*Biological Journal of the Linnean Society*, 2009, **96**, 8–12.

# Inclusive fitness in human relationships

J. PHILIPPE RUSHTON*

*The University of Western Ontario, Ontario, N6A 5C2 Canada*

*Received 6 February 2008; accepted for publication 21 April 2008*

For *Homo sapiens*, inclusive fitness theory goes well beyond 'kin'. As William Hamilton hypothesized, genes can increase the probability of their own survival by bringing about the reproduction of not only family members with whom they share copies, but also of any individuals with whom they share copies. Research with Hamilton's theory on people is less well known and remains controversial. This review shows: (1) spouses and close friends assort on blood groups and that similarity predicts fertility; (2) twin and adoption studies find genes rather than upbringing cause people to positively assort; (3) phenotype matching is more pronounced on more heritable items within sets of homogeneous traits; (4) bereavement studies find grief is greater following the death of a more similar co-twin or child; (5) studies of face perception find people prefer and trust those who look like them; and (6) DNA variance within and between ethnic groups is equivalent to that within and between families. 

ADDITIONAL KEYWORDS: behaviour genetics – coalitions – kin selection – mate choice – nepotism – neurobiology.

## INTRODUCTION

Kin-selection theory predicts that animals increase their fitness by allocating more cooperation to kin than to non-kin. Hamilton (1964) showed that altruism (or, conversely, reduced aggression) is favored when $rb - c > 0$, where $r$ is the genetic relatedness between two individuals, $b$ is the (genetic) fitness benefit to the beneficiary, and $c$ is the fitness cost to the altruist. However, to benefit kin over non-kin, altruists must be able to detect genetic relatedness. Mechanisms proposed for this to occur include familiarity, imprinting on self or others, and innate feature detectors that work in the absence of learning.

Studies show that many animal species do recognize kin and act accordingly. In a classic study of the sweat bee, *Lasioglossum zephyrum*, Greenberg (1979) bred for 14 degrees of closeness to a guard bee, which blocks the nest to intruders, and found a strong linear relationship ($r = 0.93$) between passing the guard and degree of relatedness. In a classic study of the frog, *Rana cascade*, Blaustein & O'Hara (1981) separated tadpoles before hatching, reared them in isolation, and found they later spent more time at the sibling's end of the tank. Belding's ground squirrels (*Spermophilus beldingi*) are a promiscuous species that produce litters that contain both full-siblings and half-siblings. Yet Hauber & Sherman (2001) found that, even though they have the same mother, share the same womb, and inhabit the same nest, full-siblings fight less often and come to each other's aid more. Plants too prefer kin. Dudley & File (2007) found that when sea rockets (*Cakile edentula*) share soil with non-relatives they have to grow additional roots to ensure water and mineral nutrients.

Kin recognition is also required for inbreeding avoidance and assortative mating, which occurs in plants, insects, birds, and mammals (Hauber & Sherman, 2001). Even in species that disperse, offspring show aversion to mating with close relatives. Some primates show paternal kin recognition even though identifying paternal kin is more difficult where females mate with several males (Widdig, 2007). An optimal level of outbreeding is shown in studies of zoo animals, where lower fitness accrues to offspring of distantly related individuals, perhaps due to the break-up of co-adapted genes (Edmands, 2007).

*E-mail: rushton@uwo.ca

## GENETIC SIMILARITY IN *HOMO SAPIENS*

The existence of evolved mechanisms for assessing genetic relatedness is less well known and more controversial in humans. When Hamilton (1971) applied his theory to *H. sapiens*, he showed that genetic relatedness, $r$, equated to Wright's (1951) $F_{ST}$ measure of within-group variance (typically $r \sim 2F_{ST}$). Citing an experimental study of a semi-isolated group of mice in which even random mating produced an $F_{ST}$ of 0.18, or $r = 0.31$, Hamilton concluded that the within-group mice should treat 'the average individual encountered as a relative closer than a grandchild (or half sib) but more distant than an offspring (or full sib), referring to an outbred population' (p. 77). He extrapolated the finding to human population groups and deduced that co-operation between 'non-kin' would facilitate the growth of male coalitions and make warfare 'a natural development from the evolutionary trends taking place in the hominid stock' (p. 79). Subsequently, Hamilton (1975) made it explicit that altruism could result from any degree of genetic relatedness. He wrote, 'Because of the way it was first explained, the approach using inclusive fitness has often been identified with 'kin selection' . . . as a way of establishing altruistic behaviour by natural selection. But . . . kinship should be considered just one way of getting positive regression of genotype in the recipient, and that it is this positive regression that is vitally necessary for altruism. Thus the inclusive-fitness concept is more general than 'kin-selection' (pp. 140–141).

Applying Hamilton's theory to human dyads, small groups, and even larger ones, Rushton, Russell & Wells (1984; Rushton, 1989a) dubbed their application 'genetic similarity theory'. They proposed that people maximize their inclusive fitness by marrying others similar to themselves, making friends with and helping the most similar of their neighbours, and engaging in ethnic nepotism. As the English language makes plain, 'likeness goes with liking'. Although kin-selection theory *sensu stricto* does not explain positive assortative mating because individuals seldom mate with 'kin', the literature shows that spouses and close friends are highly similar, most on sociodemographic variables such as age, ethnicity, and educational level ($r = 0.60$), next most on opinions and attitudes ($r = 0.50$), then on cognitive ability ($r = 0.40$), and least, but still significantly, on personality ($r = 0.20$) and physical traits ($r = 0.20$). But, as Thiessen & Gregg (1980) asked, is the assortment due to genetic mediation, to shared upbringing, or to other environmental effects? Does it vary positively or inversely with the heritability of its components?

### Optimal outbreeding and blood group studies

One study found women prefer the bodily scents of men with genes somewhat similar to their own, and not those of men with nearly identical genes or with genes totally dissimilar to their own (Jacob *et al.*, 2002). Each woman's choice was based on the human leukocyte antigen (HLA) (i.e. the basis for personal odors and olfactory preferences) inherited from her father, but not her mother. In a study of 1000 sexually-interacting couples of north European appearance (judged by photographs), those who produced a child together were 52% similar with respect to ten blood groups [ABO, Rhesus (Rh), MNSs, Kell, Duffy (Fy), Kidd (Jk), and HLA], whereas those who did not produce a child were only 43% similar (Rushton, 1988). On the same blood loci and from the same population, pairs of close male friends were significantly more similar to each other than were randomly matched pairs from the same sample (Rushton, 1989b). Such blood group differences are sufficient to identify more than 95% of true relatedness in paternity disputes. A significant positive association between kinship and fertility was found by Helgason *et al.* (2008) in a study of all known couples of the Icelandic population born between 1800 and 1965, with the greatest reproductive success being found in couples related at the level of third and fourth cousins.

### Twin and adoption studies

Twin and adoption studies demonstrate a moderate to strong genetic contribution to people's tendency to socially assort and match phenotypes. Heritabilities can be calculated from the comparison of monozygotic (MZ) twin pairs, who share 100% of their genes, and dizygotic (DZ) twin pairs, who share 50% of their genes. For example, Rowe & Osgood (1984) analysed several hundred adolescent MZ and DZ twins and found those genetically inclined to delinquency were also genetically inclined to seek out similar others as friends. The association between friendship and delinquency was 60% heritable. Iervolino *et al.* (2002) examined several hundred pairs of siblings from adoptive-, step-, and twin-families and found that MZ twins had more similar friends than DZ twins who had more similar friends than step- and adoptive-siblings (i.e. who share only environments). Averaged across measures, the genes accounted for 40% of the variance.

Rushton & Bons (2005) studied several hundred MZ and DZ twin pairs along with their spouses and best friends on questionnaires measuring personality traits and social attitudes. They found: (1) friends and spouses were approximately as similar as siblings ($r = 0.25$), a level of similarity not previously

recognized and (2) MZ twins chose more similar friends and spouses to their co-twin than did DZ twins. The heritability of the preference for similarity in social assortment ranged from 17% to 35% for spouse–spouse, friend–friend, and spouse–friend comparisons and, when corrected for attenuation due to measurement unreliability, 34% for all relationships. Guo (2006) found that with measures made of cognitive ability and personality, friends of MZ twins were significantly more similar to each other ($r = 0.47$) than were the friends of DZ twins ($r = 0.26$) or other full siblings, who in turn were more similar to each other than were random pairs from the same sample ($r = 0.03$). These results indicated a heritability of approximately 50%. In a study of 1800 twins, Kendler *et al.* (2007) found genetic influence on choice of peer-group increased with age, rising from 30% at 8–11 years to 50% at 15–25 years.

### Phenotype matching studies

Hamilton (1971: p. 77) noted that more heritable components within multifarious traits better reflect the underlying genotype. In line with Hamilton's prediction, research finds that social assortment is more pronounced on the more heritable components measured within sets of homogeneous anthropometric, cognitive, and social characteristics. For example, Russell, Wells & Rushton (1985), in a study of married couples, found that, across 36 physical traits, spousal similarity was greater on attributes with higher heritability such as wrist circumference (71% heritable) than on attributes with lower heritability such as neck circumference (48% heritable). On 54 indices of personality and leisure time pursuits, Rushton & Russell (1985) found that spousal similarity was greater on items with higher heritability such as 'enjoying reading' (41% heritable) than on items with lower heritability such as 'having many hobbies' (20% heritable). On 26 cognitive ability tests, Rushton & Nicholson (1988) found that spousal resemblance was greater on the more heritable subtests from the Wechsler Adult Intelligence Scale and the Hawaii Family Study of Cognition. When spouses assort on more heritable items, they report greater marital satisfaction (Russell & Wells, 1991).

In a study of close friends, Rushton (1989b) found similarity was greater on the more heritable items across a wide range of anthropometric and social attitude measures, such as agreement with 'military drill' (40% heritable) and 'church authority' (25% heritable). In an experimental study of liking in acquaintances, Tesser (1993) manipulated people's beliefs about how similar they were to others on attitudes pre-selected as being either high or low in heritability. He found that people liked others more when their similarity had been chosen (by him) on the more heritable items. In a twin study by Rushton & Bons (2005), the phenotype matching for both spouses and close friends was again on the more heritable items.

### Bereavement studies

A study of 263 child bereavements found that: (1) spouses agreed 74% of the time on which side of the family a child 'took after' the most, their own or that of their spouse, and (2) the grief intensity reported by mothers, fathers, and grandparents was greater for children who resembled their side of the family than for children resembling the other side of the family (Littlefield & Rushton, 1986). A study of bereavement in twins found that MZ twins, compared to DZ twins: (1) work harder for their co-twin; (2) show more physical proximity to their co-twin; (3) express more affection to their co-twin; and (4) show greater loss when their co-twin dies (Segal, 2000).

### Studies of face preferences

Several studies have found that people rate faces as more attractive when they resemble their own. Platek *et al.* (2002) morphed people's faces with those of toddlers and asked questions such as 'Which one of these children would you like to spend time with?' and 'Which child would you adopt?' People responded more positively toward children's faces that had been morphed with their own. During debriefing, the participants expressed surprise that any morphing had occurred. DeBruine (2002) found people trusted a stranger's face more when it had been morphed with their own than when it was left unchanged. Familiarity was ruled out by using morphs of celebrities; only self-resemblance mattered.

Bereczkei, Gyuris & Weisfeld (2004) found similarity in the faces of spouses and opposite-sex adoptive parents, a result they attributed to sexual imprinting. DeBruine (2005) found that, although self-similarity of opposite-sex faces increased ratings of trustworthiness, it had no effect on ratings of attractiveness for a long-term partner and a negative effect on attractiveness for a short-term partner. When DeBruine *et al.* (2008) reviewed the literature, she concluded it remained unclear whether self-similarity was important in promoting mate choice, although it undoubtedly influenced trust and positive attributions. Functional magnetic resonance imaging studies are beginning to demonstrate the neural correlates associated with viewing kin and facial self-resemblance (Platek, Krill & Kemp, 2008). The results suggest that the detection of resemblance is occurring below the level of conscious awareness (Platek & Thomson, 2007).

### Ethnic nepotism

The pull of genetic similarity does not stop at family and friends. Malat & Hamilton (2006) found that people prefer same-race health providers and perceive them as more trustworthy. Putnam (2004) found that the more ethnically diverse a community, the less likely its inhabitants are to trust others, from next-door neighbours to local governments.

Inclusive fitness theory has been used to explain why members of ethnic groups move into the same neighbourhoods, join together in clubs and societies, and are prone to develop ethnocentric attitudes toward those who differ in dress, dialect, and other appearance. For example, van den Berghe (1981) found that even relatively open and assimilative groups 'police' their boundaries against invasion by strangers using cultural 'badges' to mark group membership, such as scarification, linguistic accent, and clothing style. Irwin (1987) calculated coefficients of consanguinity within and between Eskimo tribes in the Hudson's Bay region of Canada and found prosocial behaviour such as wife exchange and anti-social behaviour such as the genocidal killing during warfare followed lines of genetic distance, albeit mediated by ethnic badging such as dialect and appearance.

Harpending (1979, 2006) analysed kinship within human populations. Via the equation $r \sim 2\ F_{ST}$, he found that compared to the total world genetic variance, random members of any one population are related $r \sim 0.25$. He wrote, 'Since $F_{ST}$ among human populations on a world scale is reliably 10 to 15 percent, kinship between two individuals of the same population is equivalent to kinship between grandparents and grandchildren or between half siblings' (2006, p. 327). Subsequently, Salter (2006) calculated genetic relatedness between populations using Cavalli-Sforza, Menozzi & Piazza's (1994: 75) compendium of genetic distances and showed that, if the world population were wholly English, then kinship between any two random English people would be (obviously) zero. However, if the world consisted of only English people and Danes, then two random English people (or Danes) with an $F_{ST}$ of 0.0021 would have a kinship of 0.004 and be like 1/32 of a cousin. Two English people become the equivalent of 3/8 cousin by comparison with people from the Near East; 1/2 cousins by comparison with people from India; half-siblings by comparison with people from China; and like full-siblings compared with people from sub-Saharan Africa (where the $F_{ST}$ is 0.23). Because people have many more co-ethnics than relatives, the aggregate of genes shared with co-ethnics dwarfs those shared with extended families. Rather than being a poor relation of family nepotism, ethnic nepotism is virtually a proxy for it.

## CONCLUSION

Hamilton (1996) autobiographically remarked that he 'did not anticipate the degree of relevance to humans that the findings eventually proved to have' (p. 3). In retrospect, it is not surprising that people are able to detect and prefer those who resemble themselves. Similarity, whether actual or perceived, is one of the most important factors in human relationships. It is more surprising to find just how fine-tuned the recognition process can be. The studies reviewed above show that the preference for similarity occurs within ethnic groups and within families and on the more heritable items from within sets of related traits.

## REFERENCES

**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:** 1129–1134.

**van den Berghe PL. 1981.** *The ethnic phenomenon*. New York, NY: Elsevier.

**Blaustein AR, O'Hara RK. 1981.** Genetic control for sibling recognition? *Nature* **290:** 246–248.

**Cavalli-Sforza LL, Menozzi P, Piazza A. 1994.** *The History and Geography of Human Genes*. Princeton, NJ: Princeton University.

**DeBruine LM. 2002.** Facial resemblance enhances trust. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **269:** 1307–1312.

**DeBruine LM. 2005.** Trustworthy but not lust-worthy: context specific effects of facial resemblance. *Proceedings of the Royal Society of London Series B, Biological Sciences* **272:** 919–922.

**DeBruine LM, Jones BC, Little AC, Perrett DI. 2008.** Social perception of facial resemblance in humans. *Archives of Sexual Behavior* **37:** 64–77.

**Dudley SA, File AL. 2007.** Kin recognition in an annual plant. *Biology Letters* **3:** 435–438.

**Edmands S. 2007.** Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. *Molecular Ecology* **16:** 463–475.

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

**Guo G. 2006.** Genetic similarity shared by best friends among adolescents. *Twin Research and Human Genetics* **9:** 113–121.

**Hamilton WD. 1964.** The genetical evolution of social behavior. I and II. *Journal of Theoretical Biology* **7:** 1–52.

**Hamilton WD. 1971.** Selection of selfish and altruistic behavior in some extreme models. In: Eisenberg JF, Dillon WS, eds. *Man and beast: comparative social behavior*. Washington, DC: Smithsonian Press, 57–91.

**Hamilton WD. 1975.** Innate social aptitudes of man: an approach from evolutionary genetics. In: Fox R, ed. *Biosocial anthropology*. London: Malaby Press, 133–155.

**Hamilton WD. 1996.** Shoulders of giants: the evolution of

altruistic behaviour. In: Hamilton WD, ed. *Narrow roads of gene land: the collected papers of W. D. Hamilton, Volume 1, Evolution of social behavior*. Oxford: WH Freeman, 1–8.

**Harpending H. 1979.** The population genetics of interactions. *American Naturalist* **113:** 622–630.

**Harpending H. 2006.** Kinship and population subdivision. In: Salter F, *On genetic interests: family, ethnicity and humanity in an age of mass migration (Appendix 1)*. New Brunswick, NJ: Transaction, 327–333.

**Hauber ME, Sherman PW. 2001.** Self-referent phenotype matching: theoretical considerations and empirical evidence. *Trends in Neurosciences* **24:** 609–616.

**Helgason A, Pálsson S, Guöbjartsson DF, Kristjánsson P, Stefánsson K. 2008.** An association between the kinship and fertility of human couples. *Science* **319:** 813–816.

**Iervolino AC, Pike A, Manke B, Reiss D, Hetherington EM, Plomin R. 2002.** Genetic and environmental influences in adolescent peer socialization: evidence from two genetically sensitive designs. *Child Development* **73:** 162–174.

**Irwin CJ. 1987.** A study in the evolution of ethnocentrism. In: Reynolds V, Falger VSE, Vine I, eds. *The sociobiology of ethnocentrism: evolutionary dimensions of xenophobia, discrimination, racism, and nationalism*. London: Croom Helm, 131–156.

**Jacob S, McClintock MK, Zelano B, Ober C. 2002.** Paternally inherited HLA alleles are associated with women's choice of male odor. *Nature Genetics* **30:** 175–179.

**Kendler KS, Jacobson KC, Gardner CO, Gillespie N, Aggen SA, Prescott CA. 2007.** Creating a social world: a developmental twin study of peer-group deviance. *Archives of General Psychiatry* **64:** 958–965.

**Littlefield CH, Rushton JP. 1986.** When a child dies: the sociobiology of bereavement. *Journal of Personality and Social Psychology* **51:** 797–802.

**Malat J, Hamilton MA. 2006.** Preference for same-race health care providers and perceptions of interpersonal discrimination in health care. *Journal of Health and Social Behavior* **47:** 173–188.

**Platek SM, Burch RL, Panyavin IS, Wasserman BH, Gallop GG. Jr. 2002.** Reactions towards children's faces: resemblance matters more for males than females. *Evolution and Human Behavior* **23:** 159–166.

**Platek SM, Krill AL, Kemp SM. 2008.** The neural basis of facial resemblance. *Neuroscience Letters* **437:** 76–81.

**Platek SM, Thomson JW. 2007.** Neural correlates of facial resemblance. In: Platek SM, Keenan JP, Shackelford TK, eds. *Evolutionary cognitive neuroscience*. Cambridge, MA: MIT Press, 221–243..

**Putnam RD**. (ed) **2004.** *Democracies in flux: the evolution of social capital in contemporary society*. Oxford: Oxford University Press.

**Rowe DC, Osgood DW. 1984.** Heredity and sociological theories of delinquency: a reconsideration. *American Sociological Review* **49:** 526–540.

**Rushton JP. 1988.** Genetic similarity, mate choice, and fecundity in humans. *Ethology and Sociobiology* **9:** 329–333.

**Rushton JP. 1989a.** Genetic similarity, human altruism, and group selection. *Behavioral and Brain Sciences* **12:** 503–559.

**Rushton JP. 1989b.** Genetic similarity in male friendships. *Ethology and Sociobiology* **10:** 361–373.

**Rushton JP, Bons TA. 2005.** Mate choice and friendship in twins: evidence for genetic similarity. *Psychological Science* **16:** 555–559.

**Rushton JP, Nicholson IR. 1988.** Genetic similarity theory, intelligence, and human mate choice. *Ethology and Sociobiology* **9:** 45–57.

**Rushton JP, Russell RJH. 1985.** Genetic similarity theory: a reply to Mealey and new evidence. *Behavior Genetics* **15:** 575–582.

**Rushton JP, Russell RJH, Wells PA. 1984.** Genetic similarity theory: beyond kin selection. *Behavior Genetics* **14:** 179–193.

**Russell RJH, Wells PA. 1991.** Personality similarity and quality of marriage. *Personality and Individual Differences* **12:** 406–412.

**Russell RJH, Wells PA, Rushton JP. 1985.** Evidence for genetic similarity detection in human marriage. *Ethology and Sociobiology* **6:** 183–187.

**Salter F. 2006.** *On genetic interests: family, ethny and humanity in an age of mass migration*. New Brunswick, NJ: Transaction.

**Segal NL. 2000.** *Entwined lives: twins and what they tell us about human behavior*. New York, NY: Plume.

**Tesser A. 1993.** The importance of heritability in psychological research: the case of attitudes. *Psychological Review* **93:** 129–142.

**Thiessen D, Gregg B. 1980.** Human assortative mating and genetic equilibrium: an evolutionary perspective. *Ethology and Sociobiology* **1:** 111–140.

**Widdig A. 2007.** Paternal kin discrimination: the evidence and likely mechanisms. *Biological Reviews* **82:** 319–334.

**Wright S. 1951.** The genetical structure of population. *Annals of Eugenics* **15:** 323–354.