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## **Modeling Social Evolution, 1964–1973: Inclusive Fitness Meets Population Structure**

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### **ABSTRACT**

In 1964, William Hamilton presented a mechanism for the evolution of altruism, which was perceived by its main promoters as an alternative to explanations based on “group selection,” invoking advantage to the population to account for the evolution of such traits. Less than ten years later, Hamilton used the framework developed by George Price to model the evolution of an altruistic gene in a structured population, a result that has been interpreted as a spectacular conversion to group selection. This paper revisits the modeling research on altruism and the considerable semantic ambiguities concerning the levels of selection in the late 1960s and early 1970s, by studying in close detail the reflections and exchanges among Hamilton, Price, Robert Trivers, and Ilan Eshel. The challenge in this research was not simply to find and model robust mechanisms for the evolution of altruism, but to interpret their properties in unambiguous terms that could be accepted by other researchers. The continuing debate over the levels of selection results from the tension between the properties of the models and the words used in interpreting them.

KEY WORDS: levels of selection, Hamilton, Price, inclusive fitness, sociobiology, altruism

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The following abbreviations are used: GCWP, personal papers of George C. Williams, Stony Brook University Library; GRPA, personal papers of George R. Price, British Library, London; JMSP, personal papers of John Maynard Smith, British Library; SWP, personal papers of Sewall Wright, American Philosophical Society; WDHP, personal papers of William D. Hamilton, British Library.

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## INTRODUCTION

The history of the early modeling research on the evolution of altruism in population genetics is now reasonably well known, but the interpretation of some critical episodes is still under contention.<sup>1</sup> Modeling research on altruism began with J.B.S. Haldane's formal definition of the concept in the early 1930s. Haldane called "altruistic" traits being deleterious to their bearers' fitness and advantageous to others.<sup>2</sup> For the British population geneticist, most cases of apparent altruism in nature, such as helping behavior by nonreproductive workers among social insects, did not require a specific explanation, because they were probably a simple extension of parental care. However, some behaviors, particularly among humans, were more puzzling from the point of view of evolutionary theory. Saints and recipients of the Victoria Cross found neither personal nor parental benefit in sacrificing their own survival and reproductive prospects. Interested in how altruism could evolve without kin relationships, Haldane devised a group selection model, in which the presence of altruists in a group increased the probability of survival of the group. In view of the stringent conditions for altruistic genes to be favored in this model, Haldane drew negative conclusions: it was unlikely that many altruistic genes would evolve, since individual selection against altruists seemed in most cases stronger than group selection.<sup>3</sup> The exceptional fate of saints and recipients of the Victoria Cross was likely to remain an exception.

Altruism was then a side issue in evolutionary theory. Haldane's treatment was limited to a few pages. From the 1930s to the early 1960s, formal inquiries on the problem were sketches published in appendices, book reviews, short

1. For the main references, see: Philip Kitcher, *Vaulting Ambition: Sociobiology and the Quest for Human Nature* (Cambridge, MA: MIT Press, 1985); Helena Cronin, *The Ant and the Peacock: Altruism and Sexual Selection from Darwin to Today* (Cambridge: Cambridge University Press, 1991); Elliott Sober and David Sloan Wilson, *Unto Others: The Evolution and Psychology of Unselfish Behavior* (Cambridge, MA: Harvard University Press, 1998); Ullica Segerstrale, *Defenders of the Truth: The Battle for Sociobiology and Beyond* (Oxford: Oxford University Press, 2000); Lawrence A. Dugatkin, *The Altruism Equation: Seven Scientists Search for the Origins of Goodness* (Princeton, NJ: Princeton University Press, 2011); Samir Okasha, *Evolution and the Levels of Selection* (Oxford: Clarendon Press, 2006); Marc E. Borrello, *Evolutionary Restraints: The Contentious History of Group Selection* (Chicago: University of Chicago Press, 2010).

2. John B. S. Haldane, *Causes of Evolution* (London and New York: Longmans, Green and Co., 1932), 210.

3. *Ibid.*, 121.

discussions in conference talks, or isolated papers.<sup>4</sup> Things changed in the mid-1960s, when some evolutionary biologists saw in altruism a genuine problem that had received a satisfactory answer with Hamilton's theory of inclusive fitness. In 1964, Hamilton made altruism not simply an intriguing issue, but a worst-case scenario for "individual selection." His argument, framed into a general model without group structure, seemed to show that individual selection could account for the evolution of such traits, provided that their benefits fall preferentially on the bearers' close kin.<sup>5</sup> This result found special significance in the context of the controversy on the levels of selection. For Hamilton's first readers, such as the British population geneticist John Maynard Smith and the American evolutionary biologist George C. Williams, Hamilton's treatment confirmed that "group selection" arguments, invoking long-term benefits for the population or the species, were unwarranted.<sup>6</sup> However, it is instructive to note that, for these evolutionists, little seemed to be expected from further work in this area. Maynard Smith, who popularized the mechanism described by Hamilton by calling it "kin selection," considered the problem anecdotal.<sup>7</sup> Williams considered it important, but solved, and suggested to put it to rest.<sup>8</sup>

In the late 1960s and early 1970s, this solved problem became the object of substantial modeling research. Several theoretical biologists, in part stimulated

4. See the models discussed in Sober and Wilson, *Unto Others* (ref. 1). See also James F. Crow, "General Theory of Population Genetics: Synthesis," in *Cold Spring Harbor Symposia on Quantitative Biology* 20 (Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press, 1955), 54–59.

5. William D. Hamilton, "The Genetical Evolution of Social Behaviour. I," *Journal of Theoretical Biology* 7, no.1 (1964a): 1–16; William D. Hamilton, "The Genetical Evolution of Social Behaviour. II," *Journal of Theoretical Biology* 7, no.1 (1964b): 17–52. On Hamilton, see Alan Grafen, "William Donald Hamilton. 1 August 1936–7 March 2000," *Biographical Memoirs of Fellows of the Royal Society*, 50 (2004): 109–113; William D. Hamilton, *Narrow Roads of Gene Land: The Collected papers of W. D. Hamilton*, vol. 1. *Evolution of Social Behaviour* (Oxford: W.H. Freeman/Spectrum, 1996); Ullica Segerstrale, *Nature's Oracle: The Life and Work of W. D. Hamilton* (Oxford: Oxford University Press, 2013).

6. John Maynard Smith, "Kin Selection and Group Selection," *Nature* 201, no. 4924 (1964): 1145–1147; George C. Williams, *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought* (Princeton, NJ: Princeton University Press, 1966), 252.

7. In the mid-1960s, Maynard Smith emitted doubts about the importance of altruism because he saw little evidence for it in nature. He then thought that if kin selection were to be of evolutionary significance, it would be for its possible role in other adaptations, such as sexual reproduction (Maynard Smith, *Theory of Evolution*, 2nd ed. (London: Penguin Books, 1966), 158.)

8. Williams to Hamilton, 25 Oct 1968, GCWP. George C. Williams, "Preface," in *Group Selection*, ed. G. C. Williams, (Chicago: Aldine Atherton, 1971), 1–17.

by Hamilton's papers, began to work on the evolution of altruism. They proposed alternative hypotheses and devised models to sustain their speculations. In this context, it transpired that "kin selection" and "group selection" were very elusive labels. There were no unequivocal rules explaining how to separate them or how to recognize them in the models. Furthermore, Hamilton himself refashioned his original model, producing results that allow room for conflicting interpretations. On the basis of Hamilton's last major contribution on the problem, stated in a conference given at Oxford in 1973, philosopher of science Elliott Sober and biologist David Sloan Wilson even claimed that Hamilton realized that kin selection was not substantially different from group selection.<sup>9</sup>

Sober's and Wilson's claims have been nuanced on philosophical grounds by Samir Okasha,<sup>10</sup> who presented a lucid discussion of the differences between kin selection and group selection models. My purpose is not to contribute to this conceptual discussion, but rather to revisit the study of the evolution of altruism in the critical period between 1964 and 1973, when it became the object of extended evolutionary and modeling investigations. The conflicting interpretations on the outcomes of Hamilton's research raise indeed several questions: Did Hamilton revise his views between 1964 and 1973? Why did other scientists pay interest to the study of altruism in this period, while the problem seemed either solved or anecdotal to committed neo-Darwinians such as Williams and Maynard Smith? To what extent were there overlaps, convergences, or conflicts between their results? What was the status of kin selection and group selection in these developments? The present paper answers these questions by reconstructing the course of Hamilton's thinking on social evolution during the decade 1964–1973.

The interpretation proposed here is focused on Hamilton's modeling work on inclusive fitness. In 1964, Hamilton did not simply propose an argument for the evolution of altruism. He devised a general modeling method to study social situations based on the concept of inclusive fitness. I reconstruct Hamilton's research on altruism after 1964 as an attempt to solve two distinct problems facing his method. The first problem concerned a tension between the features of his original model, and the conditions he saw as most favorable

9. Sober and Wilson, *Unto Others* (ref. 1), 77.

10. Samir Okasha, "Why won't the group selection controversy go away?," *The British Journal for the Philosophy of Science* 52, no.1 (2001): 25–50. Okasha, "Genetic Relatedness and the Evolution of Altruism," *Philosophy of Science*, 69, no. 1 (2002): 138–149.

to the evolution of altruism. In 1964, Hamilton anchored his treatment of altruism in deterministic models assuming a population of infinite size, without population structure, which were the most general family of models in population genetics at the time. He defined his main tool, the concept of inclusive fitness, in this model. Over the course of the 1960s, Hamilton came to pay increasing attention to the effect of population structure in facilitating interactions between altruists. The challenge became for him to apply his modeling method, based on the concept of inclusive fitness, to population-structured models.

A second problem was to connect the inclusive fitness method to the other mechanisms favoring altruism, being proposed in the aftermath of the publication of his papers. In the late 1960s and early 1970s, George Price, Robert Trivers, and Ilan Eshel proposed alternative hypotheses and modeling methods. Their correspondence with Hamilton, which is held in Hamilton's papers at the British Library, gives insights into the birth of a modeling field. The vocabulary is not stabilized. Problems are tackled with very different tools by individual researchers, who then face the task of establishing communication between their different hypotheses. Practically, the existence of alternative hypotheses on the evolution of altruism meant that Hamilton had to assess to what extent he could account for them with his own tools.

## **ALTRUISM AND LEVELS OF SELECTION**

### **The Problem of Altruism**

Why Hamilton considered risking PhD research on an issue that seemed to offer limited career prospects has been well documented by Ullica Segerstrale in her biography of Hamilton.<sup>11</sup> I will limit myself to quote a letter to Mary Jane West-Eberhard, in which Hamilton mentioned the deep influence exerted on his thinking by prewar popular books on Darwinism, which insisted on the individualistic dimension of natural selection and raised the problem of its consequences on human nature.

I think it was the class of this far-pre-war background with what I found myself being taught that started me thinking that there was some important unsolved puzzle about the theory: did the process work for the “benefit of the individual”, or for the “benefit of the species”, as textbooks and teachers

11. Segerstrale, *Nature's Oracle* (ref. 5).

had it? Later with stimulation from the books by [Ronald] Fisher and then [John B. S.] Haldane this worry crystallized into what I called the problem of “altruism”, *but the feeling that there was a big unsolved problem and a need for an approach through a priori reasoning rather than through any further experimentation or collecting of data was certainly with me before I left school* . . . I can remember being quite emphatic . . . that science teaching had an inappropriate down on “arm-chair philosophising” and that there was need for more of it not less, and that *I felt even a sort of contempt for “professional biology” for not having its fundamental tenets sorted out*. Indeed, I can remember feeling doubtful whether I wanted to “learn more biology” at University and fearing the “ruts” that this might put me into prior to having made my own a priori attack on the fundamentals; the proposed attack incidentally included a lot more than just pure Darwinism, such as an intention to get myself a better understanding of thermodynamics so as to understand evolution’s apparent defeat of the Second Law (this I have never followed up as I intended); and there were other grandiose schemes, such as finding mathematical descriptors of the complexity of patterns, again with evolution as the ultimate goal.<sup>12</sup>

This letter captures three issues dominating Hamilton’s thinking in the late 1950s and early 1960s: the feeling that evolutionary theory still required major clarifications of its central tenets; that these clarifications would affect the understanding of natural selection as a principle generating adaptation; and that further developments in this area should be expressed in quantitative form. These preoccupations crystallized into the problem of the evolution of altruism. If Darwinian evolution was to be taken seriously, it made sense to account for human behaviors as the result of evolution by natural selection. If natural selection was only responsible for the adaptation of the individual organism, it remained to be seen how it could generate characteristics deleterious to the survival and reproduction of their bearers.

Hamilton’s basic solution to the problem of altruism is the idea that there are two main ways for a gene to increase in frequency under natural selection. The first way is to be advantageous to its bearer, that is, to increase its fitness: this was the original, “Darwinian” mechanism. The second way is to give an advantage to other bearers of copies of the same gene. In other words, a gene can be favored if it increases the *inclusive* fitness of its bearer, that is, the proportion of its copies in the gene pool at the next generation. This second way provided the mechanism for the evolution of altruism. Hamilton argued

12. Hamilton to Mary Jane West-Eberhard, 26 Feb 1979, WDHP, Z1 X83; emphasis added.

that altruistic traits can evolve if the benefits of these characteristics fall preferentially on the bearers' close kin, simply because they have higher chances of carrying copies of the same genes. Thus, under certain conditions, it makes sense, in a Darwinian perspective, to direct altruistic behavior toward relatives, who have higher chances of sharing genes identical by descent with those of the actor than with random members of the population.

At the end of this research, Hamilton realized that the scope of his treatment went beyond the issue of altruism. Generalizing Haldane's definition, Hamilton observed that *any* character could be analyzed depending on its relative effects on the fitness of self and others. This was made explicit in a matrix providing a general classification of social behaviors. In this matrix, a character is termed "cooperative" if it has positive effects, and "spiteful" if it has negative effects, on the fitnesses of both actor and recipients. A character beneficial to the recipient and deleterious to the bearer's fitness is called "altruistic," whereas a character favoring the bearer to the detriment of the recipient is called "selfish."<sup>13</sup> This set of definitions had two consequences. First, it basically separated the study of social behaviors from psychological considerations, something that had not been entirely clear to Haldane himself.<sup>14</sup> In Hamilton's treatment, social behaviors were not conditioned by any kind of cognitive abilities. Any character, in so far as it affects the fitness of others, can have social effects. Thus, the post-reproductive lifespan of cryptic and aposematic moths studied by A. D. Blest can be considered as an altruistic trait, shaped by natural selection.<sup>15</sup> Second, Hamilton was able to propose a genetical theory that was not restricted to the problem of altruism, but applied to social behaviors in general. This theory was expressed in quantitative form.<sup>16</sup>

### Hamilton's Model

The objective of a population genetics model is to find conditions for the increase in frequency of an allele in a population. This takes the form of an equation relating  $\Delta p$  (the change in frequency of an allele at a locus) to a finite set of variables: the smaller the number of variables, the clearer the result. After

13. Hamilton, "Genetical Evolution I," (ref. 5), 15.

14. Haldane, *Causes of Evolution* (ref. 2), 131.

15. A. D. Blest, "Longevity, Palatability and Natural Selection in Five Species of New World Saturnid Moth," *Nature* 197, no. 4873 (1963): 1183–1186. See Dugatkin, *Altruism Equation* (ref. 1), 77–78, and Segerstrale *Nature's Oracle* (ref. 5), 69–70.

16. Hamilton, "Genetical Evolution I" (ref. 5).

several unfruitful attempts, Hamilton anchored his model in the deterministic theory (models of infinite population size, no genetic drift) of one-locus  $n$ -allele systems, which he had learned at Cambridge in Fisher's Department of Genetics. This was the canonical family of models in theoretical population genetics in the 1950s, being developed by Sewall Wright's as well as well as Fisher's students.<sup>17</sup> In line with this modeling tradition, Hamilton's model assumed a population of infinite size, weak selection, discrete generations, and additive effects of alleles.

The classical index of natural selection is the index of fitness ascribed to a genotype.<sup>18</sup> Hamilton used and modified this index to model social traits, which do not affect simply the fitness of their bearers, but also the fitness of other members of the population. The concept of inclusive fitness was designed to take these effects into account. Its defining feature is its focus on the effects caused by a behavior or a trait on gene frequencies. "The conceptual transformation," Alan Grafen observes, "is that the number of offspring contains all the offspring an individual has, whereas inclusive fitness contains those offspring that an individual causes to exist. Inclusive fitness accounts offspring by causation and not by parenthood."<sup>19</sup> Let us consider a behavior affecting positively the fitness of someone else. From the point of view of the actor, this effect can be partitioned into two parts. On the one hand, the behavior boosts the transmission of genes present in the genotype of the recipient, which have common ancestry with those of the actor.<sup>20</sup> This is the "effect of inclusive fitness" associated to the allele coding for this behavior. Inclusive fitness captures the effect of a genotype on the fitness of others, as weighted by their coefficient of relationship with the focal genotype. But, on the other hand, the behavior also affects the transmission of genes that *are not*

17. On the history of deterministic theory, see A.W.F. Edwards, "The Fundamental Theorem of Natural Selection," *Biological Reviews* 69, no. 4 (1994): 443–474 and J-B. Grodwohl, "The Theory was Beautiful Indeed: Rise, Fall and Circulation of Maximizing Methods in Population Genetics (1930–1980)," *Journal of the History of Biology* (2016): 1–38.

18. For a history of the concept of fitness, see Jean Gayon, "Sélection naturelle ou survie des plus aptes? Éléments pour une histoire du concept de fitness dans la théorie évolutionniste," in *Nature Histoire, Société: Essais en Hommage à Jacques Roger*, ed. Claude Blanckaert, Jean-Louis Fisher, and Roselyne Rey (Paris: Klincksieck, 1995), 263–287.

19. Grafen, "Hamilton" (ref. 5), 114.

20. Hamilton used Wright's machinery of relationship coefficients to measure the genes of common ancestry in actor and recipient. Hamilton's use of relationship coefficients raises specific issues, which will be discussed in a separate paper. See Alan Grafen, "A Geometric View of Relatedness," *Oxford Surveys in Evolutionary Biology* 2 (1985): 28–89.

identical by descent to genes present in the bearer, because, unless reproduction is clonal, recipients do not have a genome identical by descent to that of the actor. Hamilton called this second class of effects the “diluting effect” of the gene. The total effect of a behavior is the sum of its inclusive fitness effect and its diluting effect.

Hamilton wanted to make from inclusive fitness a useful descriptor in the analysis of social situations. He first obtained an equation giving the change in frequency of a gene in function of the diluting effect and of the inclusive fitness. This equation was relatively complex, and Hamilton tried to obtain a simpler descriptor. He then drew inspiration from a standard tool in mathematical population genetics, the function of mean fitness, written as  $\bar{W}$ . This function, devised in the mid-1930s by Sewall Wright, was defined as the average of the fitnesses of the genotypes present in a population, as weighted by their frequencies expected under random mating. Wright had made great use of this function, showing how to use it in the mathematical analysis of genetic systems under selection. Furthermore, the mean fitness function was held to be non-decreasing.<sup>21</sup> This was in harmony with the intuition that natural selection increases the mean fitness of populations. In Wright’s picturesque adaptive topographies, populations move under selection from valleys to peaks of mean fitness, and remain on peaks once they reach them.

Hamilton drew from Wright’s mean fitness the inspiration to build his own mathematical index presenting similar maximizing properties. Building a function of mean *inclusive* fitness, he was able to show that, under certain restrictive conditions (random mating and non-negative mean diluting effect), the mean inclusive fitness gave the direction of selection on a gene: selection favors genes that increase their bearers’ inclusive fitness. This meant that diluting effects were not informative on the direction of selection. Hamilton had thus identified, under the limitations of his model, which was an extension of the classical model at the time, a certain quantity that described the direction of selection in genetic systems with social effects.

Here then we have discovered a quantity, inclusive fitness, which under the conditions of the model tends to maximize in much the same way that fitness tends to maximize in the simpler classical model. For an important class of genetic effects where the individual is supposed to dispense benefits

21. For a simple presentation of the mathematical properties of the method in one-locus systems, see C. C. Li, “The Stability of an Equilibrium and the Average Fitness of a Population,” *The American Naturalist* 89, no. 848 (1955): 281–295.

to his neighbours, we have formally proved that the average inclusive fitness in the population will always increase.<sup>22</sup>

Hamilton expected his population genetics model to lead to guiding rules applying to the behaviors of organisms.<sup>23</sup> However, the principle of mean inclusive fitness increase proved to be too general for this purpose. Reducing the parameter space, Hamilton obtained more specific results. The first result of interest to us concerns the derivation of a condition for the evolution of an altruistic gene, known as “Hamilton’s rule.”<sup>24</sup> Under the assumptions of the original model, this condition is  $k > 1 / r$ ,  $k$  being the ratio *benefit to the recipient / cost to the bearer* of the altruistic genotype and  $r$  being the coefficient of relatedness between actor and recipient. Hamilton later called this result a “gift from God.”<sup>25</sup> The reasons for Hamilton’s surprise may appear more clearly by comparison with the results obtained by Haldane in 1932. In Haldane’s structured model, altruism was selected for only after altruists were established, or present at very high frequencies, in a group. Otherwise, altruists suffered from the presence of selfish parasites and were counter-selected. The main problem was then to determine how the altruistic gene could evolve to high frequencies in the first place: hence Haldane mentioned the role of stochastic factors in raising the frequency of the altruistic gene.<sup>26</sup> By contrast, Hamilton’s rule does not mention gene frequencies. Two quantities only are relevant in Hamilton’s rule: a variable for the ratio *benefit to the recipient / cost to the altruist* and the coefficient of relationship between partners,  $k$  and  $r$ , respectively. This meant also that the evolution of altruism did not depend on stochastic factors: the principle emerged from the sole deterministic theory of natural selection at one locus.<sup>27</sup>

22. Hamilton, “Genetical Evolution I” (ref. 5), 8.

23. E.g., “The social behaviour of a species evolves in such a way that in each distinct behaviour-evoking situation the individual will seem to value his neighbours’ fitness against his own according to the coefficients of relationship appropriate to that situation.” Hamilton, “Genetical Evolution I” (ref. 5), 13.

24. Eric L. Charnov seems the originator of the term; see Charnov, “An Elementary Treatment of the Genetical Theory of Kin-Selection,” *Journal of Theoretical Biology* 66, no.3 (1977): 541–550, on 542.

25. Hamilton, “This Week’s Citation Classic,” *Current Contents* 40 (1988): 16.

26. Haldane, *Causes of Evolution* (ref. 2), 209–210.

27. As Hamilton acknowledged, this was a property of his deterministic model. In the real world, a new altruistic mutant has no kin and is thus of direct disadvantage. Hence it must spread under drift for relatedness to build.

Hamilton obtained a second specific result, which concerned the effect of population structure on altruism. If relatedness drives altruism, then a population structure favoring interactions between kin should be particularly favorable to the evolution of altruism. Hamilton called this kind of population structure “viscous,” by analogy with the physicist’s conception of viscosity: the molecules of a viscous liquid do not diffuse and interpenetrate so rapidly as do those of non-viscous liquids.<sup>28</sup> Hamilton expected more generous dispositions in such viscous populations than in populations with high dispersal rates and panmictic structure, which should exhibit more disinhibited competition.<sup>29</sup> However, his original model did not specify population structure. At the time of his 1964 model, the compatibility between the general model and the expectation that viscosity might favor altruism was not a problem. In the following years, however, Hamilton gave increasing thought to it.

### **Kin Selection and Group Selection**

A first stimulation for investigating population structure was the formulation of the concept of “kin selection,” simultaneously coined by the British population geneticist John Maynard Smith to describe the selection on traits evolving because of their effects on the bearer’s close kin.

As documented by Ullica Segerstrale,<sup>30</sup> Maynard Smith’s involvement was closely linked to the discussions on the levels of selection triggered by the publication of Vero Copner Wynne-Edwards’ book on *Animal Dispersal in Relation to Social Behavior*.<sup>31</sup> A British ecologist interested in behaviors, Wynne-Edwards proposed a unifying and coherent perspective on a wide array of biological phenomena. Wynne-Edwards’ starting point was the hypothesis that, just as fisheries were in danger of over-exploiting fish stocks, natural populations were at risk of over-exploiting their own resources and thus going to extinction. He conjectured that, to overcome these risks, populations had evolved mechanisms enabling them to control their own growth rate. He reinterpreted a wide number of behaviors in the light of this hypothesis. An important example was territorial behavior. In territorial species, individuals take control of a site, usually to find a mate and rear offspring, and prevent

28. Hamilton to Ronaldo Zucchi, 10 December 1967, WDHP, Z1Box 89.

29. Hamilton, “Genetical Evolution II” (ref. 5), 10.

30. See Ullica Segerstrale, *Defenders of the Truth* (ref. 1).

31. Vero-Copner Wynne-Edwards. *Animal Dispersion in Relation to Social Behavior* (Edinburgh: Oliver and Boyd, 1962). For a recent reappraisal, see Borrello, *Evolutionary Restraints* (ref. 1).

conspecifics from using or breeding in this site. Serious empirical data suggested that territorial behavior limited the numbers of breeders in an area. Wynne-Edwards claimed that this was the function of territoriality. Territorial behavior was a behavioral mechanism enabling a population to control the number of potential reproducers in a given area.

For partisans of individual selection, addressing Wynne-Edwards' claims involved two kinds of responses. The first response implied clarifying the mechanism of natural selection and constraining accordingly the hypotheses on the adaptive value of behaviors. Serious thought was required to stabilize the vocabulary in evolutionary biology, and identify which kind of explanation was acceptable, and which was not, in the adaptive study of behavior. This approach was chosen by naturalists, such as David Lack, Jerram Brown, and George Williams.<sup>32</sup> The second response came from the development of population genetics models designed to show the conditions under which group selection could, or could not, occur. Maynard Smith's *Nature* paper took place among the second kind of responses.

Maynard Smith (1920–2004) had built his reputation on elegant experiments on the genetics of *Drosophila subobscura* in Haldane's laboratory at University College, London. In the early 1960s, he was making a transition from experimental genetics to model making.<sup>33</sup> In 1964, he published a note in *Nature* on "Group Selection and Kin Selection."<sup>34</sup> This note was a modified, and very much abridged, version of a manuscript titled "Territory, Group Selection and Evolution" written in collaboration with his wife, Sheila. This long manuscript was composed of two population genetics models designed to cast doubt on Wynne-Edwards' scheme. The first model accounted for territorial behavior in terms consistent with individual selection.<sup>35</sup> For unknown reasons, Maynard Smith reduced the size of the paper and deleted the model on territoriality. Hence the published paper only gave a group selection model,

32. David L. Lack, *Ecological Adaptations for Breeding in Birds* (London: Methuen and Co., 1968); Jerram L. Brown, "Types of group selection," *Nature* 211 (1966): 870. Williams, *Adaptation and Selection* (ref. 6). See also Mark E. Borrello, "Synthesis and Selection: Wynne-Edwards' Challenge to David Lack," *Journal of the History of Biology* 36, no. 3 (2003): 531–566.

33. On Maynard Smith, see Brian Charlesworth and Paul Harvey, "John Maynard Smith. 6 January 1920–19 April 2004," *Biographical Memoirs of Fellows of the Royal Society*, 51 (2005): 253–265. For Hamilton's complex relationships with Maynard Smith, see Segerstrale, *Defenders of the Truth* (ref. 1), 53–78, and Segerstrale, *Nature's Oracle* (ref. 5), 173–188.

34. Maynard Smith, "Kin Selection and Group Selection" (ref. 6).

35. John and Sheila Maynard Smith, "Territory, Group Selection, and Evolution," *JMSP*, 86 649.

the so-called haystack model.<sup>36</sup> This model assumed a population of mice, structured in semi-isolated colonies—haystacks—composed of the progeny of a single fertilized female. The altruistic allele was counter-selected in a haystack, while giving an advantage to the haystack productivity. In part because of the initial assumptions of this model, the conditions for altruism to be favored were particularly stringent. Maynard Smith claimed that another mechanism could favor more easily the spread of altruistic traits: “kin selection,” whose invention he credited to Haldane and Hamilton, and which could occur in any interaction between related individuals. Thus, kin selection seemed a distinct mechanism accounting for the presence of altruistic characters without invoking the benefit of the group.

While his discussion of kin selection in the *Nature* note was still verbal, Maynard Smith devised in 1965 a kin selection model on the evolution of alarm calls in birds.<sup>37</sup> This model exemplified the terminological difficulties that were about to impede later discussions on the levels of selection. The objective was assessing the conditions for the spread of an altruistic trait in a flock without invoking group selection. But in the model the population was composed of sib groups, and altruism evolved because of this group structure. Furthermore, the coefficient of relationship  $r$  was not used as a variable. “It would be desirable to work out the conditions for the spread of alarmism in the more general case in terms of the mean coefficient of relationship between the members of a flock,” Maynard Smith admitted. “I have been unable to do this.”<sup>38</sup> From the time of its formulation, the mechanism of kin selection was

36. As observed by Sober and Wilson, *Unto Others* (ref. 1), an assumption in this model made the haystack model a worst-case for group selection: Maynard Smith assumed very strong selection in haystacks, so that the altruistic allele was eliminated in mixed colonies before migration. In other words, group selection was between pure altruistic and pure selfish colonies. Maynard Smith’s model did not allow mixed colonies to reap benefits from the presence of altruists. See also David Sloan Wilson, “Altruism in Mendelian Populations Derived from Sibling Groups: The Haystack Model Revisited,” *Evolution* 41, no. 5, (1987): 1059–1070, on 1060.

37. John Maynard Smith, “The Evolution of Alarm Calls,” *The American Naturalist* 99, no. 904, (1965): 59–63.

38. *Ibid.*, 62–63. Maynard Smith’s model was similar to a model built previously by George and Doris Williams aiming at altruism in sib-groups, designed to account for the evolution of social adaptations in termites. George C. and Doris Williams, “Natural Selection of Individually Harmful Social Adaptations among Sibs with Special Reference to Social Insects,” *Evolution* 11, no.1 (1957): 32–39. Maynard Smith’s model improved Williams and Williams’ model by making a stability analysis of the equilibria. George Price (see below, the section bearing his name) later objected to Maynard Smith that his was a group-selection model: “You do not show a gene for altruistic behavior spreading in a flock by individual selection, but instead show selection between

thus ambiguous. According to the definition, it was distinct from group selection, since it did not require a group structure. But Maynard Smith's own use of the concept implied a structuration into groups.

The formulation of the concept of kin selection by John Maynard Smith had two effects on Hamilton. In the long term, Hamilton became known as the father of kin selection—a term of which he was certainly not the author, which he rarely employed, and about which he expressed reservations.<sup>39</sup> In the short term, he had to define his views in relation to Maynard Smith's mechanism.

### **An Internal Tension in Inclusive Fitness Theory**

A second stimulation for investigating population structure was related to the internal consistency of Hamilton's theory. Hamilton's original model had been framed into the classical theory of deterministic systems. By demonstrating that inclusive fitness was maximized in a model with one locus and  $n$  alleles, infinite population size—without drift—and no specific pattern of interaction between agents, Hamilton had shown that altruism could evolve in the class of models seemingly the most hostile to the evolution of altruism. However, population structure seemed to play a role in the selection on altruism, since a viscous population structure, facilitating interactions between kin, would be more efficient in spreading the altruistic gene. Thus, there was a tension between the classical, deterministic framework in which Hamilton had originally designed his main results and the conditions he saw as most favorable to the evolution of altruistic relationships.

Furthermore, Hamilton came to think that his model did not fit the biological situations he had in mind. All populations are of finite size, and more importantly, all of them present some degree of structuration. Hamilton was especially interested in the behavior of social Hymenoptera. He paid close attention to the problems raised by polygynous colonies of tropical wasps.

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flocks. The matter of relatedness of flock members is not directly relevant [*sic*] to the result, but is just a way to obtain (in a biologically plausible way) high intergroup variance." (Price to Maynard Smith, 19 Oct 1972, JMSP, Ms 86 597B). Maynard Smith disagreed: "I'm still inclined to think that, at least by the definition in my 1964 paper, alarm notes are a case of kin selection. If you look at my definition I think you'll agree—of course you may not like the definition!" (Maynard Smith to Price, 24 Oct 1972, JMSP, Ms 86 597B).

39. See Hamilton, "Sociobiology: The New Synthesis, by E. O. Wilson," *Journal of Animal Ecology* 46, no. 3 (1977): 975–977.

A polygynous colony is founded by several females, which cooperate during the early stage of the colony before one female eventually monopolizes reproduction. It seemed to him that the behavior of females choosing to found together a colony would make sense if they were both related and inbred. Thus, the social behavior of organisms Hamilton was especially interested in seemed to call for the consideration of inbreeding in inclusive fitness calculations.<sup>40</sup>

Hence, Hamilton came to feel that substantial modifications of his original work were required. These preoccupations were made public in his communication at the Symposium on “Man and Beast” held in Washington in May 1969. There he briefly reviewed the major topics he would investigate in a much more systematic way in the early 1970s: the evolution of spite, the limits of altruism in a viscous population owing to the competition between kin, the attempts to find a formalism that allowed dealing jointly with inclusive fitness and population structure, and the use of the prisoner dilemma in modeling social interactions.<sup>41</sup> Hamilton conjectured on the factors generating viscosity. In Wright’s island model as well as in Motoo Kimura and George Weiss’s stepping stone model,<sup>42</sup> limited dispersal maintained relatively high levels of inbreeding. But he had to connect these population-structured models to his concept of inclusive fitness, which was defined without population structure. Hamilton considered using the  $F$  statistics developed by Wright, but was not fully convinced that they were adequate to problems of social evolution, since they were devised (as coefficients of relationship) for neutral genes.<sup>43</sup>

Thus, before exchanging with Price, Hamilton was searching for a hierarchical model combining inclusive fitness and population structure. The formalism developed by George Price gave him the tool he was searching for.

40. See William D. Hamilton, “Altruism and Related Phenomena, Mainly in Social Insects,” *Annual Review of Ecology and Systematics* 3 (1972): 193–232.

41. William D. Hamilton, “Selection of Selfish and Altruistic Behavior in Some Extreme Models,” in *Man and Beast: Comparative Social Behaviour*, ed. John F. Eisenberg and Wilton S. Dillon (Washington, DC: Smithsonian Press, 1971): 57–91.

42. Sewall Wright, “Isolation by distance,” *Genetics* 28, no.2 (1943): 114–138. Motoo Kimura and George H. Weiss, “The Stepping Stone Model of Population Structure and the Decrease of Genetic Correlation with Distance,” *Genetics* 49, no.4 (1964): 561–576.

43. Hamilton to West-Eberhard, 5 Oct 1967, WDHP, Z1 Box 83.

## THE HAMILTON-PRICE COLLABORATION

### George Price

George Price (1922–1975) has been recently the center of much interest.<sup>44</sup> Oren Harman has shown in detail how, after putting an end to a first career in chemistry, Price went to London in 1967 and became interested in biological approaches to human nature. These evolutionary speculations followed a new trend after Price read Hamilton's paper on the evolution of social behaviors. Struck by Hamilton's conclusions, Price thought about the problem of altruism, tried to derive Hamilton's results in a more transparent model, and developed a new equation describing the process of selection. In July 1969, Price wrote to Hamilton that he had developed a surprisingly simple equation to study the change in genetic frequencies under the effect of selection.<sup>45</sup> Price explained that his results led to conclusions differing from those drawn by Hamilton. The subsequent exchanges between them materialized into two papers published in *Nature*, "Selection and Covariance" by Price in August 1970 and "Selfish and Spiteful Behaviour in an Evolutionary Model" by Hamilton in November of the same year.<sup>46</sup>

Price's paper was a very concise presentation of his equation. Applied to the field of genetics, the Price equation is a method for studying the change in frequency of a gene, "the basic event in biological evolution," through its statistical association with fitness.<sup>47</sup> In the first sentence of his paper, Price insisted on the generality of his equation.

The following equation . . . , which gives frequency change under selection from one generation to the next for a single gene or for any linear function of any number of genes at any number of loci, holds for any sort of dominance or epistasis, for sexual or asexual reproduction, for random or non-random mating, for diploid, haploid or polyploid species, and even for imaginary species with more than two sexes.<sup>48</sup>

44. The main reference is S. A. Frank, "George Price's Contributions to Evolutionary Genetics," *Journal of Theoretical Biology* 175, no. 3 (1995): 373–388. See also James Schwartz, "Death of an Altruist," *Lingua Franca*, 10 (2000): 51–61; and Oren S. Harman, *The Price of Altruism: George Price and the Search for the Origins of Kindness* (New York, W.W. Norton, 2010).

45. Price to Hamilton, 28 Jul 1969, WDHP, Z1 Box 89.

46. George R. Price, "Selection and Covariance," *Nature* 227 (1970): 520–521. William D. Hamilton, "Selection of Selfish and Altruistic Behaviour in an Evolutionary Model," *Nature* 228, no. 5277 (1970): 1218–1220. See Hamilton, *Narrow Roads* (ref. 5), 169–176.

47. Price, "Selection and Covariance" (ref. 46), 520.

48. *Ibid.*, 520.

This sentence deserves a comment. The classical approach, in a population genetics model, consists of starting with simplifying assumptions and adding complicating factors step by step. Thus, Sewall Wright, in describing the effect of selection on the change in gene frequencies, had built an index dependent on simplifying assumptions (his mean fitness function, dependent on the assumption of random mating and infinite population size), and modified it later depending on the problem of interest.<sup>49</sup> The Price equation takes a different approach: rather than starting with simplifying assumptions, it starts with the change in gene frequency, whatever the assumptions made about the genetic machinery implied in this system, and partitions it by isolating the component of selection from the other components.

A second unusual feature of this equation is its way of analyzing the change in gene frequencies from one generation to the next. The basic entities targeted by the Price equation are not genotypic frequencies, but individuals. To understand this focus, one can start with the idea that gave rise to it, the mechanism of kin selection. Under kin selection, the frequency of an altruistic allele is expected to increase if it favors the survival or reproduction of the bearer's kin. Price observed that, in this case, gene frequency increases or diminishes depending on the "dose" of this allele present in the genotypes of the recipients of the behavior: it increases if recipients bear this allele at high concentrations (they are related to the actor) and decreases if they bear it at low concentrations (they are less, or not related to him). Price found in this observation the inspiration to think about evolutionary change in terms of the content of the genotypes of *individuals*.

Price's approach separates, in the change in gene frequency, the component of selection from other components. In a model with separate generations, the change in gene frequency is given by:

$$\Delta q = q' - q = \frac{\text{Cov}(z_i, q_i)}{\bar{z}} + \frac{\sum_i z_i \Delta q_i}{N\bar{z}}$$

Here,  $q$  and  $q'$  are the mean frequencies of the allele of interest in a population of size  $N$  at one generation and the next. In the right-hand side of this equation, the first term is the covariance between the individual fitness  $z_i$  of individual  $i$  and its gene dosage  $q_i$ , that is, the number of copies of the allele present in its genotype (e.g., in a diploid species, the dosage can be 0, 1, or 2

49. See Sewall Wright, *Evolution and the Genetics of Populations*, Vol. 2 of *The Theory of Gene Frequencies* (Chicago: University of Chicago Press, 1969).

copies of the gene), as weighted by the mean fitness  $\bar{z}$  in the population. This is the selection component. The second term describes the fidelity of the transmission from one generation to the next. If, for example, sampling effects caused by finite population size, or newly occurring mutations, perturb the process of transmission of gene frequencies from one generation to the next, then the value of this second term will be different from zero.

Price's equation has sometimes been presented in the historiography of social evolution as the major equation searched by generations of scientists.<sup>50</sup> However, this equation hardly filled a gap in the eyes of evolutionists. "I am not sure that any other evolutionary biologist sees the interest of his covariance formula for natural selection in the way that I do . . .,"<sup>51</sup> Hamilton observed after Price's death in 1974. The interest of this equation was not immediately apparent. The advantages in terms of calculations were nonexistent. As Price admitted, "identifying a relation of covariance (or regression or correlation) is of no interest for numerical calculation."<sup>52</sup> Where would lie its interest? Price laid the emphasis on two aspects. First, it helped to clarify the evolutionary reasoning. The Price equation allowed a graphical representation of the problems involving natural selection. The information on the direction of selection was given by the sign of the regression coefficient of fitness on gene dosage. This graphical representation, suggested Price, gave a useful method to formulate problems in evolutionary biology:

at any step in constructing hypotheses about evolution through natural selection—for example, about why human canines do not protrude, why deer antlers are annually shed and renewed, why parrots mimic, why dolphins play—one can visualize such a diagram and consider whether the slope really would be appreciably non-zero under the assumptions of the theory. If there is no slope, then there is no frequency change . . . and the hypothesis is probably wrong.<sup>53</sup>

But, the reader could object, if a gene or a trait covaries with fitness, it is because it is of advantage or disadvantage. Formulating this selective advantage in terms of covariance or regression was limited to reformulating something

50. See Harman, *Price of Altruism* (ref. 44), and Dugatkin, *The Altruism Equation* (ref. 1).

51. Hamilton to Edison Price, 15 Feb 1975, WDHP, 21X102. James F. Crow and T. Nagylaki, "The Rate of Change of a Character Correlated with Fitness," *American Naturalist* 110, no. 972 (1976): 207–213.

52. Price, "Selection and Covariance" (ref. 46), 520.

53. *Ibid.*

that was already known. It was hard to see to what extent the formulation of a statistical relationship between two variables could facilitate the analysis of a given problem.

Price advanced a second asset. It was a very convenient tool to formulate problems. In his insightful presentation of the Price equation, Steven Frank has commented on this aspect:

The first steps in using the equation are often quite difficult because one has to match the problem to the strange notation. This requires labelling individuals, genotypes or groups in a nonstandard way. Once the right structure is found, solving problems seems very natural both algebraically and biologically. The gain is in forcing one, right at the start, to look for the strange twist that makes the solution inevitable.<sup>54</sup>

These gains were not immediately apparent at a first reading of Price's paper, which was a very short note. Price's original manuscript was a long and complex text, in which Price showed in detail how to use his equation and why it was useful. He applied his equation to numerous specific cases, such as group selection and sex-linked genes and considered difficulties, such as the role of reproductive value and the effects of class- or age-structuration. He chided some critics of natural selection, and gave anecdotic examples. On the contrary, the published version was disconcertingly concise. The brief, elliptic, and austere format of this paper certainly affected its reception.

To use the Price equation, one had either to be familiar with covariance reasoning or to be informed by personal contacts that it was a useful tool to formulate problems related to selection. Familiarity with covariance reasoning led to results similar to the Price equation, but not to using it. At the University of Edinburg a few years earlier, Alan Robertson had formulated the first part of Price's equation describing the rate of change of a character in function of its covariance with fitness.<sup>55</sup> C. Clark Cockerham, one of the main experts on quantitative genetics in the United States, was developing similar methods.<sup>56</sup> These quantitative geneticists were routinely manipulating variance and covariance components, but they had their own way of using this statistical machinery (the partitioning into components of genetic and phenotypic variance). Furthermore, they rarely paid attention to evolutionary issues; their

54. Frank, "George Price" (ref. 44), 379.

55. Alan Robertson, "A Mathematical Model of the Culling Process in Dairy Cattle," *Animal Production* 8, no. 95 (1966): 95–108.

56. Hamilton to Price, 5 Dec 1969, GRPA, 84 116.

efforts were focused on applied research, such as the improvement of breeding methods. This left only personal interactions for circulating the equation. Price himself played little role in making his equation known: he lost interest relatively quickly in evolutionary theory and died soon thereafter. Hence, Price's equation circulated mainly through Hamilton's own research and teachings. Hamilton prepared teaching materials on the Price equation for his students at Imperial College and, later, at Michigan University.<sup>57</sup> Most importantly, he put it to work in his own papers.

### Hamilton and Spite

Hamilton originally found in the Price equation a new method to derive his own results. In a model assuming weak selection and finite size, he was able to derive in a few steps an equation for the increase in frequency  $\Delta q$  of a gene, depending on the covariance between the gene dosage in a genotype and its inclusive fitness effect,  $x_i$ :

$$\Delta q = \frac{\text{Cov}(q_i, x_i)}{\bar{w}}$$

This reformulation of inclusive fitness theory in the formalism developed by Price enabled Hamilton to deal with a theoretical difficulty unmentioned in his 1964 paper. In 1964, Hamilton had defined spite as a trait deleterious to the fitnesses of both actor and recipient. Spite was then only a theoretical possibility—an entry in a matrix—and seemed relatively implausible as an adaptation. Consideration of the effects of finite population size gave some content to this possibility.

In his letter to Hamilton, Price suggested that indeed important modifications appeared when one gave up the assumption of infinite population size.<sup>58</sup> The major effect concerns the measure of relatedness between members of a population. In a population of infinite size, the mean relatedness between an

57. Hamilton also encouraged other researchers in correspondence to use it. In his PhD dissertation at Harvard, Jon Seger used the Price equation to build consistent indices of relatedness in kin selection models (see Jon Seger, "Kinship and Covariance," *Journal of Theoretical Biology* 91, no.1 (1981): 191–213). Seger observed to Hamilton: "after seeing what it did for my thesis, I'm convinced that Price's theorem will turn out to be a great aid to clear thinking and model construction even in, or perhaps especially in, those cases where the existence of a positive correlation between dosage and fitness is *not* obvious on reflection" (Jon Seger to Hamilton, 6 Mar 1981, WDHP, Z1 Box 63).

58. Price to Hamilton, 28 Jul 1969, WDHP (ref. 45).

individual and the other members of the population is zero. This is not true in a population of finite size, in which all members are to some extent related. This greatly affects the calculation of inclusive fitness. In a population of finite size, some members in the population can have a *negative* relatedness to the actor: they are simply less related to a given individual than a random member of the population would be. The existence of negative coefficients of relatedness is of consequence for social behaviors. It can make sense, in an inclusive fitness perspective, to decrease the representation of less-related genes in the next generation, even if this affects the actor's own prospects of survival or reproduction: in essence, spite against less-related individuals means making room for more replica genes identical to one's own genotype. Hence, on paper, spiteful adaptations could evolve under natural selection.

However, despite a real interest in the concept, Hamilton did not find a single convincing example of spiteful behavior in animals. After suggesting several plausible reasons for this absence, Hamilton concluded that it was more a theoretical curiosity than a phenomenon likely to evolve in natural populations. "Spite is unlikely to become permanent and elaborated into a complex adaptation."<sup>59</sup> The importance of the 1970 paper lay less in its apparent result—the modeling of the conditions for spite—than in its formal achievement. For Hamilton, the 1970 paper was first and foremost a confirmation of the results obtained six years earlier. "I had been delighted with the results not so much because of spite, which even now I regard as practically a non-starter for important evolutionary effects . . . but because I could reformulate all the results that I had had before in my 1964 paper in a vastly more economical and appropriate way."<sup>60</sup> The maximizing properties of inclusive fitness had been established in a new, much simpler model, without affecting the major conclusions. "Taken together these points suggest that my previous account is not seriously inaccurate for social behaviour in realistic circumstances."<sup>61</sup> In the views of its author, the theory of inclusive fitness had successfully assimilated Price's formalism.

### **Altruism, Nepotism, Spite**

Despite their intellectual affinities, Hamilton and Price viewed their two papers in a different light. When he wrote to Hamilton in 1969 to tell him

59. Hamilton, "Selfish and Altruistic Behaviour" (ref. 41), 1120.

60. Hamilton, *Narrow Roads I* (ref. 5), 175.

61. Hamilton, "Selfish and Altruistic Behaviour" (ref. 41), 1120.

the results he obtained with his equation, Price insisted that Hamilton had made a “mistake” in his 1964 paper and urged him to acknowledge it in print.<sup>62</sup> This mistake was exposed in an unpublished manuscript, the “Mathematical Genetics of Nepotism,” in which Price used his equation to claim that Hamilton’s mechanism did not favor genes beneficial to all members of a group.<sup>63</sup> When Hamilton eventually published his *Nature* paper, presenting it as vindicating his previous analysis, Price felt that Hamilton had somewhat blurred the limitations of kin selection. Later, he regretted the lack of explicit retraction by Hamilton in a letter to John Maynard Smith:

Hamilton’s 1964 mathematics is wrong and “kin selection” doesn’t work—at least not by his model. I have a clear mathematical demonstration of this, which I showed to Bill when he got back from Brazil . . . He has somewhat slurred over the matter of his being mistaken, and he does not give my full mathematical demonstration that kin selection does not work in the way he described. . . .

What “kin selection” will do is increase the frequency of a gene that causes animals to give greater benefit (or smaller harm) to near relatives, which means that more distant relatives in a group must be relatively harmed. It will not cause increase in frequency of a gene that causes animals to benefit the group as a whole: there must be some members of a group that are relatively harmed for a gene to spread in the group by Hamilton’s mechanism.<sup>64</sup>

What was Hamilton’s “mistake?” Price’s objection was stated as a mathematical derivation of kin selection, but it ultimately concerned Hamilton’s *explanandum*. Price objected to Hamilton that his mechanism did not favor the evolution of altruism, if one meant by this term the evolution of behaviors unconditionally favorable to others; he had produced a model for the evolution of nepotistic preference. A recent discussion on the semantics of spite illustrates Price’s objection.<sup>65</sup> To evolve under Hamilton’s mechanism, a spiteful behavior must be ultimately beneficial to the actor’s close kin. In other words, as paradoxical as it may seem, “spite” is a form of “altruism.” Conversely, in a population of finite size, an altruistic behavior *has* negative consequences on the fitness of nonrecipients: by favoring the fitness of genetically closer individuals, the seemingly altruistic behavior decreases likewise the representation

62. Price to Hamilton, 28 Jul 1969, WDHP (ref. 45).

63. Price, “The Mathematical Genetics of Nepotism,” WDHP.

64. Price to Maynard Smith, 19 Oct 1972, JMSP, Add. Ms 86 597B.

65. Stuart A. West and Andy Gardner, “Altruism, Spite, and Greenbeards,” *Science* 327, no. 5971 (2010): 1341–1344, on 1343.

of genes of other members of the population that are less genetically related to the donor. Here lay Price's basic objection to Hamilton: this equivalence between spite and Hamiltonian altruism made "kin selection" or "nepotism" a very poor candidate for the evolution of altruism. Hamiltonian altruism hardly provided a theory for the evolution of true goodness.

This objection did not particularly affect Hamilton. Later he admitted in his lectures that the term "altruism" could be misleading, since altruistic behaviors turn out to be little else than nepotistic strategies.

While admitting that nepotism is a poor sort of altruism, certainly not altruism in the highest human sense of the word—it does seem to me to vividly convey the character of the phenomenon we have been talking about. I felt its use was justified in the same way as the physicists' use of "work" and "power" and "energy" is justified, but I have to admit that those words are not emotionally charged quite like "altruism."<sup>66</sup>

But Hamilton had no reservations about his theory. The objective of a population genetics model is to state conditions for the increase in frequency of a gene; if these conditions are related to natural selection, this means that this gene is fitter than the others. As Robert Trivers puts it, "Models that attempt to explain altruistic behavior in terms of natural selection are models designed to take the altruism out of altruism."<sup>67</sup> Or, as Alan Grafen observes to us, from Hamilton's point of view, altruism had been the problem. Nepotism was the answer.<sup>68</sup>

### Group Selection and the Evolution of Man

Price, for his part, wanted a model that would keep the intuitive properties of altruism, being unconditionally costly to the altruist *and* unconditionally beneficial to the recipient.<sup>69</sup> He expected that group selection would provide the mechanism to select for such unconditional altruism. Despite not sharing these expectations, Hamilton strongly encouraged him to explore this direction. "In its general form I can see how one might use your formula to investigate 'group selection.' Probably this is a line of thought you have already followed, and

66. Hamilton, Lecturing notes at Imperial College, ca 1975, WDHP, Z1 Box 90.

67. Robert L. Trivers, "The Evolution of Reciprocal Altruism," *Quarterly Review of Biology* 46, no. 1 (1971): 35–57, on 35.

68. Alan Grafen, pers. communication to the author, 13 Oct 2013.

69. This aspect has been emphasized by Harman, *Price of Altruism* (ref. 44).

which has allowed you to state your belief that ‘group selection,’ as distinct from selection of inclusive fitness, really occurs.”<sup>70</sup> Even before collaborating with Price, Hamilton had kept a strong interest in the issue of the levels of selection, and he never refrained from mentioning group selection as a possible and efficient mechanism. When first trying to devise a model for the evolution of altruism in the early 1960s, he had followed the advice of his supervisors and developed Haldane’s model. It was only after realizing the limitations of this model that Hamilton turned to another mechanism.<sup>71</sup> While giving up Haldane’s model, he kept an open mind on the issue, as if he had tried to keep some corners for heterodoxy in the new orthodoxy he was forging in social evolution theory.<sup>72</sup>

A strong stimulation, in this regard, came from his interest in the evolution of humankind.<sup>73</sup> This interest had convinced him at first that altruism was a problem deserving evolutionary inquiry.<sup>74</sup> As a high school student, Hamilton had been influenced by the books of Arthur Keith (1866–1955), a paleoanthropologist famous for his “group theory,” which stated that, at its earliest stages, the human species was composed of very small isolated groups that diverged later to form the different races.<sup>75</sup> Inspired by this theory, Hamilton explained in 1965 to John Pfeiffer, a science writer interested in anthropology,

70. Hamilton to Price, 5 Dec 1969, GRPA, 84 116.

71. Hamilton to West-Eberhard, 26 Feb 1979, WDHP (ref. 12).

72. Here are some examples. In his second 1964 paper, Hamilton invoked an argument elaborated by Sturtevant based on interpopulation competition, to suggest how colonies of social insects would resist the invasion of selfish workers reproducing for themselves. See Hamilton, “Genetical Evolution II” (ref. 5), 34. At the London School of Economics, he ran computer simulations to investigate group selection effects on the frequency of a gene affecting sex ratio (William D. Hamilton, “Extraordinary Sex Ratios,” *Science* 156, no. 3774 (1967): 477–488, on 477–478). During the debate that flared up in 1968 between Crow and Kimura and Maynard Smith on the evolution of sex, Hamilton wrote to George Williams that he was favorable to the idea that long-term advantages explained the wide prevalence of sexual reproduction in nature (Hamilton to Williams, 5 Jul 1969, GCWP).

73. “Ayalat Shavit brought attention to the ideological implications associated with the emphasis on a definite “level” of selection.” The interpretation proposed here rather lays the emphasis on the evolution of humankind as a problem stimulating speculations on the evolution of social life in groups. See Ayelet Shavit, “Shifting Values Partly Explain the Debate over Group Selection,” *Studies in History and Philosophy of Science, Part C: Studies in History and Philosophy of Biological and Biomedical Sciences* 35, no.4 (2004): 697–720.

74. For a similar argument, see S. A. Swenson, “‘From Man to Bacteria’: W.D. Hamilton, the Theory of Inclusive Fitness, and the Post-War Social Order,” *Studies in History and Philosophy of Science, Part C: Studies in History and Philosophy of Biological and Biomedical Sciences* 49 (2015): 45–54.

75. Arthur Keith, *A New Theory of Human Evolution* (London: Watts and Co, 1948).

that from his point of view, group selection might well have played a role in the evolution of humankind. Partition of populations between tribes of small size would have raised coefficients of relationships inside tribes and thus reinforced the solidarity between tribe members. “Thus it may be that evolutionary arguments based on the rather vague concept ‘group selection’ are really sounder than my paper would seem to indicate, but this must depend very much on the extent to which vagrancy and exchange of genes between groups does occur.”<sup>76</sup> Even in 1965, Hamilton was not ready to accept uncritically Maynard Smith’s distinction between “kin” and “group” selection. Selection between groups would be effective if groups were composed of close kin: in this sense, kin selection could make group selection work. Hamilton was still skeptical, however, because migration rates between groups were expected to reduce differences between tribes.

This interest in humankind and group selection was shared by Price, who submitted in 1969 a grant application to the Science Research Council. This ambitious text mentioned most of the subsequent contributions of its author in the early 1970s; the concept of evolutionary stability, the problems raised by the modeling of group selection, sexual selection, and systems of limited conflicts were introduced in this research program. Price’s main objective was to develop mathematical tools for tackling the role of group selection in human evolution.

The main purpose of the work is to develop improved techniques for making inferences about hominid evolution in the Pleistocene going beyond what is directly shown by fossils and artefacts. It is felt that the most fruitful way to being is by developing (a) new mathematical treatments of evolution under conditions of complex social interactions, and (b) more simple and transparent mathematical genetics models that can provide rules-of-thumb for qualitative or semi-quantitative reasoning.<sup>77</sup>

Hamilton, who had not yet met Price at the time, was especially sensitive to this side of Price’s project.

I gather from the notes in general that his overall concern is with problems in human biology which I also consider very crucial: the extent to which all aspects of man are explicable in terms of genetical natural selection, and what “causes” the aspects which are not so explicable, if any. We hear many pleas nowadays about the need for further research into the nature of man

76. Hamilton to John Pfeiffer, 16 Feb 1965, WDHP, Z1 Box 89.

77. Price, “Proposal to the Science Research Council: On group selection, human evolution,” ca 1969, GRPA, 84 116.

rather than into the nature of the physical universe. I agree with this emphasis, and the work being offered in this application seems to me to be in just the field where enlightenment (of a philosophical kind at least) is most likely to be gained.<sup>78</sup>

### Mapping the Levels of Selection: The Variance Problem

It was only in 1972, after being urged by Hamilton to publish his views, that Price eventually published a brief and very austere paper in the *Annals of Human Genetics*, extending the mathematics of covariance and selection to the problem of the levels of selection.<sup>79</sup> Price's 1972 paper was designed as an illustration of the usefulness of his equation. This usefulness, Price had said, lay in the clarification of evolutionary problems rather than in numerical calculation. Indeed, the 1972 paper put the Price equation to work. The equation had been devised to partition the respective effects of selection and transmission in the change of gene frequency, Price showed how some algebraic substitutions could make it model different levels of selection.

Let  $G$  be a population composed of isolated subgroups  $G_i$  (no migration), in a model with separate generations. The size of subgroup  $G_i$  is  $n_i$  in the parental generation and  $n'_i$  in the next generation. Let  $P$  be the frequency of the gene  $A$  in the whole population  $G$ ;  $p$  and  $s$  are, respectively, the frequency of  $A$  and the mean fitness in a subgroup  $G_i$ . Price used his equation to show how to partition the change in frequency of  $A$  in two components:

$$\Delta P = Cov_n(s, p) + E_{n'}(\Delta p)$$

Here,  $Cov_n(s, p)$  is the covariance between mean fitness and gene frequency in the subgroups, weighted by subgroup size  $n$ . This component describes the genetic variability between groups on which group selection can act. The second term,  $E_{n'}(\Delta p)$ , is the mean change of the frequency of the gene in the groups from one generation to the next.

Since  $\Delta p$  can itself be decomposed with the Price equation, Price partitioned the second term  $E_{n'}(\Delta p)$  to obtain a more transparent result. Writing  $q$  the dosage in gene  $A$  of a given individual in a subgroup  $G$ , and  $z$  as its fitness, Price obtained the following result, expressing the change in frequency of a gene as the sum of two covariance terms:

78. Hamilton to P. H. Williams, 2 May 1969, GRPA, 84 116.

79. George R. Price, "Extension of Covariance Selection Mathematics," *Annals of Human Genetics* 35 (1972): 485–490.

$$\Delta P = Cov_n(s, p) + E_n'(Cov(z, q))$$

Price proposed to view this equation “as a ‘two-level’ selection equation involving two different ‘levels’ of selection.”<sup>80</sup> As before, the first term, which describes the covariance between mean fitness and gene frequency in a subgroup, is the index of selection between the subgroups. The second term, which describes the covariance between gene dosage and individual fitness, is the index of selection in each subgroup. Both levels of selection were thus integrated in a single equation describing the change in gene frequencies from one generation to the next. “Group selection” and “individual selection” were no longer seen as qualitative alternatives, but as processes of greater or lesser intensity. The conceptual debate on the classes of explanation acceptable in evolutionary thinking left room for a quantitative assessment of the relative efficiency of selection at different levels.

However, Price’s equation did not solve the basic problem under investigation. Consideration of the equation shows that for group selection to work, covariance between gene frequencies and fitness among subgroups is needed. On the factors generating this variance Price remained cautiously silent. He had produced a map of the operations of selection at different levels, but he had not given any hint about the mechanisms able to generate variance between groups and, thus, giving material for group selection to occur.<sup>81</sup> Genetic drift in populations, and sampling effects in the founding of new populations, may temporarily provide the needed mechanism. But this variance would soon be exhausted by group selection itself. Hamilton objected to Price: “Your formula merely shows that in certain situations the ‘group selection’ component can override the ‘individual selection’ component: you don’t discuss how such situations can arise naturally, and it is here that it seems to me essential to consider mechanisms generating a variance between populations—genetic drift, accidental constitutions of founder populations and so on.”<sup>82</sup> This problem was central to the assessment of group selection models. Hamilton wanted to identify which processes can generate, on a regular basis, between-group variance: “[E]ven the possibility of devising model circumstances in which a positive group-selection term (first-term) outweighs

80. *Ibid.*, 488.

81. Thus, Price contacted Sewall Wright to enquire whether Wright had given a mathematical treatment of the process of differential migration in interdeme selection that he had discussed in 1945 (Price to Wright, 10 May 1968, SWP).

82. Hamilton to Price, 28 Nov 1971, GRPA, 84 116.

a negative individual selection one (second term, assuming no further levels), gives no guarantee that ‘altruism’ can evolve by group selection: we have to consider whether the population can get into the specified state, and, if it can, whether its present trend will continue.”<sup>83</sup>

Thus, while Price objected to Hamilton’s theory of altruism, Hamilton had reservations of his own about Price’s treatment of the levels of selection. “However,” Hamilton concluded in his letter to Price, “I have high hopes that your covariance formulae will eventually produce an account of group selection.”<sup>84</sup>

## **ALTRUISM IN POPULATION-STRUCTURED MODELS: TRIVERS, ESHEL, HAMILTON**

### **Trivers and the Theory of Reciprocal Altruism**

In the early 1970s, two texts convinced Hamilton to use his inclusive fitness method to model the problem of altruism in structured populations. The first was “The Evolution of Reciprocal Altruism” by Robert Trivers. The second was a model on the evolution of altruism under a “neighbor effect,” by the Israeli mathematician Ilan Eshel.

A graduate student at Harvard, Robert Trivers (b. 1943) made himself known in the early 1970s as the first disciple of Hamilton’s thinking, extending kinship theory and making it understandable to larger audiences of scientists. The theory of reciprocal altruism represented his first major contribution in this area.<sup>85</sup> Trivers proposed a mechanism for the evolution of altruism that did *not* rely on kinship. Altruistic traits could evolve without kin relationships, Trivers argued, provided that their author would benefit later from their effects, usually by benefitting from the reciprocal help of the recipients. Hence, an altruistic trait could be selected because of its return effect. The main condition, for this kind of behavior to evolve, was to focus altruistic acts

83. William D. Hamilton, “Innate Social Aptitudes of Man: An Approach from Evolutionary Genetics,” in *Biosocial Anthropology*, ed. Robin Fox (London: Malaby Press, 1975), 133–155. Reprinted in Hamilton, *Narrow Roads I* (ref. 5), 315–352, on 333. References will be made to this latter version.

84. Hamilton to Price, 28 Nov 1971, GRPA, 84 116.

85. Trivers, “Reciprocal Altruism” (ref. 67). See Robert L. Trivers, “Reciprocal Altruism: 30 Years Later,” in *Cooperation in Primates and Humans*, ed. Peter M. Kappeler and Carel P. Van Schaik (Berlin: Springer-Verlag, 2006), 67–83.

toward a specific class of recipients, that is, toward altruists able to reciprocate later.

Trivers' argument was aimed at dislodging long-term advantages of cooperation typical of "group selection" arguments in favor of short-term advantages, consistent with individual fitness. However, his treatment was not devoid of ambiguities. The example of alarm calls in birds can illustrate this point. This example had been given by Hamilton in his 1964 paper, and later modeled by Maynard Smith, as a case of kin selection.<sup>86</sup> Trivers reinterpreted this example by suggesting that alarm calls could be of direct advantage to the caller, because they limit the predator's efficiency. Trivers' reasoning was as follows. The efficiency of a predator depends on its having the right search pattern for the prey. This search pattern is not innate: the predator learns it by catching preys. According to Trivers, the calling bird reduces the probability that the predator catches a conspecific prey and learns the search-image, enabling it to catch more conspecifics. By way of consequence, it limits the chance that the caller itself will end up being caught by the predator. It was unclear how alarm calls, under Trivers' mechanism, would resist being used by cheaters, benefitting from the presence of callers without taking the risk of calling themselves. Here Trivers' argument seemed very close to a group selection argument.

It does not matter that in giving a warning call the caller is helping its non-calling neighbor more than it is helping itself. What counts is that it outcompetes conspecifics from areas in which only one is giving warning calls. The non-calling neighbors of the caller (or their offspring) will soon find themselves in an area without any caller (or will be selected against) relatively to birds in an area with callers. The caller, by definition, is always in an area with at least one caller. If we assume that two callers are preferable to one and so on, then selection will favor the spread of the warning-call genes. Thus, individuals living in groups having altruists have a higher mean reproductive success than those living in groups composed of non-callers.<sup>87</sup>

Without an explicit model, this mechanism allowed for different interpretations. One could interpret it as the result of relatedness between alarm callers, due to the local structure of the population. One could as well interpret it as a kind of group selection, groups of altruists outcompeting groups of selfish members. Trivers tried to preclude this latter interpretation by arguing that

86. Maynard Smith, "The Evolution of Alarm Calls" (ref. 37).

87. Trivers, "Reciprocal Altruism" (ref. 67), 44.

group selection required isolated groups, that is, no dispersal. “Note that this model depends on the concept of open groups, whereas ‘group selection’ depends partly on the concept of closed groups.”<sup>88</sup> This contorted discussion reflects quite well the ambiguities inherent to these new speculations. The rejection of uncritical “benefit of the species” explanations led to consideration of new mechanisms. However, in these new postulated mechanisms, the distinction between individual selection and group selection was not that clear. The ambiguity resulted from the fact that population structure clearly mattered for the evolution of altruism. Repeated interactions between altruists were needed to provide an advantage to altruism and avoid parasitism. “What matters for the evolution of reciprocal altruism is that the same two individuals interact repeatedly.”<sup>89</sup>

Despite some reservations, Hamilton was impressed by Trivers’ idea.<sup>90</sup> Reciprocal altruism seemed to be a mechanism independent of relatedness. More generally, Trivers’ paper signaled to him the rise of Darwinian thinking about social behaviors. He now had followers, working along similar lines. At Harvard, Trivers enjoyed a very favorable environment to develop his views and became the main inspiring presence in a group of anthropologists and primatologists under the tutelage of the anthropologist Irven DeVore. Jeffrey Kurland, a graduate student at Harvard in the early 1970s, remembers thinking at the time that the emerging field of social evolution theory had its own holy trinity:

Hamilton, The Father, Bob Trivers, the Son and George C. Williams, The Holy Ghost (no one had met him yet and he was not known in fields like primatology, anthropology, sociology, etc.). [In Trivers’ lectures at Harvard,] an initial trial by fire was to read the first chapter of Wynne-Edwards 1963 book [*Animal Dispersion & Relation to Social Behavior*], be seduced by The Dark Side of naïve group selection arguments and then argue our way out to the glory of The Light Side of Darwinian individual-based selection. Williams’ 1966 book, *Adaptation and Natural Selection* delivered the final *coup de grâce*, putting group selection to rest.<sup>91</sup>

The research interests in Trivers’ and DeVore’s group concerned the social behavior of primates. Trivers himself intended to work on primates, and it was

88. Ibid., 44, citing Wynne-Edwards, *Animal Dispersion* (ref. 31).

89. Ibid., 42.

90. Hamilton to R. G. Smoljer, 20 Aug 1970, WDHP, Z1 Box 89.

91. J. Kurland, e-mail correspondence with the author, 29 Nov 2014.

only after much hesitation that he turned to Jamaican lizards.<sup>92</sup> Studying the langurs of Abu (India) Sarah Hrdy observed infanticides by adult males. Rather than dismissing them as abnormal behaviors, she came to consider them as adaptive strategies related the short-term tenure of dominant males in langur groups.<sup>93</sup> For his part, Kurland intended to work on the sociobiology of Japanese macaques. He sent his research project to Hamilton, who expressed interest: “it outlines just the sort of approach to wild primate behaviour that seems to me necessary, especially to help us to see the background from which human sociality arose.” However, he cautioned his correspondent against opposing too dogmatically kin selection and group selection.

I would say that you overemphasise kin selection at the expense of group selection. If troops exchange a lot of migrants then you may be justified, but if they don't, and if troops sometimes become extinct and sometimes “reproduce” by fission, then group selection may be a meaningful term. I don't regard group selection as basically different from kin selection and *claim that the concept of inclusive fitness can in principle cover any process of group selection.*<sup>94</sup>

This letter shows quite clearly that for Hamilton, once explanations in terms of good of the species had been ruled out, the question of using “group selection” or “kin selection” was largely terminological: these were terms, or labels, that could be useful to describe cases of population structuration. Inclusive fitness, however, remained in his view the modeling method for studying conditions the evolution of altruism. To Kurland, Hamilton's suggestions came as a shock.

Under Trivers' tutelage, I have just about given up any belief in group selection. So, I was almost shocked by your open acceptance of group selection as a viable evolutionary mechanism. Indeed it struck me as some Horrendous Heresy—My God, Hamilton believes in Group Selection! Actually, and very secretly, I harbored a similar heretical dogma, but only in regard to those peculiar creatures, known as insects.<sup>95</sup>

92. See Robert L. Trivers, *Natural Selection and Social Theory: Selected Papers of Robert Trivers* (New York: Oxford University Press, 2002), 208.

93. See Sarah Hardy, “Myths, Monkeys, Motherhood: An Intellectual Biography,” in *Leaders in Animal Behavior: The Second Generation*, ed. Lee Drickamer and Donald Dewsbury (Cambridge, MA: Cambridge University Press, 2010), 343–374.

94. Hamilton to Kurland, 13 Oct 1972, WDHP, Z1 Box 89; emphasis added. Kurland's reports were published in Jeffrey A. Kurland, “Kin Selection in the Japanese Monkey,” *Contributions to Primatology* 12 (1977): 1–145.

95. Kurland to Hamilton, 10 Nov 1972, WDHP, Z1 Box 89.

### Ilan Eshel and the Neighbor Effect

In the early 1970s, a second paper signaled to Hamilton the existence of another potential alternative to his principle of inclusive fitness in social evolution. A young Israeli mathematician who had worked with game theorist Robert Aumann, Ilan Eshel published a paper “on the neighbor effect and the evolution of altruistic traits.”<sup>96</sup>

It was an anthropological observation that led Eshel to consider the problem of the evolution of altruism. During the Six Days War, he observed behaviors that seemed to him in contradiction with Darwinian expectations. Humans could be so much indoctrinated that they could neglect their own survival and fight altruistically for the benefit of their fellow citizens. But, as he had ample opportunity to observe, there was also significant variation between individuals. Influenced by Sewall Wright’s views on the evolutionary process<sup>97</sup> and his emphasis on population structure, Eshel developed a population-structured model on the evolution of altruism.

This model assumed a population of haploid types, with clonal reproduction, partitioned into neighboring demes that exchange migrants and have different probabilities of survival (or extinction). The probability of survival of a deme was a function of the number of altruists in it. Genetic drift occurred in each deme, generating interdeme variance in type frequencies. Altruistic types were at a disadvantage compared to selfish types, but they limited the probability of extinction of their colony. This meant that, in this model, altruists enjoyed a direct benefit from their altruism, by reducing the probability that their own population would go extinct.<sup>98</sup>

Eshel obtained two main results. First, he demonstrated the existence of a low but non-zero migration rate threshold at which fully altruistic colonies (or, more precisely, colonies composed of 100 percent altruistic parents) reached fixation. Interestingly, Eshel suggested that this situation—isolated demes with very low migration rates—should be the most common case in nature. This vision was clearly inspired by Sewall Wright, and not by Fisher. But Eshel obtained also conditions for polymorphism of altruists and egoists in

96. Ilan Eshel, “On the Neighbor Effect and the Evolution of Altruistic Traits,” *Theoretical Population Biology* 3 (1972): 258–277.

97. Sewall Wright, “Tempo and Mode in Evolution: A Critical Review,” *Ecology* 26, no. 4 (1945): 415–419.

98. This was in contrast with the Hamiltonian altruism, which implies a non-retrievable loss in fitness for the bearer of the altruistic gene. See J. W. Pepper, “Relatedness in Trait Group Models of Social Evolution,” *Journal of Theoretical Biology* 206, no.3 (2000): 355–368.

the meta-population. If the migration rate was higher than a certain quantity (equivalent to the relative fitness of altruists), and if the probability of extinction of fully selfish demes was sufficiently high, both pure equilibria were unstable and neither type reached fixation. Altruists and egoists then coexisted in a world partitioned into semi-isolated colonies that vanished when they were overwhelmed with selfish types.

It was relatively unclear, however, which mechanism was responsible for the increase in the number of fully altruistic colonies for a sufficiently low migration rate. In his verbal discussion, Eshel stated that in his model, both group selection and kin selection were particular cases of a more general process that he called the “neighbor effect.” Under the neighbor effect, Eshel claimed, the probability of success of an altruistic gene depends on the social environment of its bearers. If this environment (the deme) is composed of altruists, then the gene is selected: altruists help each other, and their colony is less vulnerable to extinction. Conversely, an altruistic type is expected to decrease, and the proportions of selfish types to increase, in a mixed deme. But this turns out to be fatal to selfish colonies. By agglomerating, selfish types accelerate their own probability of extinction. “Thus on a purely statistical basis the non-altruistic type is more likely to suffer such a disaster, simply because, on the average, it appears with higher frequency in disaster areas.”<sup>99</sup> This phenomenon depends crucially on migration rates. If migration rates are too high, then the altruistic type is counter-selected by selfish types coming from the other demes.

This new mechanism, at the borders between kin selection and group selection, seemed hard to classify. Eshel remembers receiving two laudatory letters in reaction to his paper.<sup>100</sup> In the first letter, his work was praised for showing that altruism could evolve without group selection. In the second letter, the same paper was being credited for showing that, contrarily to Williams’ conclusions, group selection could favor the evolution of altruism. With hindsight, this ambiguity might well have been an effect of the discrepancy between Eshel’s mathematical model and his verbal discussion.

The paper was structured into theorems, corollaries, and mathematical proofs, some of them being more than two pages long. This approach was certainly consistent with the standards of the journal in which it was published, the recently founded *Theoretical Population Biology*, which strove for an

99. Eshel, “Neighbor effect” (ref. 96), 261.

100. Eshel, e-mail correspondence with the author, 7 Nov 2011.

unprecedented level of mathematical rigor in theoretical biology, but it was certainly of limited help to biologists trying to cope with this difficult paper. Several biologists wrote to Hamilton to ask him his opinion about Eshel's paper. The mathematics was intimidating, but the author seemed to know his affair. Could his conclusions be trusted?<sup>101</sup> Hamilton skimmed through the mathematical sections and fell under the charm of Eshel's discussion of the consequences on human evolution. Eshel suggested that mechanisms of self-limitation of births to avoid overpopulation could have evolved before the Neolithic, at a time of low migration rate, and that this adaptation would have been later disturbed by the high rates of mobility following the Neolithic.

It may be that some intrinsic human drives, altruistic in nature, that are fundamental for the establishment of any human civilization, could possibly evolve only under precivilization demographic conditions. And it is possible that just those selection forces imposed by civilization itself act to reduce the frequency of these fundamental drives within human population, thus leading it into the course of misadaptation.<sup>102</sup>

Sewall Wright wrote to Eshel his full agreement with this suggestion.<sup>103</sup> Hamilton himself rejoiced. At least, he thought, a population geneticist was seriously considering the problems raised by the evolution of fertility rates in the course of human history. Overpopulation had been one of his main subjects of concern since the early 1960s. He wrote to Eshel to ask for a reprint and to tell him the results of his own considerations about the evolution of crime in human societies. However, he objected to Eshel's claim that kinship was *not* a prerequisite for the evolution of altruism.

That upsets a long held tenet of faith of mine that my concept of "inclusive fitness" should cover any kind of altruism, being only, perhaps, rather cumbersome when applied to the cases that usually go by the name of "group selection." However, I had to admit an exception in Trivers' "reciprocal altruism," so maybe I will have to admit one in yours too. I must think. At present I look askance at your claim that it is *necessary* to talk of your "neighbour effect" in order to deal with the whole lot.<sup>104</sup>

101. For example, Jerram Brown to Hamilton, 13 Jul 1972, WDHP, Z1 Box 89.

102. Eshel, "Neighbor Effect" (ref. 96), 262. For criticisms of these views by a leading physical anthropologist, see Sherwood L. Washburn, "Animal Behavior and Social Anthropology," *Society* 15, no. 6 (1978): 35–41.

103. Wright to Eshel, 24 Jan 1973, SWP.

104. Hamilton to Eshel, 30 Oct 1972, WDHP, Z1 Box 89.

In his answer, Eshel insisted on the primacy of the neighbor effect over kin selection. The neighbor effect in a model with explicit population structure was not the only possible approach to the problem, but it had the merit of making explicit an aspect that, in his view, Hamilton had left more or less implicit in his 1964 panmictic model: for an altruistic trait to spread, the population has to be “badly mixed,” to increase the probabilities of preferential interaction between selfish and between altruistic types.

I do believe that in many cases the concept of “inclusive fitness” and this of “neighbor effect” may apply to the same situation, thus, a “bad mixing” of the population will increase, on a statistical basis, the inclusive fitness of the altruist, relative to this of the non-altruist, simply because it will increase its chance of inadvertently helping its own kin. The model of neighbor effect just helps us to analyze this on a probabilistic, rather than on a statistical level. As a matter of fact, I had some troubles trying to apply the concept of inclusive fitness to well-mixed populations, i.e., populations without a neighbor effect active within them.<sup>105</sup>

This clarification probably helped Hamilton to see that Eshel’s mechanism presented some similarities with the one he had postulated in 1964. In Hamilton’s formulation, Eshel laid the emphasis on population “viscosity.” In a population with limited migration, viscosity compensates for the disadvantages suffered by altruists, because the recipients of altruistic behaviors have high chances of being themselves the bearers of the altruistic gene. Hamilton intended to explain this point to his colleagues—by making a model.

### **The Conference on Biosocial Anthropology: Hamilton’s Model**

Hamilton took the opportunity of a conference on biosocial anthropology held at Oxford, in July 1973, to present his new views on the mathematics of the levels of selection.<sup>106</sup> A significant part of Hamilton’s talk was devoted to conjectures on the evolution of humankind, including the recent history of Western civilization. In this context, Hamilton presented a model on altruism in a group-structured population. Hamilton’s objective was to overcome the verbal and elusive distinction between kin selection and group selection, and to focus on the conditions involved in the selection of an altruistic gene. The main tool for this purpose was the Price equation, which Hamilton used

105. Eshel to Hamilton, 17 Nov 1972, WDHP, Z1 Box 89.

106. Hamilton, “Innate Social Aptitudes” (ref. 83).

to analyze three particular cases of structured population: (1) a group structure without extinction and migration between groups; (2) a group structure including migration, with random assortment between the different migrants; and (3) a group structure in which assortment between migrants is not random.

The first case concerned a population partitioned into isolated groups without extinction and migration between groups. This was a variant of the model that Haldane had proposed in 1932 to account for the evolution of altruism.<sup>107</sup> On paper, these conditions seemed especially favorable to group selection, since in the absence of migration a colony of altruists does not incur the risk of being infected by selfish migrants from the other colonies. Hamilton commented that, under these conditions, the meta-population frequency of the altruistic gene would indeed increase, as a result of the increased productivity of colonies comprising more altruists. However, the gene frequency in the meta-population would *not* overcome the maximal value  $q_m$  of the colony where the gene was initially the most frequent. Furthermore, the altruistic gene would still be counter-selected within colonies. If one took into account the weak plausibility of the initial assumptions, Haldane's scenario seemed unlikely for showing the efficiency of group selection in the evolution of altruistic traits.

The second situation included migration, with random assortment between the different migrants in groups of size  $n$ . This represented a situation almost opposite that in the first case: here groups dissolved and recomposed at each generation. Hamilton considered the case of a haploid model, with asexual reproduction and separate generations, in which the asexual type gives up  $k$  units of its fitness to increase  $K$  units to the fitness of its  $(n - 1)$  companions. When the composition in a group results from random sampling of migrants, the change in the frequency of the altruistic allele is:

$$\bar{w}\Delta q = -k(1 - q)q$$

The frequency of the altruistic gene diminishes in proportion to the factor  $k$ , the cost in fitness to the altruist. In other terms, in case of random assortment, altruism cannot evolve.

The third situation gave up the assumption of random assortment by introducing the assumption of preferential assortment between migrants. In this last case, Hamilton observed, altruism could indeed be selected. Altruism

107. Haldane, *Causes of Evolution*, Appendix (ref. 2).

evolved because altruists aggregated among themselves. The key to the evolution of altruism in group-structured populations was preferential assortment. “The easiest way to see the basis of generality is to notice that the benefits of altruism do not now fall on a random section of the population and therefore do not simply enlarge the existing gene pool; instead they fall on individuals more likely to be altruists than are random members of the population.”<sup>108</sup> Hamilton then interpreted this result with his own tools. Defining  $F$  as the degree of assortment between migrants, and  $k$  and  $K$  being, respectively, the costs to the bearer and benefits to the recipients of the altruistic type, Hamilton was able to derive the condition  $F > k / K$  for the selection of an altruistic gene. This condition could easily be reinterpreted as another formulation of Hamilton’s rule  $r > I / k$ . In the view of its author, Hamilton’s rule thus emerged as the condition for the evolution of altruism, in structured as well as unstructured population. This condition accounted both for reciprocal altruism and neighbor effect.

As noted by Hamilton, and underscored by Sober and Wilson in their review of group-selection models, an important component was changed in Hamilton’s rule. This change concerned the meaning of “relatedness.”  $F$  now described a rate of assortment (a correlation coefficient) rather than a relatedness coefficient. Hence Sober and Wilson have argued that genealogy lost its monopoly as the prime mover of altruism, in favor of statistical interactions between interactors.<sup>109</sup>  $F$  can be caused by relatedness, but also by other factors (preferential interactions between altruists, such as permitted by shared habitat preferences between altruists). However, as pointed out by Robert Trivers in a letter to Hamilton, relatedness was still expected to be the major force driving altruism, because it generates common interests between genes at all loci.<sup>110</sup> Let us consider an altruistic gene favoring the survival of unrelated bearers of the same gene at the cost of its bearer’s fitness. This gene interferes with the interests of the *other* genes present in the altruist’s genome; their own probability of replication is affected, since the altruistic gene decreases the bearer’s fitness. Relatedness solves this potential conflict of interest, because relatedness generates common interests between genes at all loci. If the recipients of altruistic behaviors are related to the actors, they are expected to convey the

108. Hamilton, “Innate Social Aptitudes” (ref. 83), 336.

109. Sober and Wilson, *Unto Others* (ref. 1), 77.

110. Trivers to Hamilton, ca. 1975, WDHP. See especially Grafen, “Geometric View on Relatedness” (ref. 20), and Okasha, “Group Selection Controversy” (ref. 10), 142.

bearer's own genes at the other loci as well, according to the probabilities given by a pedigree. Hence, Hamilton continuously emphasized the heuristic benefits of concentrating on relatedness, seeing in it the main source of insights in social evolution, because it represented in his view the most stable basis for the development of social adaptations.

The interpretation proposed here is conservative. Hamilton neither converted to group selection nor promoted it as a major source of insights. He rather accepted that the label could present some heuristic value in some definite contexts. This was so because he maintained the priority of his own modeling method in dealing with both structured and unstructured populations. This method was originally devised by refashioning tools available in the toolkit of his field, that of mean fitness maximization. In a second step, he tried to apply it to other situations and to connect his new formalism to the apparently complementary or alternative mechanisms appearing in the literature, aiming to build a framework general enough to derive various results as special cases. Nonetheless, Hamilton's 1973 communication signals a change in the understanding of inclusive fitness as a modeling method. In 1964, Hamilton's model was focused on the ambition of obtaining a maximizing principle in the study of social behaviors. His fundamental result was showing that the mean inclusive fitness of a genotype, exhibiting maximizing properties similar to those of classical mean fitness, was a satisfactory descriptor in the study of social situations. Hamilton's rule was then derived as a particular application of the general method. In 1973, the relation between inclusive fitness and Hamilton's rule was reversed: inclusive fitness was now primarily a modeling method based on Hamilton's rule. Later modeling work followed this emphasis. Kin selection models are defined by Hamilton's rule. They are devised to partition the conditions for the evolution of a trait in two different terms, a term for the statistical association between interactors and a term for the *benefit for the recipient / cost for the actor* component. At this stage, kin selection had become synonym with Hamilton's rule. As a result, the fates of inclusive fitness and Hamilton's rule have diverged. Among behavioral ecologists, inclusive fitness maximization has circulated as a qualitative generalization rather than as a general basis for models. Conversely, the term "inclusive fitness" has disappeared in the modeling literature of the 1970s and 1980s, being replaced by "kin selection." In the early 1980s, a theoretical biologist working on kin selection felt confident in stating frankly: "Inclusive fitness in Hamilton's 1964 paper was just a tool used in the construction of the rule, and the only reason we have dealt with it at length is that it is surrounded by so much confusion.

Hamilton's rule is more important and more illuminating than inclusive fitness; it is also easier to apply data to it."<sup>111</sup>

## CONCLUSION

In 1998, John Maynard Smith wrote a review of Elliott Sober's and David Sloan Wilson's *Unto Others*. Pleading in favor of group selection as a respectable modeling method, Sober and Wilson reviewed the history of the modeling research on altruism in this perspective. In line with their definition of group selection, they also reinterpreted various results and modeling methods usually catalogued in the "individual selection" family, such as kin selection and the evolutionary theory of games, as exemplars of group selection models. Maynard Smith objected to this very liberal use of the concepts. "Although I have been a participant, I find it quite hard to decide what the current debate is about. Is it about what the world is like, or about the best words to use when we describe it? When I first became interested, back in the 1960s, it seemed fairly clear."<sup>112</sup> Maynard Smith reiterated his view that the original issues under contention in the 1960s concerned how to account for the adaptations of organisms: Did they evolve because of their benefit to the populations or the species to which they belonged, or because of the advantage they gave to their bearers? This basic issue, Maynard Smith regretted, was lost in sight in current discussions of group selection.

However, things had not been that simple when Maynard Smith first turned his attention to this issue. The scientists laying the foundations of the mathematical theory of altruism in the late 1960s and early 1970s came from very different backgrounds. They were students or newcomers, rather than established researchers, deciding to venture on an unexplored path. Hamilton worked on altruism as a solitary PhD student at University College. George Price put an end to a career in chemistry to make a brief career as an evolutionary biologist. A graduate student in mathematics in Israel, Ilan Eshel turned to altruism as one of his first inquiries in theoretical population genetics. Robert Trivers was a graduate student at Harvard working in theoretical

111. Alan Grafen, "Natural Selection, Kin Selection and Group Selection," in *Behavioural Ecology: An Evolutionary Approach*, ed. Nicholas E. Davies and John Krebs (Oxford: Blackwell Scientific Publications, 1984), 62–84, on 69.

112. Maynard Smith, "The Origin of Altruism. Book review of *Unto Others: The Evolution and Psychology of Unselfish Behavior*," *Nature* 393 (1998) 639–640.

ecology. Influenced by Hamilton's papers, he saw in the study of altruism a reason to switch to the growing field of sociobiology. What led these *homines novi* to consider altruism as a significant problem was a common interest in the evolution of humankind. This interest materialized in very different ways. Hamilton found in this interest the stimulation for exploring the effects of population structure on altruism. Price felt that human altruism required an explanation that would be other than nepotism. Ilan Eshel related his mathematical results on the importance of migration rates to conjectures on the past history of the species. Interested in the sociobiology of primates, including humans, Robert Trivers used anthropomorphic reasoning as a way of generating insights into the evolution of social behaviors. Clearly, there were very different ways of being interested in the evolution of humankind.

Turning to a new issue, these researchers came with their own vocabulary, their own expectations, and their own standards about what a satisfactory solution of the problem of altruism would be. It gradually appeared that the challenge was not simply to find and model robust mechanisms for the evolution of altruism, but to interpret their properties in terms that could be accepted by other researchers trained in other modeling traditions. These terminological disagreements are yet to be solved. The field of social evolution theory still presents a great diversity of modeling approaches and of labels. Terminological disagreements and replications of results between different modeling schools remain among the features of the field. In his review, Maynard Smith admitted that these terminological disagreements could not be dismissed single-handedly. The search for appropriate words is an important issue for theoretical biologists, because it guides the modeler's intuition.

Does it matter what words we use to describe a model if we agree about its consequences? Perhaps it does. We need formal models, but we also need intuition about why the models give the results they do, and the words used guide our intuitions and tell us what to look for. A group selection terminology leads us to look for factors causing a difference between variation within and between groups; a kin selection model leads us to look for relatedness (. . .). If this is right, the argument is not about what the world is like, or even about how we should model it (that is, what simplifying assumptions are adequate to explain it), but about what words we should use to explain our model.<sup>113</sup>

113. Ibid.

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