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# Fluctuating asymmetry, facial masculinity, and offspring sex ratio
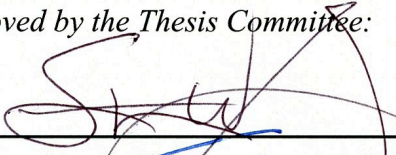
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**FLUCTUATING ASYMMETRY, FACIAL MASCULINITY,**
**AND**
**OFFSPRING SEX RATIO**


**BY**


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THESIS

Submitted in Partial Fulfillment of the
Requirements for the Degree of

**Master of Science**
**Psychology**

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Albuquerque, New Mexico

**August, 2010**

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**Melissa A. Heap**

**B.S., Psychology, Arizona State University, 2004**
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## ABSTRACT

Research on offspring sex ratios and parental condition indicate that parents in better condition may benefit from biasing their offspring toward sons. While measures of phenotypic quality and offspring sex ratio have been examined in other animals, the current study was designed to look at this relationship within human families. I investigated the relationship between fluctuating asymmetry and facial masculinity, both possible measures of phenotype, and offspring sex ratio within families. The results were mixed. The fluctuating asymmetry of one sibling covaried negatively with the overall offspring sex ratio within their family. The significant negative correlation between the two provides partial support for adaptive biasing in offspring sex ratio. However, no relationship was detected between male facial masculinity, female facial masculinity, and sex ratio within families.

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## Introduction

Differences in individual reproductive success may be due to differences in individual quality or condition and the underlying levels of associated traits. As individuals vary in their condition, it is expected that an individual's "optima" for offspring sex ratio may vary as well.  Essentially, whenever offspring of one sex will have greater opportunity for reproductive success, an advantage may be had by those parents able to bias their offspring ratio in response to the relative fitness of their possible offspring.  Parental ability to bias their offspring sex ratio toward one sex or another is dependent on the assumption that parental condition will differentially impact the offspring's reproductive success.   The offspring sex toward which parents bias their reproduction should have greater reproductive success than the other sex, due to their parents' condition.  In other words, the sex toward which parents bias their offspring should yield more grandchildren than offspring of the opposite sex.  Preliminary evidence corroborates this.  Male billionaires produce more sons than daughters and in turn their sons beget more grandchildren than do their daughters (Cameron & Dalerum, 2009).

Several theories attempt to predict adaptive offspring sex ratios based on parental condition.  First, the Trivers-Willard hypothesis (TWH) predicts that in polygynous species, parents in good condition will benefit by biasing their offspring toward the sex with the highest reproductive variance, while parents in poor conditions will benefit by biasing their offspring toward the sex with the lowest reproductive variance (Trivers & Willard, 1973).  Secondly, while general condition may promote adaptive bias of offspring sex ratio, the specific traits parents can offer male and female offspring may be

just as important in influencing offspring fitness as the general condition of the parent. Different selection pressures for males and females may result in sexually dimorphic traits, traits with separate sex-specific optimal levels. Such traits are often related to one's attractiveness to the opposite sex, thereby impacting reproductive success. Thus if heritable, parents' individual levels of sexually dimorphic traits may differentially influence their male and female offspring's levels of similar traits, impacting their attractiveness as mates. Consequently, parents may adaptively bias the sex ratio of their offspring based on their levels of sexually dimorphic traits to maximize reproductive success.

**Trivers-Willard Hypothesis**

TWH predicts that when one sex has more variable reproductive success than the other, natural selection should favor parents that are able to manipulate their offspring sex ratio toward the sex that will maximize their own fitness (Trivers & Willard, 1973). In many mammals, males typically have higher variance in reproductive success than females. Males in good condition have the most offspring, thus the highest reproductive success. Increased size and/or attractiveness to females lead to better competitive ability, increased opportunity for mating, and the possibility for multiple mates at one time. Males in poor condition, on the other hand, face the possibility of zero mating opportunities and the consequent lack of any reproductive success. Due to constraints on the number of offspring a female can produce, high quality female mammals in many species cannot produce the large number of offspring that a male counterpart could produce. At the same time, most females have some mating opportunity, making the likelihood of zero reproductive success much lower for females in poor condition. Thus,

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females in good condition may not produce as many offspring as males in good condition. Yet females in poor condition may out produce males in poor condition.

Male offspring in good condition are expected to have higher reproductive success than their female counterparts, thus in most cases TWH leads to the prediction that parents in good condition will bias their offspring sex ratio toward males to maximize their own reproductive success. Female offspring in poor condition have higher reproductive success than males in poor condition.  As a result, in most cases parents in poor condition may benefit by biasing their offspring sex ratio toward female offspring.   Since Trivers & Willard made their proposal, hundreds of researchers have tested this hypothesis on nutritional/material condition and extended it to included indicators of genetic condition. Reviews of this research have suggested that it is parental, mainly maternal, condition at time of conception that has the most robust influence on offspring sex ratio (Cameron, 2004).

**Quality Indicators in Animals**

Traits related to quality in animals show support for the TWH demonstrating that high quality parents tend to have more sons.  Mothers displaying traits related to high quality have more sons.  Female Weddell seals, with higher lifetime reproductive success, birth more male offspring (Proffitt, Garrott, & Rotella, 2008).  Dominant female red deer have a high sex ratio of offspring (Clutton-Brock, Albon, & Guiness, 1984).   Mothers with higher quality mates also have more sons.  In house wrens, the offspring sex ratio of birds fathered by extra-pair mates is higher than the offspring sex ratio of within-pair mates. Purportedly, males given the opportunity for extra-pair copulations have higher fitness than other males (Johnson, Thompson, Sakaluk, Neuhauser, Johnson, Soukup, Forsythe,

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& Masters, 2009).  Furthermore, female guppies with attractive mates produce more sons than those with unattractive mates, particularly when the chosen mate is strongly preferred (Karino & Sato, 2009).

As TWH predicts that parents will bias offspring in the direction of the sex with highest potential for reproductive success, sometimes high quality parents have more daughters. Female springboks in good condition bias their offspring toward daughters.  It is suspected that this maximizes grandchildren, as daughters (6 months) can reproduce earlier than sons (2 years) (Kruger, Radford, Anderson, & Liversidge, 2005). In some cases high status women may be able to manipulate the success of their daughters more than their sons.  Indeed, female billionaires produce more daughters than sons, contrary to male billionaires (Cameron & Dalerum, 2009).

Researchers have also experimented with markers of quality in animals and find that parents appear to bias offspring sex ratio in the direction of the experimentally enhanced "higher quality" parent.  Burley (1981) manipulated zebra finches attractiveness by putting colored bands on males and females legs.  These bands had previously been shown to be highly preferred or un-preferred by the opposite sex birds.  Male birds with attractive band colors had more male offspring.  And female birds with attractive band colors had more daughters.  Manipulations of quality may actually be picking up on parental assessment of change in condition, rather than current condition.  Reduction of UV reflectance in crown feathers of blue tits resulted in differing offspring sex ratio. Males that had previously been high in UV reflectance had fewer sons after UV reduction than did males that were previously low in UV reflectance (Delhey, Peters, Johnsen, & Kempenaers, 2007).  Such research is also supportive of the idea that maternal condition

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plays a larger role in biasing offspring sex ratio than paternal condition.  Female juncos with experimentally whitened tails produced more sons, while female juncos partnered with males with experimentally enhanced tails did not produce more sons than those partnered with unenhanced males (Ferree, 2007).

**Quality Indicators in Humans**

The literature suggests that, similar to non-human animal parents of higher quality, human parents in better social conditions also bias the sex ratio of their offspring toward sons.  Parents in better social conditions, higher status or wealthier, may have greater access to resources or may be higher quality themselves, allowing them to produce higher quality offspring. Thus, these parents may optimize reproductive success by biasing offspring toward sons. Males with high status, as determined by occupation, are more likely to have sons than low status males (Hopcroft, 2005).  Similarly, members of the executive branch and United States Presidents produce more sons than normally expected (Betzig & Weber, 1995).   Relatedly, economic status influences sex ratio.  As already noted, male billionaires produce more sons than other males (Cameron & Dalerum, 2009).

Maternal social conditions also appear to play a role in offspring sex ratio.  In humans, married women and those with higher education produce more sons than other women (Almond & Edlund, 2007). Low ranking wives (3rd wife or lower) in Rwandan polygynous societies produce fewer sons than both monogamous wives and 1st and 2nd wives.  These wives may receive fewer resources from their husband and incur more household stress than other wives.  Additionally, one may assume that given the opportunity, a lower ranked wife would have chosen to be the only or higher ranked wife of a different man (Pollet, Fawcett, Buunk, & Nettle, 2009).

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**"Good genes" quality indicators in humans**

As human parents bias offspring sex ratio in relation to non-genetic cues of condition or material benefits, it is expected that similar adaptive biases may be associated with direct measures of genetic quality. In humans, traits such as low fluctuating asymmetry (FA) (Moller & Swaddle, 1997; Gangestad, Thornhill, & Yeo, 1994) may be reflections of genetic quality. Thus, the relationship between adaptive bias of offspring sex ratio and the genetic quality of offspring could be examined using FA as a variable. Extending TWH to genetic markers of quality in humans, if parents in good genetic condition can bias their offspring sex ratio in response to the anticipated relative genetic fitness of their offspring, one would expect increased production of sons when offspring will inherit their parents "good genes" and have lower FA.

**Fluctuating Asymmetry**

FA is a measure of developmental instability, resulting from exposure to genetic and environmental factors that can cause perturbations during periods of growth/development. More specifically, FA refers to the aggregate measure of random deviations from bilateral symmetry that occurs due to "stress" caused by poor genes or a challenging environment. Thus, FA may be a measure of an individual's "good genes." The association between adaptive bias of offspring sex ratio and FA is based on the assumption that the trait is somewhat heritable. Developmental instability does appear to have a significant, moderate additive genetic component when assessed using aggregate measures of FA (Johnson, Gangestad, Segal, & Bouchard, 2008) and has been indicated as a measure of phenotype. Thus parents with lower FA may be able to pass on their higher genetic quality to offspring, and therefore may benefit by biasing their offspring toward sons, whereas parents with higher FA may adaptively bias toward daughters.

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This optimizes parents' reproductive success, as more symmetrical sons are more appealing to females (out competing less symmetrical males) and potentially out-reproduce symmetrical daughters.

**Fluctuating Asymmetry and Ecological Condition**

As FA may measure phenotype, environmental conditions, in addition to genes, are also expected influence it. Animal studies have yielded results showing environment components to FA. For example, temperature fluctuations (Bradley, 1980) and nutrition (Swaddle & Witter, 1994; Picton, Palmisciano, & Nelson, 1990) influence FA. Environmental conditions at time of conception may in part determine how much stress the gamete will experience during conception and early development. Thus, FA may possibly tap into both parental conditions relating to "good genes" inheritance and relating to environment/resource availability. To maximize the fitness of their offspring, parents in good environment conditions, as well as genetic condition, may bias their offspring toward sons, as the stress leading to FA will be lower. Research supports this, and in humans, sex ratio has been shown to vary as a function of ecological conditions. Warm ambient temperatures are associated with higher sex ratios at birth in populations (Helle, Helama, & Jokela, 2007; and Helle, Helama & Lertola, 2009) and nutritional status of the mother is also associated with the proportion of sons born (Navara & Nelson, 2009; Matthews, Johnson, & Neil, 2008). Relatedly, mothers experiencing psychological stress during conception and pregnancy are less likely to have sons (Obel, Henriksen, Secher, Eskenazi, & Hedegaard, 2007). Maternal body conditions relating to items such as food intake appear to be the most consistent and strongly supported influences on offspring sex ratio in the literature (Cameron, 2004).

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**Predictions**

While evidence for TWH suggests that parents may bias the sex ratio of their offspring based on potential phenotypic quality of their offspring, the previous research does not directly address this issue in humans. Previous research in humans used measures that assess parental ability to supply non-genetic material benefits to offspring, thereby only indirectly assessing phenotype. One purpose of this study is to examine whether physical measures of phenotype are related to skews in offspring sex ratio. It is unknown whether potential offspring phenotype may function to adaptively skew offspring sex ratios. In humans, one might expect that when there is potential for high quality male offspring (for example, when fluctuating asymmetry is low), it would be beneficial to the parents to have more male children. Conversely, if quality offspring were uncertain due to poor parental condition, female offspring fitness would be higher and one might expect to see more female offspring than male. It is expected that when parents are able to produce high quality offspring, as reflected by FA, they will bias their offspring sex ratio toward males. This leads to the first study prediction.

**Prediction 1.** According to TWH and general offspring sex ratio theory, offspring with lower fluctuating asymmetry will have more brothers than offspring with higher fluctuating asymmetry.

**Sexual Antagonism and Masculinity/Femininity**

In mammals different selection pressures on males and females have created discrete optimal levels of specific traits. For example, as size may be important in competition, taller than average human males may have higher reproductive success then shorter males. Conversely, the highest reproductive success for females occurs in those women whose

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height is just under average (Nettle, 2002a; Nettle 2002b).  Many of such traits with distinct optimal levels for men and women are likely those involved in attractiveness and may be mediated by testosterone and estrogen (Penton-Voak & Chen, 2004, Ellison, 2003).  One trait, facial masculinity, has noticeably different optimal levels for males than for females.  Men with higher facial masculinity are also found to be preferred by women, especially as short term partners (Penton-Voak & Chen 2004; Johnston, Hagel, Franklin, Fink, & Grammer, 2001).  High facial masculinity in males and facial femininity in females may advertise developmental stability and therefore be a measure of phenotype quality (Scheib, Gangestad, & Thornhill, 1999; Gangestad & Thornhill, 2003). The opposite, facial femininity, may be an indicator of quality in females.

Evidence suggests that testosterone levels and the traits it mediates, such as facial masculinity, may be heritable.  In a study of twin families, monozygotic twins had more similar levels of testosterone than dizygotic twins.  Mothers and daughters also had correlated testosterone levels (Harris, Vernon, and Boomsma, 1998).  Additional evidence suggests that opposite sex twins have similar testosterone levels prior to puberty (Hoekstra, Bartels, & Boomsma, 2006).   Thus while there is support that testosterone levels may be related within sex in families, it is unclear whether male and female testosterone levels covary within families after puberty.  Traits purportedly mediated by testosterone may also be heritable.  Fathers' and sons' facial masculinity are correlated (Cornwell & Perret, 2008) and arm strength may also be heritable within families (Thomis, Beunen, Van Leemputte, Maes, Blimkie, Claessens, Marchal, Willems, & Vlietinck, 1998).  However, while implying that traits related to masculinity and femininity are inherited, these studies do not establish whether female and male

masculinity covary within families.   None of these studies, aside from the pre-puberty evidence, address the heritability of traits related to masculinity/femininity within the family across the sexes.

Traits related to testosterone and masculinity may be inherited from both parents but expressed differentially in the two sexes of offspring.  As many of these traits are sexually dimorphic, traits related to masculinity/femininity may not just be relevant in examining offspring sex ratio in relation to phenotype, but also how intralocus sexual conflict may impact offspring sex ratio (Rice, 1992).  Different selection on the loci of a gene can create preferences for specific alleles depending on the sex of the individual.  One allele might be favored when the individual is male and a different allele may be favored for females.   In some cases this results in sex-limitation of the gene, where the opposing selection is eliminated.  When a trait is sex-limited, the underlying gene(s) is/are only expressed in individuals of one sex, and not at all in the opposite sex.  However, sexually dimorphic traits are not always sex-limited.  Differential selection pressures across the sexes can maintain variation at the loci of the gene and the traits affected by these loci.  One implication of antagonistic sexually dimorphic traits is that high quality males may have unfit female relatives, while high quality females may have unfit male relatives.   Sexually antagonistic genes may reduce the direct benefits of having parents who are have high levels of sexually dimorphic traits, as they may hurt the reproductive success of the opposite sex offspring.  For example, feminine mothers could have more feminine sons and masculine fathers could have more masculine daughters.

The TWH predicts that parents in good condition transfer material and/or genetic benefits to male and female offspring equally.  In contrast, sexual antagonism predicts that the

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fathers' quality may impede the quality of female offspring, but promote male offspring quality. Where as the mother's quality may impede male offspring quality and promote female offspring quality. Parents may maximize their reproductive success by biasing offspring sex ratio in relation to their own relative levels of masculinity and femininity.

Evidence in animals suggests that this is the case. Long-tailed male guppies have the same total length of short-tailed male guppies, but have different proportions of body and tail length. Females display a preference for total length, but do not favor either long-tailed or short-tailed males. Thus having a long tail does not increase attractiveness, but appears to enable long tailed males to invest less in growth, as a longer tail is not as costly to grow as a larger body. Female offspring of such long-tailed are likely to be small, as they may inherit the smaller body size of their father but not receive the long tail that males grow. Thus, female offspring of long-tailed male guppies will not have as much reproductive success as male offspring and parents should bias the ratio of their offspring toward males. Indeed, female guppies with long-tailed male mates do produce more sons than those with short-tailed mates (Karino, Kobayashi, & Orita, 2006). Burley's (1981) study manipulating attractiveness of parents by giving zebra finches colored leg bands, found that zebra finches appear to bias their offspring sex ratio toward the more attractive parent when parent attractiveness differed. However, when both parents had equal levels of attractive band color an equal number of both sexes were produced.

Human research is less conclusive. Humans vary in their sociosexuality from restricted to unrestricted. Before entering into a sexual relation, restricted individuals require more time, commitment from their partner, and attachment to their partners in comparison to

unrestricted individuals.    Unrestricted individuals would thus be expected to have more premarital partners than restricted individuals.  If sociosexuality is heritable, unrestricted parents may optimize their own reproductive success by having more sons, as son's reproductive success would benefit from unrestricted sociosexuality. Restricted parents may maximize offspring reproductive success by having more daughters, as their restricted sons may have low reproductive success due to competition from unrestricted males.  In fact, females with more premarital partners do have more sons than females with less premarital partners (Simpson & Gangestad, 1990; Kanazawa & Apari, 2009).  However, these findings could also be easily explained by TWH, much like the previously mentioned findings for house wrens where offspring fathered by extra-pair mates were more male-biased (Johnson et al., 2009).    Females who prefer "good gene" indicators in mates may have more extramarital partners, and therefore may have more sons as a result of their high quality partners.  Including data about the father's quality and about the offspring's quality may be important in differentiating the reasons for the sex ratio skew.

Additional research on humans does show support for the idea that parents bias the sex ratio of their offspring in relation to their relative level of specific traits.   As expected, taller and bigger parents have higher offspring sex ratios than is expected, while shorter and smaller parents have lower offspring sex ratios (Kanazawa, 2005).  Large size and strength may be linked to masculinity and should benefit male offspring's potential for reproductive success and may hurt female offspring's.  Stronger mothers (mid upper arm muscle are) are more likely to have had a son than other mothers (Gibson & Mace, 2003).  Additionally, masculinized parents may be able to pass these traits to their sons,

furthering their reproductive success, when it would hinder their daughters.  Parents with

low 2D:4D have more male offspring than parents with high 2D:4D (Manning, Martin,

Trivers, & Soler, 2002).  This is a trait that is purportedly related to testosterone levels in

utero.  Conversely, highly attractive parents have more female offspring than other

parents (Kanazawa, 2007).  As previously discussed, many traits related to masculinity

and femininity are related to attractiveness.  It is possible that being perceived as "very

attractive" may be linked to being less masculine and more feminine.  Males displaying

lower levels of masculine traits may not fare as well as other males.   Thus, it may

behoove parents to bias the sex of their offspring toward females.

If traits related to masculinity and femininity are sexually antagonistic, then parents

should bias offspring toward the sex who will inherit levels of the trait closer to the

optimal level of masculinity.

**Predictions**

The possibility of sexually antagonistic genes has not been studied in humans as it relates

to adaptive biases in offspring sex ratio.  Previous research indicates that parents may

benefit from biasing their offspring dependent on their relative levels of

masculinity/femininity, but does not directly study traits related to masculinity/femininity

in both parents. As facial masculinity is related to quality and may have differing optimal

levels for males and females, one purpose of this study is to examine whether offspring

sex ratio within families varies as a function of parental facial masculinity.

**Prediction 2.1.**  If traits related to masculinity and femininity are not sexually

antagonistic, TWH and general offspring sex ratio theory predict that male masculinity

and female femininity will covary positively with offspring sex ratio and sibling sex ratio.

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**Prediction 2.2.** In contrast, if traits related to masculinity and femininity are sexually antagonistic, male masculinity and female masculinity will covary positively with offspring sex ratio and sibling sex ratio.

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**Methods**

University of New Mexico undergraduates were recruited from the UNM community using flyers posted around campus and from the introduction to psychology courses. Participants ranged between the ages of 18 and 37. Consisting of 117 females and 51 males, 168 individuals were recruited from 140 families. Of these participants, 56 of the individuals were from 28 sibling pairs.

During the study, participants' faces were photographed by a researcher using a digital camera. Participants whose siblings also came in were asked to obtain photographs of their parents, as researchers had already collected photos of two children in the family. Individual participants were asked to obtain digital photos of their parents and one sibling over the age of 18. All photos were taken in front of a plain, light-colored background from the shoulders up by a researcher, the participant, or another family member (if the participant lived in a separate location from their family members). Participants faced straight forward, without tilting or turning their head, and maintained a neutral expression on their face for their photos. Participants and their family members were accordingly instructed to take photographs at home using the same method.

Participants also had a variety of physical measurements taken (height, weight, body fat, length of finger lengths, wrist width, chest/waist/hip measurements, and bicep circumference for men); and filled out a variety of questionnaires including information on family composition, relationship status, and age.

**Offspring Sex Ratio**

Participants reported on family size. Participants were asked to separately list the number, age, and sex of all full siblings, half siblings, and step siblings. Total number of male

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siblings (including the participant, if male) was calculated and then divided by the total number of siblings (including the participant) to get the offspring sex ratio (SR). Siblings that did not share both biological parents with the related participant, half and step siblings, were excluded from these calculations.

**Fluctuating Asymmetry of Hands**

FA measurements were added later in the study, so the initial seventeen families do not have participant FA measurements, leaving 113 families with an FA measures for participants. Measures for FA were taken using digital calipers by one of two trained measurers. Participant's second (index) through fifth (pinky) finger lengths and wrist width were measured for both right and left sides. All five traits were measured twice on each side. For all five traits left and right side traits were separately averaged. The absolute value of the difference between the average right side and average left side was then calculated for each of the five traits.

Mean trait size was calculated separately for male participants and female participants by averaging across both right and left sides. Participant asymmetry measures were then calculated, according to Gangestad and Thornhill (2003) for each of the five traits by dividing the absolute value of the difference between right and left sides by the average trait size for that participant's sex. The aggregate FA score was calculated by summing the individual FA scores for each participant.

**Facial Masculinity**

Not all members of each participant's family chose to participant. Other members of the family took photos that were not usable, as their faces were turned, tilted, or they were

smiling, distorting the measurements that were needed to produce reliable masculinity/femininity scores.  Usable photographs were obtained from 137 participants, 47 males and 90 females; 138 siblings, 52 male siblings and 59 female siblings; 124 mothers; and 106 fathers. These photos were subsequently analyzed to generate a facial masculinity/femininity score for each individual.  Photographs were imported into NIH Image 1.65. To compensate for head tilt, all faces were aligned such that the center of the pupils were on the same horizontal axis. Following Grammer, Fink, Juette, Ronzal, and Thornhill (2002), and Gangestad and Thornhill (2003), 25 standard points were placed on each face. Based on these coordinates, seven sexually dimorphic facial traits were measured: chin length (distance from the mouth to the bottom of the chin), jaw width (distance side-to-side across the face at the level of the mouth), eye height (mean height of the eye, from bottom of upper lid to top of lower lid), eye width (mean width from corner to corner), lip height (top of upper lip to bottom of lower lip), mouth width (corner to corner) interpupillary distance (pupil to pupil). To standardize measures for overall face size, "height measures" (e.g., chin length, eye height) were divided by overall face length (hairline to bottom of chin) and "width measures" (e.g., jaw width, interpupillary distance) were divided by face width (distance between outermost extensions across the cheekbones).

Using a principal components analysis and non-orthogonal rotation of the factors, two factors were calculated from the seven measured sexually dimorphic facial traits.   The first of these factors contained the eye height, eye width, width of jaw, and length of the chin.  The second factor contained lip height, mouth width, interpupillary distance, and eye width.  Participant scores for each factor were calculated using a regression-based

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methods, then discriminant analysis of both sets of factor scores were used to predict sex. Lastly, weighted combinations of the two factor scores, discriminant function scores, were calculated for each participant. The discriminant function scores were then multiplied by -1, such that higher values reflect higher facial masculinity while lower values reflect higher facial femininity.

**Results**

To avoid problems with heterogeneity of data (repeating data from the same family twice), one sibling from each data set was excluded from this analysis. In cases where both siblings were the same sex, one sibling was randomly excluded. Because of the disproportionate number of male and female participants, in cases where the siblings were opposite sex, the male sibling was retained and the female sibling excluded. The resulting numbers of female participants were 91 and of males were 49. The average age was 19.93 (sd = 2.93).

Additionally, small and restricted family sizes reported in this study may not provide an accurate assessment of any potential biases in offspring sex ratio. Larger families may offer more precise estimation of biased offspring sex ratio. To test this, families with less than three (3) children were excluded. This left 26 male participants, 45 female participants, 25 male siblings, 34 female siblings, 46 fathers, and 55 mothers with usable facial masculinity measures. This left 74 families with offspring sex ratio data and 54 families with participant FA scores.

**Fluctuating Asymmetry**

To test the prediction that offspring FA will predict sibling sex ratio, I performed a univariate GLM analysis with sex ratio of offspring in the family as the dependent variable and three predictors: sex of the participant from the family in the study, FA of that participant, and the interaction of sex and FA. Sex had a significant main effect (F=31.544, p<0.000), but the effect is not meaningful as the sex ratio of families where the participant was male would naturally be more male-biased than those where the participant was female. FA covaried negatively with sibling sex ratio (F=6.386, p=0.015),

such that participants with lower FA (more symmetrical) were from families with higher sex ratios.  The unstandardized beta weight for FA is B=-0.080 (SE=0.032), thus sibling sex ratio changes by -0.080, with every standard deviation increase in FA.  The partial correlation between FA and sibling sex ratio is -0.327 (p=0.015).  The interaction between FA and sex was not significant, F=2.508, p=0.119.

Separate bivariate correlations for females and males were also examined.  Female participants' FA did not significantly covary with the sex ratio of their parents' offspring (r=-0.139, p=0.427).  Male participants' FA did significantly and negatively covary with their parents' offspring sex ratio, r=-0.571, p=0.006. As noted above, however, the interaction between sex and FA was not statistically robust. Hence, any difference between the sexes must be interpreted cautiously.

**Facial Masculinity**

Two analyses were performed to test the relationship between male masculinity, female masculinity, and sex ratio within families. First, the relationship between mother facial masculinity, father facial masculinity, and offspring sex ratio was tested.  Second, offspring facial masculinity and sibling sex ratio were examined.

**Parental facial masculinity.**  To test whether mother's facial masculinity, father's facial masculinity, or an interaction between mother's and father's facial masculinity accurately predicts offspring sex ratio, I performed a univariate GLM analysis with offspring sex ratio as the dependent variable. Mother's facial masculinity, father's facial masculinity, and the interaction between mother's and father's facial masculinity were used as predictor variables.  The interaction between mother's and father's facial masculinity was included to examine whether different levels of parental

facial masculinity might have stronger effects in influencing offspring sex ratio.  For example, the interaction would examine whether extremely masculine fathers has a stronger effect on offspring sex ratio than the simple additive effect of father facial masculinity.   Parental facial masculinity was not related to the sex ratio of their offspring (mothers $F=0.494$, $p=0.486$; fathers $F=-0.033$, $p=0.856$, and mother by father $F=0.447$, $p=0.507$).  The unstandardized beta weights for mother's facial masculinity was $B=-0.072$, $SE=0.102$ (partial correlation $-0.109$, $p= 0.486$) and father's facial masculinity was $B=-0.010$, $SE =0.054$ (partial correlation $-0.029$, $p=0.856$).

**Offspring facial masculinity.**  To test whether offspring facial masculinity accurately predicts sibling sex ratio, I performed a univariate GLM analysis, using sibling sex ratio as the dependent variable.  The facial masculinity of the participant within the family, that participant's sex, and the interaction between participant facial masculinity and participant sex were used as independent variables.  As with participant FA, sex had a significant effect ($F=28.082$, $p<0.000$), though it is not meaningful, as the participant sex is included in the offspring sex ratio within their family.  .  Participant facial masculinity did not have a significant effect ($F=0.046$, $p=0.831$), nor did the interaction between participant facial masculinity and sex ($F=0.916$, $p=0.342$).  The unstandardized beta weight for participant FA was $B=0.009$, $SE=0.037$ (partial correlation $0.029$). Thus no relationship was detected between offspring facial masculinity and sibling sex ratio.

**Summary**

Two qualities purportedly associated with phenotypic quality, fluctuating asymmetry and facial masculinity, were looked at to assess their association with offspring sex ratio. In accordance with TWH I predicted that higher quality offspring, as reflected by FA in participants, would come from families with more males than lower quality offspring. TWH predictions for offspring sex ratio may be inaccurate in cases where parental quality is determined by traits with separate optima for males and females, due to the prospect that such traits are sexually antagonistic. Taking into account this possibility, I made two contrasting predictions for the relationship between male and female facial masculinity and the sex ratio of offspring within families. First, according to TWH male facial masculinity and female facial femininity would covary positively with sex ratio within families. Thus high quality parents and high quality offspring would have male-biased family sex ratios. Low quality parents and offspring would have female-biased family sex ratios. Conversely, if the genes related to facial masculinity are sexually antagonistic, male facial masculinity and female facial masculinity may covary positively with sex ratio within families. Thus more masculine parents and offspring should have male-biased family sex ratios. More feminine parents and offspring should have female-biased family sex ratios.

**Fluctuating asymmetry**

My first prediction that symmetrical, higher quality participants are more likely to have brothers than less symmetrical, lower quality participants was supported. Parents of symmetrical offspring do appear to bias their offspring in the direction of sons.

**Possible mechanisms used to bias offspring sex ratio in relation to FA.** There is a lack of a coherent research picture explaining the mechanism through which human offspring sex ratios are biased.   In humans, an individual's biological sex begins with spermatogenesis (whether a sperm cell produced is X or Y) and ends with conception (whether the sperm cell fertilizing the egg is X or Y).   50.3% of sperm cells are male, Y-bearing, but 51.3% of offspring at birth are male.  The two do not significantly differ, nor does there appear to be age based difference in number of Y-bearing sperm (Graffelman, Fugger, Keyvanfar, & Schulman, 1999).  Thus for biased sex ratios on the population level, and for age related offspring sex ratio effects, the manipulation of offspring sex ratio seems to occur after spermatogenesis but before birth.  However, individual differences in number of X or Y sperm, in addition to differences in sperm viability and motility may exist.

Oxidative stress is one little investigated mechanism that could affect offspring sex ratio through individual differences in the ratio of viable X and Y sperm.  Oxidative stress is known to have destructive effects on sperm through damaged DNA and decreased motility (Aitken, Gordon, Harkiss, Twigg, Milne, Jennings, & Irvine, 1998; Aitken & Krausz, 2001).  It is possible that oxidative stress has more harmful effects on Y bearing sperm (Aitken & Krausz, 2001), influencing whether fathers in good condition will be more likely to have daughters or sons.  A mother's level of oxidative stress could also influence offspring sex ratio.  Oxidative stress in the uterine environment could also differentially damage Y and X bearing sperm.  These damaged sperm would be less likely to fertilize an egg or create a viable gamete, as male gametes are more susceptible

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to loss.  As oxidative stress may be linked with FA, parents with lower oxidative stress and lower FA may differentially conceive and/or produce male offspring.

Researchers have hypothesized various mechanisms that may influence the sex of offspring by differential fertilization by X or Y sperm cells of eggs cells.  Parental hormones at time of conception may moderate differential fertilization. (James, 2008; Grant & Irwin, 2009).  Explorations of this mechanism have yielded support.  For example, older fathers and mothers have fewer male offspring (Matsuo, Ushioda, Udoff, 2009).  It is suggested that higher concentrations of follicular testosterone appear to aid fertilization for Y bearing sperm (Grant, Irwin, Standley, Shelling, & Chamley, 2008).  As previously discussed, hormone levels and FA may be indicative of fitness.  Mothers who are more likely to have symmetrical sons may be able maintain high hormone levels, resulting in a higher sex ratio of offspring.

Glucose may also be a mechanism through which maternal condition influences offspring sex ratio. (Grant & Irwin, 2009)  Uterine glucose levels appear to hinder female blastocyst growth, while benefiting male blastocyst growth.   This results in parents with high nutritional status, particularly glucose, biasing fertilization in the direction of sons.  Since nutrition can be important for developmental stability (Swaddle & Witter, 1994; Picton et al., 1990), parents with better nutrition, are likely lower in FA, and may also be more likely to have symmetrical sons.  Therefore, due to nutrition intake, parents producing symmetrical offspring are also more likely to have sons than daughters.

Lastly, males are more vulnerable in utero and a disproportionate loss of males may result in a skewed sex ratio.  Male fetuses have a higher risk of stillbirth which is

associated with birth weight (Smith, 2000).   Mothers carrying male fetuses are more likely to have preterm birth (Di Renzo, Rosati, Sarti, Cruciani, & Cutuli, 2007) and are more vulnerable to pregnancy complications like preeclampsia, gestational diabetes, and umbilical cord issues (Di Renzo et al., 2007;  Vatten & Skjaerven, 2004).  As male embryos seem more vulnerable and at higher risk for problems, male offspring with potential for higher FA may be disproportionately lost in utero, due to less stable developmental conditions, combined with increased male vulnerability.  Thus parents, particularly mothers, in good condition (providing for more developmental stability) would be more likely to carry male embryos to term, than mothers in poor condition.

**Facial masculinity**

My predictions regarding a relationship between male facial masculinity, female facial femininity, and the sex ratio of offspring within families were not supported.   I detected no relationship between male facial masculinity, female facial masculinity (or femininity), and sex ratio within families.  The results of this study do not support ideas that female facial masculinity, male facial masculinity, or an interaction between the two influence adaptive biases in offspring sex ratio.

It is possible that facial masculinity and femininity are not heritable, though this seems unlikely given existing research on heritability of masculine traits and hormone levels (Cornwell & Perret, 2008; Hoekstra et al., 2006; Harris et al., 1998; and Thomis et al., 1998).  However, past research shows that only father and son were related in masculinity (Cornwell & Perret, 2008) and only mother and daughter in testosterone level (Harris et al., 1998) indicating that different genetic mechanisms may influence testosterone levels and the traits it mediates over an individual's lifetime.  Age differences between parent

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and offspring may make it difficult to determine the heritability of testosterone and the traits it mediates across the sexes.

Research does suggest that hormone levels decrease with age (Dabbs, 1990; Deslypere & Vermeulen, 1984; Lamberts, van den Beld, & van der Lely, 1997; Zumoff, Strain, Miller, & Rosner, 1995; and Ferrini & Barrett-Conor, 1998). Traits related to testosterone also change as individuals age, making it difficult to compare older parents' quality to quality of their young offspring or to offspring sex ratios. Additionally, plastic surgeons note that facial features change with age (Coleman & Grover, 2006; Ferrario, Sforzia, Serrao, Ciusa, & Dellavia, 2003; Gunn, Rexbye, Griffiths, Murray, Fereday, Catt, Tomlin, Strongitharm, Perret, Catt, Mayes, Messenger, Green, van der Ouderaa, Vaupel, & Christensen, 2009). Thus, the possibility exists that our measures of current parent facial masculinity and offspring facial masculinity were not an accurate measure of parental condition during their reproductive period. Parent facial masculinity at the time of conception may correlate with offspring sex ratio, while offspring facial masculinity and current parent facial masculinity do not.

**Conclusions**

While phenotypic quality and offspring sex ratio has been looked at in other animals, this is the first known study to look at physical measures of phenotype in humans and adaptive biasing of offspring sex ratio. The results are mixed. FA of one sibling significantly predicted overall sibling sex ratio, and the negative correlation between the two provide partial support for the TWH of adaptive biasing in offspring sex ratio. Parents who are able to produce higher quality offspring, with lower FA, may manipulate the sex ratio of their offspring, such that they have more sons.

However, neither maternal nor paternal facial masculinity, nor an interaction between the two, predicted offspring sex ratio. Additionally the facial masculinity of one sibling did not predict the sex ratio within their family. This does not support my predictions for adaptive biases in offspring sex ratio. A relationship between parent/offspring quality, as related to facial masculinity and sex ratio within families was not detected. It may be that parents do not bias their offspring sex ratio in relation to their individual levels of sexually dimorphic traits. Alternately, parents may bias their offspring sex ratio in relation to their facial masculinity, but this study did not have the sufficient power to detect these biases.

Future research is needed on the mechanism(s) through which parents bias the sex ratio of their offspring. Identifying the means through which parents bias offspring sex ratio and the time frame, may help clarify which parental conditions trigger such biases. Additionally, it is still unknown how, if at all in humans, parents may bias offspring sex ratio in situations where inherited traits are sexually antagonistic. Research is needed determining which traits are sexually antagonistic and whether parents adaptively bias their offspring sex ratio in accordance with their relative levels of such traits.

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# Figure 1

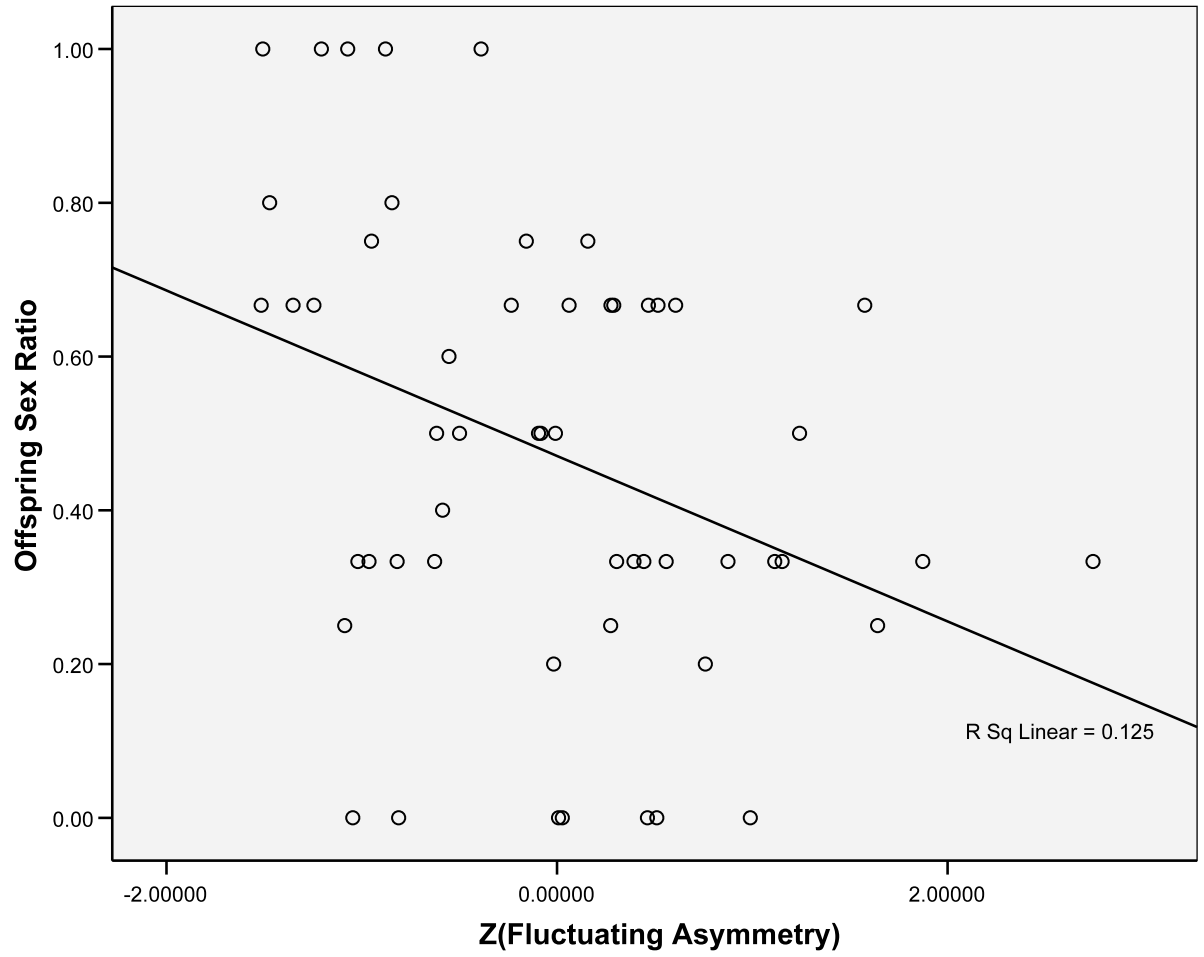### Offspring Sex Ratio and Fluctuating Asymmetry

**Table 1**

Correlations Between Parental and Offspring Facial Masculinity

| | | MP | FP | FS | MS | Mother | Father |
|---|---|---|---|---|---|---|---|
| Male Participant (MP) | Pearson Correlation | 1 | .(a) | .321 | .699 | .359 | -.279 |
| | Sig. (2-tailed) | | . | .285 | .054 | .156 | .356 |
| | N | 26 | 0 | 13 | 8 | 17 | 13 |
| Female Participant (FP) | Pearson Correlation | .(a) | 1 | .359 | .308 | .317 | .100 |
| | Sig. (2-tailed) | | | .131 | .246 | .060 | .592 |
| | N | 0 | 45 | 19 | 16 | 36 | 31 |
| Female Sibling (FS) | Pearson Correlation | .321 | .359 | 1 | .(a) | .215 | .095 |
| | Sig. (2-tailed) | .285 | .131 | | . | .272 | .646 |
| | N | 13 | 19 | 34 | 0 | 28 | 26 |
| Male Sibling (MS) | Pearson Correlation | .699 | .308 | .(a) | 1 | .365 | .066 |
| | Sig. (2-tailed) | .054 | .246 | . | | .087 | .793 |
| | N | 8 | 16 | 0 | 25 | 23 | 18 |
| Mother | Pearson Correlation | .359 | .317 | .215 | .365 | 1 | .080 |
| | Sig. (2-tailed) | .156 | .060 | .272 | .087 | | .600 |
| | N | 17 | 36 | 28 | 23 | 55 | 45 |
| Father | Pearson Correlation | -.279 | .100 | .095 | .066 | .080 | 1 |
| | Sig. (2-tailed) | .356 | .592 | .646 | .793 | .600 | |
| | N | 13 | 31 | 26 | 18 | 45 | 46 |

a  Cannot be computed because at least one of the variables is constant.