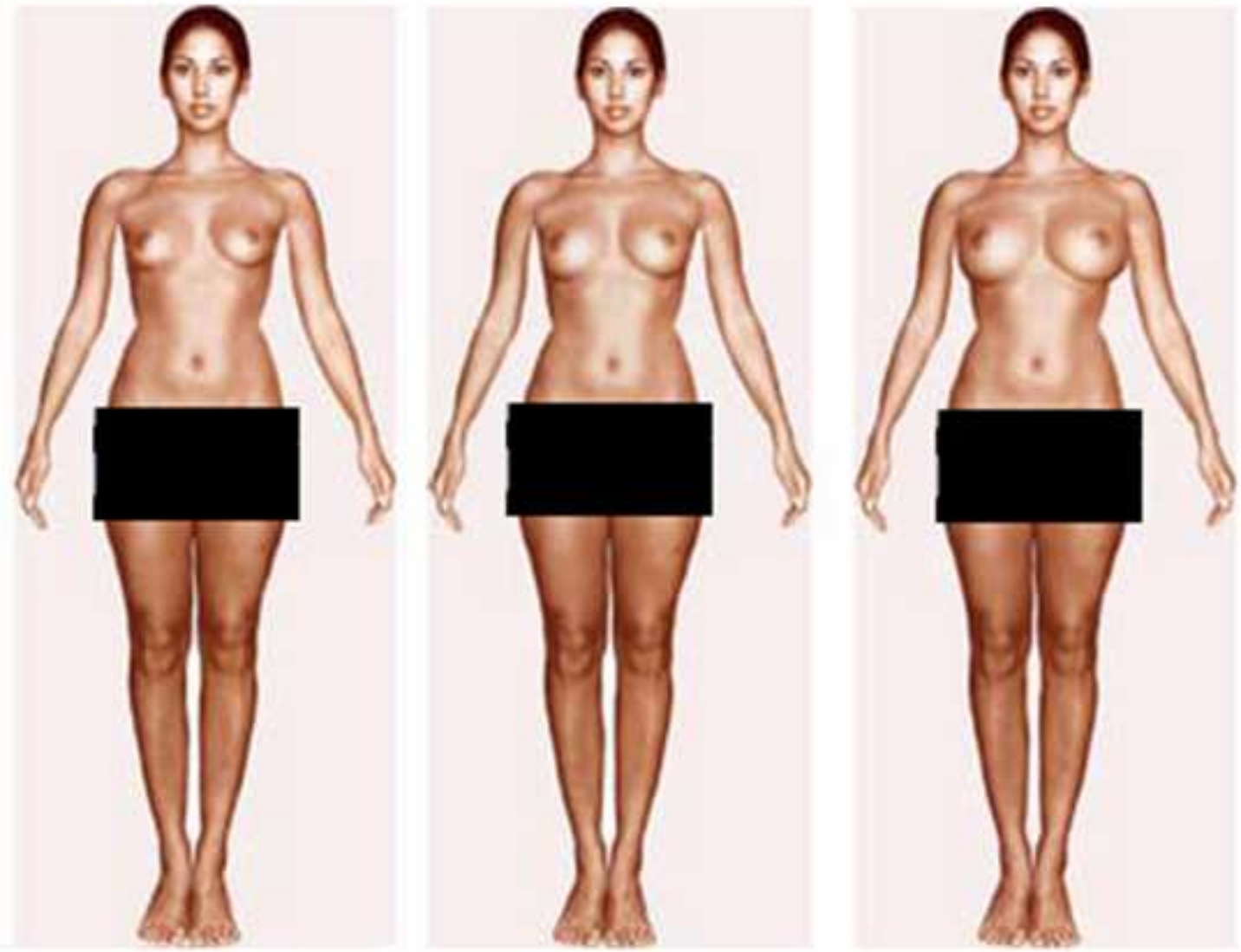


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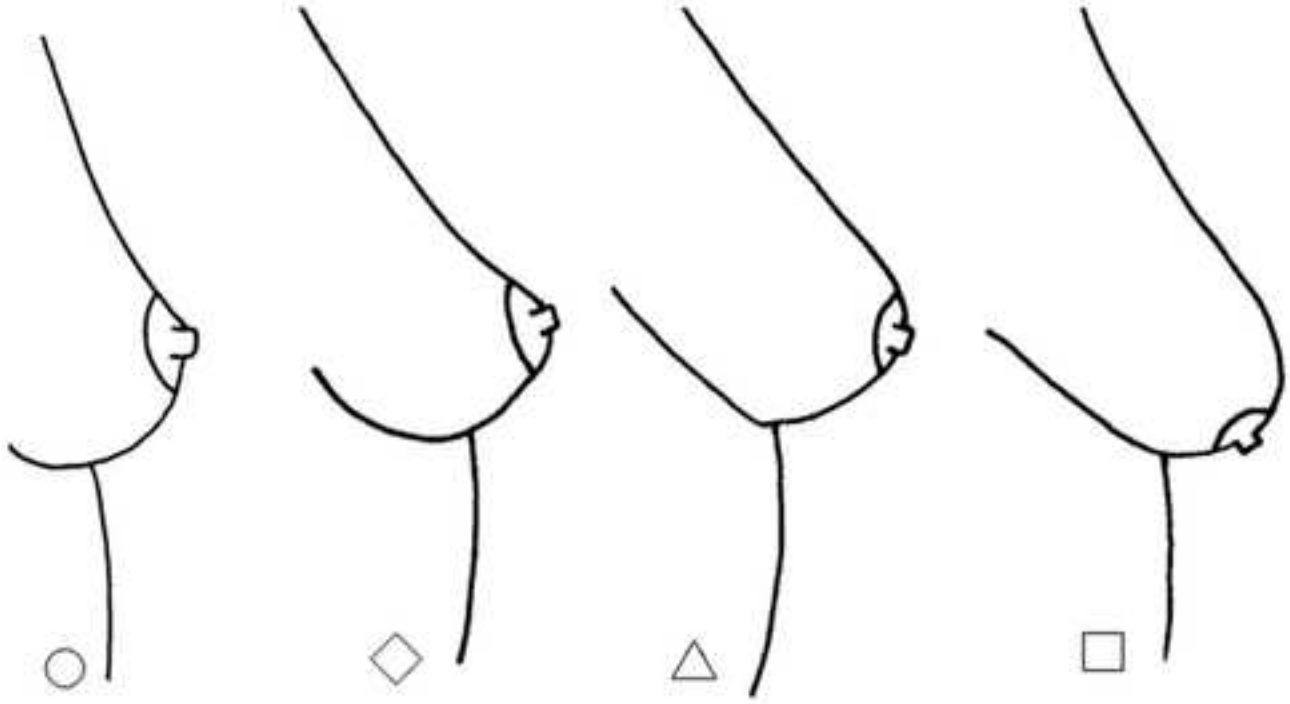


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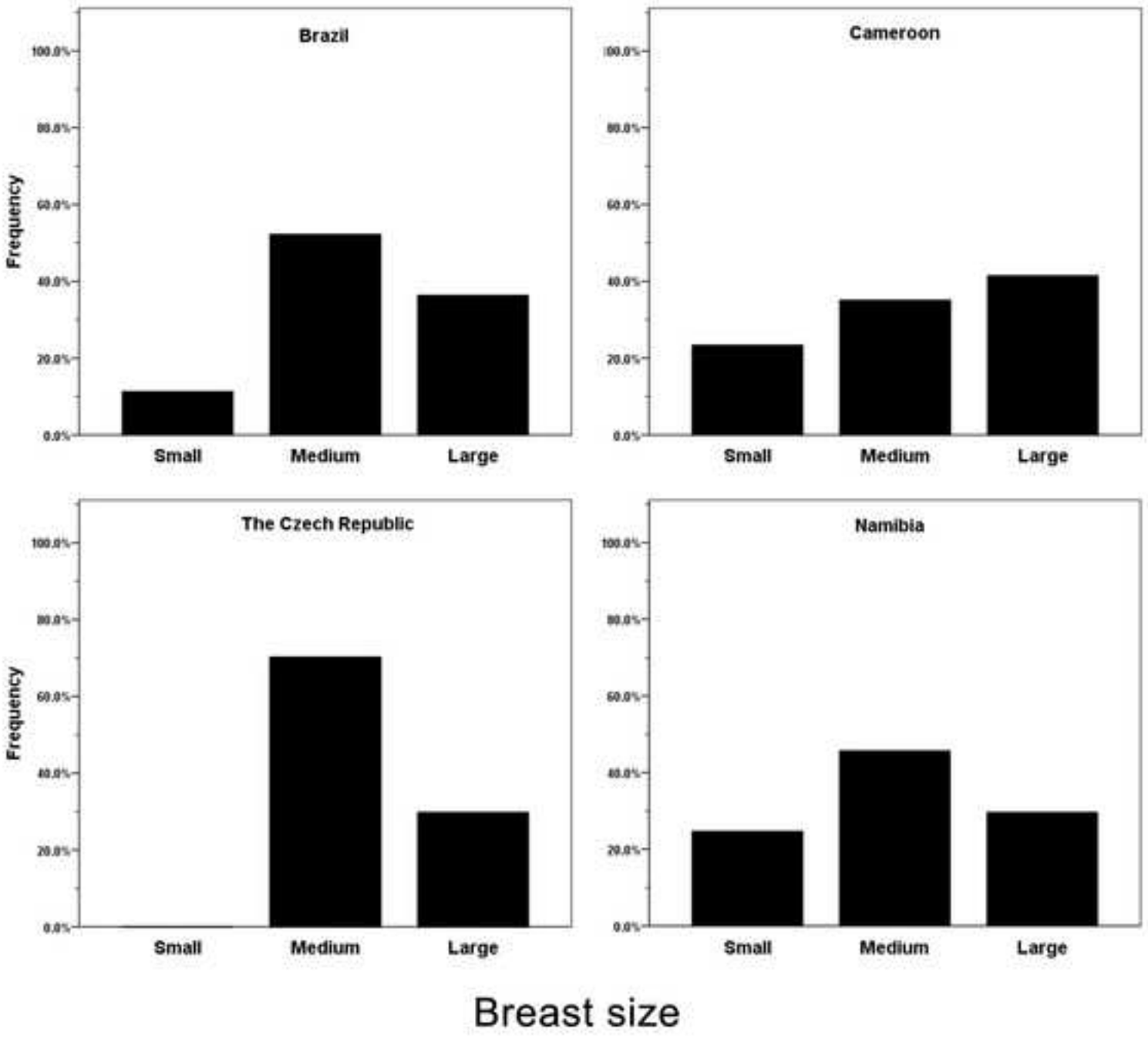


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