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Original Article

Facial attractiveness and fertility in populations with low levels of modern birth control

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Abstract

Evolutionary models of human mate choice generally assume that physical attractiveness has evolved through sexual selection, i.e., it has been associated with higher mating opportunities and subsequent reproductive success across our evolutionary history. Here we investigate whether facial attractiveness is related to fertility in order to understand the extent to which selection can operate on attractive traits in modern populations. We used data from two populations where the prevalence of modern birth control methods is low and thus unlikely to disconnect mating opportunities from reproductive success: men and women from contemporary rural Senegal and men from the West Point Military Academy in the USA who graduated in 1950. We found that facial attractiveness negatively predicts age-specific reproduction in both sexes in Senegal and is independent from lifetime reproductive success in men from the USA. Overall, the results suggest that facial attractiveness is not under positive selection and raise questions about methodological approaches currently used to assess attractiveness.

Keywords: Sexual selection; Preferences; Mate choice; Reproductive success; Fitness

1. Introduction

Attractiveness can be defined as the ability of being preferred as a mate, and thus attractive traits are expected to indicate the reproductive value of an individual (Rhodes, Simmons, & Peters, 2005). There are two main hypotheses for the evolution of mating preferences: a runaway process (Fisher, 1930), predicting that an initial random preference for a trait can eventually lead to an increase in its frequency if attractive individuals have more offspring, and the good genes hypothesis (Hamilton & Zuk, 1982), which predicts that traits genuinely reflecting genetic quality are preferred. In humans, attractiveness encompasses several physical and psychological traits (Buss, 1989; Gangestad & Scheyd, 2005), and the facial phenotype, conveying critical information such as sex and health, is likely to play a key role in a mate choice context. There is also some evidence that facial attractiveness is more relevant than body attractiveness in hypothetical mate choice decisions (Currie & Little, 2009).

So far, three main properties have been suggested to influence facial attractiveness: symmetry, averageness, and sexual dimorphism (Rhodes, 2006). While several studies have found a relationship between these attractive traits and markers of mate quality (e.g., Rhodes, Chan, Zebrowitz, & Simmons, 2003; Thornhill & Gangestad, 1999), a considerable number of studies have failed to detect any significant link (e.g., Rhodes & Simmons, 2007; Zebrowitz & Rhodes, 2004). In addition, it is unclear whether markers of mate quality reflect genetic quality or are instead cues of the phenotypic condition of the individual, unrelated to genetic quality.

Finally, even if preferences towards facially attractive individuals have now been well established (Langlois et al., 2000), only a few studies have investigated whether these preferences are adaptive, i.e., whether facial attractiveness

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is heritable and is associated with higher fertility. Livshits & Kobyliansky (1989) found evidence for phenotypic similarity between parents and offspring for a combined measure of body and facial symmetry, while for the majority of specific facial measures, only a weak correlation was found. More recently, a study based on a sample of parent–offspring pairs from Scotland reported a significant positive correlation between parents' and daughters' facial attractiveness but not between parents and sons (Cornwell & Perrett, 2008). The association between facial attractiveness and reproductive success is also not clear. In the Ache of Paraguay, for instance, women with the most attractive faces were found to have 1.6 times higher fertility than those of average attractiveness (Hill & Hurtado, 1996: 312). In contrast, a study in Poland failed to find a correlation between women's facial attractiveness and the number of offspring (Pawlowski, Boothroyd, Perrett, & Kluska, 2008). However, according to a study based on a large sample of individuals from the USA, attractive men and women have, respectively, 12% and 16% more children than less attractive individuals (Jokela, 2009). Finally, a recent study found that attractive individuals in a sample of Slovak men are more likely to be married and consequently have higher number of children than unattractive individuals (Prokop & Fedor, 2011; but see Prokop, Obertová, & Fedor, 2010)

Besides the Ache study (Hill & Hurtado, 1996: 312), no other research has been conducted in a high-fertility and polygynous population with intense mating competition, although this socioecological setting is the most frequent among human societies (Marlowe, 2003). Moreover, in other studies, only short-term measures of reproductive success have been used (i.e., number of children). However, since the transition to low fertility rates observed in postindustrial populations is hypothesized to result from a higher demand of parental investment per child which possibly maximizes long-term reproductive success (Lawson & Mace, 2011), the use of multigenerational data may be required to investigate the fitness outcomes of facial attractiveness in modern populations.

The main objective of this study is to investigate whether facial attractiveness brings reproductive benefits in contemporary populations with low uptake of modern contraceptive methods. Indeed, modern birth control may not only lead to a disconnection between mating opportunities and fertility in men (Pérusse, 1993), but it is also possible that it affects mate preferences in both men and women (see Alvergne & Lummaa, 2010 for review). First, we used multigenerational historical data from the USA (men from the West Point Military academy born in the 1930s and graduating in the 1950s; note that the first birth control pill was available in 1960) to test whether facially attractive men have more children (completed fertility) and grandchildren. Second, we used data from contemporary rural Senegal where contraceptive prevalence is low [<15% (Wickstrom, Diagne, & Smith, 2006)] to investigate the link between facial attractiveness and age-specific reproduction in both men and women.

2. Materials and methods

2.1. Study populations

2.1.1. West Point Military Academy, VA, USA (35 men)

The sample is constituted of 35 men from the West Point Military Academy who graduated in the class of 1950 (see Mueller & Mazur, 1997 for details). Sociodemographic data were obtained in 1991 through postal questionnaires (Table 1). In the 1960s USA, fertility was moderate [total fertility rate in 1960=3.7 (World Bank, 2010)]; the sampled individuals are mostly Christians (82%), and remarriage is uncommon (14%). All participants gave their informed consent for the data collected to be used for research purposes.

2.1.2. Rural Senegal (62 men, 80 women)

In rural Senegal, fertility and mortality are high [total fertility rate=5.3 and infant mortality rate=61 deaths per 1000 births (APHRC, 2008)]. Most people are Muslims (>90%) and polygynous marriages are allowed (see Alvergne, Faurie, & Raymond, 2009 for details). Data were collected in 2006 through questionnaires administered in four villages situated around Sokone, a small town (~10,000 inhabitants) in southern Senegal (Table 2). Most people in the sampled populations are small-scale agriculturalists. However, the transition to a market economy has started (e.g., cash crops becoming more common than subsistence crops), and people frequently have secondary jobs in the main town. We obtained clearance from both the French National Committee of Information and Liberty and the ethical committee of the Senegalese National Research Council for Health, and also obtained informed consent from all participants.

2.2. Assessment of facial attractiveness

2.2.1. Pictures

We used 35 black and white facial pictures of men from the West Point Academy from the graduate class of 1950 taken at the time of graduation, with the ages of the individuals ranging from 21 to 26 years (mean±S.D.=22.7±1.4). We also used black and white pictures of 62 men and 80 women living in contemporary Senegal taken in 2006, with ages ranging from 26 to 69 years (mean±S.D.=46.4±9.2) in men and 18 to 53 years in women

Table 1
Descriptive statistics—USA (men)

	Mean (S.D.)	*n*
Age	22.7 (1.4)	35
Number of children	3.9 (1.7)	35
Number of grandchildren	3.7 (2.7)	35
Rank		35
Lieutenant colonel		7
Colonel		18
Brigadier general		3
Major general		2
Lieutenant general		1
"Full" general		4

Table 2
Descriptive statistics—Senegal (men and women)

	Men		Women	
	Mean (S.D.)	*n*	Mean (S.D.)	*n*
Age	46.7 (9.2)	62	36.2 (8.0)	80
Number of children	5.5 (3.2)	62	5.4 (2.6)	80
Number of wives	1.4 (0.6)		–	
1		44	–	–
2		16	–	–
3		1	–	–
4		1	–	–
Wealth (FCFA)	2,814,456 (3,128,257)		3,064,446 (3,338,459)	
1st quartile	734,957 (416,651)	14	940,654 (370,106)	15
2nd quartile	1,671,857 (257,498)	17	1,723,657 (241,732)	26
3rd quartile	2,544,947 (349,836)	14	2,507,410 (345,332)	16
4th quartile	6,047,063 (4,710,779)	17	6,128,141 (4,746,063)	23
Level of education	1.1 (0.8)		0.5 (0.3)	
University		1		0
Secondary school		20		3
Primary school		28		18
No schooling		13		59

(mean±S.D.=36.2±8.0). In both samples, each facial picture depicts an individual in a front view and displaying a neutral facial expression (see Fig. 1). All the backgrounds were homogenized using Photoshop CS3.

2.2.2. Principle

Facial pictures were presented in pairs to judges of the opposite sex. Each judge was then asked in his or her native language to indicate who represented the most

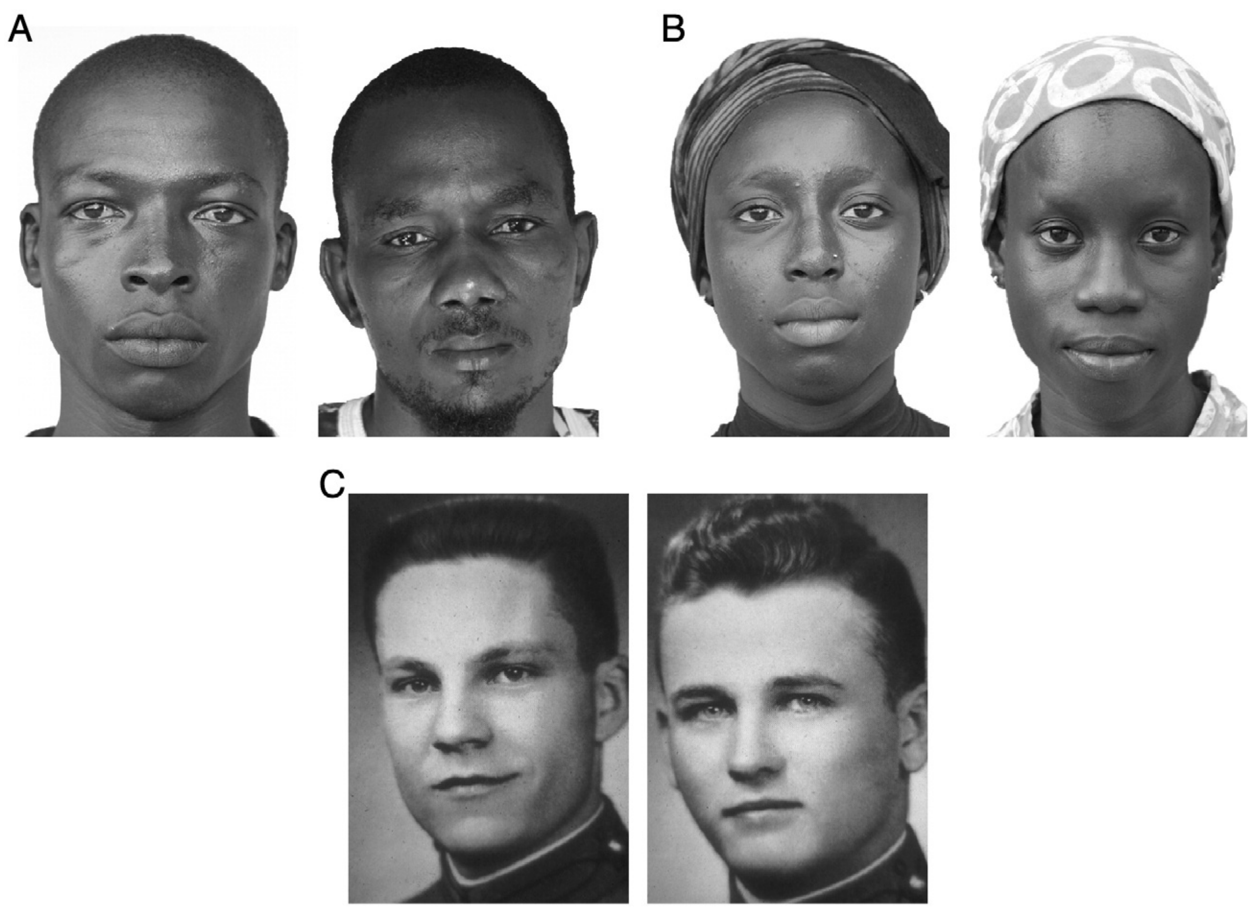

Fig. 1. Photos of Senegalese and American individuals similar to the ones used in the attractiveness tests. Due to ethical issues, the individuals in these photos are not the same as the ones included in the analysis (A, Senegalese men; B, Senegalese women; C, American men).

attractive individual within the same-sex pair (Fig. 1). We used this method in order to sample all possible pairs of individuals multiple times. An alternative scaled rating technique, such as a Likert scale, can arguably introduce variation that does not reflect genuine variation of the attractiveness of an individual but is in fact an artifact of the rating scale (Friedman & Amoo, 1999), while in paired choice method, the variation comes mostly from the pictures.

We used a computer program (written in Delphi 7) to randomize the order and the side (left or right) of the screen on which each image was displayed. Each judge was confronted with paired images, and each pair of images was presented only once to each judge, with the pair composition randomly assigned by the program. The paired images were randomly selected within a 10-year age range of each other; for example, the image of a 35-year-old man was only displayed alongside images of men ranging from 30 to 40 years.

The validity of the test was checked as follows. At the end of each test, three previously shown pairs (excluding the last one) were displayed again to evaluate the consistency of the judge. A score of 0 to 3 was recorded depending on whether the judge's choice was the same as in the previous tests or not. Judges with scores of 0 and 1 were excluded from the analysis.

2.2.3. Ratings

The attractiveness ratings for the men of the West Point Military Academy were performed by Caucasian women. These tests were conducted over two weeks in June 2010 at a café at the UCL campus in London, UK (61 judges, 3150 tests). Each picture was judged on average 51 times. The facial attractiveness of Senegalese men and women was rated by Senegalese judges in Senegal. The tests were conducted in July 2010 in the same region but in different villages from where the participants originated in order to avoid familiarity bias when judging the attractiveness of individuals (Hume & Montgomerie, 2001). A total of 240 judges (N men=120, N women=120) performed a total of 15,676 valid comparisons, with each picture being shown an average of 73 times. The judge's age was also recorded (mean±S.D.=30.±12.4). In order to prevent the loss of concentration by the judges rating the photos, we designed the tests to last less than 10 min for each judge.

Interjudge agreement on facial attractiveness is a nonlinear function of mean facial attractiveness. Each judge has seen a given pair only once, so the proportion of similar ratings for an individual within a given pair can be taken as a proxy for interjudge agreement. In all samples, interjudge agreement was high for individuals with high and low attractiveness, but low for individuals with intermediate attractiveness (Figure 2 in Supplementary Web Material, available on the journal's Web site at www.ehbonline.org).

2.3. Demographic and socioeconomic data

2.3.1. West Point Military Academy

Reproductive success corresponds to (1) the number of surviving offspring (completed fertility) and (2) the number of surviving grand-offspring. Note that this latter measure is likely to be incomplete for some men as some might have had more grand-offspring after the year of data collection (average age of men±S.D. at the time of data collection=62.7±1.4). Remarriage was not considered as a proxy for reproductive success as it only concerns five men in this sample. Age and military rank were previously found to be associated with reproductive success in this population (Mueller & Mazur, 1997) and were thus considered as control variables. In particular, the highest military rank achieved was used to infer socioeconomic status (SES). It corresponds to a continuous variable in ascending order: major, lieutenant colonel, colonel, brigadier general, major general, lieutenant general, and "full" general.

2.3.2. Rural Senegal

Age-specific reproduction corresponds to the marital status for men (N monogamous=44, N polygynous=18) and the number of surviving children to age 1 for both men and women. Two variables were used to describe SES (1) the accumulated monetary value [in the local currency (FCFA)] of the area of owned land and the number and type of livestock (weighed by their monetary value) that each individual possessed in 2006 (continuous variable) and (2) the highest level of education that the individual had completed (ordinal variable: no school, primary schooling, secondary school, and university). Finally, age was obtained from multiples sources that were then compared, i.e., birth certificates when available, interviews with the individuals and with family members, and information on major political or historical events around the time of birth.

2.4. Statistical analysis

Analyses have been performed separately for the two populations. As several judges rated a participant's facial picture (and in a different pair for each judge), the overall data set was characterized by pseudoreplication. This was taken into account by using mixed-effect models in which the identity of the participant was included as a random effect. The use of best unbiased linear predictors allows correcting effect sizes for the correlation between the pseudoreplicates within each group (Bates & Sarkar, 2007; Crawley, 2007).

First, a model was built to investigate the characteristics of the judges on attractiveness ratings (i.e., mixed models in which the age of the judge was included as a fixed effect). Judge's age was not found to influence attractiveness ratings and was not included in the working models. Second, whether attractiveness plays a role in fitness-related traits was investigated. As the variable describing attractiveness of a given participant is relative to the attractiveness of the participant he/she is paired with (binary variable: 1=chosen, 0=not chosen), all other variables were created so as to represent differences between the paired individuals in each test (e.g., difference in number of offspring, difference in SES). Several generalized linear mixed models were then run in which the following response variables were considered: (1) difference in number of living children (Senegal and USA), (2) difference in number of living grandchildren (USA), and (3) difference in the number of wives (Senegal). All response variables were normally distributed (Shapiro test $p<.001$). Facial attractiveness was included as an explanatory variable, along with confounding control variables (see Tables 1 and 2). We also ran models to investigate whether facial attractiveness mediates age at first reproduction, as individuals from the Senegal sample had not all completed their reproductive period. We used a smaller subsample of Senegalese men and women for whom we had these data available.

Model selection based on information theoretic methods using the Akaike information criterion (AIC) was used to quantify the strength of evidence for the competing alternative models (Akaike, 1974; Burnham & Anderson, 1998) that were constructed in order to understand the effect of facial attractiveness on individual's reproductive behavior. Models were ranked by second-order AIC (AICc) to account for the small sample sizes. Akaike weights (w_i), based on the likelihood of a candidate model explaining the data given the model set, were then used to compare the different models (Burnham & Anderson, 1998). Parameters' estimates were calculated through model averaging across models in order to reduce the uncertainty and relative bias of calculating parameters' estimates using only the best fitted model (Anderson, Burnham, & Thompson, 2000). All analyses have been carried out using the lme4 (Bates & Sarkar, 2007) and AICcmodavg (Mazerolle, 2011) packages for R 2.12.1 (R Development Core Team, 2011).

3. Results

Using data from two contemporary populations where the use of modern contraception is limited, we did not find support for facial attractiveness being under positive selection. We found facial attractiveness to be negatively associated with age-specific number of grandchildren in the USA and with age-specific number of children in men and women in rural Senegal, and independent from the completed number of children in the USA. This suggests that attractive individuals do not achieve a higher fitness. Results are provided in Tables 3 and 4.

3.1. Men from the West Point Military Academy, USA

3.1.1. Is facial attractiveness associated with reproductive success?

First, facial attractiveness is not associated with lifetime reproductive success [i.e., the number of children, fertility completed; β=−0.06, 95% confidence interval (CI) (−0.19, 0.06); Table 4]. The relationships are controlled for age on the picture [β=−0.28, 95% CI (−0.33, −0.24); Table 4] and the highest military rank achieved [β=−0.05, 95% CI (−0.09; −0.01); Table 4]. That facial attractiveness is a poor predictor of lifetime reproductive success is also supported by the low weight associated with the model assuming a relationship (w_i=0.37; Table 3). Second, facial attractiveness is negatively

Table 3
Sets of candidate models and model selection

Model	K	logLik	ΔAICc	w_i
Number of children—Senegal (men; *n*=62)				
Control 1 (wealth+education+no. wives+age)+attractiveness	8	−11,394.11	0.0	0.93
Control 1 (wealth+education+no. wives+age)	7	−11,397.73	5.2	0.07
Control 2 (wealth+education+age)+attractiveness	7	−11,583.03	375.9	<0.01
Null model	3	−11,831.76	865.3	<0.01
Number of wives—Senegal (men; *n*=62)				
Control (wealth+education+age)	6	−4302.79	0.0	0.68
Control (wealth+education+age)+attractiveness	7	−4302.56	1.5	0.32
Null model	3	−4372.04	132.5	<0.01
Number of children—Senegal (women; *n*=80)				
Control (wealth+education+no. co-wives+age)+attractiveness	8	−10,149.93	0.0	0.64
Control (wealth+education+no. co-wives+age)	7	−10,151.51	1.2	0.36
Null model	3	−10,684.98	1060.1	<0.01
Number of children—USA (men; *n*=35)				
Control (rank+age)	5	−6165.02	0.0	0.63
Control (rank+age)+attractiveness	6	−6164.54	1.1	0.37
Null model	3	−6239.71	145.4	<0.01
Number of grandchildren—USA (men; *n*=35)				
Control 2 (no children+rank+age)+attractiveness	7	−7348.07	0.0	1
Control 2 (no children+rank+age)	6	−7385.21	72.3	<0.01
Control 1 (rank+age)	5	−7592.25	484.4	<0.01
Null model	3	−7608.00	511.9	<0.01

Models are ranked according to their AICc. *K*, number of parameters in the model; logLik, log likelihood; ΔAICc, difference between AIC values; w_i, Akaike weights which indicate the strength of evidence that the model is the best approximating model for the data given the candidate model set.

associated with the number of grandchildren. Surprisingly, attractive men were found to have 0.83 less grandchildren than unattractive men [β=−0.83; 95% CI (−1.01, −0.64); Table 4]. This effect is likely to be strong, as the weight of the model including facial attractiveness is nearly 1 (Table 3). The role of facial attractiveness in predicting the number of grandchildren is unlikely to be mediated by its effect on the number of children, as it remains unchanged after the inclusion of this variable. It cannot be excluded, however, that children from attractive individuals start reproducing later than children from less attractive individuals, which could explain why facially attractive individuals have less grandchildren for their age. The relationship is controlled for military rank achieved at the end of the career and age at graduation when the picture was taken, with both having a positive effect in relation to age-specific number of grandchildren. Models ran without controlling for rank did not substantially alter the effect of facial attractiveness on either the number of children or the number of grandchildren.

3.2. Men and women from rural Senegal

3.2.1. Is facial attractiveness associated with age-specific reproduction in men?

First, we found that facially attractive men are not married to more wives for their age than less attractive individuals [β=−0.01, 95% CI (−0.04, 0.02); Table 4], which is further supported by the weak weight of the model including facial attractiveness (w_i=0.32, Table 3). Second, the results show that attractive men have 0.16 less surviving offspring for their age than unattractive men [β=−0.16; 95% CI (−0.28, −0.04); Table 4]. This is further supported by the large weight associated with the model including this variable (w_i=0.93; Table 3). The relationships are controlled for SES variables (wealth and education), age, and number of wives (Table 4). The effect of facial attractiveness on age-specific reproduction is not mediated by the number of wives, as excluding this variable from the models does not substantially alter the estimates [β=−0.17, 95% CI (−0.29, −0.05); unpublished results]. It is possible, however, that attractive individuals reproduce later than their less attractive counterparts, which would explain a negative link between facial attractiveness and age-specific reproduction. We thus ran a model on a subsample of individuals for whom we knew the age at first reproduction (N=32), but we did not find any evidence that facial attractiveness played a role in explaining the variation of the age at first birth (Table 4). We also ran models without controlling for SES, but the direction of the effect of facial attractiveness on the number of wives, number of children, and age at first birth remained.

3.2.2. Is facial attractiveness associated with age-specific reproduction in women?

Attractive women appear to have fewer children than unattractive women, but this effect is not strong [β=−0.09; 95% CI (−0.20, −0.01); Table 4]. The number of co-wives

Table 4
Model averaged estimates and unconditional CIs [β; (95% CI)]

USA (men)

Model	No. of children	No. of grandchildren
Predictor		
Attractiveness	−0.06 (−0.19, 0.06)	−0.83 (−1.01, −0.64)
Age	−0.28 (−0.33, −0.24)	0.14 (0.08, 0.21)
Rank	−0.05 (−0.09, −0.01)	0.23 (0.17, 0.29)
No. children	–	0.55 (0.50, 0.60)

Senegal (men)

Model	No. children	No. wives	Age at first birth
Predictor			
Attractiveness	−0.16 (−0.28, −0.04)	−0.01 (−0.04, 0.02)	−0.43 (−1.00, 0.13)
Age	0.19 (0.17, 0.21)	0.02 (0.01, 0.02)	0.38 (0.28, 0.47)
Wealth	−0.16 (−0.21, −0.1)	0.06 (0.05, 0.08)	−2.23 (−2.56, −1.90)
Education	−0.30 (−0.38, −0.22)	−0.05 (−0.07, −0.03)	1.20 (0.72, 1.68)
No. children	–	–	–
No. wives	1.08 (0.97, 1.19)	–	–

Senegal (women)

Model	No. children	Age at first birth
Predictor		
Attractiveness	−0.09 (−0.20, −0.01)	0.01 (−0.16, 0.18)
Age	0.22 (0.20, 0.24)	0.26 (0.23, 0.29)
Wealth	0.32 (0.27, 0.36)	0.63 (0.55, 0.71)
Education	−0.64 (−0.74, −0.54)	−0.60 (−0.77, −0.43)
No. children	–	−0.02 (−0.04, 0.00)
No. co-wives	−0.74 (−0.81, −0.67)	–

and the level of education also have a negative effect on the number of children, while wealth and age both have a positive effect (Table 4). We also ran a model for a subsample of the Senegalese women (N=47) with age at first birth as a response variable, but again, facial attractiveness did not play an important role in explaining the variation observed (Table 4). The effect of facial attractiveness did not substantially change when running the models without SES variables.

4. Discussion

Human mate preferences towards attractive individuals are now well established (Langlois et al., 2000), but whether these preferences are adaptive in contemporary populations is unclear. This study investigates the link between facial attractiveness and fertility in two populations where mating opportunities are likely to be translated into reproduction (i.e., rural Senegal and 1950s USA). Overall, the results suggest that facial attractiveness is not under positive selection in the populations studied, and in fact, we found that facial attractiveness is negatively associated with age-specific reproduction in women and men of Senegal and in men of the USA. Interestingly, in the case where lifetime reproductive success was informed (i.e., completed number of offspring in the military sample), it is found to be independent from facial attractiveness.

Why facial attractiveness either predicts lower age-specific reproduction or is independent from lifetime reproductive success is intriguing. One possibility is that preferences towards attractive individuals in experimental situations may not translate into actual mate choice. Still, other studies have found that attractive men have more sexual encounters (Rhodes et al., 2005; Weeden & Sabini, 2007) and are more likely to get married (Prokop & Fedor, 2011), which is expected to lead to a higher reproductive success, especially in societies with low prevalence of modern fertility control. Extrapair copulations (EPCs), although not measured in this study, are possibly facilitated by facial attractiveness, which could help explain the low recorded number of children of attractive men in Senegal. This could be related to differential strategies of parental investment, where unattractive individuals invest more in their offspring, increasing their survival chances, while attractive individuals can choose a strategy of low parental investment and increased number of EPCs. Our sample of American military men is likely to be skewed towards individuals who spend a long time away from their family and with a more dominant behavior than the general population, which could indicate reduced parental investment and higher occurrence of EPCs in this sample. The results for Senegal could also speculatively be explained by a reverse causality, where the attractiveness of an individual is altered due to the costs associated with raising children in a resource poor environment, and as a result, less attractive individuals could be found to have more children. The fact that the number of children in both men and women in Senegal predicted lower facial attractiveness, while controlling for age and SES, does give some support to this theory [men: β=−0.02, 95% CI (−0.04, 0); women: β=−0.02, 95% CI (−0.04, 0); unpublished results].

Taking into account the factors above could possibly shed further light on the proximate mechanisms mediating lower age-specific reproduction of attractive men, but this is nevertheless a surprising result. In contrast to the findings of this study, Jokela (2009) found attractive individuals to have higher number of children than unattractive individuals. This is possibly related to the large sample size used (1244 women and 997 men) which allowed to detect a weak directional selection gradient for facial attractiveness (β=0.06 in women, β=0.07 in men).

We are unsure how to interpret the differences found between the studies investigating the effect of facial attractiveness on reproductive success, but in the face of the negative nature of the results from this study and the lack of clear evidence from other studies on the selective pressures on facial attractiveness (Cornwell & Perrett, 2008; Pawlowski et al., 2008; Prokop et al., 2010), it is pertinent to question the current methodological approaches to quantify facial attractiveness. In this study, we are confident in the assessment of facial attractiveness from the two-dimensional (2D) frontal images shown, as demonstrated by the cross-cultural agreement between the Senegalese and British judges on the attractiveness of a subsample (N=16) of pictures of American individuals [r=0.60, 95 CI (0.10, 0.80), p=.02; unpublished results]. However, this does not indicate that we have actually measured the real-life attractiveness of the individuals in the photos, which may not have been captured by the static 2D images used in this study. Mate preferences have evolved through various cues which might not be fully detected by static photographs. Motion, for instance, is likely to play a crucial role in assessing facial attractiveness, and studies have indeed shown that facial attractiveness judgments significantly change between dynamic and static stimuli (Riggio, Widaman, Tucker, & Salinas, 1991; Rubenstein, 2005).

Mate choice preferences towards attractive individuals may have evolved in the past as a response to attractive traits being cues of mate quality (Hamilton & Zuk, 1982) and/or as result of a Fisherian runaway process where a random preference for a trait leads to the fixation of that preference in a population, even though that trait may be unrelated to quality (Fisher, 1930). Such preferences do not appear to be adaptive in the two populations studied, with facial attractiveness appearing to be under negative or no selection, suggesting that it may not be a reliable marker of mate quality. Indeed, studies have shown that preferences towards attractive individuals may not be related to accurate measures of mate quality, with the correlation between attractiveness and perceived health being significantly stronger than that with the actual health status of the individuals (Kalick, Zebrowitz, Langlois, & Johnson, 1998; Rhodes et al., 2003).

Alternatively, real-life attractiveness of individuals is not in fact being captured by static 2D images normally used in facial attractiveness research, and a broader set of stimuli should be used to assess attractiveness. We hope that these findings will spur further research into the selective pressures that act on facial attractiveness in contemporary populations.

Supplementary Materials

Supplementary data to this article can be found online at doi:10.1016/j.evolhumbehav.2012.01.002.

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References

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*, 716–723.

Alvergne, A., Faurie, C., & Raymond, M. (2009). Father–offspring resemblance predicts paternal investment in humans. *Animal Behaviour*, *78*, 61–69.

Alvergne, A., & Lummaa, V. (2010). Does the contraceptive pill alter mate choice in humans? *Trends in Ecology & Evolution*, *25*, 171–179.

Anderson, D. R., Burnham, K. P., & Thompson, W. L. (2000). Null hypothesis testing: problems, prevalence, and an alternative. *The Journal of Wildlife Management*, *64*, 912–923.

Bank, W. (2010). World development indicators. Washington, DC, USA: World Bank.

Bates, D., & Sarkar, D. (2007). lme4: linear mixed-effects models using S4 classes [CRAN Package].

Burnham, K. P., & Anderson, D. R. (1998). *Model selection and inference: a practical information-theoretic approach*. New York, U.S.A.: Springer-Verlag.

Buss, D. M. (1989). Sex differences in human mate preferences: evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, *12*, 1–14.

Center, A. P. H. R. (2008). *Africa population datasheet:* Population Reference Bureau and African Population & Health Research Center.

Cornwell, R. E., & Perrett, D. I. (2008). Sexy sons and sexy daughters: the influence of parents' facial characteristics on offspring. *Animal Behaviour*, *76*, 1843–1853.

Crawley, M. J. (2007). The R book. London, U.K.: Wiley.

Currie, T. E., & Little, A. C. (2009). The relative importance of the face and body in judgments of human physical attractiveness. *Evolution and Human Behavior*, *30*, 409–416.

Fisher, R. A. (1930). The genetical theory of natural selection. Oxford, U.K.: Clarendon.

Friedman, H. H., & Amoo, T. (1999). Rating the rating scales. *Journal of Marketing Management*, *9*, 114.

Gangestad, S. W., & Scheyd, G. J. (2005). The evolution of human physical attractiveness. *Annual Review of Anthropology*, *34*, 523–548.

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

Hill, K., & Hurtado, A. M. (1996). Ache life history: the ecology and demography of a foraging people. New York, U.S.A.: Hawthorne.

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

Jokela, M. (2009). Physical attractiveness and reproductive success in humans: evidence from the late 20th century United States. *Evolution and Human Behavior*, *30*, 342–350.

Kalick, S. M., Zebrowitz, L. A., Langlois, J. H., & Johnson, R. M. (1998). Does human facial attractiveness honestly advertise health? Longitudinal data on an evolutionary question. *Psychological Science*, *9*, 8–13.

Langlois, J. H., Kalakanis, L., Rubenstein, A. J., Larson, A., Hallam, M., & Smoot, M. (2000). Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychological Bulletin*, *126*, 390–423.

Lawson, D., & Mace, R. (2011). Parental investment and the optimisation of human family size. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 333–343.

Livshits, G., & Kobyliansky, E. (1989). Study of genetic variance in the fluctuating asymmetry of anthropometrical traits. *Annals of Human Biology*, *16*, 121–129.

Marlowe, F. W. (2003). The mating system of foragers in the standard cross-cultural sample. *Cross-Cultural Research*, *37*, 282–306.

Mazerolle, M. J. (2011). AICcmodavg [CRAN Package].

Mueller, U., & Mazur, A. (1997). Facial dominance in *Homo sapiens* as honest signaling of male quality. *Behavioral Ecology*, *8*, 569–579.

Pawlowski, B., Boothroyd, L. G., Perrett, D. I., & Kluska, S. (2008). Is female attractiveness related to final reproductive success? *Collegium Antropologicum*, *32*, 457–460.

Pérusse, D. (1993). Cultural and reproductive success in industrial societies: testing the relationship at the proximate and ultimate levels. *Behavioral and Brain Sciences*, *16*, 267–283.

Prokop, P., & Fedor, P. (2011). Physical attractiveness influences reproductive success of modern men. *Journal of Ethology*, *29*, 453–458.

Prokop, P., Obertová, Z., & Fedor, P. (2010). Paternity cues and mating opportunities: what makes fathers good? *Acta ethologica*, *13*, 101–107.

R Development Core Team (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. URL: http://www.R-project.org/.

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

Rhodes, G., Chan, J., Zebrowitz, L. A., & Simmons, L. W. (2003). Does sexual dimorphism in human faces signal health? Proceedings of the Royal Society of London. *Series B: Biological Sciences*, *270*, S93–S95.

Rhodes, G., & Simmons, L. W. (2007). Symmetry, attractiveness and sexual selection. In R. I. M. Dunbar, & L. Barret (Eds.), *Oxford handbook of evolutionary psychology* (pp. 333–364). Oxford: Oxford University Press.

Rhodes, G., Simmons, L. W., & Peters, M. (2005). Attractiveness and sexual behavior: does attractiveness enhance mating success? *Evolution and Human Behavior*, *26*, 186–201.

Riggio, R. E., Widaman, K. F., Tucker, J. S., & Salinas, C. (1991). Beauty is more than skin deep: components of attractiveness. *Basic and Applied Social Psychology*, *12*, 423–439.

Rubenstein, A. J. (2005). Variation in perceived attractiveness. *Psychological Science*, *16*, 759–762.

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

Weeden, J., & Sabini, J. (2007). Subjective and objective measures of attractiveness and their relation to sexual behavior and sexual attitudes in university students. *Archives of Sexual Behavior*, *36*, 79–88.

Wickstrom, J., Diagne, A., & Smith, A. (2006). Repositioning family planning—Senegal case study: promising beginnings, uneven progress. New Work: EngenderHealth/The ACQUIRE Project.

Zebrowitz, L. A., & Rhodes, G. (2004). Sensitivity to "bad genes" and the anomalous face overgeneralization effect: cue validity, cue utilization, and accuracy in judging intelligence and health. *Journal of Nonverbal Behavior*, *28*, 167–185.