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7 **Parental preferences for the facial traits of their offspring's partners can enhance**

8 **parental inclusive fitness.**

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10

11   **Abstract**

12   Physical appearance provides a wealth of information concerning an individual's biological

13   fitness and reproductive quality, but we do not know whether parents make use of this

14   information when evaluating potential partners for their offspring. This is critical to our

15   understanding of human mate choice, because parents frequently influence their offspring's

16   mating decisions, either directly, for instance through arranged marriages, or indirectly,

17   through manipulating their offspring's partner choice. Here, we used facial images that varied

18   in attractiveness, masculinity, health, and symmetry to assess both reproductively-aged

19   daughters' and their parents' preferences in potential mates for the daughters. In line with our

20   predictions, both daughters and their parents had clear preferences for markers of genetic

21   quality, although the daughters showed significantly stronger preferences for these markers

22   than their parents. Contrary to previous research, parents and daughters did not have stronger

23   preferences for markers of genetic quality if they perceived the daughter to be more

24   attractive. Parents' preferences for the facial markers of genetic quality in their offspring's

25   partner may help maximise inclusive fitness.

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28   **Keywords:** mate choice, parental investment, parent-offspring conflict, face preferences,

29   inclusive fitness

Introduction

Parental involvement in their offspring's mate choice appears to be ubiquitous across human cultures (Apostolou, 2007; Goode, 1959; Menon, 1989; Minturn, Grosse, & Haider, 1969). In contemporary societies, the degree of parental involvement varies from relatively superficial, such as approval or disapproval of the offspring's choice, through to much more extensive, such as arranged marriage practices (Apostolou, 2007; 2013; Buunk, Park, & Duncan, 2010). Some level of parental involvement has probably been evident throughout our evolutionary history (Apostolou, 2010a,b; 2012; 2013; Buunk et al., 2010). As such, parental involvement in mate choice has likely been subject to evolutionary pressures, and humans may have developed specialised mechanisms for choosing suitable mates for their offspring, perhaps independent from mechanisms involved in their own mate choice.

Appearance plays an important role in mate choice, as has been convincingly demonstrated numerous times (see e.g. Penton-Voak, 2011). This is perhaps with good cause: physical traits can convey critical information concerning the suitability and genetic quality of an individual as a reproductive partner, including their genetic quality, their health status and their fertility (e.g. Thornhill, & Gangestad, 2006; Rhodes, 2006). Much research has shown that people readily and accurately discern these markers of genetic quality in others (e.g. Rhodes, 2006). Yet we do not know whether parents also exploit physical markers of genetic quality when judging potential partners for their offspring, despite the clear benefits of doing so. Indeed, research has indicated that women's judgements of the attractiveness of male faces may change at menopause, when markers of genetic quality in a partner become less relevant (Jones et al., 2011; Little et al., 2010), but we hypothesise that menopause should leave intact a woman's ability to assess markers of genetic quality of potential sons-in-law so that she can appropriately judge potential partners for her offspring so as to maximize her

55 inclusive fitness, i.e. the benefits to her fitness if her offspring successfully produces

56 offspring of high genetic quality in turn.

57

58 Mate choice is often portrayed as a market, where individuals adjust their preferences

59 according to their own desirability (Waynforth & Dunbar, 1995). This strategic adjustment

60 contributes to assortative mating, whereby people tend to choose a partner of approximately

61 equal mate value to themselves. Assortative mating has been established for a range of traits

62 including physical appearance (Jones et al., 2005; Little et al., 2001), and might support long-

63 term relationship bonds. The pursuit of a partner of equivalent mate value allows people to

64 maximise their reproductive potential by focussing their time and efforts on a partner who is

65 maximally high-quality while still being attainable. We hypothesise that parents may also

66 adjust their evaluation of a potential partner's suitability according to their perceived mate

67 value of their offspring.

68

69 Men can provide both direct benefits (investment) and indirect benefits (heritable fitness) as

70 reproductive partners, and may trade off one against each other. For example, males with

71 high facial masculinity, a marker of genetic quality (Perrett et al., 1998), show fewer

72 investing traits (Boothroyd et al., 2008) and are perceived as less investing compared to

73 males with lower levels of facial masculinity (Perrett et al., 1998). Similarly, men with higher

74 attractiveness, or higher facial symmetry, also markers of genetic quality (Little et al., 2001),

75 are less co-operative and offer fewer resources in experimental settings (Sanchez-Pages &

76 Turiegano, 2010; Takahashi et al., 2006; Zaatari & Trivers, 2007). Accordingly, women may

77 need to trade off investment and genetic quality when choosing a mate (Perrett et al., 1998;

78 Roney et al., 2006).

79

80 Parents and their daughters benefit in different ways from the genetic quality and investment

81 of the daughter's partner, and thus the ideal trade-off point might be different for parents

82 compared to daughters (Andersson, 1994; Buunk, Park, & Dubbs, 2008). The genetic quality

83 of a daughter's partner provides relatively greater benefits to that daughter than to her

84 parents, because any children born to the daughter are related 0.5 to her, but only 0.25 to the

85 daughter's parents. A daughter therefore might be happy to sacrifice a partner with good

86 investment potential for one who has high genetic quality. In contrast, the daughter's parents

87 will be less willing to relinquish traits that make a partner valuable but which do not

88 constitute genetic quality. Further, parents might have additional specific preferences for a

89 partner with good investment potential, to reduce the risk that they might have to shoulder

90 some of the costs arising from low paternal investment by the daughter's partner to the

91 detriment of their investment in other (grand-)offspring (Buunk et al., 2008; Apostolou 2011,

92 2015). This position is supported by questionnaire studies. Parents put more emphasis on

93 traits indicating investment (e.g. 'kind', 'housekeeper') while their offspring judged markers

94 of genetic quality (e.g. 'attractive') as more important (Perilloux, Fleischman, & Buss; 2011).

95 Similarly, people indicated that they would have greater preferences for good looks in a

96 partner than in a son- or daughter-in-law, alongside greater preferences for a good family

97 background in a son- or daughter-in-law than a partner (Apostolou, 2011). Finally, children

98 (aged 16+) rated good looks more important in a prospective spouse than their parents did in

99 a prospective son- or daughter-in-law (Apostolou 2015).

100

101 In the present study, we recruited parents with daughters of reproductive age, and tested the

102 preferences of the parents and their daughters for markers of genetic quality in potential

103 partners for the daughters. We predicted that: 1) parents would show directional preferences

104 for facial markers of genetic quality (attractiveness, masculinity, health, and symmetry) in an

105 offspring's potential partner, and these preferences would not be affected by the menopause;

106 2) facial markers of genetic quality would be more attractive to daughters judging the

107 attractiveness of a potential partner than to parents judging a potential partner for their

108 daughter; and 3) parents and daughters would adjust their preferences in accordance with

109 their perception of the daughter's mate quality (attractiveness).

110

111 **Methods**

112 *Participants*

113 Participants consisted of 210 parents (111 female; mean age = 52 yrs, age range = 37-73yrs)

114 and 125 of their daughters (mean age = 20.57 yrs, age range = 18-29). Eighty seven daughters

115 had both parents participate, there were no sisters in the sample. All participants self-

116 identified as white and lived in the UK. The daughters were recruited predominantly from a

117 large Psychology undergraduate teaching class. Participants were only included if daughters

118 were between 18 and 30 years old, so that daughters were in the peak reproductive phase, and

119 were of roughly equivalent age to the male face stimuli used. Additionally, daughters had to

120 have lived with both their biological parents until at least age 16. This restriction was applied

121 to ensure that all parents had invested substantially and extensively in their daughters. All

122 participants gave informed consent. The study was approved by the XXXXXXX.

123

124 *Stimuli*

125 Daughter-aged male face stimuli were created from 15 male base identities. Each identity was

126 a composite of three photographs drawn from a white student image set generated at the

127 University of St Andrews. These images were combined to create a composite to avoid

128 individuals being identified. Each identity was then transformed for attractiveness, health,

129 masculinity, and symmetry. Attractiveness transforms were conducted by applying ±25% of

6

130   the shape and colour difference of an attractive and unattractive prototype, taken from

131   Todorov and colleagues (Todorov et al., 2013; Todorov & Oosterhof, 2011). For health

132   transforms, a ±17% carotenoid colouration transform was applied (Lefevre et al., 2013). For

133   masculinity, base images were transformed by ±50% of the shape and colour difference

134   between an average male and average female (Perrett et al., 1998). Finally, to create stimuli

135   differing in symmetry, base faces were symmetrised while the untransformed base faces were

136   used as the low-symmetry versions of each face (Little et al., 2001). Example stimuli are

137   shown in Figure 1. These stimuli were presented in pairs in a forced choice paradigm in an

138   online study. Each face pair contained two versions of the same identity, with high and low

139   levels (each level randomly presented on the left/right) of one of the four manipulations,

140   presented in random order.

141

142   Parent-aged male face stimuli were created from 15 male faces (mean age=45.9yrs) from the

143   FACES database (Ebner, Riediger, & Lindenberger, 2010). Faces were transformed for

144   attractiveness, health, masculinity, and symmetry using the methods described above, and

145   presented in the online survey as described above.

146

147   Daughter-aged female face stimuli ($n = 20$) were taken from a set of photographs taken at the

148   University of St Andrews. They were all white and of undergraduate student age. We

149   attempted to choose a range of attractiveness levels for these stimuli.

150

151   ---- insert Figure 1 about here -----

152

153   **Procedure:** The daughter participants were first shown the pairs of daughter-aged male face

154   stimuli. For each pair, they were asked to select the face that they found more attractive. This

155 allowed us to calculate a 'high preference score' representing the proportion of trials on

156 which the high trait face was chosen. Next, the daughter participants were asked to compare

157 themselves to each of the daughter-aged female face stimuli, and to state whether they

158 considered themselves more or less attractive than each (Clark, 2004). Subsequent to

159 participation in the study, they were contacted to ask if they would like to invite their parents

160 to take part in a related study. Those who agreed forwarded details of the study to their

161 parents.

162

163 Parental participants were first shown the same set of daughter-aged male face stimuli that

164 their daughters saw. They were asked to refer to the daughter who participated in the study,

165 and to select the face that would be more suitable as a partner for the daughter[1]. This allowed

166 us to calculate a 'high preference score' representing the proportion of trials on which the

167 high trait face was chosen. Next, the parental participants saw the same daughter-aged female

168 face stimuli that their daughters saw, and were asked to rate whether the daughter was more

169 or less attractive than each. Thirty-two participants (14 female) chose to skip this step. In

170 addition, female parental participants completed an additional facial preference test. In this

171 test, the parent-age male face pairs were presented in random order as above, and women

172 were asked to choose the more attractive face in each pair. They also reported whether they

173 had stopped menstruating due to menopause (43 stopped cycling; 2 unsure).

174

175 **Results**

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[1] We have no evidence that the question wording might have affected responses: in a separate study with a similar cohort of white, heterosexual females (N=114, mean age=20.06) we presented participants with the same face pairs as described in this paper but randomly assigned them to answer either the question 'Who is more attractive' or the question 'Who would be a more suitable partner for you'. A repeated measures ANOVA with question as a between subjects factor indicated no main effect of question (p=.69) and no interaction between face transform and question (p=.89). This cohort was recruited from the same large undergraduate psychology class, but one year later than the cohort described in the main study.

176 *Directional preferences*

177 One-sample t-tests against chance (0.5) indicated directional preferences of parents and

178 daughters for facial markers of genetic quality (all p<.001; see Table 1).

179

180 Table 1: Mean preference scores, representing the proportion of times participants selected

181 the high-trait face. All scores are significantly above chance (all p<.001).

	Mean (SD) preference of…		
	Daughter	Mother	Father
Attractiveness	.79 (.15)	.76 (.18)	.70 (.20)
Health	.76 (.15)	.68 (.19)	.67 (.18)
Masculinity	.75 (.21)	.70 (.23)	.68 (.23)
Symmetry	.64 (.19)	.66 (.19)	.66 (.16)

182

183 Additionally, attractiveness, health, and masculinity preferences were weakly to moderately

184 correlated, while symmetry preferences were independent (Table 2). Fathers and mothers

185 showed a significant correlation in attractiveness preferences (r_{rho}=.25, p=.02). There were no

186 other significant correlations between parents (all p>.12) or parents and daughters (all p>.10).

187

188 Table 2: Zero-order correlations of parental trait preferences.

Preference for…	Attractiveness	Health	Masculinity
Health	.53**		
Masculinity	.21**	.41**	
Symmetry	.10	.10	-.02

189 Note. **p<.01.

190

191 *Parent-offspring conflict*

192 Next, for those families were daughter, mother, and father participated (N=87), we next ran a

193 3x4 repeated measures ANOVA with rater (daughter, mother, father) and rating

194 (attractiveness, health, masculinity, and symmetry) as repeated measures. The test revealed a

195 main effect of rater (F(2,85)=5.60, p=.005), a main effect of rating (F(3,84)=17.68, p<.001),

196 and a rater by rating interaction (F(6,81)=3.01, p=.01). The main effect of rater was driven by

197 daughters showing stronger preferences than both their mothers (p=.04) and their fathers

198 (p=.002). There was no significant difference in preference between mothers and fathers

199 (p=.33). The main effect of rating was driven by the high attractive face having been chosen

200 significantly more frequently than the 'high' face of any of the other traits (all p<.01) and the

201 high health and high masculinity faces having been chosen significantly more often than the

202 high symmetry face (ps<.01). The interaction between rater and rating was resolved using

203 sub-sequent independent repeated measures ANOVAs for each rating. For attractiveness,

204 mothers and daughters did not differ in their ratings (p=.46), but fathers and daughters did

205 (p<.01). For health, daughters chose the 'high' face significantly more often than both their

206 mothers (p=.003) and fathers (p<.001). For masculinity, daughters showed a marginally

207 stronger preference for 'high' faces than their mothers (p=.08) and a significantly stronger

208 preference than their fathers (p=.02). Finally, for symmetry there was no difference between

209 daughters and their parents (all p>.34; Figure 2). Mothers and fathers did not differ in their

210 ratings for any traits, although for attractiveness, mothers showed a marginally stronger

211 preference (p=.05). Finally, in order to assess whether menopause influenced mothers' ratings

212 we ran an additional repeated measures ANOVA including only mothers with rating as a

213 repeated measure and controlling for menopause and age. This test revealed no effect of

214 either age (p=.67) or menopause (p=.47).

215

216   --- Insert Figure 2 here ---

217

218 To determine whether the parents' lesser preferences for markers of genetic quality were

219 driven by judging faces much younger than themselves, we used paired-samples t-tests to

220 compare the mothers' ratings of the suitability of daughter-aged male faces for their

221 daughters with their ratings of the attractiveness of parent-aged male faces for themselves.

222 With the exception of health (t(104)=0.79, p=.43, d=.15), mothers showed significantly

223 stronger preferences for markers of genetic quality when making judgements for their

224 daughters than when judging potential partners for themselves (attractiveness: t(104)=5.01,

225 p<.001, d=0.98; masculinity: t(104)=4.73, p<.001, d=0.93; symmetry: t(104)=3.94, p<.001,

226 d=0.77).

227

228 *Effect of daughter's attractiveness*

229 Next, we assessed whether participants adjusted their preferences for potential partners

230 according to the daughter's attractiveness. Spearman's correlations revealed that the

231 associations between preferences for markers of genetic quality and assessments of

232 daughters' attractiveness were generally negative and non-significant (Table 3). Results were

233 similar for fathers and mothers.

234

235 Table 3: Zero-order correlations between preferences for facial markers of genetic quality in

236 the daughter's potential partner and rated attractiveness of the daughter

Preference for…	Parent preference and parent-perceived daughter attractiveness		Daughter preference and self-perceived daughter attractiveness	
	r	p	r	p
Attractiveness	-.15	.05	-.15[‡]	.09
Health	-.15	.04	-.13	.16
Masculinity	-.03	.73	-.14	.13
Symmetry	-.02	.77	.11	.21

237

Discussion

239 Our results are the first demonstration that parents show clear preferences for facial markers

240 of genetic quality when assessing potential partners for their daughters. Parents thus have

241 mechanisms that assess facial markers of genetic quality when assessing their daughters'

242 partners, and could use this information to inform their dealings with potential sons-in-law.

243

244 We also saw diverging patterns of preferences between parents and their daughters.

245 Daughters showed stronger preferences for attractiveness, health, and masculinity than their

246 fathers, and stronger preferences for health and marginally for masculinity than their mothers.

247 Fathers and mothers did not differ in their levels of preference. Parent-offspring conflict

248 predicts that daughters should have greater preferences than their parents for markers of

249 genetic quality in order to maximise their own fitness through mating with a high quality

250 partner, whereas parents should have stronger preferences for partners who are likely to

251 invest resources into offspring (Buunk et al., 2008). While our data are consistent with this

252 prediction, we did not explicitly test parental preferences for investment but rather inferred

253 these following previous research that indicates that markers of genetic quality are traded off

254 with investment traits (Perrett et al., 1998). It is unlikely that parents should disregard

255 markers of genetic quality completely, and this is also evident in our findings. We did not

256 find the same pattern of results for symmetry judgements, perhaps due to stimuli being harder

257 to distinguish, although both parents and daughters showed above chance preferences for

258 symmetrical faces. Our results are further corroborated by a previous study (Kruger, 2006)

259 where university students were asked to imagine their preferences if they had a grown-up

260 daughter, and demonstrated a stronger preference for feminised male faces (i.e. more rather

261 than less investing) as potential sons-in-law compared to other contexts, including dating,

262 marriage, and sexual relations. The differences in judgements between parents and daughters

263 in our study is unlikely to be attributable to the possibility that the parents struggled to

264 properly judge genetic quality in faces younger than themselves; indeed mothers showed

265 stronger preferences for genetic quality in daughter-aged male faces than in parent-aged male

266 faces.

267

268 Menopause did not change the mothers' assessments of the faces, irrespective of whether

269 they were judging daughter-aged faces in terms of their suitability as a partner for their

270 daughter, or age-matched faces in terms of their attractiveness to themselves. This latter point

271 stands in contrast to previous work showing that menopause reduces women's preferences for

272 facial markers of genetic quality when assessing potential partners for themselves in age-

273 matched and younger faces (Jones et al., 2011; Little et al., 2010). Given the potential benefit

274 to inclusive fitness, maintained ability to assess mate quality for their daughters might be

275   independent from the hormonal effects of the menopause that could affect own mate choice.

276   In line with this, mothers demonstrated stronger preferences for markers of genetic quality in

277   their daughters' partners than in partners for themselves. This seems to run counter to the

278   parent-offspring conflict hypothesis, as genetic quality should be more important in a

279   reproductive partner than in an in-law. On the other hand, we cannot directly compare ratings

280   of daughter-aged and parent-aged stimuli because the stimuli themselves were different and

281   so properties of the stimuli could have interacted with properties of the manipulations. In

282   addition, even though the majority of the mothers were pre-menopausal, genetic quality could

283   still be of lesser strategic importance than investment in a potential partner for women who

284   have more years of potential grandparenting than potential reproduction in the near future.

285

286   Finally, we did not find that parents and daughters had stronger preferences for markers of

287   genetic quality if they perceived the daughter to be more attractive. Indeed, we found weak

288   evidence for the contrary: parents had stronger preferences for healthy male faces if they

289   perceived their daughters to be less attractive, and there were non-significant negative

290   relationships between perceptions of daughter attractiveness and preferences for other facial

291   markers of genetic quality (Table 3). While this is surprising given the existing literature on

292   assortative mating (Jones et al., 2005; Little et al., 2001), parents and daughters appeared to

293   be behaving similarly, indicating an analogous mechanism at play. It is possible that physical

294   appearance is somewhat less critical in partner choice if a daughter is very attractive and

295   accordingly carries many markers of genetic quality. In this instance, a trade-off towards

296   caring personality traits might be made by both parents and women choosing partners. Our

297   results run contrary to a recent study (Apostolou & Papageorgi, 2014) however, showing that

298   parents preferred sons-in-law who were similar in attractiveness to their daughter, although

299 this study assessed attractiveness equivalence using a single Likert-scale item, rather than

300 rating both partners' and own daughter's attractiveness on a large number of trials.

301

302 We did not collect data on hormonal contraceptive usage. Women who use hormonal

303 contraceptives show weaker preferences for male facial masculinity than women who do not

304 (e.g. Little et al. 2013). Use of oral contraceptives by women in the UK declines sharply

305 throughout adulthood (Lader, 2009; Lifestyle Statistics, Health and Social Care Information

306 Centre, 2014). Accordingly, hormonal contraceptive usage should create stronger preferences

307 for male facial femininity in the daughters, and stronger preferences for male facial

308 masculinity in the mothers. This was opposite to what we found, and indicates that the effects

309 we noted might have been even stronger if we had taken account of hormonal contraceptive

310 usage. Overall, here, we found that the masculinised rather than feminised male facial stimuli

311 tended to be preferred; research studies have previously reported findings of enhanced

312 attractiveness both in masculinised and also in feminised male facial stimuli (Rhodes 2006).

313 These differences likely result from a complex combination of the features of the stimuli and

314 individual variables relating to the raters (Rhodes 2006). For our research study, the key

315 question was not whether male facial masculinity or feminity overall was preferred, but how

316 parents' preferences compared with those of their daughters.

317

318 We chose to focus on female rather than male participants and their parents. Females can

319 incur higher potential costs than males in mate choice (Trivers 1972). We would anticipate

320 that, in respect of sons, the parents would have similar preferences for markers of genetic

321 quality in daughters-in-law, and would also have weaker preferences than their sons for

322 markers of genetic quality (Apostolou, 2011, 2015; Perilloux, Fleischman, & Buss; 2011).

323

15

324 The current study did not assess whether the parents in the study were influential in their

325 daughter's actual mate choice, although a wealth of evidence shows the existence of this

326 phenomenon (Apostolou, 2007; Goode, 1959; Menon, 1989; Minturn, Grosse, & Haider,

327 1969). Likewise, like almost every study on attractiveness preferences, we did not test how

328 the preferences that we assessed would translate into real-world encounters. While several

329 studies have shown a relationship between ideal and actual partner choice, the former does

330 not necessarily predict the latter (Campbell & Stanton 2014; Eastwick et al. 2014). For

331 consistency with the wealth of existing literature on human mate choice, we asked the

332 daughters to indicate the more attractive male face in the pair. This exact question could not

333 be used directly to ask parents about their preferences for their daughter, and so, instead, we

334 asked them to select which face was more suitable as a partner for their daughter. To check

335 whether the wording difference could have contributed to the difference in preferences, we

336 ran a further study recruited from the same teaching class but amongst the students in the

337 following year's cohort. Participants were randomly allocated to answer one question or the

338 other. The question wording did not influence stated preferences. However, the difference in

339 question wording for the parents compared to the daughters is a potential limitation of the

340 study.

341

342 Taken together, we present evidence for parental preferences for sons-in-law being

343 directional and supportive of inclusive fitness. Our data are consistent with parent-offspring

344 conflict, which may be the driving force behind parental involvement in their offspring's

345 mate choice. Contemporary western research seeks to understand universal patterns of human

346 mate choice by extrapolating from measurements of individual preferences, but human mate

347 choice across cultures is often modified by parental wishes (Apostolou, 2007; Goode, 1959;

348 Menon, 1989; Minturn, Grosse, & Haider, 1969). In showing commonalities and differences

349　between an individual's preferences for their own partner, and parents' preferences for an in-

350　law, we show how research on physical attraction within WEIRDs (western, educated,

351　industrialised, rich, democratic people; Henrich, Heine, & Norenzayan, 2010) can be

352　integrated with cross-cultural, historical and anthropological data that highlight the role of the

353　family in marriage and partnership choices.

354

355

360

361 ***Figure Caption:***

362 *Figure 1: Example stimuli pairs.*

363 *Figure 2: Differences between parent and offspring preferences for each marker of genetic*

364 *quality, where 0.5 would indicate preferences at chance levels (mean +/- SE). *p<.05;*

365 ***p<.01; ***p<.001 (Bonferroni corrected).*

366

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