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Why do blue-eyed men prefer women with the same eye color?

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Abstract The human eye color blue reflects a simple, predictable, and reliable genetic mechanism of inheritance. Blue-eyed individuals represent a unique condition, as in their case there is always direct concordance between the genotype and phenotype. On the other hand, heterozygous brown-eyed individuals carry an allele that is not concordant with the observed eye color. Hence, eye color can provide a highly visible and salient cue to the child's heredity. If men choose women with characteristics that promote the assurance of paternity, then blue-eyed men should prefer and feel more attracted towards women with blue eyes. To test these predictions, close-up photos of young women and adult men with either blue or brown eyes were rated for their attractiveness by young women and men observers with either blue or brown eyes (N=88). The eye color in the photographs of each model was manipulated so that a same face would be shown with either the natural eye color (e.g., blue) or with the other color (e.g., brown). Both blue-eyed and brown-eyed female participants showed no difference in their attractiveness ratings for male models of either eye color. Similarly, brown-eyed men showed no preference for either blue-eyed or brown-eyed female models. However, blue-eyed men rated as more attractive the blue-eyed women than the brown-eyed ones. We interpret the latter preference in terms of specific mate selective choice of blue-eyed men, reflecting strategies for reducing paternity uncertainty. In a second study, a group of young adults (N=443) of both sexes and different eye colors (blue, brown, and green) were asked to report the eye and hair color of their romantic partners. Their responses indicated the presence of assortative mating by eye color as well as, to a less degree, for hair color. Most importantly, blue-eyed male respondents were the group with the largest proportion of partners of same eye color. These findings 1) indicate that blue-eyed men do prefer women with the same eye color and 2) specifically suggest the presence of a male adaptation for the detection of extra-pair paternity based on eye color, as a phenotypically based assurance of paternity (i.e., when the father's and offspring's phenotypes match) as well as a defense against cuckoldry (i.e., when the phenotypes do not match).

Keywords Assortative mating · Eye color · Paternity confidence

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Why do blue-eyed men prefer women with the same eye color?

Eye color has been the first character in humans to be recognized as Mendelian in its inheritance. Hurst (1908) examined the eyes within several families and pointed out that the blue and brown eyes form a Mendelian pair of characters. Among the earliest to study human heredity of iris color, Halfdan Bryn (1920) examined the prevalence of eye color types within Norwegian families (notice that in many human populations brown is the only iris phenotype; Eiberg and Mohr 1996) and confirmed the Mendelian character of eye color's inheritance by observing that: 1) if both parents have blue eyes the children will have blue eyes; 2) if both parents have brown eyes, the children will be on average 1/4 blue-eyed and 3/4 brown-eyed; 3) blue is found recessive to all grades of brown. Thus, eye color reflects a simple, predictable, and reliable genetic mechanism of inheritance. Importantly, blue-eyed individuals represent a unique condition, as in their case there is always direct concordance between the genotype and phenotype. On the other hand, heterozygous brown-eyed individuals carry an allele that is not concordant with the observed eye color.

Apparently, quite apart from the above observation of eye-color heredity, it is well-known that the genetic costs of parental investment exert strong selective pressures (Trivers 1972; Maynard Smith 1977). Such pressures should favor behavioral propensities that increase the probability that parental investment is not misdirected to non-relatives (Williams 1975; Alexander and Noonan 1979; Buss and Schmitt 1993; Hrdy 2000), and such propensities should be strongest with men. It is also self-evident that maternal uncertainty is generally not an issue and therefore parental uncertainty may be a "uniquely male" adaptive problem. In conclusion, we would expect that a man would be more attracted toward a woman exhibiting a trait that increases the man's paternal confidence or a trait that increases the likelihood of uncovering the mate or spouse's *deception* (cuckoldry or sexual infidelity).

From the above considerations that a) eye color provides a highly visible and salient cue to the child's heredity, and that b) men choose women with characteristics that promote the assurance of paternity, we then reasoned that blue-eyed men should prefer and feel more attracted towards women with blue eyes. The paternal uncertainty of brown-eyed men neither decreases nor increases when mating with blue-eyed women. In fact, the choice of a blue-eyed mate by another blue-eyed individual would guarantee the presence of this salient phenotypic trait in all of their offspring. Importantly, a child born of two blue-eyed parents without the same trait would signal that the blue-eyed "father" did not sire the child. In contrast, brown-eyed men lack such constraint and women lack the need for developing abilities to detect parental certainty. However, it can be argued that women are under selective pressure to increase their ability to successfully cuckold a man. Thus, the blue-eyed women may actually prefer brown-eyed men (cf. Feinman and Gill 1978). On the other hand, a blue-eyed woman could promote her mate's assurance that an offspring is his own by mating with a blue-eyed man. Hence, a clear-cut prediction of what women should do in general to increase their inclusive fitness remains unclear, and it is likely that the specific context would decide which strategy a blue-eyed woman would choose to adopt.

Interestingly, the iris (notably of Caucasian infants) starts out with a clear blue color and soon becomes brown in the more melanized individual or remains blue in the less melanized one (Bito et al. 1997). Thus, infants appear to be born with "neutral" eye color. As the eye is exposed to sunlight, the iris begins to produce melanin pigment and the eye color gradually changes towards its adult coloring, reaching complete pigmentation by age 3. One could speculate that brown-eyed infants hide their "true" phenotype as an evolved strategy (cf. Pagel 1997). One consequence of this age-dependent change is that the "father" may initially treat offspring with respect to eye color without being sure that they have acted adaptively.

All of the above considerations are based on the assumption that sexual infidelity that results in illegitimate offspring is not at all a minor possibility, either in the present or in the evolutionary past, and that its occurrence can have serious consequences for the couple and/or for the illegitimate children. In a large cross-cultural study, Betzig (1989) confirmed that infidelity is the most cited reason for divorce. Sigusch and Schmidt (1971) found that 6% of their female informants stated that they would have casual sexual intercourse with someone else than their current partner (see also Kinsey et al. 1953; Greiling and Buss 2000; Schackelford 2003; Schmitt et al. 2004). According to several researchers (e.g., Laumann et al. 1994; Wiederman 1997; Shackelford et al. 2000), estimates of infidelity appear to range from 20 to 75%, depending on age, type of relationship, and its duration. Gaulin and Schlegel (1980) concluded that only 55% of 135 societies have high paternity confidence.

Most importantly, studies on the incidence of genetic mismatches (i.e., cases in which the presumed father of the child is not the actual biological father; cf. Pena and Chakraborty 1994) show that the number of children who may be the result of infidelity, concealed adoption, or another event, is not negligible (e.g., 2.3%, Ashton 1980; 6%, Fuster 1984). A recent review (Anderson 2006) of 67 studies estimates a median non-paternity of 3.9% (range 0.4–32.0). Individual studies can place the prevalence of non-paternity at much higher levels (about 10% on average; see Baker and Bellis 1995; Cerda-Flores et al. 1999; Neale et al. 2002; Sasse et al. 1994; Sykes and Irven 2000), and it is likely that cultural and contextual factors can influence the frequency of non-paternities.

In addition, at least in modern Western societies, women are more prone to fantasize or have sexual intercourse with a man other than their current partner during the fertile phase of the cycle (Gangestad et al. 2002). The resemblance among children and their parents is also a common topic of/with parents and paternal resemblances of children commonly draw more interest than maternal (Daly and Wilson 1982; Regalski and Gaulin 1993; McLain et al. 2000; Platek et al. 2002, 2004). Studies conducted within modern Western societies show that fathers appear to invest in parenting in direct proportion to the children's resemblance to themselves (Apicella and Marlowe 2004); and aunts and uncles show a matrilineal bias in their investment towards their nieces or nephews (Alexander 1979), even in groups presumed to have high paternity certainty (i.e., among Orthodox Jews, McBurney et al. 2002).

In many societies, the discovery of non-paternity can have serious consequences for the partner and offspring. As mentioned earlier, infidelity is the most cited reason for divorce (Betzig 1989). But other consequences may include desertion, reduced male care, and reduced transfer of resources from the "father" to the children, which could in turn increase the mortality rates of children from the illegitimate births (Fuster 1984). In some societies, where paternal investment can be crucial for the successful raising of offspring, an extramarital conception can lead to infanticide, either paternal or maternal (e.g., six out of 15 instances of infanticide among the Eipo of New Guinea; Schiefenhovel 1989). However, among societies in which paternal investment is less crucial to the successful raising of offspring, infanticide rates tend to be low (Hrdy 1992).

Among the various factors that would seem particularly relevant for developing mate preferences is what we may label 'early-age-based *koinophilia*' (cf. Koeslag and Koeslag 1994), leading to a preference for family resemblances. According to this view, exposure during developmental sensitive periods to the immediate kin is the first and foremost influential model from which relevant positive features are abstracted (cf., DeBruine 2005). There is already evidence that individuals prefer mates who resemble their parents (Zei et al. 1981; Wilson and Barrett 1987; Perrett et al. 2002; Little et al. 2003). Specifically, there seems to be a "quasi-oedipal" or "parental imprinting" effect of mothers' traits onto their sons' preferences and of the fathers' traits onto their daughters' preferences. One would also predict that blue-eyed individuals with both blue-eyed parents might be more likely to have partners with blue eyes than participants with only the father or the mother showing the blue eyes phenotype.

Finally, another factor that may be particularly relevant for developing mate preferences for lightly colored eyes is the phenomenon that in many societies, men tend to prefer women with lighter colored skin (van den Berghe and Frost 1986). Symons (1995) argued that such a preference derives from the fact that across a wide range of populations, women have on average lighter skin than men and both aging and successive pregnancies progressively darken the skin. Hence, men could use complexion as a cue to desirable feminine traits as nubility and fecundity. Specifically, sex differences in complexion arise at puberty and adult men can have a ruddier and browner complexion than women as a result of differing melanin and hemoglobin levels in the skin's outer layers (Jablonski and Chaplin 2000). Thus, one could hypothesize that also other visible traits, like having blue eyes or blond hair, that are correlated to light skin color would also be preferred by men in general.

Although there is value in such an alternative view, we believe that it does not apply well to the specific situation. First of all, as van den Berghe and Frost (1986) point out, the sex difference in complexion color decreases from strongly to weakly pigmented people and is not significant in the Dutch (i.e., the least pigmented people yet examined; Ritgers-Aris 1973). Thus, if the Dutch are already close to the physiological limit of human depigmentation and their complexion cannot lighten any further (a "ceiling effect"; see Frost 2006), one would easily assume that among the Scandinavians or light-skinned populations in general (cf., Relethford et al. 1985), eye color cannot be used as a reliable cue to femininity, as the two sexes are likely not to differ in complexion at any age.

In sum, if men choose women with characteristics that promote the assurance of paternity, then blue-eyed men should prefer and feel more attracted towards women with blue eyes. To test these predictions, in a first study, frontal close-up photos of young female and male adults with either blue or brown eyes were rated for their attractiveness by young female and male observers, also with either blue or brown eyes. The eye color in the photographs of each model was manipulated so that for each model's face two versions were shown, one with the natural eye color (blue/brown) and another with a different color (brown/blue). Participants were requested to give attractiveness ratings to models of either eye colors.

Study 1

This study used exclusively photos of faces of young Norwegian adults that were manipulated so as to create for each model, a "double" of the face with the eye color transformed (see Fig. 1). All other facial characteristics were kept identical in the manipulated photos. The participants were asked to judge the degree of attractiveness of each individual model. Different groups of subjects saw only one version of each face, so as to increase the likelihood that during the experiment the eye color manipulation would go unnoticed. No mention was made about the fact that half of the models displayed in the photos had artificial eye coloring. We predicted that blue-eyed men should prefer women with blue eyes, whereas all the other groups of participants would not show specific preferences based on the eye colors of the models.

Materials and methods

Participants Eighty-eight individuals took part voluntarily in an experiment on judgments of facial attractiveness. All participants were Norwegians and none were immigrants or

Fig. 1 Examples of two of the models used in study 1: left-sided photos show each model's natural eye color, whereas the right-sided pictures show the same faces with transformed eye color (*top*: *brown* to *blue*; *bottom*: *blue* to *brown*). *Colors* can be seen in the electronic, on-line version of this Figure

born of immigrant parents. They were all university students within the 5-year psychology program (mean age=23.2; SD=3.7) at the University of Tromsø, Norway. Participants were selected so as to form four groups with 22 participants each: the blue-eyed men; the brown-eyed men; the blue-eyed women, and the brown-eyed women. Individuals were personally contacted by the investigators, and if presenting other eye colors (e.g., green) were excluded from this study and recruited instead for a different psychology experiment. In fact, in some medical studies, green and brown can be collapsed in one category (e.g., Regan et al. 1999); however, genetic models show that blue eyes implicate one genotype and brown eyes implicate two genotypes, green eyes implicate no specific genotype (Hasstedt 1995).

Stimuli and apparatus A Kodak DC-120 digital camera was used to photograph young adults (the "models") of both sexes. Eyes were categorized as blue or brown by three independent judges. Models showing differences in the brightness of the brown or blue hues (e.g., hazel or gray) were included into the brown or blue category, but ambiguous cases (e.g., brownish-green) were not included in the stimulus sample. However, pure eye colors may be rare among humans (Rife 1933). The finally selected set of photos for the study consisted of 60 models (30 women).

Each picture was a full frontal, close-up of the face, with an equal number (i.e., 15) of naturally blue-eyed or brown-eyed models (unfamiliar to the participants) in each sex group. Adobe PhotoShop 4.0 or 7.0 were used to edit the color images. The models' irises were outlined to enable color adjustments. For each model a "mutant clone" was created, i.e., an individual with the exact same characteristics except for eye color. The final number of 120 pictures was divided into two sets, each with an equal number of men and women with "natural" and "altered" versions of eye color. Only one of the alternate copies of each model was included in a set so that every participant would see each model in only one eye-color version. A Macintosh PowerBook 1400cs/133, screen set to "millions of colors," presented the stimuli and collected responses. The letter keys just above the space bar were labeled with numbers 1 to 5. Each picture was displayed full-screen.

Procedure Participants were tested individually within a time period of 9 months in a windowless laboratory room and were randomly assigned to one of the two experimental sets, counter-balancing the groups for sex and eye color. The task was self-paced. Each image remained on the computer screen until the participant made a key press (on one the 1–5 keys on the number pad). The task was to judge the attractiveness of each of the models by rating, with 1 the least attractive and with 5 the most attractive. The PC recorded each key press using the SuperLab software. The 60 trials were ordered pseudo-randomly (i.e., no more than two consecutive presentations of models of either the same sex or eye color were allowed).

At the end of the experiment, all participants were asked to provide, with the use of a questionnaire, their own eye color and that of their biological parents. No additional questions were added in the attempt to disguise the purpose of the study; however, participants were specifically requested to report in writing their guesses about the purpose of the experiment and whether they had noticed "something unusual" in the pictures. In addition, ten of the participants (five women) were also specifically asked whether they had noticed "something unusual" about some of the models' eyes. In the debriefing phase of the experiment, it was explained that the experiment investigated the effects of eye color on esthetic judgments.

Results

Preliminary ANOVAs showed no main effects ($F<1$) or interactions with the factors of stimulus set and of iris (natural/altered). Hence, the following analyses were based on results pooled over the two sets of faces and manipulations of the iris. The obtained means for the remaining factors were entered as cells in repeated-measures ANOVA with sex of participant (female/male) and eye color of participant (blue/brown) as the between-subjects factor, and sex of models (female/male), eye color (blue/brown) as the within-subject factors.

The analysis revealed a significant four-way interactive effect between the factors of sex of participant, eye color of participant, model's sex, and model's eye color; $F(1, 84)=8.8$, $p=0.0041$. As predicted, the blue-eyed male subjects gave higher ratings to blue-eyed female models (mean=3.29; SD=0.45) than to the brown-eyed female models (mean=2.79; SD=0.44), Cohen's $d=1.11$. A Newman–Keuls post hoc test, performed over 16 comparisons, confirmed the predicted difference between the blue-eyed male participants' ratings of blue- and brown-eyed female models (i.e., MSE=0.12; $W_7=0.436$; difference=0.487). In addition, the blue-eyed male participants' ratings of blue-eyed women were significantly larger than the blue-eyed female participants' ratings of blue-eyed men (i.e., MSE=0.12; $W_2=0.302$; difference=0.317). In contrast, the brown-eyed men did not show the same eye-color-based preference for female models (blue-eyed women: mean=2.82; SD=0.46; brown-eyed women: mean= 2.99; SD=0.47) and, in fact, according to the Newman–Keuls post hoc tests, there was no reliable difference in their ratings of models with different eye colors (i.e., MSE=0.12; $W_2=0.302$; difference=0.17). Similarly, female participants did not show a significant eye-color-based preference for either male or female models, and male participants (regardless of their eye color) did not show a preference for male models of either eye color (see Fig. 2).

The interaction of sex of participant and model's sex was significant, $F(1, 84)=21.9$, $p<0.0001$. Not surprisingly, female participants rated the male models as more attractive than the female models, whereas the male participants showed the reverse preference. No other factors or interactions reached the significance level of $\alpha<0.05$.

In addition, we identified those participants ($N=72$) who had parents of either blue or brown eye colors (excluding those with a green-eyed parent) and performed a separate ANOVA on ratings with sex (sons and daughters), eye color of child (blue-eyed and brown-eyed), and eye color of parents (blue-eyed mothers and brown-eyed fathers, both blue-eyed, brown-eyed mothers and blue-eyed fathers, both brown-eyed) as the between-subjects factors. There was no significant effect of eye color of parents, $F(3, 81)= 1.2$, $p=0.27$, or interactive effects with the other factors (for $p<0.05$).

No participant commented spontaneously in the debriefing phase about the possibility that in some pictures the eye color looked unnatural or strange. Within a group of ten participants who were specifically asked if they had noticed something unusual with the eye colors, only one female participant commented that some of the models might have been wearing 'colored contact lenses'. No participants guessed correctly that the study investigated the effects of eye color on attractiveness responses. Instead, several participants mentioned the possibility that the study was aimed at measuring the effect of 'facial symmetry'.

Discussion

Men with blue eyes rated as more attractive women with blue eyes than women with brown eyes. On the other hand, men with brown eyes did not show any significant preference of eye color. Similarly, women showed no difference in their ratings of men with either blue or brown eyes. Finally, same-sex attractiveness ratings failed to show any advantage based on eye color. The high specificity of these findings was predicted by a simple hypothesis: We argued that 1) human males make mate choices that reduce their paternal uncertainty and 2) blue-eyed men avail of a simple and reliable method for increasing their paternal confidence and uncover sexual infidelity from their mates, which resulted in illegitimate births.

It is remarkable that blue-eyed men showed such a clear preference for women with the same eye color, given that the present experiment did not request participants to

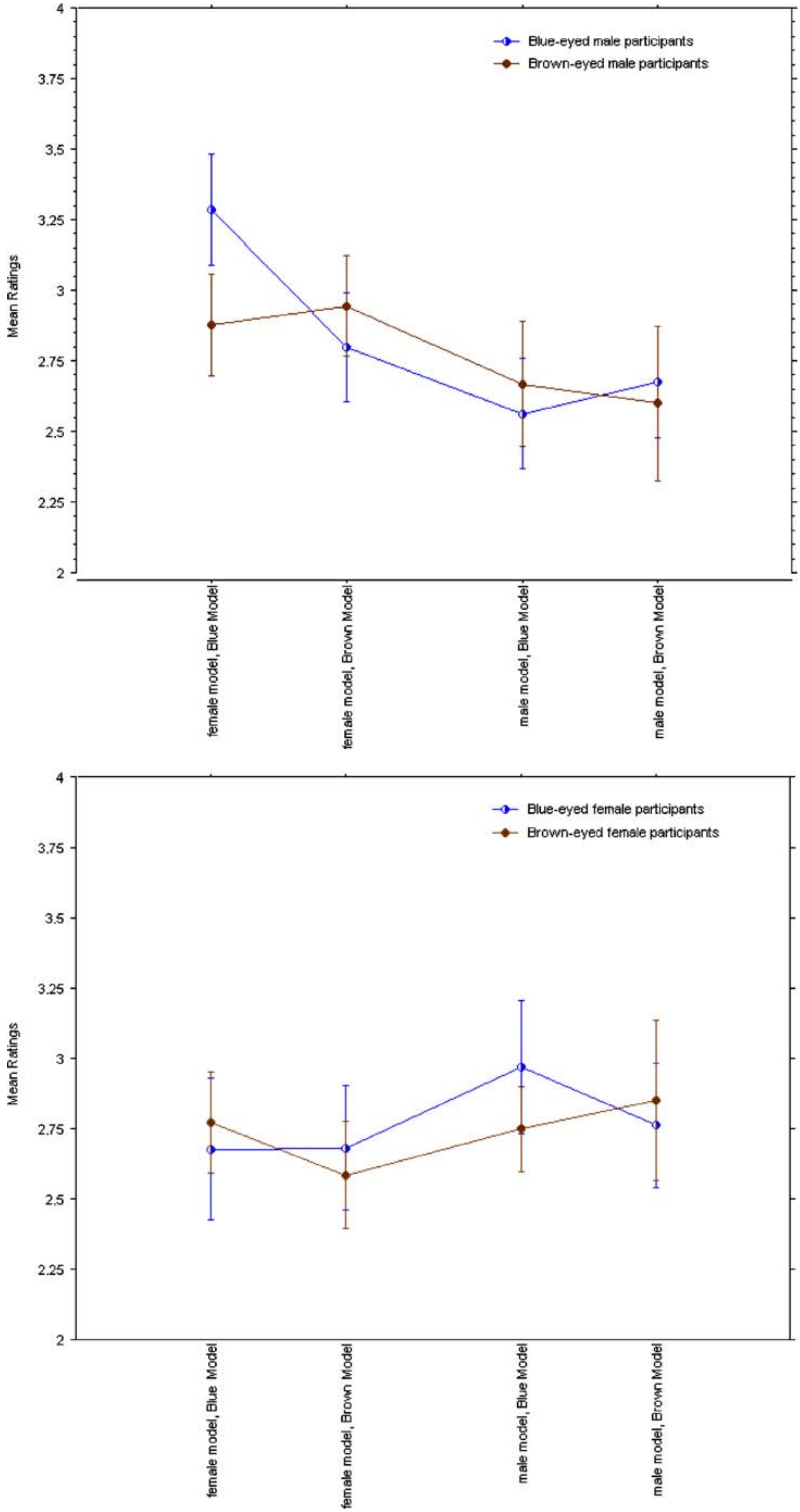

Fig. 2 Means of ratings of female and male models with *blue* or *brown* eyes for the group of male participants (*top panel*) and of female participants (*bottom panel*), split by *blue* (*half filled circles*) and *brown* eyes (*filled circles*). *Bars* show 95% confidence intervals

choose prospective sexual mates, but only to provide their esthetic or attractiveness responses that were exclusively based on face close-up photographs of same-age strangers. However, several studies have shown that those individuals judged to have attractive faces would also be preferentially chosen by the observers as their sexual mates (e.g., Walster et al. 1966). Interestingly, the iris alterations went largely unnoticed by the participants, an event which supports our interpretation of the present results as reflecting choices based on what participant perceived to be a model's "true" phenotype.

We also observed significant preferences for the models of the opposite sex, regardless of eye color of the participant. These generic effects may simply reflect the generally heterosexual orientation of our groups of respondents, but may also indicate the presence of some degree of intrasexual competition, whereby the attractiveness reported for individuals of the same sex is lowered (cf., Fisher 2004).

Finally, we found no evidence that 1) brown-eyed men would prefer blue-eyed women to the same extent or more than the blue-eyed men, which was a strong prediction of the hypothesis that eye color preferences reflect generic male preferences for women with lighter complexion and eye/hair color; and no evidence that 2) blue-eyed individuals with both blue-eyed parents had a greater preference for this trait than the other groups, which was a strong prediction of the hypothesis that eye color preferences reflect generic preferences for "family resemblances."

Study 2

Within an experimental setting as the one used in the previous study, facial variables other than eye color can be controlled and only the target variable (i.e., eye color) manipulated; but in the ecological situation, several psychological and social variables (e.g., economical, cultural, geographic, developmental, and personality factors) could enter in the choice of actual mates (including elements of opportunity, risk, and chance; cf. Lykken and Tellegen 1993; Symons 1995: Miller and Todd 1998; Widemo and Sæther 1999; Gangestad and Simpson 2000; Schmitt 2005). Yet, if preferences for eye colors reflect sexual strategies, then actual mate choices should reflect to some degree the influence of these factors.

Unfortunately, many studies on actual partners' assortment for somatic traits have not considered eye color (Price and Vanderberg 1980). Nevertheless, using Franz Boas's data (1928), Willoughby (1933) calculated a coefficient of contingency of 0.67 (N=293) for "homogamy" (i.e., assortative mating) in eye color and, practically, null in hair color. Two studies by Karl Pearson (Pearson and Lee 1903; Pearson 1907) found small, but significant, positive correlations (r=0.10 and r=0.26). A few studies have shown no significant or weak relations (Elston 1961; Beckman 1962; Thiessen et al. 1997). Recently, in an Internet-based survey of 697 participants, Little et al. (2003) found that the best single predictor of both male and female partner eye color was the opposite-sex parent's eye color. Hasstedt (1995) examined assortative mating for specific eye colors and found evidence for it in 62 spouse pairs, but the correlation between eye colors was negative (that is, blue-eyed and brown-eyed matings occurred in excess of matings with same eye color). We suspect that the small sample size may have spuriously influenced the results (cf. Jorjani et al. 1997) and it remains unclear whether a greater prevalence of blue-eyed women with brown-eyed husbands was mainly responsible for the effect. Thus, in the present study, we examined interrelations between specific eye colors. Information about physical characteristics like their own eye color and hair color, of their biological parents, and that of the current partners, was collected by use of a questionnaire.

Materials and methods

Participants and questionnaire Four hundred and forty-three individuals (women: N=239; men: N=204) completed a questionnaire that collected information about their own eye and hair colors, their current partners' (if any) and of the previous two partners (if any). In addition, they were asked to provide the eye and hair colors of their biological parents. All participants were Caucasian, non-immigrant Scandinavians, from the Tromsø community (mean age of women=27.2; SD=11; mean age of men=28.6; SD=12). Originally, 455 individuals volunteered to take part in various psychology experiments (e.g., studies of the Stroop effect, individual differences in color vision, perception and memory for faces, etc.); the questionnaire was administered at the end of each experimental session.

This included items probing each respondent's sex, age, place of birth, educational level, and profession. Respondents could place a checkmark in a box next to a color label (eyes: blue, brown, or green; hair: black, blond, brown, or red). If none of the labels described well the color, the participant left the boxes unchecked. Previous studies on heredity of physical traits have shown that a few color categories are sufficient to obtain reliable information (e.g., Burks 1938). Participants who reported having no partners at all in their lifetime (i.e., 2.8% of the total sample) were excluded from the analyses. Among the rest of the participants, 71% reported they had three or more partners in their lifetime. The present analyses are based on the 443 participants who reported at least one partner.

Results

Eye color Chi-square analyses were performed on the female and male participants' distributions of eye color traits and those of their partners. There was a significant difference in frequencies reported by male participants with blue, brown, and green eyes, in their mate choices for female partners' eye colors, $\chi^2(4)=33.7$, $p<0.0001$. Table 1 shows the males' observed frequencies, the expected values as well as the respective post hoc cell contributions (these values indicate which cells in the Table contribute to the χ^2 statistics; specifically, values greater than 4 for a 0.0001 probability indicate that the cell in question provides significant information about the combination of groups of the variables whose occurrence is different than would be expected). Thus, partners of the same eye color of the respondents were observed in excess to the expected value. Interestingly, although there appears to be assortative mating for all eye colors, the blue-eyed men with blue-eyed female partners were the group that differed the most from the expected values ($z=4.98$).

There was also a significant difference in frequencies reported by female participants with blue, brown, and green eyes, in their mate choices for male partners' eye colors, $\chi^2(4)=11.6$, $p=0.019$. Table 2 shows the women's choices. Females with male partners of the same eye color were observed in excess to the expected value. Moreover, the brown-eyed women with brown-eyed male partners was the group differing the most from the expected values. However, it is important to note that these differences are weaker than those seen earlier for the male respondents (as indicated by the lower values of the respective post hoc cell contributions).

Table 1 Distribution of male participants [i.e., Self (M)] with blue, brown, and green eyes and their female partners [i.e., Partner (F)] with blue, brown, and green eyes

Observed frequencies for self (M), partner (F)				
	Blue (F)	Brown (F)	Green (F)	Totals
Blue (M)	78	23	13	114
Brown (M)	19	23	12	54
Green (M)	11	9	16	36
Totals	108	55	41	204
Expected values for self (M), partner (F)				
	Blue (F)	Brown (F)	Green (F)	Totals
Blue (M)	60.353	30.735	22.912	114.000
Brown (M)	28.588	14.559	10.853	54.000
Breen (M)	19.059	9.706	7.235	36.000
Totals	108.000	55.000	41.000	204.000
Post hoc cell contributions for self (M), partner (F)				
	Blue (F)	Brown (F)	Green (F)	
Blue (M)	4.985	−2.458	−3.488	
Brown (M)	−3.049	3.019	0.454	
Green (M)	−2.965	−0.292	4.017	

From top to bottom: observed frequencies, expected values, and post hoc cell contributions

Table 2 Distribution of female participants [i.e., self (F)] with blue, brown, and green eyes and their male partners [i.e., partner (M)] with blue, brown, and green eyes

Observed frequencies for self (F), partner (M)				
	Blue (M)	Brown (M)	Green (M)	Totals
Blue (F)	82	28	12	122
Brown (F)	31	25	5	61
Green (F)	33	12	11	56
Totals	146	65	28	239
Expected values for self (F), partner (M)				
	Blue (M)	Brown (M)	Green (M)	Totals
Blue (F)	74.527	33.180	14.293	122.000
Brown (F)	37.264	16.590	7.146	61.000
Green (F)	34.209	15.230	6.561	56.000
Totals	146.000	65.000	28.000	239.000
Post hoc cell contributions for self (F), partner (M)				
	Blue (M)	Brown (M)	Green (M)	
Blue (F)	1.983	−1.506	−0.923	
Brown (F)	−1.906	2.804	−0.990	
Green (F)	−0.379	−1.109	2.108	

From top to bottom: observed frequencies, expected values, and post hoc cell contributions

In addition, we performed 12 separate Chi-square analyses on sons or daughters of blue-, brown-, and green-eyed mothers and fathers in relation to their partners' eye color. Only one Chi-square analysis yielded significant differences: daughters of blue-eyed fathers were biased in their mate choices ($\chi^2=13.1$, $p=0.011$); specifically, only the blue-eyed and green-eyed women had partners of the same eye color in excess to the expected values. In contrast, male respondents showed no biases due to their parents' eye colors (including the sons of blue-eyed fathers, $\chi^2=4.2$, $p=0.33$, or mothers, $\chi^2=3.7$, $p=0.43$). Finally, based on the blue-eyed participants' data only, we grouped frequencies of partners' eye colors in relations to whether a) the mother and father both had blue eyes, b) the mother had blue eyes, but the father had brown eyes, and c) the father had blue eyes, but the mother had brown eyes. There were no significant differences, $\chi^2=0.9$, $p=0.62$.

Hair color Chi-square analyses were also performed on the female and male participants' and their partners' distributions of two hair color traits ('blond' or 'brown'), as there were too few instances of reports of other hair colors (e.g., "black" or "red"). There were significant differences among the male participants in their mates' hair colors, $\chi^2(1)=9.3$, $p=0.0022$. Table 3 shows the men's observed frequencies,

Table 3 Distribution of male participants [i.e., self (S)] with blond and brown hair and their female partners [i.e., partner (P)] with blond and brown hair

Observed Frequencies for self (M), partner (F)			
	Blond (P)	Brown (P)	Totals
Blond (S)	61	37	98
Brown (S)	36	54	90
Totals	97	91	188
Expected Values for self (M), partner (F)			
	Blond (P)	Brown (P)	Totals
Blond (S)	50.564	47.436	98.000
Brown (S)	46.436	43.564	90.000
Totals	97.000	91.000	188.000
Post hoc cell contributions for self (M), partner (F)			
	Blond (P)	Brown (P)	
Blond (S)	3.049	−3.049	
Brown (S)	−3.049	3.049	

From top to bottom: observed frequencies, expected values, and post hoc cell contributions

the expected values, and the respective post hoc cell contributions. Partners of the same hair color were observed in excess to the expected value. Although there was positive assortment for hair color, this did not differ between hair color types.

Female participants also showed significant biases in their partners' hair colors, $\chi^2(1)=7.4$, $p=0.0061$. Table 4 shows the women's observed frequencies, the expected values, and the respective post hoc cell contributions. Again, partners of the same hair color were observed in excess of the expected value. The women's positive assortment for hair color appeared weaker (as indicated by the lower values of the post hoc cells contributions) than that observed for the male participants.

Table 4 Distribution of female participants [i.e., self (S)] with blond and brown hair and their male partners [i.e., partner (P)] with blond and brown hair

Observed frequencies for self (F), partner (M)			
	Blond (P)	Brown (P)	Totals
Blond (S)	51	36	87
Brown (S)	30	50	80
Totals	81	86	167
Expected values for self (F), partner (M)			
	Blond (P)	Brown (P)	Totals
Blond (S)	42.198	44.802	87.000
Brown (S)	38.802	41.198	80.000
Totals	81.000	86.000	167.000
Post hoc cell contributions for self (F), partner (M)			
	Blond (P)	Brown (P)	
Blond (S)	2.728	−2.728	
Brown (S)	−2.728	2.728	

From top to bottom: observed frequencies, expected values, and post hoc cell contributions

Discussion

The present findings support the presence of positive assortment for eye and hair color. Individuals carrying the same traits showed higher than 'expected' pairings, regardless of eye colors and sex. However, the relative degrees of assortative mating were the largest for eye color and in blue-eyed men. Although to a smaller extent than the male groups, the brown-eyed women that assorted positively for eye color were in excess. The latter finding could be interpreted within the present account as an indication that brown-eyed women may have difficulty in finding "available" blue-eyed men. One should note that even in a large sample the assortment for hair or eye color can be stronger for one group than another, despite that couples are composed of men and women.

In fact, at any one time, not every individual in the general population will be "coupled" into a relationship with a member of the opposite sex. One would think that there would be symmetry only if individuals in the population could never be unpaired. That obviously does not happen: Some of us have been "singles" or currently are, or will be in the future, and some (by choice or destiny) will never have a companion of the opposite sex. In the present sample, of all respondents, 2.8% reported having no partners at all. Of the remaining individuals who had a heterosexual relationship, 29% were "singles" at the time of testing (and therefore reported the eye/hair color of their latest partner). Given such fluctuations in human mating, we believe one should not expect perfect symmetry.

One should also note that, at least among Scandinavians (cf., Lock-Andersen et al. 1998), the two traits of eye and hair colors are not randomly distributed with regards to one another. Hence, there is the possibility that one trait may appear as assortative because it covaries with another preferred trait. We suspect that positive assortment for hair color may simply piggyback that for eye color. Both from a theoretical standpoint (i.e., the inheritance of eye color is Mendelian, hair color is not) and from the present empirical evidence (i.e., the differences from chance assortment were greater for eye color than for hair color and assortment for light hair color was weaker than those for light eye colors), there are grounds for arguing that it is the preference for eye color that is relevant.

Finally, we found only weak support to the hypothesis that exposure to a family prototype or sex-specific "template" could influence preference for eye colors. In study 1, there were no effects of the parents' eye colors on ratings of attractiveness and, in study 2, participants with both blue-eyed parents were no more likely to have partners with blue eyes than participants with only the father or the mother showing the blue eyes phenotype. In addition, only the blue-eyed and green-eyed daughters of blue-eyed fathers showed a bias towards partners of the same eye color. Nevertheless, the findings of study 2 partially replicate those of Little and colleagues (2003) who found a tendency in both men and women (regardless of their specific eye colors) towards having partners with the opposite-sex parent's trait (i.e., a "quasi-oedipal" or "parental imprinting" effect of mothers' traits onto their sons' preferences and of the fathers' traits onto their daughters' preferences).

General discussion

Men with blue eyes had a stronger preference for the same trait in women. We propose that such a preference is an adaptation reflecting the selective pressure to increase the men's ability to detect extra-pair paternity and decrease paternal uncertainty; that is, both as a phenotypically based assurance of paternity (i.e., when the father's and offspring's phenotypes match) as well as a defense against cuckoldry (i.e., when the phenotypes do not match). One could assume here that the positive advantage accrued by those individuals who expressed the trait in past history was sufficient to favor the evolution (and maintenance) of such specific trait in blue-eyed men. Moreover, there could be selection *in favor* of the expression of the trait in blue-eyed men, without a complementary selection *against* the expression of the same trait in brown-eyed men (or, more generally non-blue-eyed men). Alternatively, if all is inherited is general "rules" for assortative mating and this can increase phenotypic resemblance of the offspring, blue-eyed individuals may have learned to attend and value a physical trait that can facilitate recognition of own kin.

It is unclear whether such an increased 'attention' towards eye color evokes corresponding conscious awareness that the trait in question is desirable. In general, would it be necessary to have explicit knowledge of the probabilities of children inheriting a certain eye color from the parents? We believe that such knowledge may just as well be implicit and that blue-eyed men may not be necessarily thinking about having blue-eyed children when they feel attracted towards a woman with the same eye color. In other words, this preference would be "unconscious" and blue-eyed men may either not know about the genetic meaning of this preference or not attend to it and therefore they may not make a voluntary decision when selecting for blue eyed women.

However, as shown by a developmental study by Solomon et al. 1996, even small children can have a rather explicit understanding of some basic laws of inheritance. In that study, children were told a story about a little boy born to a king/queen and adopted by a shepherd or one in which a little boy is born to a shepherd and adopted by a king/queen. Children showed an understanding of inheritance of physical traits when answering questions about resemblance of traits of parents (biological/adoptive) and child (e.g., "The king has green eyes and the shepherd has brown eyes. When the little boy is all grown up and is a young man, do you think that he will have green eyes like the king or brown eyes like the shepherd?"). It is interesting that this study used inheritance of eye color, as the test situation and even preschool children (e.g., 5 years old) showed some intuitive understanding of the inheritance and permanence of physical traits based on resemblance to family members. It would seem that a full appreciation of the Mendelian laws of inheritance would have to wait formal schooling for most children.

In addition, one cannot neglect the possibility that some of these preferences described in this paper do not necessarily reflect evolutionary pressures and adaptations, but may be due to stereotypes and prejudices that can be common within specific societies (Gergen 1967; Maddox 2004). Without a doubt, Scandinavians are not immune from varying degrees of negativism regarding immigrant populations (e.g., from Africa and the Middle East) that, incidentally, may almost entirely be brown-eyed. Given that hair can be easily dyed in blonde or light colors (a whole industry has thrived on this; cf. Gladwell 1999), eye color may then be used as reliable cue to discern artificiality in the visible composition of the traits of a woman (e.g., seeing brown eyes paired with blonde hair).

In other words, the following argument, which would be "cultural" or not evolutionary-based, could be constructed: eye color could be used as a way to "discriminate" members of the Scandinavian ethnic group from those who are likely to be from another. One could also propose that such a discriminating bias would be stronger among Scandinavian men than women, because 1) it is the men who are already motivated to seek partners with lighter complexion than their own and 2) because women may generally be less prejudiced than men about having sexual relationship with individuals outside of their own ethnic group (i.e., women show more "erotic plasticity" than men, see Baumeister 2000). However, if men prefer in general women with lighter complexion than their own, then also the brown-eyed individuals should prefer the blue-eyed women to the brown-eyed ones and to an extent that should be superior to that of the blue-eyed men (i.e., the blue-eyed and blonde women would present for the brown-eyed men a "super-stimulus" of femininity). Clearly, such a result was not obtained in the present findings.

At any rate, historical reasons also cast doubts on the equation that 'brown eyes equal strangers', as the percentage of brown-eyed Scandinavians is rather large and the national statistics of 1970 show that the largest immigration group into Norway (see Forgaard and Dzamarjia 2004) was from Northern Europe (44.8%; e.g., Sweden, Denmark, northern Russia, and the Baltic states), followed by Western Europe (e.g., 25.7% Germany, Great Britain, the Netherlands), North America (13.7%; e.g., USA), Eastern Europe (9.8%; e.g., Poland), and last Asia and Africa (6.0%; e.g., Pakistan, Somalia). In more recent years, these proportions have somewhat leveled off (Forgaard and Dzamarjia 2004). Importantly, among the above-listed populations that may have contributed most immigrants within the last four generations, the proportions of blue-eyed individuals would be high. Thus, in Norway, eye colors or their combinations with hair colors may not provide any reliable association with the ethnic origin of an individual.

On the basis of the present study's findings, one could also conclude that blue-eyed men are "choosier" than other men, or women in general, for the trait of eye color. However, it is not necessary to propose that blue-eyed men do restrict the potential range of possible partners. In fact, the results of the present experiment with photographic stimuli indicate that blue-eyed men can have a heightened response towards blue-eyed women without a significant decrease in attractiveness towards the brown-eyed women. Nevertheless, we must assume the existence of enough variability in eye color within the population to confer enough positive advantage for the expression of the trait. Otherwise, the proposed adaptation may provide only a slight defense against being cuckolded when the predominant eye color of the population is indeed blue.

Consequently, its expression could be weakened in populations where a blue iris is the most common trait, like among Scandinavians and other populations living around the Baltic Sea. In fact, the present survey of 445 Norwegians in Tromsø, a coastal town in the Arctic at 69°7′ N, showed that the blue iris color is predominant (55%); however, the presence of other color traits is not negligible (22% brown-eyed and 23% green-eyed). Similarly, surveys in Denmark showed 50.7% blue-eyed, 15.9% brown-eyed, and 33.4% in other eye color classes (Vinding 1990; see also Lock-Andersen et al. 1998). In countries of central and southern Europe, blue-eyed individuals are a minority but still a substantial one (Beals and Hoijer 1965, p. 213). A survey in France of 10,064 individuals (Gloor et al. 1981) showed that blue-eyed individuals comprised 30% of the sample. In a random sample of 1,795 individuals from Italy (Zanetti et al. 1996), 24% were blue eyed. The more frequent within a society the blue eye trait is, the less reliably the birth of blue-eyed offspring from blue-eyed parents would index that infidelity and philandering did not occur. The extra-pair father may have been in fact another man carrying the same, common, genetic trait. Hence, it is remarkable that the present study, conducted within one of the world's populations with the highest prevalence of blue-eyed individuals, was able to reveal clear-cut biases for eye color in mate choices.

Finally, one may wonder whether the percentages of blue-eyed Norwegians are fixed at 55% and about what keeps brown-eyed alleles around if there is a strong preference for blue: why have larger proportions of blue-eyed individuals not been reached? First of all, we should not forget that a strong preference for blue eyes is likely to exist only for the blue-eyed individuals. Moreover, even assuming that all individuals, independently of their individual eye color or sex, do prefer other blue-eyed individuals, this should result in the blue individuals choosing each other (i.e., mating assortatively by choice), but leaving the majority of the remaining individuals free to mate (i.e., mating assortatively by default). Thus, the presence of extreme mate choices might not necessarily result in the disappearance of other, non-preferred, traits (cf., Burley 1982). Yet, one could argue that if the preferences for blue-eyed women by blue-eyed men were indeed very strong, then even if others mate randomly, the number of brown-eyed women left out of the mating pool (or who have poorer sires for their offspring because they are not highly sought after) would be larger than that of blue-eyed women, leading to selection against brown eyes.

Nonetheless, even within this scenario, other counter-selective pressures are likely to exist and these may maintain a proportion of brown eyes in the population. Interestingly, a few researchers have proposed that the unusually diverse variety of human hair and eye color in northern and eastern Europe may have been the result of sexual selection (Cavalli-Sforza et al. 1994; Frost 2006). That is, color traits and color polymorphisms diversified as a result of sexual selection on early Europeans living in the extremely harsh environment of the continental tundra. According to Frost (2006), in this ecozone the sex ratio was likely to be strongly skewed towards a male shortage, and polygyny was unlikely to be a viable mating strategy and, as a result, there was increased pressure of sexual selection on women for color polymorphisms (to provide a "rare-color advantage").

In other ecological situations (i.e., at latitudes lower than those of northern Europe), there may in fact have been rather strong "natural selection" pressures against color polymorphism and towards the dark or brown eye type as well as darker skin to protect the eyes, and the body surface in general (Jablonski 2004), from exposure to toxic UV rays (Dolin 1994; Javitt and Taylor 1995; Singh et al. 2004). Moreover, dark eyes can have better visual acuity in bright light than blue eyes (Bornstein 1973), whereas, blue eyes are more subject to light refraction and scattering so as to result in lower acuity in bright light. However, blue eyes provide better color vision for the short wavelengths (i.e., blue and purple end of the color spectrum; Bornstein 1973) and they might have better visual acuity in the dim light of circumpolar regions and misty maritime environments. Finally, a lighter skin may provide protection from cold injury (Post 1975) and foster the production of vitamin D in environments with low levels of solar irradiation (Jablonski and Chaplin 2000).

Hence, in locations where blue eyes are not a disadvantage, the relaxed selection against blue eyes at high latitudes may have allowed for the selection for a blue-eyed preference. Nevertheless, even if we assumed that there were no trade-offs between disadvantages/advantages for the visual performance of blue/brown eyes, the desired 50% of blue-eyed individuals could be obtained (see S1, the Evolutionary Game or computer simulation, available on-line as a supplementary material for this article), if the relative pay offs for mating with a blue-eyed woman were such that 1) paternal certainty is low for a blue-eyed man when his "opponent" (i.e., the extra-pair male) has the same eye color; but 2) paternal certainty for the blue-eyed man is high when the opponent has brown eyes; 3) paternal certainty is low for a brown-eyed man when the opponent has the same eye color; 4) the paternal certainty of the brown-eyed man is only slightly higher when the opponent has blue eyes (as the brown-eyed man may carry the blue eye recessive allele).

Specifically, we surmise that a small advantage for the brown men when their opponents are blue, together with a larger pay off (perhaps double) for the blue men when their opponents are brown, would be sufficient to maintain the proportion of blue-eyed individuals near the levels observed in our Norwegian sample.

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References

Alexander RD (1979) Darwinism and human affairs. University of Washington, Seattle, WA

Alexander RD, Noonan KM (1979) Concealment of ovulation, parental care, and human social evolution. In: Chagnon NA, Irons W (eds) Evolutionary biology and human social behavior: an anthropological perspective. Suxbury, North Scituate, MA, pp 402–435

Anderson KG (2006) How well does paternity confidence match actual paternity? Evidence from worldwide nonpaternity rates. Curr Anthropol 48:511–518

Apicella CL, Marlowe FW (2004) Perceived mate fidelity and paternal resemblance predict men's investment in children. Evol Hum Behav 25:371-378

Ashton GC (1980) Mismatches in genetic markers in a large family study. Am J Hum Genet 32:601–613

Baker RR, Bellis MA (1995) Human sperm competition: copulation, masturbation and infidelity. Chapman & Hall, London, UK

Baumeister RF (2000) Gender differences in erotic plasticity: the female sex drive as socially flexible and responsive. Psychol Bull 126:347–374

Beals RL, Hoijer H (1965) An introduction to anthropology (3rd edn) MacMillan, New York

Beckman L (1962) Assortative mating in man. Eugen Rev 54:63–67

Betzig L (1989) Causes of conjugal dissolution: a cross-cultural study. Curr Anthropol 30:654–676

Bito LZ, Matheny A, Cruickshanks KJ, Nondahl DM, Carino OB (1997) Eye color changes past early childhood. The Louisville twin study. Arch Ophthalmol 115:659–663

Boas F (1928) Materials for the study of inheritance in man. Columbia University Press, New York

Bornstein MH (1973) Color vision and color naming: a psychophysiological hypothesis of cultural difference. Psychol Bull 80:257–285

Bryn H (1920) Researches into anthropological heredity: I. On the inheritance of eye-colour in man; II. The genetical relation of index cephalicus. Hereditas 1:186–212

Burks BS (1938) Objectivity of report in family studies of heredity: a preliminary analysis. J Heredity 29:505–509

Burley N (1982) The meaning of assortative mating. Ethol Sociobiol 4:191–203

Buss DM, Schmitt DP (1993) Sexual strategies theory: an evolutionary perspective on human mating. Psychol Rev 100:204–232

Cavalli-Sforza LL, Menozzi P, Piazza A (1994) The history and geography of human gene. Princeton University Press, Princeton, NJ

Cerda-Flores RM, Barton SA, Marty-Gonzales LF, Rivas F, Chakrborty R (1999) Estimation of nonpaternity in the Mexican population of Nuevo Leon: a validation study with blood group markers. Am Journal Phys Anthropol 109:281–293

Daly M, Wilson M (1982) Whom are newborn babies said to resemble? Ethol Sociobiol 3:69–78

DeBruine LM (2005) Trustworthy but not lust-worthy: context-specific effects of facial resemblance. Proc R Soc Edinb Sect B Biol Sci 272:919–922

Dolin PJ (1994) Ultraviolet radiation and cataract: a review of the epidemiological evidence. Br J Ophthalmol 78:478–482

Eiberg H, Mohr J (1996) Assignment of genes coding for brown eye colour (BEY2) and brown hair colour (HCL3) on Chromosome 15q. Eur J Hum Genet 4:237–241

Elston R (1961) Assortative mating in man. Transactions of the second international congress of human genetics, Rome

Feinman S, Gill GW (1978) Sex differences in physical attractiveness preferences. J Soc Psychol 105:43–52

Fisher ML (2004) Female intrasexual competition decreases female facial attractiveness. Biol Lett 271:283–285

Forgaard TS, Dzamarjia MT (2004) Innvandrerbefolkningen. In: Tronstad KR (ed) Innvandring og invandrere 2004, Statistisk Sentralbyrå, Oslo, Norway, pp 17–54

Frost P (2006) European hair and eye color: a case of frequency-dependent sexual selection? Evol Hum Behav 27:85–103

Fuster V (1984) Extramarital reproduction and infant mortality in rural Galicia (Spain). J Hum Evol 13:457–463

Gangestad SW, Simpson JA (2000). The evolution of human mating: trade-offs and strategic pluralism. Behav Brain Sci 23:573–644

Gangestad SW, Thornhill R, Garver CE (2002) Changes in women's sexual interests and their partners' mate-retention tactics across

the menstrual cycle: evidence for shifting conflicts of interest. Proc R Soc Lond B 269:975–982
Gaulin SJC, Schlegel A (1980) Paternity confidence and paternal investment: a cross-cultural test of a sociobiological hypothesis. Ethology and Sociobiology 1:301–309
Gergen KJ (1967) The significance of skin color in human relations. Daedalus 96:390–406
Gladwell M (1999) True colors: hair dye and the hidden history of postwar America. New Yorker 3/22/99:70–81
Gloor PA, Houdaille J, Menk R (1981) Taille et couleur des yeux: 10'064 élèves de l'Ecole Polytechnique de Paris, 1794–1874. Archives Suisses d'anthropologie générale 45:17–29
Greiling H, Buss DM (2000) Women's sexual strategies: the hidden dimension of extra-pair mating. Pers Individ Differ 28:929–963
Hasstedt SJ (1995) Phenotypic assortative mating in segregation analysis. Genet Epidemiol 12:109–127
Hrdy SB (1992) Fitness trade-offs in the history and evolution of delegated mothering with special references to wet-nursing, abandonment, and infanticide. Ethol Sociobiol 13:409–442
Hrdy SB (2000) Mother nature. Random House, London, UK
Hurst CC (1908) On the inheritance of eye-colour in man. Proc Roy Soc B 85–96
Jablonski NG (2004) The evolution of human skin and skin color. Annu Rev Anthropol 33:585–623
Jablonski NG, Chaplin G (2000) Skin deep. The Scientific American, October 2002, pp 74–81
Javitt JC, Taylor HR (1995) Cataract and latitude. Documenta Ophthamologica 88(3–4):307–325
Jorjani H, Engstrõm G, Liljedahl LE (1997) Genetic studies of assortative mating: a simulation study. I. Characteristics of the control populations. Acta Agric Scand 47:65–73
Kinsey AC, Pomeroy AB, Martin CE, Gebhard PH (1953) Sexual behavior in the human female. Saunders, Philadelphia
Koeslag JH, Koeslag PD (1994) Koinophilia. J Theor Biol 167:55–65
Laumann EO, Gagnon JH, Michael RT, Michaels S (1994) The social organization of sexuality. University of Chicago, Chicago, IL
Little AC, Penton-Voak IS, Burt DM, Perrett DI (2003) Investigating an imprinting-like phenomenon in humans: partners and opposite-sex parents have similar hair and eye colour. Evol Hum Behav 24:43–51
Lock-Andersen J, Wulf HC, Knudstorp ND (1998) Interdependence of eye and hair colour, skin type and skin pigmentation in a Caucasian population. Acta Derm Venereol (Stockholm) 78:214–219
Lykken DT, Tellegen A (1993) Is human mating adventitious or the result of lawful choice? J Pers Soc Psychol 65:56–58
Maddox KB (2004) Perspectives on racial phenotypicality bias. Pers Soc Psychol Rev 8:383–401
Maynard Smith J (1977) Parental investment: a prospective analysis. Anim Behav 25:1–9
McBurney DH, Simon J, Gaulin SJC, Geliebter A (2002) Matrilineal biases in the investment of aunts and uncles: replication in a population presumed to have high paternity certainty. Hum Nat 13:391–402
McLain DK, Setters D, Moulton MP, Pratt AE (2000) Ascription of resemblance of newborns by parents and nonrelatives. Evol Hum Behav 21:11–23
Miller GF, Todd PM (1998) Mate choice turns cognitive. Trends Cogn Sci 2:190–198
Neale MC, Neale BM, Sullivan PF (2002) Nonpaternity in linkage studies of extremely discordant sib pairs. Am J Hum Genet 70:526–529
Pagel M (1997) Desperately concealing father: a theory of parent–infant resemblance. Anim Behav 53:973–981
Pearson K (1907) Reply to certain criticisms of G.U. Yule. Biometrika 8:159–315
Pearson K, Lee A (1903) On the laws of inheritance in man: I. Inheritance of physical characters. Biometrika 2:357–462
Pena SDJ, Chakraborty R (1994) Paternity testing in the DNA era. Trends Genet 10:204–209
Perrett DI, Penton-Voak IS, Little AC, Tiddeman BP, Burt DM, Schmidt N, Oxley R, Barrett L (2002) Facial attractiveness judgments reflect learning of parental age characteristics. Proc R Soc Lond B 269:873–880
Platek SM, Burch RL, Panyavin IS, Wasserman BH, Gallup GG Jr (2002) Reactions to children's faces: resemblance affects males more than females. Evol Hum Behav 23:159–166
Platek SM, Raines DM, Gallup GG Jr, Mohamed FB, Thomson JW, Myers TE, Panyavin IS, Levin SL, Davis JA, Fonteyn LCM, Arigo DR (2004) Reactions to children's faces: males are more affected by resemblance than females are, and so are their brains. Evol Hum Behav 25:394–405
Post PW (1975) Cold injury and the evolution of "white" skin. Hum Biol 47:65–80
Price RA, Vanderberg SG (1980) Spouse similarity in American and Swedish couples. Behav Genet 10:59–71
Regalski JM, Gaulin SJC (1993) Whom are Mexican infants said to resemble? Monitoring and fostering paternal confidence in the Yucatan. Ethol Sociobiol 14:97–113
Regan S, Judge HE, Gragoudas ES, Egan KM (1999) Iris color as a prognostic factor in ocular melanoma. Arch Ophthalmol 117:811–814
Relethford JH, Lees FC, Byard PJ (1985) Sex and age variation in the skin color of Irish children. Curr Anthropol 26:396–397
Rife DC (1933) Genetic studies of monozygotic twins. J Heredity 24:407–414
Ritgers-Aris CAE (1973) A reflectance study of the skin in Dutch families. J Hum Evol 2:123–136
Sasse G, Muller H, Chakrborty R, Ott J (1994) Estimating the frequency of nonpaternity in Switzerland. Hum Hered 44:337–343
Schiefenhovel W (1989) Reproduction and sex-ratio manipulation through preferential female infanticide among the Eipo, in the highlands of western New Guinea. In: Rasa AE, Vogel C, Voland E (eds) The sociobiology of sexual and reproductive strategies. Chapman & Hall, New York, pp 170–193
Schmitt DP (2005) Fundamentals of human mating strategies. In: Buss DM (ed) The handbook of evolutionary psychology. Wiley, Hoboken, NJ, pp 258–291
Schmitt DP, Alcalay L, Allik J, Angleitner A, Ault L, Austers I et al (2004) Patterns and universals of mate poaching across 53 nations: the effects of sex, culture, and personality on romantically attracting another person's partner. J Pers Soc Psychol 86:560–584
Shackelford TK (2003) Preventing, correcting, and anticipating female infidelity: three problems of sperm competition. Evolution and Cognition 9:90–96
Shackelford TK, LeBlanc GJ, Drass E (2000) Emotional reactions to infidelity. Cogn Emot 14:643–659
Sigusch V, Schmidt G (1971) Lower-class sexuality: some emotional and social aspects in West German males and females. Arch Sex Behav 1:29–44
Singh AD, Rennie IG, Seregard S, Giblin M, McKenzie J (2004) Sunlight exposure and pathogenesis of uveal melanoma. Surv Ophthalmol 49:419–428
Solomon GEA, Johnson SC, Zaitchik D, Carey S (1996) Like father, like son: young children's understanding of how and why offspring resemble their parents. Child Dev 67:151–171
Sykes B, Irven C (2000) Surnames and the Y chromosome. Am J Hum Genet 66:1417–1419
Symons D (1995) Beauty is in the adaptations of the beholder: the evolutionary psychology of human female sexual attractiveness.

In: Abramson PR, Pinkerton SD (eds) Sexual nature, sexual culture. The University of Chicago, Chicago, pp. 80–118

Thiessen D, Young RK, Delgado M (1997) Social pressures for assortative mating. Pers Individ Differ 22:157–164

Trivers R (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man: 1871–1971. Aldine, Chicago, pp. 136–179

Van den Berghe PL, Frost P (1986) Skin color preferences, sexual dimorphism, and sexual selection: a case of gene-culture co-evolution? Ethn Racial Stud 9:87–113

Vinding T (1990) Pigmentation of the eye and hair in relation to age-related macular degeneration. An epidemiological study of 1000 aged individuals. Acta Ophthalmol 68(1):53–58

Walster E, Aronson V, Abrahams D, Rottman L (1966) Importance of physical attractiveness in dating behaviour. J Pers Soc Psychol 4:508–516

Wiederman MW (1997) Extramarital sex: prevalence and correlates in a national survey. J Sex Res 34:167–174

Widemo F, Sæther SA (1999) Beauty is in the eye of the beholder: causes and consequences of variation in mating preferences. Trends Ecol Evol 14:26–31

Williams GC (1975) Sex and evolution. Princeton University Press, Princeton, NJ

Willoughby RR (1933) Somatic homogamy in man. Hum Biol 5:690–705

Wilson GD, Barrett PT (1987) Parental characteristics and partner choice: Some evidence for oedipal imprinting. J Biosoc Sci 19:157–161

Zanetti R, Rosso S, Martinez C, Navarro C, Scraub S, Sancho-Garnier H et al (1996) The multicentre south European study “helios” I: skin characteristics and sunburns in basal cell and squamous cell carcinomas of the skin. Br J Cancer 73:1440–1446

Zei GP, Astolfi P, Jayakar SD (1981) Correlation between father’s age and husband’s age: a case of imprinting. J Biosoc Sci 13:409–418