# Individual selection and altruistic relationships: the legacy of W. D. Hamilton

Ilan Eshel[1] and Marcus W. Feldman[2]

[1] Department of Statistics

Tel-Aviv University

Tel-Aviv 69978, Israel

[2] Department of Biological Sciences

Stanford University

Stanford, CA 94305-5020

October 30, 2000

Bill Hamilton, one of the most influential Darwinian thinkers of our time, was, above all, immensely curious. He was intrigued by nature s riddles, whether they arose in his backyard or in the faraway rain forests of Brazil or Africa, where he recently came to his tragic death. Walking with him in the woods or in the desert, sometimes even in a crowded street in the midst of a city, one had to expect an adventure; an uncommon beetle or some unexplained behavior of a bird could turn an innocent journey into a research expedition.

There was a continuity between the curiosity of the person as revealed in his backyard research, and the most basic questions dealt with in his scientific work. Why do we grow old (Hamilton 1966)? Why does the sex ratio come close to even in one population but deviate from it in another (Hamilton 1967)? Why is it that we so often observe gregarious behavior of a potential prey when such behavior could apparently only be of advantage to its predator (Hamilton 1971a, b)? Why is it that the investment in dispersal is so often high even in cases where the expected reproductive success far from home is apparently no larger than it is close to home (Hamilton and May 1977, 1980)? And finally, a central theme in his last 20 years of research - Why do we reproduce sexually (e.g. Hamilton, 1980, Hamilton et. al, 1981, Hamilton and Zuk 1982 and many later works)? Hidden in these papers are many concepts and ideas that later would become widely accepted as being central to the quantitative theory of evolution. Perhaps the most prominent example is that of the Unbeatable Strategy (Hamilton 1967), which foreshadowed the future development of the concept of ESS (Maynard Smith and Price 1973). Yet, for most biologists and social scientists, Hamilton s name was, and still is, connected most intimately with the evolution of altruistic behavior (Hamilton 1963, 1964 I, II, 1970, 1971b, 1972). In the present note we concentrate on that part of his work. However, almost any subject that he studied can be interpreted in terms of the basic philosophy that led him to his insights about the evolution of altruistic traits.

Altruistic traits, a term first coined by Haldane (1932), are those that decrease the fitness of their carrier but increase that of other individuals in the population. While still an undergraduate student in Cambridge, Hamilton wondered how can natural selection maintain traits that, even if advantageous for the population, apparently reduce the number of their carriers below their share in the population? The answer he gave to this question is now referred to as *Hamilton s rule*: An inherited behavior is selected for in a population if and only if it results in an increase in the number of genes, *identical by descent* to those of the individual doing that behavior, namely those genes carried by the offspring of the individual in question or by its other relatives. To measure the effect of one's behavior on the number of his or her genes in the population, Hamilton first employed *Wright s kinship coefficient* (Wright 1922), measuring relatedness by the chance *r* that an allele carried by one individual would be identical by descent to an allele carried by its relative. Employing this measure of relatedness, Hamilton concluded that natural selection would favor altruism toward a relative if and only if the ratio between the cost to the helper and the benefit to that relative were less than *r*, cost and benefit being measured in terms of fitness.

This answer became one of the central dogmas of the modern theory of evolution. It has undergone many revisions and, in some technical aspects, remains controversial. However, this reason for the evolution of an individually deleterious trait in a population has now become part of the general knowledge of any modern student of evolution. But this was far from the case in 1964. Reproductive restraints that prevent overpopulation, behavioral or even physiological mechanisms minimizing harm inflicted on co-species opponents, eusocial behavior in hymenoptera and termites, were all assumed to have evolved simply because of their importance for *the survival of the species*. In a very influential book of that time, *Animal Dispersal in Relation to Social Behavior*, Wynne-Edwards (1962) maintained that mechanisms of reproductive self restraint should be an inevitable product of biological evolution because, by preventing overpopulation, they protected the population from extinction in the

future. The same line of reasoning can be found in Lorenz s *On Aggression* (1963), in connection with the evolution of mechanisms, either behavioral or physiological, that prevent competing males from seriously damaging their opponents. Although apparently costly in terms of the individual, such restrictions were supposed to be maintained in the population because of their contribution to the survival of the species.

While Fisher (1930, 1958) and Wright (1948) had already shown this sort of argument to be false, their theoretical work was never accepted by Cambridge biologists of the time as having any empirical relevance (to be distinguished from Fisher s well-accepted contributions to statistical inference). To illustrate this attitude, Hamilton (1996) gives the following passage from *The Life of Insects,* a book published by the Cambridge professor Sir Vincent Wigglesworth in 1964 (coincidentally, the same year as Hamilton s The genetic evolution of social behavior ):

> *Insects do not live for themselves alone. Their lives are devoted to the survival of the species whose representative they are indeed we have now reached the heart of the matter The aim and purpose (as far as we can understand them) of the life of insects .*

Under the influence of Fisher, it was clear to Hamilton, even as a student, that no genetically inherited trait disfavored by natural selection within a population can possibly be maintained in a population only because of its importance to the future survival of this population. Yet he realized that the alternative to group selection might not be restricted to individual selection. The *kin selection* mechanism described above, first suggested in his 1963 paper, was based on the gene rather than on the individual as a unit of selection. Later, this led Dawkins (1976) to use the term s*elfish gene* for any allele under natural selection, a reemphasis of Hamilton s belief that altruistic traits could only evolve on the individual level, if they allow the spread of the selfish allele which determines them.

Hamilton is often misleadingly regarded an advocate of a view that places the evolution of altruistic traits at the center of the Darwinian theory of natural selection. This is far from the truth. Haldane (1932) had attempted unsuccessfully to model the evolution of altruism, but few scholars (e.g., Williams 1966) recognized the importance of the phenomenon and the need to explain its evolution in quantitative terms. A fact quite often overlooked is that Hamilton s rule was suggested not only as a sufficient but also as a necessary condition for the evolutionary success of an altruistic trait, a condition that in most natural situations is not easily met. It is thus worth recalling that this very rule was employed to predict the limitation of workers altruism in ants  nests (Hamilton 1971b, 1972) as well as that of parents toward their offspring (Trivers 1974). Also important is the crucial role of Hamilton s rule in clarifying a much wider range of conditions under which only those traits that exclusively promote the welfare of their individual carrier can evolve. This point is illustrated by the way different authors have treated the phenomenon of gregarious behavior of a potential prey. As mentioned by Hamilton (1971a):

> *Most writers on the subject of animal aggregation seem to have believed that the evolution of gregarious behaviour must be based on some advantage to the aggregation as a whole. Many well known biologists have subscribed, outspokenly or by implication, to this view. At some time some  for example Hesse et al (1937)  and Lorenz (1966)  have admitted that the nature of the group advantage remains obscure in many cases.*

Indeed, one (though not the only) possible  advantage to the aggregation as a whole , suggested by Lorenz, was that of mutual defense against predators. The theoretical difficulty of the individual advantage of defection in such cases was not even realized as a problem by Lorenz. He was perplexed, instead, by those cases in which there appeared to be no mutual defense on part of the potential prey, in some of which gregarious behavior appears just to facilitate predation. Hamilton, however, addressed both cases. On one hand, an apparently altruistic tendency toward mutual

defense is well predicted by the theory of kin-selection, in relatively small groups of more or less permanent structure (Hamilton 1963, 1964 I, II 1970, 1971b, 1972, but see also Trivers 1971 and Axelrod and Hamilton 1981 for the possibility of reciprocal altruism in this case). On the other hand, this is not likely to occur in large anonymous aggregations; this was the subject of Hamilton s article  On the geometry of the selfish herd  (1971a), from which the quotation in the previous paragraph is taken. As Hamilton explained, the possible group-detrimental behavior of the aggregation is an inevitable result of the individually advantageous (hence selfish) behavior of each member of it. Struggling to be as close as possible to other members of the aggregation, preferably in the middle of it, such a member thereby seeks the relative safety from being the first taken by the predator.

Here, instead of the prey-predator two-player game tacitly envisaged by Lorenz, Hamilton developed his analysis in terms of the spatial structure of a population game in which the payoff is individual survival and the players are the potential members of the aggregation. He again used the population game structure (Hamilton 1967), and with his concept of unbeatable strategy he anticipated the later applications of game theory to evolutionary reasoning by Maynard Smith and Price (1973).

To those who knew Hamilton, his approach of first resorting to the simplest explanation of direct individual selection was quite natural. Actually, it was just this approach that led him to look for deeper explanations when direct individual selection appeared to fail. This was indeed the case with apparently altruistic behavior for which one of the first examples given in his 1964 article was that of warning calls. Thirty years later, visiting the field observatory of Amotz Zahavi at Hazeva in the south of Israel, he was still eager to learn a new explanation for this phenomenon among Arabian bubblers, based on individual reproductive success. Other phenomena, not explained on the basis of direct individual selection, soon added themselves to his list. There were  extraordinary sex ratios  that deviated from Fisher s principle of the maximization of the expected number of grand offspring. There were deviations from

Fisher s criterion for dispersal as a means to maximize the expected success of one s seeds. Some aspects of sexual reproduction and sexual selection can also be added to this list.

Concerning the theory of sex allocation, Hamilton (1967) first noticed that selection on genes located on the Y chromosome could not possibly operate to maximize the expected number of grand offspring. It would operate, instead, to maximize the number of *male* grand offspring born to *male* offspring, since those are the only ones to inherit the Y chromosome. An inevitable result, in such a case, would be a drastically male-biased sex ratio, reducing the dispersal of either autosomal alleles or those located on the X-chromosome. Hamilton suggested that this sort of an intragametic conflict could explain the shortening through translocations of the Y-chromosome. Kin selection in a deme-structured population, on the other hand, was shown to cause a female-biased sex ratio.

Widely observed over-investment in seed dispersal was explained by Hamilton, in collaboration with May, on the basis of two factors, both, again, invoking the gene's view . First, dispersal gives the advantage of competing for new sites in which the migratory allele is under-represented (Hamilton and May 1977, 1980). Then, in a distant empty site, the advantage in terms of future dispersal of genes is likely to be larger than can be accounted for by the success of one seed. Indeed, a new empty site may provide better conditions for future descendents.

A variation of this latter argument is repeated as a crucial component of Hamilton s combined theory for the evolution of sexual reproduction and sexual selection. On the face of it, these two appeared to be contradictory. On the one hand, Hamilton s theory for the evolution of sexual reproduction assumes that the pressure of continuously evolving parasites on a currently successful combination of genes is the most crucial factor of natural selection. Sex and recombination, according to this view, are tools to get rid of the currently successful combinations of genes (sooner or later to become obsolete) without eliminating the genes involved in these

combinations. Yet Hamilton s theory for the evolution of sexual preference assumes, quite on the contrary at first sight, that male sexual display is aimed to demonstrate immunity to parasites now present in the population. But this immunity would be characteristic of exactly that combination of genes soon to become deleterious and hence to be discarded by recombination and natural selection. The resolution of the apparent contradiction is again based on the concept of the long-term perspective of the gene rather than on that of the individual. It was shown by Eshel and Hamilton (1984), that even when recombination does not increase the average fitness of the direct offspring (and, under the plausible conditions of not too rapid cycling, it does not), the longer-term reproductive contribution of the few most successful combinations may provide to sexual reproduction a long-term selective advantage even against the cost of meiosis. At the same time, in such a case, natural selection is shown to favor females genes for mating with the fittest males.

Throughout Hamilton s career, each of his new ideas became a subject of controversy. This was true, above all, for his most influential contribution, the theory of kin selection. Reservations about the theory in his famous 1964 article can be sorted into three categories:

a) Ambiguity concerning the very concept of relatedness and, hence, of inclusive fitness.
b) The limitation of the theory, at least in its first version, to directed altruism among well-recognized relatives.
c) Most importantly, possible contradictions between the quantitative predictions of the theory and those obtained by the analysis of exact population genetic models.

Ambiguity concerning the concept of relatedness, as used by Hamilton in his 1964 paper, stemmed from its use of Wright s concept of *identity by descent*. Hence,

the inclusive fitness was first defined by Hamilton as the expected increase in the number of genes in the population that are identical by descent to those of the acting individual. With this definition in mind, one can imagine a group of sibs colonizing an isolated island. Hamilton s rule, in terms of Wright s definition of relatedness, would predict selective advantage to a high level of altruism on that island. Yet it is easy to see that if a gene for highly competitive or even spiteful behavior were carried by some of the sibs, it would be the one to survive on that island. Another crucial question raised more generally was how far back should one look for common descent. Going back far enough, it might be that all members of a species would be found to be close relatives, much like the imaginary sibs on the island. This question appeared to be especially important in highly inbred, spatially structured, non-panmictic populations, and these soon became a major arena for the study of altruistic traits. Moreover, concentrating the focus on such populations, the most apparent examples of biological altruism were those of physiological or biochemical altruism such as metabolic self-restraint, traits which by their very nature should serve all neighbors of the individual, regardless of relatedness. The first version of the theory presented by Hamilton, instead, was explicitly restricted to directed altruism, discriminating between related and unrelated neighbors.

In order to explain the phenomenon of non-directed altruism, an alternative quantitative theory was developed, much in line with Wright s idea about the evolutionary role of partial isolation of local groups in the population (e.g., Wright 1945). Pure probabilistic analysis of the chance of like individuals to encounter each other in such a situation led to explicit conditions under which non-directed altruism could evolve.

Committed to his original opposition to the old concept of group selection, as envisaged by Wynne Edwards and Lorenz, Hamilton was initially reluctant to accept any new version, even modified, of this concept. His position on the matter changed only when he learned of Price s covariance formula for natural selection (Price 1970)

and was convinced to re-define relatedness so as to adjust the concept of inclusive fitness to the dynamics predicted by this new formula. This was done by defining relatedness as the regression coefficient of the number of representatives of a given allele, carried by one individual, on the number of representatives of this same allele, carried by its relative (Hamilton 1970, 1972). In the absence of selection, this regression coefficient is easily shown to be uniquely defined, regardless of the locus and of the distribution of alleles carried at this locus in the population. Moreover, with random mating, the regression coefficient is equal to Wright s coefficient of relatedness, employed by Hamilton in his 1964 paper. From Price s formula it followed that, given this regression coefficient, selection should always operate to increase the inclusive fitness. Hence Hamilton s rule was re-established without resorting to the ambiguous concept of identity by descent. As an important by-product, the concept of relatedness was now extended to include neighbors in spatially structured populations. In this way, Hamilton s rule could now be used to account for group selection and the evolution of non-directed altruism (see also Uyenoyama and Feldman 1980).

It remained to consider the effect of natural selection on the relatedness between two individuals as determined by the regression coefficient. Ignoring this effect, Hamilton s theory of kin selection still led to predictions not always in agreement with those obtained by the analysis of exact population genetic models. For example, conditions for the initial increase of an altruistic allele may not be the same as those for its ultimate fixation (Cavalli-Sforza and Feldman 1978), an effect which emerges from a formal genotypic analysis of Hamilton s model. By moving away from the Hardy-Weinberg structure, the effect on individuals of the selection for altruism is actually clarified, as is the effect of Hamilton s assumption of additivity of fitness gains and losses.

This criticism was rejected by Maynard Smith (1980), who favored inclusive fitness models over the exact population genetic framework that deals with individual

fitnesses because the approximations inherent in the latter produce significantly simpler analysis, especially for relatives more distant than first degree. Hamilton was clearly aware of the distinction. In an overview introduction to his 1964 article, published in his 1996 book (p 27), Hamilton, however, wrote:

> *My long endeavour to generalize a maximizing property of the classical selection model was vitiated by my relatedness coefficient being only properly defined if there were no selection, which was obviously not true in my model. Indeed, selection was the whole point. So the proof I came up with was really only suggestive to what would happen, not a watertight demonstration. Nevertheless, it was easy to see that the argument must apply with increasing accuracy as selection in the model was made weak I was and still am a Darwinian gradualist for most of the issues of evolutionary change. Most change comes, I believe, through selected alleles that make small modifications to existing structure and behaviour*

Formal population genetic models of altruistic behavior involve the dynamics of genotype frequencies that cannot be transformed into gene frequencies. Hamilton (1964, p.2) recognized that the use of allele frequencies was an approximation to the exact genotypic dynamics that was valuable when selection was weak. In fact, he later wrote:

> *At least as we humans perceive the matter, it is not genes but we whole diploid organisms that make the decisions, so I had been delighted to find something approaching an individualistic view that I could justify for whole genotypes .*

Of course, the exact increase in the frequency of an allele depends on its marginal fitness, which is a function of genotype frequencies. The weak-selection approximation in terms of allele frequencies permits intuitive calculation of the inclusive fitness.

A formal and robust justification of Hamilton s conjecture about the asymptotic validity of his argument in the case of weak selection was, in fact, given by Taylor

(1989). The assumption of moderate selection forces was again made in a later study by Taylor (1992), in which selection in a spatially structured (viscous) population was studied. It was demonstrated how inclusive fitness is determined by the demographic mobility in such a population and how the direction of selection can then be interpreted in terms of Hamilton s rule. Different results were obtained, however, by Matessi and Karlin (1984), even for arbitrarily weak selection when the advantage accruing to a group member is not a linear function of the number of potential helpers in the group. Hamilton also worried about the limitations imposed by the assumptions in his 1964 paper. As he wrote in 1996 (p. 27):

> *Another limitation was that my model, complicated as it seemed already, had only one locus variable at time. This, however, was the same restriction as was required to get a maximization property in the classical model; in this respect the limitation of my results appeared to be no worse  Later I came to feel that my struggle to include multiple alleles had been rather pointless. On the other hand, my confidence that I had proved a maximization of inclusive fitness, with or without multiple alleles under weak selection for the one locus case, was important to me.*

Even when strong selection forces in several loci are involved, one can easily verify that the only *unbeatable strategies* (Hamilton 1967) in a population game of the prisoner s dilemma among relatives are those (either  Help  or  Defect ) that maximize one s inclusive fitness. In other words, this is the only strategy that, when fixed in the population, is immune to any non-epistatic mutation that affects the relevant behavior of its carrier. As mentioned elsewhere (Eshel 1997), Hamilton s concept of unbeatable strategy corresponds to the process of long-term evolution, according to which (rare) occasionally successful mutations, followed by natural selection, repeatedly shift the population from the vicinity of one (short term) genetic equilibrium to that of another. An important question, concerning long-term evolution and inclusive fitness, is whether monomorphic genetic equilibria that maximize the

inclusive fitness are the only ones immune to all non-epistatic mutations that affect the relevant behavior of their carriers. This is the kind of conundrum that Bill Hamilton would have enjoyed.

REFERENCES


Axelrod, R. and W. D. Hamilton. 1981. The evolution of cooperation. Science 211: 1390-1396,

Cavalli-Sforza, L.L., and M.W. Feldman. 1978. Darwinian selection and altruism . Theor. Pop. Biol. 14: 268-280.

Dawkins, R. 1976. *The Selfish Gene*. Oxford University Press, Oxford.

Eshel, I. 1997. On the changing concept of population stability as a reflection of a changing problematics in the quantitative theory of evolution. J. Math. Biol. 34: 485-510.

Eshel, I., and W.D. Hamilton. 1984. Parent-offspring correlation in fitness under fluctuating environment. Proc. Royal Soc. Lond. B 222: 1-14.

Feldman, M.W. and L.L. Cavalli-Sforza, 1981. Further remarks on Darwinian selection and ‘‘altruism . Theor. Pop. Bio. 19: 251-260.

Fisher, R.A. 1958. The Genetical Theory of Natural Selection. 2nd edition. (First edition 1930). Dover, New York.

Haldane, J. B. S. 1932. The Causes of Evolution. Cornell Univ. Press. Ithaca, N.Y.

Hamilton, W.D. 1963. The evolution of social behavior. The American Naturalist. 97: 354-356.

Hamilton, W.D. 1964. The genetic evolution of social behaviour, I-II. Journal of Theoretical Biology 7: 1-52.

Hamilton, W.D. 1966. The moulding of senescence by natural selection. Journal of Theoretical Biology 12: 12-45.

Hamilton, W.D. 1967. Extraordinary sex-ratios. Science. 156: 477-488.

Hamilton, W.D. 1970. Selfish and spiteful behaviour in an evolutionary model. Nature 228: 1218-1220.

Hamilton, W.D. 1971a. Geometry of the selfish herd. Journal of Theoretical Biology 31: 295-311.

Hamilton, W.D. 1971b. Selection of selfish and altruistic behaviour in some extreme models. In J.F. Fisenberg and W.S. Dillon (eds), *Man and Beast: Comparative Social Behavior,* pp. 57-91. Smithsonian Press, Washington D.C.

Hamilton, W.D. 1972. Altruism and related phenomena. Annual Review of Ecological Systems.

3: 193-232,

Hamilton, W.D. 1980. Sex versus non-sex versus parasite. Oikos 35: 282-290.

Hamilton, W.D. 1996. *Narrow Roads of Gene Land I. Evolution of Social Behaviour.* Freeman&Spektrum. Oxford, N.Y.

Hamilton, W.D., P.A. Henderson and N.A. Moran, 1981. Fluctuation of environment and coevolved antagonist polymorphism as factors in the maintenance of sex. In ‘‘Natural Selection and Social Behavior , R.D. Alexander and D.W. Tinkle (eds.) Chiron Press, New York.

Hamilton, W.D. and R. M. May. 1977. Dispersal in stable habitats. Nature 269: 578-581.

Hamilton, W.D. and R. M. May. 1980. Evolutionarily stable dispersal strategies. Journal of Theoretical Biology 82: 205-230.

Hamilton, W.D. and Zuk, M. 1982. Heritable true fitness and bright birds: A role of parasites? Science 218: 384-387.

Hesse, R., W.C. Allee, and K.P. Schmidt, Ecological Animal Geography. Chapman and Hall, London. Wiley, N.Y.

Lorenz, K. 1963. *On Aggression*. English translation 1966. Harcourt, Brace & World, N.Y.

Matessi, C., and Karlin, S. 1984. On the evolution of altruism by kin selection. Proc. Natl. Acad. Sci. USA 81: 1754-1758.

Maynard Smith, J. 1980. Models of the evolution of altruism. Theor. Pop. Biol. 18: 151-159.

Maynard Smith, J. and G. R. Price. 1973. The logic of animal conflict. Nature 246. 15-18.

Price, G. R. 1970. Selection and covariance. Nature 227: 520-521.

Taylor, P. 1989. Evolutionary stability in one-parameter models under weak selection. Theoretical Population Biology 36: 125-143.

Taylor, P. 1992. Altruism in viscous populations - an inclusive fitness model. Evol. Ecol. 6: 352-356.

Trivers, R.L. 1971. The evolution of reciprocal altruism. Quarterly Review of Biology. 46. 35-57.

Trivers, R.L. 1974. Parent offspring conflict. American Zoologist 14: 249-264.

Uyenoyama, M. and M.W.Feldman. 1980. Theory of kin and group selection: A population genetics perspective. Theor. Pop. Biol. 17: 380-414.

Williams, 1966. *Adaptation and Natural Selection*. Princeton University Press, Princeton, N.J.

Wigglesworth, V.B. 1964. *The Life of Insects*. Wiedenfeld and Nicholson. London.

Wynne-Edwards, V.C. 1962. *Animal Dispersal in Relation to Social Behavior.* Hafner. N.Y.

Wright, S. 1922. Coefficients of inbreeding and relationship. Amer. Natur. 56: 330-338.

Wright, S. 1945. Tempo and mode in evolution, a critical review. Ecology 26: 415-419.

Wright, S. 1948 (1961 printing). Genetics of populations. In Encyclopedia Britannica 10: 111 A-D, 112.