

# Sexual imprinting in human mate choice

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Animal and human studies have shown that individuals choose mates partly on the basis of similarity, a tendency referred to as homogamy. Several authors have suggested that a specific innate recognition mechanism, phenotypic matching, allows the organism to detect similar others by their resemblance to itself. However, several objections have been raised to this theory on both empirical and theoretical grounds. Here, we report that homogamy in humans is attained partly by sexual imprinting on the opposite-sex parent during childhood. We hypothesized that children fashion a mental model of their opposite-sex parent's phenotype that is used as a template for acquiring mates. To disentangle the effects of phenotypic matching and sexual imprinting, adopted daughters and their rearing families were examined. Judges found significant resemblance on facial traits between daughter's husband and her adoptive father. Furthermore, this effect may be modified by the quality of the father–daughter relationship during childhood. Daughters who received more emotional support from their adoptive father were more likely to choose mates similar to the father than those whose father provided a less positive emotional atmosphere.

**Keywords:** evolved mating preferences; homogamy; sexual imprinting; phenotype matching

## 1. INTRODUCTION

Research has shown that human sex partners resemble each other in many traits (Mascie-Taylor 1988, 1995; Weisfeld *et al.* 1992; Jaffe & Chacon-Puignau 1995; Keller *et al.* 1996; Bereczkei *et al.* 1997; Thiessen 1999). Positive correlations have been found between their socio-economic status, age, intellectual ability, education, personality variables, physical attractiveness, vocational interests and anthropometric measures. Although homogamy, or positive assortative mating, appears to be under the influence of many cultural factors that presumably render married couples more compatible, its ubiquity across cultures and species requires an evolutionary explanation. One possible explanation is genetic-similarity theory, an extension of kin-selection theory (Thiessen & Gregg 1980; Rushton 1989). If organisms can identify genetic similarity in strangers, they might exhibit altruism towards them, with a consequent increase in inclusive fitness. This altruism could take the form of homogamy, which increases the degree to which parents share genes with offspring, thereby enhancing genetic representation in future generations. Homogamy might also prevent genetic complexes coadapted to the local environment from being disrupted, thereby enhancing reproductive success (Read & Harvey 1988). Obviously, an extreme degree of homogamy can impose serious reproductive costs (inbreeding depression effects) (Blouin & Blouin 1988). It has been argued that an adaptive compromise has evolved between the opposing selection pressures of inbreeding and outbreeding, with individuals choosing a mate with a moderate degree of homogamy (Bateson 1983). Accordingly, homogamy between non-relatives has been found to enhance marital stability and fertility, and to lower the rate

of miscarriage in humans (Mascie-Taylor 1988; Rushton 1988; Thiessen *et al.* 1997).

How is homogamy thought to be achieved? Some animals have been found to prefer genetically similar mates (Blaustein *et al.* 1991; Holmes 1995; Pfennig & Sherman 1995). This may occur by phenotypic matching to self, through which they use their own phenotype to choose others with similar phenotypic cues. Obviously, this can occur only if there is a high correlation between genetic similarity and phenotypic similarity on traits that individuals use to distinguish potential mates. Much experimental evidence shows that various animals are able to recognize genetic similarity in unfamiliar individuals on the basis of shared olfactory and visual cues. For example, a study of Belding's ground squirrels (*Spermophilus beldingi*) revealed that biological sisters reared apart could recognize one another and engaged in a significantly lower rate of aggressive interactions than non-siblings (Holmes & Sherman 1983).

However, very few studies have examined the possibility that humans recognize gene-related 'strangers' based on similarity to their own phenotype. These studies have yielded controversial results. One has shown that a woman prefers the odour of a man who has significantly more human leucocyte antigen (HLA) allele matches to her own alleles than the man with the least preferred odour (Jacob *et al.* 2002). Another study revealed that female students tended to prefer the scent of men who possessed dissimilar HLA genotypes (Wedekind & Furi 1997). It is not known what perceptual mechanisms are involved in this feature detection, and what part of the similarity detection system is based on innate mechanisms and associative learning. Furthermore, critics argue that the theory of genetic similarity via phenotypic matching has a possible theoretical fallacy (Archer 1989; Krebs 1989; Daly *et al.* 1997). As relatedness decreases, the probability that individuals share the gene responsible for altruism will be lower, and distant relatives or strangers are not likely to carry that

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gene, even though they may be similar in certain traits. Therefore, discriminatory altruism on the basis of phenotypic similarity is uncorrelated with the likelihood of sharing an altruism gene, and would be selected out. As a consequence, genetic similarity theory will be reduced to kin recognition.

Imprinting-like mechanisms have been suggested as an alternative explanation for the mediation of homogamy in humans (Daly 1989; Bereczkei *et al.* 2002; Little *et al.* 2002). Similarity between spouses would arise if individuals acquired mate-choice criteria templates through exposure to their parents. In cases of sexual imprinting, as the ethologists called it, an early fixation to a set of family characteristics will shape mate preferences during adulthood (Bateson 1964; Lorenz 1965; Bolhuis & Horn 1992). Cross-fostering experiments with birds and mammals have revealed that adults prefer sexual partners that are similar to the opposite-sex parent that reared them (Immelmann *et al.* 1991; Oetting *et al.* 1995; Kendrick *et al.* 1998). For example, supporting his optimal outbreeding theory, Bateson (1988) found that Japanese quail (*Coturnix japonica*) prefer to mate with birds that differ slightly in appearance from their parents and siblings.

Sexual imprinting on the observed features of the opposite-sex parent during a sensitive period in early childhood might be responsible for shaping people's later mate-choice criteria. Children might internalize their opposite-sex parent's phenotype as a template and, at sexual maturity, prefer those who resemble this mental model. In a recent study comparing more than 300 facial photographs of family members and controls, the subjects correctly matched wives to their husband's mother (Bereczkei *et al.* 2002). Furthermore, a higher degree of similarity was perceived between the husband's mother and his wife than between the husband and his wife. These results suggest that sons fashion a representation of their mother's physical appearance and use it for choosing mates. In another study, similarity was observed between the facial photographs of husbands and their wife's biological father (Gyuris 2003). The subjects correctly matched husbands to their father-in-law at a significantly higher mean rate than expected by chance, and a significantly higher frequency than matching between husbands and wives.

However, a crucial limitation of these investigations is the difficulty of separating the effects of phenotype matching to self and sexual imprinting. Similarity between one's spouse and his/her opposite-sex parent might be an artefact, given the 50% overlap between the parents' and offspring's genetic material. Therefore, if homogamy works via phenotype matching, it would be responsible for the similarity between spouse and opposite-sex parent. In this case, our results about resemblances between family members may be a result of innate similarity detection between spouses, not sexual imprinting on the mother. However, certain studies suggest that imprinting-like mechanisms may occur in human mate choice. One study revealed greater importance of the opposite-sex parent over the same-sex parent in predicting the hair and eye colour of actual partners (Little *et al.* 2002). Similarly, women were found to prefer the odours of men with HLA alleles that resembled her father's HLA alleles but not her mother's (Jacob *et al.* 2002).

To disentangle these effects further, the present study aimed at investigating the mate choices of women from adoptive families. In light of our hypothesis, sexual imprinting will have a long-term effect on one's mate choice, whether the child and the caring adult were relatives or not. We predicted, therefore, that the women would choose a mate who resembled their father even though he was not a biological relative. Alternatively, if phenotypic matching theory is correct, the women would prefer mates similar to themselves but not to their adoptive father.

## 2. METHOD

### (a) *Subjects*

To test this hypothesis, we applied a method that was used in an earlier study (Bereczkei *et al.* 2002). Subjects were shown photographs of wives, and rated the similarity between each of them and four possible husbands, one of whom was the actual spouse. They also rated the degree of similarity between the wife's adoptive father at the age when his adopted daughter was between 2 and 8 years, and her possible husbands. Similarly, facial photographs of the wife and her adoptive mother were compared. These photographs were provided by 26 Caucasian families. Advertisements were placed in three newspapers in Pecs (Hungary), stating that researchers at the University of Pecs needed volunteers who had been reared in an adoptive family. Additional photographs, as controls, were taken of 198 young men at the age comparable with that of the husbands (mean age of 28.3 years). They were randomly chosen from undergraduate and graduate students at university. We took black-and-white photographs because many of the mothers' and fathers' portraits had been taken several decades ago in this format. The photographs of the adoptive parents had been taken when they were young, i.e. when their adopted children were growing up. All of the photographs were developed and scanned into a computer, using the Corell PHOTOPAINT program.

Three sets of tableaux were made of these individual photographs. They were standardized for age, length and colour of hair, position of their head in the photograph, and certain other traits, to minimize the possible differences between the faces of target persons and controls. One tableau contained the wife (left side), and her husband and three controls (right side). The other set of tableaux was made of the same photographs, with the exception that the wife was replaced by her adoptive father (figure 1). The third set showed the adoptive mother next to the same group photographs (one husband, three controls). Finally, we had three sets of tableaux, with a total of 182 photographs of individual faces.

In all, 242 undergraduate (128 female, 114 male) psychology students were used as independent judges to evaluate similarity. They were not aware of the aim of the study, and were not personally acquainted with any of the persons in the photographs. Eighty-four subjects participated in the first study (wife-husband matching), 82 in the second study (husband-father) and 76 in the third study (husband-mother).

### (b) *Procedure*

Each tableau was projected on a screen in a seminar room, where up to 10 subjects participated in the experiment at a time. The subjects were instructed to look at each of the 3 × 26 tableaux thoroughly, match the photographs of the index person with four possible matches, one of which was the true match.

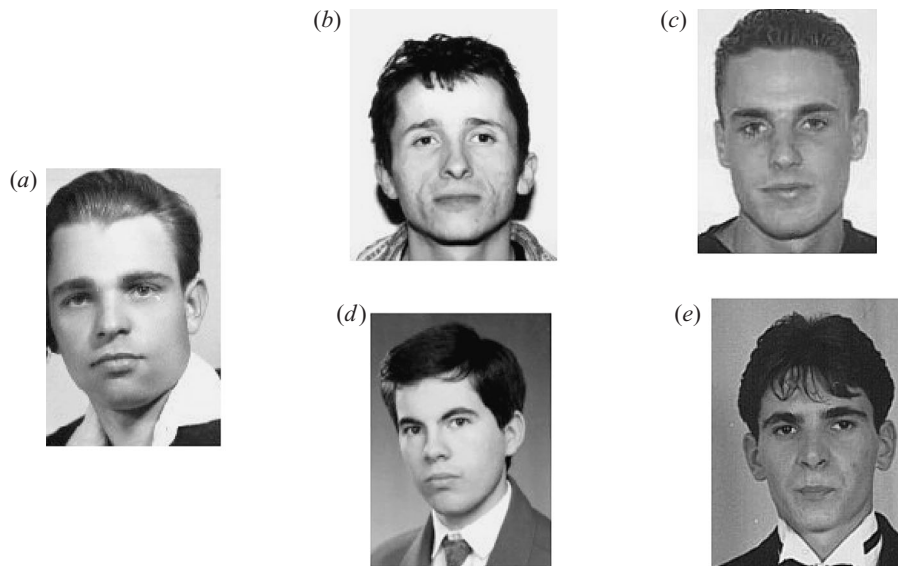


Figure 1. The tableau shows adoptive father when his daughter was between 2 and 8 years old (a) and four possible sons-in-law (b)–(e). Subjects were asked to make an assessment about the rank of similarity between them. The appropriate match was (d).

The subjects ranked the pairs individuals on the basis of similarity. They marked the degree of similarity with numbers from 1 (the most similar) to 4 (the least similar). In the first three studies, they judged the similarity between the husband and wife, between the husband and his wife's adoptive father, and between the husband and his wife's adoptive mother, respectively.

In the final study, wives were asked to complete a retrospective attachment test, the EMBU, which assesses adults' perceptions of their parents' rearing behaviour during childhood. The short form of the EMBU, with 23 items, provides three factorially derived subscale measures: rejection (e.g. 'my parents criticized me and told me how lazy and useless I was in front of others'); emotional warmth (e.g. 'my parents showed with words and gestures that they liked me'); and overprotection (e.g. 'my parents wanted to decide how I should be dressed or how I should look'). In an examination among samples of 2442 students from four countries, internal consistency and reliability has been high (Arindell *et al.* 1999). In our study, the test was administered in the subject's home by a research assistant who was naive about the point of the study. For each EMBU item, participants rated themselves on a scale ranging from 1 (no, never) to 4 (yes, most of the time). Finally, the perceived degree of similarity between husband and his father-in-law was correlated with the test scores on the EMBU.

### 3. RESULTS

#### (a) Study 1: husband–wife matching

As figure 2 shows, the resemblance between husbands and their wives exceeded chance. The judges correctly matched husbands to wives at a significantly higher mean rate than 25% (31.10%, Wilcoxon  $z = -5.86$ ,  $p < 0.01$ ). This percentage significantly exceeds the rate at which a control was chosen as most similar (22.9%,  $z = -6.124$ ,  $p < 0.001$ ). No sex difference was found in the estimation of similarity; approximately the same proportion of male and female subjects made the appropriate matches (Mann–Whitney  $U = 234.3$ ,  $p > 0.05$ ).

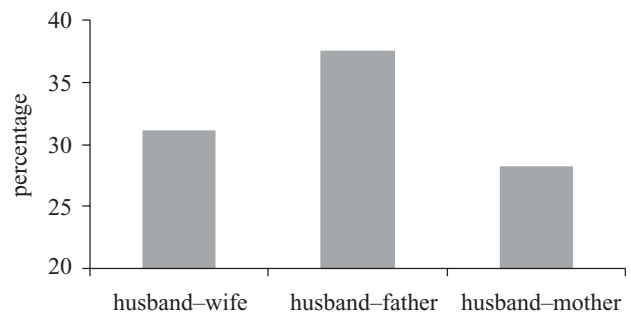


Figure 2. The percentage of matches of husband to wife, husband to wife's adoptive father, and husband to wife's adoptive mother. Significant resemblance was ascribed between husband and wife, and between husband and wife's adoptive father, with a significant difference between the two mean rates.

#### (b) Study 2: husband–father matching

Even more similarity was perceived between husbands and their wives' adoptive father (figure 2). The subjects correctly chose the husband as being the most similar to his father-in-law, on average, in 37.7% of the tableaux, which exceeds chance level ( $z = -7.81$ ,  $p < 0.001$ ). Husbands were ranked first on the similarity scale almost twice as often as controls (20.7%,  $z = -7.618$ ,  $p < 0.001$ ). No sex difference was found between subjects ( $U = 324.3$ ,  $p > 0.05$ ).

Comparing the results of studies 1 and 2, a higher degree of similarity was perceived between the wife's husband and the wife's adoptive father than between the husband and his wife. The subjects correctly matched husbands to their fathers-in-law at a significantly higher frequency than to their wives (37.7% versus 31.1%,  $z = -2.85$ ,  $p < 0.01$ ).

#### (c) Study 3: husband–mother matching

The percentage of matches of husband to wife's mother was not significantly above chance level (27.2%,



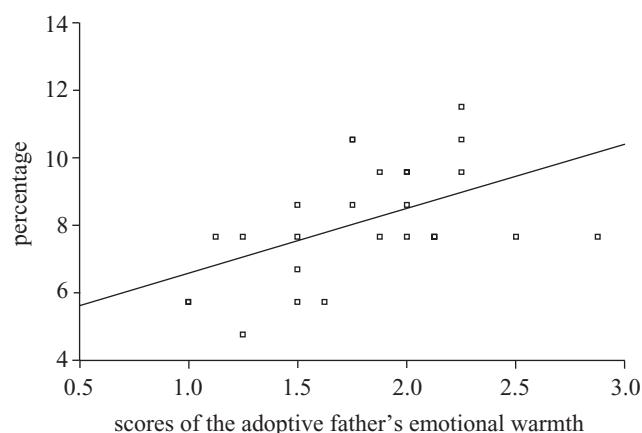


Figure 3. Percentage of husband-wife adoptive father matching as a function of the father's emotional warmth. The more emotional warmth the adoptive daughters received during their childhood, the more similarity was judged between their husband and adoptive father.

$z = -0.86$ ,  $p > 0.5$ ). No resemblance was found in facial appearance between husbands and wives' adoptive mother.

#### (d) Study 4: exposure to adoptive father

The degree of perceived similarity between the husband and the wife's adoptive father was plotted against the mean scores on the three subscales of the EMBU (figure 3). A regression of emotional warmth on matching frequencies by judges showed a significant positive relationship: women who had been more emotionally supported by their fathers during childhood were more likely to choose mates similar to their fathers on facial traits ( $\beta = 0.510$ ,  $t = 2.90$ ,  $p < 0.01$ ). No significant relationship was found for the other subscales: rejection ( $\beta = -0.288$ ,  $t = -1.285$ ,  $p > 0.05$ ) and overprotection ( $\beta = -0.128$ ,  $t = -0.633$ ,  $p > 0.05$ ).

This result suggests that those fathers who had provided emotional warmth for their adopted daughters during childhood were judged as being more similar to their daughters' husbands than those fathers who did not provide a positive atmosphere. In other words, those fathers who were most frequent matches to their sons-in-law had shown more emotional warmth towards their adopted daughters.

## 4. DISCUSSION

Our results showed that: (i) significant resemblance was found between husbands and their wives; (ii) an even higher degree of similarity was perceived between husband and the wife's father (husband's father-in-law); and (iii) the more emotional warmth the father provided for his adopted daughter, the more similarity was perceived between him and his son-in-law. These findings suggest that sexual imprinting-like mechanisms play a role in human mate choice. Although homogamy via phenotypic matching to self could not be excluded, homogamy may be achieved more by exposure to the opposite-sex parent early in life. Preferences for ensuring positive assortative mating seem to be shaped during the process of bonding to the opposite-sex parent, and long-term mates will be selected partly on the basis of resemblance to that parent.

Our results could also be explained as a result of a familiarization effect; people generally respond positively to familiar stimuli. In this case, mother and father alike should influence their offspring's homogamous mating, and people would be attracted to faces with some characteristics of both parents. However, because no resemblance was revealed between husband and the adoptive same-sex parent, that rival hypothesis was rejected.

The recent study and our several earlier researches on sexual imprinting (Bereczkei *et al.* 2002; Gyuris 2003) found significant facial resemblance between wife and husband. These results are not inconsistent with the possibility that homogamy is promoted by phenotype matching. Phenotype matching seems to influence kin recognition. Studies have revealed that various vertebrates can recognize relatives that were reared apart from them (Blaustein *et al.* 1991; Pfennig & Sherman 1995). An innate capacity for kin recognition would be especially adaptive for species that disperse when young (Weisfeld *et al.* 2003). In this case, an assessment of the degree of kinship would promote altruism and cooperative behaviour towards individuals with shared genes.

There is some evidence that people are able to recognize relatives who share similar facial or olfactory features. A study found that mothers who had limited contact with their newborns immediately after birth could recognize them by olfactory cues alone (Porter 1987). Adult judges could also match the odours of mothers with those of their infants, but were unable to match husbands with wives (Porter *et al.* 1985). Using visual cues, adult subjects could match mothers', fathers', and their newborn infants' facial photographs (Christenfeld & Hill 1995). Recently, Weisfeld *et al.* (2003) found that participants were able to identify the odour of most of their first-degree relatives, but mothers could not recognize their stepchildren, nor could children recognize their stepsiblings.

We suggest that phenotype matching has less influence on interpersonal relationships beyond the circle of kinship. A genetically canalized learning process (sexual imprinting), rather than direct genetic similarity detection via phenotype matching, is responsible for the similarity between spouses. Our studies found that similarity between oneself and one's spouse was significantly exceeded by the similarity between one's spouse and one's opposite-sex parent. A recent study has revealed that eye and hair colour were positively correlated between partners but the best predictor of the partner's eye and hair colour was the opposite-sex parents' colour traits (Little *et al.* 2002).

Our results support the notion of a long-lasting effect of attachment during childhood on later mating preferences. In the recent study a positive relationship was found between the degree of facial similarity between the daughters' husband and their father and the scores of emotional warmth provided by these fathers. Similarly, a previous study revealed a negative correlation between maternal rejection towards son and spouse similarity (Bereczkei *et al.* 2002). All of these results suggest that mate choice depends on physical and emotional exposure to the opposite-sex parent, as the sexual imprinting model predicts. In accordance with this theory, individuals shape a mental model of their opposite-sex parent's appearance, and search for a partner who possesses certain traits

similar to that perceptual schema. An important difference between imprinting-like mechanisms and phenotype matching is that the development of the former definitely needs social interaction. In this theoretical framework, homogamy is shaped not by a genetically prescribed recognition of similarity, but during a learning process that occurs in a specific direction that is advantageous to genetic reproduction.

One of the referees suggested that emotional investment by the father to the adopted daughter may be mediated by their facial resemblance. Fathers may invest more in adopted daughters who resemble them and so daughters selecting partners who resemble themselves would also result in a link between the father–husband facial similarity. A recent study has shown that males react more favourably to children's faces that have been morphed to resemble their own (Platak *et al.* 2002). These are the children whom males are most likely to adopt, and with whom they would like to spend the most time. If the father's investment on adoptive daughters (including emotional closeness) depends on the degree of their facial resemblance, it would explain the similarity between daughters and husbands which would further support the imprinting-like effect on mate choice. In a future study, this effect could be tested by evaluating similarity between the fathers' and adopted daughters' facial photographs.

At present, however, we do not know the particular attachment and learning mechanisms that are responsible for homogamy. It is possible that duration of co-residence or the amount of physical contact would influence the developmental processes through which individuals acquire mate-choice criteria from exposure to their parents. A longer period of co-residence might strengthen the impact of sexual imprinting. However, this hypothesis was not supported, in that we did not find a significant relationship between the age at which daughters were adopted and the degree of similarity between daughter's husband and daughter's adoptive father. It is highly probable that a complex array of environmental factors and multiple social contacts with parents shapes a mental model of potential partners. Recent research has shown that certain contextual family variables, such as presence or absence of father, trustworthiness of family members, intensity of emotional stress and security of attachment, tend to change later life-history traits, including the onset of maturation, the age of first sexual experience, the length of stable pair-bonding (Belsky *et al.* 1991; Kim & Smith 1998; Bereczkei & Csanaky 2001). However, it is not yet well understood how these adaptive trajectories are linked to the effects of the opposite-sex parent. Much more research is needed based on the perspectives of life-history strategy and sexual imprinting to provide a coherent picture of these developmental phenomena.

## REFERENCES

- Archer, J. 1989 Why help friends when you can help sisters and brothers? *Behav. Brain Sci.* **12**, 519–520.
- Arindell, W. A. (and 11 others) 1999 The development of a short form of the EMBU: its appraisal with students in Greece, Guatemala, Hungary and Italy. *Pers. Individ. Diff.* **27**, 613–628.
- Bateson, P. P. G. 1964 An effect of imprinting on the perceptual development of domestic chicks. *Nature* **202**, 421–422.
- Bateson, P. P. G. 1983 Optimal outbreeding. In *Mate choice* (ed. P. P. G. Bateson), pp. 257–277. Cambridge University Press.
- Bateson, P. P. G. 1988 Preferences for close relations in Japanese quail. In *Acta XIX. Congress Int. Ornith.*, vol. 1 (ed. H. Quellet), pp. 961–972. University of Ottawa Press.
- Belsky, J., Steinberg, J. & Draper, P. 1991 Childhood experience, interpersonal development, and reproductive strategy: an evolutionary strategy. *Child Dev.* **62**, 647–670.
- Bereczkei, T. & Csanaky, A. 2001 Stressful family environment, mortality, and child socialization: life-history strategies among adolescents and adults from unfavourable social circumstances. *Int. J. Behav. Dev.* **25**, 501–508.
- Bereczkei, T., Vörös, A., Gál, A. & Bernáth, L. 1997 Resources, attractiveness, family commitment: reproductive decisions in mate choice. *Ethology* **103**, 681–699.
- Bereczkei, T., Gyuris, P., Koves, P. & Bernáth, L. 2002 Homogamy, genetic similarity, and imprinting; parental influence on mate choice preferences. *Pers. Individ. Diff.* **33**, 677–690.
- Blaustein, A. R., Bekoff, M., Byers, J. A. & Daniels, T. J. 1991 Kin recognition in vertebrates: what do we really know about adaptive value? *Anim. Behav.* **41**, 1079–1083.
- Blouin, S. F. & Blouin, M. 1988 Inbreeding avoidance behaviors. *Trends Ecol. Evol.* **3**, 230–233.
- Bolhuis, J. J. & Horn, G. 1992 Generalization of learned preferences in filial imprinting. *Anim. Behav.* **44**, 185–187.
- Christenfeld, N. J. S. & Hill, E. A. 1995 Whose baby are you? *Nature* **378**, 669.
- Daly, M. 1989 On distinguishing evolved adaptation from epiphenomena. *Behav. Brain Sci.* **12**, 520.
- Daly, M., Salmon, C. & Wilson, M. 1997 Kinship: the conceptual hole in psychological studies of social cognition and close relationships. In *Evolutionary social psychology* (ed. J. A. Simpson & D. T. Kenrick), pp. 265–296. Lawrence Erlbaum Associates.
- Gyuris, P. 2003 Homogamy, imprinting, evolution: mate choice of women and men rearing in various family environments. PhD thesis, University of Pécs, Hungary. [In Hungarian.]
- Holmes, W. G. 1995 The ontogeny of littermate preferences in juvenile golden-mantled ground squirrels: effects of rearing and relatedness. *Anim. Behav.* **50**, 309–322.
- Holmes, W. G. & Sherman, P. W. 1983 Kin recognition in animals. *Am. Sci.* **71**, 46–55.
- Immelmann, K., Pröve, R., Lassek, R. & Bischof, H. 1991 Influence of adult courtship experience on the development of sexual preferences in zebra finch males. *Anim. Behav.* **42**, 83–89.
- Jacob, S., McClintock, M. K., Zelano, B. & Ober, C. 2002 Paternally inherited HLA alleles are associated with women's choice of male odor. *Nature Genet.* **30**, 175–179.
- Jaffe, K. & Chacon-Puignau, G. 1995 Assortative mating: sex differences in mate selection for married and unmarried couples. *Hum. Biol.* **67**, 111.
- Keller, M. C., Thiessen, D. & Young, R. K. 1996 Mate assortment in dating and married couples. *Pers. Individ. Diff.* **21**, 217–221.
- Kendrick, K. M., Hinton, M. R. & Atkins, K. 1998 Mothers may irreversibly determine male social and sexual preferences. *Nature* **395**, 229–230.
- Kim, K. & Smith, P. K. 1998 Retrospective survey of parental marital relations and child development. *Int. J. Behav. Dev.* **22**, 729–751.
- Krebs, D. 1989 Detecting genetic similarity without detecting genetic similarity. *Behav. Brain Sci.* **12**, 533–534.

- Little, A. C., Penton-Voak, I. S., Burt, D. M. & Perrett, D. I. 2002 Investigating an imprinting-like phenomenon in humans. Partners and opposite-sex parents have similar hair and eye colour. *Evol. Hum. Behav.* **24**, 43–51.
- Lorenz, K. 1965 *Evolution and modification of behavior*. University of Chicago Press.
- Mascie-Taylor, C. G. N. 1988 Assortative mating for psychometric characters. In *Human mating patterns* (ed. C. G. N. Mascie-Taylor & A. J. Boyce), pp. 61–82. Cambridge University Press.
- Mascie-Taylor, C. G. N. 1995 Human assortative mating: evidence and genetic implications. In *Human populations: diversity and adaptations* (ed. A. J. Boyce & V. Reynolds), pp. 86–105. Oxford University Press.
- Oetting, S., Pröve, E. & Bischof, H. 1995 Sexual imprinting as a two-stage process: mechanisms of information storage and stabilization. *Anim. Behav.* **50**, 393–403.
- Pfennig, D. W. & Sherman, P. W. 1995 Kin recognition. *Sci. Am.* **272**, 68–73.
- Platek, S. M., Burch, R. L., Panyavin, I. S., Wasserman, B. H. & Gallup, G. G. 2002 Reactions to children's faces. Resemblance affects males more than females. *Evol. Hum. Behav.* **23**, 159–166.
- Porter, R. H. 1987 Kin recognition: functions and mediating mechanisms. In *Sociobiology and psychology: ideas, issues, and applications* (ed. C. Crawford, M. Smith & D. Krebs), pp. 175–204. London: Lawrence Erlbaum Associates.
- Porter, R. H., Cernoch, J. M. & Balogh, R. D. 1985 Odor signatures and kin recognition. *Physiol. Behav.* **34**, 445–448.
- Read, A. F. & Harvey, P. H. 1988 Genetic relatedness and the evolution of animal mating patterns. In *Human mating patterns* (ed. C. G. N. Mascie-Taylor & A. J. Boyce), pp. 115–131. Cambridge University Press.
- Rushton, J. P. 1988 Genetic relatedness, mate choice, and fecundity in humans. *Ethol. Sociobiol.* **9**, 329–333.
- Rushton, J. P. 1989 Genetic similarity, mate choice, and group selection. *Behav. Brain Sci.* **12**, 503–518.
- Thiessen, D. 1999 Social influences on human assortative mating. In *The descent of mind. Psychological perspectives on hominid evolution* (ed. M. C. Corballis & S. G. Lea), pp. 311–323. Oxford University Press.
- Thiessen, D. & Gregg, B. 1980 Human assortative mating and genetic equilibrium: an evolutionary perspective. *Ethol. Sociobiol.* **1**, 111–140.
- Thiessen, D., Young, R. K. & Delgado, M. 1997 Social pressures for assortative mating. *Pers. Individ. Diff.* **22**, 157–164.
- Wedekind, C. & Furi, S. 1997 Body odour preferences in men and women: do they aim for specific MHC combinations for simply heterozygosity? *Proc. R. Soc. Lond. B* **264**, 1471–1479. (DOI 10.1098/rspb.1997.0204.)
- Weisfeld, G. E., Russell, R. J. H., Weisfeld, C. C. & Wells, P. A. 1992 Correlates of satisfaction in British marriages. *Ethol. Sociobiol.* **13**, 125–145.
- Weisfeld, G. E., Czilli, T., Phillips, K. A., Gall, J. A. & Lichtman, C. M. 2003 Possible olfaction-based mechanisms in human kin recognition and inbreeding avoidance. *J. Exp. Child Psychol.* **85**, 279–295.