Father–offspring resemblance predicts paternal investment in humans

Alexandra Alvergne [a,b,*], Charlotte Faurie [a,b], Michel Raymond [a,b]

[a] University of Montpellier II
[b] CNRS, Institute of Evolutionary Sciences of Montpellier (UMR 5554)

ARTICLE INFO

In species in which paternal care of offspring is important but paternity is uncertain, evolutionary theory suggests that kin recognition mechanisms (e.g. phenotype matching) should evolve. Fathers are expected to discriminate between their children and others' on the basis of phenotypic similarities, and they should allocate resources accordingly. However, studies showing that males assess paternity by phenotype matching are rare. In a polygynous human population of rural Senegal, we examined the relationships between (1) actual father–child resemblance through both the facial and the olfactory phenotypes; (2) fathers' investment of resources in each child; and (3) child nutritional condition. We found that paternal investment was positively related to both face and odour similarities between fathers and children. Additionally, such discriminative paternal investment was linked to the children's health: children who received more investment had better growth and nutritional status. This is the first evidence that paternal investment is associated with father–child resemblance in real human families, and, furthermore, that these discrepancies in paternal investment result in differences in fitness-related traits in children.

© 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Because of resource allocation trade-offs, males that provide parental investment to their existing offspring do so at the cost of investing in future reproduction (Trivers 1972; Clutton-Brock 1991). According to inclusive fitness theory, this costly behaviour is expected to have been favoured only if it was preferentially directed towards related offspring (Hamilton 1963). However, in species where females mate with multiple partners, males are generally uncertain about their paternity. Paternal investment combined with paternity uncertainty challenges the importance of kin selection. This challenge would nevertheless be resolved, however, if recognition mechanisms that allow males to discriminate kin from nonkin had evolved. Indirect evidence that putative fathers use cues of paternity to direct their investment is provided by studies showing that males of many species adjust their paternal effort according to the risk of cuckoldry (Dixon et al. 1994; Sheldon & Ellegren 1998; Wright 1998; Sheldon 2002; Simmons 2002). However, direct support for relatedness-based parental investment decisions is rare, and, to our knowledge, only available in the bluegill sunfish, *Lepomis macrochirus*, where males' parental investment depends on their paternity, which is assessed through odours emanating from fry after eggs hatch (Neff & Gross 2001; Neff & Sherman 2003, 2005).

The estimates of nonpaternity rates in humans range from 0.8% to 30% depending on the population (Bellis & Baker 1990; Sasse et al. 1994; Cerda-Flores et al. 1999; Bellis et al. 2005; Anderson 2006), with an average rate of 3.3% (Anderson 2006). Such paternity uncertainty influences paternal investment: in a comparison of 135 human societies, the level of paternity confidence was positively associated with the level of paternal investment at the population level (Gaulin & Schlegel 1980). Paternity uncertainty explains why alloparenting from the maternal lineage is higher than from the paternal lineage (Euler & Weitzel 1996; Gaulin et al. 1997; McBurney et al. 2001).

There is some evidence that human fathers use cues directly related to kinship to adjust their investment decisions. These cues refer to the assessment of phenotypic similarities (i.e. phenotype matching: Lacy & Sherman 1983; Hauber & Sherman 2001). For instance, perceived facial resemblance to self is more important for men than for women in hypothetical adoption decisions (Volk & Quinsey 2002). Additionally, fathers' perceptions of children's physical and psychological resemblance predict reported investment (Apicella & Marlowe 2004), as well as the self-reported quality of the men's relationships with their children (Burch & Gallup 2000). However, reported paternal investment, which may be influenced by social factors, may not translate into actual investment. Similarly, perception of phenotypic similarities may

* Correspondence: A. Alvergne, Institut des Sciences de l'Evolution (UMR 5554), Université Montpellier 2 (C. C. 065), F-34095 Montpellier cedex 05, France.
E-mail address: alexandra.alvergne@univ-montp2.fr (A. Alvergne).

not reflect actual resemblance but can instead be the result of social learning through cohabitation or social manipulation by mothers. Indeed, it has been shown that mothers preferentially ascribe resemblance to the fathers, and a father's perception of a child's resemblance is highly correlated with what other people have told the father (Burch & Gallup 2000). Finally, empirical studies have yielded mixed results. By manipulating pictures of faces, different studies have shown that self-referent facial phenotype influences either paternal but not maternal decisions of investment (Platek et al. 2002, 2003), or maternal but not paternal decisions of investment (Bressan et al., in press) or both (DeBruine 2004). The assessment of investment varies widely among these studies, as do the computational methods used to create artificial facial resemblance (i.e. the way pictures of adults are manipulated and mixed with pictures of children to create artificial faces, as well as the degree to which artificial faces resemble the adults to whom the pictures are presented as stimuli). Although recent studies suggest that individuals respond similarly to real and transformed faces (Jones et al. 2004) and to faces transformed using different methods (DeBruine et al. 2008), one may not exclude the possibility that the various processes of picture mixing, creating artificial faces, have introduced unforeseen biases. It is thus difficult to draw a definitive conclusion based on these reports, and studies in nonexperimental settings are warranted.

The possibility that paternal investment is discriminative according to father–child phenotypic similarities has never been investigated in natural conditions using measures of paternal investment and phenotypic resemblance that are independent of fathers' reports. In addition, facial phenotype may not be the only cue on which phenotype matching is based.

One interesting possibility is odour phenotype matching. Individuals of various taxa identify their kin through the assessment of individual-specific odours, for example social insects (Greenberg 1979; Gamboa et al. 1986), fish (Neff & Sherman 2003, 2005), and rodents (Holmes 1994; O'Riain & Jarvis 1997; Heth et al. 2003; Mateo 2003). According to these studies, odour cues are used by individuals to discriminate their kin from nonkin in the directions predicted by inclusive fitness theory (i.e. nepotism, avoiding inbreeding with kin). In humans, contrary to previous thought, olfactory capacities are effective enough for odour cues to be used in social recognition (Shepherd 2004). Studies have revealed that human odour similarities inform kinship relationships independently of shared environment (Weisfeld et al. 2003), and odour cues are used in a mate choice context to avoid inbreeding (Wedekind & Furi 1997; Weisfeld et al. 2003). In a mate choice context, there is now increasing evidence in house mice, *Mus musculus*, and humans that the assessment of relatedness through the olfactory system is based on scents associated with the major histocompatibility complex (MHC), a highly polymorphic gene (reviewed in Penn & Potts 1999). In a parent–progeny recognition context, the role of the MHC has been proven in mice (Yamazaki et al. 2000), but such genetic data are not available for humans. There is, none the less, some evidence that odour cues are involved in the recognition of newborns by both mothers (Porter & Moore 1981; Porter & Cernoch 1983) and fathers (Porter et al. 1986; but see Russel et al. 1983 for an exception). Moreover, paternal recognition of children through odour cues may extend until adolescence (Weisfeld et al. 2003). There is thus a possibility that human putative fathers use odour cues (possibly informed by MHC similarities) to assess their paternity and modulate their investment accordingly.

Finally, whether father–offspring phenotypic similarities influence offspring fitness by affecting paternal investment has never been directly tested in any species. In other words, if fathers discriminate among their children on the basis of phenotypic similarities, does this translate into developmental variation among children of a given father?

This study investigated (1) the role of father–child phenotypic resemblance in paternal investment allocation, using both visual and olfactory cues, and (2) the relationship between paternal investment allocation and child nutritional status. For the first time, resemblance of children to their fathers and paternal investment were simultaneously and quantitatively assessed in real families. We used data collected from a rural and polygynous human population, where access to limited resources, such as alimentation, education and medical care, largely depends on a father's decisions and behaviour. Consequently, we predicted that in such settings, fathers may discriminate among their children on the basis of phenotypic similarities and allocate resources accordingly.

METHODS

Study Population

The study was conducted in traditional villages located in the Sine Saloum area of Senegal, on the west coast of Africa. The most common ethnic groups in this area are the Sereer, the Wolof and the Peuhl. The subsistence mode is mainly agriculture, especially of cash crops such as peanuts and cashew nuts, but also of subsistence crops, such as millet. The inheritance mode is patrilineal, and the residence is patrilocal. Polygynous marriages are common, with a maximum of four wives as permitted by the local interpretation of Islam, which most people practise.

Participants, Demographic and Anthropometric Data

The protocols used to recruit families and to collect data were approved by both the French National Committee of Information and Liberty (CNIL) and the ethical committee of the Senegalese National Research Council for Health, and informed consent was obtained from all participants. Among villagers, all families with at least two children aged 2–7 years were asked to take part in the test. Participants were not paid, but gifts such as school or farming equipment were given to the head of the village, who was in charge of reallocating items among the villagers. Thirty families were involved in the project (two children per family, excluding step- or foster children, chosen among the youngest children present at the time of interview), leading to a total sample of 60 children (32 boys: $\overline{X} \pm SD = 4.2 \pm 1.4$ years; 28 girls: 4.2 ± 1.6 years). For each child, information on his/her age, sex and birth order was collected. Moreover, two indexes of child condition were measured: body mass index (BMI) and mid-arm circumference (MAC; Visweswara & Singh 1970). These indexes reflect different aspects of child condition (growth and nutritional status, respectively; Visweswara & Singh 1970).

In addition, the ages of both parents were collected, as well as, for the father, number of wives, number of children, land possession and number of working hours per day.

Evaluation of Father–Child Phenotypic Resemblance

General procedure

We conducted two tests of father–offspring phenotypic resemblance, one of which was visual (test 1) and the other olfactory (test 2). The stimuli in test 1 were facial photographs, while the stimuli in test 2 were T-shirts worn by father and offspring for 1 night each. The two tests were conducted separately, involving different sets of raters. To assess father–child resemblance, a given rater was presented with stimuli associated with several individuals at the same time, namely, a child and several adult men (three men for visual

cues and two men for olfactory cues), one of the men being the true father (see Fig. 1 for an example of test 1). Fewer stimuli were presented to a given rater for the odour to avoid a saturation effect in the ability to perceive odours. A decreasing ability to perceive odour similarity was indeed observed during a preliminary experiment in this population.

For both tests 1 and 2, each rater was asked to identify the true father of the child from the men presented. For each child, for a given rater, the score in picking out the correct father was recorded as zero for failure or one for success. For each child, the expected percentage of correct matches from all raters varied between the rate expected by chance (33% for the visual test and 50% for the odour test), which corresponds to no resemblance, and the rate expected if all raters correctly identified the father (100% for both tests), which corresponds to perfect resemblance. A total of 109 raters aged 15–60 years were asked to perform test 1 (57 men: $\overline{X} \pm SD = 23.7 \pm 9.7$ years; 52 women: 25.6 ± 9.5 years). Three hundred raters aged 15–70 years, different from those performing test 1, performed test 2 (140 men: 29.5 ± 15 years; 160 women: 28.5 ± 11.2 years). The methods used to collect stimuli and to assess father–child resemblance are further detailed below.

Detailed procedure

Test 1 (visual cues). To assess father–child facial similarities, participants were photographed in a front view and at a distance of about 1 m using the same digital camera (Canon EOS 20D) with the same general settings. People were asked to maintain an expressionless face and to look directly at the camera. All pictures were taken outdoors and in the shade to avoid overexposure, and people stood in the same place in each village. To homogenize luminosity between pictures taken in different villages, photographic sessions were performed only on sunny mornings. All photographs were processed using Adobe Photoshop 7 to normalize the contrast and the luminosity and also to turn all backgrounds to white. Note that only backgrounds and external accessories such as earrings were masked in white, while the hair, neck and ears were not.

A computer program (written in Delphi, version 7) was used to randomize and to assist each part of the test (the order in which children's pictures were presented, the position of the pictures depicting possible fathers, and the association between correct fathers and 'false' fathers). Each picture was seen by a given rater only once, to avoid a rater's choice being influenced by a previous choice. The raters were chosen from distant villages (2 h by cart, the traditional and most common means of transport) so that they would be unable to recognize people presented on photographs. However, in a few cases (seven times out of 109×20 sets of four pictures), a rater recognized an individual, and these data were removed. Each rater was asked to identify the true father of a child among three possible men by looking at facial pictures, and this was repeated for 20 children from different families. Raters were not given a time limit.

Test 2 (olfactory cues). To collect olfactory stimuli, participants were asked to wear a T-shirt for 1 night. The T-shirts were new, white, 100% cotton and all identical except in size. They were stored in transparent zipped plastic bags, on which participants' identities were indicated, and given to families. After wearing T-shirts for 1 night, people were asked to put the T-shirt back in the plastic bag upon waking up. Each plastic bag was collected in the morning and stored at the lowest temperature available (between 0 and 4 °C). In this population, there is only one kind of soap for washing (clothes, dishes or body), and alimentation is homogeneous between families. Traditional meals are prepared in the same way by all women, specific meals devoted to either lunches or dinner being identical for the families studied. It is thus likely that the environment plays a restricted role in this population, compared to previous studies in occidental settings. It was not possible to ask people to change their sleeping habits. However, the mother was asked with whom the child had slept during that night, and there were no significant differences in father–child odour resemblance between children who slept in the same bed as their fathers and those who did not (ANOVA: $F_{1,48} = 0.09$, $P = 0.76$). A computer program (written in Delphi, version 7) was used to randomize each part of the experiment, such as the order of presentation of T-shirts to raters and the associations between correct and 'false' fathers. The program also facilitated the double blind procedure when the transparent plastic bags containing the T-shirts were put in larger black plastic bags with new labels. These new labels were randomly assigned by the computer program, and the relabelling was performed by a research assistant, so the experimenter was blind to the correct associations. To keep storage time equal among all T-shirts (approximately 10 days at the end of the testing), they were all used simultaneously in a given experimental session, during which all children's T-shirts were smelled once. To avoid odour saturation, each rater was asked to identify, by smelling the T-shirts, the true father among only two possible men for each child. Prior to the test, raters were given a towel and asked to wipe their face to avoid contamination. They were also given gloves to handle the T-shirts. They were allowed to smell each T-shirt as long as they needed. When all children had been tested once, the black plastic bags were relabelled. All T-shirts were used by raters the same number of times.

Quantification of Paternal Investment

Paternal investment was estimated through detailed reports from both mother and father (mothers/fathers were interviewed in private, in the absence of their spouses). The levels of direct and indirect paternal investment (towards the child and towards the mother, respectively), as well as the level of marital conflict, were assessed. The level of marital conflict was taken as an inverse measure of global paternal investment because the quality of the marital relationship is strongly negatively related to the father–child interaction quality (Parke et al. 2005). Before the survey, the questionnaire was translated into the local languages and recorded on a dictaphone. The basics of the local languages, to the extent necessary to record the answers unambiguously, were known by

Figure 1. Assessment of father–child facial similarities. Raters were asked to find the correct father of a child among three possible men. The correct answer for this example is the picture on the left.

the researcher. This procedure was used to conduct a private conversation between the parent and the researcher, thereby avoiding social biases associated with the presence of the locally known guide. Data on direct fathers' investment were collected from mothers' reports, whereas data on indirect fathers' investment and marital conflict were collected through both mothers' and fathers' reports. The use of questionnaires may introduce biases caused by social desirability (e.g. people do not want to be seen to give what they perceive to be a socially unacceptable answer), which leads responses to accumulate in the middle of the proposed scale. To minimize this social desirability bias, the scales used in this study lacked midpoints (Garland 1991).

Direct fathers' investment

Mothers were asked about the amount of time the father spent per day with each of the two children involved in the study. In practice, mothers described the previous day in detail, hour by hour, stating whether the child was interacting with the father or not. From this information, the number of hours that the fathers had spent the previous day with each of their children was calculated. The mothers were asked about father–child relationships using 10 questions focused on attachment, responsibility and education (adapted from the Inventory of Father Involvement, Hawkins et al. 2002). For each question, mothers could answer 'yes' (1 point) or 'no' (0 points), leading to a score between 0 and 10.

Indirect fathers' investment

Mothers and fathers separately answered two questions: whether the father supported the mother emotionally and whether the father gave her money for the children. For each question, four answers were possible: 'not at all' (1 point), 'a little bit' (2 points), 'much' (3 points), or 'very much' (4 points), leading to a general score of fathers' indirect investment between 2 and 8 for each parental report.

Marital conflict

Both parents were specifically asked about the level of marital conflict they experienced together (concerning money, jealousy, education of children, drugs and time spent together). For each conflict type, participants were able to choose between four possible answers: 'not at all' (1 point), 'a little bit' (2 points), 'much' (3 points) or 'very much' (4 points), leading to a general score of marital conflict between 5 and 20, for each parental report.

Statistical Analyses

Father–child phenotypic match

To compare actual recognition rates to those expected by chance, general linear mixed models (GLMM) were used to account for the structure of the data (repeated measures for both raters and children in test 1 and children in test 2; Crawley 2007) and a GLMM was built for each cue (odour and face). The response variable was modelled as binary, and the model contained no fixed effects. The 95% confidence intervals around the predicted value of the mean were then compared to the rate expected by chance. To investigate the effects of the raters' characteristics, the recognition scores were analysed using a similar model on overall data. The type of test (face recognition: test 1; odour recognition: test 2), the rater's sex, the child's sex and all the corresponding interactions were fitted as fixed effects. The identities of both the raters and the children were fitted as cross-random effects to account for the fact that one rater assessed several children (in the case of the facial recognition test) and that one child was evaluated by several raters. Moreover, as the same children were not assessed by the same number of raters in the two matching tests (50 raters for test 1 and five raters for test 2),

an interaction term between the type of test (fixed effect) and the identity of the child (random effect) was fitted to take into account the different variability between children between the two tests. Then, following Bates & Sarkar (2007), P values were calculated using a sample generated after 10 000 simulations from the posterior distribution of the parameters of the fitted model using Markov Chain Monte Carlo (MCMC) methods (P_{MCMC}).

Two indexes of resemblance to the father were built, one for faces and one for odours. For each child, each index of resemblance corresponds to the average score obtained by the raters in the corresponding test.

Paternal investment index

We used a principal components analysis (PCA) to extract a single factor termed 'paternal investment index', which reflects the father's inclination to invest in his offspring. The Kaiser–Meyer–Olkin index KMO (Kaiser 1974), an index that measures the interrelation among the six variables of paternal investment) was used to evaluate the pertinence of a PCA. For each variable associated with paternal investment, a measure of sampling adequacy (MSA) was performed (where MSA corresponds to the KMO for the correlation between individual variables). Variables were removed if the measure of sampling adequacy was below 0.5, and this included the variables associated with the mother's report of both marital conflict and indirect paternal investment. The KMO measures of the four remaining variables were 0.58, which is adequate for PCA analysis (Kaiser 1974).

Relations between father–child phenotypic resemblance, paternal investment and child condition

In all the analyses described below, the following variables were entered into the models to control for potential sources of variation: the father's age, the father's number of children, the father's land possessions, the child's age, the child's sex and the child's birth order. A full model containing these variables was first built, and stepwise regression was not used. We avoided stepwise regression to reduce a number of problems associated with this technique, such as the inflation of type I errors that results from the large number of tests or the bias in the estimation of parameters that results from parameter inference (i.e. testing whether parameters were significantly different from zero at each step of model selection; Whittingham et al. 2006). Therefore, the full model was not reduced. Those variables that were significant in this full model, as determined by F tests, were entered as confounding variables in a second model specifically testing the effects of interest, namely (1) odour resemblance and facial resemblance to the father in the analysis of their effect on paternal investment, or (2) paternal investment index in the analysis of its effect on either MAC or BMI. The model was not reduced, and the significance of the terms was determined using F tests. Then, normality, heteroscedasticity and autocorrelation of residuals were verified.

The effects of father–child odour and facial resemblance on the index of paternal investment were analysed together using a generalized linear model (GLM). The response term (paternal investment index) was fitted to a gamma error structure (as its variance was found to be proportional to the square of its mean). Father–child facial and odour resemblances were both considered in the model as main fixed effects. Residuals of the final model were normally distributed (Shapiro test: $W = 0.9$, $P = 0.8$), homoscedastic (Breusch–Pagan test: $BP_2 = 3.1$, $P = 0.2$) and not autocorrelated (Durbin–Watson test: $DW = 1.58$, $P = 0.06$).

The effects of paternal investment index on the two indexes of child condition were analysed using two separate linear models. For both BMI and MAC analyses, the response term was fitted to a normal error structure, and the paternal investment index was fitted as the main fixed effect. Residuals of the final model

explaining variation in MAC were normally distributed (Shapiro test: $W = 0.9$, $P = 0.8$), homoscedastic (Breusch–Pagan test: $BP_2 = 0.94$, $P = 0.62$) and not autocorrelated (Durbin–Watson test: $DW = 1.94$, $P = 0.42$). Similarly, residuals of the final model explaining variation in BMI were normally distributed (Shapiro test: $W = 0.97$, $P = 0.52$), homoscedastic (Breusch–Pagan test: $BP_2 = 1.40$, $P = 0.49$) and not autocorrelated (Durbin–Watson test: $DW = 2.2$, $P = 0.67$). All statistical analyses were carried out with R software version 2.4.1 (R Development Core Team, Vienna, Austria).
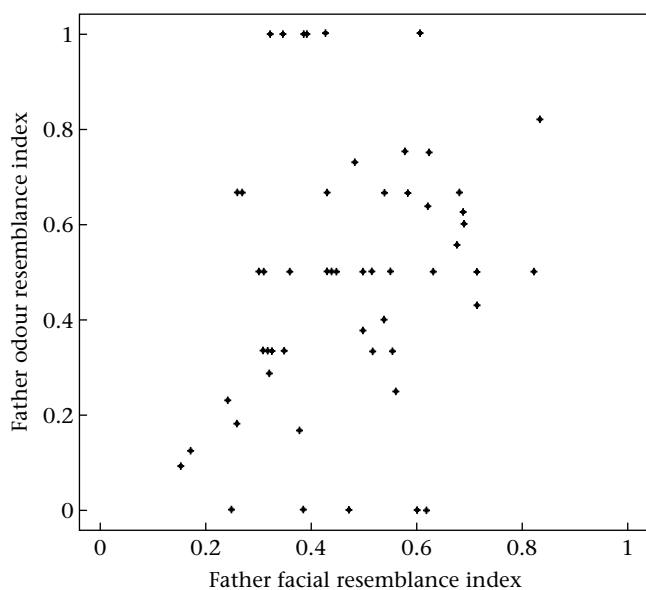
RESULTS

Resemblance Indexes

We found that unfamiliar raters were able to detect phenotypic similarities between fathers and their children at a rate greater than chance when looking at faces (prediction values of 0.47 ± 0.02, while the rate under chance expectancies would be 0.33), but not when smelling odours (prediction values of 0.50 ± 0.03, while the rate under chance expectancies would be 0.50). However, we found that the degree to which a child resembled his/her father through odour similarities varied widely among children, with approximately 40% of children resembling their fathers more than expected by chance. Importantly, while men and women showed equal performance at detecting facial similarities, women were less good than men at detecting odour similarities (the average level of correct assignments was ca. 0.58 for men and ca. 0.40 for women, a significant difference: $P_{MCMC} = 0.03$). Therefore, for each child, the index of odour resemblance was defined as the average score obtained by male raters only, whereas the index of facial resemblance was the average score obtained by raters of both sexes.

These two indexes of resemblance to the father (faces and odours) were positively correlated (Spearman rank correlation: $r_S = 0.28$, $N = 53$, $P < 0.05$; Fig. 2).

Paternal Investment and Paternity Cues

Both cues of phenotypic resemblance were positively related to the value of the investment index (facial resemblance: $F_{1,47} = 4.2$, $P < 0.05$; odour resemblance: $F_{1,47} = 7.11$, $P < 0.05$), after we controlled for the effect of father's number of children (which was negatively correlated with the amount of paternal care received by each child: $F_{1,40} = 5.76$, $P < 0.05$). Therefore, children who resembled their fathers the most were also those who, on average, received the most paternal investment (Fig. 3a, b). However, the paternal investment index was not significantly associated with the child's age ($F_{1,40} = 0.51$, $P = 0.43$), the child's sex ($F_{1,40} = 0.33$, $P = 0.56$), the child's birth order ($F_{1,40} = 1.53$, $P = 0.93$), the father's age ($F_{1,40} = 1.60$, $P = 0.21$), the father's working hours per day ($F_{1,40} = 1.05$, $P = 0.31$) or the father's land possessions ($F_{1,40} = 0.55$, $P = 0.41$). These results show that both facial and odour similarities between fathers and children were positively related to the fathers' investment of resources in their offspring.
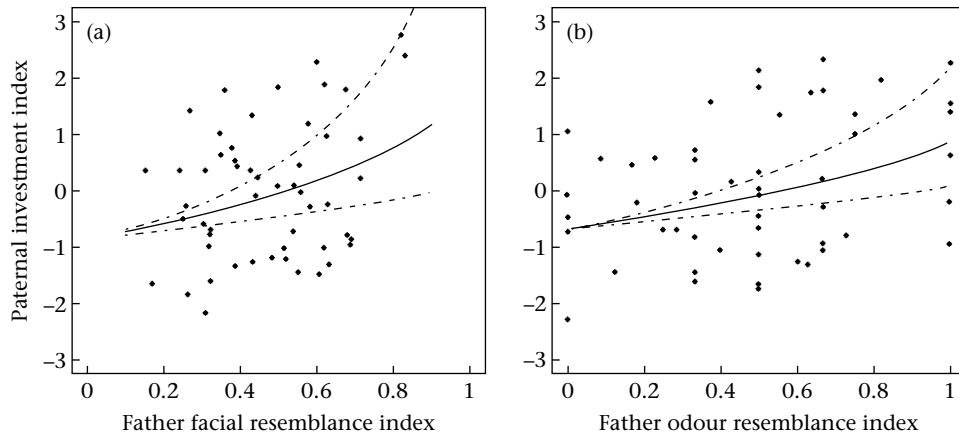
Paternal Investment and Child Condition

Two indexes of child condition (MAC and BMI) were correlated in the present sample (Spearman correlation: $r_S = 0.49$, $N = 38$, $P < 0.001$). First, there was a significant and positive effect of paternal investment on MAC ($F_{1,42} = 9.32$, $P < 0.01$; Fig. 4a), after we controlled for the child's age (which positively influenced the MAC: $F_{1,28} = 10.38$, $P < 0.01$). Children receiving the most paternal investment had better nutritional status. MAC was not associated with the child's sex ($F_{1,28} = 0.71$, $P = 0.40$), the child's birth order ($F_{1,28} = 1.16$, $P = 0.29$), the father's age ($F_{1,28} = 0.84$, $P = 0.36$), the father's number of children ($F_{1,28} = 0.03$, $P = 0.86$), the father's working hours per day ($F_{1,28} = 0.38$, $P = 0.54$) or the father's land possessions ($F_{1,28} = 1.69$, $P = 0.20$).

Second, paternal investment had a significant and positive effect on the BMI ($F_{1,39} = 22.93$, $P < 0.001$; Fig. 4b), after we controlled for the father's land possessions ($F_{1,29} = 4.15$, $P = 0.05$). Children having the highest BMI were also those who received the most paternal care. However, no significant effects on BMI were found concerning the child's sex ($F_{1,29} = 1.54$, $P = 0.22$), the child's birth order ($F_{1,29} = 0.19$, $P = 0.66$), the child's age ($F_{1,29} = 1.15$, $P = 0.29$), the father's age ($F_{1,29} = 1.58$, $P = 0.22$), the father's number of children ($F_{1,29} = 1.70$, $P = 0.20$) or the father's working hours per day ($F_{1,29} = 2.84$, $P = 0.10$). Our results thus demonstrate that discriminative paternal investment was positively linked to two different and important fitness-related traits in offspring.

DISCUSSION

Across species where females may have multiple mates and males provide paternal care, males face paternal uncertainty, so they must take this into account when making investment decisions in offspring (Krebs & Davies 1993; Ihara 2002). Kin selection theory predicts that, in this context, fathers should estimate their paternity using reliable indicators of relatedness. The use of indirect cues, such as cohabitation (Lieberman et al. 2007), is not appropriate for paternal investment decisions because paternal investment is costly, and spatial cues are particularly unreliable for estimating the probability of paternity. Males involved in paternal care are thus expected to use more direct cues, such as phenotypic similarities (i.e. phenotype matching; Hain & Neff 2007). Direct evidence that males recognize their offspring through phenotype matching is rare, however (see Neff & Gross 2001 for evidence in the bluegill sunfish), and the effects of father–offspring resemblance on children's fitness-related traits have not been quantified. Here, we investigated father–child resemblance through both visual and olfactory cues in a human rural polygynous population, where access to limited resources mainly depends on male provisioning, leading to high levels of competition among offspring for paternal investment. As the raters used to assess resemblance did

Figure 2. Father–offspring facial and odour resemblance. The level of phenotypic resemblance to the father as assessed by independent raters for each child (53 children in total) is given for facial and odour cues.
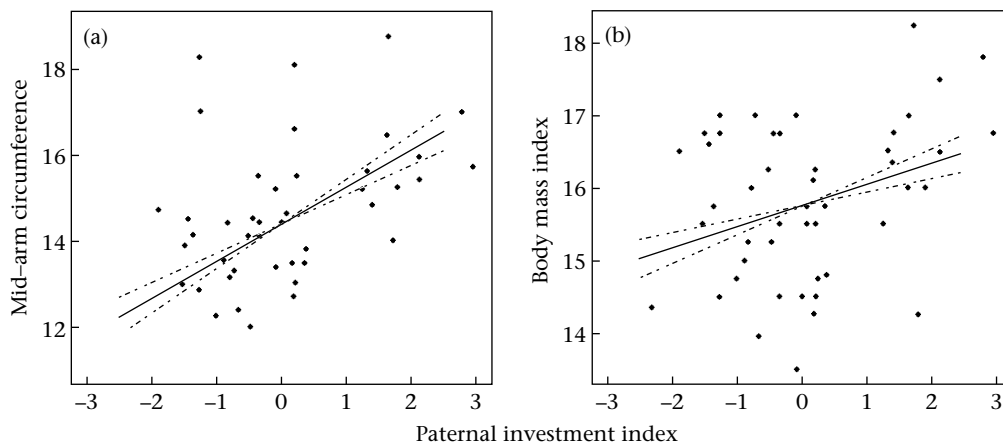
Figure 3. Paternal investment index and father–child phenotypic resemblance. The fitted relations between paternal investment and father–child resemblance are drawn (plain line), with the 95% standard confidence intervals of the fitted model (dotted-dashed lines). Raw data adjusted for the other index of resemblance are indicated by dots. (a) Effect of facial resemblance to the father. (b) Effect of odour resemblance to the father.

not know the families, our study avoided the effects of shared experience (familiarity) on the assessment of phenotypic similarities. We showed that paternal resemblance was significantly and positively related to paternal investment for both cues, and paternal investment was significantly and positively related to two indexes of child condition (BMI and MAC).

The observed link between father–child phenotypic resemblance and paternal investment could be interpreted with the opposite causal link, that is, as a result of the influence of paternal investment on resemblance. In the case of facial resemblance, this would be possible through the process of imitation, which is possibly increased when father–child interactions are more frequent. However, imitation is unlikely to explain our results entirely, as facial resemblance was assessed on motionless images of people presenting an expressionless face. Concerning olfactory signals, similarities between a father and his offspring could result from a nongenetic cause, such as odour contamination from interactions between individuals, that is, time spent together. While some contamination surely acts on odour resemblance between a father and his offspring, its effect is probably weak. Previous studies have indeed revealed that odour similarities between kin may be inferred independently of shared environment (Weisfeld et al. 2003). Furthermore, our study showed that a given child did

not express a higher odour resemblance to his/her father after spending the night in the same bed, compared to children who slept apart from their fathers. None the less, the nature of odour similarities resulting from nongenetic causes and their influence on discriminative paternal investment should be further explored. Is this a by-product of increased paternal investment at first influenced by genetic similarities? What is the relative influence of genetic similarities on odour similarities involved in discriminative paternal investment? Addressing these questions will give insight into the adaptive nature of the use of olfactory similarities in the context of paternity uncertainty and paternal investment.

Another interpretation of the correlation between phenotypic similarities and discriminative paternal investment is that highly investing fathers are also those who generally have strong resemblances to their children, without any causal link. If this were true, the level of resemblance to the father would be more similar between siblings than between nonrelated children. Rather, our results suggest that fathers did adjust the amount of paternal care that they provided to their children as a function of phenotypic similarities. Indeed, the variability in the level of father–child resemblance was similar between and within families (the scaled percentage of variation of resemblance was 17% between families and 23% within families).

Figure 4. Child condition and paternal investment index. The fitted relations between paternal investment and two indexes of child condition are drawn (plain line), with the 95% standard confidence intervals of the fitted models (dotted-dashed lines). Raw data are indicated by dots. (a) Effect of paternal investment on mid-arm circumference. (b) Effect of paternal investment on body mass index.

One can argue that some fathers may not be the genetic fathers in the tested sample, a possibility that cannot be tested without DNA paternity testing. If we adjust for some amount of extrapair children, then the level of father–offspring resemblance, as detected by the raters, is lower than expected, which would make our results conservative. Moreover, given the mean rate of nonpaternity worldwide (ca. 3.3%, Anderson 2006) and the small size of the studied villages, it is likely that the nonpaternity rate is low in this sample.

In this study, although we sampled two children per family, we did not have the ability to investigate the link between the variation within families in the degree of resemblance and in the level of investment. This is due to a low variability in paternal investment, as reported by the mother within families (less than 1%, whereas variability between families was 29%). This could be because fathers allocate their resources equally among all their children, whatever their characteristics. Although studies on differential investment among children of the same father based on resemblance are currently lacking, differential investment based on either sex or birth order is frequently observed in human societies (e.g. Mace 1996; Draper & Hames 2000; Beise & Voland 2002; Bereczkei & Dunbar 2002; Hertwig et al. 2002). The absence of any variation in paternal investment in our study sample may thus suggest that differences in the level of paternal investment received by two children of the same family were underreported by the mothers because of social norms, cultural beliefs and/or social desirability. This underreporting could be resolved by the use of an objective measure of paternal investment, based on observations instead of mothers' reports, as well as specific data on both how resources are allocated from fathers to offspring and the extent to which mothers can compensate for loss of paternal investment. Such an approach would be capable of revealing the variability of paternal investment and therefore allow the investigation of within-family effects.

Differential investment among a father's children on the basis of phenotypic similarities could be maladaptive, from the father's point of view, in cases where he is equally related to all of his children (although investment in equally related offspring need not necessarily be equal to be adaptive). In the context of female infidelity, however, the probability of paternity can vary among his children (Westneat & Sherman 1993). For each child, fathers must balance the risk of investing resources in an unrelated child with the risk of not providing care to a related child. The evolution of distinctive paternal signatures in response to paternity uncertainty has previously been modelled, and the more realistic model finds that the optimal strategy for both fathers and offspring is one in which the child's phenotype reveals the paternity (Johnstone 1997).

One might wonder whether external raters and fathers are equally good at detecting phenotypic similarities. First, more than half of the raters in this study were themselves parents (57%). Additionally, the activation of specific brain areas in men, when confronted with self-facial resemblance, has been observed in a sample of young men who were likely to be nonfathers (undergraduate students), suggesting that the sensitivity to facial resemblance is already present before fatherhood (Platek et al. 2004, 2005). If nonparents are nevertheless poorer detectors than parents, the use of a mixed sample of raters (parents and nonparents) makes our resemblance results conservative.

One remaining question concerns the methods by which fathers know their own facial phenotype, since mirrors are a recent innovation. It is possible that water reflection of the face, used as a mirror in the ancestral environment, is sufficient for such learning. It is also possible that fathers rely on what their kin tell them about actual resemblance ('social mirror'; Burch & Gallup 2000) or that they use the phenotype of relatives known unambiguously as 'kin template'. Much less is known about olfactory cues. Whether men know their own odours is questionable, as young men are apparently unable to detect their own axillaries' secretion when presented with five possible choices, while young women detect their own odour accurately (Platek et al. 2001). However, Platek et al. (2002) have shown that an inability to self-recognize morphed faces consciously does not prevent the observation of investment decisions based on self-facial resemblance. Thus, the possible absence of self-odour recognition does not contradict the interpretation of our results, which suggest that men are able to detect odour similarities between themselves and their children and adjust investment decisions accordingly.

The proximate signals of relatedness associated with facial and olfactory phenotypes remain to be elucidated. For the face, signals of relatedness seem to be located mainly in the upper half, since masking this area decreases the recognition rate of siblings by unrelated raters by 65% (Dal Martello & Maloney 2006), whereas masking the lower half decreases recognition by only 5.3%. For the odour, signals of relatedness may be mediated by chemosignals associated with the MHC. The MHC phenotype is a likely candidate for father–child odour resemblance, as it is involved both in parent–progeny recognition in mice (Yamazaki et al. 2000) and in mate choice in humans (Wedekind & Furi 1997).

The observed link between paternal investment and child condition may result from greater access to food resources, which are mainly controlled by men in this population. If mothers were not observed to be biased in their food allocation among their children, an unequal food repartition may nevertheless result from male behaviour. We often observed fathers collecting 'little things' for their children, such as fruits, cookies and other edibles, throughout the day. Also, when fathers came back home for a meal, some children who had eaten earlier (generally one or two per family) often ate a second time on their fathers' laps. Moreover, the likelihood that fathers buy or provide food to a particular child is probably associated with the time spent with each child. In this study, the time fathers spent with each child was the variable accounting for most of the variability of the paternal investment index. The link between paternal investment and child condition was still significant when the father's social status, reflecting access to resources, was taken into account. Thus, resembling their father benefits the nutritional condition of children, possibly through increased time spent with their father, which leads to increased access to food resources.

This study provides the first evidence in humans that paternal investment is predicted by father–child phenotypic similarities, as detected by the human brain independently of social manipulation, through both the face and the odour. Furthermore, this investment positively influenced the condition of the child. These findings have important implications for illuminating the evolution of paternal investment and paternity cues in response to paternity uncertainty.

members of the Senegalese ethical committee for their interest and recommendations and two anonymous referees for their helpful suggestions. This study was supported by the Agence Nationale pour la Recherche 'BIOEVOLHUM' project (NT05-1_43865) and the European Commission (Marie Curie Intra-European Fellowship: project 24796). This is contribution 2009.030 of the Institut des Sciences de l'Evolution de Montpellier (UMR CNRS 5554).

References

Anderson, K. G. 2006. How well does paternity confidence match actual paternity? Evidence from worldwide nonpaternity rates. *Current Anthropology*, **47**, 513–519.

Apicella, C. L. & Marlowe, F. W. 2004. Perceived mate fidelity and paternal resemblance predict men's investment in children. *Evolution and Human Behavior*, **25**, 371–378.

Bates, D. & Sarkar, D. 2007. lme4: Linear Mixed-effects Models using S4 Classes. Vienna: R Development Core Team.

Beise, J. & Voland, E. 2002. Differential infant mortality viewed from an evolutionary biological perspective. *History of the Family*, **7**, 515–526.

Bellis, M. A. & Baker, R. R. 1990. Do females promote sperm competition? Data for humans. *Animal Behaviour*, **40**, 997–999.

Bellis, M. A., Hughes, K., Hughes, S. & Ashton, J. R. 2005. Measuring paternal discrepancy and its public health consequences. *Journal of Epidemiology and Community Health*, **59**, 749–754.

Bereczkei, T. & Dunbar, R. I. M. 2002. Helping-at-the-nest and sex-biased parental investment in a Hungarian gipsy population. *Current Anthropology*, **43**, 804–812.

Bressan, P., Bertamini, M., Nalli, A. & Zanutto, A. In press. Men do not have a stronger preference than women for self-resemblant child faces. *Archive of Sexual Behavior*, doi:10.1007/s10508-008-9350-0

Burch, R. L. & Gallup Jr., G. G. 2000. Perceptions of paternal resemblance predict family violence. *Evolution and Human Behavior*, **21**, 429–435.

Cerda-Flores, R. M., Barton, S. A., Marty-Gonzalez, L. F., Rivas, F. & Chakraborty, R. 1999. Estimation of nonpaternity in the Mexican population of Nuevo Leon: a validation study with blood group markers. *American Journal of Physical Anthropology*, **109**, 281–293.

Clutton-Brock, T. H. 1991. *The Evolution of Parental Care*. Princeton, New Jersey: Princeton University Press.

Crawley, M. J. 2007. *The R Book*. Chichester: J. Wiley.

Dal Martello, F. D. & Maloney, L. T. 2006. Where are kin recognition signals in the human face? *Journal of Vision*, **6**, 1356–1366.

DeBruine, L. M. 2004. Resemblance to self increases the appeal of child faces to both men and women. *Evolution and Human Behavior*, **25**, 142–154.

DeBruine, L. M., Jones, B. C., Smith, F. G. & Little, A. C. 2008. Are attractive men's faces masculine or feminine? The importance of controlling confounds in face stimuli. *Journal of Experimental Psychology: Human Perception and Performance*, **34**, 884–893.

Dixon, A., Ross, D., O'Mallay, S. L. C. & Burke, T. 1994. Paternal investment inversely related to degree of extra-pair paternity in the reed bunting. *Nature*, **371**, 698–700.

Draper, P. & Hames, R. 2000. Birth order, sibling investment, and fertility among Ju/'hoansi (! Kung). *Human Nature*, **11**, 117–156.

Euler, H. & Weitzel, B. 1996. Discriminative grandparental solicitude as reproductive strategy. *Human Nature*, **7**, 39–59.

Gamboa, G. J., Reeve, H. K. & Ferguson, I. D. 1986. Nestmate recognition in social wasps: the origin and acquisition of recognition odours. *Animal Behaviour*, **34**, 685–695.

Garland, R. 1991. The mid-point on a rating scale: is it desirable? *Marketing Bulletin*, **2**, 66–70.

Gaulin, S. J. C. & Schlegel, A. 1980. Paternal confidence and paternal investment: a cross cultural test of a sociobiological hypothesis. *Ethology and Sociobiology*, **1**, 301–309.

Gaulin, S. J. C., McBurney, D. & Brakemann-Wartell, S. 1997. Matrilateral biases in the investment of aunts and uncles: a consequence and measure of paternity uncertainty. *Human Nature*, **8**, 139–151.

Greenberg, L. 1979. Genetic component of bee odor in kin recognition. *Science*, **206**, 1095–1097.

Hain, T. J. A. & Neff, B. D. 2007. Multiple paternity and kin recognition mechanisms in a guppy population. *Molecular Ecology*, **16**, 3938–3946.

Hamilton, W. D. 1963. The evolution of altruistic behavior. *American Naturalist*, **97**, 354–356.

Hauber, M. E. & Sherman, P. W. 2001. Self-referent phenotype matching: theoretical considerations and empirical evidence. *Trends in Neurosciences*, **24**, 609–616.

Hawkins, A. J., Bradford, K. P., Palkovitz, R., Christiansen, S. L., Day, R. D. & Call, V. R. A. 2002. The inventory of father involvement: a pilot study of a new measure of father involvement. *Journal of Men's Studies*, **10**, 183–196.

Hertwig, R., Davis, J. N. & Sulloway, F. J. 2002. Parental investment: how an equity motive can produce inequality. *Psychological Bulletin*, **128**, 728–745.

Heth, G., Todrank, J. & Busquet, N. 2003. Genetic relatedness assessment through individual odour similarities in mice. *Biological Journal of the Linnean Society*, **78**, 595–603.

Holmes, W. G. 1994. The development of littermate preferences in juvenile Belding's ground-squirrels. *Animal Behaviour*, **48**, 1071–1084.

Ihara, Y. 2002. A model for evolution of male parental care and female multiple mating. *American Naturalist*, **160**, 235–244.

Johnstone, R. A. 1997. Recognition and the evolution of distinctive signatures: when does it pay to reveal identity? *Proceedings of the Royal Society of London, Series B*, **264**, 1547–1553.

Jones, B. C., Little, A. C., Feinberg, D. R., Penton-Voak, I. S., Tiddeman, B. P. & Perrett, D. I. 2004. The relationship between shape symmetry and perceived skin condition in male facial attractiveness. *Evolution and Human Behavior*, **25**, 24–30.

Kaiser, H. F. 1974. An index of factorial simplicity. *Psychometrika*, **39**, 31–36.

Krebs, J. R. & Davies, N. B. 1993. *An Introduction to Behavioural Ecology*. Oxford: Blackwell Science.

Lacy, R. C. & Sherman, P. W. 1983. Kin recognition by phenotype matching. *American Naturalist*, **121**, 489–512.

Lieberman, D., Tooby, J. & Cosmides, L. 2007. The architecture of human kin detection. *Nature*, **445**, 727–731.

McBurney, D. H., Simon, J. & Gaulin, S. J. C. 2001. Matrilateral biases in the investment of aunts and uncles. *Human Nature*, **13**, 391–402.

Mace, R. 1996. Biased parental investment and reproductive success in Gabbra pastoralists. *Behavioral Ecology and Sociobiology*, **38**, 75–81.

Mateo, J. M. 2003. Kin recognition in ground squirrels and other rodents. *Journal of Mammalogy*, **84**, 1163–1181.

Neff, B. D. & Gross, M. R. 2001. Dynamic adjustment of parental care in response to perceived paternity. *Proceedings of the Royal Society of London, Series B*, **268**, 1559–1565.

Neff, B. D. & Sherman, P. W. 2003. Nestling recognition via direct cues by parental male bluegill sunfish (*Lepomis macrochirus*). *Animal Cognition*, **6**, 87–92.

Neff, B. D. & Sherman, P. W. 2005. In vitro fertilisation reveals offspring recognition via self-referencing in a fish with paternal care and cuckoldry. *Ethology*, **111**, 425–438.

O'Riain, M. J. & Jarvis, J. U. M. 1997. Colony member recognition and xenophobia in the naked mole-rat. *Animal Behaviour*, **53**, 487–498.

Parke, R. D., Dennis, J., Flyr, M. L., Morris, K. L., Leidy, M. S. & Schofield, T. J. 2005. Fathers: cultural and ecological perspectives. In: *Parenting: an Ecological Perspective* (Ed. by T. L. L. Okagaki), pp. 103–146. London: L. Erlbaum.

Penn, D. J. & Potts, W. K. 1999. The evolution of mating preferences and major histocompatibility complex genes. *American Naturalist*, **153**, 145–164.

Platek, S. M., Burch, R. L. & Gallup Jr., G. G. 2001. Sex differences in olfactory self-recognition. *Physiology and Behavior*, **73**, 635–640.

Platek, S. M., Burch, R. L., Panyavin, I. S., Wasserman, B. H. & Gallup Jr., G. G. 2002. Reactions to children's faces: resemblance affects males more than females. *Evolution and Human Behavior*, **23**, 159–166.

Platek, S. M., Critton, S. R., Burch, R. L., Frederick, D. A., Myers, T. E. & Gallup Jr., G. G. 2003. How much paternal resemblance is enough? Sex differences in hypothetical decisions but not in the detection of resemblance. *Evolution and Human Behavior*, **24**, 81–87.

Platek, S. M., Raines, D. M., Gallup Jr., G. G., Mohamed, F. B., Thomson, J. W., Myers, T. E., Panyavin, I. S., Levin, S. L., Davis, J. A., Fonteyn, L. C. M. & Arigo, D. R. 2004. Reactions to children's faces: males are more affected by resemblance than females are, and so are their brains. *Evolution and Human Behavior*, **25**, 394–405.

Platek, S. M., Keenan, J. P. & Mohamed, F. B. 2005. Sex differences in the neural correlates of child facial resemblance: an event-related fMRI study. *NeuroImage*, **25**, 1336–1344.

Porter, R. H. & Cernoch, J. M. 1983. Maternal recognition of neonates through olfactory cues. *Physiology and Behavior*, **30**, 151–154.

Porter, R. H. & Moore, J. D. 1981. Human kin recognition by olfactory cues. *Physiology and Behavior*, **27**, 493–495.

Porter, R. H., Balogh, R. D., Cernoch, J. M. & Franchi, C. 1986. Recognition of kin through characteristic body odors. *Chemical Senses*, **11**, 389–395.

Russel, M. J., Mendelson, T. & Peeke, H. V. S. 1983. Mothers' identification of their infant's odor. *Ethology and Sociobiology*, **4**, 29–31.

Sasse, G., Muller, H., Chakraborty, R. & Ott, J. 1994. Estimating the frequency of nonpaternity in Switzerland. *Human Heredity*, **44**, 337–343.

Sheldon, B. C. 2002. Relating paternity to paternal care. *Philosophical Transactions of the Royal Society of London, Series B*, **357**, 341–350.

Sheldon, B. C. & Ellegren, H. 1998. Paternal effort related to experimentally manipulated paternity of male collared flycatchers. *Proceedings of the Royal Society of London, Series B*, **265**, 1737–1742.

Shepherd, G. M. 2004. The human sense of smell: are we better than we think? *PLoS Biology*, **2**, 572–575.

Simmons, W. 2002. Confidence of paternity and paternal care: covariation revealed through the experimental manipulation of the mating system in the beetle *Onthophagus taurus*. *Journal of Evolutionary Biology*, **15**, 784–795.

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

Visweswara, R. & Singh, D. 1970. An evaluation of the relationship between nutritional status and anthropometric measurements. *American Journal of Clinical Nutrition*, **23**, 83–93.

Volk, A. & Quinsey, V. L. 2002. The influence of infant facial cues on adoption preferences. *Human Nature*, **13**, 437–455.

Wedekind, C. & Furi, S. 1997. Body odour preferences in men and women: do they aim for specific MHC combinations or simply heterozygosity? *Proceedings of the Royal Society of London, Series B*, **264**, 1471–1479.

Weisfeld, G. E., Czilli, T., Phillips, K. A., Gall, J. A. & Lichtman, C. M. 2003. Possible olfaction-based mechanisms in human in recognition and inbreeding avoidance. *Journal of Experimental Child Psychology*, **85**, 279–295.

Westneat, D. F. & Sherman, P. W. 1993. Parentage and the evolution of parental behavior. *Behavioral Ecology*, **4**, 66–77.

Whittingham, M. J., Stephens, P. A., Bradbury, R. B. & Freckleton, R. P. 2006. Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology*, **75**, 1182–1189.

Wright, J. 1998. Paternity and paternal care. In: *Sperm Competition and Sexual Selection* (Ed. by T. R. Birkhead & A. P. Møller), pp. 117–145. London: Academic Press.

Yamazaki, K., Beauchamp, G. K., Curran, M., Bard, J. & Boyse, E. A. 2000. Parent-progeny recognition as a function of MHC odortype identity. *Proceedings of the National Academy of Sciences, U.S.A.*, **97**, 10500–10502.