Sexy sons and sexy daughters: the influence of parents' facial characteristics on offspring

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Choosing a mate to maximize fitness underlies all sexual selection theories. Key to understanding mate choice is the inheritance of particular traits. Using family photos, we evaluated the predictions made by sexual selection theories for human mate choice concerning the inheritance of facial characteristics and assortment in facial appearance of parents. We found that both fathers' and mothers' attractiveness predicted the facial attractiveness of daughters: 'sexy daughters'. Fathers and sons were related to each other in facial masculinity but not attractiveness, providing only partial evidence for 'sexy sons'. Mothers and sons did not relate in masculinity–femininity; neither did fathers and daughters. Parents were similar in attractiveness but masculine men were not partnered to feminine women. Our findings support some predictions of Fisherian selection processes and 'good genes' theory but are less consistent with 'correlated response theory' and the immunocompetence handicap principle.

Current theories of sexual selection include Fisher's (1915, 1930) 'sexy-son hypothesis', Trivers's (1972) parental investment theory, Zahavi's (1975) 'good genes', Grafen's (1990) handicap principle and Hamilton & Zuk's (1982) theory of heritable fitness. Inheritance is necessary for all of these theories.

Fisher's Runaway Process

Fisher's theory is most often used to explain exaggerated male ornamentation. Heritable female preference for a heritable male trait generates nonrandom mating within a population (Fisher 1915). Given a differential reproductive potential between males and females (i.e. males can produce much higher numbers of offspring), a female can increase her own reproductive success by choosing 'sexy mates' who provide the genes enabling her to produce 'sexy sons'. This theory has found support across a number of species (Etges 1996; Jones et al. 1998; Wedell & Tregenza 1999; Brooks 2000). Although Fisher expressly discussed his theory in the light of human evolution and mate choice, less has been done to examine its usefulness in explaining sexual dimorphism in humans.

Fisher noted that in many species, especially those that share in parenting duties and that establish monogamous pair bonds, similar traits and the preferences for them can be found in both sexes. Lande (1980) suggested that female ornamentation is simply a product of correlated response. Natural selection would act more strongly on females to subdue sexual ornamentation and hence decrease predation on both females and their young. Lande's argument has received some support (Lande & Arnold 1985; Muma & Weatherhead 1989; Wolf et al. 2004) but there is an alternative argument that female ornamentation is a product of sexual selection and female–female competition (Hill 1993; Amundsen et al. 1997; Langmore 1998; Amundsen 2000; Amundsen & Forsgren 2003; Jawor & Breitwisch 2003; Jawor et al. 2004). Jawor et al. (2004) found that multiple ornaments (e.g. plumage colour, bill colour, crest length and face mask) in female cardinals, *Cardinalis cardinalis*, a biparental

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care species, provided honest signals to condition and maternal behaviour. Fisherian processes, then, can be responsible for exaggerated ornamentation in both males and females.

In humans, as a biparental care species, we should expect that both males and females are choosy when selecting long-term mates. Humans should have evolved preferences for opposite-sex features and behavioural characteristics, increasing their frequency. How the traits are passed down through the maternal or the paternal line will increase understanding of sexual selection in human evolution. We therefore examined transmission of facial characteristics.

'Good Genes' Theory

We suggest that qualities such as parenting behaviour (Storey et al. 2000) and generosity are related to phenotypic signals, and are heritable. Genes controlling the expression of such characteristics could be referred to as good genes (e.g. Wolf et al. 1999; Wade & Shuster 2002; e.g. Wolf et al. 1997). Instead, in the literature we find the label of 'good genes' overwhelmingly applies to those genes responsible for resistance to disease. While this is usually taken to mean superior immunocompetence, survival and health depend on genes responsible for the efficient function of all bodily systems.

'Good genes' theory (Trivers 1972; Zahavi 1975; Andersson 1994) suggests that sexually dimorphic characteristics signal genetic superiority (e.g. parasite resistance). Researchers have suggested that masculine characteristics in human males signal good genes (Gangestad & Simpson 2000; Fink & Penton-Voak 2002) although they also signal lower paternal investment, likelihood of abandonment, and other negative personality traits such as coldness or dishonesty (Perrett et al. 1998). A female must therefore make trade-offs, weighing the benefits of good genes, which she can pass on to her offspring and thus gain indirect benefits therefrom, against the direct and indirect benefits gained through male parenting skills and ability to provide resources for her and her offspring. If the principal reason for a woman to choose a masculine partner is to pass good genes on to her offspring, the inheritance of these good genes (masculinity) should be manifest in her offspring, at least by the time the offspring reach reproductive age.

Testosterone can have a negative impact on health since it may suppress the immune system and, more generally, it diverts bodily energy to building and maintaining muscle mass leaving less energy for maintaining other systems and so increases susceptibility to failure of these systems as well as to infectious disease and cancer. The immunocompetence handicap principle (Folstad & Karter 1992) suggested only males healthy and vigorous enough to withstand the deleterious (immunosuppressive) effects of testosterone are capable of displaying exaggerated sexually dimorphic characteristics but this theory is not without criticism (Kimball & Ligon 1999; Getty 2002; Owen-Ashley et al. 2004; Roberts et al. 2004). Good genes increase resistance to maladies and environmental stress, thereby increasing averageness and symmetry (Palmer & Strobeck 1986; Parsons 1990; Møller 1995, 1996; Badyaev

et al. 2000). These beneficial processes should be equally apparent in the phenotype of male and female offspring.

In women, feminine characteristics may signal good immunocompetence with oestrogen acting as a handicap (Thornhill & Grammer 1999). If oestrogen can suppress aspects of immunocompetence, we might expect feminine facial characteristics to be evident in daughters of more masculine fathers. The role of female gonadal hormones on immunity is controversial (Da Silva 1999; Seli & Arici 2002; Kumru et al. 2004). Oestrogen is, however, necessary for women's fertility (Lipson & Ellison 1996); thus men should prefer those characteristics that reliably signal female reproductive health and fitness. These findings explain why men prefer feminine characteristics in women (Singh 1993; Perrett et al. 1998; Ishi et al. 2004). This is especially true in biparental care species where males and females form pair bonds and both devote their time and resources to offspring, but it is also found in lekking species where males give preference to signals of genetic quality in females (Werner & Lotem 2003; Dosen & Montgomerie 2004).

Human Sexual Dimorphism

Epigamic (sexually dimorphic) traits in humans are moderate compared to many other primates (Lee 2001). These sex differences, although slight, are important to human mating strategies (Cunningham et al. 1990; Perrett et al. 1998; Hume & Montgomerie 2001; Johnston et al. 2001; Penton-Voak & Perrett 2001; Penton-Voak et al. 2001, 2003; Swaddle & Reierson 2002; Ishi et al. 2004; Penton-Voak & Chen 2004). Humans, like all other animals, are subject to sexual selection, and evidence for it should be testable. We evaluated two possible genetically heritable characteristics: the attractiveness and sexual dimorphism of faces, using photos taken in the laboratory and family photographs. All sexual selection models rely on traits being heritable, and therefore predict commonality in facial appearance across generations. Theories can be used to predict specific relationships.

Hypotheses

Same-sex parent-to-offspring relationships

Fisherian selection leads to Hypothesis 1a: father's masculinity predicts son's masculinity. A good-genes process makes a similar prediction. Fisherian selection could also exist for traits other than masculinity. Good genes in general will enhance symmetry, averageness and skin quality. These qualities will affect attractiveness; thus Fisherian processes and good genes theory lead to Hypothesis 1b: father's attractiveness predicts son's attractiveness. These hypotheses underpin the notion of 'sexy sons' where masculinity and attractiveness are presumed to underlie male allure and are inherited. The commonality in father's and son's appearances depends on shared genes controlling androgenic response or genes influencing body growth.

If Fisherian processes are contributing to female facial characteristics, then maternal influences should be apparent

in female offspring. Similarly, good genes theory also predicts maternal influences in offspring. Hence, Hypothesis 2a: mother's femininity predicts daughter's femininity; and Hypothesis 2b: mother's attractiveness predicts daughter's attractiveness. Such hypotheses are symmetric to those underlying 'sexy sons' and correspond to the matrilineal equivalent concept of 'sexy daughters'.

Opposite-sex parent-to-offspring relationships

From correlated response theory (Lande 1980), paternal characteristics may also appear in opposite-sex offspring. This gives Hypothesis 3a: daughter's facial masculinity correlates (positively) with father's facial masculinity; and for parity, Hypothesis 3b: son's facial femininity correlates positively with mother's facial femininity.

Genes aiding immunity and growth in their owner should benefit symmetry, averageness and skin condition of males and females alike. Good-genes consideration therefore predicts (Hypothesis 3c) a positive correlation between father's and daughter's facial attractiveness. In the same way good genes controlling mother's facial attractiveness should also predict son's facial attractiveness (Hypothesis 3d). One can derive similar predictions from considering the heritability of physiognomy; facial appearance of offspring should reflect genes from both father and mother.

As noted earlier, handicap theory gives Hypothesis 3e: father's facial masculinity should predict daughter's facial femininity. The ability to tolerate the handicap of sex hormones should allow accentuation of sex-typical traits in men or women. Similarly, we can predict from handicap theory that mother's femininity and son's masculinity should be correlated (Hypothesis 3f).

Note that while there are many theories producing similar predictions, none predicts a negative correlation between parent and offspring of the same sex. Correlated response is unique in predicting a detrimental impact on attractiveness of parents on opposite-sex offspring. This is most obvious for daughters since masculinity inherited from fathers (Hypothesis 3c) should detract from daughters' attractiveness.

Parental relationships

Both males and females are choosy which predicts assortment of level of attractiveness in parents. Hypothesis 4a: attractiveness of mothers and fathers should be positively correlated. Attractive feminine women show stronger preferences for masculine male faces for long-term partners compared to preferences of less attractive and more masculine women (Little et al. 2001; Penton-Voak et al. 2003). Such preferences in women coupled with men's preference for femininity in female faces (e.g. Cornwell et al. 2004) leads us to predict that feminine women will partner with masculine men (Hypothesis 4b).

We conducted two studies, the first examining the relationship between parents and female offspring and the second examining the relationship between parents and male offspring. Ethical approval was obtained from the University of St Andrews School of Psychology Ethics Committee.

STUDY 1: FEMALES

Methods

Stimuli

Undergraduate students were asked if we could contact their family to obtain family photos. For those students who gave permission, a letter was sent to their parent(s) explaining the nature of our work, along with a short questionnaire and a request for a number of separate family images. The short questionnaire asked for the ages of the individuals in the photos at the time that the photo was taken, as well as information on biological relatedness (e.g. whether the individual is the biological parent or step-parent). Only images of biological parents with the known age at time of photography were used. This gave images of 108 female undergraduates of White European descent (mean age $\pm$ SD = 19.70 $\pm$ 1.44 years, range 17−23), with 95 images of the biological fathers (mean age $\pm$ SD = 48.37 $\pm$ 7.50 years, range 25−73) and 104 images of the biological mothers (mean age $\pm$ SD = 46.44 $\pm$ 6.54 years, range 23−64).

All images were scanned using an Epson 1200s, cropped to expose mainly the face, and sized to approximately 4.0 MB, uncompressed, and then converted to JPG format. These images were presented with some hair and clothing visible.

Photos of the students were taken in a laboratory setting, under diffuse lighting. Students were asked to pose with a neutral expression. A digital camera captured the images uncompressed, at a resolution of 1200 × 1000 pixels, with 24-bit RGB (red, green, blue) colour encoding.

Participants

Participants judging the photos were undergraduates recruited from the University of St Andrews (14 females, age range 19−31, mean = 22.5 years; and 3 males, age range 22−23, mean = 22.3 years).

Presentation

Images were presented in randomized blocks, and each block consisted of randomized images of mothers, fathers or female students, as well as filler items. Participants were asked to rate each image on masculinity and attractiveness. For the masculinity scale, participants were asked 'Does this student (or 'parent') look more masculine or feminine?' and could choose from one of eight possibilities: (1) very feminine; (2) normally feminine for a female; (3) slightly masculine for a female; (4) androgynous female; (5) androgynous male; (6) slightly feminine for a male; (7) normally masculine for a male; (8) very masculine. Attractiveness ratings were done on a 7-point Likert-type scale with very attractive (7) and not at all attractive (1) as the end points.

Analyses

To determine the relationship between each parent and his or her offspring we used correlation and linear regression. Before these analyses, steps were required to control for factors such as parent and student age. We controlled for age for two reasons: (1) the parent images varied greatly in age from early 20s to early 70s; (2) age was positively correlated

with father's masculinity (Pearson correlation: $r_{93} = 0.253$, $P = 0.013$), negatively correlated with mother's femininity ($r_{102} = -0.197$, $P = 0.045$), negatively correlated with mother's attractiveness ($r_{102} = -0.212$, $P = 0.031$), and negatively correlated with female student's femininity ($r_{106} = -0.211$, $P = 0.028$).

Prior to running our zero-order correlations to evaluate the relationship between students' perceived attractiveness and masculinity and that of their parents, we ran an initial linear regression analysis to adjust for effects of age. Each of our dependent variables (mother's masculinity, mother's attractiveness, father's masculinity, father's attractiveness, student's masculinity and student's attractiveness) were run with the appropriate age (i.e. mother's age, father's age or student's age) as the independent variable with the standardized residuals retained. All further analyses used these residuals (i.e. attractiveness or masculinity controlling for age).

Results

Cronbach's alpha

Ratings were examined using Cronbach's alpha for observed reliability coefficient. For mothers' images judged for attractiveness, $\alpha = 0.92$, masculinity $\alpha = 0.87$; fathers' images judged for attractiveness, $\alpha = 0.92$, masculinity $\alpha = 0.71$; female students' images judged for masculinity, $\alpha = 0.89$, attractiveness $\alpha = 0.93$. Given the high degree of agreement, further analysis was run on average ratings.

Zero-order correlations

Our Spearman rank zero-order correlations revealed that among our female students, attractiveness and femininity (for clarity, we substitute the term 'femininity' rather than 'masculinity' when discussing the sexually dimorphic characteristics of females) were positively correlated ($r_S = 0.805$, $N = 108$, $P < 0.001$), as was mother's attractiveness and femininity ($r_S = 0.823$, $N = 104$, $P < 0.001$). For fathers we found no relationship between attractiveness and masculinity ($r_S = -0.026$, $N = 95$, $P = 0.805$).

In terms of parent–offspring relationships (Table 1), we found that mother's femininity and daughter's (female student's) femininity and attractiveness were positively correlated. Mother's attractiveness and daughter's attractiveness and femininity were also positively correlated. Father's attractiveness was related both to daughter's attractiveness and daughter's femininity, whereas father's masculinity was not related to either daughter's attractiveness or daughter's femininity.

Father's attractiveness was positively correlated with both mother's attractiveness and femininity (Table 2). Father's masculinity showed a nonsignificant tendency to be negatively correlated with mother's attractiveness and was negatively correlated with mother's femininity (Table 2).

Linear regression

The data were checked for normality using SPSS collinearity diagnostics, and a tolerance value of 0.904 met the criteria for linear regression. Mahalanobis distances were inspected, and there were no outliers outside the critical value. A standard linear regression analysis was performed between the dependent variable, female student attractiveness, and the independent variables, father's attractiveness and mother's attractiveness. Because mother's femininity and attractiveness were highly correlated, only one of these two variables could be used in our analysis. We used the maternal attractiveness, as this variable produced the strongest correlation with daughter's attractiveness. The two variables explained 18% of the variance (adjusted $R^2 = 0.176$, $F_{2,88} = 10.62$, $P < 0.001$). Father's attractiveness was a stronger predictor of daughter's attractiveness ($\beta = 0.313$, $P = 0.005$) than was mother's attractiveness ($\beta = 0.228$, $P = 0.026$).

Similar analysis revealed that daughter's femininity was predicted by father's attractiveness and mother's femininity (adjusted $R^2 = 0.203$, $F_{2,88} = 12.47$, $P < 0.001$). Father's attractiveness was again a stronger predictor ($\beta = 0.360$, $P < 0.001$) than mother's femininity ($\beta = 0.219$, $P = 0.027$).

Figure 1 illustrates the similar attractiveness of parents and daughters. Each image is a composite made by averaging the shape and colour of 10 component faces (Perrett et al. 1998; Jones et al. 2005). The composite images of female students were constructed based on the attractiveness of parents and without reference to the student's attractiveness, yet the average appearance of the daughters follows the appearance of their parents in terms of attractiveness.

STUDY 2: MALES

Methods

Stimuli

Images were collected in the same manner as in study 1, and again only images of biological parents were included, giving us 64 images of male undergraduates of White European descent (mean age $\pm$ SD = 20.2 ± 1.57 years, range 18–23), with 64 images of the biological fathers (mean age $\pm$ SD = 47.52 ± 10.06 years, range 18–67) and 61 (mean age $\pm$ SD = 46.26 ± 8.80 years, range 20–61) images of the biological mothers. All images and photos were processed in the same way as in study 1.

Participants

Participants judging the photos were undergraduates recruited from the University of St Andrews (20 females, age range 18–41, mean = 21.4 years; 14 males, age range 18–22, mean = 19.07 years).

Presentation

Images were presented in randomized blocks, and each block consisted of randomized images of mothers, fathers or male students as well as filler items. Because we collected fewer family images from male students than from female students, we opted to use a more sensitive scale to investigate the heredity of facial masculinity and thus changed our rating scale from a 4-point (each sex) to

Table 1. Relationship in facial characteristics of parents and daughters (study 1)

	Mother's				Father's			
	Attractiveness		Femininity		Attractiveness		Masculinity	
Daughter's	r_S	P	r_S	P	r_S	P	r_S	P
Attractiveness	0.310	0.001	0.297	0.002	0.362	<0.001	−0.138	0.184
Femininity	0.316	0.001	0.312	0.001	0.403	<0.001	−0.046	0.660

$N = 104$ for mothers, 95 for fathers.

a 7-point scale. Thus, participants were asked to rate each image on masculinity and attractiveness on 7-point Likert-type scales.

Analyses

Analyses for the second study were carried out in the same manner as in study 1.

Results

Cronbach's alpha

For mothers' images judged for attractiveness, $\alpha = 0.97$, masculinity $\alpha = 0.97$; fathers' images judged for attractiveness, $\alpha = 0.93$, masculinity $\alpha = 0.89$; male students' images judged for attractiveness $\alpha = 0.94$, masculinity $\alpha = 0.94$. Owing to the high agreement between evaluators average ratings are analysed below.

Zero-order correlations

Prior to our Spearman rank zero-order calculations, we ran linear regressions on each of our variables to control for age, and the standardized residuals were retained. As with study 1, the parent images spanned a large age range (20s−70s) and, as previously found, mother's age was negatively correlated with both attractiveness ($r_S = -0.413$, $N = 61$, $P = 0.001$) and femininity ($r_S = -0.447$, $N = 61$, $P < 0.001$). We also found a positive but nonsignificant trend between father's age and masculinity ($r_S = 0.239$, $N = 66$, $P = 0.057$). All

Table 2. Relationship of facial characteristics between parents (studies 1 and 2)

	Mother's			
	Attractiveness		Femininity	
Father's	r_S	P	r_S	P
Study 1				
Attractiveness	0.305	0.003	0.306	0.003
Masculinity	−0.203	0.053	−0.223	0.034
Study 2				
Attractiveness	0.389	0.002	0.312	0.016
Masculinity	0.018	0.892	−0.044	0.740

$N = 91$ in study 1 and 59 in study 2.

further analyses were done with these residuals (i.e. attractiveness or masculinity controlling for age).

Our zero-order correlations revealed that among our male students, attractiveness and masculinity were positively correlated ($r_S = 0.323$, $N = 64$, $P = 0.009$), as was mother's attractiveness and femininity ($r_S = 0.912$, $N = 61$, $P < 0.001$). For fathers, unlike Study 1, we found a positive relationship between attractiveness and masculinity ($r_S = 0.443$, $N = 64$, $P < 0.001$).

In terms of parent−offspring relationships (Table 3), we did not find a relationship between mother's femininity and son's masculinity or son's attractiveness. Nor did we find that mother's attractiveness and son's attractiveness or son's masculinity were related. We also did not find a relationship between father's attractiveness and son's attractiveness or son's masculinity. We did find a relationship between father's masculinity and son's masculinity, but there was no relationship with son's attractiveness.

Figure 2 illustrates the similarity in masculinity of fathers and sons. The composite images of male students are constructed (as Fig. 1) based on the masculinity of fathers and without reference to the student's masculinity, yet the average appearance of sons follows the appearance of the average appearance of their fathers in terms of masculinity.

As in study 1, we also looked at the relationship between mothers and fathers (Table 2), and found that father's attractiveness was positively correlated with both mother's attractiveness and femininity. Similar to the findings of study 1, father's masculinity was unrelated to mother's attractiveness, or to mother's femininity.

As we found a contribution of father's masculinity evident only in male offspring trait characteristics, linear regressions (to determine independent parent contributions) were not performed.

DISCUSSION

We made one overarching hypothesis: parents' facial characteristics would be apparent in their offspring's facial characteristics. We found that daughters' looks (femininity and attractiveness) were accounted for by both maternal and paternal facial attractiveness. The facial appearance of sons was less clearly related to that of parents; the only link we found was that between the masculinity of father and son. Our evidence for inheritance of facial characteristics in female offspring is strong

Table 3. Relationship in facial characteristics of parents and sons (study 2)

| Son's	Mother's				Father's			
	Attractiveness		Femininity		Attractiveness		Masculinity	
	r_S	P	r_S	P	r_S	P	r_S	P
Attractiveness	0.078	0.557	0.084	0.529	0.031	0.810	−0.083	0.520
Masculinity	0.003	0.980	0.009	0.949	0.062	0.635	0.314	0.013

$N = 59$ for mothers, 62 for fathers.

and would survive stringent Bonferroni corrections for multiple tests. The link between facial masculinity of father and son was of a similar statistical effect size to the link between face characteristics of parents and daughters, although study 2 had less statistical power owing to the smaller photograph collection.

We made hypotheses pertaining to specific mate selection theories and discuss each in turn. Our data appear to support some theories but not others, although we note that negative results do not disprove a theory since tests may lack sensitivity.

Our first prediction (Hypothesis 1a) is based on Fisherian processes and 'good genes' theory that father's masculinity would predict son's masculinity. Our data supported this hypothesis. Also under the rubric of Fisherian processes and 'good genes' theory, we predicted
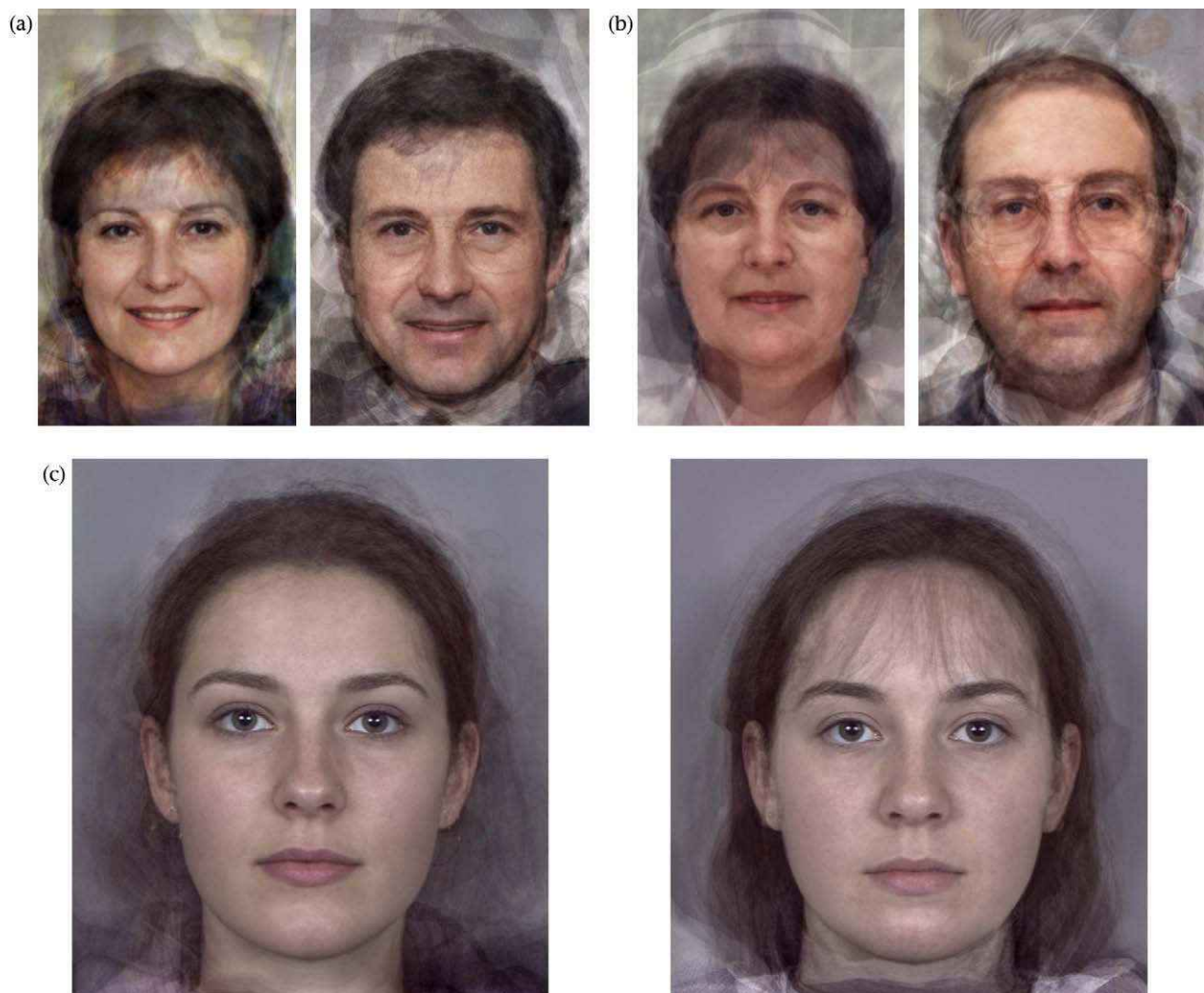
Figure 1. Image trios of parents and daughters were selected on the basis of the average of the two parents' attractiveness. (a, b) Composite images of 10 parents with high (a) and 10 with low (b) attractiveness (mother's age at photo: $\overline{X} \pm SD = 44.0 \pm 6.7$, 44.9 ± 8.6 years, respectively; father's age: 45.9 ± 7.4, 48.3 ± 7.0 years). (c) Composites of their 10 daughters (age: 19.7 ± 1.6, 19.0 ± 1.7 years).
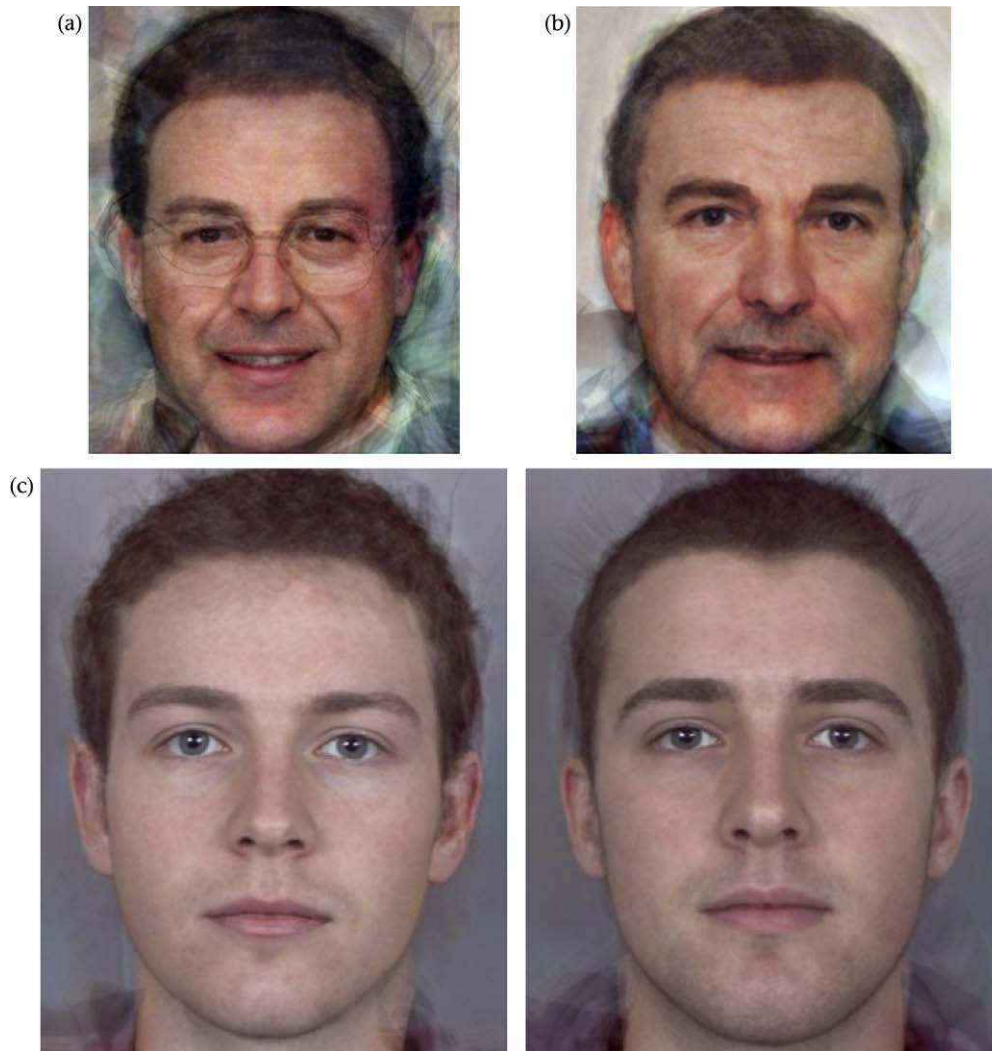
Figure 2. Image pairs of fathers and sons were selected on the basis of the father's facial masculinity. (a, b) Composite images of 10 fathers with low (a) and 10 with high (b) masculinity (age at photo: $\overline{X} \pm SD = 51.5 \pm 4.4$, 50.2 ± 3.4 years, respectively). (c) Composites of their 10 sons (age: 20.9 ± 1.0, 20.1 ± 1.1 years).

(Hypothesis 1b) that father's attractiveness would predict son's attractiveness, but this was not supported.

In our next set of predictions, we hypothesized (Hypothesis 2) that if Fisherian processes were contributing to female facial characteristics, maternal influences should be apparent in female offspring. This hypothesis was supported, as mother's facial femininity predicted both daughter's facial femininity (Hypothesis 2a) and attractiveness. As femininity and attractiveness were highly correlated for both mothers ($P < 0.001$) and daughters ($P < 0.001$), one can also state that mother's attractiveness predicted daughter's attractiveness and femininity (Hypothesis 2b).

We evaluated the correlated response theory (Lande 1980; Hypothesis 3a) that paternal masculine facial characteristics would influence daughter's facial characteristics. We did not find support for this hypothesis. Nor did we find support for the mirror hypothesis (3b) that mother's femininity would be related to son's facial characteristics.

We did find support for Hypothesis 3c (good genes theory) that daughter's facial attractiveness and femininity were

predicted by father's facial attractiveness. We did not find support for Hypothesis 3e (immunocompetence handicap principle) that father's facial masculinity should predict daughter's femininity. The relationship we found between father and daughter aligns most closely with the good genes theory and not the immunocompetence handicap principle.

We did not find support for Hypotheses 3b, 3d, or 3f that mother's facial characteristics would influence son's facial characteristics.

In our final set of hypotheses based on assortative mating, we predicted (Hypothesis 4a) that attractiveness of the parents should be correlated and this was supported by the data. That is, mother's attractiveness and father's attractiveness were positively correlated. Concerning Hypothesis 4b, we did not find that father's masculinity and mother's femininity were positively correlated, and in fact found that mother's attractiveness and father's masculinity were negatively correlated in study 1.

Although possible, we did not make predictions concerning correlations between male masculinity and

attractiveness, and our data from the two studies are inconsistent. In the first study we did not find a relationship between father's masculinity and attractiveness ($P = 0.805$); in study 2 we found that father's masculinity and attractiveness were positively correlated ($P < 0.001$) and son's masculinity and attractiveness were also positively correlated ($P = 0.009$). We discuss the possible reasons for this discrepancy below.

Daughters

Our findings are supportive of both Fisherian processes and good genes theory. Both parents contributed to the attractiveness and femininity of daughters. We found that daughter's attractiveness was predicted independently by father's attractiveness and mother's femininity (and therefore, by default, mother's attractiveness). Fisherian selection processes would suggest that men have evolved preferences for sexually dimorphic facial characteristics in opposite-sex partners, and through human evolution these preferences have increased the frequency of feminine facial characteristics such as a slender chin, full lips and large eyes in women. Good genes theory predicts the same finding, although it suggests that feminine facial characteristics must by definition signal good quality, including possible cues to immunocompetence, fertility, youthfulness, health and perhaps even maternal tendencies (Deady et al. 2006). Our study was not designed to determine the honesty of or the information conveyed by the signals of attractive or sexually dimorphic facial characteristics; thus we cannot differentiate between Fisherian processes and good genes theory. We should note that one prediction based on good genes theory in which masculinity is a signal of superior genetic quality (e.g. Thornhill & Gangestad 1999; Gangestad & Simpson 2000) would be that masculine fathers would produce attractive sons and daughters, yet we did not find any support for this prediction.

The immunocompetence handicap principle as proposed by Folstad & Karter (1992) makes a much more specific assertion, in that testosterone acts as an immunosuppressant and thus only those men with the constitution to withstand the ill-effects of testosterone are capable of producing exaggerated sex-specific testosterone-mediated traits. The prediction based on the immunocompetence handicap principle was that masculine fathers would produce attractive and feminine daughters; we found no evidence for this. On the other hand, Thornhill & Grammer (1999) suggested that oestrogen could also act as an immunosuppressant, and thus feminine-looking mothers would be expected to produce feminine-looking daughters. While we did find that maternal femininity predicts daughter's femininity, we do not claim to have provided evidence for the immunocompetence handicap principle because oestrogen and progesterone appear to enhance immunity (Da Silva 1999). Still, we cannot rule out our finding as having supported Thornhill & Grammer's proposition.

We can rule out evidence to support Lande's correlated response theory as father's masculinity did not predict any facial characteristics in daughters.

Sons

In males, we found only father's masculinity influenced son's facial characteristics. We did not find any evidence that father's attractiveness or mother's femininity or attractiveness influenced the facial characteristics of male offspring. Thus we have no evidence for good genes via the mother's contribution and correlated response theory.

Our finding that male facial masculinity is passed down from father to son is supportive of both Fisherian processes and good genes theory. It is also consistent with the immunocompetence handicap principle, in that a son may inherit the genes coding for superior immunocompetence and thus can support higher levels of testosterone which in turn will produce exaggerated sexually dimorphic traits.

We are perplexed as to why we did not find any evidence for the inheritance of attractiveness in males, through either the female or male parent. Attractiveness, by its own definition, should be sexy, and while we found evidence for sexy parents–sexy daughters, we did not find the parallel in male offspring. While masculine dads produced masculine sons, in this study, sexy parents did not produce sexy sons.

Parent's Assortative Mating

Parents represent real mating effort and competition in the 'mating market' should result in positive assortment. We therefore predicted (Hypothesis 4a) that attractive mothers would be paired with attractive fathers, and (Hypothesis 4b) feminine mothers would be paired with masculine fathers. We found support for the first but not the second hypothesis.

Asymmetries in Parent–Offspring Characteristics

Both Fisherian processes and good genes theory posit that members of one sex select traits in the opposite sex, and that these traits pass to offspring. Above we outlined the evidence for some traits being passed from parent to offspring, but not all the data fit the postulated selection process.

To begin with the tidiest findings: our data show men select for traits of femininity and attractiveness in partners (Hypothesis 4a) and these traits are passed to female offspring. Additionally we found that women select for attractiveness in partners (Hypothesis 4b), and attractive traits are passed to daughters.

While we found that women select for attractiveness in male partners, we did not find evidence of selection resulting in attractiveness passing to sons. One explanation for such discrepancy derives from the equivocal relationship between male attractiveness and masculinity. Study 1 found no relationship between father's masculinity and attractiveness whereas study 2 found a positive relationship between father's masculinity and attractiveness as well as between son's masculinity and attractiveness. Such disparate findings pervade the literature. Most studies reveal a slight positive association between attractiveness

and masculinity in male faces (Grammer & Thornhill 1994; Scheib et al. 1999; Penton-Voak & Perrett 2001; Rhodes 2006), but some studies report an opposite negative relationship (Perrett et al. 1998; Penton-Voak et al. 1999, 2003; Swaddle & Reierson 2002). No studies report attraction to extreme masculinity. More importantly, there are individual differences in women: some are attracted to masculinity but others are averse to masculine traits (Little et al. 2001; Penton-Voak et al. 2001).

Diversity in women's opinions about whether masculinity is attractive will detract from father—son correlation in perceived attractiveness, but not correlation in perceived masculinity. Indeed, heritability of male traits coupled with heritable or culturally transmitted variance in female attraction to masculinity sets the stage for rapid enhancement or diminution of sexual dimorphism in a species. Such flexibility could help radiation of species into niches in which raised masculinity is beneficial (e.g. for male competition or immune profile), and niches where reduced masculinity is beneficial (e.g. for greater cooperation or paternal care).

We found evidence for facial masculinity passing from father to son. This supports both Fisherian processes and good genes theory but we did not find any evidence for selection maximizing or maintaining dimorphism in partnerships, at least in the parents of university students. In study 1, feminine and attractive women had selected feminine-looking husbands and in study 2 we did not find a relationship between husband's masculinity and wife's facial characteristics. The apparent lack of consistency between selection and inheritance may be the result of individual differences between our evaluators in combination with the wide age range of the parent photos. It would be best to recruit photos of the parents at the time of the marriage.

A further possible caveat of the study is that our parent cohort were long-term partners (we had few divorced parents in our Scottish sample). The low separation rate may not be typical of the species or of prehistoric humans. It has been posited that testosterone in both men and women can increase the likelihood of abandonment and marriage dissolution (Mazur & Booth 1998). We may have tapped into a subgroup within the general population of men and women selected for long-term relationships, and thus this particular group of women would not have had a strong preference for masculinity traits in a partner. A relevant point in this context is that daughter's facial masculinity is associated with stressful environments including early parental divorce and parental discord (Boothroyd & Perrett 2006). So we may be missing the fathers that could contribute to a positive association between father's and daughter's masculinity. To resolve such a possibility would require further study of a different population perhaps following partnerships from an earlier stage.

There is one more piece of the puzzle that should be addressed in future research: are parents' preferences inherited by their offspring? Research has provided support for offspring preferring opposite-sex parent characteristics in potential mates (Jacob et al. 2002; Perrett et al. 2002; Little et al. 2003). Such relationships may arise from

imprinting (Bereczkei et al. 2004) which is widespread in birds and mammals. The relationships may reflect heritable preferences, or a combination of genetic and nongenetic transgenerational effects.

While our evidence for immunocompetence theory was weak in terms of the attractiveness of male facial masculinity, men and women may still be selecting for good immune systems. There are other signals to health (Jones et al. 2001, 2005; Boothroyd et al. 2005) that influence attractiveness. Symmetry, normal proportions, skin texture and colour, demeanour and even odour may give cues to superior immunocompetence and influence mate choice.

Family photographs present a valuable resource in studies of mate choice and the extent that traits pass across generations. Here, we have demonstrated how this resource can be tapped with simple perceptual assessments to provide some evidence on how evolutionary theory applies to human mate choice. Overall we found evidence from facial photographs that attractive parents beget attractive 'sexy daughters', but we found no support for the 'sexy sons' phenomenon. We did not find that attractive fathers (or attractive mothers) produce attractive sons. For the male line, we found only that facial masculinity conforms to the rule 'like father—like son'.

References

Amundsen, T. 2000. Why are female birds ornamented? *Trends in Ecology & Evolution*, **15**, 149—155.

Amundsen, T. & Forsgren, E. 2003. Male preference for colourful females affected by male size in a marine fish. *Behavioral Ecology and Sociobiology*, **54**, 55—64.

Amundsen, T., Forsgren, E. & Hansen, L. T. T. 1997. On the function of female ornaments: male bluethroats prefer colourful females. *Proceedings of the Royal Society of London, Series B*, **264**, 1579—1586.

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Badyaev, A. V., Foresman, K. R. & Fernandes, M. V. 2000. Stress and developmental stability: vegetation removal causes increased fluctuating asymmetry in shrews. *Ecology*, **81**, 336—345.

Bereczkei, T., Gyuris, P. & Weisfeld, G. E. 2004. Sexual imprinting in human mate choice. *Proceedings of the Royal Society of London, Series B*, **271**, 1129—1134.

Boothroyd, L. G. & Perrett, D. I. 2006. Facial and bodily correlates of family background. *Proceedings of the Royal Society of London, Series B*, **273**, 2375—2380.

Boothroyd, L. G., Jones, B. C., Burt, D. M., Cornwell, R. E., Little, A. C., Tiddeman, B. P. & Perrett, D. I. 2005. Facial masculinity is related to perceived age but not perceived health. *Evolution and Human Behavior*, **26**, 416—431.

Brooks, R. 2000. Negative genetic correlation between male sexual attractiveness and survival. *Nature*, **406**, 67—70.

Cornwell, R. E., Boothroyd, L., Burt, D. M., Feinberg, D. R., Jones, B. C., Little, A. C., Pitman, R., Whiten, S. & Perrett, D. I. 2004. Concordant preferences for opposite-sex signals? Human pheromones and facial characteristics. *Proceedings of the Royal Society of London, Series B*, **271**, 635–640.

Cunningham, M. R., Barbee, A. P. & Pike, C. L. 1990. What do women want? Facialmetric assessment of multiple motives in the perception of male facial physical attractiveness. *Journal of Personality and Social Psychology*, **59**, 61–72.

Da Silva, J. A. P. 1999. Sex hormones and glucocorticoids: interactions with the immune system. *Annals of the New York Academy of Science*, **22**, 102–117.

Deady, D. K., Law Smith, M. J., Sharp, M. A. & Al Dujaili, E. A. S. 2006. Maternal personality and reproductive ambition in women is associated with salivary testosterone levels. *Biological Psychology*, **71**, 29–32.

Dosen, L. D. & Montgomerie, R. 2004. Female size influences mate preferences of male guppies. *Ethology*, **110**, 245–255.

Etges, W. J. 1996. Sexual selection operating in a wild population of *Drosophila robusta*. *Evolution*, **50**, 2095–2101.

Fink, B. & Penton-Voak, I. S. 2002. Evolutionary psychology of facial attractiveness. *Current Directions in Psychological Science*, **11**, 154–158.

Fisher, R. A. 1915. The evolution of sexual preference. *Eugenics Review*, **7**, 184–192.

Fisher, R. A. 1930. *The Genetic Theory of Natural Selection*. Oxford: Oxford University Press.

Folstad, I. & Karter, A. J. 1992. Parasites, bright males and the immunocompetence handicap. *American Naturalist*, **139**, 603–622.

Gangestad, S. W. & Simpson, J. A. 2000. The evolution of human mating: trade-offs and strategic pluralism. *Behavioral and Brain Sciences*, **23**, 573–644.

Getty, T. 2002. Signaling health versus parasites. *American Naturalist*, **159**, 363–371.

Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology*, **144**, 517–546.

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

Hamilton, W. D. & Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science*, **218**, 384–387.

Hill, G. E. 1993. Male mate choice and the evolution of female plumage coloration in the house finch. *Evolution*, **47**, 1515–1525.

Hume, D. K. & Montgomerie, R. 2001. Facial attractiveness signals different aspects of 'quality' in women and men. *Evolution and Human Behavior*, **22**, 93–112.

Ishi, H., Gyoba, J., Kamachi, M., Mukaida, S. & Akamatsu, S. 2004. Analyses of facial attractiveness on feminised and juvenilised faces. *Perception*, **33**, 135–145.

Jacob, S., McClintock, M. K., Zelano, B. & Ober, C. 2002. Paternally inherited HLA alleles are associated with women's choice of male odor. *Nature Genetics*, **30**, 175–179.

Jawor, J. M. & Breitwisch, R. 2003. A unique ornament display in female northern cardinals. *Wilson Bulletin*, **115**, 464–467.

Jawor, J. M., Gray, N., Beall, S. M. & Breitwisch, R. 2004. Multiple ornaments correlate with aspects of condition and behaviour in female northern cardinals, *Cardinalis cardinalis*. *Animal Behaviour*, **67**, 875–882.

Johnston, V. S., Hagel, R., Franklin, M., Fink, B. & Grammer, K. 2001. Male facial attractiveness. Evidence for hormone-mediated adaptive design. *Evolution and Human Behavior*, **22**, 251–267.

Jones, T. M., Quinnell, R. J. & Balmford, A. 1998. Fisherian flies: benefits of female choice in a lekking sandfly. *Proceedings of the Royal Society of London, Series B*, **265**, 1651–1657.

Jones, B. C., Little, A. C., Penton-Voak, I. S., Tiddeman, B. P., Burt, D. M. & Perrett, D. I. 2001. Facial symmetry and judgements of apparent health. Support for a 'good genes' explanation of the attractiveness − symmetry relationship. *Evolution and Human Behavior*, **22**, 417–429.

Jones, B. C., Perrett, D. I., Little, A. C., Boothroyd, L. G., Cornwell, R. E., Feinberg, D. R., Tiddeman, B. P., Whiten, S., Pitman, R. M., Hillier, S. G., Burt, D. M. & Stirrat, M. R. 2005. Pregnancy, menstrual cycle and hormonal contraceptive use alter attraction to apparent health in faces. *Proceedings of the Royal Society of London, Series B*, **272**, 347–354.

Kimball, R. T. & Ligon, J. D. 1999. Evolution of avian plumage dichromatism from a proximate perspective. *American Naturalist*, **154**, 182–193.

Kumru, S., Godekmerdan, A. & Yilmaz, B. 2004. Immune effects of surgical menopause and estrogen replacement therapy in peri-menopausal women. *Journal of Reproductive Immunology*, **63**, 31–38.

Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, **34**, 292–305.

Lande, R. & Arnold, S. J. 1985. Evolution of mating preference and sexual dimorphism. *Journal of Theoretical Biology*, **117**, 651–664.

Langmore, N. E. 1998. Functions of duet and solo songs of female birds. *Trends in Ecology & Evolution*, **13**, 136–140.

Lee, S.-H. 2001. Patterns of skeletal sexual dimorphism in human, chimpanzee, and gorilla. *Journal of Human Evolution*, **40**, A13.

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

Little, A. C., Burt, D. M., Penton-Voak, I. S. & Perrett, D. I. 2001. Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proceedings of the Royal Society of London, Series B*, **268**, 39–44.

Little, A. C., Penton-Voak, I. S., Burt, D. M. & Perrett, D. I. 2003. Investigating an imprinting-like phenomenon in humans: partners and opposite-sex parents have similar hair and eye colour. *Evolution and Human Behavior*, **24**, 43–51.

Mazur, A. & Booth, A. 1998. Testosterone and dominance in men. *Behavioral and Brain Sciences*, **21**, 353–397.

Møller, A. P. 1995. Leaf-mining insects and fluctuating asymmetry in elm *Ulmus glabra* leaves. *Journal of Animal Ecology*, **64**, 697–707.

Møller, A. P. 1996. Parasitism and developmental instability of hosts: a review. *Oikos*, **77**, 189–196.

Muma, K. E. & Weatherhead, P. J. 1989. Male traits expressed in females: direct or indirect sexual selection? *Behavioral Ecology and Sociobiology*, **25**, 23–31.

Owen-Ashley, N. T., Hasselquist, D. & Wingfield, J. C. 2004. Androgens and the immunocompetence handicap hypothesis: unraveling direct and indirect pathways of immunosuppression in song sparrows. *American Naturalist*, **164**, 490–505.

Palmer, A. R. & Strobeck, C. 1986. Fluctuating asymmetry: measurement, analysis, patterns. *Annual Review of Ecology and Systematics*, **17**, 391–421.

Parsons, P. A. 1990. Fluctuating asymmetry: an epigenetic measure of stress. *Biological Review of the Cambridge Philosophical Society*, **65**, 131–145.

Penton-Voak, I. S. & Chen, J. Y. 2004. High salivary testosterone is linked to masculine male facial appearance in humans. *Evolution and Human Behavior*, **25**, 229–241.

Penton-Voak, I. S. & Perrett, D. I. 2001. Male facial attractiveness: perceived personality and shifting female preferences for male

traits across the menstrual cycle. *Advances in the Study of Behavior*, **30**, 219–259.

Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Burt, D. M., Kobayashi, T., Murray, L. K. & Minamisawa, R. 1999. Menstrual cycle alters face preferences. *Nature*, **399**, 714–742.

Penton-Voak, I. S., Jones, B. C., Little, A. C., Baker, S., Tiddeman, B. P., Burt, D. M. & Perrett, D. I. 2001. Symmetry, sexual dimorphism in facial proportions and male facial attractiveness. *Proceedings of the Royal Society of London, Series B*, **268**, 1617–1623.

Penton-Voak, I. S., Little, A. C., Jones, B. C., Burt, D. M., Tiddeman, B. P. & Perrett, D. I. 2003. Female condition influences preferences for sexual dimorphism in faces of male *Homo sapiens*. *Comparative Psychology*, **117**, 264–271.

Perrett, D. I., Lee, K. J., Penton-Voak, I. S., Rowland, D. R., Yoshikawa, S., Burt, D. M., Henzi, S. P., Castles, D. L. & Akamatsu, S. 1998. Effects of sexual dimorphism on facial attractiveness. *Nature*, **394**, 884–887.

Perrett, D. I., Penton-Voak, I. S., Little, A. C., Tiddeman, B. P., Burt, D. M., Schmidt, N., Oxley, R., Kinloch, N. & Barrett, L. 2002. Facial attractiveness judgements reflect learning of parental age characteristics. *Proceedings of the Royal Society of London, Series B*, **269**, 873–880.

Rhodes, G. 2006. The evolutionary psychology of facial beauty. *Annual Review of Psychology*, **57**, 199–226.

Roberts, M. L., Buchanan, K. L. & Evans, M. R. 2004. Testing the immunocompetence handicap hypothesis: a review of the evidence. *Animal Behaviour*, **68**, 227–239.

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*, **266**, 1913–1917.

Seli, E. & Arici, A. 2002. Sex steroids and the immune system. *Immunology and Allergy Clinics of North America*, **22**, 407–433.

Singh, D. 1993. Body shape and women's attractiveness: the critical role of waist-to-hip ratio. *Human Nature*, **4**, 297–321.

Storey, A. E., Walsh, C. J., Quinton, R. L. & Wynne-Edwards, K. E. 2000. Hormonal correlates of paternal responsiveness in new and expectant fathers. *Evolution and Human Behavior*, **21**, 79–95.

Swaddle, J. P. & Reierson, G. W. 2002. Testosterone increases perceived dominance but not attractiveness in human males. *Proceedings of the Royal Society of London, Series B*, **269**, 2285–2289.

Thornhill, R. & Gangestad, S. W. 1999. Facial attractiveness. *Trends in Cognitive Sciences*, **3**, 452–460.

Thornhill, R. & Grammer, K. 1999. The body and face of woman: one ornament that signals quality? *Evolution and Human Behavior*, **20**, 105–120.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man: 1971–1971* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.

Wade, M. J. & Shuster, S. M. 2002. The evolution of parental care in the context of sexual selection: a critical reassessment of parental investment theory. *American Naturalist*, **160**, 285–292.

Wedell, N. & Tregenza, T. 1999. Successful fathers sire successful sons. *Evolution*, **53**, 620–625.

Werner, N. Y. & Lotem, A. 2003. Choosy males in a haplochromine cichlid: first experimental evidence for male mate choice in a lekking species. *Animal Behaviour*, **66**, 293–298.

Wolf, J. B., Moore, A. J. & Brodie, E. D., III. 1997. The evolution of indicator traits for parental quality: the role of maternal and paternal effects. *American Naturalist*, **150**, 639–649.

Wolf, J. B., Brodie, E. D., III & Moore, A. J. 1999. The role of maternal and paternal effects in the evolution of parental quality by sexual selection. *Journal of Evolutionary Biology*, **12**, 1157–1167.

Wolf, W. L., Casto, J. M., Nolan, V., Jr. & Ketterson, E. D. 2004. Female ornamentation and male mate choice in dark-eyed juncos. *Animal Behaviour*, **67**, 93–102.

Zahavi, A. 1975. Mate selection: a selection for a handicap. *Journal of Theoretical Biology*, **53**, 205–214.