

Paternity cues and mating opportunities: what makes fathers good?

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Abstract Human males provide facultative paternal investment to their offspring; that is, the male care is not necessary for the survival of his offspring. It is expected that the degree of male investment (1) increases with growing paternity certainty, (2) increases when investment increases the survival and later reproductive prospect of offspring and (3) declines when there are opportunities to mate with multiple females. Using a large sample of adult offspring and their fathers ($n=245$), we first investigated the role of two factors possibly involved in the assessment of paternity and subsequently regulating the level of paternal investment: (a) father–child facial resemblance and (b) assortative mating for eye colour. Second, because mating opportunities are inversely related to paternal investment, we also investigated how male facial attractiveness (a cue of mate opportunities) correlates with paternal investment. In line with paternal investment theory, male investment positively correlated with offspring facial resemblance. However, paternal investment were neither higher among blue-eyed couples, nor there were preferences of blue-eyed men to marry with blue-eyed women. Moreover, father facial attractiveness was unrelated to paternal investment. These results indicate that resemblance between

offspring and their fathers still plays an important role in paternal investment decision later in offspring's life.

Keywords Facial attractiveness · Facial resemblance · Paternal investment

Introduction

Parental investment has been defined as “any investment by the parent in an individual offspring that increases the offspring's reproductive success at the cost of the parent's ability to invest in other offspring” (Trivers 1972, p. 139). Human males are one of <10% of mammals species in which males do provide resources to their offspring (Clutton-Brock 1991). This behaviour is, however, facultatively expressed in humans; that is, it is not always critical for the survival of his offspring (Sear and Mace 2008), and the optimal level of investment that is favoured varies according to socio-ecological factors. In particular, since paternal investment is costly in terms of loss of mating opportunities and as fathers face paternity uncertainty when making investment decisions (mean rate is ~ 4% worldwide; Anderson 2006), inclusive fitness theory (Hamilton 1963) predicts father investment to evolve if fathers (1) favour their related offspring over others (Houston 1995; Daly and Wilson 1998; Marlowe 1999; Houston and McNamara 2002; Geary 2006) and (2) invest less when they have more opportunities to reproduce (Heath and Hadley 1998; Geary 2006).

First, there is some evidence that paternal care is negatively correlated with paternity uncertainty. Previous research on non-human animals revealed that males of some fish, such as the bluegill sunfish (*Lepomis macrochirus*), adjusted parental care in response to perceived paternity in the field (Neff 2003; Magee and Neff 2006). Males of some non-human

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primates, such as mountain gorillas (*Gorilla beringei beringei*), Japanese macaques (*Macaca fuscata*) or Hanuman langurs (*Semnopithecus entellus*), also discriminate between kin and non-kin offspring and protect them against infanticide by other males (reviewed by Widding 2007). In humans, it is cross-culturally well documented that the level of father investment is lower for stepchildren than for biological children (Marlowe 1999, Anderson et al. 1999a, b; Zvoch 1999), which indicates that relatedness plays a role in decisions of father investment. Moreover, in situations where men have been attributed the paternity, it has been shown that men use cues of paternity to direct their investment. Indeed, the level of care provided by fathers is higher when the perceived fidelity of the mother is higher (Apicella and Marlowe 2004), and paternal care is positively related to the level of child physical resemblance to the father, the level of father resemblance being either perceived (Apicella and Marlowe 2004, 2007; Burch and Gallup 2000; Fox and Bruce 2001) or measured objectively (in experimental conditions, Platak et al. 2002, but see DeBruine 2004 in natural conditions; Alvergne et al. 2009, 2010).

Although this research suggests that children's resemblance to the father positively influences paternal investment, as far as we are aware, (1) not one study investigated the influence of father resemblance on adult children and (2) the child's feelings about father investment. If the father-child resemblance is a cue used by fathers to assess their paternity and adjust their investment accordingly, we predict that father's ascription of resemblance should match objective resemblance made by objective raters.

An alternative male strategy, which is not mutually exclusive from judging facial resemblance of the child, is assortative mating with similarly eyed female. It was found that blue-eyed men preferentially chose women with the same eyes (Laeng et al. 2007). No similar patterns are, however, expected for heterozygous brown eyes because only if both parents have blue eyes is the probability of having children with blue eyes highest (Bryn 1920). Laeng et al. (2007) suggest that preferences of blue-eyed men for blue-eyed women promote assurance of paternity. It would be therefore suggested that blue-eyed fathers who married with blue-eyed mothers and have blue-eyed children should invest to their offspring more than other fathers, all else being equal. Furthermore, blue-eyed couples are expected to be not randomly distributed, which means that blue-eyed men should be married with blue-eyed women more frequently than with brown-eyed women. To our knowledge, however, no one research examined whether assortative mating in humans influences paternal investment.

Second, there is some support that male care is traded off with mating opportunities in species where males do provide care (Neff 2003). This trade-off is mediated by socio-ecological factors (e.g. the availability of mates) and

intrinsic characteristics of the male (e.g. attractiveness or the ability to attract many mates; Houston et al. 2005; Kokko 1998; Magrath and Komdeur 2003; Von Hippel 2000). As a result, the cost of paternal investment in terms of reduction of future mating opportunities is expected to be higher for attractive males, and male attractiveness is expected to correlate negatively with the amount of paternal care (Møller and Thornhill 1998). In humans, men who are more facially attractive have greater mating success than less attractive males (Rhodes et al. 2005; Thornhill and Gangestad 1994), and as predicted, men with higher perceived mate value provide less paternal care than men with low perceived mate value (Apicella and Marlowe 2007). However, we are not aware about any study that investigated the relationships between objective male physical attractiveness (e.g. facial attractiveness) and paternal investment.

In this study, we investigated (1) the link between objective and subjective father facial resemblance, (2) the frequency of assortative mating for blue eyes and (3) how paternal investment, as quantified by the quality of relationships between fathers and his offspring, is predicted by both paternity cues (facial resemblance and combination of eye colours) and father's facial attractiveness. We predict (1) that subjective facial resemblance is linked with objective facial resemblance, (2) that the frequency of blue-eyed fathers married with blue-eyed women will be higher and (3) that blue eyed couples will invest to offspring more, and (4) facial attractiveness in fathers is negatively linked with paternal investment.

Materials and methods

Study population and demographic data

The study was conducted in Slovakia. Grade 1 university students ($n=323$) were asked at the beginning of the winter semester 2008 to voluntarily provide current colour facial photograph of themselves as well as their biological father. Students who participated in this study were given an extra credit in human biology course. To avoid discrimination of fatherless students, these students were provided a chance to ask their friends for requested data. Basic demographic data (age of participants, current age of father), total number of father's children, birth order, marital status of participants' parents (married or divorced) and colour of mother' and father' eyes were asked at the beginning of the questionnaire (Table 1).

Out of 294 students who agreed in the participation in this research, 49 were excluded due to missing data. Thus, 245 participants remained in further analyses. Mean age of participants (24 males and 221 females) was 19.6 years ($SD=1.34$, range = 16–33, $n=245$). Only 20 participants (8%) had

Table 1 Distribution of fathers with brown, blue and green eyes and their female partners (i.e. mothers with brown, blue and green eyes)

		Mothers' eyes			Total
		Blue	Brown	Green	
Fathers' eyes	Brown	40	45	29	114
	Blue	31	28	19	78
	Green	12	23	18	53
	Total	83	96	66	245

divorced parents. Out of these, 17 participants lived with their mother only, two lived with their father, and one lived with both mother and father in a single flat despite parents were divorced.

Father–offspring facial resemblance

Subjective rating Students received a seven-point scale (1 = not similar, 7 = very similar) measuring father–offspring facial resemblance. We explicitly asked each father “How do you think your child [participant] facially resembles to yourself?” Because this latter measure was done subjectively by fathers of our participants, we termed this variable “subjective rating”.

Objective rating Male and female ratings (36 females and 6 males) of facial resemblance between participants and their biological fathers were collected by asking an independent set of raters “How do you think the student on the photo A facially resembles to his father on the photo B?” Facial resemblance was rated on a seven-point scale (1 = not similar; 7 = very similar). Facial resemblance score for each participant’s photo was calculated by averaging across all raters. The mean age of this rater set was 20.7 years (SD=0.94, range = 19–23, $n=42$). The reliability (Cronbach’s alpha) of facial resemblance score was 0.84.

Father–offspring relationship

Each participant completed a 22-item Likert-type questionnaire focused on father–offspring relationships adapted from Schacht et al. (2007). Each item was answered by participants from 1 (from strongly disagree) to 5 (strongly agree). Negatively worded items were scored in reverse order. The reliability of father–offspring relationships was satisfactory (Cronbach’s $\alpha = 0.79$).

Father facial attractiveness

Female ratings of attractiveness for each father face were collected according to the method outlined by Rhodes et al.

(2005). Attractiveness was rated on a seven-point scale (1 = not attractive; 7 = very attractive) in the context of a short-term sexual partner (i.e. when women seek genetic benefits rather than paternal investment; Little et al. 2002), and women raters were encouraged to use the whole range of the scale. The order of presentation of pictures was randomized. An attractiveness score for each father’s face was calculated by averaging across all raters. The mean age of this rater set was 21.2 years (SD=1.40, range = 18–25, $n=25$). The reliability (Cronbach’s alpha) of facial attractiveness score was 0.93.

Students participating in rating photographs (both resemblance and attractiveness) were volunteers from various grades, unfamiliar with presented pictures. Neither student raters nor participants who were asked for providing photographs and questionnaires were aware of the reason for the study or the hypotheses being tested. Attractiveness and resemblance was judged by different groups of students and the order of pictures was randomized. Each rater judged all pictures included in the research.

Frequency of distribution of eye colours among married couples

The distribution of blue-, brown- or green-eyed parents was compared according to data obtained from students following Laeng et al. (2007).

Results

Objective and subjective ratings

Perception of facial resemblance by fathers is found to reflect actual resemblance. Father’s subjective rating of facial resemblance between himself and his offspring is correlated with objective ratings of independent raters (Pearson’s $r=0.17$, $P=0.008$, $n=245$; Fig. 1). This result remained unchanged even after controlling for offspring sex. Mean scores of objective and subjective ratings were not different (t test, $t=-0.97$, $P=0.33$).

Are blue-eyed couples more frequent?

Chi-square analyses were performed on the mothers’ and fathers’ distributions of eye colour traits according to Laeng et al. (2007). There was no significant difference in the distribution of eye combinations reported by fathers with blue, brown and green eyes in their mate choices for mothers’ eye colours (Pearson’s $\chi^2=4.53$, $df=4$, $P=0.34$; Table 1). These results remained unchanged even after pooling persons with blue- and green-coloured eyes.

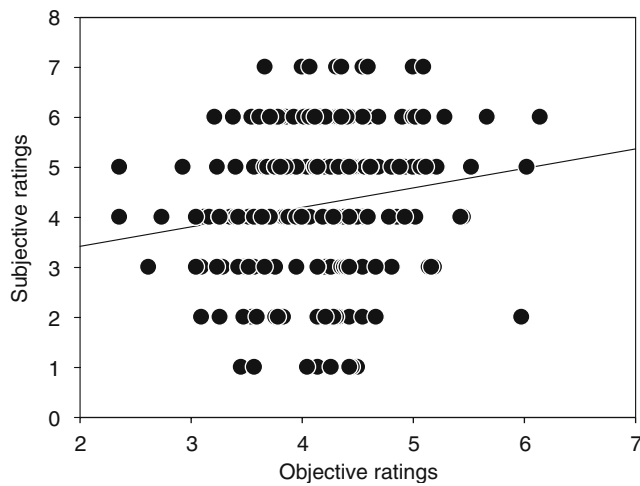


Fig. 1 Positive relationships between objective and subjective ratings of father-offspring facial resemblance

Does facial resemblance and fathers’ attractiveness influence father-offspring relationship?

We found that father investment is related to objective father-child facial resemblance, but not to father facial attractiveness (multiple regression, $R^2=0.04$, $F(2,242)=5.19$, $P=0.006$; Table 2). As shown in Table 2, only father-child facial resemblance and combination of parents’ eye colour entered the multiple regression model. These results are not biased because the analysis was controlled for father’s age, offspring sex, divorce and birth order. Only the objective rating of facial resemblance (Fig. 2), but not the combination of parents’ eye colour or facial attractiveness (excluded from the model; Fig. 3), was significantly related to father-offspring relationship score. If the subjective rating of offspring facial resemblance was used instead of objective ratings, the model was not significant.

Discussion

This study investigated the associations between paternal investment, offspring facial resemblance and fathers’ facial attractiveness. As far as we are aware, this is the first paper assessing paternal investment from the point of view of children. We suggest that assessing paternal investment

Table 2 Linear multiple regression (forward stepwise method) on father-offspring relationship score

	β	$t(243)$	P
Objective father-offspring resemblance	0.19	3.11	0.002
Combination of parents’ eye colour	0.07	1.11	0.27

Father facial attractiveness was excluded from the model

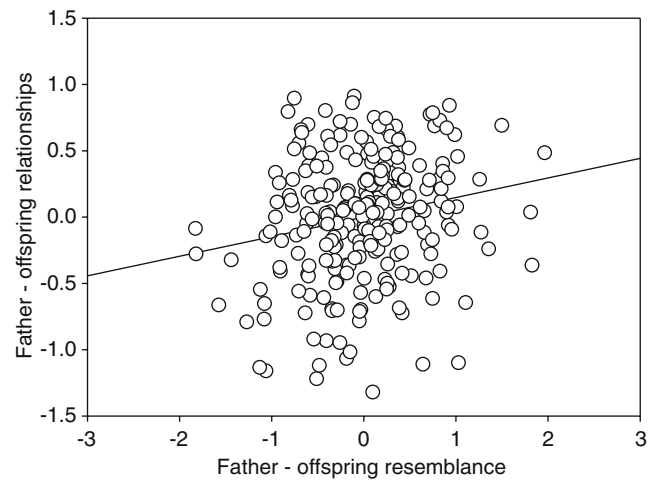


Fig. 2 Positive relationships between father-offspring resemblance and paternal investment measured by father-offspring relationships. Values are residuals of regression described in “Results”

from offspring is important as compared to assessing investment from fathers because it makes these measurements more objective. We found support for the paternal investment theory which predicts that paternal investment positively correlates with offspring facial resemblance with their fathers (e.g. Daly and Wilson 1982; Alvergne et al. 2009, 2010). However, we did not find any significant association between either men’s facial attractiveness or assortative mating and paternal investment based on eye colour.

Subjective and objective father facial resemblance

We found that subjective and objective father facial resemblances are significantly correlated, although the effect size is weak. We suggest that deviations of fathers’ subjective ratings

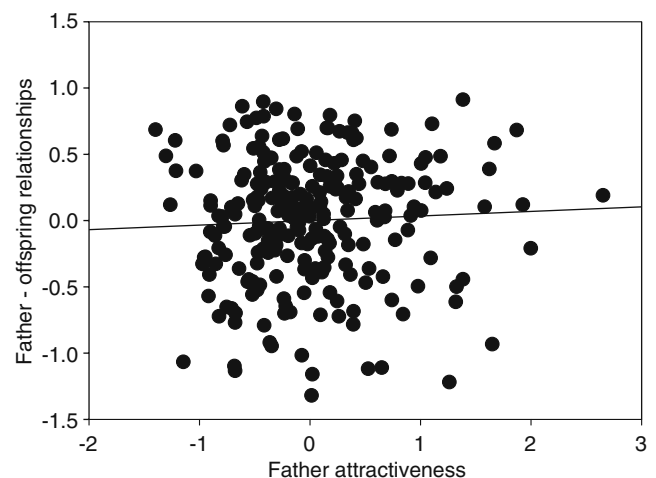


Fig. 3 Non-significant relationships between father facial attractiveness and paternal investment measured by father-offspring relationships. Values are residuals of regression described in “Results”

from scores of objective raters could first be influenced for example because fathers can be influenced by mothers' claims, which are women's strategies that limit the problems of paternity uncertainty (Daly and Wilson 1982; McLain et al. 2000, Alvergne et al. 2007). Similarly, father's perception of a child's resemblance could be influenced by what other people have told the father (Burch and Gallup 2000). Second, when assessing facial resemblance, the judges in our study were aware about offspring–parent relatedness, which may also artificially increase the level of father–child resemblance detected by the person making the assessment (Oda et al. 2005). Third, it would be best to know true genetic relatedness between putative fathers and offspring because at least some of the offsprings involved in this study may not be the true children (although the mean rate is low, ~4% worldwide; see Anderson 2006). That is, unrelated offspring could be excluded from the sample, which would make the results stronger. Fourth, we suggest that this deviation may result from social experience between the father and his child. In contrast with previous works, participants in the present study were of older age, which increases the opportunity for children to imitate their fathers more easily than 3-year-old children. However, the correlation between objective and subjective ratings of father–offspring resemblance was statistically significant and the mean scores of these ratings were similar, which means that ratings by fathers were in line with real facial resemblance.

Facial resemblance and paternal investment

Although we found significant relationship between paternal investment and father–offspring facial resemblance, one would argue that low effect sizes make our results less convincing. In contrast to the present study, some previous researchers used combined data from facial and behavioural resemblance of children (Apicella and Marlowe 2004, 2007) or used “resemblance” without distinction between facial and behavioural resemblance (Burch and Gallup 2000), which could mask the effect of facial resemblance alone. Thus, although correlation coefficients were low, our results support the hypothesis that facial resemblance in adult children per se is an important cue for male parental investment decisions (Daly and Wilson 1982; Platak et al. 2002; Alvergne et al. 2009, 2010). We suggest that greater correlations between paternal investment and resemblance in previous researches reflect additive effects of children's behavioural and facial resemblance on their putative fathers and/or children age.

Effects of men's attractiveness

We predicted that fathers' facial attractiveness (a cue of the number of potential mates that a man can have) would negatively correlate with paternal investment. Male with

more attractive faces are expected to have more extra-pair partners (Thornhill and Gangestad 1994; Rhodes et al. 2005) and consequently to invest less in their own offspring. Several explanations can be proposed why this hypothesis is not supported. First, men's facial attractiveness need not correlate with other body features like waist–hip ratio or height (Weeden and Sabini 2007) which are important in female mate choice (reviewed by Geary et al. 2004). Thus, facial attractiveness alone does not have to be necessarily associated with the number of extra-pair partners. In addition, male mate value is strongly influenced by his control over material resources (reviewed by Geary et al. 2004), which was not controlled for in our research. Second, it is not excluded that some intrinsic differences between attractive and non-attractive men were not controlled for, thus possibly masking the predicted link between attractiveness and paternal investment.

It is possible that attractive men are able to camouflage their extra-pair interests in such a way that their children could not feel possible differences in emotional involvement between faithful and unfaithful fathers. Moreover, attractive men have children resembling them more than unattractive (correlation between attractiveness and objective resemblance is significant, Pearson $r=0.19$, $P=0.002$, $n=245$), which could mask the difference between investment and attractiveness (Apicella and Marlowe 2004, 2007).

It is worth noting that father's facial attractiveness was not linked to the number of children (data not shown in “Results”, partial correlation controlled for the effect of fathers' age, divorce and eye colour combination between parents, $r=-0.04$, $P=0.49$, $n=245$); thus, a link between attractiveness and paternal investment in this sample is not expected. We suggest that failure between facial attractiveness and reproductive success could be influenced either by scoring attractiveness of older men instead of scoring younger men in the peak of reproductive activity and/or the absence of unmarried men. For example, Jokela (2009), examining relationships between facial attractiveness and reproductive success, used ratings of attractiveness based on participants' photographs being 18.1 years of age. The mean age of our participants was, however, 47.7 years. Regarding the latter, having unmarried, childless men, who are expected to be less facially attractive, would importantly influence statistical relationships between attractiveness and reproductive success. From this point of view, our sample would be considered to be based towards attractive men; thus, no definite conclusion of whether facial attractiveness influences reproductive success could be made.

Effects of assortative mating

We found no support for assortative mating hypothesis based on preferences on blue-eyed men for blue-eyed women

(Laeng et al. 2007). Neither blue-eyed fathers married more frequently with blue-eyed women, nor was paternal investment higher in blue-eyed couples.

The inability to replicate the results of Laeng et al. (2007) could be explained by demographic differences in samples of participants. Laeng et al. (2007) asked university students for mate preferences of faces with different eye colours and their actual preferences of eye colour of their romantic partners. In contrast, we retrospectively examined preferences in eye colours in married couples. It has been shown based on speed dating experiments that reported preferences may not always correspond to actual mate choices (Todd et al. 2007); thus, attractiveness of blue-eyed females for blue-eyed males does possibly not have to result in marriage.

Conclusion and future research

This research extends the importance of facial resemblance as a cue of paternity certainty in modern humans based on a large sample size. Our finding that facial resemblance and paternal investment are related also on a sample of adult offspring extends previous knowledge based on a research on young children. Somewhat unexpectedly, this study casts doubt on the role of male facial attractiveness and paternal investment. Future research should further investigate relationships between male physical attractiveness, material resources and paternal investment with data from larger, more diverse samples.

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