LETTER TO THE EDITOR

Comment on Genetic Similarity Theory

Linda Mealey[1,2]

Genetic similarity theory, a purported extension of the concept of inclusive fitness, is not only unnecessary, but also logically flawed. In this paper, the author (1) discusses the definition of inclusive fitness; (2) identifies the major logical flaw of genetic similarity theory; and (3) refers readers to earlier, more thorough discussions of several common misunderstandings of kin selection and assortment.

In an earlier issue of this journal (Vol. 14, No. 3, 1984), Rushton, Russell, and Wells presented their genetic similarity theory (GST), as a purported extension of Hamilton's (1964a) concepts of kin selection and inclusive fitness. GST is intended to explain a variety of data on altruism and assortment, of which they claim kin selection is only a special case. The behaviors addressed included kin recognition in animals reared apart, assortative mating, intrafamilial relations, human friendship and altruism, and ethnic nepotism.

In their review of the literature, the authors produced data which indicate that (1) individuals positively assort across a wide variety of species and relationships, (2) this assortment is associated with cooperative behavior, and (3) the degree of assortment and cooperation tends to be positively related to the degree of similarity of the assorting individuals. GST, however, is not necessary to explain these data. In the following paragraphs, I attempt to show (1) that Hamilton's concept of inclusive fitness is broader than Rushton *et al.* indicate, in that it is not synonymous with kin selection; (2) that to the extent that GST does go

[1] Department of Psychology, University of Texas at Austin, Austin, Texas 78712.
[2] Present address: Department of Psychology, College of St. Benedict, St. Joseph, Minnesota 56374.

beyond Hamilton's concept, it is logically flawed; and (3) that the be-
haviors GST attempts to explain can already be explained using Hamil-
ton's version of inclusive fitness and other more parsimonious
mechanisms.

In Hamilton's (1964a) paper, inclusive fitness is defined as the sum
of an individual's "basic unit" of fitness (i.e., the population mean), the
effect of his personal genotype (i.e., the individual component), and *the
"effects on him due to his neighbors, which will depend on their genotypes"*
(pp. 2–3; emphasis added). As stated, the effect of neighbors is consequent
to the genotypes of the neighbors, not to their relatedness. Only in a
situation where altruistic behavior is a consequence of a new mutation
is relatedness the issue. In such a situation, it is easy to calculate the
likelihood that kin and nonkin also carry the new allele (r and 0, respec-
tively) and, thus, to demonstrate a mechanism whereby altruistic behavior
can evolve. This is what Hamilton did, and as his intent was to illustrate
the origin and spread of altruism, his paper did not address the situation
in which a nonrelative could also be a carrier of the altruism allele. In a
later paper, however (Hamilton, 1975), he laments not emphasizing the
greater implications of his theory, stating,

> Because of the way it was first explained, the approach using inclusive fitness has
> often been identified with "kin selection" . . . but . . . kinship should be considered
> just one way of getting positive regression of genotype in the recipient, and . . . 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)

Dawkins (1979) also points out this misunderstanding of Hamilton's work.

Rushton *et al.* (1984) are thus correct, but not new, in saying that a
gene can ensure its own survival by "acting so as to bring about the
reproduction of any organism in which copies of itself are to be found"
(p. 181). But beyond that, their argument fails. Rushton *et al.* combine
several logical fallacies in their argument, each of which has appeared in
print frequently enough that Dawkins felt a need to address them. In a
beautiful, but little-cited paper (Dawkins, 1979), he discusses 12 misun-
derstandings of kin selection, 5 of which are attributable to GST.

Rather than recite Dawkins' work, I refer Rushton *et al.* and other
readers to it and briefly discuss the main fallacy of GST. This is as follows:
it is not the *proportion* of genes shared with another which is relevant
for altruistic behavior; it is the *probability* that the two individuals share
the "altruism gene." The probability that sibs share such an allele iden-
tical by descent (ibd) is 0.5. This is an exact figure and is not equivalent
to the average 50% proportion of genes ibd that sibs share. That altruism
can evolve is by virtue of this 0.5 probability of sharing the altruism allele
and is totally independent of the fact that genes at other loci are also

shared. Altruistic behavior, therefore, is contingent solely on the likelihood that another shares this particular allele at a particular locus, not on overall genetic or phenotypic similarity. (Humans are not expected to be altruistic to chimps because we share 98% of their genes.)

In relation to my third point, it is possible that phenotypic similarity may be an indicator of the likelihood that another individual carries the same altruism allele, but this is true only if (1) the phenotypic similarity is actually due to relatedness or (2) the phenotypic trait(s) in question is (are) linked genetically to the altruism locus. The former would be a case of kin recognition using similarity to self (or nestmates) as a proximate mechanism. The latter would be a case of Dawkins' (1976) "green beard" phenomenon, with the effect being due to the action of multiple, linked genes, rather than to the pleiotropic effects of a single allele. Many examples of cooperation and altruism based on phenotypic similarity cited by Rushton *et al.* can be classified into one of these types of discrimination (which, by the way, were not lost on Hamilton; see his 1964b paper). Discriminatory altruism, on the other hand, which is based on phenotypic similarity uncorrelated with the likelihood of sharing the altruism allele, would be selected out.

Finally, there are some cases of assortment, cooperation, and altruism found among similar individuals who would not be expected to be more likely than others to share an altruism allele. These cases can be parsimoniously explained by mechanisms other than phenotypic matching, particularly reciprocal altruism (Trivers, 1971) but also others [see several given by Burley (1983)]. Many cases are due to the fact that self-selection of one's environment leads to assortment of like individuals into like environments, where by virtue of repeated encounters, individuals are benefited by setting up (conscious or unconscious) reciprocation arrangements. Clubs and organizations, in which individuals share similar interests which may or may not be related to underlying genetics, provide an excellent example of this. Other cases may be due to actual increases in individual fitness which are consequent to positive assortment, e.g., similar mates may have more congruent and, therefore, more effective parenting behaviors than dissimilar mates [see Thiessen and Gregg (1980) and references therein for such data in humans]. Assortment may also be an epiphenomenon of sexual selection in monogamous species—the best get the best, leaving the worst for the worst (see Burley, 1983). There are many parsimonious explanations for positive assortment and differential altruism without necessitating GST. Indeed, most data demonstrating such behavior were collected with the intent to support Hamilton's theory and do not require any additional explanation.

Many misunderstandings of Hamilton's theory have become common belief [see Mealey (1980) for another misunderstanding in addition to those discussed by Dawkins (1979)]. Together with the methodological problems inherent to the study of human sociobiology (see, e.g., Mealey and Young, 1985), these mistakes have unfortunately provided antisociobiologists with justified reason for suspicion. As a sociobiologist, I am confident that these problems will eventually be cleared up, but for now, we need to be much more critical of our own work and that of others in our field.

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