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CHAPTER SEVENTEEN

**GENETIC SIMILARITY THEORY,
ETHNOCENTRISM, AND GROUP
SELECTION**

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Introduction

Genetic similarity theory, an extension of the kin-selection theory of altruism, postulates that people detect genetic similarity in others ("nonkin" as well as "kin") in order to provide mutually supportive environments, such as marriage, friendship, and social groups. In line with prediction, studies using blood antigens and heritabilities reveal that sexually interacting couples and same-sex friendships are based partly on genetic similarity (Rushton 1989a; 1995). As such, a new theory of attraction and friendship is constituted, and the conditions for the evolution of human altruism are enhanced. Genetically biased preferences are not limited to social partners but extend to adopting other cultural practices maximally compatible with genotypes. Ethnocentrism and patriotism may be fitness-enhancing mechanisms that enable group selection to occur.

Choosing social partners is among the most important decisions individuals make affecting their social environment. The tendency is to choose similarity. For example, spouses tend to resemble each other in such characteristics as age, ethnic back-

ground, socioeconomic status, physical attractiveness, religion, social attitudes, level of education, family size and structure, intelligence, and personality. The median assortative mating coefficient for standardized intelligence tests averages about 0.35. Correlations tend to be higher for opinions, attitudes, and values (0.40 to 0.70) and lower for personality traits, personal habits, and physical features (0.02 to 0.30).

Most explanations of the role of similarity in human relationships focus on immediate, environmental effects, for example, their reinforcement value. Recent analyses, however, suggest that genetic influences may also be involved. According to "genetic similarity theory," genetic likeness exerts subtle effects on a variety of relationships and has implications for the study of social behavior in small groups and even in large ones, both national and international. The main purpose of genetic similarity-seeking is to enhance altruism.

The Paradox of Altruism

As recognized by Darwin (1871), altruism represents a paradox for theories of evolution: How could altruism evolve through "survival of the fittest" when, on the face of it, altruistic behavior diminishes personal fitness? If the most altruistic members of a group sacrifice themselves for others, they run the risk of leaving fewer offspring to pass on the very genes that govern the altruistic behavior. Hence, altruism would be selected against, and selfishness would be selected for.

The resolution of the paradox of altruism is one of the triumphs that led to the new synthesis called sociobiology. By a process known as kin selection, individuals can optimize their inclusive fitness rather than only their individual fitness by increasing the production of successful offspring by both themselves and their genetic relatives (Hamilton 1964). According to this view, the unit of analysis for evolutionary selection is not the individual organism but its genes. Genes are what survive and are passed on, and some of the same genes will be found not only in direct offspring but in siblings, cousins, and nephews and nieces, as well as more distant kin. If an animal sacrifices its life for its siblings' offspring, it ensures the survival of common genes because, by common descent, it shares 50 percent of its distinct genes with each sibling and 25 percent with each sibling's offspring.

From an evolutionary perspective, altruism is a means of helping genes to propagate. By being most altruistic to those with whom we share genes, we help copies of our own genes to replicate. This makes "altruism" ultimately "selfish" in purpose. Promulgated in the context of animal behavior, this idea became known as "kin selection" and provided a conceptual breakthrough by redefining the unit of analysis away from the individual organism to his or her genes, for it is these that survive and are passed on. Another way sociobiologists have suggested that altruism could evolve is through reciprocity. Here there is no need for genetic relatedness; performing an altruistic act need only lead to an altruistic act in return.

Detecting Genetic Similarity

In order to pursue a strategy of directing altruism toward kin, the organism must be able to recognize degrees of relatedness. There is clearly no such thing as "genetic extrasensory perception." For individuals to direct altruism selectively to genetically similar individuals, they must respond to phenotypic cues. This is typically accomplished by detecting similarities between self and others in physical and behavioral cues. Four processes have been suggested by which animals recognize relatives: (1) innate feature detectors, (2) matching on appearance, (3) familiarity, and (4) location. They are not mutually exclusive. If there are evolutionary advantages to be gained from the ability to detect genetic similarity, all the mechanisms may be operative.

Innate feature detectors. Individuals may have "recognition alleles" that control the development of innate mechanisms allowing them to detect genetic similarity in strangers. Dawkins (1976) suggested a thought experiment to illustrate how this could come about, known as the "green beard effect." In this, a gene has two effects: it causes individuals who have it (1) to grow a green beard and (2) to behave altruistically toward green-bearded individuals. The green beard serves as a recognition cue for the altruism gene. Altruism could therefore occur without the need for individuals to be directly related.

Matching on appearance. The individual may be genetically guided to learn its own phenotype, or those of its close kin, and then to match new, unfamiliar individuals to the template it has

learned—for example, Dawkins' (1982) "armpit effect." Individuals that smell (or look or behave) like oneself or one's close kin could be distinguished from those that smell (or look or behave) differently. This mechanism would depend on the existence of a strong correlation between genotype and phenotype.

Familiarity or association. Preferences may also depend on learning through social interaction. This may be the most common means of kin recognition in nature. Individuals that are reared together are more likely to be kin than nonkin.

Location. The fourth kin recognition mechanism depends on a high correlation between an individual's location and kinship. The rule states: "If it's in your nest, it's yours." Where an individual is and whom the individual encounters can also be based on similar genes, for example, if parents exert discriminatory influence on where and with whom their offspring interact.

Kin Recognition in Animals

There is dramatic experimental evidence that many animal species recognize genetic similarity. For example, bees block the nest to prevent intruders from entering. In one study, bees bred for 14 different degrees of genealogical relationship were introduced near nests (Greenberg 1979). There was a strong linear relationship ($r=0.93$) between the ability to pass the guard bee and the degree of genetic relatedness.

Mammals are also able to detect degrees of genetic relatedness (reviewed in Fletcher and Michener 1987). For example, squirrels produce litters that contain both sisters and half-sisters. Despite the fact that they shared the same womb and inhabit the same nest, full sisters fight less often than half-sisters, come to each other's aid more, and are less prone to chase one another out of their home territory. Recent experiments with squirrels demonstrate how rearing (together or apart) and relatedness (littermates or non-littermates) affect juveniles' social interactions. Play-bout frequencies were ordered (high to low): littermates reared together > non-littermates reared together > littermates reared apart > non-littermates reared apart. Statistical analysis revealed that both rearing and relatedness contributed to this ordering (Holmes 1995).

Similarity Recognition in Humans

In earlier papers, my colleagues and I extended the kin-selection theory of altruism to the human case by proposing that, if a gene can ensure its own survival by acting so as to bring about the reproduction of family members with whom it shares copies, then it can do so by benefiting any organism in which copies of itself are to be found (Rushton, Russell and Wells 1984; Rushton 1989a). Rather than merely protecting kin at the expense of strangers, organisms might identify genetically similar others so as to exhibit altruism toward these "strangers" as well as toward "kin." Kin recognition would be just one form of genetic similarity detection.

Humans are capable of learning to distinguish kin from nonkin at an early age. Infants can distinguish their mothers from other women by voice alone at 24 hours of age, know the smell of their mother's breast before they are 6 days of age, and recognize a photograph of their mother when they are 2 weeks old. Mothers are also able to identify their infants by smell alone after a single exposure at 6 hours of age, and to recognize their infant's cry within 48 hours of birth.

Human kin preferences follow lines of genetic similarity. For example, among the Ye'Kwana Indians of South America, the words "brother" and "sister" cover four different categories ranging from individuals who share 50 percent of their distinctive genes (identical by descent) to individuals who share only 12.5 percent of their genes. Hames (1979) has shown that the amount of time the Ye'Kwana spend interacting with their biological relatives increases with their degree of relatedness, even though their kinship terminology does not reflect this correspondence.

Anthropological data also show that in societies where certainty of paternity is relatively low, males direct material resources to their sisters' offspring (to whom their relatedness is certain) rather than to their wives' offspring (Kurland 1979). Paternity uncertainty exerts other predictable consequences. Grandparents spend 35 to 42 percent more time with their daughters' children than with their sons' children (Smith 1981). Following bereavement, grandparents grieve more for their daughters' children than for their sons' children (Littlefield and Rushton 1986). Family members feel only 87 percent as close to the fathers' side of the family as they do to the mothers' side (Russell and Wells 1987). Finally, mothers of newborn children and her relatives spend more time commenting on resemblances between the baby and

the putative father than they do about the resemblance between the baby and the mother (Daly and Wilson 1982).

When the level of genetic similarity within a family is low, the consequences can be serious. Children who are unrelated to a parent are at risk: a disproportionate number of battered babies are stepchildren. Children of preschool age are 40 times more likely to be assaulted if they are stepchildren than if they are biological children (Daly and Wilson 1988). Unrelated people living together are more likely to kill each other than are related people living together. Converging evidence shows that adoptions are more likely to be successful when the parents perceive the child as similar to them.

Mate Choice

A well-known phenomenon that is readily explained by genetic similarity theory is positive assortative mating, that is, the tendency of spouses to be nonrandomly paired in the direction of resembling each other (described in the introduction). This tendency even extends to socially undesirable characteristics, including aggressiveness, criminality, alcoholism, and psychiatric disorders such as schizophrenia and the affective disorders. Although alternative reasons can be proposed for this finding, such as unsuccessful competition for the most attractive and healthiest mates, it does suggest that the tendency to seek a similar partner may override considerations such as mate quality and individual fitness.

A study of cross-racial marriages in Hawaii found more similarity in personality test scores among males and females who married across ethnic groups than among those marrying within them (Ahern, Cole, Johnson, and Wong 1981). The researchers posit that, given the general tendency toward homogamy, couples marrying heterogamously with respect to ethnicity tend to "make up" for this dissimilarity by choosing spouses more similar to themselves in other respects than do persons marrying within their own ethnic group.

Assortative mating is found in taxa ranging from insects to birds to primates, and it can be observed in the laboratory as well as in nature (Fletcher and Michener 1987). Assortative mating also occurs in plants (Willson and Burley 1983). To have evolved independently in such a wide variety of species, assortative mating

must confer substantial advantage. Advantages thought to accrue in human mates include (1) increased marital stability, (2) increased relatedness to offspring, (3) increased within-family altruism and (4) greater fecundity.

The upper limit on the fitness-enhancing effect of assortative mating for similarity occurs with incest. Too much genetic similarity between mates increases the chances that harmful recessive genes may combine. The negative effects of "inbreeding depression" have been demonstrated in many species, including humans. As a result, the "incest taboo" has been hypothesized to have an evolutionary basis, possibly mediated through negative imprinting on intimate associates at an early age (van den Berghe 1983). Optimal fitness, then, may consist in selecting a mate who is genetically similar but not actually a relative. Van den Berghe (1983) speculates that the ideal percentage of relatedness is 12.5 percent identical by descent, or the same as that between first cousins.

Other animal species also avoid inbreeding. For example, several experiments have been carried out with Japanese quail, birds that, although promiscuous, proved particularly sophisticated. They preferred first cousins to third cousins, and both of these relatives to either unrelated birds or siblings, thus avoiding the dangers of too much or too little inbreeding (Bateson 1983).

I tested the hypothesis that human mating followed lines of genetic similarity by examining blood antigen analyses from nearly 1,000 cases of disputed paternity (Rushton 1988). Seven polymorphic marker systems (ABO, Rhesus (Rh), MNSs, Kell, Duffy (Fy), Kidd (Jk), and HLA) at 10 loci across six chromosomes were examined in a sample limited to people of North European appearance (judged by photographs kept for legal identifications). These blood groups are sufficient to correctly identify more than 95 percent of cases in paternity disputes. They also reliably distinguish between fraternal twins. My results showed that genetic similarity within pairs related to (1) whether the pair was sexually interacting or randomly generated from the same sample, and (2) whether the pair produced a child. Sexually interacting couples shared about 50 percent of measured genetic markers, part way between mothers and their offspring, who shared 73 percent, and randomly paired individuals from the same sample, who shared 43 percent. Couples who produced a child together were 52 percent similar on this metric, whereas those who did not were only 44 percent similar ($p < 0.05$).

In other tests of the genetic similarity theory of assortative mating, studies show that mate choice is greater on the more heritable of a set of homogeneous items. This prediction follows from the theory because more heritable items better reflect the underlying genotype. Examples of differing heritabilities used to establish the theory include: for physical characters, 80 percent for mid-finger length versus 50 percent for upper arm circumference; for intelligence, 80 percent for the general factor versus less than 50 percent for specific abilities; for personality, 41 percent for having a preference for reading versus 20 percent for having many different hobbies; and for attitudes, 51 percent for agreement with the death penalty versus 25 percent for agreement with Bible truth. Thus, Russell, Wells, and Rushton (1985) found spouses were more similar on the more heritable of 36 anthropometric variables, 5 perceptual judgment variables, and 11 personality variables. Rushton and Russell (1985) found heritabilities predicted similarity between spouses for 54 personality traits, 15 cognitive tests, and 13 anthropometric variables. Rushton and Nicholson (1988) found that spouses were most similar on the more heritable of 15 IQ subtests from the Hawaii Family Study of Cognition and 11 subtests from the Wechsler Adult Intelligence Scale.

Intrafamilial Relationships

One consequence of genetic similarity between spouses is an increase of within-family altruism. Several studies have shown that not only the occurrence of relationships but also their degree of happiness and stability can be predicted by the degree of matching on personal attributes (reviewed in Rushton 1989a).

A related prediction can be made about parental care of offspring that differ in similarity. Sibling differences within families have often been overlooked as a topic of research. Positive assortative mating makes some children genetically more similar to one parent or sibling than to another. For example, if a father gives his child 50 percent of his genes, 10 percent of which he shares with the mother because of parental similarity, and the mother gives the child 50 percent of her genes, 20 percent of which she shares with the father because of parental similarity, then the child will be 60 percent similar to the mother and 70 percent similar to the father.

Genetic similarity theory predicts that parents and siblings will tend to favor those who are most similar. Littlefield and Rushton (1986) tested this hypothesis in a study of bereavement following the death of a child. Respondents picked which side of the family the child "took after" more, their own or their spouse's. Spouses agreed with each other 74 percent of the time on this question. Both mothers and fathers grieved more intensely for children perceived as resembling their side of the family.

Other evidence of within-family preferences comes from a review by Segal (1988) of feelings of closeness, cooperation, and altruism in twin pairs. Compared with fraternal twins, identical twins worked harder for their co-twins on tasks, maintained greater physical proximity, expressed more affection, and suffered greater loss following bereavement. Subsequently, Segal, Wilson, Bouchard, and Gitlin (1995) found that degree of genetic relatedness predicted degree of bereavement and that the loss of a co-twin resulted in the same level of grief as the loss of a child or a spouse.

A Genetic Basis for Friendship

Friendships also form on the basis of similarity, whether as perceived by the friends or for a variety of objectively measured characteristics, including activities, attitudes, needs, personality, and anthropometric variables. Moreover, in the experimental literature on who likes whom and why, one of the most influential variables is perceived similarity. Apparent similarity of personality, attitudes, or any of a wide range of beliefs has been found to generate liking in subjects of varying ages and from many different cultures.

The tendency to choose similar others as friends is genetically influenced. In a study of delinquency among 530 adolescent twins by Rowe and Osgood (1984), path analysis revealed not only that antisocial behavior was about 50 percent heritable, but that the correlation of 0.56 between the delinquency of an individual and the delinquency of his friends was mediated genetically. Adolescents genetically disposed to delinquency were genetically inclined to seek each other out for friendship. In a study of 396 adolescent and young adult siblings from both adoptive and non-adoptive homes, Daniels and Plomin (1985) found that genetic influences were implicated in choice of friends: biological siblings

were more similar to each other in the types of friends they had than were adoptive siblings.

In a study to examine similarity among male friendship pairs, I used the same blood markers and differential heritabilities as in my study of sexual partners. The best friends were 54 percent similar to each other using 10 loci from 7 polymorphic blood systems (ABO, Rhesus (Rh), MNSs, P, Duffy (Fy), Kidd (Jk), and HLA). An equal number of randomly chosen pairs from the same overall sample were significantly less similar. Stratification effects were unlikely because within-pair differences in age, education, and occupation did not correlate with the blood similarity scores. Similarity between friends was strongest on the more heritable of 36 conservatism items and 81 personality items.

Independent corroboration that attitudes with high heritability are stronger than those with low heritability has come from a series of studies by Tesser (1993). Each subject responded "Agree" or "Disagree" to attitudes with known heritabilities. Attitudes higher in heritability were responded to more quickly, were more resistant to change when attempts were made at social influence, and were more predictive of liking of others who shared similar attitudes. For example, similarity on more heritable attitudes correlated higher with attraction to a stranger imagined as a potential friend, a romantic partner, and a spouse than did similarity on less heritable items.

Epigenetic Rules in Social Development

Both the evolutionary and social sciences err in not making more explicit that social learning is dependent upon the innate capacities and biases of the learner. For example, most models of cultural transmission within the family (i.e., vertical, from parent to child, and horizontal, from sibling to sibling) imply that siblings will resemble each other, over and above shared genes, as a result of a common family environment. An epigenetic model, in contrast, in which genes incline individuals to acquire patterns of behavior best fitting their particular genotype, leads to the expectation that siblings will differ from each other. While it may seem intuitively correct to assume that common family environment shapes individual development, consideration of data reveals quite a different set of relationships.

Social development is guided by epigenetic rules that incline individuals to particular learning experiences. As in the studies of friendship formation among delinquents described in the last section, behavior genetic designs provide powerful tests of alternative hypotheses about the genetic and social influences on family resemblances. Comparing 573 pairs of adult monozygotic and dizygotic twins who had been reared together, Rushton, Fulker, Neale, Nias, and Eysenck (1986) examined the cultural and genetic inheritance of individual differences in altruism and aggression. We found not only a strong association of genetic factors with the characteristics in question but also a negligible influence of the twins' shared environment. Rather, the distinct experiences of the individual accounted for almost all the environmental influence.

The discovery that common family environment plays a very limited role in social development (even for traits that parents are expected to indoctrinate, such as altruism) runs counter to prevailing theories of personality development that assume that the important environmental variance is between families, not within. Yet the observation that the environmental factors that influence development are those that are specific to each sibling, rather than common, is robust, having been replicated using other research designs (like adoption studies) and other social characteristics. Regardless of whether one considers the transmission of socially undesirable traits, such as crime, obesity, and schizophrenia, or more normative personality characteristics, such as vocational interests and value systems, the evidence reveals that whereas genetic influences have an important role to play, the common family environment alone has little apparent effect.

A compelling test of models of transmission has been made in the context of social attitudes. Since attitudes are more flexible than personality, purely cultural models of transmission might be considered especially likely, with at least some vertical transmission occurring from parent to child. Yet in one compilation of results, Eaves, Eysenck, and Martin (1989) showed that social scientists have typically misconceived the role of cultural inheritance in attitude formation. Individuals acquire little from their social environment that is incompatible with their genotype.

So far the discussion has been limited to individual social development. However, the potential of epigenetic rules to bias behavior and affect society goes well beyond ontogeny. Via cognitive phenotypes and group action, altruistic inclinations may be amplified into charities and hospitals, creative and educative dis-

positions into academies of learning, and martial tempers into institutes of war. Such macrocultural innovations can be expected to influence the genetic composition of future generations.

Ethnocentrism

The implications of the finding that people moderate their behavior as a function of genetic similarity and epigenetic biases are far-reaching. They suggest a biological basis for ethnocentrism. Despite enormous variance within populations, it can be expected that two individuals within an ethnic group will, on average, be more similar to each other genetically than two individuals from different ethnic groups. According to genetic similarity theory, people can be expected to favor their own group over others.

Ethnic conflict and rivalry, of course, is one of the great themes of historical and contemporary society. Local ethnic favoritism is also displayed by group members who prefer to congregate in the same area and to associate with each other in clubs and organizations. Understanding modern Africa, for example, is impossible without understanding tribalism there. Many studies have found that people are more likely to help members of their own race or country than they are to help members of other races or foreigners, and that antagonism between classes and nations may be greater when a racial element is involved.

Traditionally, political scientists and historians have seldom considered intergroup conflict from an evolutionary standpoint. That fear and mistrust of strangers may have biological origins, however, is supported by evidence that animals often show fear of and hostility toward strangers, even when no injury has ever been received. Analogies may be drawn between the way monkeys and apes repel intruding strangers of the same species and the way children attack another child who is perceived as being an outsider.

Many of those who have considered nationalist and patriotic sentiment from a sociobiological perspective, however, have emphasized its apparent irrationality. Johnson (1986) formulated a theory of patriotism in which indoctrination through socialization and conditioning engage kin-recognition systems so that people behave altruistically toward in-group members as though they were genetically more similar than they actually are. In Johnson's analysis, for example, patriotism may often be an ideology indoc-

trinated by the ruling class to induce the ruled to behave contrary to their own genetic interests, while increasing the fitness of the elite. He noted that patriotism is built by referring to the homeland as the "motherland" or "fatherland," and that bonds between people are strengthened by referring to them as "brothers" and "sisters."

According to genetic similarity theory, patriotism is more than just "indoctrinated" altruism working to the individual's genetic detriment. It is a strategy by which genes typically replicate copies of themselves more effectively. The developmental processes that Johnson (1986) and others have outlined undoubtedly occur, as do other forms of manipulated altruism. However, if these were sufficient to explain the human propensity to feel strong moral obligation toward society, patriotism would remain an anomaly for evolutionary biology. From the standpoint of optimization, one might ask whether ethical systems would survive very long if they consistently led to reductions in the inclusive fitness of those believing in them.

If epigenetic rules do incline people toward constructing and learning ideologies which increase their fitness, then patriotic nationalism, religious zealotry, class conflict, and other forms of ideological commitment can be seen as genetically influenced cultural choices that individuals make that, in turn, influence the replication of their genes. Religious, political, and other ideological battles may become as heated as they do partly because of implications for fitness; some genotypes may thrive more in one ideological culture than in another. According to this view, Karl Marx did not take the argument far enough: ideology serves more than economic interest; it also serves genetic fitness.

Two sets of falsifiable propositions follow from this interpretation. First, individual differences in ideological preference are partly heritable. Second, ideological belief increases genetic fitness. There is evidence to support both propositions. With respect to the heritability of differences in ideological preference, it has generally been assumed that political attitudes are mostly determined by the environment; however, as mentioned, both twin and adoption studies reveal significant heritabilities for social and political attitudes as well as for stylistic tendencies (Eaves, Eysenck, and Martin 1989). Of course, no behavioral geneticist believes that genes are 100 percent responsible for complex social behavior. The battle is between those who believe 100 percent in

environmental determinism and those who think that both genes and environments affect behavior.

Examples of ideologies that increase genetic fitness include religious beliefs that regulate dietary habits, sexual practices, marital customs, infant care, and childrearing (Reynolds and Tanner 1983). Amerindian tribes that believed it important to cook maize with alkali had higher population densities and more complex social organizations than tribes that did not, partly because cooking with alkali releases the most nutritious parts of the cereal, enabling more people to grow to reproductive maturity (Katz, Hodiger, and Valleroy 1974). The Amerindians did not know the biochemical reasons for the benefits of alkali cooking, but their cultural beliefs had evolved for good reason, enabling them to replicate their genes more effectively than would otherwise have been the case.

By the way of objection, it could be argued that although some religious ideologies confer direct benefits on the extended family, ideologies like patriotism decrease fitness (hence, most analyses of patriotism rest on indoctrination and social manipulation). Genetic similarity theory may provide a firmer basis for an evolutionary understanding of patriotism, for benefited genes do not have to be only those residing in kin. Members of ethnic groups, for example, often share the same ideologies, and many political differences are genetic in origin. One possible test of genetic similarity theory in this context is to calculate degrees of genetic similarity among ideologues in order to examine whether ideological "conservatives" are more homogeneous than the same ideology's "liberals." Preserving the "purity" of an ideology might be an attempt to preserve the "purity" of the gene pool.

Because ethnic conflict has defied explanation by the standard social science disciplines, genetic similarity theory may represent an advance in understanding. Eibl-Eibesfeldt (1989b) agreed with me that if attraction toward similarity has a genetic component then it provides a basis for xenophobia as an innate trait in human beings. He reiterated that ethnocentrism is a phenomenon manifested in all cultures so far studied and presented his view that generalized altruism began with maternal caretaking, a turning point in the evolution of vertebrate social behavior, which up to that time had been based on dominance and submission. The mother-child bond established the possibility of gradients in familiarity-trust/strangeness-suspicion.

Van den Berghe (1989) also endorsed the genetic similarity perspective, stating that ethnicity had a "primordial dimension." In his 1981 book, *The Ethnic Phenomenon*, he had suggested that ethnocentrism was a case of extended nepotism, with even relatively open and assimilative ethnic groups policing their ethnic boundaries against invasion by strangers by using badges as markers of group membership. These were likely to be cultural rather than physical, he argued, such as linguistic accent or clothing style. Now, it seemed to him (van den Berghe 1989), identifying fellow ethnics using shared traits of high heritability provided a more reliable method than cultural, flexible ones, although these other membership badges could also be used.

Adopting a gene-based evolutionary perspective for ethnic conflict may prove illuminating, especially in the light of the conspicuous failures of environmentalist theories. With the breakup of the Soviet bloc, many Western analysts have been surprised at the outbreak of the fierce ethnic antagonisms long thought over. Lynn (1989, 534) put it directly:

Racial and ethnic conflict is occurring throughout the world—between Blacks and Whites in the United States, South Africa, and Britain; Basques and Spaniards in Spain; and Irish and British in Northern Ireland. These conflicts have defied explanations by the disciplines of sociology, psychology, and economics ... genetic similarity theory represents a major advance in the understanding of these conflicts.

Lynn (1989) raised the question of why people remain as irrationally attached as they do to languages, even almost dead ones such as Gaelic and Welsh. One function of language barriers, he suggested, was to promote inbreeding among fellow ethnics. The close mapping recently found to occur between linguistic and genetic trees is compatible with Lynn's hypothesis. Cavalli-Sforza, Menozzi, and Piazza (1994) combined 120 allele frequencies from 42 populations into a phylogenetic tree based on genetic distances and related it to a taxonomy of 17 linguistic phyla. Despite the apparent volatility of language and its capacity to be imposed by conquerors at will, considerable parallelism between genetic and linguistic evolution was found.

The theoretical stance taken so far predicts that the ease of producing patriotic sentiment and internal harmony varies with the genetic homogeneity of the national group. As van den Berghe (1981, 27) put it: "Ethnicity can be manipulated but not manufactured." Since ethnic aspirations are rarely justified in terms of

naked genetic self-interest, any analysis will necessarily have to be conducted at a deeper level than surface ideology. Political interests are typically couched in the highest of ethical terms, no matter how utilitarian, transparent, or heinous these appear to opponents.

Genetic similarity is only one of many possible influences operating on political alliances. Obviously, causation is complex, and it is not intended to reduce relationships between ethnic groups to a single cause. Fellow ethnics will not always stick together, nor is conflict inevitable between groups any more than it is between genetically distinct individuals. As indicated, people can be manipulated into working for "other groups." People also work for other motives, such as economic success as well as reproductive success. However, as van den Berghe (1981) pointed out, from an evolutionary perspective, the ultimate measure of human success is not production, but reproduction.

While cultural evolution and organic evolution are undoubtedly different, they are linked reciprocally in complicated ways and seem to share certain properties. Both appear to "strive" to replicate their units, if necessary at the expense of the other system's units (alleles in the case of organic evolution; "memes" or "culturgens" in the case of cultural evolution). Their seat of battle is the individual human mind, which only dimly perceives the consequences of its choices, based as they are on many competing elements. Thus, ideologies can arise which have the paradoxical effect of dramatically decreasing fitness. A classic example of such a lethal culturgen is found among the Shakers, a religious sect which considers sex to be so sinful that it imposes celibacy upon even its married members. This ideology has nonetheless been quite successful in replicating itself through several generations, new adherents being recruited, largely via adoptions. The members' genes, of course, fail to replicate.

Selection of Groups

Humans have obviously been selected to live in groups. Typically, they hold a territory in common that they fill with symbols of their group and that they are willing to defend (Eibl-Eibesfeldt 1989a). The line of argument presented so far may have implications for determining whether group selection occurs among humans. Although the idea of group selection, defined as "selection that

operates on two or more members of a lineage group as a unit" (E. O. Wilson 1975, 585) was popular with Darwin, Spencer, and others, in recent decades it has often been thought not to play a major role in evolution. Hamilton's (1964) theory of inclusive fitness, for example, has been typically regarded as an extension of individual selection, not group selection (Dawkins 1976; 1982).

Group selection was brought to center stage by Wynne-Edwards (1962) in the context of altruism. He suggested that whole groups of animals collectively refrained from overbreeding when the density of population became too great, even to the point of killing their offspring. Such self-restraint, he argued, protected the animals' resource base and gave them an advantage over groups that did not practice restraint and became extinct as a result of their profligacy. This extreme form of the group selection claim was immediately disputed, and a great deal of argument and data was marshaled against the idea (Williams 1966). There did not seem to exist a mechanism (other than favoring kin) by which altruistic individuals could leave more genes than selfish individuals who cheated.

A compromise was offered by E. O. Wilson (1975), who suggested that although genes are the units of replication, their selection could take place through competition at both the individual and the group levels; for some purposes these can be viewed as opposite ends of a continuum of nested, ever enlarging sets of socially interacting individuals. Kin selection is thus seen as intermediate between individual and group selection. Group selection may have been prematurely rejected due to a failure to see that with genes as "replicators," it is irrelevant whether it is individuals, social groups, or still higher-level entities that are the "vehicles" of selection (for an extended discussion see D. S. Wilson and Sober 1994).

Among humans, genetic similarity theory makes group selection especially likely because altruism is conferred beyond immediate kin. Through language, law, religious imagery, and patriotic nationalism, all replete with kin terminology, ideological commitment extends altruistic behavior enormously. Groups made up of people genetically disposed toward honesty, trust, temperance, willingness to share, loyalty, and self-sacrifice will have a distinct genetic advantage over groups that do not have this makeup. In addition, if strong socialization pressures, including "mutual monitoring" and "moralistic aggression," are used to shape values

within the group, a mechanism is provided for controlling, and even removing, the genes of cheaters.

As indicated, social learning is genetically biased. Social psychological studies of cultural transmission show that people pick up trends more readily from role models who are similar. It is likely that different ethnic groups learn from different trendsetters and that the variance among groups is increased, thereby increasing the efficacy of group selection. Those groups adopting an optimum degree of ethnocentric ideology may have replicated their genes more successfully than those that did not. Evolution under bioculturally driven group selection, including migration, war, and genocide, may account for a substantial amount of change in human gene frequencies. E. O. Wilson (1975, 573–74) put it forcefully:

If any social predatory mammal attains a certain level of intelligence, as the early hominids, being large primates, were especially predisposed to do, one band would have the capacity to consciously ponder the significance of adjacent social groups and to deal with them in an intelligent organized fashion. A band might then dispose of a neighboring band, appropriate its territory, and increase its own genetic representation in the metapopulation, retaining the tribal memory of this successful episode, repeating it, increasing the geographic range of its occurrence, and quickly spreading its influence still further in the metapopulation. Such primitive cultural capacity would be permitted by the possession of certain genes.... The only combination of genes able to confer superior fitness in contention with genocidal aggressors would be those that produce either a more effective technique of aggression or else the capacity to preempt genocide by some form of pacific maneuvering. Either probably entails mental and cultural advance. In addition to being autocatalytic, such evolution has the interesting property of requiring a selection episode only very occasionally in order to proceed as swiftly as individual-level selection. By current theory, genocide or genosorption strongly favoring the aggressor need take place only once every few generations to direct evolution. This alone could push truly altruistic genes to a high frequency within the bands.

References

- Ahern, F. M., Cole, R. E., Johnson, R. C., and Wong, B. (1981). Personality attributes of males and females marrying within vs. across racial/ethnic groups. *Behaviour Genetics*, 11, 181–94.
- Cavalli-Sforza, L. L., Menozzi, P., and Piazza, A. (1994). *The history and geography of human genes*. Princeton University Press, Princeton.

- Daly, M. and Wilson, M. (1982). Whom are newborn babies said to resemble? *Ethology and Sociobiology*, **3**, 69–78.
- . (1988). *Homicide*. Aldine de Gruyter, New York.
- Daniels, D. and Plomin, R. (1985). Differential experience of siblings in the same family. *Developmental Psychology*, **21**, 747–60.
- Darwin, C. (1871). *The descent of man*. Murray, London.
- Dawkins, R. (1976). *The selfish gene*. Oxford University Press, Oxford.
- . (1982). *The extended phenotype*. Freeman, San Francisco, Cal.
- Eaves, L. J., Eysenck, H. J., and Martin, N. G. (1989). *Genes, culture and personality*. Academic, London.
- Eibl-Eibesfeldt, I. (1989a). *Human ethology*. Aldine de Gruyter, New York.
- . (1989b). Familiality, xenophobia, and group selection. *Behavioural and Brain Sciences*, **12**, 503–59.
- Fletcher, D. J. C. and Michener, C. D. (1987). *Kin recognition in animals*. Wiley, New York.
- Greenberg, L. (1979). Genetic component of bee odor in kin recognition. *Science*, **206**, 1095–97.
- Hames, R. B. (1979). Relatedness and interaction among Ye'Kwana: A preliminary analysis. In *Evolutionary biology and human social behavior* (ed. N. A. Chagnon and W. Irons), pp. 238–49. Duxbury, North Scituate, Mass.
- Hamilton, W. D. (1964). The genetical evolution of social behaviour: I and II. *Journal of Theoretical Biology*, **7**, 1–52.
- Holmes, W. G. (1995). The ontogeny of littermate preferences in juvenile golden-mantled ground squirrels: Effects of rearing and relatedness. *Animal Behaviour*, **50**, 309–22.
- Johnson, G. R. (1986). Kin selection, socialization, and patriotism: An integrating theory (with commentaries and response). *Politics and the Life Sciences*, **4**, 127–54.
- Katz, S. H., Hodiger, M. L., and Valleroy, L. A. (1974). Traditional maize processing techniques in the new world. *Science*, **223**, 1049–51.
- Kurland, J. A. (1979). Paternity, mother's brother, and human sociality. In *Evolutionary biology and human social behavior* (ed. N. A. Chagnon and W. Irons), pp. 145–80. Duxbury, North Scituate, Mass.
- Littlefield, C. H. and Rushton, J. P. (1986). When a child dies: The sociobiology of bereavement. *Journal of Personality and Social Psychology*, **51**, 797–802.
- Lynn, R. (1989). Balanced polymorphism for ethnocentric and nonethnocentric alleles. *Behavioural and Brain Sciences*, **12**, 535.
- Reynolds, V. and Tanner, R. E. S. (1983). *The biology of religion*. Longman, New York.
- Rowe, D. C. and Osgood, D. W. (1984). Heredity and sociological theories of delinquency: A reconsideration. *American Sociological Review*, **49**, 526–40.
- Rushton, J. P. (1988). Genetic similarity, mate choice, and fecundity in humans. *Ethology and Sociobiology*, **9**, 329–33.
- . (1989a). Genetic similarity, human altruism, and group selection (with commentaries and author's response). *Behavioral and Brain Sciences*, **12**, 503–59.
- . (1989b). Genetic similarity in male friendships. *Ethology and Sociobiology*, **10**, 361–73.
- . (1995). *Race, evolution, and behaviour*. Transaction Publishers, New Brunswick, N.J.
- Rushton, J. P., Fulker, D. W., Neale, M. C., Nias, D. K. B., and Eysenck, H. J. (1986). Altruism and aggression: The heritability of individual differences. *Journal of Personality and Social Psychology*, **50**, 1192–8.

- Rushton, J. P., and Nicholson, I. R. (1988). Genetic similarity theory, intelligence, and human mate choice. *Ethology and Sociobiology*, 9, 45–57.
- Rushton, J. P., Russell, R. J. H., and Wells, P. A. (1984). Genetic similarity theory: Beyond kin selection. *Behaviour Genetics*, 14, 179–93.
- Russell, R. J. H. and Wells, P. A. (1987). Estimating paternity confidence. *Ethology and Sociobiology*, 8, 215–20.
- Russell, R. J. H., Wells, P. A., and Rushton, J. P. (1985). Evidence for genetic similarity detection in human marriage. *Ethology and Sociobiology*, 6, 183–87.
- Segal, N. L. (1988). Cooperation, competition, and altruism in human twinships: A sociobiological approach. In *Sociobiological perspectives on human development* (ed. K. B. MacDonald), pp. 168–206. Springer-Verlag, New York.
- Segal, N. L., Wilson, S. M., Bouchard, T. J., Jr., and Gitlin, D. G. (1995). Comparative grief experiences of bereaved twins and other bereaved relatives. *Personality and Individual Differences*, 18, 511–24.
- Smith, M. (1981). Kin investment in grandchildren. Unpublished doctoral thesis, York University, Toronto, Ontario, Canada.
- Tesser, A. (1993). The importance of heritability in psychological research: The case of attitudes. *Psychological Review*, 93, 129–42.
- van den Berghe, P. L. (1981). *The ethnic phenomenon*. Elsevier, New York.
- . (1983). Human inbreeding avoidance: Culture in nature (with commentaries and author's response). *Behavioural and Brain Sciences*, 6, 91–123.
- . (1989). Heritable phenotypes and ethnicity. *Behavioural and Brain Sciences*, 12, 544–45.
- Williams, G. C. (1966). *Adaptation and natural selection*. Princeton University Press.
- Willson, M. F. and Burley, N. (1983). *Mate choice in plants*. Princeton University Press.
- Wilson, D. S. and Sober, E. (1994). Reintroducing group selection to the human behavioural sciences. *Behavioural and Brain Sciences*, 17, 585–654.
- Wilson, E. O. (1975). *Sociobiology: The new synthesis*. Harvard University Press, Cambridge, Mass.
- Wynne-Edwards, V. C. (1962). *Animal dispersion in relation to social behaviour*. Oliver and Boyd, Edinburgh.