This is the authors' version of the manuscript that was accepted for publication.

Full citation details of the published article are: Saxton, T. K., Steel, C., Rowley, K., Newman, A.V., & Baguley, T. (in press). Facial resemblance between women's partners and brothers. *Evolution and Human Behavior*. doi: <u>http://doi.org/10.1016/j.evolhumbehav.2017.04.006</u>

1	Facial resemblance between women's partners and brothers
2	
3	Tamsin K. Saxton*a, Catherine Steela, Katie Rowleya, Amy V. Newmana, Thom Baguleyb.
4	
5	* corresponding author. tamsin.saxton@northumbria.ac.uk. +44(0)191 227 4486.
6	
7	^a Evolution, Perception & Behaviour Research Group, Psychology Department, Northumbria
8	University, Northumberland Building, Ellison Place, Newcastle, NE1 8ST.
9	
10	^b Department of Psychology, School of Social Sciences, Nottingham Trent University, 50 Shakespeare
11	Street, Nottingham NG1 4FQ.
12	
13	Abstract
14	Research on optimal outbreeding describes the greater reproductive success experienced on average
15	by couples who are neither too closely related, nor too genetically dissimilar. How is optimal outbreeding
16	achieved? Faces that subtly resemble family members could present useful cues to a potential
17	reproductive partner with an optimal level of genetic dissimilarity. Here, we present the first empirical
18	data that heterosexual women select partners who resemble their brothers. Raters ranked the facial
19	similarity between a woman's male partner, and that woman's brother compared to foils. In a multilevel
20	ordinal logistic regression that modeled variability in both the stimuli and the raters, there was clear
21	evidence for perceptual similarity in facial photographs of a woman's partner and her brother. That is,
22	although siblings themselves are sexually aversive, sibling resemblance is not. The affective responses
23	of disgust and attraction may be calibrated to distinguish close kin from individuals with some genetic
24	dissimilarity during partner choice.

25 **1. Introduction**

26 In selecting a partner, the most reproductively successful individuals are those that avoid partners who 27 are too closely or too distantly related, thereby avoiding both inbreeding and outbreeding (see e.g. 28 Edmands 2007). Inbreeding is biologically detrimental due to the accumulation of harmful recessive 29 genes, a reduction in useful genetic heterozygosity, the possibility of increased competitiveness 30 between similar offspring, and a reduction in offspring variability (Bateson 1983). Excessive 31 outbreeding, on the other hand, may separate genes that work well together, disrupt the inheritance of 32 traits that have been adapted to work well in the local environment, and increase the costs of altruism 33 (Bateson 1983; Rushton 1989). Empirical data that support the value of intermediate relatedness 34 ('optimal outbreeding') have been presented for many species, including humans. For example, a study 35 of all known couples born in Iceland during a 165-year period found that the optimal level of relatedness 36 in that population in terms of number of grandchildren was around the level of third or fourth cousin 37 (Helgason, et al. 2008).

38

39 How do people avoid both inbreeding and excessive outbreeding? The avoidance of inbreeding appears 40 to be operationalised by the Westermarck effect, whereby people are not sexually attracted to those 41 with whom they socialise during childhood (reviewed in Rantala and Marcinkowska 2011). An aversion 42 to siblings as sexual partners seems to develop through maternal perinatal association and co-43 residence duration (De Smet, et al. 2014; Lieberman 2009; Lieberman, et al. 2007). To avoid excessive 44 outbreeding however, slight physical resemblance might provide an appropriate cue. Features found in 45 parental faces might be one of the most useful cues to genetic similarity, particularly in the environment 46 in which humans evolved, without frequent exposure to views of themselves in reflective surfaces. Data 47 support this: several studies have found that people choose partners and prefer faces that resemble 48 their parents (Bereczkei, et al. 2002; Bereczkei, et al. 2004; Dixson, et al. 2013; Heffernan and Fraley 49 2013; Jedlicka 1980; Jedlicka 1984; Little, et al. 2003; Marcinkowska and Rantala 2012; Perrett, et al. 50 2002; Rantala, et al. 2010; Saxton 2016; Seki, et al. 2012; Wilson and Barrett 1987; Zei, et al. 1981); 51 see also (Fraley and Marks 2010; Rantala and Marcinkowska 2011); but see (Nojo, et al. 2011).

52

However, parental appearance is an incomplete source of information. Maternal appearance provides
just one point of reference. Reliance on paternal faces is potentially problematic: serial relationships in

55 both traditional (Hill and Hurtado 1996) and modern societies (Cherlin 1981) mean that the father might 56 no longer be present. In addition, the putative father is not the biological father in cases that may 57 average around 2% of births worldwide (see Bressan and Kramer 2015). Sibling facial features 58 therefore could be a useful point of reference, especially given the extensive presence of siblings during 59 an individual's childhood in historically high-fertility populations. Additionally, younger brothers are more 60 readily detected as kin than older brothers (Lieberman, et al. 2007), and thus might be the better referent 61 for kin resemblance. Accordingly, our study used a multilevel ordinal logistic regression analysis to 62 investigate resemblance between a woman's partner and her brother, alongside the possible 63 moderating effects of absolute and relative age, in two separate samples.

64

65 2. Material and Methods

All of the research described herein was granted ethical approval by the Northumbria University
 Psychology Department Ethics Committee.

68

69 2.1 Stimuli creation

70 Stimuli were obtained in two ways: through the provision of photographic images by consenting 71 individuals ('volunteer sample'), and by the collection of appropriate photographic images available 72 online ('online sample'). The volunteer sample consisted of 32 female participants who passed on 73 details of the study to their brother and male partner, who in turn supplied photographs of themselves. 74 The 32 brothers (aged 18 - 40; mean +/- SD = 24 + -5 years) and 32 partners (aged 20 - 37; mean +/-75 SD = 23 +/- 4 years) were requested to provide good quality, recent, colour facial photographs, with a 76 neutral facial expression, although participants were often smiling in the photographs that they supplied. 77 The online sample consisted of 48 photographs (24 brothers, 24 partners) that were located online by 78 a researcher (A.N.) who had been instructed to find relatively recent facial photographs of brothers and 79 partners of public figures or celebrities. All individuals in the photographs were aged 18 or over, and 80 exact ages were identified for all but two of the siblings; 22 of the brothers were aged 21 - 53 (mean +/- SD = 31 +/- 8 years), and the 24 partners were aged 22 - 50 (mean +/- SD = 34 +/- 9 years). The 81 82 researcher was asked to find brothers and partners who appeared to be of white ethnicity, where the 83 face of a single individual was apparent with a fairly neutral facial expression and unadorned features 84 (i.e. without glasses, make-up, etc.) The photographs had to be sourced from a site that allowed the 85 usage of photographs in research (i.e. non-commercially), and the photographs had to be taken in a 86 venue where the individual in the photograph could reasonably expect to be observed by strangers, 87 following ethical guidelines for the research use of information available online (Hewson and Buchanan 88 2013). Across the whole sample, 28 of the brothers were older than the woman whose partner's 89 photograph was in the study, and 28 of the brothers were younger (or, in one instance, a twin, who was 90 categorised here as a younger brother). Three of the men had features consistent with Asian ethnicity, 91 while all of the others appeared to be of white ethnicity. We performed an additional check of our 92 statistical model by adding a categorical term to distinguish these three men along with one man who 93 was a half brother, but found no significant effect.

94

95 The photographs were grouped into sets of four brothers and four partners, keeping separate the 96 volunteer and online sample to increase within-set consistency in photograph quality and cultural or 97 demographic variables. The photographs were grouped so that six of the sets only contained younger 98 brothers, six of the sets only contained older brothers, and two of the sets (one from the volunteer 99 sample and one from the online sample) contained a mixture (3:1) of younger and older brothers. The 100 photographs were arranged into tableaux following the methodology of previous work on preferences 101 for parental resemblance in faces (Bereczkei, et al. 2002; Bereczkei, et al. 2004), and printed in colour 102 on A4 sheets of paper. Photographs varied a little in size, but each was around 5cm x 6cm. Photographs 103 were cropped to focus in on the face, so typically would be cropped from just below the chin to just 104 above the top of the hair. On the right-hand side, the four photographs of the four partners in a set were 105 displayed; this set of four photographs was repeated identically across four sheets of paper. On the left-106 hand side of these four sheets, the photograph of one of the brothers from the same set was displayed, 107 with a different brother on each of the four sheets. In addition, four versions of each of the two tableaux 108 that contained a mixture of older and younger brothers were created, so that the placement on the 109 stimulus sheet of the photograph of the single younger/older brother could be fully counterbalanced in 110 the four possible positions (top/bottom left/right). After these constraints, the selection of photographs 111 for each set was based on ordered partner age from youngest to oldest, so that the people in the photographs were as similar as possible in age. The age difference between the oldest and youngest 112 113 of the four partners in each set ranged from 0 to 16 years, with a mean age difference of 5 years

between the oldest and youngest partner in each set. Age and relative age (older or younger) wereincluded as variables in the models (see below).

116

117 2.2 Photograph rating

118 An opportunity sample of 32 female raters aged 19 to 40 (mean +/- SD = 24 +/- 5 years) were presented 119 with the 56 tableaux in random order. Female raters were chosen because the volunteer and online 120 sample were all female, and so we wanted to focus on female facial perception. For each tableau, they 121 were asked to rank the four men on the right hand side (the partner plus three foils) in terms of their 122 similarity to the man on the left hand side (the brother). A sample size of 32 raters was selected based 123 on pilot work (see Supplementary Online Material 2). Raters were not told that the individuals in the 124 photographs were related, but only that the study was investigating perceptions of facial similarity. 125 Participants were quizzed and debriefed afterwards, and no-one reported guessing the aims of the 126 study. 23 out of a possible 1792 of the raters' responses (1.3%) were unclear (e.g. a rater listed the 127 same photo as both most and third most similar) and these were treated as missing data in the model. 128 Data were collected from one additional rater, but were discarded prior to analysis because the tableaux 129 were erroneously provided in numerical rather than randomised order, meaning that the same image 130 of the same four brothers was presented on the right-hand side of all of the first four tableaux, then the 131 same four brothers were presented on the second four tableaux, and so on.

132

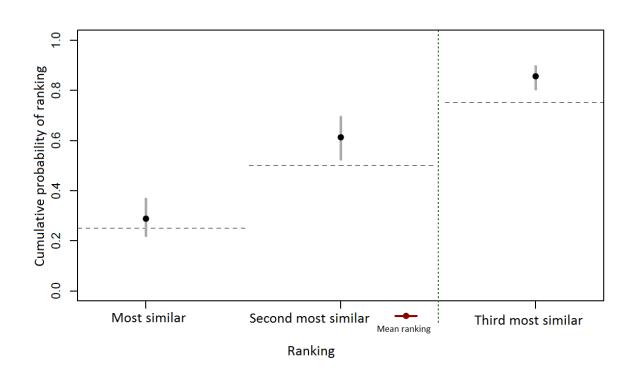
133 3. Results

134 Rating data were modelled using multilevel ordinal logistic regression implemented in the ordinal package (Christensen 2015) within R (http://www.R-project.org/). Using an ordinal model permitted us 135 136 to model the cumulative probability of the brother and partner being ranked as 1) most similar to each 137 other; 2) most or second most similar; and 3) most, second most or third most similar. The advantage 138 of a multilevel model is that variability in both faces and raters can be incorporated into the model as 139 fully crossed random effects. Traditional analyses that ignore variability in either faces or raters, either 140 by treating ratings as independent or by modelling variability by raters or by faces in isolation, are known to inflate Type I error (see e.g. Baguley 2012; Judd, et al. 2012). Our initial model therefore included 141 142 two random effects (face and rater) and three intercepts representing the thresholds in the ordinal

143 logistic regression model on a log odds scale. In this intercept-only model, the estimate of face variability 144 is 1.251 while the rater variability is negligible (1.7 x 10⁻⁵) suggesting individual differences in the 145 resemblance of brothers to partners, but near independence of rankings within raters in our sample. 146 The estimated thresholds for the ratings were -1.02, 0.34 and 1.67 corresponding to a cumulative 147 probability of .27, .59 and .84. The raters were choosing from four photos, and so if they were picking at chance levels, they should have chosen the correct pair at a rate of .25. The probability of ranking 148 the brother most (.27), second (.32), or third (.26) most similar to the partner therefore appears elevated 149 150 relative to chance (.25), while the probability of ranking the brother least similar to the partner is 151 depressed (.16) (Figure 1).

152

153



154

155

Figure 1: Cumulative probability of ranking the correct brother-boyfriend pairing as most, second most, and third most similar, while controlling for participant age and sample source (see section 2 Materials and Methods and section 3 Results). Observed values (mean +/- 95% CIs) are indicated by solid vertical lines, while chance values for each ranking are marked by dashed horizontal lines. A 95% CI for the mean rankings are indicated as calculated using the intercept-only model (red horizontal line) and under the null hypothesis of equiprobability (vertical dotted line). 162 To test whether the joint pattern of ratings was consistent with guessing we simulated a 95% CI for the 163 mean rating by parametric bootstrapping of the intercept only model (incorporating the random effects 164 of both faces and raters). This simulation (with 5000 replicated data sets) estimated the mean ranking 165 as 2.335, 95% CI [2.28, 2.39] and close to the observed mean ranking of 2.338 (to 3 d.p.). The potential 166 impact of missing data (1.3% of the expected total data; see subsection 2.2 Photograph rating) was 167 simulated by replacing simulated data with missing values with a fixed probability equal to that observed 168 in the real data set. This is equivalent to treating data as missing completely at random (though with so 169 few missing cases the impact on inferences is neglible). A null hypothesis test of the observed mean 170 ranking was obtained by simulating an equiprobability model (fixing the probability of each ranking at 171 (0.25) with the same random effects. Under the equiprobability model the mean ranking was 2.50 (SE = 172 0.0287) and not consistent with the observed mean of 2.34, z = 5.64, p < .0001.

173

174 A further model was fitted to determine the influence of other variables on the rankings. This model 175 included the woman's age (centred) as a continuous predictor, and several categorical predictors: 176 brother's relative age (older or younger), partner's relative age (older or younger), and whether the 177 photo came from the volunteer sample or the online sample. All categorical predictors were effect coded 178 for this analysis and effects were tested by a likelihood ratio test. Only partner's relative age was close 179 to statistical significance, $G^2(1) = 2.76$, p < .10 (with other effects $G^2 < 1$). There is thus little evidence 180 that any of these variables influenced the ratings. Including these predictors also had little impact on 181 the thresholds; Figure 1 shows the cumulative probability of rating the sibling as most, second most or 182 third most similar when these predictors were included. Although stimuli were counterbalanced we also 183 checked the impact of tableaux version and position of the correct match by including version, position 184 and all version by position interactions. None of the effects reached statistical significance and the 185 overall change in fit was negligible, $G^2(15) = 10.2$, p = .81. As a final check we tested the hypothesis 186 that ratings were driven merely by the similarity or dissimilarity in age of the partners and brothers or of 187 the women and their brothers. To this end we added the absolute difference in ages to the model for 188 each of these comparisons; neither was close to statistical significance, $G^2 < 1$.

189

190 4. Discussion

191 We present clear evidence that women select partners who resemble their brothers. This is true 192 irrespective of whether the sample is based around a student or a celebrity population. People 193 experience strong aversion and disgust towards incest (Antfolk, et al. 2012). However, identity is not 194 the same as resemblance; the proper domain of kinship detecting mechanisms (Lieberman, et al. 2007) 195 might entail the creation of aversion to siblings themselves, and not to those that resemble them. Our 196 results suggest that affective responses during partner choice (disgust and attraction) could be 197 calibrated to distinguish actual close kin from those who might be somewhat genetically similar and 198 could thereby support optimum outbreeding. That is, people are disgusted by thinking about engaging 199 in relationships with siblings (Lieberman, et al. 2007), but seem to pick partners who show some slight 200 resemblance to siblings.

201

202 Facial resemblance can indicate relatedness even beyond immediate family members (Davidson 1993; 203 Kaminski, et al. 2009). Although contextual cues such as kinship nomenclature and family histories also 204 indicate relatedness, automated cue-based processes might function alongside and independently of 205 explicit knowledge, and have a deeper evolutionary history (Park, et al. 2008). Humans can detect 206 kinship on the basis of appearance similarity in mother-daughter pairs in mandrills, gorillas, 207 chimpanzees and macagues (Alvergne, et al. 2009; Vokey, et al. 2004). Non-human primates can also 208 detect visual similarity in kin (e.g. Kazem and Widdig 2013; Parr and de Waal 1999; Pfefferle, et al. 209 2014). For much of human history, a preference for partners who demonstrated subtle resemblances 210 to close family members might have supported the selection of a reproductive partner who was neither 211 too closely nor too distantly related.

212

213 Facial cues to kinship play a role in sexual, parental and social behaviours (Lewis 2011; Park, et al. 214 2008). People are more likely to trust and invest in those whose familiar facial appearance indicates 215 possible family membership (DeBruine 2005; Platek, et al. 2002). As attraction affects every level of 216 interpersonal interaction, our results also suggest a possible mechanism by which nepotism could be 217 scaffolded. Although we focussed on women's choices, the same tendencies should apply to men. 218 Indeed, men might find sibling-resemblance less aversive than women do (Marcinkowska, et al. 2013), 219 and this can be explained by men's lesser reproductive investment and hence lower risk in a sub-220 optimal partner (Haig 1999).

222 Siblings resemble parents, and individuals have been previously shown to select partners who resemble 223 their parents. Our work suggests that the effect sizes for each are similar (see Supplementary Material 224 1); parents and siblings could both provide reference points. Zebra finches (Kruijt, et al. 1983), snow 225 geese (e.g. Cooke, et al. 1976; Cooke and McNally 1975; Walter 1973), bullfinch (Nicolai 1956), and 226 mallards (Klint 1978) demonstrate preferences for sibling characteristics that are independent of 227 preferences for parental characteristics. Siblings might provide a source of information on familial 228 resemblance that is more extensive than that provided by parents. Future research should contrast 229 parental, sibling and self resemblance explicitly, in order to parse their contributions to partner choice.

230

231 Previous research that has looked at the effects of siblings on attractiveness judgements of facial 232 images does not support the interpretation that sibling resemblance unambiguously enhances 233 judgements of attractiveness per se. One previous research study investigated the impact of sibling-234 resemblance on attraction by computer-manipulating facial images so that they resembled the raters' 235 siblings or the raters themselves. The study found that men rated sibling-resembling faces as 236 significantly more attractive than self-resembling faces but not significantly different from control faces, 237 whereas women rated sibling-resembling faces as significantly less attractive than control faces and no 238 different from self-resembling faces (Marcinkowska, et al. 2013). Men with sisters have been found to 239 be less likely to judge feminised women's faces attractive than men without sisters do (Marcinkowska, 240 et al. 2016), although in contrast, adolescent boys in a single-sex school environment (i.e. with limited 241 daytime visual exposure to girls) have been found to judge female facial femininity as more attractive if 242 they have sisters than if they do not (Saxton, et al. 2009). Attractiveness judgements assessed in a 243 laboratory context may not always map directly onto patterns of relationship formation and maintenance 244 when other factors come into play.

245

One limitation of our study was that the photographs were not fully standardised; they portrayed facial features, but also facial expressions, hairstyles, and some elements of clothing and background. We reduced the possible impact of these elements as much as possible by asking participants to provide standardised photographs, by cropping photographs to focus on the face, and by presenting the raters with photographs from the online sample separately from the volunteer sample (see Material and 251 Methods section). We asked the raters to judge facial similarity, but these non-standardised elements 252 likely contributed somewhat to their decisions. Therefore, it is possible that our raters were not matching 253 the photographs merely on facial structural similarity, but also on elements such as emotionality 254 (perceived through facial expressions), and socio-economic status and cultural cues (perceived through 255 clothing and hairstyle). Nevertheless, we note that previous research that used non-standardised 256 photographs (Bereczkei, et al. 2002; Bereczkei, et al. 2004) to examine similarity between individuals' 257 partners and their parents revealed similar results to research that used standardised photographs 258 (Vukovic, et al. 2015). Future research might undertake the logistically more complicated step of 259 creating standardised photographs of all participants.

260

261 Our study focussed on contemporary western populations. Although our biologically-based hypotheses 262 should apply cross-culturally, other cultures remain to be tested. Indeed, we found substantive inter-263 individual variability in the extent to which a woman's brother and partner were similar: not all women 264 select partners who resemble their brothers. Accordingly, the effect will be weaker in contexts that 265 amplify the variables that reduce preferences for brother-resemblance. We did not find that older 266 compared to younger brothers had differential effects. Future research might investigate other possible 267 individual predictors of brother-partner similarity, such as emotional closeness between brother and 268 sister (Bereczkei, et al. 2002; Bereczkei, et al. 2004). However, here we demonstrate perceptual 269 similarity between women's brothers and partners in a contemporary population.

270

Data Availability: The data associated with this research are available in the Supplementary Online
Materials 3.

273

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

276

277 5. References

Alvergne A, Huchard E, Caillaud D, Charpentier MJE, Setchell JM, Ruppli C, Féjan D, Martinez L,
Cowlishaw G, Raymond M. 2009. Human ability to recognize kin visually within primates. *International Journal of Primatology* 30(1):199-210. DOI: 10.1007/s10764-009-9339-0

- Antfolk J, Karlsson M, Bäckström A, Santtila P. 2012. Disgust elicited by third-party incest: the roles of
 biological relatedness, co-residence, and family relationship. *Evol. Hum. Behav.* 33(3):217 223. D0l: <u>http://dx.doi.org/10.1016/j.evolhumbehav.2011.09.005</u>
- Baguley T. 2012. Serious Stats: A guide to advanced statistics for the behavioral sciences.
 Basingstoke: Palgrave.
- Bateson P. 1983. Chapter 11: Optimal outbreeding. In: Bateson P, editor. Mate Choice. Cambridge:
 Cambridge University Press. p 257-
- Bereczkei T, Gyuris P, Koves P, Bernath L. 2002. Homogamy, genetic similarity, and imprinting;
 parental influence on mate choice preferences. *Pers. Indiv. Differ.* 33(5):677-690. DOI:
- Bereczkei T, Gyuris P, Weisfeld GE. 2004. Sexual imprinting in human mate choice. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 271(1544):1129-1134. DOI:
- Bressan P, Kramer P. 2015. Human kin detection. Wiley Interdisciplinary Reviews: Cognitive Science
 6(3):299-311. DOI: 10.1002/wcs.1347
- Cherlin AJ. 1981. Marriage, Divorce, Remarriage: Social trends in the United States. Cambridge,
 Massachusetts: Harvard University Press.
- 296 Christensen RHB. 2015. ordinal Regression models for ordinal data. R package version 2015.1-21.
- 297 Cooke F, Finney GH, Rockwell RF. 1976. Assortative mating in lesser snow geese (Anser
- 298 caerulescens). Behav. Genet. 6(2):127-140. DOI: 10.1007/bf01067143
- Cooke F, McNally CM. 1975. Mate selection and colour preferences in lesser snow geese. *Behaviour* 53(1):151-169. DOI: doi:<u>http://dx.doi.org/10.1163/156853975X00588</u>
- 301 Davidson HR. 1993. A large family with patent ductus arteriosus and unusual face. J. Med. Genet.
- 302 30(6):503-505. DOI: 10.1136/jmg.30.6.503
- 303 De Smet D, Van Speybroeck L, Verplaetse J. 2014. The Westermarck effect revisited: a
- 304 psychophysiological study of sibling incest aversion in young female adults. *Evol. Hum.*
- 305 Behav. 35(1):34-42. DOI: http://dx.doi.org/10.1016/j.evolhumbehav.2013.09.004
- 306 DeBruine LM. 2005. Trustworthy but not lust-worthy: context-specific effects of facial resemblance.
 307 *Proc. Biol. Sci.* 272(1566):919-922. D0I:
- 308 Dixson BJ, Tam JC, Awasthy M. 2013. Do women's preferences for men's facial hair change with
- 309 reproductive status? Behav. Ecol. 24(3):708-716. DOI: 10.1093/beheco/ars211

- 310 Edmands S. 2007. Between a rock and a hard place: evaluating the relative risks of inbreeding and
- 311 outbreeding for conservation and management. *Mol. Ecol.* 16(3):463-475. DOI:

312 10.1111/j.1365-294X.2006.03148.x

- Fraley RC, Marks MJ. 2010. Westermarck, Freud, and the incest taboo: Does familial resemblance
- 314 activate sexual attraction? *Pers. Soc. Psychol. B.* 36(9):1202-1212. DOI:
- 315 10.1177/0146167210377180
- Haig D. 1999. Asymmetric relations: Internal conflicts and the horror of incest. *Evol. Hum. Behav.*20(2):83-98. DOI: http://dx.doi.org/10.1016/S1090-5138(98)00042-7
- 318 Heffernan ME, Fraley RC. 2013. Do early caregiving experiences shape what people find attractive in
- 319 adulthood? Evidence from a study on parental age. Journal of Research in Personality

320 47(4):364-368. DOI: 10.1016/j.jrp.2013.03.003

- Helgason A, Pálsson S, Guðbjartsson DF, Kristjánsson þ, Stefánsson K. 2008. An association
- between the kinship and fertility of human couples. *Science* 319(5864):813-816. DOI:
- 323 10.1126/science.1150232
- Hewson C, Buchanan T. 2013. Ethics Guidelines for Internet-mediated Research. Leicester, UK:
 British Psychological Society
- Hill K, Hurtado AM. 1996. Ache Life History: The ecology and demography of a foraging people. New
 York: Aldine de Gruyter.
- Jedlicka D. 1980. A test of the psychoanalytic theory of mate selection. *J. Soc. Psychol.* 112(2):295.
 D0I:
- 330 Jedlicka D. 1984. Indirect parental influence on mate choice: A test of the psychoanalytic theory.

331 Journal of Marriage and Family 46(1):65-70. D0I: 10.2307/351864

- 332 Judd CM, Westfall J, Kenny DA. 2012. Treating stimuli as a random factor in social psychology: A
- new and comprehensive solution to a pervasive but largely ignored problem. *J. Pers. Soc. Psychol.* 103(1):54-69. DOI:
- Kaminski GI, Dridi S, Graff C, Gentaz E. 2009. Human ability to detect kinship in strangers' faces:
 effects of the degree of relatedness. *Proc. Biol. Sci.* 276(1670):3193-3200. DOI:
- 337 10.1098/rspb.2009.0677
- Kazem AJN, Widdig A. 2013. Visual phenotype matching: Cues to paternity are present in rhesus
 macaque faces. *PLOS ONE* 8(2):e55846. DOI: 10.1371/journal.pone.0055846

- Klint T. 1978. Significance of Mother and Sibling Experience for Mating Preferences in the Mallard
 (Anas platyrhynchos). *Z. Tierpsychol.* 47(1):50-60. DOI: 10.1111/j.1439-0310.1978.tb01822.x
- Kruijt JP, Ten Cate CJ, Meeuwissen GB. 1983. The influence of siblings on the development of
 sexual preferences of male zebra finches. *Dev. Psychobiol.* 16(3):233-239. DOI:
- 344 10.1002/dev.420160309
- Lewis DMG. 2011. The sibling uncertainty hypothesis: Facial resemblance as a sibling recognition cue. *Pers. Indiv. Differ.* 51(8):969-974. DOI: <u>http://dx.doi.org/10.1016/j.paid.2011.08.002</u>
- Lieberman D. 2009. Rethinking the Taiwanese minor marriage data: evidence the mind uses multiple
 kinship cues to regulate inbreeding avoidance. *Evol. Hum. Behav.* 30(3):153-160. DOI:
- 349 <u>http://dx.doi.org/10.1016/j.evolhumbehav.2008.11.003</u>
- 350 Lieberman D, Tooby J, Cosmides L. 2007. The architecture of human kin detection. Nature
- 351 445(7129):727-731. DOI:
- 352 http://www.nature.com/nature/journal/v445/n7129/suppinfo/nature05510_S1.html
- 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(1):43. DOI:
- Marcinkowska UM, Moore FR, Rantala MJ. 2013. An experimental test of the Westermarck effect: sex
 differences in inbreeding avoidance. *Behav. Ecol.* 24(4):842-845. DOI: 10.1093/beheco/art028
- Marcinkowska UM, Rantala MJ. 2012. Sexual imprinting on facial traits of opposite-sex parents in
 humans. *Evolutionary Psychology* 10(3):621-630. D0I:
- Marcinkowska UM, Terraube J, Kaminski G. 2016. Imprinting and flexibility in human face cognition.
 Scientific Reports 6:33545. DOI: 10.1038/srep33545
- 362 Nicolai J. 1956. Zur Biologie und Ethologie des Gimpels (Pyrrhula pyrrhula L.) D. 77. *Z. Tierpsychol.* 363 13(1):93-132. DOI: 10.1111/j.1439-0310.1956.tb01549.x
- Nojo S, Ihara Y, Furusawa H, Akamatsu S, Ishida T. 2011. Facial resemblance and attractiveness: an
 experimental study in rural Indonesia. *Letters on Evolutionary Behavioral Science* 2(1):9-12.
 D0I:
- 367 Park JH, Schaller M, Van Vugt M. 2008. Psychology of human kin recognition: Heuristic cues,
- 368 erroneous inferences, and their implications. *Rev. Gen. Psychol.* 12(3):215-235. DOI:
- 369 10.1037/1089-2680.12.3.215

- 370 Parr LA, de Waal FBM. 1999. Visual kin recognition in chimpanzees. *Nature* 399(6737):647-648. DOI:
- 371 Perrett DI, Penton-Voak IS, Little AC, Tiddeman BP, Burt DM, Schmidt N, Oxley R, Kinloch N, Barrett
- 372 L. 2002. Facial attractiveness judgements reflect learning of parental age characteristics.
- 373 Proceedings of the Royal Society of London Biological Sciences (Series B) 269(1494):873-

374 880. DOI: 10.1098/rspb.2002.1971

- 375 Pfefferle D, Kazem Anahita JN, Brockhausen Ralf R, Ruiz-Lambides Angelina V, Widdig A. 2014.
- 376 Monkeys spontaneously discriminate their unfamiliar paternal kin under natural conditions
- 377 using facial cues. *Curr. Biol.* 24(15):1806-1810. DOI:

378 <u>http://dx.doi.org/10.1016/j.cub.2014.06.058</u>

- Platek SM, Burch RL, Panyavin IS, Wasserman BH, Gallup JGG. 2002. Reactions to children's faces:
 Resemblance affects males more than females. *Evol. Hum. Behav.* 23(3):159. DOI:
- Rantala M, Marcinkowska U. 2011. The role of sexual imprinting and the Westermarck effect in mate
 choice in humans. *Behav. Ecol. Sociobiol.* 65(5):859-873. DOI: 10.1007/s00265-011-1145-y
- Rantala MJ, Polkki M, Rantala LM. 2010. Preference for human male body hair changes across the
 menstrual cycle and menopause. *Behav. Ecol.* 21(2):419-423. D0I: 10.1093/beheco/arp206
- Rushton JP. 1989. Genetic similarity, human altruism, and group selection. *Behav. Brain Sci.*

386 12(03):503-518. DOI: doi:10.1017/S0140525X00057320

387 Saxton TK. 2016. Experiences during specific developmental stages influence face preferences. *Evol.*

388 *Hum. Behav.* 37(1):21-28. DOI: <u>http://dx.doi.org/10.1016/j.evolhumbehav.2015.06.001</u>

- 389 Saxton TK, Little AC, DeBruine LM, Jones BC, Roberts SC. 2009. Adolescents' preferences for
- 390 sexual dimorphism are influenced by relative exposure to male and female faces. *Pers. Indiv.*

391 *Differ.* 47:864-868. DOI: 10.1016/j.paid.2009.07.005

- Seki M, Ihara Y, Aoki K. 2012. Homogamy and imprinting-like effect on mate choice preference for
 body height in the current Japanese population. *Ann. Hum. Biol.* 39(1):28-35. DOI:
- doi:10.3109/03014460.2011.635695
- Vokey JR, Rendall D, Tangen JM, Parr LA, de Waal FBM. 2004. Visual kin recognition and family
- 396 resemblance in chimpanzees (*Pan troglodytes*). J. Comp. Psychol. 118(2):194-199. DOI:
- 397 10.1037/0735-7036.118.2.194

- 398 Vukovic J, Boothroyd LG, Meins E, Burt DM. 2015. Concurrent parent–child relationship quality is
- 399 associated with an imprinting-like effect in children's facial preferences. *Evol. Hum. Behav.*
- 400 36(4):331-336. DOI: 10.1016/j.evolhumbehav.2015.03.004
- 401 Walter MJ. 1973. Effects of parental colouration on the mate preference of offspring in the zebra finch,
- 402 Taeniopygia guttata castanotis Gould. *Behaviour* 46(1):154-173. DOI:
- 403 doi:<u>http://dx.doi.org/10.1163/156853973X00229</u>
- 404 Wilson GD, Barrett PT. 1987. Parental characteristics and partner choice: some evidence for Oedipal
- 405 imprinting. J. Biosoc. Sci. 19(02):157-161. D0I: doi:10.1017/S0021932000016758
- 406 Zei GP, Astolifi P, Jayakar SD. 1981. Correlation between father's age and husband's age: a case of
- 407 imprinting. J. Biosoc. Sci. 13:409-418. DOI:
- 408
- 409