



Breast Asymmetry, Sexual Selection, and Human Reproductive Success

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Breasts of human females are large compared to those of closely related primate species, and they can thus be hypothesized recently or currently to have been subject to directional sexual selection. Here we show that (1) large breasts have higher levels of fluctuating asymmetry than small breasts, (2) breast fluctuating asymmetry is higher in women without children than in women with at least one child, (3) breast fluctuating symmetry is a reliable predictor of age-independent fecundity, and (4) breast fluctuating symmetry appears to be associated with sexual selection. These conclusions were similar in studies from two cultures differing in fecundity and breastfeeding traditions (Spain; New Mexico, U.S.A.). Choosy males that prefer females with symmetrical breasts may experience a direct fitness benefit in terms of increased fecundity and an indirect benefit in terms of attractive or fecund daughters.

KEY WORDS: Breasts; Breast asymmetry; Developmental instability; Fecundity; Fluctuating asymmetry; Humans; Sexual selection.

Size dimorphism in breasts of humans is exaggerated compared to that of closely related primate species (Darwin 1871), suggesting that recent directional selection has played a role in the evolution of adult female breast size. There is little evidence that the size of breasts in human

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females is a reliable predictor of lactation ability or milk composition in current industrial societies (reviews in Anderson 1983; Cant 1981; Low et al. 1987), and the functional significance of breast size therefore remains obscure. The exaggerated size of female breasts, their rapid development prior to and during puberty, and their apparent role in male-female interactions suggest that breasts may be involved in sexual selection (Alexander 1971; Low 1979). A directional male preference for large breasts (or an associated feature) may account for the evolutionary increase in breast size in humans as compared to related primate taxa. Because of a recent evolutionary history of directional selection and a net evolutionary change, breasts are expected to demonstrate higher levels of developmental instability than other morphological characters (Møller and Pomiankowski 1993). Directional selection covaries with low levels of developmental stability because selection for increased size simultaneously results in (1) selection against genetic modifiers that control the stable development of the character in question and (2) selection of uncommon alleles that sometimes confer high phenotypic trait values disrupting a coadapted genome (Møller and Pomiankowski 1993).

Developmental stability reflects the ability of an individual to generate the same phenotype under different environmental conditions (Ludwig 1932; Palmer and Strobeck 1986; Parsons 1990). Measures of developmental instability include deviations from bilateral symmetry such as phenotypic deviants and fluctuating asymmetry. Morphological characters usually demonstrate small, random deviations from the optimal phenotype of perfect bilateral symmetry that are termed fluctuating asymmetry (reviews in Ludwig 1932; Palmer and Strobeck 1986; Parsons 1990). Individuals with high degrees of fluctuating asymmetry often show low levels of environmentally and genetically caused health (Møller 1993; Palmer and Strobeck 1986; Parsons 1990; Watson and Thornhill 1994). Therefore, conspecifics and heterospecifics potentially are able to use the level of fluctuating asymmetry as a reliable health certificate of an individual, because it is very difficult to produce a perfectly symmetrical phenotype, particularly if it is exaggerated in size and subject to intense directional selection.

Developmental stability may play an important role in sexual selection because deviations from bilateral symmetry provide individuals with important information reflecting direct and indirect fitness benefits of mate choice (Møller 1990, 1992a, 1993; Thornhill 1992a, 1992b; Watson and Thornhill 1994). As characters become exaggerated due to net directional sexual selection, the levels of fluctuating asymmetry increase and become a perceivable and reliable indicator of general health. The character per se and its fluctuating asymmetry thus become the targets of sexual selection. A number of studies have now shown that symmetrical individuals have higher-than-average mating success, apparently because symmetrical mates are preferred over asymmetrical ones (reviews in Møller 1993; Thornhill and Gangestad 1994; Watson and Thornhill 1994).

In this paper we hypothesize that breast symmetry in human females is a target of sexual selection, because breast symmetry reliably reflects environmentally and genetically caused health, and that males by choosing females with symmetrical breasts obtain a direct fitness benefit in terms of increased fecundity

and potentially an indirect benefit in terms of fecund daughters with an attractive phenotype. This is studied by determining the relationship between breast symmetry and fecundity in two study samples from Spain and the United States.

METHODS

We obtained data sets of breast measurements from two culturally different populations. The average fecundity was higher and breastfeeding ubiquitous in our Spanish population, while fecundity was lower and breastfeeding less common in our U.S. population. These differences may be important because lactation as well as childbirth may affect the appearance of breasts by affecting their level of fluctuating asymmetry.

Measurements in our Spanish sample originate from 172 women that contacted Dr. F. Machado Quintana, M.D., in Granada, Spain. The women were asked to contribute to a research project by allowing the doctor to make two repeated measures of their breasts. All women agreed, and there was thus no bias in the sample caused by women not agreeing to participate. The doctor was asked to measure twice to the nearest mm the maximum circumference of each breast from the midpoint of the sternum to the meeting point between the *Musculus pectoralis* and the ribs. Absolute fluctuating asymmetry was estimated as the unsigned left-minus-right circumference of the breasts (Palmer and Strobeck 1986). Breast size was estimated as the mean of the circumference of the left and the right breast. Relative fluctuating asymmetry in breast size was estimated as absolute fluctuating asymmetry divided by breast size (Palmer and Strobeck 1986). This measure of relative fluctuating asymmetry is thus expressing absolute fluctuating asymmetry as a proportion of mean character size. During the consultation, each woman provided information on age, number of biological children, height, mass, and history of breast plastic surgery (none in the sample).

Breast size and breast fluctuating asymmetry were measured precisely because the repeatability (Becker 1984; Falconer 1981) based on one measurement of the left and the right breast and a subsequent remeasurement in the Spanish sample gave a value of $R = 0.988$ ($SE = 0.002$, $F = 150.10$, $df = 171,172$, $p < .0001$) for breast size and a value of $R = 0.982$ ($SE = 0.003$, $F = 110.31$, $df = 171,172$, $p < .0001$) for absolute breast fluctuating asymmetry.

The American subjects were all female patients of an Albuquerque, New Mexico, plastic surgeon (Patrick Hudson, M.D.) that came in for a breast consultation on either size reduction or augmentation during 1993. The mere fact that these women consulted a plastic surgeon suggests that they have a high degree of dissatisfaction about their breast morphology. The American sample may thus be biased as compared to the overall population. We discuss this potential bias at length in the Discussion. None of the 50 subjects had had previous surgical breast alteration. The subjects were selected haphazardly from a larger file of recent patients without previous breast surgery by a research assistant who was unfamiliar with the research hypothesis. At the time of the consultation, the subject was photographed in frontal perspective from the shoulders to the

waist at a distance of 1 m from the camera. Photo images were 3- × 5-inch color prints.

During the consultation, each woman provided information on age, number of biological children, height, mass, history of plastic surgery (none in the sample analyzed). At this time, each woman signed a statement releasing the photo and personal history data for scientific use.

The photographs of women from New Mexico were used by the research assistant (Sharon Shaw) for estimating absolute breast asymmetry as the distance from the suprasternal notch to the center of each of the nipples. Absolute fluctuating asymmetry was defined as the unsigned left minus right distances. All measures were made with steel calipers to the nearest 1 mm. Breast size was defined as the mean of the distance from the notch to the left and the right nipple, respectively. Relative breast fluctuating asymmetry was simply defined as absolute fluctuating asymmetry divided by breast size (Palmer and Strobeck 1986). The doctor measured the distance from the notch to the left and right nipple, respectively, on eight subjects, and the doctor's estimate of absolute fluctuating asymmetry was simply the unsigned difference between the distance to the left and the right nipple, respectively. The research assistant's and the doctor's measures of absolute fluctuating asymmetry are highly positively correlated (Pearson's $r = 0.83$, $p = .007$).

Breast size in the Spanish sample did not demonstrate directional asymmetry, which is a fundamentally different kind of asymmetry characterized by the trait of one side of the body consistently demonstrating higher values than the other, because mean signed left-minus-right character values did not deviate from zero (Palmer and Strobeck (1986); mean (SE) = -0.03 (0.12), one-sample t -test: $t = 0.25$, $df = 171$, $p > .20$). Breast size did not demonstrate antisymmetry (a second, different kind of asymmetry characterized by a deficiency of symmetrical phenotypes) because the distribution of signed left-minus-right character values did not deviate from a normal distribution (Kolmogorov-Smirnov test, $p > .20$). Breast size in the U.S. sample did not demonstrate directional asymmetry because mean signed left-minus-right character values did not deviate from zero (mean (SE) = 0.01 (0.12), one-sample t -test: $t = 0.17$, $df = 49$, $p > .20$). Breast size did not demonstrate antisymmetry because the distribution of signed left-minus-right character values did not deviate from a normal distribution (Kolmogorov-Smirnov test, $p > .20$).

We determined the relationship between lifetime fecundity and breast fluctuating asymmetry in a stepwise linear regression by first forcing presumably important variables to enter the regression model. Age had to be entered as a variable in order to obtain an age-independent estimate of lifetime fecundity. We also forced breast size to enter in order to control for any direct relationships between fecundity and breast size. Absolute fluctuating asymmetry was then forced to enter as a third variable in order to test whether absolute asymmetry was able to explain any residual variation. Finally, body height and body mass were allowed to enter the regression model in an attempt to test whether they were able to explain any additional residual variation in fecundity. We used absolute fluctuating breast asymmetry rather than relative fluctuating asymmetry because the

effects of breast size were controlled by first forcing this independent variable to enter the regression model.

RESULTS

There was considerable variation in breast size, breast fluctuating asymmetry, and the confounding variables in both the Spanish and the U.S. samples (Table 1). Absolute fluctuating asymmetry in breast size was large in both samples (Table 1), as was relative fluctuating asymmetry. The relative fluctuating asymmetry values were large compared to those of other morphological characters in humans, which are usually less than 1% (Livshits and Kobylansky 1991; Thornhill and Gangestad 1994). When breast fluctuating asymmetry was assessed as a discrete variable, more than 10% of healthy women were classified as having asymmetric breasts (Capraro and Gallego 1975; Normelli et al. 1986). This frequency of phenodeviants was high compared to that of other morphological characters in humans for which the frequency of deviants is usually only a couple of percent (Rasmuson 1960).

Absolute breast fluctuating asymmetry was positively related to breast size in both the Spanish and the New Mexico samples (Spain: Pearson $r = 0.21$, $N = 172$, $p = .005$; New Mexico: $r = 0.29$, $N = 50$, $p = .04$). Therefore, we have controlled for size-related absolute fluctuating asymmetry in the following analyses by using both absolute and relative breast fluctuating asymmetry as independent variables in the statistical analyses. Absolute breast fluctuating asymmetry was unrelated or only weakly related to the other variables (Spain: age: Pearson $r = 0.13$, $N = 172$, $p = .09$; height: Pearson $r = 0.04$, $N = 172$, $p = .52$; body mass: Pearson $r = 0.18$, $N = 172$, $p = .02$; New Mexico: age: Pearson $r = 0.08$, $N = 50$, $p = .58$; height: Pearson $r = -0.02$, $N = 46$, $p = .88$; body mass: Pearson $r = 0.01$, $N = 46$, $p = .95$).

Surprisingly, women that had given birth to children had on average 19% less absolute breast fluctuating asymmetry than women without children in the Spanish sample and 54% less in the New Mexico sample, both differences being statistically significant (Table 2). Comparable differences were also found when relative breast fluctuating asymmetry was analyzed (Table 2).

Table 1. Summary Statistics for Breast Measurements and Other Variables in the Two Samples of Women

	Spain ($N = 172$)			New Mexico ($N = 50^{\dagger}$)		
	Mean	SE	Range	Mean	SE	Range
Breast size* (cm)	24.75	0.43	14-44	4.86	0.15	2.40-7.30
Absolute FA* (cm)	1.23	0.08	0-5.5	0.22	0.03	0-1.00
Relative FA*	0.051	0.004	0-0.316	0.045	0.006	0-0.208
Height (cm)	158.7	0.5	143-176	164.4	0.9	152-175
Body mass (kg)	63.17	0.75	44-93	59.12	1.17	44-80
No. of children	2.23	0.12	0-7	1.54	0.20	0-5
Age (years)	43.83	0.79	16-73	32.36	1.38	14-68

* Breast size and fluctuating asymmetry were not estimated in the same way in the two samples (see Methods).

[†] $N = 46$ for height and body mass.

Table 2. Breast Fluctuating Asymmetry in Women with and without Children

Asymmetry variable	No. of children		<i>t</i>	<i>p</i>
	None	One or more		
Spain				
Absolute asymmetry	1.46(0.08)	1.18(0.03)	3.29	<.001
Relative asymmetry	0.064(0.004)	0.047(0.001)	4.14	<.001
<i>N</i>	34	138		
New Mexico				
Absolute asymmetry	0.35(0.08)	0.16(0.03)	2.88	.006
Relative asymmetry	0.067(0.014)	0.034(0.001)	2.57	.004
<i>N</i>	17	33		

Values are means (*SE*). Breast fluctuating asymmetry was not estimated in the same way in the two samples (see Methods).

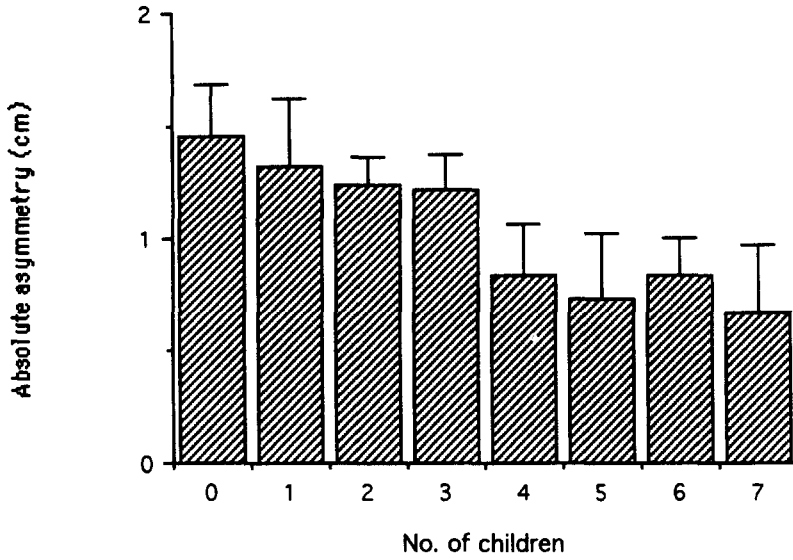
For each sample there was a positive relationship between age and fecundity measured as the number of biological children, while there was no statistically significant effect of breast size (Table 3). Age was forced to enter as the first variable in a multiple stepwise linear regression, because fecundity then is expressed as estimated lifetime fecundity. Similarly, breast size was forced to enter in order to control statistically for any direct effects of breast size on fecundity. Absolute fluctuating asymmetry in breast size explained a statistically significant proportion of the residual variance in fecundity (Table 3; according to partial *F* tests, the change in variance explained by forcing absolute breast asymmetry to enter was as follows: Spain: partial *F* = 23.11, *df* = 1,168, $r^2 = 0.06$, $p < .01$; New Mexico: Partial *F* = 8.85, *df* = 1,46, $r^2 = 0.14$, $p < .01$). Breast asymmetry was thus negatively related to fecundity (Figure 1). Neither body mass nor body height entered as statistically significant independent variables in additional stepwise regression analyses of either of the two samples.

Table 3. Stepwise Linear Regressions with Number of Children as the Dependent Variable, and Age and Breast Size Forced to Enter as the Independent Variables in Order to Control for Age-Dependent and Breast-Size-Dependent Fecundity

Spain	
<i>Initial model: F</i> = 8.88, <i>df</i> = 2,169, $r^2 = 0.14$, $p < .001$	
β(age)	0.39
β(breast size)	0.10
<i>Asymmetry model: F</i> = 14.10, <i>df</i> = 3,168, $r^2 = 0.20$, $p < .001$	
β(age)	0.40
β(breast size)	0.13
β(absolute breast asymmetry)	-0.14
New Mexico	
<i>Initial model: F</i> = 3.25, <i>df</i> = 2,47, $r^2 = 0.12$, $p = .048$	
β(age)	0.35
β(breast size)	-0.21
<i>Asymmetry model: F</i> = 5.31, <i>df</i> = 3,46, $r^2 = 0.26$, $p = .003$	
β(age)	0.35
β(breast size)	-0.10
β(absolute breast asymmetry)	-0.38

In the asymmetry regression model absolute breast fluctuating asymmetry was forced to enter as an independent variable. β values are standardized regression coefficients.

(a)



(b)

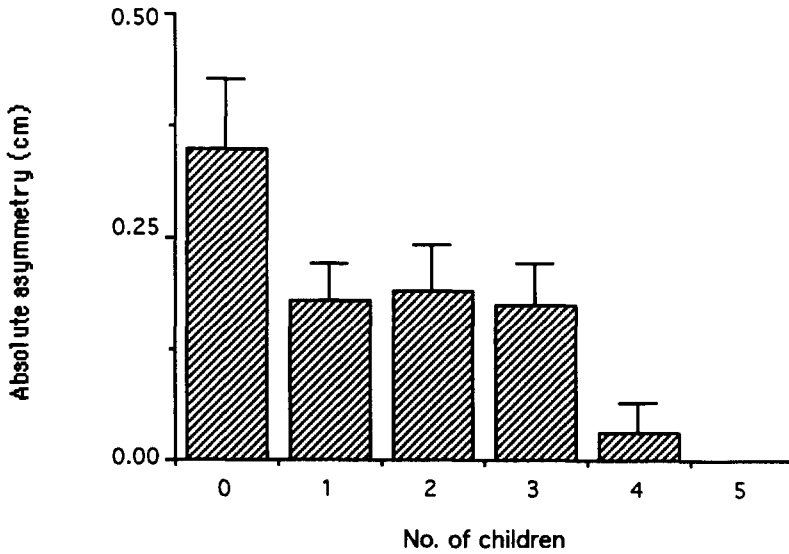


FIGURE 1. The relationship between fluctuating asymmetry in breast size (cm) and fecundity (number of children) in (a) Spain and (b) New Mexico. Values are means (SE). Note that breast fluctuating asymmetry was not estimated in the same way in the two populations (see Methods). In (b) there is a single observation of 0 asymmetry at 5 children.

DISCUSSION

This study demonstrates that one measure of developmental instability of breast size is large in two human populations, breast fluctuating asymmetry is positively related to breast size, and breast fluctuating asymmetry is a reliable predictor of age-independent fecundity.

Before discussing these results, it may be appropriate to consider a number of potential biases that may have affected our conclusions. First, we have not used random samples of women from the study populations. This problem is particularly important for the sample from New Mexico, which consisted of women that had contacted a plastic surgeon. It is highly likely that these women had a high degree of dissatisfaction about their breasts. Women that contact medical doctors may be hypothesized to have lower levels of breast fluctuating asymmetry than women in the overall population, because pregnant women automatically contact a medical doctor and because women approaching plastic surgeons generally do so in order to augment the size of their breasts. Because absolute breast asymmetry is positively related to breast size, the sample of women from New Mexico is likely to have had smaller breasts with smaller degrees of fluctuating asymmetry than women in the population. The fact that we obtained qualitatively similar results from the two samples suggests that our conclusions are robust despite potential sampling biases.

Second, several persons have drawn our attention to the fact that gestation and especially lactation tend to result in an increase in breast size and an increase in cordoidal strain on the breasts. Although we have been unable to empirically verify these effects through the literature, we assume that they are real phenomena. These increases should result in relatively high levels of breast asymmetry in women who have given birth or nursed their children. This general trend toward increased breast asymmetry over the course of a parous woman's reproductive career should mitigate any direct negative relationship between fecundity and breast asymmetry. The negative relationship between fecundity and breast asymmetry may actually underestimate the real magnitude of the relationship. A more direct test of our hypothesis could be based on estimates of breast asymmetry in post-pubescent nulligravidas and subsequent longitudinal assessment of their reproductive careers.

Third, we have used two different techniques for estimating fluctuating asymmetry in breasts. Both techniques are far-from-perfect estimates of overall fluctuating asymmetry in breast size because breasts are three-dimensional structures. It is common knowledge that some women have wide-based, short breasts while other have small-based, but long breasts. If breast size in one dimension (say, length) is negatively correlated with breast size in another dimension (say, width), fluctuating asymmetry in breast size in one dimension would automatically be positively correlated with that in the other dimension. The reason for this is that a bilateral size difference in one direction, for example, for breast length would result in an oppositely directed difference for breast width. This effect would not cause any bias in our linear estimates of breast fluctuating asymmetry. If breast asymmetry in one dimension is not negatively correlated with breast asymmetry in another dimension, an unbiased estimate of three-dimensional asymmetry is the cube of our estimate of absolute fluctuating asymmetry

in breast size. The optimal estimate of breast asymmetry could be obtained from casts of each breast that were subsequently used to estimate breast volume. However, we were forced to estimate breast asymmetry in a single linear dimension because there are limits to the kinds of requests that you can make to subjects and medical doctors without causing other kinds of biases in your samples. The fact that we obtained qualitatively similar results by using two different measures of fluctuating asymmetry in breasts suggests that our conclusions are robust.

Finally, our conclusions were based on two samples from current industrial societies in which environmentally caused stress due to lack of nutrition is relatively unimportant. The levels of fluctuating asymmetry in breasts in cultures currently subject to severe nutritional stress and in prehistoric societies may have been considerably larger than in current industrial societies. In conclusion, we find it unlikely that our consistent results from two different samples can arise as a consequence of systematic bias in our data sets. However, it is likely that the true relationship between fecundity and fluctuating asymmetry in breasts may have been underestimated for the reasons given above.

We hypothesize that breast fluctuating asymmetry may play an important role in sexual selection and mate choice in humans because it is a reliable indicator of age-independent fecundity. Developmental stability has recently been suggested to play an important role in sexual selection in nonhuman species because acquisition of a developmentally stable partner may result in both direct and indirect fitness benefits to choosy individuals (Møller 1990, 1992a, 1993; Thornhill 1992a, 1992b; Watson and Thornhill 1994). Sexual selection also appears to be related to developmental stability in humans as evidenced from a series of recent studies (Grammer and Thornhill 1994; Thornhill and Gangestad 1994; Thornhill et al. in press).

The size of breasts in human females is large compared to that of other primate species, and there has thus been a recent evolutionary change in breast size. Human breasts are characterized by their large size and rapid development prior to and during puberty, when growth of other body parts also reaches a high level. They can thus be considered costly structures in terms of energy use. Heterogeneity in development will depend on the rate of relative growth and therefore generate the largest magnitude of fluctuating asymmetry early during development when growth is relatively rapid (e.g., Balinsky 1975; Torrey and Feduccia 1979). Compensational growth at later stages of development may therefore reduce the magnitude of initially large fluctuating asymmetries (Corruccini and Potter 1981). This is also the case in some studies of age-related differences in breast fluctuating asymmetry ("The Adolescent Breast" 1971; Benedek et al. 1979; Dewhurst 1969), but not in others (Normelli et al. 1986)

Heavy investment in breast development during puberty may seem puzzling because the functional significance of breasts is far from obvious. There is no or little relationship between breast size and production and composition of milk in current industrial societies (reviews in Anderson 1983; Cant 1981; Low et al. 1987), and breasts have therefore been hypothesized to constitute a deceptive signal used by women to attract preferred mates (Low et al. 1987). In prehistoric human populations, conditions may have been different, when mother's milk

was the sole source of nutrition for young children and when resources often may have been more limited than in present industrial societies. In this study we show that large breasts tend to be more asymmetric than small breasts. In prehistoric societies, where resources were likely to be less available or more unevenly distributed among women, breast asymmetries are likely to have been much larger than in present industrial societies with relatively easy access to resources. Environmentally caused fluctuating asymmetries can arise as a consequence of the quality and quantity of food (Palmer and Strobeck 1986; Parsons 1990), and stress-induced fluctuating asymmetries are often disproportionately large in extravagant traits such as secondary sexual characters (Manning and Chamberlain 1993; Møller 1992b). If the relationship between breast size and fluctuating asymmetry is robust, we hypothesize that a directional preference for large, symmetrical breasts, as apparently found in some cultures (Ellis 1954), can be maintained in the population because selection for large breasts will be balanced by selection against asymmetrical breasts.

We also show that breast symmetry is a reliable predictor of age-independent fecundity, and that choosy males that use breast symmetry as a cue in their mate choice will experience an advantage in terms of reproductive success. Breast symmetry can thus be considered a reliable signal used in intersexual communication. The relationship between breast fluctuating asymmetry and fecundity was similar in the two populations currently differing in fecundity and breastfeeding preferences. This suggests that our conclusions are robust and to some extent independent of cultural differences. The causes of breast fluctuating asymmetry have been hypothesized to include intrauterine disturbance, endocrine imbalance, and hereditary effects (Bishop 1969; Maliniac 1950; Neifert et al. 1985). Choosy males may thus experience direct (high fecundity) as well as indirect fitness benefits (attractive and genetically high-quality fecund daughters) from their choice of females with symmetrical breasts.

The negative relationship between breast fluctuating asymmetry and fecundity need not be causal, but can be due to a third variable affecting both breast fluctuating asymmetry and fecundity. First, fluctuating asymmetry in breasts and fecundity may have a common hormonal basis, if hormonal imbalances result in both increased fluctuating asymmetry (Bishop 1969) and reduced fecundity. This hypothesis assumes that hormonal imbalances cause an increase in breast fluctuating asymmetry and that such imbalances as a side effect reduce fecundity. Breast fluctuating asymmetry may, however, not be a cue used directly by males in mate-choice situations.

Second, if breasts are considered secondary sexual characters, breast fluctuating asymmetry may be used as a cue in mate choice (Møller 1990, 1992a, 1993; Thornhill 1992a, 1992b; Watson and Thornhill 1994). The negative relationship between fluctuating asymmetry and fecundity could then be the outcome of sexual selection against fluctuating asymmetry reliably signaling fecundity or sexual attractiveness. As a direct result of our study, recent evidence from an experiment suggests that men judge figures of women with symmetrical breasts as more attractive and healthy than figures with slightly asymmetrical breasts (Singh in press). This sexual selection hypothesis is also supported by anecdotal evidence.

One of us (A.P.M.) asked male acquaintances whether they have had female partners with breast asymmetry, and eight responded affirmatively. All these relationships were terminated by the men at the stage of questioning that may suggest that men selectively left women with asymmetrical breasts. Furthermore, all eight men told unsolicited that breast asymmetry was a considerable psychological problem to their partners. This acute female consciousness of breast symmetry may be interpreted as reflecting (1) a history of the importance of developmental stability of breasts for mate choice in humans, or (2) a recent consciousness caused by culturally determined attitudes. We predict that mating success will be negatively and time to pair bond will be positively related to fluctuating asymmetry in breast size. It is known that women with scoliosis, who also have high levels of breast asymmetry (Normelli et al. 1986), more frequently remain single for life than other women (e.g., Zorab 1977). However, this relationship may be due to mating success being negatively related to symptoms of scoliosis in general.

Third, fluctuating asymmetry in breasts could reflect overall, organism-wide fluctuating asymmetry in morphological characters (Livshits and Kobylansky 1991). Various fitness components are known to be negatively related to levels of fluctuating asymmetry (Møller 1993; Palmer and Strobeck 1986; Watson and Thornhill 1994), and a reduced fecundity among women with asymmetric breasts may be due to an overall high level of fluctuating asymmetry. For example, several fitness components are known to be negatively associated with overall skeletal fluctuating asymmetry in humans (Livshits and Kobylansky 1991). Correlations between fluctuating asymmetries in different morphological characters are most likely to arise as a consequence of the different characters being developmentally and genetically linked (Sakai and Shimamoto 1965). Breast size is unrelated to a number of other morphological characters, including height (this study), suggesting that breast fluctuating asymmetry is unlikely to reflect overall differences in individual developmental stability. This study has shown that breast asymmetry reflects specific quality properties related to fecundity, and this is the main reason why breast symmetry may become the target of a directional male mate preference.

Breast asymmetry has been suggested to have a heritable basis (Maliniac 1950). This claim is consistent with the conclusion of a recent review of heritability of developmental stability demonstrating a small but statistically highly significant additive genetic component (Møller and Thornhill unpublished manuscript). Males that acquire mates with low levels of breast fluctuating asymmetry will thus also tend to sire daughters with little breast fluctuating asymmetry. This will provide choosy males with a sexual selection advantage because their daughters may experience higher mating success, earlier reproduction, and higher fecundity. Mutation will be a source of continuous input of asymmetric phenotypes to the population, and mate choice for fecund females with symmetrical breasts can thus continuously be maintained in the population.

In conclusion, breast fluctuating asymmetry in humans is common and large compared to the asymmetry of other morphological characters. Breast fluctuating asymmetry reliably predicts fecundity and may be a cue used directly by males in their choice of fecund and attractive partners.

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