

William D. Hamilton: A Tribute

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In the presentation of his collected papers (Hamilton, 1996), W. D. Hamilton writes that for most of his young years as a researcher he was extremely lonely. I did not know the man, only some of his works. I met him once in Santa Fe in 1987. One night I saw him, alone, walking in the street looking at shop windows. I was with other people and I invited him to join us. He declined,

I first became interested in Hamilton's works in 1980. I was then a postdoc working on sex ratio evolution with Sam Karlin at Stanford University. Triggered by Ilan Eshel and Marc Feldman's study on evolutionary genetic stability (EGS) of the sex ratio, we were trying to provide more mathematical rigor to Fisher's verbal argument for the evolution and maintenance of equal investment in the two sexes in Mendelian populations. The cases where Fisher's argument fails were of prime interest to a biologist. Hamilton's paper on extraordinary sex ratios (Hamilton, 1967), published 13 years earlier was concerned with situations where certain underlying assumptions of Fisher's argument do not hold. These were sex-linked drive, which is a genetic factor, and local competition for mates, which involves population structure. This paper is one of the more analytical ones W. D. Hamilton, a non-mathematician, ever wrote alone. It is also one of which he is more proud than almost any other: "*Perhaps this is most of all because I believe it helped sex-ratio theory well on its way to being the section of evolutionary theory that best proves the power and accuracy of the Neodarwinian paradigm as a whole.*" (Hamilton, 1996, p. 132). Hamilton believed that sex ratio, an easily observable trait, had a status practically unsurpassed in evolutionary theory as an exact science: it was more suitable than any other trait for testing predictions about evolution.

One of the main contributions of Hamilton's paper on extraordinary sex ratios, besides the illustration of possible conflicts within the genome and between different levels of selection, is the introduction of game theoretic ideas to

sex ratio evolution and the introduction of the notion of an "*unbeatable strategy*," a precursory to Maynard Smith and Price's notion of ESS, "*evolutionarily stable strategy*": "*This required that, relative to a type I designated "unbeatable," no other type, no matter in what frequency in a mixture, would be able to increase. Maynard Smith's ESS only required that it be shown that if almost all individuals in the population are using the ESS, no other strategy starting from a low frequency can invade that population*" (Hamilton, 1996, pp. 373–374). In haploid or haploid-like models like the ones studied by Hamilton, no polymorphic equilibrium can exist and, when a strategy has a selective advantage over another at some frequency, then it has a selective advantage over the other at any frequency. Consequently an ESS is *de facto* unbeatable. But in general the conditions for an ESS in a defined microevolutionary context are less restrictive, since they bear only on the final strategies that can resist invasions once they are fixed in the population. The generality and simplicity of application of this concept have made it very popular among evolutionary biologists for pointing out the presumed endpoints of evolution.

But Hamilton's formulation raises a more difficult question: will there be evolution toward the ESS by natural selection when it exists? The EGS property, when it holds, ensures that the population tends toward an ESS, at least initially after enough generations have passed, when a mutant allele invades the population at any other equilibrium. When the next attainable equilibrium is closer to the ESS, as happens in some sex ratio evolution models, we have the EGS property over successive possible equilibria. But global convergence according to such a scheme has been demonstrated only for a few cases. The long-term evolutionary trends, as mutant genes are introduced one at a time into game theoretic evolution models or sex ratio evolution models, remain exciting theoretical challenges.



Like many others, I have been puzzled by kin selection theory, which is considered the major contribution of W. D. Hamilton to evolutionary theory. This theory, which was introduced as an alternative to group selection to explain the evolution of altruistic behaviors, has had a profound influence on the way we think of, and treat, evolution today. It is remarkable that a Ph.D. thesis written by a solitary worker appeals to so many concepts and tools that are at the heart of a discipline. Kin selection theory is indeed in the main stream of population genetics. In his first paper on the subject, Hamilton refers only to three authors, Fisher, Haldane, and Wright, nothing less than the fathers of population genetics. They were all concerned with a satisfactory explanation for cases “*where an animal behaves in such a way to promote the advantages of other members of the species not its direct descendants at the expense of its own*” (Hamilton, 1963). Haldane may have been the one who came closest to Hamilton’s principle when he discussed whether a genetic trait causing someone to risk his life to save a relative in danger could evolve. But the principle was already foreshadowed in Fisher’s remark of the evolution of distastefulness in insects. Roughly speaking, Hamilton’s principle says that an altruistic behavior will evolve if the loss to the altruist is less than the total gain to its relatives weighted by coefficients of relatedness. The main point is that the beneficiaries of the altruistic act must be related to the altruist. Hamilton (1964) proved that the inclusive fitness which transfers benefits of altruistic acts from beneficiaries to actors, weighted by coefficients of relatedness, is maximized by natural selection in much the same way that fitness is maximized in the simpler classical model according to the fundamental theorem of natural selection. When understood as an increase of the mean fitness, Hamilton’s proof may lack some mathematical rigor. But its corollary for the initial increase of an altruistic gene has generally proved to be sound when the costs, benefits and coefficients of relatedness are defined in an appropriate manner and selection is weak enough.

As shown later on, the change in frequency of an altruistic gene is correlated to inclusive fitness via Price’s covariance formula (Hamilton, 1970), which leads to an approximate adaptive topography in Wright’s sense based on inclusive fitness when selection is weak. Moreover, the coefficient of relatedness originally defined for diploid outbred populations as Wright’s symmetric correlation coefficient of relationship can be extended to haplodiploid populations if reproductive values of the two sexes are taken into account (Hamilton, 1972). It extends to inbred populations if defined as a regression coefficient or more generally as a covariance ratio which can be

expressed in terms of Malécot’s coefficient of kinship and Gillois’ coefficients of identity under weak selection (Michod and Hamilton, 1980). This covariance ratio can be extended to the case of multiple alleles, but in general it is not symmetric and depends on the allele frequencies and the probabilities of performing an altruistic act according to the genotypes. Alternatively, it can be replaced when selection is weak by the expected fraction of genes identical by descent to at least one of the genes at a single locus in the altruist, given that these genes are identical by descent or not. Such a fraction corresponds to the original definition given by Hamilton for outbred populations.

Hamilton claimed several times that his theory applies provided selection is slow, as suggested by an inclusive fitness function which additively combines weighted changes in fitness. This additive model is actually an approximation when selection is weak, the linear part of a Taylor expansion. Moreover, several authors have confirmed that weak selection is a necessary ingredient for the validity of Hamilton’s theory. His theory has motivated many studies of selection models with kin interactions as multiplicative models in family-structured populations and general frequency-dependent selection models in group-structured populations. Thanks to Hamilton, we know more today about all of those models. Moreover, although some kin selection models may be cast in the framework of fertility-viability selection or group selection, the inclusive fitness approach is quite intuitive and has an undeniable appeal. It has simplified to a great extent the finding of optimal (actually, EGS) strategies or sex ratios and it has rapidly spread among population biologists. It has become an indispensable tool for advancing evolutionary theory.

But what I like most in kin selection theory is that it is a genetic theory. There is a pervasive idea among some evolutionary biologists that the underlying genetics is not decisive in evolution, that the genetics does not really count to predict evolutionarily stable strategies. Kin selection theory takes the opposite view since it is centered on relatedness, which is essentially based on identity of genes. It is impossible to study kin selection without knowing the population structure, the mating pattern, the genetic system, everything that can affect inbreeding and relationship. Population geneticists are still in business.

That the evolution of sex was one of the more recent research interests of Hamilton (1990) is not surprising. This is one of the central unsolved questions in population genetics. That his explanation is based on host-parasite coevolution is also not fortuitous. Hamilton spent a great

deal of his professional life studying interactions between individuals. These latest works are typical of Hamilton's view.

REFERENCES

- Hamilton, W. D. 1996. "Narrow Roads of Gene Land: The Collected papers of W. D. Hamilton, volume 1: Evolution of Social Behaviour" (W. H. Freeman, Ed.), Spektrum, Oxford, Macmillan Press.
- Hamilton, W. D. 1967. Extraordinary sex ratios, *Science* **156**, 477–488.
- Hamilton, W. D. 1963. The evolution of altruistic behavior, *Am. Nat.* **97**, 354–356.
- Hamilton, W. D. 1964. The genetical evolution of social behaviour, I and II, *J. Theor. Biol.* **7**, 1–52.
- Hamilton, W. D. 1970. Selfish and spiteful behaviour in an evolutionary model, *Nature* **228**, 1218–1220.
- Hamilton, W. D. 1972. Altruism and related phenomena, mainly in social insects, *Ann. Rev. Ecol. Syst.* **3**, 193–232.
- Michod, R. E., and Hamilton, W. D. 1980. Coefficients of relatedness in sociobiology, *Nature* **288**, 694–697.
- Hamilton, W. D., Axelrod, R., and Tanese, R., 1990. Sexual reproduction as an adaptation to resist parasites (A review), *Proc. Natl. Acad. Sci. USA* **87**, 3566–3573.