Evolution and Human Behavior 42 (2021) 517–523

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.elsevier.com/locate/ens

Breast symmetry, but not size or volume, predicts salivary immunoglobulin-A (sIgA) in women[☆]

Ashley Locke, Steven Arnocky[*]

Nipissing University, 100 College Drive, North Bay, Ontario P1B8L7, Canada

ARTICLE INFO

Keywords:
Immunocompetence
Breasts
Breast symmetry
Fluctuating asymmetry
Salivary immunoglobulin A
Immunoglobulin
Signaling

ABSTRACT

Human breasts are larger and more enduring than reproductively necessary. It is thus unclear why this costly, yet conspicuous phenotype has been selected for, or what information they might convey about the underlying quality of the female. Following previous research on fluctuating asymmetry, we postulated that breast symmetry would predict a marker of mucosal immunity (salivary immunoglobulin-A; sIgA). Anthropometric breast measurements were provided by 97 young women. Controlling for Body Mass Index (BMI), breast size, and volume, results demonstrated that breast asymmetry predicted lower sIgA, whereas size and volume did not. Results support the hypothesis that symmetrical female breasts are a cue to underlying immunocompetence.

1. Introduction

The female breast is one of our species' most conspicuous secondary sex characteristics. Adult breasts are, on average, much larger than necessary to facilitate their primary job of lactation. In comparison, the breasts of other primates are flatter, yet are still able to produce sufficient milk for feeding their young (Morris, 1967). In other mammals, breasts develop at first pregnancy whereas human females develop breasts during puberty (Short, 1976). Humans are also the only species who retain enlarged breasts permanently throughout life regardless of lactation requirements, unlike other primates (Arieli, 2004). Breast morphology appears to be a sexually selected trait that is highly heritable (Kościński, Makarewicz, & Bartoszewicz, 2020; Pomiankowski & Møller, 1995). Morris (1967) suggested that female breasts evolved as sexual stimuli to replace the buttocks during the transition to bipedal locomotion. Breasts provide a clear signal in upright bipeds (Morris, 1967). There is also a plethora of evidence that the human female breast is very attractive to males (e.g., Dixson, Grimshaw, Linklater, & Dixson, 2011a, 2011b; Duncan, 2010). Across cultures, men's reported ideal breast size in a partner varies, but breasts are considered an erotic stimulus across various cultures (e.g., Ford & Beach, 1951; Prokop et al., 2020). In hunter-gatherer cultures such as the Hadza, men find breasts erotic, even though women do not usually cover their breasts (Marlowe, 1998). In a study by Dixson, Grimshaw, et al. (2011b), men spent significantly more time looking at the breasts than other areas of the body or head when viewing nude images of women. Moreover, cross-cultural evidence suggests that shape (i.e., firmness) weighs more heavily upon breast attractiveness than does size. Specifically, whereas breast size was highly variable in its cross-cultural association with attractiveness, a preference for firmness was more ubiquitous (Havlíček et al., 2017).

What information is conveyed by breast morphology, however, is much less well-understood. Some have suggested that breast size honestly indicates fat reserves and ability to survive and invest in offspring (Cant, 1981; Gallup, 1982; Huss-Ashmore, 1980). The nubility hypothesis proposes that breast size and shape are a signal of age and residual reproductive value (Marlowe, 1998). Similarly, Gallup (1982) suggested that breast size and shape have evolved to indicate probability of ovulating, age, and nutritional status. Some empirical evidence has supported links to fecundity. According to Jasienska, Ziomkiewicz, Ellison, Lipson, and Thune (2004), women with larger breasts have better reproductive health, as assessed by biological markers of fecundity such as higher daily levels of 17-β-oestradiol (E2) and progesterone, particularly when paired with having a narrow waist. These hormones are associated with higher rates of conception (Lipson & Ellison, 1996). Conversely, two other studies were not able to replicate the finding

---

[☆] This research was funded by a Natural Sciences and Engineering Research Council of Canada Discovery grant awarded to Steven Arnocky (file # RGPIN-2019-05988). Correspondence regarding this research should be directed to Steven Arnocky (stevena@nipissingu.ca). We are grateful to Vicki Schlosser and Tracy Westerlund for their assistance in conducting the breast measurements.

[*] Corresponding author.
E-mail address: stevena@nipissingu.ca (S. Arnocky).

https://doi.org/10.1016/j.evolhumbehav.2021.05.001
Received 1 October 2020; Received in revised form 21 April 2021; Accepted 12 May 2021

linking breast size to estrogen, nor did they find an association between breast size and testosterone (T) levels - a predictor of poor reproductive health in women (Grillot, Simmons, Lukaszewski, & Roney, 2014; Kościński et al., 2020; Steinberger, Smith, Tcholakian, & Rodriguez-Rigau, 1979).

Although most research on the signaling and cueing properties of breasts has focused on size, there is reason to suspect that symmetry might also convey important information about the underlying quality of a female. A large body of research has demonstrated that symmetrical morphological features are considered attractive (e.g., Gangestad & Thornhill, 1997; Gangestad, Thornhill, & Yeo, 1994; Grammer, Fink, Møller, & Thornhill, 2003; Grammer & Thornhill, 1994; Rhodes, Simmons, & Peters, 2005; Scheib, Gangestad, & Thornhill, 1999). This is also true of breast morphology, such that men prefer more symmetrical breasts (e.g., Dixson et al., 2011; Duncan, 2010; Singh, 1995). For example, Duncan (2010) found that participants rated images of symmetrical breasts as significantly more attractive than asymmetrical comparisons. Increasing levels of asymmetry systematically decreased ratings of attractiveness (Duncan, 2010). Similarly, Singh (1995) found that line drawings of female bodies with low waist-to-hip ratios and symmetrical breasts were judged to be most attractive. Recent research has shown cross cultural consistency in men's preference for symmetrical breasts (Dixson, Vasey, et al., 2011). Furthermore, women with more symmetrical breasts are more likely to marry, more likely to have more children and have them earlier in life compared to women with asymmetrical breasts (Manning, Scutt, Whitehouse, & Leinster, 1997; Møller, Soler, & Thornhill, 1995). Yet, despite the breadth of research highlighting the importance of female breast symmetry as attractive, little research has explored what, if any, information breast symmetry might convey to the perceiver about the underlying quality of the female.

Overall, preferences for symmetry can provide both direct (i.e., avoiding pathogens, marker of health) and indirect (i.e., providing good genes to offspring) benefits to the perceiver, and there is some evidence that perceivers can identify potential links between FA and underling immunocompetence. For example, Grammer and Thornhill (1994) found that facial symmetry was perceived as a sign of health in males. Additional studies have since replicated and extended these findings, and found perceived health was significantly positively correlated with symmetry in both male and female faces (Fink, Neave, Manning, & Grammer, 2006; Rhodes et al., 2001). Similar findings have been observed in men's ratings of female breasts; images of women with symmetrical breasts are rated as healthier than women with asymmetrical breasts (Duncan, 2010), indicating that men might consider this characteristic as a cue to developmental stability and underlying female immunocompetence.

1.1. Developmental instability and asymmetry

Developmental instability refers to one's inability to resist adverse effects of developmental disturbances, which can include illness and/or stress on the body (Van Dongen & Gangestad, 2011). The system that regulates symmetrical development does not function as well in times of stress. Accordingly, small, random deviations from perfect bilateral symmetry, termed fluctuating asymmetry (FA), arise in response to genetic and environmental stressors during development (Gangestad & Thornhill, 1997; Manning et al., 1997; Møller, 1993; Møller et al., 1995; Palmer & Strobeck, 1986; Thornhill, 1992). Accordingly, FA is considered as a proximate or indirect index of developmental instability (e.g., Van Dongen & Gangestad, 2011). Stressors can include toxins, mutations, food deficiency, pesticides, and inbreeding (Møller & Pomiankowski, 1993; Parsons, 1990). Since these asymmetries occur during development, they are thus considered to represent an individual's ability to fight off extrinsic health threats. Applying this reasoning to male ornaments, Møller (1990) suggested that FA should be a reliable measure of an individual's ability to produce extravagant sexual traits, because only those in the best physical condition should be able to produce both large and symmetrical ornaments. Similarly, Thornhill and Møller (1998) identified a lack of fluctuating asymmetry as the best measure of genetic quality (see also: Møller & Pomiankowski, 1993; Watson & Thornhill, 1994).

In support of this, FA is negatively related to fitness indicators across diverse species (Møller, 1994; Thornhill, 1992; Thornhill & Gangestad, 1994; Watson & Thornhill, 1994). In other species, there is evidence that FA is negatively associated with measures of immunocompetence (e.g., Hammouda et al., 2012), however, there is limited research on this relationship in humans. Shackelford and Larsen (1997) found that individuals with low facial FA have better health as measured by self-report symptoms including runny nose, congestion, and headaches. Thornhill and Gangestad (2006) found that facial and body asymmetry were correlated positively with the number of respiratory illnesses reported. One recent meta-analysis on the relationship between FA and health found that across six broad categories (including health and disease, psychological maladaptation, and attractiveness) the mean effect size for associations with FA was about $r = 0.20$ (Van Dongen & Gangestad, 2011). FA has also previously been related to genetic stresses such as congenital defects (Adams & Niswander, 1967) and number of serious illnesses experienced (Waynforth, 1998). Milne et al. (2003) found a relationship between a composite measure of FA for six body traits and reporting two or more past health conditions, the strongest relationship being hepatitis and major surgery. Nevertheless, some research has observed null links between FA and markers of immunocompetence. Pawlowski, Borkowska, Nowak, Augustyniak, and Drulis-Kawa (2018) found little evidence of FA measured across six body regions and T CD3 and B CD19 lymphocytes, total IgA and IgG and response to flu vaccine.

One glaring issue with extant research is that most studies examine markers of FA that are not clear secondary sex characteristics, such as asymmetries of the hand and feet (e.g., Jasienska, Lipson, Ellison, Thune, & Ziomkiewicz, 2006; Pawlowski et al., 2018) which are unlikely to be attended to during naturalistic mate choice. Møller and Pomiankowski (1993) noted that:

> "The patterns of fluctuating asymmetry in secondary sexual characters differ from those seen in other morphological traits. Secondary sexual characters show much higher levels of fluctuating asymmetry. Also, there is often a negative relationship between fluctuating asymmetry and the absolute size of ornaments, whereas the relationship is typically U-shaped in other morphological traits. The common negative relationship between fluctuating asymmetry and ornament size suggests that many ornaments reliably reflect individual quality" (pp. 267).

From this perspective, it is imperative to focus more directly upon our species most elaborate secondary sex characteristics, such as the female breast. As breast size increases, so too does bilateral asymmetry (Manning et al., 1997). Given the female breast is one of our species' most sexually dimorphic features to which men selectively attend and are universally attracted to, and given that men appear to use breast symmetry to inform their perceptions of female health, it is important for research to directly examine potential links between breast symmetry and immunocompetence to determine whether such secondary sex characteristics may serve as a cue to the ability of an individual to cope with immunological challenges in their environment.

To date, breast asymmetry has been linked to some health problems including cancer (Kayar & Çilengiroğlu, 2015; Scutt, Manning, Whitehouse, Leinster, & Massey, 1997), and women with more symmetrical breasts are more fecund (Møller et al., 1995), suggesting that breast symmetry may act as a valid cue to health. Yet, very little research has investigated relationships between breast symmetry and direct markers of immunocompetence. The goal of the present study was to examine whether breast asymmetry correlates with a marker of mucosal immunocompetence, salivary immunoglobulin A (sIgA). sIgA is a key component of the immune system's initial defence against microbial invasion and pathogens (Marcotte & Lavoie, 1998). Specifically, it plays an important role in protection against infections caused by viruses in both human and animal models, limits local inflammatory reactions, and inhibits bacterial adherence to epithelial cells (Marcotte & Lavoie, 1998). Low levels of sIgA have previously been linked to increased infection (Nakamura, Akimoto, Suzuki, & Kono, 2006; Volkmann & Weekes, 2006), and there is evidence that sIgA is negatively correlated with mortality, particularly from cancer and respiratory disease in later life (Phillips, Carroll, Drayson, & Der, 2015).

Beyond symmetry, researchers have been interested in other morphological characteristics of the breast, such as size and volume. Breast size is negatively associated with symmetry (Møller et al., 1995), and larger breast size has also been linked to specific health problems (Kościński et al., 2020; Ray, Mohllajee, van Dam, & Michels, 2008). Previous research has demonstrated that breast size is also positively correlated with body mass (Brown et al., 2012; Kościński et al., 2020), and women with higher BMIs tend to have lower levels of sIgA (Starzak, Konkol, & McKune, 2016). There is also evidence that both body asymmetry and more specifically, breast asymmetry, and body weight are positively correlated (Manning, 1995; Manning et al., 1997). Accordingly, we predicted that breast symmetry would positively predict sIgA in women, controlling for BMI, breast size and volume as covariates in the model (Hypothesis 1).

Whereas breast symmetry is expected to serve as a cue to underlying immunocompetence, it is unclear whether breast size or volume (i.e., ornament size as an overt sexual signal) should be expected to correlate with sIgA. Zahavi and Zahavi (1997) speculated that breast size might be explained by the handicap principle, but to date there is little evidence in support of this explanation. The immunocompetence handicap hypothesis (ICHH; Folstad & Karter, 1992) attempts to explain the development of hormonally modulated sexual ornaments and immunocompetence. It proposes that elaborate ornaments are costly to develop and/or maintain and are selected for by the opposite sex because they honestly signal the underlying quality of the bearer (Zahavi, 1975). The ICHH suggests that specific hormones are complicit in both developing the sexual signal and in suppressing immune function (Folstad & Karter, 1992). Although the ICHH is primarily applied to testosterone and male traits, "the model would accommodate any biochemical substance that is self-regulated and exerts the two-pronged effect of compromising the immune system and stimulating trait expression" (Folstad & Karter, 1992, p.605).

Correlational and experimental studies have shown both positive and negative relationships between estrogen and immune function (see Foo, Nakagawa, Rhodes, & Simmons, 2017; Klein, 2004; McDade, 2003; Roved, Westerdahl, & Hasselquist, 2017 for review). Specific to sIgA, some research has demonstrated a positive relationship between estradiol and sIgA in healthy women (van Anders, 2010). However, another study found that estradiol associated with lower sIgA in females (Hodges-Simeon, Asif, Gurven, Blackwell, & Gaulin, 2019). Moreover, directionality issues pervade handicap modeling, such that either positive or negative correlations could be interpreted as support for the theory (Getty, 2006). Moreover, traits that are positively linked to immunocompetence do not necessarily indicate a handicap but rather could serve as an index signal (Maynard Smith & Harper, 1995), whereby the signal honesty relies not upon its cost, but rather upon the "function of internal processes that cannot be faked" (Weaver, Koch, & Hill, 2017, p.2), such as parasite resistance (Hamilton & Zuk, 1982). In support of this, many studies have found that individual survival is associated with the expression of secondary sexual characteristics (Jennions, Møller, & Petrie, 2001), and studies of human secondary sexual traits have been positively linked to markers of immunocompetence (e.g., Rantala et al., 2012), including sIgA (Arnocky, Hodges-Simeon, Ouellette, & Albert, 2018). Accordingly, we examined the effects of breast size and volume in an exploratory manner in the main regression analysis.

2. Methods

2.1. Participants

The research was approved by the institutional Research Ethics Board. To determine an appropriate sample size, we used a-priori power analysis (G*Power 3.1; Faul, Erdfelder, Buchner, & Lang, 2009). To obtain statistical power at the .80 level, with alpha set at .05 and medium effect size, $p^2 = 0.14$, we aimed to collect a minimum of 95 participants. Participants were recruited from a small university in Northern Ontario, Canada. The final sample consisted of 97 undergraduate females between the ages of 18 and 29 ($M_{age} = 20$, $SD = 1.98$). The ethnic distribution was as follows: $n = 91$ Caucasian/White, $n = 3$ Asian, $n = 2$ South Asian, $n = 6$ Native/Aboriginal, $n. = 1$ Latin-American. Participants were remunerated with course partial credit.

2.2. Materials and procedures

Participants were instructed not to eat, drink (except water), smoke, or exercise for at least 1 h prior to their testing session. They were also instructed to reschedule the session if they were sick. After obtaining informed consent, participants provided a saliva sample via passive drool into a transparent 5 ml polystyrene culture test tube which was then stored at −20 °C. Participants then had their height and weight measured by a research assistant using a Detecto Apex digital physician scale with sonar height rod (Webb City, Missouri, USA). BMI was calculated using the height and weight measurements (BMI = weight [kg]/height [m]2). Subsequently, participants completed a self-report questionnaire on a computer which consisted of a demographics section (age and ethnicity). Prior to testing, participants reported having no children and no history of surgical procedures such as breast implants, breast reduction, or other procedures (e.g., tumour removal) that might alter the shape of their breast(s).

2.2.1. Immunoglobulin-A (sIgA) concentrations

sIgA was assayed using commercially available enzyme linked immunoassay (ELISA) kits (DRG International, NJ, USA). Research shows there is a diurnal pattern for sIgA (Hodges-Simeon et al., 2020), and it is suggested that sIgA samples should be taken at a standardized time of day (Bellussi, Cambi, & Passali, 2013). In this study, sIgA samples were taken within a precise window; all participants gave their sample between 8 am and 10 am on the data collection day. Samples were assayed in duplicate and the average of the duplicates. The inter- and intra-assay coefficients of variation for sIgA were both below 5%. Previous research has shown that salivary flow rate corresponds to measurable sIgA levels (Arnocky et al., 2018; Eliasson, Österberg, & Carlén, 2006). Thus, flow rate (ng/ml) was controlled by multiplying the concentration by flow rate to create a flow rate adjusted concentration value (ng/s). Finally, we log transformed the flow rate adjusted value, and the resulting value was used in all analyses.

2.2.2. Measured breast size and asymmetry

In a private testing room, one of two trained female healthcare professionals completed the breast size and symmetry measurements. Participants were asked to stand fully erect with feet together, and shoulders relaxed with arms hanging freely. Measurements were taken in centimetres (cm) using a soft measuring tape for all markers except for mammillary projection and the vertical distance from the nipple to the infra mammary fold on the lateral view, which require use of a ruler. For breast size, the following measures were taken: (1) the chest circumference measured at the infra mammary fold (under bust) and (2) the circumference of the chest (full bust). Breast size was calculated by subtracting the under bust from the full bust circumference (Garver-Apgar, Eaton, Tybur, & Emery Thompson, 2011; Grillot et al., 2014;

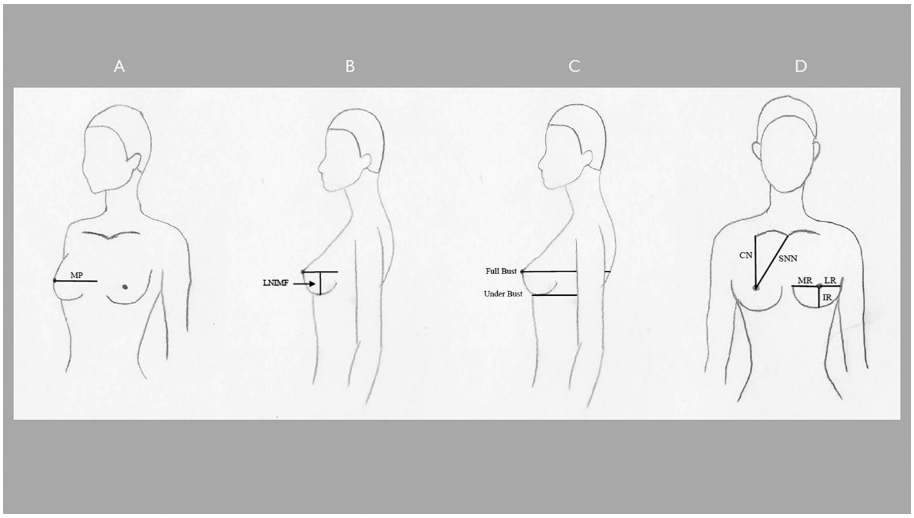

Fig. 1. Panel A = Mammillary projection (MP) (breast projection) measurement, Panel B = The vertical distance from the nipple to the inframammary fold on the lateral view (LNIMF) measurement, Panel C = Breast size measurements, Panel D = Inferior breast radius (IR) (from the nipple to the midpoint of the inframammary fold), medial breast radius (MR) (medial radius from the nipple), lateral breast radius (LR) (lateral radius from the nipple), from the nipple to the clavicle notch (CN) and nipple to the sternal notch (SNN) measurements.

Table 1
Inter-rater correlations between nurse measurements.

Breast Marker	Inter-rater Correlation
Nipple to Clavicle Notch (CN) Right	$r = 0.96, p = .001$
Nipple to Clavicle Notch (CN) Left	$r = 0.88, p = .010$
Nipple to Sternal Notch (SNN) Right	$r = 0.97, p = .001$
Nipple to Sternal Notch (SNN) Left	$r = 0.94, p = .003$
Nipple to Infra Mammary Fold (LNIMF) Right	$r = 0.59, p = .110$
Nipple to Infra Mammary Fold (LNIMF) Left	$r = 0.64, p = .085$
Inferior Breast Radius (IR) Right	$r = 0.98, p < .001$
Inferior Breast Radius (IR) Left	$r = 0.99, p < .001$
Medial Breast Radius (MR) Right	$r = 0.98, p < .001$
Medial Breast Radius (MR) Left	$r = 0.97, p = .001$
Lateral Breast Radius (LR) Right	$r = 0.97, p < .001$
Lateral Breast Radius (LR) Left	$r = 0.99, p < .001$
Mammillary Projection (MP) Right	$r = 0.89, p = .008$
Mammillary Projection (MP) Left	$r = 0.87, p = .013$

Note: Pearson correlations, 1-tailed.

Jasienska et al., 2004). For breast volume (markers which also served as unique symmetry markers), the following four measurements were taken for each breast: (1) inferior breast radius (IR) (from the nipple to the midpoint of the infra mammary fold radius), (2) medial breast radius (MR) (medial radius from the nipple), (3) lateral breast radius (LR) (lateral radius from the nipple) and (4) mammillary projection (MP) (breast projection). Breast volume was calculated by inserting the measured IR, MR, LR, and MP values for each participant: breast volume (in cubic centimetres) $= \pi/3 \times MP^2 \times (MR + LR + IR - MP)$ (Kayar et al., 2011; Qiao, Zhou, & Ling, 1997). These measures were used as individual markers of breast asymmetry in conjunction with the following: (1) the vertical distance from the nipple to the infra mammary fold on the lateral view for each breast (LNIMF), (2) from each nipple to the clavicle notch (CN), and (3) from each nipple the sternal notch (SNN) (Huang et al., 2017). Measurements are depicted in Fig. 1. Six participants agreed to have the measurement procedure completed successively by both healthcare practitioners, (counterbalanced), in order to assess inter-rater reliability between them. Neither had access to the other individuals' measurements. Rater measurements of the left and right breast markers (CN, SNN, IR, MR, LR, MP) were all highly positively correlated, except for LNIMF (See Table 1). We expect this is because LNIMF measurements were most difficult as they required the use of two rulers at the same time. In order to obtain this measurement, one ruler measured the horizontal distance and the other measured the vertical distance from the nipple to the infra mammary fold on the lateral view for each breast. Based on this information, the total asymmetry variable combined the difference scores between the left and right breast measurements (valences removed) for each individual measurement except for LNIMF, by summing the scores to create a total asymmetry (in centimetres) score. We then log transformed this variable because it was not normally distributed.

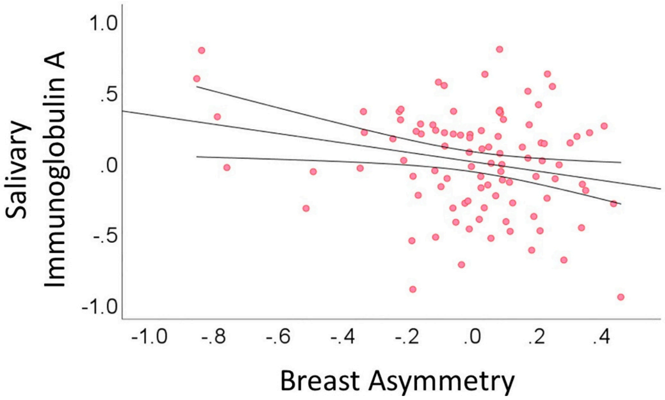

Fig. 2. Partial regression plot with confidence intervals for the relationship between breast asymmetry and salivary immunoglobulin-A (sIgA).

3. Results

Outliers were winsorized for breast volume, BMI, measured size, and measured asymmetry. For all variables, fewer than 10% of the cases were winsorized.[1] First, we ran zero-order correlations (two-tailed) between predictors. Breast asymmetry was positively correlated with BMI ($r = 0.22, p = .03$), breast size ($r = 0.24, p = .02$), and breast volume ($r = 0.32$, $p = .001$). Then, a multiple regression was conducted to predict sIgA from breast asymmetry, BMI, breast size, and breast volume. There was linearity as assessed by partial regression plots and a plot of studentized residuals against the predicted values. There was independence of residuals, as assessed by a Durbin-Watson statistic of 1.85. There was homoscedasticity, as assessed by visual inspection of a plot of studentized residuals versus unstandardized predicted values. There was no evidence of multicollinearity, as assessed by tolerance values greater than 0.1. There were no studentized deleted residuals greater than ±3 standard deviations, and no values for Cook's distance above 1. There

---

[1] Using raw (not winsorized) values does not meaningfully change any of the relationships reported herein.

Table 2
Multiple regression results for sIgA.

sIgA	*B*	95% CI for *B*		*SE B*	β	R^2	Adj. R^2	Sig.
		LL	*UL*					
Model						0.072	0.032	0.138
Constant	−0.369	−0.829	0.091	0.232				0.115
Breast Asymmetry	−0.330	−0.613	−0.047	0.142	−0.248			0.023
BMI	0.009	−0.008	0.025	0.007	0.123			0.298
Breast Size	−0.008	−0.031	0.014	0.011	−0.081			0.473
Breast Volume	0.000028	0.000	0.000	0.000	0.078			0.538

was one case with a leverage value greater than 0.2, but when this case was removed from the analysis, it did not significantly change the model. The assumption of normality was met, as assessed by a visual inspection of a histogram and P-P Plot.

R^2 for the overall model was 7% with an adjusted R^2 of 3%, a small size effect according to Cohen (1988). The multiple regression model did not overall statistically significantly predict sIgA levels, $F(4,92) = 1.79$, $p = .14$. Breast asymmetry statistically significantly predicted sIgA levels, $p = .023$, showing that women with more asymmetrical breasts were lower in sIgA than women with more symmetrical breasts, supporting Hypothesis 1 (Fig. 2). Regression coefficients and standard errors can be found in Table 2. Conversely, there was no relationship for measured breast size, BMI, or volume with sIgA. These findings suggest that breast asymmetry predicts lower sIgA levels in women regardless of breast size, and that it is symmetrical women on the whole, rather than women with symmetrical and large breasts who are highest in one marker of immunocompetence.

4. Discussion

To date, most research on human breast morphology has focused on size and its putative links to fecundity. In contrast, little research has examined the potential role of breast symmetry as a cue to developmental stability. Much extant work linking fluctuating asymmetry to immunocompetence has focussed on relatively innocuous traits instead of overt secondary sexual characteristics that (1) draw more attention from the opposite sex, and (2) more strongly influence attractiveness. Previous research has shown that breast symmetry is an important evaluation criterion used by men to gauge female attractiveness and health (Duncan, 2010; Singh, 1995). Identifying healthy mating partners is an important adaptive challenge with implications for reproductive fitness (see Arnocky, Pearson, & Vaillancourt, 2015). The fact that men appear to use breast symmetry to make judgements about underlying female immunocompetence could be predicated upon breast tissue acting as an honest signal of that quality. In this study, we tested whether breast morphology might serve as a cue to one marker of immunocompetence, sIgA.

Results demonstrated that measured breast asymmetry predicted sIgA, regardless of BMI, breast size and volume, none of which in turn related to sIgA. This finding suggests that it is breast symmetry, not size, that matters for predicting one marker of immunocompetence in women. In other species, there is evidence that FA is negatively associated with measures of immunocompetence (e.g., Hammouda et al., 2012). More specifically, our finding aligns with previous research linking fluctuating asymmetry of sexual ornaments to worse immune function (Lagesen & Folstad, 1998). Although to date little research has examined corresponding asymmetry of sexual ornaments in human females, our finding does also align with those linking fluctuating asymmetry of non-sexual ornaments with both a high BMI and poor health outcomes in young adult women (e.g., Milne et al., 2003). Further, our findings align with research that both body asymmetry and more specifically, breast asymmetry, and body weight are positively correlated (Manning, 1995; Manning et al., 1997).

Previous research has shown strong positive relationships between breast size and breast asymmetry across various cultures including New Mexico, Spain, and England (Manning et al., 1997; Møller et al., 1995). The results from the current research supports these findings. Interestingly, we did not find a significant relationship for breast size or volume with sIgA. Recent research has highlighted that cross-culturally, other morphological characteristics of the breast, such as firmness, are more consistently rated as attractive compared to size (Havlíček et al., 2017). Perhaps these characteristics (i.e., symmetry and firmness) are more robustly rated as attractive because they might serve as a more reliable cue to underlying female quality. Recently, a device called a breast durometer, which measures tissue firmness, has been considered as a tool for measuring breast firmness with potential applications for cosmetic surgery (Brown, Brown, & Murphy, 2017). Using this device, future research could consider whether firmer breasts are (1) also more symmetrical, and (2) correlate independently with female immunocompetence and/or with youth and nulliparity (e.g., Marlowe, 1998). Considering the inconsistent findings from previous studies exploring individual differences in breast size as a marker of fertility, and the null findings of this study regarding breast size and in relation to a marker of immunocompetence, it is evident that more work is required to better understand the evolution of the female breast as one of our species' most pronounced secondary sex characteristics.

This research was limited in the following ways. The restricted demographic characteristics of our samples (e.g., age, ethnicity) may have narrowed the natural variability in measured size that exists in the broader population. Thus, it is possible that the measured breast size variable was unable to detect an effect. Future research should reexamine potential links between measured breast size and immunocompetence using a larger sample size. Further, like much of the research in evolutionary psychology, participants were drawn from a relatively healthy, "WEIRD" (Western, educated, industrialized, rich and democratic) population (Henrich, Heine, & Norenzayan, 2010). Young adults are generally healthier which may restrict variance within the sample relative to the broader population. However, using a greater age range presents the difficulty that the natural breasts have been affected due to pregnancy and breast-feeding. It would also convolute any findings with potentially correlated variables that the breast could signal, such as youth or fertility. Additionally, levels of breast asymmetry in cultures more subject to severe nutritional stress and in more traditional societies might be considerably different than in current industrial societies. Thus, future research should aim to replicate these results in more traditional societies.

It is important to consider that biological immunity cannot be determined from the measurement of one single index (sIgA). The use of a single biomarker does not present a full picture of overall immune function, since immunity is often considered a composite trait made up of many subcomponents. Despite sIgA's validity as a known biomarker relevant to infections, particularly those of the respiratory tract (Drummond & Hewson-Bower, 1997; Fahlman & Engels, 2005; Nakamura et al., 2006; Volkmann & Weekes, 2006), as well as mortality from cancer and respiratory illness (Phillips et al., 2015), future research should extend to more diverse indices of immunocompetence. Similarly, composite indices of FA may better characterise an individual's developmental stability and genetic quality, rather than relying on the FA of a single trait. Future research could extend the current findings by looking at additional markers of biological and self-report health, and also by adding FA of the breast into more composite measures of body FA. To the extent that fluctuating asymmetry matters for mate choice, it seems logical that traits most strongly linked to organism quality might be those that bear most heavily upon mate choice. As Møller and Pomiankowski (1993) noted, fluctuating asymmetry in secondary sexual characteristics should be better indicators of underlying quality.

To date, breast asymmetry has been linked to some health problems including cancer (Kayar & Çilengiroğlu, 2015; Scutt et al., 1997), and women with more symmetrical breasts are more fecund (Møller et al., 1995), suggesting that breast symmetry may act as a valid cue to health. Yet, very little research has investigated relationships between breast symmetry and direct markers of immunocompetence. The present study addressed this important gap in knowledge showing preliminary evidence supporting a link between breast asymmetry and lower sIgA levels. Further research using larger and more diverse samples along with more diverse biological markers of immunocompetence is necessary before making firm conclusions about the link between breast morphology and immunocompetence.

References

Adams, M. S., & Niswander, J. D. (1967). Developmental "Noise" and a congenital malformation. *Genetics Research, 10*(3), 313–317.

Arieli, R. (2004). Breasts, buttocks, and the camel hump. *Israel Journal of Ecology and Evolution, 50*(1), 87–91.

Arnocky, S., Hodges-Simeon, C. R., Ouellette, D., & Albert, G. (2018). Do men with more masculine voices have better immunocompetence? *Evolution and Human Behavior, 39* (6), 602–610. https://doi.org/10.1016/j.evolhumbehav.2018.06.003.

Arnocky, S., Pearson, M., & Vaillancourt, T. (2015). Health, anticipated partner infidelity, and jealousy in men and women. *Evolutionary Psychology, 13*(3), 1–10. https://doi.org/10.1177/1474704915593666.

Bellussi, L., Cambi, J., & Passali, D. (2013). Functional maturation of nasal mucosa: Role of secretory immunoglobulin A (sIgA). *Multidisciplinary Respiratory Medicine, 8*(46), 1–3. https://doi.org/10.1186/2049-6958-8-46.

Brown, N., White, J., Milligan, A., Risius, D., Ayres, B., Hedger, W., & Scurr, J. (2012). The relationship between breast size and anthropometric characteristics. *American Journal of Human Biology, 24*(2), 158–164.

Brown, T., Brown, S., & Murphy, T. (2017). Breast durometer (mammometer): A novel device for measuring soft-tissue firmness and its application in cosmetic breast surgery. *Aesthetic Plastic Surgery, 41*(2), 265–274. https://doi.org/10.1007/s00266-017-0783-5.

Cant, J. G. H. (1981). Hypothesis for the evolution of human breasts and buttocks. *American Naturalist, 117*, 199–204. https://doi.org/10.1086/283699.

Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed.). New York: Psychology Press.

Dixson, B. J., Grimshaw, G. M., Linklater, W. L., & Dixson, A. F. (2011a). Eye tracking of men's preferences for female breast size and areola pigmentation. *Archives of Sexual Behavior, 40*(1), 51–58.

Dixson, B. J., Grimshaw, G. M., Linklater, W. L., & Dixson, A. F. (2011b). Eye-tracking of men's preferences for waist-to-hip ratio and breast size of women. *Archives of Sexual Behavior, 40*, 43–50. https://doi.org/10.1007/s10508-009-9523-5.

Dixson, B. J., Vasey, P. L., Sagata, K., Sibanda, N., Linklater, W. L., & Dixson, A. F. (2011). Men's preferences for women's breast morphology in New Zealand, Samoa, and Papua New Guinea. *Archives of Sexual Behavior, 40*, 1271–1279. https://doi.org/10.1007/s10508-010-9680-6.

Drummond, P., & Hewson-Bower, B. (1997). Increased psychosocial stress and decreased mucosal immunity in children with recurrent upper respiratory tract infections. *Journal of Psychosomatic Research, 43*(3), 271–278. https://doi.org/10.1016/S0022-3999(97)00002-0.

Duncan, M. (2010). *Sexual Selection and Human Breast Morphology. (Master's Thesis)*.

Eliasson, L., Österberg, B. D., & Carlén, A. (2006). Minor salivary gland secretion rates and immunoglobulin a in adults and the elderly. *European Journal of Oral Sciences, 114*(6), 494–499. https://doi.org/10.1111/j.1600-0722.2006.00413.x.

Fahlman, M. M., & Engels, H. J. (2005). Mucosal IgA and URTI in American college football players: A year longitudinal study. *Medicine and Science in Sports and Exercise, 37*, 374–380. https://doi.org/10.1249/01.MSS.0000155432.67020.88.

Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods, 41*, 1149–1160.

Fink, B., Neave, N., Manning, J. T., & Grammer, K. (2006). Facial symmetry and judgements of attractiveness, health and personality. *Personality and Individual Differences, 41*(3), 491–499. https://doi.org/10.1016/j.paid.2006.01.017.

Folstad, I., & Karter, A. J. (1992). Parasites, bright males, and the immunocompetence handicap. *American Naturalist, 139*(3), 603–622. https://doi.org/10.2307/2462500.

Foo, Y. Z., Nakagawa, S., Rhodes, G., & Simmons, L. W. (2017). The effects of sex hormones on immune function: A meta-analysis. *Biological Reviews, 92*, 551–571. https://doi.org/10.1111/brv.12243.

Ford, C. S., & Beach, F. A. (1951). *Patterns of sexual behavior* (Harper).

Gallup, G. G. (1982). Permanent breast enlargement in human females: A sociobiological analysis. *Journal of Human Evolution, 11*(7), 597–601.

Gangestad, S. W., & Thornhill, R. (1997). Human sexual selection and developmental stability. *Evolutionary Social Psychology*, 169–195.

Gangestad, S. W., Thornhill, R., & Yeo, R. A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology, 15*(2), 73–85.

Garver-Apgar, C. E., Eaton, M. A., Tybur, J. M., & Emery Thompson, M. (2011). Evidence of intralocus sexual conflict: Physically and hormonally masculine individuals have more attractive brothers relative to sisters. *Evolution and Human Behavior, 32*, 423–432. https://doi.org/10.1016/j.evolhumbehav.2011.03.005.

Getty, T. (2006). Sexually selected signals are not similar to sports handicaps. *Trends in Ecology & Evolution, 21*(2), 83–88. https://doi.org/10.1016/j.tree.2005.10.016.

Grammer, K., Fink, B., Møller, A. P., & Thornhill, R. (2003). Darwinian aesthetics: Sexual selection and the biology of beauty. *Biological Reviews, 78*(3), 385–407.

Grammer, K., & Thornhill, R. (1994). Human facial attractiveness and sexual selection: The role of symmetry and averageness. *Journal of Comparative Psychology, 108*(3), 233–242.

Grillot, R. L., Simmons, Z. L., Lukaszewski, A. W., & Roney, J. R. (2014). Hormonal and morphological predictors of women's body attractiveness. *Evolution and Human Behavior, 35*, 176–183. https://doi.org/10.1016/j.evolhumbehav.2014.01.001.

Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science, 218*(4570), 384–387. https://doi.org/10.1126/science.7123238.

Hammouda, A., Selmi, S., Pearce-Duvet, J., Chokri, M. A., Arnal, A., Gauthier-Clerc, M., & Boulinier, T. (2012). Maternal antibody transmission in relation to mother fluctuating asymmetry in a long-lived colonial seabird: The yellow-legged gull Larus michahellis. *PLoS One, 7*(5). https://doi.org/10.1371/journal.pone.0034966.

Havlíček, J., Třebický, V., Varella Valentova, J., Kleisner, K., MbeAkoko, R., Fialová, J., … Roberts, S. C. (2017). Men's preferences for women's breast size and shape in four cultures. *Evolution and Human Behavior, 38*(2), 217–236. https://doi.org/10.1016/j.evolhumbehav.2016.10.002Get.

Henrich, J., Heine, S. J., & Norenzayan, A. (2010). The weirdest people in the world? *Behavioral and Brain Sciences, 33*, 61–135. https://doi.org/10.1017/S0140525X0999152X.

Hodges-Simeon, C. R., Asif, S., Gurven, M., Blackwell, A. D., & Gaulin, S. J. (2019). Testosterone is positively and estradiol negatively associated with mucosal immunity in Amazonian adolescents. *American Journal of Human Biology, 31*(5). https://doi.org/10.1002/ajhb.23284.

Hodges-Simeon, C. R., Grail, G. P. O., Albert, G., Landry, N., Ortiz, T. L., Carre, J. M., … Arnocky, S. A. (2020). Testosterone, cortisol, and secretory immunoglobulin-A within a single day and across two sequential days among trans- and cis-gender men. *Steroids, 160*, 1–9. https://doi.org/10.1016/j.steroids.2020.108640.

Huang, N. S., Quan, C. L., Mo, M., Chen, J. J., Yang, B. L., Huang, X. Y., & Wu, J. (2017). A prospective study of breast anthropomorphic measurements, volume and ptosis in 605 Asian patients with breast cancer or benign breast disease. *PLoS One, 12*(2), 1–10. https://doi.org/10.1371/journal.pone.0172122.

Huss-Ashmore, R. (1980). Fat and fertility: Demographic implications of differential fat storage. *American Journal of Physical Anthropology, 23*(S1), 65–91. https://doi.org/10.1002/ajpa.1330230506.

Jasienska, G., Lipson, S. F., Ellison, P. T., Thune, I., & Ziomkiewicz, A. (2006). Symmetrical women have higher potential fertility. *Evolution and Human Behaviour, 27*, 390–400. https://doi.org/10.1016/j.evolhumbehav.2006.01.001.

Jasienska, G., Ziomkiewicz, A., Ellison, P. T., Lipson, S. F., & Thune, I. (2004). Large breasts and narrow waists indicate high reproductive potential in women. *Proceedings of the Royal Society of London Series B, 271*, 1213–1217. https://doi.org/10.1098/rspb.2004.2712.

Jennions, M. D., Møller, A. P., & Petrie, M. (2001). Sexually selected traits and adult survival: A meta-analysis. *The Quarterly Review of Biology, 76*(1), 3–36. https://doi.org/10.1086/393743.

Kayar, R., & Çilengiroğlu, Ö. V. (2015). Breast volume asymmetry value, ratio, and cancer risk. *Breast Cancer: Basic and Clinical Research, 9*, 87–92. https://doi.org/10.4137/BCBCR.S32789.

Kayar, R., Civelek, S., Cobanoglu, M., Gungor, O., Catal, H., & Emiroglu, M. (2011). Five methods of breast volume measurement: A comparative study of measurements of specimen volume in 30 mastectomy cases. *Breast Cancer: Basic and Clinical Research, 5*, 43–52. https://doi.org/10.4137/BCBCR.S6128.

Klein, S. L. (2004). Hormonal and immunological mechanisms mediating sex differences in parasite infection. *Parasite Immunology, 26*, 247–264.

Kościński, K., Makarewicz, R., & Bartoszewicz, Z. (2020). Stereotypical and actual associations of breast size with mating-relevant traits. *Archives of Sexual Behaviour, 49*, 821–836. https://doi.org/10.1007/s1050 8-019-1464-z.

Lagesen, K., & Folstad, I. (1998). Antler asymmetry and immunity in reindeer. *Behavioral Ecology and Sociobiology, 44*(2), 135–142.

Lipson, S. F., & Ellison, P. T. (1996). Comparison of salivary steroid profiles in naturally occurring conception and non-conception cycles. *Human Reproduction, 11*(10), 2090–2096.

Manning, J. T. (1995). Fluctuating asymmetry and body weight in men and women: Implications for sexual selection. *Ethology and Sociobiology, 16*, 145–153.

Manning, J. T., Scutt, D., Whitehouse, G. H., & Leinster, S. J. (1997). Breast asymmetry and phenotypic quality in women. *Evolution and Human Behavior, 18*, 223–236.

Marcotte, H., & Lavoie, M. C. (1998). Oral microbial ecology and the role of salivary immunoglobulin a. *Microbiology and Molecular Biology Reviews, 62*(1), 71–109. https://doi.org/10.1128/MMBR.62.1.71-109.1998.

Marlowe, F. W. (1998). The nubility hypothesis: The human breast as an honest signal of residual reproductive value. *Human Nature, 9*(3), 263–271.

Maynard Smith, J., & Harper, D. G. C. (1995). Animal signals: Models and terminology. *Journal of Theoretical Biology, 177*(3), 305–311. https://doi.org/10.1006/jtbi.1995.0248.

McDade, T. W. (2003). Life history theory and the immune system: Steps toward a human ecological immunology. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists, 122*(S37), 100–125.

Milne, B. J., Belsky, J., Poulton, R., Thomson, W. M., Caspi, A., & Kieser, J. (2003). Fluctuating asymmetry and physical health among young adults. *Evolution and Human Behavior, 24*(1), 53–63. https://doi.org/10.1016/S1090-5138(02)00120-4.

Møller, A. P. (1990). Fluctuating asymmetry in male sexual ornaments may reveal male quality. *Animal Behaviour, 40*, 1185–1187. https://doi.org/10.1016/S0003-3472(05)80187-3.

Møller, A. P. (1993). Developmental stability, sexual selection and speciation. *Journal of Evolutionary Biology, 6*, 493–509.

Møller, A. P. (1994). Sexual selection in the barn swallow (Hirundo rustica). IV. Patterns of Fluctuating asymmetry and selection against asymmetry. *Evolution, 48*(3), 658–670.

Møller, A. P., & Pomiankowski, A. (1993). Fluctuating asymmetry and sexual selection. *Genetica, 89*, 267–279.

Møller, A. P., Soler, M., & Thornhill, R. (1995). Breast asymmetry, sexual selection, and human reproductive success. *Ethology and Sociobiology, 16*, 207–219.

Morris, D. (1967). *The naked ape: A zoologist's study of the human animal*. Vintage Books.

Nakamura, D., Akimoto, T., Suzuki, S., & Kono, I. (2006). Daily changes of salivary secretory immunoglobulin a and appearance of upper respiratory symptoms during physical training. *Journal of Sports Medicine and Physical Fitness, 46*(1), 152–157.

Palmer, R. A., & Strobeck, C. (1986). Fluctuating asymmetry: Measurement, analysis, patterns. *Annual Review of Ecological Systems, 17*, 391–421.

Parsons, P. A. (1990). Fluctuating asymmetry: An epigenetic measure of stress. *Biological Reviews of the Cambridge Philosophical Society, 65*(2), 131–145.

Pawlowski, B., Borkowska, B., Nowak, J., Augustyniak, D., & Drulis-Kawa, Z. (2018). Human body symmetry and immune efficacy in healthy adults. *American Journal of Physical Anthropology, 167*(2), 207–216. https://doi.org/10.1002/ajpa.23617.

Phillips, A. C., Carroll, D., Drayson, M. T., & Der, G. (2015). Salivary immunoglobulin a secretion rate is negatively associated with cancer mortality: The west of Scotland twenty-07 study. *PLoS One, 10*(12), 1–11. https://doi.org/10.1371/journal.pone.0145083.

Pomiankowski, A., & Møller, A. P. (1995). A resolution of the lek paradox. *Proceedings of the Royal Society of London Series B, 260*, 21–29.

Prokop, P., Dylewski, L., Woźna, J. T., & Tryjanowski, P. (2020). Cues of woman's fertility predict prices for sex with prostitutes. *Current Psychology, 39*(3), 919–936. https://doi.org/10.1007/s12144-018-9807-9.

Qiao, Q., Zhou, G., & Ling, Y. (1997). Breast volume measurement in young Chinese women and clinical applications. *Aesthetic Plastic Surgery, 21*, 362–368.

Rantala, M. J., Moore, F. R., Skrinda, I., Krama, T., Kivleniece, I., Kecko, S., & Krams, I. (2012). Evidence for the stress-linked immunocompetence handicap hypothesis in humans. *Nature Communications, 3*, 694. https://doi.org/10.1038/ncomms1696.

Ray, J. G., Mohllajee, A. P., van Dam, R. M., & Michels, K. B. (2008). Breast size and risk of type 2 diabetes mellitus. *Canadian Medical Association Journal, 178*(3), 289–295. https://doi.org/10.1503/cmaj.071086.

Rhodes, G., Simmons, L. W., & Peters, M. (2005). Attractiveness and sexual behavior: Does attractiveness enhance mating success? *Evolution and Human Behavior, 26*(2), 186–201. https://doi.org/10.1016/j.evolhumbehav.2004.08.014.

Rhodes, G., Zebrowitz, L. A., Clark, A., Kalick, S. M., Hightower, A., & McKay, R. (2001). Do facial averageness and symmetry signal health? *Evolution and Human Behavior, 22*(1), 31–46.

Roved, J., Westerdahl, H., & Hasselquist, D. (2017). Sex differences in immune responses: Hormonal effects, antagonistic selection, and evolutionary consequences. *Hormones and Behavior, 88*, 95–105. https://doi.org/10.1016/j.yhbeh.2016.11.017.

Scheib, J. E., Gangestad, S. W., & Thornhill, R. (1999). Facial attractiveness, symmetry and cues of good genes. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 266*(1431), 1913–1917. https://doi.org/10.1098/rspb.1999.0866.

Scutt, D., Manning, J. T., Whitehouse, G. H., Leinster, S. J., & Massey, C. P. (1997). The relationship between breast asymmetry, breast size and the occurrence of breast cancer. *British Journal of Radiology, 70*(838), 1017–1021. https://doi.org/10.1259/bjr.70.838.9404205.

Shackelford, T. K., & Larsen, R. J. (1997). Facial asymmetry as an indicator of psychological, emotional, and physiological distress. *Journal of Personality and Social Psychology, 72*(2), 456–466.

Short, R. V. (1976). The evolution of human reproduction. *Proceedings of the Royal Society of London Series B, 195*, 3–24.

Singh, D. (1995). Female health, attractiveness, and desirability for relationships: Role of breast asymmetry and waist-to-hip ratio. *Ethology and Sociobiology, 16*, 465–481.

Starzak, D. E., Konkol, K. F., & McKune, A. J. (2016). Effects of cardiorespiratory fitness and obesity on salivary secretory IgA and alpha-amylase in south African Children. *Children (Basel, Switzerland), 3*(3), 12. https://doi.org/10.3390/children3030012.

Steinberger, E., Smith, K. D., Tcholakian, R. K., & Rodriguez-Rigau, L. J. (1979). Testosterone levels in female partners of infertile couples: Relationship between androgen levels in the woman, the male factor, and the incidence of pregnancy. *American Journal of Obstetrics and Gynecology, 133*, 133–138.

Thornhill, R. (1992). Fluctuating asymmetry and the mating system of the Japanese scorpionfly, Panorpa japonica. *Animal Behaviour, 44*(5), 867–879.

Thornhill, R., & Gangestad, S. W. (1994). Human fluctuating asymmetry and sexual behavior. *Psychological Science, 5*(5), 297–302.

Thornhill, R., & Gangestad, S. W. (2006). Facial sexual dimorphism, developmental stability and susceptibility to disease in men and women. *Evolution and Human Behavior, 27*(2), 131–144. https://doi.org/10.1016/j.evolhumbehav.2005.06.001.

Thornhill, R., & Møller, A. P. (1998). The relative importance of size and asymmetry in sexual selection. *Behavioral Ecology, 9*(6), 546–551.

Van Anders, S. M. (2010). Gonadal steroids and salivary IgA in healthy young women and men. *American Journal of Human Biology, 22*, 348–352. https://doi.org/10.1002/ajhb.20997.

Van Dongen, S., & Gangestad, S. W. (2011). Human fluctuating asymmetry in relation to health and quality: A meta-analysis. *Evolution and Human Behavior, 32*(6), 380–398. https://doi.org/10.1016/j.evolhumbehav.2011.03.002.

Volkmann, E. R., & Weekes, N. Y. (2006). Basal SIgA and cortisol levels predict stress related health outcomes. *Stress and Health, 22*(1), 11–23. https://doi.org/10.1002/smi.1077.

Watson, P. J., & Thornhill, R. (1994). Fluctuating asymmetry and sexual selection. *Trends in Ecology & Evolution, 9*, 21–25.

Waynforth, D. (1998). Fluctuating asymmetry and human male life-history traits in rural Belize. *Proceedings of the Royal Society of London. Series B, 265*, 1497–1501.

Weaver, R. J., Koch, R. E., & Hill, G. E. (2017). What maintains signal honesty in animal colour displays used in mate choice? *Philosophical Transactions of the Royal Society, B: Biological Sciences, 372*, 20160343. https://doi.org/10.1098/rstb.2016.0343.

Zahavi, A. (1975). Mate selection—A selection for handicap. *Journal of Theoretical Biology, 53*, 205–214.

Zahavi, A., & Zahavi, A. (1997). *The handicap principle: A missing piece of Darwin's puzzle*. New York, NY: Oxford University Press.