Does attractiveness in men provide clues to semen quality?

M. PETERS,*, † G. RHODES † & L. W. SIMMONS*

*Centre for Evolutionary Biology, School of Animal Biology, University of Western Australia, Crawley, WA, Australia †School of Psychology, University of Western Australia, Crawley, WA, Australia

Keywords:

attractiveness; averageness; masculinity; mate quality; semen quality; symmetry.

Abstract

The psychological mechanisms underlying attractiveness judgements in humans are thought to be evolved adaptations for finding a high quality mate. The phenotype-linked fertility hypothesis proposes that females obtain reliable information on male fertility from male expression of sexual traits. A previous study of Spanish men reported that facial attractiveness was positively associated with semen quality. We aimed to determine whether this effect was widespread by examining a large sample of Australian men. We also extended our study to determine whether cues to semen quality are provided by components of attractiveness: masculinity, averageness and symmetry. Each male participant was photographed and provided a semen sample that was analyzed for sperm morphology, motility and concentration. Two independent sets of women rated the male photographs for attractiveness, and three further sets of 12 women rated the photographs for masculinity, symmetry or averageness. We found no significant correlations between semen quality parameters and attractiveness or attractive traits. Although male physical attractiveness may signal aspects of mate quality, our results suggest that phenotype-linked cues to male fertility may not be general across human populations.

Introduction

Attractiveness is associated with mate choice and mating success in humans (Rhodes *et al.*, 2005), and is thought to be an evolved adaptation for finding healthy and fertile mates because attractiveness honestly indicates genotypic and phenotypic quality (Andersson, 1994; Thornhill & Gangestad, 1999). Obtaining a good quality mate may provide genetic benefits or resources that can help to increase an individual's reproductive success. For example, females may acquire indirect genetic benefits for offspring, and/or direct material benefits such as resources and/or parental care (Andersson, 1994; and see Gangestad & Scheyd, 2005 for a review). One direct benefit proposed to be associated with attractiveness is male fertility. The aim of the present study was to examine the association between attractiveness and semen quality in

Correspondence: Marianne Peters, School of Psychology, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia. Tel: +61 8 6488 3573; fax: +61 8 6488 1006; e-mail: marianne@psy.uwa.edu.au

humans, in order to explore whether an attractive male is preferred because of his reproductive potential.

Reproductive health or fertility is perhaps the most important aspect of mate quality, particularly in the context of mate choice, because the ultimate goal of mate selection is to maximize reproductive success. The phenotype-linked fertility hypothesis argues that females can obtain reliable information on male fertility from the expression of male secondary sexual traits (Sheldon, 1994). Although not universal (e.g. Birkhead & Petrie, 1995; Birkhead et al., 1997; Pizzari et al., 2004), some studies have reported positive relationships between attractive male sexual traits and semen quality. For example, in red deer, males with larger antlers produce sperm with greater swimming velocity (Malo et al., 2005). Likewise in guppies, males with greater areas of orange pigmentation produce faster swimming sperm of greater viability (Locatello et al., 2006) (see also Wagner & Harper, 2003; Kortet et al., 2004). For humans, Soler et al. (2003) reported significant correlations between semen quality parameters (sperm motility, morphology and concentration) and facial attractiveness in a sample

of 66 adult men. In that study, a second group of women rated a sub-sample of 12 male faces for attractiveness at high and low fertility risk phases of the menstrual cycle. This sub-sample yielded even higher correlations between attractiveness and semen quality, but there was no difference between the two fertility levels. To date, Soler *et al.*'s (2003) study has never been replicated, nor has any further data been published on attractiveness and fertility in men. We sought to determine the generality of the relationship between attractiveness and semen quality in human males by following Soler *et al.*'s (2003) study using a large sample of Australian men.

Masculinity, symmetry and averageness are three traits that contribute to men's attractiveness to women (Rhodes et al., 2005; Rhodes, 2006). Masculine traits are characterized by a large jaw, prominent brow ridge and cheekbones, whereas asymmetries arise from deviations from perfect symmetry in bilateral traits (Rhodes, 2006). Average faces and bodies have the arithmetic mean of traits values for a population. Individuals who are high in averageness are low in distinctiveness (Rhodes, 2006). Masculinity, symmetry and averageness of human faces and bodies are thought to be signals of mate quality in humans (Thornhill & Gangestad, 1999). Masculinity may signal immunocompetence (Folstad & Karter, 1992), and facial masculinity is associated with health during adolescent development in males (Rhodes et al., 2003). Symmetry and averageness are thought to reflect an individual's ability to cope with environmental and genetic stresses throughout the development (Fink & Penton-Voak, 2002). In particular, measured body fluctuating asymmetry (FA) has been linked to general health (for a review, see Thornhill & Moller, 1997) as well as to semen quality in men (Manning et al., 1998; Firman et al., 2003). The potential for masculinity, symmetry and averageness to signal aspects of mate quality, and the established link between body FA and semen quality, prompted us to extend our study to investigate the relationships between rated perceptions of these attractiveness traits and semen quality.

To examine the phenotype-linked fertility hypothesis in humans, we assessed semen quality in a large sample of adult males and compared this with ratings of attractiveness. Because both face and body attractiveness contribute to overall attractiveness (Peters et al., 2007), which is generally the most relevant to mate choice. ratings for both were collected and then combined into a single attractiveness component. A number of studies have found increases in female preferences for putative signals of mate quality at the fertile point of the menstrual cycle (Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000; DeBruine et al., 2005; and see Puts, 2006 for a review). Like Soler et al. (2003), we therefore included attractiveness ratings from high- and low-fertile points of the menstrual cycle from a second group of females. This additional group of raters also provided an independent set of attractiveness ratings. Our study extends that of Soler *et al.*'s by using a larger male sample, examining the associations between semen quality and both face and body ratings of attractiveness, and determining which, if any of the attractive traits masculinity, symmetry and averageness, are linked with male fertility.

Method

Participants

One hundred and eighteen male participants (mean age 22.5, SD 4.9, range 18–35 years) were recruited by advertisement at the University of Western Australia. All males were heterosexual and caucasian. An upper age limit of 35 years was set for this study in order to avoid the potential decrease in semen quality that can occur beyond this age (Rolf & Nieschlag, 1997, 2001; Piñón, 2002).

Participant procedure

Each male participant was photographed wearing a white fitted singlet and dark-coloured shorts. Both full-length body and close-up face photos were taken. The participants were asked to adopt a neutral expression and to stand with their feet slightly apart, with their arms relaxed by their sides.

Each participant completed a questionnaire regarding lifestyle factors that can potentially affect semen quality. This questionnaire was based on that of Kilgallon & Simmons (2005), and contained questions about medications, sedentary patterns, alcohol consumption, cigarette use, illicit drug use, caffeine consumption, weekly sexual activity, location of childhood upbringing, mobile phone placement, dietary habits and exposure to other environmental factors. Participants also returned self-measured (using vernier callipers) testes dimensions, from which testes volume was calculated using the formula for an ovoid $[4/3 \times \pi \times (\text{length/2}) \times (\text{width/2})^2]$. Self-measured testes volume is highly repeatable and provides a good estimate of testes size (Simmons *et al.*, 2004a).

Ratings of appearance variables

Attractiveness

Female ratings of attractiveness for each male face and body were collected according to the method outlined by Rhodes *et al.* (2005). The face photograph of one participant was excluded because it was out of focus. Attractiveness was rated on a seven-point scale (1 = notattractive; 7 = very attractive), in the context of a short-term sexual partner, and raters were encouraged to use the whole range of the scale. Photographs were presented in two blocks, one comprising faces only and the other comprising bodies only (randomized within each block), and each photograph remained on the screen until a rating was made. An attractiveness score for each male face and body was calculated by averaging across all raters. The mean age of the first rater set was 19.9 years (SD = 3.8, range = 17-28, n = 12). There were no specific participation requirements for these women other than being caucasian and heterosexual, as for to the male sample.

A second set of 27 caucasian, heterosexual females not using any form of hormonal contraception, and with regular menstrual cycles was recruited to rate the photographs for attractiveness at a high- and low-fertile point of the menstrual cycle. Each rater used an OvuPlan (Key Pharmaceuticals, NSW, Australia) or Confirm (Mentholatum Australia, Victoria, Australia) ovulation predictor kit that determines a surge in luteinizing hormone - the hormone that triggers ovulation. Two of these females did not ovulate, thus, were excluded from the analyses. The mean age of the remaining 25 raters was 28.9 years (SD = 3.4, range = 23-34). During the high-fertile testing session, females rated the faces and bodies within 48 h of a luteinizing hormone surge, which are the days most likely to result in conception following intercourse (Wilcox et al., 2001). Females were also tested during the luteal phase of the menstrual cycle. This phase occurs after ovulation but before the onset of menses, and is associated with a very low chance of conception. Half of the participants rated the photographs first at ovulation and second during the luteal phase and half vice versa. Inter-rater agreement was very high for both sets of raters, and across ratings made by females tested at high and low fertility (all Cronbach's $\alpha \ge 0.9$).

Attractive traits

Face and body ratings of attractive traits (masculinity, symmetry and distinctiveness) were also collected on a seven-point scale using the same method as described earlier. A verbal description of symmetry and masculinity was given to participants prior to commencement of the testing session. Participants were asked to rate distinctiveness (in terms of 'how much would this face/body stand out in a crowd') rather than averageness because it is easier to conceptualize and explain. Distinctiveness ratings were then reverse-scored in order to produce averageness scores (i.e. a face given a distinctiveness score of 1 was reverse-scored to have an averageness score of 7, a distinctiveness score of 2 was reverse-scored as 6, etc). Each of the three appearance variables was rated by a different group of 12 females to ensure each variable was independently assessed. The mean age of all raters was 21.6 years (SD = 4.9, range = 17-34, n = 36). Inter-rater agreement was high for ratings of face and body masculinity (Cronbach's $\alpha \ge 0.9$) and symmetry (Cronbach's $\alpha \ge 0.7$), but lower for distinctiveness (averageness) ratings (face = 0.6 and body = 0.4). A score for each appearance variable was calculated by averaging across raters.

Semen analyses

Each participant was given clear instructions regarding collection of the semen sample. Participants were asked to abstain from intercourse and masturbation for a minimum of 48 h and a maximum of 6 days prior to providing the sample. The semen sample was collected by masturbation into a sterile vial. Vials were wrapped in insulating foil to maintain temperature, and delivered to the laboratory within 1 h of collection in order to minimize the risk of reduction in motility over time. Participants were asked to record how long it took to collect their semen sample, the exact time of semen collection, and the time since their previous ejaculation.

Sperm concentration, motility and morphology were assessed according to World Health Organization (WHO) protocol (WHO, 1999). To ensure accurate assessment of semen quality, one of the experimenters (Marianne Peters) was trained by a qualified seminologist at the Hollywood Fertility Centre (Nedlands, WA, Australia) and assessed using the Fertility Society of Australia's External Quality Assurance Scheme for Reproductive Medicine. Marianne Peters' results fell within the range of results obtained by fertility clinics in the Australiasian region.

Immediately after delivery of the semen sample to the laboratory, and following liquefaction, the reduction in viscosity that occurs in normal semen samples within 60 min (WHO, 1999), the sample was assessed for motility. A 10-µL aliquot was placed onto a slide, with a cover slip and examined under 400× magnification using bright-field illumination. One hundred and thirty spermatozoa per sample were categorized into four motility categories: (A) rapid progressive (> 5 head lengths per second), (B) slow or sluggish progressive, (C) nonprogressive but still motile (velocity < 5 μ m s⁻¹) and (D) immotile. For further analyses, the proportion of sperm exhibiting A and B motility categories was summed and provided an estimate of progressive motile sperm (World Health Organization, 1999). Sperm concentration (number of sperm \times 10⁶ mL⁻¹ semen) was determined following dilution in fixation medium, by counting sperm present in $5 \times 1 \text{ mm}^2$ cells in each of two chambers of a Neubauer haemocytometer, at 400× magnification. The count from each of the two chambers was averaged to provide a measure of sperm concentration. To assess morphology, smears were prepared from a $5-\mu L$ drop of semen. These were left to air dry and stained using the Diff-Quik stain (Baxter Diagnostics, Inc., McGraw Park, IL, USA). Two hundred sperm cells were examined under oil immersion at 1000× magnification, and categorized as 'normal' or 'abnormal', according to World Health Organization (1999) guidelines. The percent of sperm with normal morphology was used in subsequent analyses.

Data reduction and statistical analyses

All data were tested for normality with the Shapiro-Wilks normality test and transformed where necessary (face and body attractiveness ratings from Set 1 female raters were log transformed, and sperm motility was arcsin square root transformed). Note that although 118 males participated, the maximum *n* in this study is 116. Data were missing for some of the variables, in particular because of participants failing to complete the lifestyle questionnaire of fully and also because of equipment failure when semen samples were delivered to the laboratory. As a consequence of these empty cells in the data files, there is some minor variation in *n* (ranging from 101 to 116), dependent on which variables were used in each statistical analysis. Additionally, data from one male participant were excluded from all analyses because of an abnormally high sperm concentration $(626 \times 10^6 \text{ sperm})$ per millilitre). All analyses for this study were performed using spss 13 for Mac OSX (SPSS Inc., Illinois, USA).

To reduce face and body ratings to a single overall appearance component for each phenotypic variable, separate principal component analyses (PCAs) were performed to combine face and body ratings of attractiveness, masculinity, symmetry and averageness, respectively (Table 1). The four resulting appearance principal component scores (PCSs) were used in subsequent analyses.

Following Soler *et al.* (2003), we also conducted a PCA that incorporated all the three semen quality parameters (i.e. sperm motility, morphology and concentration) into a single measure, which is the score on the first principal component that we refer to as the Sperm Index (eigenvalue = 1.35; variance explained = 45.1%; eigenvector motility = 0.60, morphology = 0.63, concentration = 0.50).

Semen quality is highly sensitive to environmental and lifestyle factors (Aitken *et al.*, 2004). To control for factors associated with lifestyle, we ran general linear models with each semen quality parameter as the dependent variable and lifestyle factors entered as independent variables. We also entered testes size and the potentially important procedural variables, time to produce the

Table 1 Principal component analyses

 combining ratings of appearance variables for

faces and bodies.

semen sample, time since previous ejaculation and time from ejaculation to semen analysis, as independent variables. Each nonsignificant variable was removed by stepwise deletion, and the model was re-run at each step until only significant variables remained. Significant models were obtained for sperm concentration and the Sperm Index, but no significant lifestyle or procedural factors were associated with sperm motility or morphology in our sample. For sperm concentration, variables remaining in the final model ($F_{5,90} = 7.16$, P < 0.001) were time since last ejaculation ($F_{1.90} = 8.97$, P < 0.01), exposure to toxins (e.g. lead, pesticides and organic solvents; $F_{1,90} = 7.18$, P < 0.01), use of antibiotics and/ or medication ($F_{1.90} = 4.86$, P = 0.03), exposure to heat (including fever, wearing tight underwear and regular exposure to a heated environment; $F_{1,90} = 8.82$, P < 0.01) and time taken to produce the ejaculate $(F_{1.90} = 3.99, P < 0.05)$. The only significant variable remaining for the Sperm Index model was amount of sexual activity per week ($F_{1,100} = 8.25$, P < 0.005). The residuals from each of these significant final models were used for subsequent analyses of sperm concentration and Sperm Index.

Results

Descriptive statistics for each of the semen quality parameters are shown in Table 2. Each of the mean values obtained from this sample of males was above the minimum criteria for normal semen as outlined by World Health Organization (1999) (motility > 50%) sperm with forward progression; morphology > 15% normal forms; concentration > 20×10^6 sperm per millilitre). Screening analyses revealed very high correlations between the three sets of attractiveness ratings (Set 1 females, Set 2 females, low fertility and Set 2 females, high fertility) (Table 3). Attractiveness was also significantly correlated with masculinity and symmetry but not with averageness (Table 3). We note that averageness may not have been attractive in this sample because of a low inter-rater agreement for these ratings. Analyses of averageness scores nevertheless have been included for completeness.

	Attractiveness				
Attractiveness [†]	LF‡	HF‡	Masculinity	Symmetry	Averageness
1.49	1.47	1.44	1.47	1.16	1.08
74.50	73.64	72.10	73.4	57.84	53.77
0.71	0.86	0.85	0.71	0.71	0.71
0.71	0.86	0.85	0.71	0.71	0.71
	Attractiveness [†] 1.49 74.50 0.71 0.71	Attractiveness* Attractiveness* 1.49 1.47 74.50 73.64 0.71 0.86 0.71 0.86	Attractiveness* Attractiveness 1.49 1.47 1.44 74.50 73.64 72.10 0.71 0.86 0.85 0.71 0.86 0.85	Attractiveness HF [‡] Masculinity 1.49 1.47 1.44 1.47 74.50 73.64 72.10 73.4 0.71 0.86 0.85 0.71 0.71 0.86 0.85 0.71	$\begin{array}{c c c c c c c c c c c c c c c c c c c $

Separate PCAs were performed for each appearance variable.

[†]Female raters from Set 1.

[‡]Female raters from Set 2.

LF, Low fertility ratings; HF, High fertility ratings.

Table 2 Average values (± SD) for semen quality variables.

Mean (± SD)	п	
62.4 (± 16.8)	105	
35.0 (± 8.2)	113	
90.7 (± 62.2)	108	
0.0 (± 1.1)	102	
	Mean (± SD) 62.4 (± 16.8) 35.0 (± 8.2) 90.7 (± 62.2) 0.0 (± 1.1)	

Semen quality was analyzed according to World Health Organization (1999) criteria.

Motility = percentage of sperm with forward progression.

Morphology = percentage sperm with normal forms.

Concentration = number of sperm $\times 10^6$ mL⁻¹ semen.

Attractiveness ratings from both sets of female raters were not correlated with the semen quality parameters in this sample, even when females rated males at the fertile point of the menstrual cycle (Table 4). Furthermore, there were no significant correlations between semen quality parameters and any of the attractive traits (masculinity, symmetry or averageness) (Table 5).

Our sample contained 44 men who had one or more semen parameters that fell below the minimum WHO criteria for normal semen. These men did not differ in appearance variables from the 72 men with normal semen parameters (attractiveness: $t_{114} = 0.550$, P = 0.583; masculinity: $t_{114} = 1.057$, P = 0.293; symmetry: $t_{114} = -1.069$, P = 0.287; averageness: $t_{114} = -1.131$, P = 0.0.261).

The use of raw semen quality data (without controlling for lifestyle factors) or separate face and body ratings (rather than the combined face/body PCS) in our analyses made no qualitative or quantitative differences to the results.

Discussion

Using a large sample of Australian men, we found no associations between attractiveness and semen quality, even when women rated attractiveness at the fertile

Table 4	Zero-order	correlations	between	attractiveness	and	semen
quality v	ariables.					

	Females – Set 1	Females – Set 2			
		Low fertility risk	High fertility risk		
Motility ($n = 104$)	0.035	-0.052	-0.020		
Morphology ($n = 112$)	0.001	-0.091	-0.058		
Concentration ($n = 107$)	-0.053	-0.054	-0.075		
Sperm Index ($n = 101$)	-0.007	-0.029	-0.026		

Attractiveness ratings are by two independent sets of females.

 Table 5
 Zero-order correlations between attractive traits and semen quality variables.

.000

point of their menstrual cycle, when male fertility might be expected to be of greatest importance. Furthermore, no relationship was found between semen quality and masculinity, symmetry or averageness. Insofar as attractiveness indicates mate quality, our study suggests that the visual attractiveness does not provide women with cues to male reproductive potential.

Our data do not support the findings of Soler *et al.* (2003). The importance of replication, even when methods differ, has been clearly demonstrated by studies examining the relationship between attractiveness and health (see Weeden & Sabini, 2005 for a review). There are strong arguments that attractiveness is a certificate of health (Grammer *et al.*, 2003; Weeden & Sabini, 2005), and certainly attractiveness is correlated with rater perceptions of health (Kalick *et al.*, 1998; Jones *et al.*, 2001; Henderson & Anglin, 2003; Rhodes *et al.*, 2003).

		Attractiveness			
	Attractiveness [†]	LF [‡]	HF [‡]	Masculinity	Symmetry
Attractiveness [†]	1				
Attractiveness LF [‡]	0.926***	1			
Attractiveness HF [‡]	0.927***	0.960***	1		
Masculinity	0.668***	0.716***	0.703***	1	
Symmetry	0.479***	0.457***	0.440***	0.407***	1
Averageness	-0.074	-0.038	-0.069	0.032	-0.083

***P < 0.001.

[†]Female raters from Set 1.

[‡]Female raters from Set 2.

LF, Low fertility ratings; HF, High fertility ratings.

n = 116. Note some individuals had missing cells for semen data, making n < 116 for analyses

of semen parameters (see Table 2 for values of *n*).

Table 3 Zero-order correlations betweenoverall attractiveness ratings, and ratings ofcomponents of attractiveness: symmetry,masculinity and averageness.

However, studies investigating the correlation between attractiveness and actual health yield mixed results, particularly for males (Weeden & Sabini, 2005). For example, Henderson & Anglin (2003) and Shackelford & Larsen (1999) found significant, positive correlations for men, whereas those by Hume & Montgomerie (2001) and Kalick *et al.* (1998) found no correlations. Consequently, evolutionary biologists exercise caution when making assumptions about health benefits of an attractive mate. Although of significant value, attempts to replicate studies in ecology and evolution are generally lacking (Palmer, 2000).

There are a number of key differences between our study and that of Soler et al. (2003) that could account for the different findings. Firstly, our ratings were on a seven-point scale as opposed to the 10-point scale used by Soler et al. (2003). Although a seven-point scale may reduce the variance of ratings, variance in ratings collected using a seven-point scale has been sufficient to produce significant correlations with other attractive traits and with sexual behaviour (see Rhodes et al., 2005). Secondly, Soler et al. (2003) studied only faces. We have improved on this by including bodies as well in our analyses, because both faces and bodies are important when making mate choice decisions (Peters et al., 2007). Incorporation of body appearance improves the biological relevance of our study. Thirdly, the determination of ovulation differs between the two studies; Soler et al. (2003) estimated ovulation using self-reported cycle lengths, and approximated fertility levels based on the probability of conception following sex on the day of testing. However, self-reported menstrual cycle length is prone to very high measurement error (Small et al., 2007). We therefore used ovulation predictor kits to confirm if and when ovulation occurred, which provided a more accurate and precise method of determining ovulation.

Although raw mean data for each of the semen quality variables collected during this study closely resemble those described in Soler et al. (2003), suggesting that our semen measurements are typical of an adult male population, our study did not reproduce the correlations found between attractiveness and semen quality parameters. In their study of 66 men, Soler et al. (2003) found significant correlations of approximately 0.3 between attractiveness and sperm motility, morphology and Sperm Index, but no correlation between attractiveness and sperm concentration. In a second experiment, Soler et al. chose a sub-sample of 12 men and classed them into groups of high, normal and low semen quality comprising four individuals per group. With this limited sample, they found higher correlations of around 0.6 between attractiveness and all semen quality parameters except sperm concentration. The semen quality of Soler et al.'s low group was considerably lower than the WHO criteria for normal semen, and it could be argued that their significant associations between attractiveness and semen quality could be due to the inclusion of these infertile men. However, our studies were based on a comparatively large sample of 118 men: a sample size that is greater than that of a number of other studies investigating phenotypic cues to semen quality (e.g. Firman *et al.*, 2003; n = 50; Manning *et al.*, 1998; n = 61; Soler *et al.*, 2003, n = 66). Importantly, our sample included 44 men with one or more semen traits that would be classified as below normal by WHO standards. The attractiveness of these men did not differ from that of men with normal or above normal semen quality.

Although our results suggest that females are not sensitive to visual cues to semen quality that are available in a static photograph, other studies suggest that male fertility is nonetheless reflected phenotypically via measured body FA (Manning et al., 1998; Firman et al., 2003). Both Manning et al. (1998) and Firman et al. (2003) found significant negative relationships between FA and semen quality parameters. Using ratings of symmetry, rather than measurements, the present study did not find a relationship between (a)symmetry and semen quality. It may be that measurement represents a more sensitive method for assessing the subtle phenotypic expression of traits that correlate with semen quality. Studies of face perception show that humans are finely attuned to the accurate detection of FA in faces (Simmons et al., 2004b), although the same may not be true for bodies (Rhodes & Simmons, 2007). Our data suggest that even if body asymmetry correlates with semen quality in humans, women may be unable to accurately perceive these phenotype-linked cues to fertility.

Several studies suggest that olfactory cues may be important in signalling mate quality. Body odour provides cues to genes associated with immune function [the major histocompatibility complex (MHC)], such that women are attracted to the smell of men with genes dissimilar to their own at the MHC (Wedekind & Furi, 1997). Furthermore, women show a preference for the scent of men with relatively low body asymmetry, particularly at the fertile point of the menstrual cycle, when conception is most likely (Thornhill *et al.*, 2003). Therefore, given the important cues to mate quality that can be conveyed through body odour, research incorporating olfactory cues may be useful to further investigate whether females are sensitive to signals of male fertility.

Determining biological markers of mate quality that are signalled by attractiveness in humans is a challenging task, particularly because of individual differences in grooming and lifestyle habits. Despite controlling for these variables, this study found no evidence that physically attractive males provide females with reproductive benefits via increased semen quality. Therefore, the phenotype-linked fertility hypothesis does not seem to be generally applicable to human mate choice.

Acknowledgments

The authors thank Phillip Matson from Hollywood Fertility Centre for providing semen analysis training; Bonds for donating singlets for the male participants; and Key Pharmaceuticals and Mentholatum Australasia for donating ovulation predictor kits. This work was supported by the University of Western Australia and the Australian Research Council. All research was approved by the UWA Human Research Ethics Committee (Project number: 1074).

References

- Aitken, R.J., Koopman, P. & Lewis, S.E.M. 2004. Seeds of concern. *Nature* 432: 48–52.
- Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton.
- Birkhead, T.R. & Petrie, M. 1995. Ejaculate features and sperm utilization in peafowl pavo cristatus. *Proc. R. Soc. Lond. B Biol. Sci.* **261**: 153–158.
- Birkhead, T.R., Buchanan, K.L., Devoogd, T.J., Pellatt, E.J., Szekely, T. & Catchpole, C.K. 1997. Song, sperm quality and testes asymmetry in the sedge warbler. *Anim. Behav.* 53: 965– 971.
- DeBruine, L.M., Jones, B.C. & Perrett, D.I. 2005. Women's attractiveness judgments of self-resembling faces change across the menstrual cycle. *Horm. Behav.* **47**: 379–383.
- Fink, B. & Penton-Voak, I. 2002. Evolutionary psychology of facial attractiveness. *Curr. Dir. Psychol. Sci.* 11: 154–158.
- Firman, R.C., Simmons, L.W., Cummins, J.M. & Matson, P.L. 2003. Are body fluctuating asymmetry and the ratio of 2nd to 4th digit length reliable predictors of semen quality? *Hum. Reprod.* **18**: 808–812.
- Folstad, I. & Karter, A.J. 1992. Parasites, bright males, and the immunocompetence handicap. *Am. Nat.* **139**: 603–622.
- Gangestad, S.W. & Scheyd, G.J. 2005. The evolution of human physical attractiveness. *Annu. Rev. Anthropol.* 34: 523–548.
- Grammer, K., Fink, B., Moller, A.P. & Thornhill, R. 2003. Darwinian aesthetics: sexual selection and the biology of beauty. *Biol. Rev.* **78**: 385–407.
- Henderson, J.A. & Anglin, J.M. 2003. Facial attractiveness predicts longevity. *Evol. Hum. Behav.* 24: 351–356.
- Hume, D.K. & Montgomerie, R. 2001. Facial attractiveness signals different aspects of 'quality' in women and men. *Evol. Hum. Behav.* **22**: 93–112.
- 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. *Evol. Hum. Behav.* 22: 417–429.
- Kalick, S., Zebrowitz, L.A., Langlois, J.H. & Johnson, R.M. 1998. Does human facial attractiveness honestly advertise health? Longitudinal data on an evolutionary question *Psychol. Sci.* **9**: 8–13.
- Kilgallon, S. & Simmons, L.W. 2005. Image content influences men's semen quality. *Biol. Lett.* 1: 253–255.
- Kortet, R., Vainikka, A., Rantala, M.J. & Taskinen, J. 2004. Sperm quality, secondary sexual characters and parasitism in roach (Rutilus rutilus L.). *Biol. J. Linn. Soc.* **81**: 111–117.

- Locatello, L., Rasotto, M.B., Evans, J.P. & Pilastro, A. 2006. Colourful male guppies produce faster and more viable sperm. *J. Evol. Biol.* **19**: 1595–1602.
- Malo, A.F., Roldan, E.R.S., Garde, J., Soler, A.J. & Gomendio, M. 2005. Antlers honestly advertise sperm production and quality. Proc. R. Soc. Lond. B Biol. Sci. 272: 149–157.
- Manning, J.T., Scutt, D. & Lewis-Jones, D.I. 1998. Developmental stability, ejaculate size, and sperm quality in men. *Evol. Hum. Behav.* 19: 273–282.
- Palmer, A.R. 2000. Quasi-replication and the contract of error: lessons from sex ratios, heritabilities and fluctuating asymmetry. *Annu. Rev. Ecol. Syst.* **31**: 441–480.
- Penton-Voak, I.S. & Perrett, D.I. 2000. Female preference for male faces changes cyclically: further evidence. *Evol. Hum. Behav.* 21: 39–48.
- Penton-Voak, I.S., Perrett, D.I., Castles, D.L., Kobayashi, T., Burt, D.M., Murray, L.K. & Minamisawa, R. 1999. Menstrual cycle alters face preference. *Nature* **399**: 741–742.
- Peters, M., Rhodes, G. & Simmons, L.W. 2007. Contributions of the face and body to overall attractiveness. *Anim. Behav.* 73: 937–942.
- Piñón, R. Jr 2002. Biology of Human Reproduction. University Science Books, Sausalito.
- Pizzari, T., Jensen, P. & Cornwallis, C.K. 2004. A novel test of the phenotype-linked fertility hypothesis reveals independent components of fertility. *Proc. R. Soc. Lond. B Biol. Sci.* 271: 51–58.
- Puts, D.A. 2006. Cyclic variation in women's preferences for masculine traits: potential hormonal causes. *Hum. Nat.* 17: 114–127.
- Rhodes, G. 2006. The evolutionary psychology of facial beauty. *Annu. Rev. Psychol.* **57**: 199–226.
- Rhodes, G. & Simmons, L. 2007. Symmetry, attractiveness, and sexual selection. In: Oxford Handbook of Evolutionary Psychology (L. Barrett & R. Dunbar, eds), pp. 333–364. Oxford University Press, Oxford.
- Rhodes, G., Chan, J., Zebrowitz, L.A. & Simmons, L.W. 2003. Does sexual dimorphism in human faces signal health? *Proc. R. Soc. Lond. B Biol. Sci.* 270: S93–S95.
- Rhodes, G., Simmons, L.W. & Peters, M. 2005. Attractiveness and sexual behavior: does attractiveness enhance mating success? *Evol. Hum. Behav.* 26: 186–201.
- Rolf, C. & Nieschlag, E. 1997. Senescence. In: Andrology (E. Nieschlag & H. M. Behere, eds), pp. 397–407. Springer, Berlin.
- Rolf, C. & Nieschlag, E. 2001. Reproductive functions, fertility and genetic risks of ageing men. *Exp. Clin. Endocrinol. Diabetes* **109**: 68–74.
- Shackelford, T.K. & Larsen, R.J. 1999. Facial attractiveness and physical health. *Evol. Hum. Behav.* **20**: 71–76.
- Sheldon, B.C. 1994. Male phenotype, fertility, and the pursuit of extra-pair copulations by female birds. *Proc. R. Soc. Lond. B Biol. Sci.* 257: 25–30.
- Simmons, L.W., Firman, R.C., Rhodes, G. & Peters, M. 2004a. Human sperm competition: testis size, sperm production and rates of extrapair copulations. *Anim. Behav.* 68: 297–302.
- Simmons, L.W., Rhodes, G., Peters, M. & Koehler, N. 2004b. Are human preferences for facial symmetry focused on signals of developmental instability? *Behav. Ecol.* 15: 864–871.
- Small, C.M., Manatunga, A.K. & Marcus, M. 2007. Validity of selfreported menstrual cycle length. Ann. Epidemiol. 17: 163–170.
- Soler, C., Nunez, M., Gutierrez, R., Nunez, J., Medina, P., Sanchoa, M., Alvarez, J. & Nunez, A. 2003. Facial attractiveness

in men provides clues to semen quality. *Evol. Hum. Behav.* 24: 199–207.

- Thornhill, R. & Gangestad, S.W. 1999. Facial attractiveness. *Trends Cogn. Sci.* **3**: 452–460.
- Thornhill, R. & Moller, A.P. 1997. Developmental stability, disease and medicine. *Biol. Rev. Camb. Philos. Soc.* **72**: 497–548.
- Thornhill, R., Gangestad, S.W., Miller, R., Scheyd, G., McCollough, J.K. & Franklin, M. 2003. Major histocompatibility complex genes, symmetry, and body scent attractiveness in men and women. *Behav. Ecol.* **14**: 668–678.
- Wagner, W.E. & Harper, C.J. 2003. Female lifespan and fertility are increased by the ejaculates of preferred males. *Evolution* **57**: 2054–2066.
- Wedekind, C. & Furi, S. 1997. Body odour preferences in men and women: do they aim for specific MHC combinations or

simply heterozygosity? Proc. R. Soc. Lond. B Biol. Sci. 264: 1471–1479.

- Weeden, J. & Sabini, J. 2005. Physical attractiveness and health in western societies: a review. *Psychol. Bull.* **131**: 635–653.
- Wilcox, A.J., Dunson, D.B., Weinberg, C.R., Trussell, J. & Baird, D.D. 2001. Likelihood of conception with a single act of intercourse: providing benchmark rates for assessment of postcoital contraceptives. *Contraception* 63: 211–215.
- World Health Organization 1999. WHO Laboratory Manual for the Examination of Human Semen and Sperm-Cervical Mucus Interaction, 4th edn. Cambridge University Press, Cambridge.

Received 16 August 2007; revised 1 November 2007; accepted 9 November 2007