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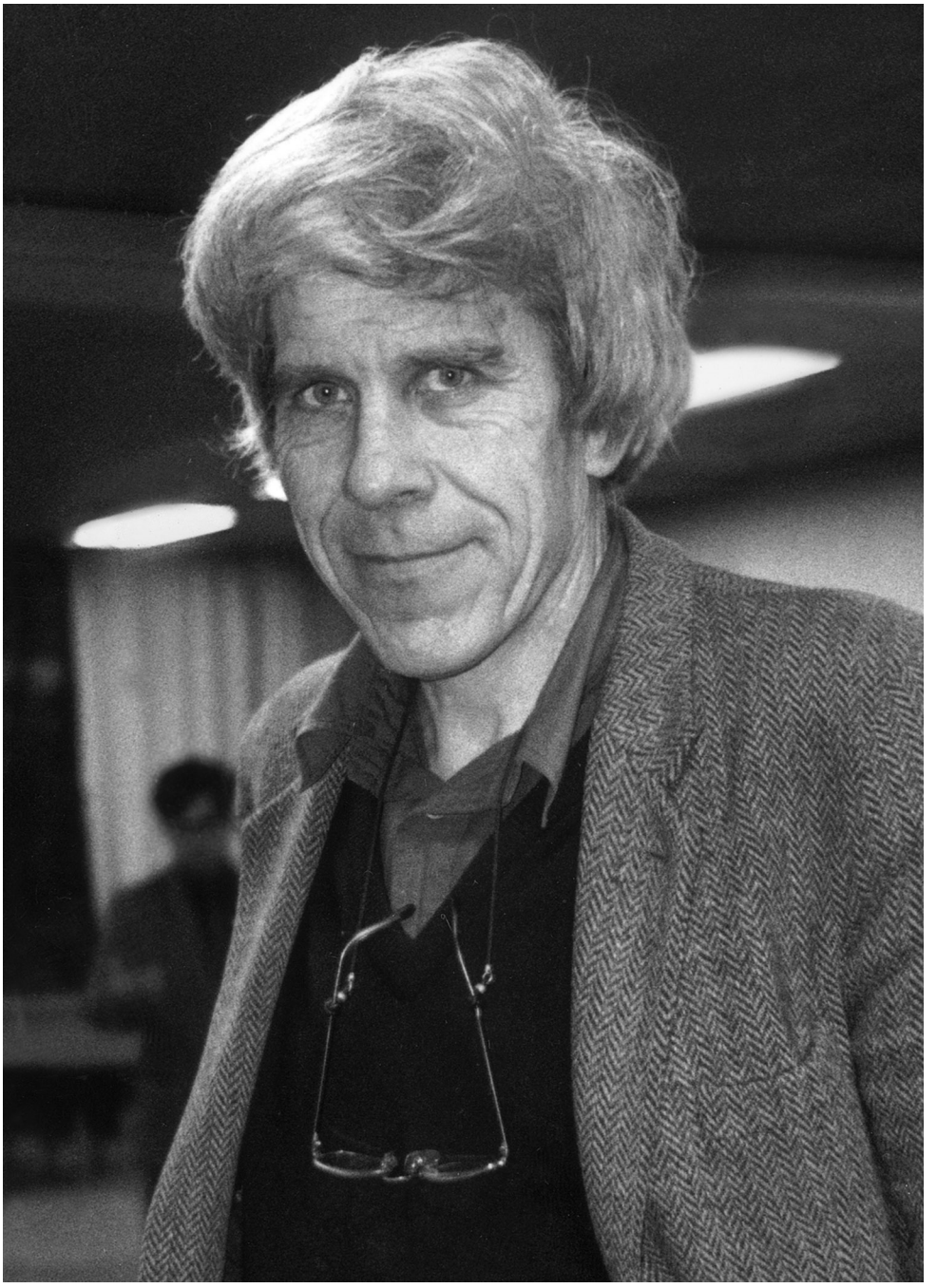

W. D. Hamilton

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Elected FRS 1980

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Introduction

William Donald Hamilton was born in 1936 in Cairo to New Zealander parents, and was brought up for the most part in a rural and wooded part of Kent, England. He described his childhood as idyllic, full of freedom to roam, and of maternal inspiration and encouragement, and himself as a great burrower. He was fascinated by insects from an early age. A great-aunt gave him her insect collection, whose cases he used for his own (later rueing his discarding of the insects themselves), and also lent him a translation from Fabre, the great French naturalist and one of the first to study behaviour scientifically. A birthday present from his parents was a much coveted copy of E. B. Ford's *Butterflies* (Ford 1945) in Collins's New Naturalist Series, which introduced the 12-year-old to genetics, to a scientific sensibility that looked down on 'mere collecting', to mathematical biology in the shape of Mendelian segregation ratios, and to the modern study of evolution. After reading Ford, he asked for a copy of Darwin's *Origin of Species* as a school prize. To have inspired this one young biologist would by itself justify Ford's efforts in writing *Butterflies*.

Another childhood interest was bombs. At about the time of *Butterflies*, he unearthed cases of materials belonging to his father, connected with wartime research on grenades, which had been hidden in a rabbit hole for safety. Retrieving them from a further hiding place, the young Hamilton proceeded to cause a near-fatal explosion. A thoracotomy in King's College Hospital saved his life, but some fingers were shortened, and brass remained implanted in his chest.

Hamilton itched to travel, and did visit France after staying on at Tonbridge School for an extra term to take Cambridge entrance. Before university were two years of compulsory National Service in 1955–57, during which his early bomb injuries prevented an overseas posting. Ironically, he was commissioned as a drafting officer in the Corps of Royal Engineers,

sending others abroad. Bill once told me a revealing story about a formal dinner. He broke a rule that no one must leave before the most senior officer present, and escaped to the countryside, pursued by a search party; he succeeded in his aim of remaining free until he could give himself up in the morning light. It is a characteristic Bill who found a formal social event tiresome and fled to huddle under bushes for the night, close to the natural world he loved, hiding from the agents of authority, playing and winning a game of his own making, for his own satisfaction.

Primed in many ways for biological study, particularly study combining mathematics, genetics and natural selection, Hamilton went up to St John's College, Cambridge, in 1957 with a State Scholarship to study Natural Sciences.

Cambridge, Fisher and theoretical biology

Cambridge was a frustrating place for Hamilton, because the undergraduate course was old-fashioned in its approach to natural selection and contained little mathematical biology. Hamilton escaped the confines of his teachers and discovered in his college library the book that would set his course in some detail until the mid-1970s, and its general direction for a lifetime, *The genetical theory of natural selection* (Fisher 1930). Then, to his surprise, he found Sir Ronald himself, still in post as Arthur Balfour Professor of Genetics.

To appreciate the influence of the book, read Hamilton's endorsement on the back cover of the 1999 Variorum edition of *The genetical theory*, written at a time when his 'ultimate graduation' was tragically and unforeseeably near:

> This is a book which, as a student, I weighed as of equal importance to the entire rest of my undergraduate Cambridge BA course and, through the time I spent on it, I think it notched down my degree. Most chapters took me weeks, some months; even Kafka whom I read at the same time couldn't depress me like Fisher could on, say, the subject of charity, nor excite me like his theory of civilisation. Terrify was even the word in some topics and it still is, so deep has been the change from all I was thinking before. And little modified even by molecular genetics, Fisher's logic and ideas still underpin most of the ever broadening paths by which Darwinism continues its invasion of human thought.
>
> … Unlike in 1958, natural selection has become part of the syllabus of our intellectual life and the topic is certainly included in every decent course in biology. By the time of my ultimate graduation, will I have understood all that is true in this book, and will I get a First? I doubt it. In some ways some of us have overtaken Fisher; in many, however, this brilliant, daring man is still far in front.

The pages of *The genetical theory* do take weeks and months to work through, and biology is richer for every student who takes the trouble. Hamilton's investment paid off a hundredfold, as we shall see. What might not be obvious today is how little influence *The genetical theory* had at that time (Edwards 2000). It was disregarded by Hamilton's teachers, who, amazingly as it now seems, viewed Fisher as only a statistician, lacking standing in biology.

Much time at Cambridge was spent not on the formal teaching, but on his own work, and he spent his third year attached to the Department of Genetics, in which the retired Fisher still reigned before the appointment of his successor. Hamilton reports getting on well with Fisher. His own work seems to have been in large part a 'theory of ethics', of which I can find no details, based on new understandings gleaned from Fisher's book, and which may have been a forerunner of his work on altruism. Hamilton was a prolific postcard writer, frequently cross-

writing in different colours. A card sent to his sister Mary, now Mary Bliss, suggests that he had worked out at least part of the sex ratio theory of his 1967 paper (3)* in February 1960, a few months before his final examinations. He had been assigned to help A. W. F. Edwards, then a graduate student of Fisher's and later his distinguished successor, with an experiment intended to test Fisher's sex ratio theory, and this may have provided the stimulus for his own work.

Hamilton continued in that postcard, 'I begin to think that my ambition to be a theoretical biologist can be more than a dream in spite of my poor mathematical ability'. Such percipience and self-knowledge are remarkable in an undergraduate. As we shall see, Hamilton's achievements with his 'poor mathematical ability' put to shame those of us who practise biology with greater mathematical skills but to less biological effect.

Inclusive fitness

Hamilton's graduate student life is the period of his greatest scientific work. Rebuffed nearly everywhere he applied for his topic of genetics and altruism, he eventually enrolled for an MSc in Human Demography at the London School of Economics (LSE), and was initially supervised for research work by Norman Carrier, who crucially also secured for him a Leverhulme Research Studentship for one year, and then a Medical Research Council Scholarship. He transferred as the work became more mathematical to John Hajnal of the LSE, and as it became more genetical to a joint supervision by Cedric Smith of University College London. In *Narrow roads of gene land*, vol. 1 ((21), p. 4), Hamilton reports a general suspicion in the institutions to which he belonged that he might have been 'a sinister new sucker budding from the recently felled tree of Fascism' simply through using words like 'gene' and 'behaviour' in the same sentence.

A vital influence for the project was an appreciation of Fisher's 'fundamental theorem of natural selection', which more or less states that natural selection should result in individuals that are well designed to produce as many offspring as possible given all the circumstances of their lives. The power and generality of the theorem greatly impressed Hamilton, but there were difficulties in applying it to social behaviour. Darwin had noticed in *The origin of species* the difficulty in explaining the evolution of honeybee workers' structures and habits (which incidentally to Darwin's point, but germane to Hamilton's, are social traits) through natural selection. The derivation of the fundamental theorem assumed that an individual's number of offspring depended on its own genotype and not on the genotypes of others. There was fundamental work to do to incorporate social behaviour into the best contemporary Darwinian theory, and Hamilton took up that challenge.

Hamilton's situation might be hard to understand for a modern biologist, because Fisher's result is not widely seen today as very interesting or important. Indeed, the situation was probably rather similar in 1960. Perhaps only Fisher and Hamilton, who so far as we know never discussed it, viewed Fisher's fundamental theorem as 'holding the supreme position among the biological sciences' (Fisher 1930, p. 37).

The initial idea was that sharing of genes altered calculations. Selection could quite easily favour helping siblings, but less often second cousins. Hamilton built up many models of

* Numbers in this form refer to the bibliography at the end of the text.

special cases, each with a different genealogical link between actor and recipient. These were unsatisfactory because clearly there was some more general phenomenon going on than these scattered separate cases, particularly as in each of them the gene frequency more or less magically dropped out from the condition for spread. More deeply, they could not aspire to provide the generalization of Fisher's fundamental theorem that was so necessary on conceptual grounds. It would be deeply unsatisfying to have a correct theory of altruism, which would disprove Fisher's fundamental theorem and throw evolutionary biology (at least as understood by Hamilton and Fisher) back into disorder. It is important to understand that references to 'the classical theory' both in the 1964 paper (2) and in *Narrow roads of gene land*, vol. 1 ((21), for example on page 27) are in fact references to the fundamental theorem, perhaps so much taken for granted that it need not be given a name, perhaps strategically veiled to deflect the reader from recalling the attacks on the theorem's truth.

At some point, Hamilton saw how to produce a general model. It employed Wright's coefficient of relatedness, which was a correlational measure of closeness of kinship. More significantly, the model encompassed a broad range of kinds of social interaction, and involved a maximization principle. Thus essentially the whole of social behaviour had been embraced by a generalization of Fisher's fundamental theorem. According to that theorem, individuals should be expected to maximize their reproductive success, or 'fitness'. In Hamilton's model, the quantity that individuals were expected to act as if maximizing was named 'inclusive fitness'.

Inclusive fitness has been much admired but also much misunderstood (Grafen 1982). It was, in the words of his 1964 paper (2), 'its production of adult offspring … stripped of all components which can be considered as due to an individual's social environment … then augmented by certain fractions of the harm and benefit which the individual himself causes to the fitnesses of his neighbours. The fractions in question are simply the coefficients of relationship.' Mathematically, we assume an additive representation such that the number of offspring of individual j is the sum of contributions s_{ij} made by individuals i, formally $1 + \sum_i s_{ij}$. The inclusive fitness of individual i is then defined as $1 + \sum_j r_{ij}s_{ij}$, where r_{ij} is the relatedness between individuals i and j. The conceptual transformation 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.

The fundamental theorem provided a mathematical and conceptual underpinning for Darwinian natural selection and clarified what 'fitness' was. Inclusive fitness, erected on the theorem, went further and extended the very concept of natural selection, so that it now satisfactorily accounted for the worker honeybee which had puzzled Darwin, and stood ready for the assault on understanding social behaviour in general, which continues today.

There are many remarkable aspects of the papers reporting this work. A short paper in *American Naturalist* (1) was published first, but written second: the paper submitted to *Journal of Theoretical Biology* (2) was split into two on the advice of a referee, but Hamilton consistently referred to these two papers as Part 1 and Part 2 of a single paper. The short paper is a lucid verbal explanation of what has become known as 'Hamilton's rule', with some applications, and it also offers the gene-centred view of selection that Hamilton always viewed as an informal aid to thinking requiring the backing of a population genetics model. In this case, the backing was in the 1964 paper (2). This gene-centred view was later developed by Dawkins (1976, 1982) into his powerful conceptual unification of Darwinian theories.

Part 1 of the 1964 paper (2) contains the model, set perfectly in context, with special cases worked out, objections to the model raised and discussed, and the conceptual implications thought through. This part has an undeserved reputation for obscurity. The main message and content are lucid when read today, and the notation and mathematical argument present no serious obstacle for those with mathematical training.

Following the theoretical triumph of Part 1, Part 2 is an extraordinary *tour de force* of synthesis. Hamilton shows, across the range of biology, how his theory transforms the study of social traits. His logical application of the ideas combined with his deep immersion in biology led to many discussions that today look highly prophetic. The early standard examples are all given, such as distastefulness in insects, alarm calls, mutual preening and grooming. He outlines the logic of kin recognition, today a whole subject of its own, quite extensively. He discusses multicellularity in terms of the relatedness of the cells, and collaboration in other kinds of colonies, and he solves what would now be called games between relatives. Moving on to social insects, he first discusses the famous '3/4' principle, which is the only argument that many later commenters noticed. It was the social insects to which his theory had given the first evolutionary key, because most of their significant behaviour is clearly social, and he accordingly gives an in-depth discussion encompassing multiple mating, multiple insemination, pleometrosis, aggression in relation to sterility, nest usurpation, and the origins of eusociality. He also discusses the possibility that females should mate only once to reduce the conflict between their offspring. These cases are not merely mentioned; rather, they are discussed with relevant facts, and considering apparent exceptions. The final section is on anomalies to the theory as a whole.

The extraordinary coherent power of the theory is nowhere more apparent than in his taxonomically distant analogy between ant queens collaborating to build a nest, and sporelings of a branching red alga, as competing and potentially related. Only a strong theory can abstract from all the details of ant biology and phycology in this way, but Hamilton was clearly in no doubt about the scale of his *magnum opus*.

It is worth pausing to see Hamilton's methods, for they vary remarkably little throughout his career. The problem must be evolutionary, and the formal solution is a population genetics model. Very extensive reading of relevant literatures was a preparation. The range of facts, in terms both of species and type, is wide, and most of them were not collected for Hamilton's purpose. Thus, the facts often require sophisticated handling and defy easy interpretation, closer to history or astronomy—indeed to Darwin's own arguments—than to the more straightforward experimental methodology that became more and more dominant during the twentieth century. A crucial role is usually played by anthropomorphic thinking. He would often make remarks like 'Now if I were the Ebola virus…', going on to explain a cunning strategy by which it could increase its spread. The problem itself is usually felt important by Hamilton because of a perceived hiatus between theory and facts, and it was his utter confidence that one should be able to explain the other that drove him forward to seek solutions.

Just how revolutionary was this work? There were frequent accusations of lack of originality, which were found hurtful. However, the view cannot be sustained that Hamilton's work was merely an elaboration of an idea that should be credited to Haldane or Fisher. They had both previously published some of the ingredients, but neither had seen or even partly understood the magnitude and significance of the problem that Hamilton identified. Fisher never pointed out that his argument about aposematism contradicted the assumptions of his fundamental theorem. Haldane published his 24-line passage in a paper (Haldane 1955) in a

semi-popular journal. Neither Fisher nor Haldane indicated that there was a general problem about how natural selection acted on social behaviour, and so naturally neither claimed to be tackling it. Neither gave the impression they attached more importance to these arguments than to the others on adjacent pages. In the large, then, there is no question of pre-emption. Even with a more detailed point, it is easy to overvalue the earlier work. A modern audience reads Haldane's use of the chances of sharing a gene and, being familiar with inclusive fitness, immediately thinks of the coefficient of relatedness, and is then tempted to credit Haldane with the importance of relatedness in social behaviour. But there is no evidence that Haldane ever made that leap from gene-sharing with particular relatives to relatedness in general. There was, however, a definite moment at which Hamilton realized the significance of the coefficient of relatedness and found that, in place of separate models making special assumptions, he could instead construct a single general model in which relatedness had a crucial role. Finally, the idea that individuals acted as if maximizing some quantity that generalized Darwinian fitness was not even hinted at by Haldane or Fisher. Indeed, so novel was this idea that I know of no passage in their work in which such a hint could even have found a natural place. Yet it is precisely this aspect of inclusive fitness that forms the centrepiece of Hamilton's achievement.

Thus, inclusive fitness was a major conceptual advance in biology, wholly original with Hamilton. We have seen how Hamilton viewed the problem and worked on it. We turn now to how other biologists reacted to this masterly reshaping of social biology.

The reception of inclusive fitness

One strand in the reception of inclusive fitness was very positive. Whole areas of biology now depend on it, and it has survived essentially unchallenged as the evolutionary theory underlying social behaviour. Hamilton received many honours and awards in recognition of his achievements. Another strand, located in the population genetics tradition, has been negative and dismissive, and sometimes worse. These strands have interplayed in important ways.

It has often been remarked that Hamilton's 1964 paper is much more frequently cited than read. Four influential books seem to have been mainly responsible for publicizing inclusive fitness and conveying its message to biologists. There is a long and serious exposition and discussion on pages 328–334 in *The insect societies* (Wilson 1971), which took it as a given that inclusive fitness theory is right as a general theory of social behaviour, and then focused on whether this theory can account for the greater incidence of eusociality in the Hymenoptera. (Incidentally, Wilson anticipated that further work would suggest that it cannot, which is still a respectable point of view.) Also in 1971, the collection of papers *Group selection* (Williams 1971) reprinted the 1964 paper, making them more available and drawing attention to their relevance. In 1975, the widely read and highly controversial *Sociobiology* (Wilson 1975) appeared and mentions inclusive fitness briefly. By 1976, Dawkins could still refer in his powerful and influential *The selfish gene* to the papers as 'among the most important contributions to social ethology ever written' and yet 'so neglected by ethologists'. It was *The selfish gene* that synthesized a unified evolutionary understanding from inclusive fitness and other current ideas. The history of this fascinating period is expertly illuminated and well documented by Segerstråle (2000), who is currently writing Hamilton's biography (Segerstråle 2005).

Generations of biologists have learnt about inclusive fitness through secondary sources, and today textbooks in animal behaviour, behavioural ecology and evolution introduce inclusive fitness as an uncontroversial central principle. In the succeeding decades since publication, the 1964 papers received an annual average citation rate of less than 10 (1964–73), about 60 (1974–83), about 100 (1984–93) and about 160 (1994–2002). Their total citations between 1981 and 2002 are greater than those of comparably iconic biological works (all books) of the same era such as Williams (1966), Macarthur & Wilson (1967), Wilson (1971) and Lack (1966, 1968). Inclusive fitness became a major, dominating theme in biology within 15 years of its publication.

Honours and prizes were important to Hamilton, as recognition that inclusive fitness really was accepted, and for the opportunity to travel that some prizes offered. His medals include the Scientific Medal of the Zoological Society of London (1975), the Darwin Medal of The Royal Society (1988), the Scientific Medal of the Linnean Society (1989) and the Frink Medal of the Zoological Society of London (1991). His memberships and fellowships of academies, sometimes foreign or corresponding memberships, include the American Academy of Arts and Sciences (1978), The Royal Society (1980), the Royal Society of Sciences of Uppsala (1987), the Brazilian Academy of Sciences (1993), the Academy of Finland (1997) and the American Philosophical Society (1999). Major prizes included the Albert Wander Prize (1992), the Crafoord Prize (1993), the Kyoto Prize (1993) and the Fyssen Prize (1996). The Crafoord is the closest that biology comes to the Nobel: the Swedish Royal Academy awards a biological prize (frequently shared, in Hamilton's case with Seymour Benzer) usually every three years. The transformation of biology for which Hamilton was responsible was fully recognized by the scientific establishments of the world.

Such was Hamilton's standing by the time of his death that his papers were taken to join the unsurpassed collection of manuscripts of the British Library, most fittingly including those of Darwin and Alfred Russel Wallace. Over 200 boxes of Hamilton's materials are in the process of being catalogued. Many of Hamilton's 'papers' are unpublished computer documents (now termed eMSS), bearing witness to the use of computers in science from near the beginning in the 1960s up to 2000. The library is devising new ways of archiving, most especially concerning how to capture, preserve and make available the information on 80-column punch cards, paper tape, and floppy and hard disks of many generations. Hamilton is as pathbreaking in death as in life.

Against this background, the existence of the strand that never accepted inclusive fitness looks very puzzling but is readily understandable in its historical context. Inclusive fitness theory provided a maximizing principle, namely that natural selection causes organisms to act so as to maximize their inclusive fitness. It was a generalization of Fisher's fundamental theorem of natural selection.

The reception of Fisher's theorem is described by Edwards (1994). It had mainly been ignored, but at just the time that Hamilton was developing and extending it, population geneticists were beginning to pay attention to it, and they found it wanting. Failing to understand the derivation, they also misunderstood the statement of the theorem, taking it to imply that mean fitness must always increase. A succession of models then proved that mean fitness does not always increase. It was conclusively established that population genetic systems did not in general *have* a quantity that would always be increased.

Believing the fundamental theorem to be false in a simple situation without social interactions, population geneticists had little patience with inclusive fitness, which claimed to

establish a maximization principle in the presence of social interactions. There are two recent lines of work that might retrospectively unpick this negative reception and finally convince population geneticists. The fundamental theorem itself is now understood much better (Price 1972*a*; Ewens 1989; Edwards 1994): Fisher's derivation was intelligible and correct after all, and crucially the theorem does not imply that mean fitness always increases. Thus, population genetics regains a theorem and loses an Aunt Sally. And I myself have undertaken a project to represent in formal mathematical terms the link between population genetics and fitness maximization principles (Grafen 1999, 2000, 2002).

Based though it may have been on misunderstandings, the presence of this negative strand has been important. Lacking support from mathematical population geneticists, Hamilton's derivation of inclusive fitness has been patronized and overlooked. There are many rederivations of inclusive fitness, presented with the clear implication that the original derivation was somehow dubious. A curious literature results, in which inferior derivations are presented as improvements, and as avoiding special assumptions which were never made in the first place. The 1964 paper (2) acknowledged all the limitations of the analysis presented and gave excellent justifications for the assumptions made.

The first derivation to improve on the original is Hamilton's own rederivation in 1970 (4), inspired by the covariance selection mathematics of Price (1970, 1972*b*; and see Frank 1995). George Price himself was a remarkable figure, and Hamilton's involvement with him is described in *Narrow roads of gene land*, vol. 1 (21) and by Schwartz (2000), who shows that Price had the central insight that led to the rederivation but turned down the co-authorship that Hamilton offered. The only further paper to improve on either of Hamilton's derivations is Taylor (1990; see also Taylor 1996), whose brief appendix provides a still somewhat cryptic expansion of the 1970 argument. It is utterly remarkable that the approaches of Hamilton's two derivations have been so neglected, while the concept of inclusive fitness has become so pervasive in biology and elsewhere, and won such renown and recognition for its inventor.

The lack of support from population geneticists for inclusive fitness also led to an overemphasis on the informal arguments that make Hamilton's rule, a simple and convenient version of the inclusive fitness conclusion, so plausible. The rule is that if a social action adds b to the recipient's number of offspring, and subtracts c from the actor's, then it will be favoured by selection if $rb - c > 0$, where r is the coefficient of relatedness. Interpreting r as the fraction of genes shared between actor and recipient, $rb - c$ is simply the net effect of the action on the number of copies in the next generation of an allele in the actor.

This argument is so simple and appealing that it became the justification for inclusive fitness to generations of biologists. It brings to mind T. H. Huxley's response to natural selection itself ('How stupid not to have thought of that'), although, tellingly, Darwin expressed privately the view that Huxley did not actually explain it very well (Burkhardt *et al.* 1993, page 84) and so perhaps did not understand it very well either. In fact, the real argument for inclusive fitness is more complex, as the original papers make perfectly clear. Hamilton himself developed methods further in the 1970 paper already mentioned (4), in his 1975 paper (6), and in his 1980 paper (9) with Richard Michod on coefficients of relatedness.

Even though most biological students of social behaviour fully accepted inclusive fitness eventually, typically for Hamilton's work it took about 15 years to become mainstream, having been regarded initially almost as crackpot science. The consensus among practitioners that is such an important element in the workings of science does act against new and original ideas,

and we will see that Hamilton spent his later years trying to encourage more open-mindedness. Radical ideas are hard to assimilate, however elegantly or clearly they are expressed, because readers start from what they (think they) know. Now, most challenges to orthodoxy are not works of genius but are trivial mistakes or confusions in intellectual terms, and are often self-promoting works in careerist terms. They are appropriately resisted by most scientists. However, the resistance appropriate to the majority seems, in retrospect, scandalous when applied to the few ultimately successful challenges. Hamilton's prophet-like status persisted throughout his working life, so that his current work, whatever it may have been, was frequently regarded as odd and obscure and often rather embarrassing. Although he did complain, for example in *Narrow roads of gene land*, vol. 2 ((27), page 18), about the lack of interest in his present as against his well-established ideas, it must be said that the position of dissident seemed quite natural to him.

Inclusive fitness has had far-reaching effects in biology, reflecting its standing as the only significant extension to Darwinism of the twentieth century. The concepts of inclusive fitness, relatedness, altruism, spite and selfishness are firmly embedded in biology, and will remain central to the study of social behaviour.

Completing a unified theoretical framework for social behaviour

We return to 1963, after the inclusive fitness work had been done but before all the papers had been published. No one else realized the significance of Hamilton's work, and there was little sign that they would. A new side of his life began with his visit to Brazil, to work with Dr W. E. Kerr in Rio Claro. His purpose was to study social insects further, with a view to collecting data relevant to the predictions of his new theory, and indeed some made it into the 1964 paper. On the day of publication of the 1964 paper, he was on the road from Brasilia to Belém, on his way to Canada and then Britain.

This section will look at Hamilton's work after the 1964 papers and before the sex project that occupied, roughly, the 1980s. Hamilton began this period as an unknown and unappreciated graduate student, and ended it with considerable fame. He took up a lectureship at Imperial College, London, in 1964, and was based at the field station at Silwood Park. In 1967 he married Christine Ann Friess, who was training as a dentist. Bill and Christine had three daughters; Helen is now a senior ecologist for an environmental firm, Ruth has recently completed a PhD in parasitology at Cambridge, and Rowena graduated with a first-class honours degree in Fine Art. Rowena was born in the USA, after Bill had left Silwood Park in 1977, spent time as a visiting professor in Harvard and then joined the University of Michigan as a professor in 1978, persuaded there by one of the leading American champions of inclusive fitness in animal and human affairs, Richard Alexander.

The 1963 expedition was the first of many. He returned with Christine to Brazil in 1968 with the Royal Society and Royal Geographical Society expedition to central Brazil. The official report (Smith 1971) has an extraordinary picture of each taken by the other, after being attacked by wasps whose tree they had just felled, as well as a hair-raising account of Bill's driving that was immediately recognizable to one more recent passenger. He later made many further visits to Brazil, particularly the Amazon. The immediate intellectual fruits of these expeditions seem few and minor, but they clearly fed Bill's imagination and fulfilled a deep need. Perhaps the jungle offered a respite from etiquette and compromise. During his final

decade, he was engaged in research on Amazonian plant communities and was actively involved in the Mamirauá Project based in Tefé. There is now a 'Centro Itinerante de Educação Ambiental e Científica Bill Hamilton' there, a floating school for scientific and environmental education. Hamilton might well, had he lived, have gone on to make significant contributions to plant ecology.

His and others' recollections of expeditions are vivid. Bill prided himself, in the friendliest possible way, on his physical fitness and ability to cope. Mike Worobey, who accompanied him on the second Congo expedition, himself a Judo black belt and a fireman, and 30 years younger, describes Bill as the toughest man he has ever known. He also relates that in the Congo, Bill did not purchase a machete from the posh shop with gleaming blades, but in the back streets. Once in the jungle, the others' tools were soon discarded, and Bill was doing all the hacking away of creeper and undergrowth with a blade built for business not beauty. Bill enjoyed relating how he swam under a hull on the Amazon to plug a hole, knowing full well that his explanation ('the dangers of piranhas were much over-rated') would impress much of his audience. Bill was a self-constructed hero from a boyhood comic, relishing putting his skills and his practical knowledge to the test, and succeeding. He had a great love for improvisation and originality in practical and intellectual affairs.

Returning, then, to Silwood Park in 1964, he ruefully described being one of two applicants for this job, and not the first to be offered it. Students routinely complained to the director, first O. W. Richards FRS and then Richard (later Sir Richard) Southwood (FRS 1977), asking that in view of the nature of the teaching, the marks from Hamilton's course should not be counted towards their degrees.

Silwood Park was the 'entomological Mecca of Britain' ((21), p. 92) and Hamilton developed a characteristic niche as a resident genius; he was regularly to be found engaged in evolutionary interaction with graduate students and others in the conservatory where morning and afternoon coffee breaks were held. Managing an intellectually brilliant but pedagogically poor lecturer is difficult. Richard Southwood later moved to Oxford and secured a Royal Society Research Professorship there for Bill—a solution unfortunately not available to him while at Silwood.

Scope for recognizing and accommodating exceptional individuals has been diminishing in British universities ever since. Hamilton published relatively few papers, in generally low-status journals, and gained only a handful of grants much later in life. Bureaucratic measures of performance are increasingly important and judge the impact of an article only by the journal it is published in. This seriously undervalues radical originality, which although extremely rare is utterly vital to science. It is disturbing that a young Bill Hamilton today would probably find an academic career even more difficult to pursue.

Hamilton's general research direction in these Silwood years was to explore the selection of social behaviour. I will mainly consider only four papers that together represent conceptual extension and consolidation of the inclusive fitness approach. They together develop the justification for a regulated anthropomorphism, remove unnecessary assumptions, and uncover theoretical questions that still concern us.

The first, 'Extraordinary sex ratios' in 1967 (3), develops a theme of Fisher's but transforms it into new metal. Fisher's sex ratio conclusion was that investment in the two sexes should be equal at the end of the period of parental investment, but his argument was verbal and was too modern in that it viewed parents as maximizing agents. Shaw & Mohler (1953), Bodmer & Edwards (1960) and Kolman (1960) had provided mathematical versions of

Fisher's argument in more conventional terms, and Verner (1965) had made the interesting point that with very small populations there would be selection for reduced variance.

Hamilton showed his deep understanding of Fisher's argument by exploring the consequences of varying the central assumption of panmixia, whose consequence was that each additional son gained on average the same number of extra grandchildren for the parent. Hamilton considered the case in which the sons of a small number of mothers are competing for the daughters. In this case there are diminishing returns to sons as increasingly they compete among themselves. This variation produces female-biased sex ratios, matching what Hamilton showed to be a common pattern in nature. This striking confirmation of a model put theory to an empirical test that was unusually stringent, especially for the 1960s. The resulting literature still provides the most quantitative tests in modern Darwinian biology (Hardy 2002).

What this paper goes on to do is of deeper significance for the whole approach of viewing organisms as maximizing agents. Hamilton did not follow Fisher in using reproductive values but employed his usual population genetics models, with one locus determining sex ratio in a species with XY sex determination. The key step he did take was to consider the possibilities that this locus might be on an autosome, on an X chromosome or on a Y chromosome. He concluded that different parts of the genome 'wanted' different sex ratios, and so discovered what is now called 'intragenomic conflict' (Haig 1997; Burt & Trivers 2004). He explained it as resulting from the different relatednesses in the different parts of the genome. Thus, while the rest of biology still had no inkling of the importance of relatednesses, or of the formal possibilities of modelling individuals as maximizing agents, Hamilton was continuing to encounter and resolve fundamental questions in his new subject, still wholly his in 1967, and in terms of its basic theoretical framework.

The 'unbeatable strategy' is an equilibrium concept introduced in the paper, a formalization of Fisher's procedure in the sex ratio argument. It is often compared to the evolutionarily stable strategy (ESS), announced six years later by Maynard Smith & Price (1973). Hamilton's concept lacked the final formal separation from dynamics that the ESS achieved, but it explicitly embraced all the rest of the bundle of ideas that launched game theory so productively and spectacularly into biology.

This short paper embodies Hamilton's work of the time: energetic, powerful developments of Fisherian themes, which simultaneously embrace empirical findings much more intimately than Fisher ever could, and lay out theoretical paths for the decades ahead. The logical structure turns out to be an extension of inclusive fitness, in which relatednesses and maximization have central roles.

The 1970 paper in *Nature* (4) has already been discussed. It provides a new and more general derivation of inclusive fitness using Price's covariance selection mathematics, and introduces 'regression coefficients of relatedness' instead of the assumption of weak selection. Along with the 1971 addendum to the reprinting of the papers in *Group selection* (Williams 1971), it shows a further characteristic Hamiltonian trait. In the 1964 paper (2), Hamilton had made one outright mistake (on sex ratio in haplodiploids under maternal control), and one unnecessary approximation (Wright's coefficient of relatedness gives the chance of gene sharing only under weak selection). Whereas many authors claim to improve or correct when nothing of the kind is required, it was almost always Hamilton himself who tackled his genuine mistakes. There is a distinct note of regret in discovering that the golden ratio does not after all have a central role in haplodiploid sex ratios, but the introduction of regression coefficients of relatedness has proved of vital significance.

The third paper in the theoretical core of this period is 'Innate social aptitudes of Man' (6) from 1975, and is in part a homage to George Price, who had died by his own hand in January of that year. In technical terms, a hierarchical expansion of the Price equation allowed the extension of inclusive fitness to structured populations. This permitted inclusive fitness to embrace and reinterpret existing theories of group selection, and more generally exhibited the power of inclusive fitness to apply when panmixia failed and, by extension, to apply to real population structures. Hamilton chose to employ this theory in relation to the evolution of humans, making an implicit claim that the new extension of natural selection allowed biology to explain the essence of human-ness. This radical suggestion met with extreme rebuttals from the distinguished anthropologist Sherwood Washburn, among others. Hamilton enjoyed and adopted Robert Trivers's reference to this as his 'fascist paper', as a mockery of one school of objections to it.

The final core paper is a joint publication with the political scientist Robert Axelrod in 1981, 'The evolution of cooperation' (10). Hamilton believed that cooperation, along with the existing work on relatedness and population structure, completed the selective forces relevant to social behaviour. The Iterated Prisoner's Dilemma is defended as a paradigm of social interaction, and previous findings of Axelrod (1980*a*,*b*, 1984) about Tit-for-Tat are extended using the logic of evolutionarily stable strategies. The key evolutionary ideas are that how well a strategy does against itself is centrally important (following the ideas of the ESS), and that relatedness between interactants can increase the effective concentration of a new mutant strategy, so that the initial hurdle of meeting mainly an incumbent type can be easier to overcome. These central points hold despite technical difficulties with the precise conclusions of the paper. Hamilton discussed in *Narrow roads of gene land*, vol. 2 ((27), p. 132) the fact that, contrary to the paper, there is no ESS in the Iterated Prisoner's Dilemma (see Lorberbaum 1994), and there remain various serious technical issues surrounding the game in general. But whether these are ultimately resolved by fastening on to a new equilibrium concept or by studying a perhaps more realistic game with fewer technical ambivalences, the key points of this paper will undoubtedly remain.

There are two more papers from this period that should be mentioned because of their great influence in ecology. 'Geometry for the selfish herd' (5) and 'Dispersal in stable habitats' ((7), jointly with Robert (later Lord) May (FRS 1979; PRS 2000–)) bring an essential evolutionary individualist view to spatial distribution. Animals aggregate on plains because each individual is safer if it places conspecifics between itself and predators: no species advantage is required; neither is mystic or cuddly communitarianism. Similarly, considerable dispersal is favoured even in the face of very high extra mortality, simply because a stay-at-home strategy can never colonize other sites and so can never increase its representation, whereas a strategy with some probability of dispersal has the chance to spread, and is unthreatened on home sites unless there is significant dispersal in the population as a whole. The remarkable finding of Hamilton and May in one simple model was that no matter how high the extra mortality was, the ESS implied that at least half the offspring should disperse. The intellectual angle of both papers shows the importance of individual selfishness in aggregate behaviour, parallel to the significance of genetic selfishness in meiotic drive a level lower. More generally, these papers show a characteristic combination of apparent quirkiness with profound and original insight. This memoir has to focus on a central narrative with a few themes and so, regrettably, cannot cover all Hamilton's papers; many biologists may find their favourite paper omitted.

Returning to the core work of this period, the current authoritative mathematical source for inclusive fitness theory comprises two papers of Taylor (Taylor 1990, 1996). Hamilton greatly

approved of a systemization by Frank (1998) of ideas and methods in the natural selection of social behaviour, building on and extending these mathematical developments, even though at a technical level it emphasized personal rather than inclusive fitness. The key point was that Frank's work allows optimization techniques to be applied to social evolution, where Hamilton himself always had to return to population genetics models for his formal arguments.

These four core papers set out a framework, based on relatedness and agents maximizing inclusive fitness, for the evolutionary study of social behaviour. There are literatures that employ this framework, but there have been no significant additions to the framework itself. In issues such as group selection, some authors choose not to use the tools provided, but it is of enormous significance for biology that the study of social behaviour can all be treated within a single coherent theoretical structure, which is Hamilton's greatest legacy.

Sex and sexual selection

By 1980, Hamilton had begun his last major research project, to solve the outstanding problem in Darwinian biology: sexual reproduction. An important and popular subject, it was receiving serious attention in books by Williams (1975), Maynard Smith (1978) and Bell (1982), but none of these seemed to Hamilton to provide a satisfactory resolution. Looking for a single explanation, and unwilling to accept that a lack of asexual mutants played a major role, Hamilton needed a model that explained the hardest case. The culminating paper (16) claims to provide a simulation model that meets the 'challenging conditions' of 'very low fecundity, realistic patterns of genotype fitness and changing environment, and frequent mutation to parthenogenesis, even while sex pays the full twofold cost'.

The starting point was that an advantage to sex required strong continuing selection, despite outward appearances of stability of phenotypes. There was in 1980 a consensus among biologists that heritability of fitness was bound to be low, because advantageous alleles would rapidly spread to fixation. Hamilton rejected inanimate selective forces, because they would not retain variation. Eventually, drift would eliminate or fix an allele. The two classic biological situations in which variability would be positively retained *and* in which there would be continual change were those producing cycling, namely predator–prey models and host–parasite models. They were ecological models, and the cycling quantities were densities of species rather than genotypes, but Hamilton thought that sauce for the ecological goose might be sauce for the evolutionary gander. He selected the host–parasite interactions for further development because all species partake in them—viruses acting as parasites on the smallest species—and because they are more species-specific, which encourages cycling.

There followed a series of six papers in which this idea was extended and developed. The methodological difficulty was that useful current methods in population genetics allowed only an analysis of stable states in simple models. Hamilton wanted a multi-species model in which each species had varying loci and in which one of the species had more than two loci, and he wanted to show that sexual reproduction was maintained by simultaneous (possibly irregular) cycling of gene frequencies at many loci. There was no precedent for studying such a model. Hamilton felt he had the makings of an answer in a general sense but that models were absolutely required, not only to persuade himself and other scientists but also to discover more particularly the significance of the different ingredients. How, though, to proceed?

Through the six papers, Hamilton moves from a simple, parable-like model to a much more realistic and richly detailed model, which consummated the project for him. Hamilton, Henderson and Moran (11) presented an analytical treatment of a species with different genotypes subject to environmentally fluctuating fitnesses, and then in 1980 Hamilton (9) made the environmental fluctuations implicitly due to parasites by introducing genotype-specific frequency dependence. The next two papers were sideshoots from the main line: Eshel and Hamilton (13) studied heritabilities of fitness under slowly fluctuating selection pressures, and Hamilton (14) investigated how ecological competition between host species affected parasite-induced cycling. So far, the methods had all been analytic, with equations sometimes solved numerically. Returning to the central theme, Seger and Hamilton (15) first continued this approach and applied numerical methods to deterministic equations to render precise many intuitions about host–parasite systems. They went on to employ individual-based modelling, in which each individual host was separately represented in the computer model, to look at a multi-locus system, although the parasites remained implicit in a host-genotype-specific frequency dependence. In the final paper Hamilton, Axelrod and Tanese (16) applied individual-based modelling to the host species and up to seven species of parasite. This completely individual-based approach made it possible to apply various assumptions that rendered the model more realistic.

It is characteristic of individual-based models that they are so complex that they need to be studied phenomologically themselves, and this leaves room for doubt about the generality of the conclusions. But it is fair to say that the model shows that there are circumstances in which host–parasite interactions can create a robust advantage for sexual reproduction in the face of the ‘challenging conditions’ referred to above.

For Hamilton, this model completed his task, although he did publish about 10 later papers on related matters. The application of the ultimately crucial methodology, individual-based models, was conducted with co-authors who, in addition to their other contributions, actually performed the computations. Thus Hamilton’s central role in the whole project was to possess and refine the key biological insights, and to encourage others to collaborate when he needed extra technical resources.

The unity of the papers is striking, because the long-term goal is always clear and the provisional nature of all but the final paper is fully acknowledged. One offshoot of this subject is not only important in itself but illuminates how Hamilton felt his way through the complex of ideas. The first two papers had involved fitness regimes in which the fitness of a given genotype swung violently up and down in succeeding generations. Hamilton had a ‘eureka moment’ in which he asked himself what an individual in the species should be trying to do. The perverse answer was to mate with the sickest individual, because that will provide the genes that do best in the next generation. This showed Hamilton two things simultaneously: first, that sexual selection and mate choice were linked with the question of sex, and fluctuations of fitness would affect both, and second, that he should be looking for slower fitness cycles to support sex, as a mating preference for sickness seemed unlikely to be realistically advantageous. This second point led on to the joint paper with Eshel already cited, whereas the first led on to the paper by Hamilton and Zuk (12). It is worth noting some features of this turning point in the sex theory. Like so much of Hamilton’s work, it was inspired by an optimizing-agent view. It was a simple idea, and yet no one but Hamilton could have had it at that time, because it made sense only within a conceptual world into which other biologists had not yet entered.

Hamilton's attention to sexual selection transformed the subject, and the idea of choosy females as conducting a medical examination of potential mates has been extremely influential. There was a long and animated debate over the theoretical predictions of and empirical support for Hamilton and Zuk's ideas, continued with great energy in the appendix to chapter 6 in *Narrow roads of gene land*, vol. 2 (27). The emphasis on 'sosigonic selection', and the theoretical importance given to extra-pair copulations, are two important legacies, whatever may be the final verdict on the particular predictions.

In 1984, after a year's hesitation caused by the property slump in Ann Arbor, Hamilton accepted a Royal Society Research Professorship, then arguably the best job in science. He was persuaded by Richard Southwood, formerly his head of department at Imperial College, to take it up in his new department, the Zoology Department of Oxford University, with a Professorial Fellowship at New College, where Hamilton remained for the rest of his career. With Christine and their daughters Helen, Ruth and Rowena, he moved to a university house in the nearby village of Wytham, whose wood is an active research base. Bill conducted his own projects there, including the (illegal) introduction of exotic burying beetles, using a badger's skull protected by wire mesh.

Autobiography, eugenics and science

During the last 10 years, Bill's personal life changed dramatically. Christine moved to Orkney to pursue her career as a dentist. Bill met Luisa Bozzi, an Italian science journalist, who became his partner for what would prove to be only the last six years of his life. As well as continuing to publish some dozens of papers continuing the project on sex, sexual selection and parasites, he opened up two new activities. He used his by then considerable prestige to support theories which he viewed as unjustly rejected by fellow scientists through prejudice and narrow-mindedness. The second activity was autobiography.

It was not in Hamilton's nature to build an institutional empire, as most similarly distinguished scientists would have done by this point in their careers, and he continued to work as a solitary scholar. He retained throughout his life a youthful political innocence, and a disdain for authority that led to various conflicts with senior figures. He gave at least as much courtesy and attention to the views of a graduate student as to those of a Fellow of The Royal Society, and inspired enormous personal affection among junior colleagues throughout his academic life, not least those who accompanied him on expeditions to the Amazon and the Congo.

The scientific output of the final decade comprises about 30 papers. One thread (including (19) and (28)) continues the sex theme, pursuing multi-locus models, and contains the discovery of new phenomena as well as the development of methods of attacking necessarily complex simulations in which a purely mathematical approach had so far been of little use. Further papers introduce interesting ideas. Hurst and Hamilton (17) argue that the basic logic of the sexes is that male gametes delete cytoplasmic DNA, whereas female gametes do not. Hamilton and Lenton (23) and Welsh, Viaroli, Hamilton and Lenton (24) argue that clouds might be dispersal mechanisms for marine microorganisms, an idea used in the extremely moving words spoken by Luisa Bozzi over Bill's open grave (quoted in Richard Dawkins' preface to the second volume of *Narrow roads*, and now inscribed on a bench near the grave). Hamilton and Brown (26) suggest that autumn colours might result from signalling by trees to

aphids. The paper on autumn leaves is already well cited given its recent publication, and Atkinson (2001) referred to 'a tantalizing idea that will no doubt spark an explosion of new research. Autumn will never be the same again.' Amazonian plant communities were a major theme in his thinking in his final years, but unfortunately no major publication emerged before his death.

Hamilton also used his prestige to support ideas that he felt were unfairly rejected by scientists. He was providing the kind of support that he felt his own early theory should have received from the famous scientists of the 1960s. Edward Hooper was helped by Hamilton to promote his polio vaccine theory of the origin of HIV, with a coauthored paper in *The Lancet* (22) and a preface by Hamilton to *The river* (Hooper 1999). It was hard to publish on the theory, and powerful interests were at work. If the theory were true, medicine would have killed more people than it had saved in its entire history, early experiments on black Africans by white European scientists would have been the cause, and pharmaceutical companies and individual scientists might have been liable in court. It was idealistic to hope to discuss such a theory with scientific dispassion, but Hamilton deeply resented what he saw as the suppression of debate by vested interests, and thought that important implications, for example for xenotransplantation, were being missed. It now seems likely that HIV did not arise through the polio vaccines, although other iatrogenic involvement in the spread of HIV is still discussed. Hamilton's support for the theory included two expeditions to the Congo to collect samples of chimpanzee faeces, to obtain relevant evidence. During the second expedition, which determined to find samples from adult wild, not juvenile urban, chimpanzees, Bill contracted malaria in the Congo, collapsed with haemorrhaging soon after returning to London, and died without fully recovering consciousness a few weeks later, at the age of only 63 years.

In the course of supporting this theory, Hamilton persuaded The Royal Society, with some difficulty, to hold a Discussion Meeting on an urgent topic at short notice. The meeting was held posthumously (reported in *Phil. Trans. R. Soc. Lond.* B **356** (2001)) and is recognized as an important precedent: procedures now allow such meetings to be proposed and held rapidly. This substantial political success suggests that Hamilton might not have been quite as unworldly as he appeared. The report includes a tribute by Lord May, President of the Society (May 2001).

The other major theory that Hamilton tried to rescue from unjustified scientific neglect was Lovelock's Gaia (Lovelock 2000). There are sympathetic remarks in a couple of the late papers, but always accompanied by his logical objections. Hamilton was determined to remain open to strange ideas and to reject the fossilization of intellect that comes with intolerance. But in the case of Gaia, unlike the polio vaccine theory, this openness did not bring him even close to conversion.

Hamilton's hero Fisher had published five volumes of collected papers, with short notes by Fisher introducing a few of them. Perhaps inspired by this example, Hamilton created a new form of scientific autobiography in his collected papers, *Narrow roads of gene land*. Michael Rodgers, who had published *The selfish gene* and knew this part of biology well, first approached Hamilton in 1980 about publishing the collected papers, and there is a reference to 'short, linking commentaries' in the resulting publishing proposal. After renewed negotiations in 1993, the commentaries had become 'prefaces', and the first volume was published in 1996 (21). Each paper is preceded by an essay in which Hamilton relates his personal life around the time of writing the paper, the intellectual issues of the time, and contemporary reflections on the paper and the issues. The second volume was almost complete when

Hamilton died, and was published with some further light editing in 2001 (27). Hamilton had written no introductions for the third volume, which will appear, under the editorship of Mark Ridley, with introductions written by his co-authors (29). The project had caught up with itself, in the sense that the period of the papers in the third volume was mainly the period in which *Narrow roads* itself was being written.

Narrow roads is an extraordinarily useful publication for the original papers, as Hamilton published in a wide variety of places, including multi-author volumes that can be hard to get hold of. The essays in *Narrow roads* provide a vivid testimony to the life of a great scientist and a remarkable man. They contain evocations of childhood and a bygone age, compelling glimpses of inner thoughts and feelings, vivid depictions of jungle scenes, marvellous portrayals of animals and plants, true-to-life pen portraits, all done with extensive though unoppressive literary references, and more. There are other essentially autobiographical essays in this period: 'Inbreeding in Egypt and in this book; a childish view' (18), 'On first looking into a British treasure' (20), and 'My intended burial and why' (25). Bill also wrote an unpublished novel from which an excerpt was read at his funeral.

The figure who emerges is a romantic Englishman, a great reader and lover of literature. Russian novels were one passion and poetry another, including Flecker, Housman and Lafcadio Hearn. A solitary rebel proud of his physical fitness, he loved nature and was proud of his knowledge of it and ability to cope in it. A restless thinker ill-at-ease with politeness and decorum, he might in a past age have colonized new lands, but instead conquered intellectual territories. Shy and diffident, he was nevertheless a marvellous story-teller and an unparalleled natural history guide. Jeremy John saw a resemblance to a prospector whose wild appearance disturbs sedate townsfolk, but who has in fact struck gold. The unexamined life, according to Socrates, is not worth living: in the abundant autobiographical writing of this period, Bill shares with us an extended self-examination. Bill's technical writing is sometimes described as difficult to understand—in fact even this is grossly unfair because the style is literary and approachable—but reading *Narrow roads* and other essays is a delight and a privilege.

Reading the essays provides an experience very similar to talking to Bill. The diversions and footnotes, the footnotes to the diversions, and then the diversions within the footnotes, show a multi-layered restless intellect at work, able and eager to move along narrow paths indeed from viewpoint to vista in an intensely wrought and highly productive mental landscape. Biology, literature and the lessons of life fuse together for the listener and reader as they did for Bill. We owe to Robert Trivers the remark that while most of us think in single notes, Bill thought in chords.

One non-scientific and even political theme recurs throughout the autobiographical essays, and it is one that troubles many readers. Hamilton develops a eugenic argument, which was deeply felt and persistently argued. It was not a conventional eugenic argument: its recommendation of interracial marriage would hardly gain the support of the political right wing. However, it shocks many readers when Hamilton advocates infanticide, suggests the denial or in more emollient mode the strict regulation of fertility treatment, and worries about the long-term effects of saving the lives of mother and neonate with a Caesarean section.

The first context into which these views must be placed is the final five chapters of *The genetical theory*, in which Fisher lays out an evolutionist's prescription for avoiding the downfall of modern civilization. These five chapters, virtually ignored by biologists, seem, more than 70 years after they were written, to emerge from the particular social position of the writer, articulated though they may be with exactly the same language and approach as the first

eight, seminal, chapters. They were unquestionably written out of social conscience, and might in a private calculus have compensated for Fisher's inability to enlist in World War I. Both scientists had wide interests in history and believed deeply that their subjects provided insights of practical assistance in matters of the highest public importance. Hamilton's determination to express eugenic enthusiasm later may have been fuelled by his early experience with the Royal Society Population Study Group in the mid-1960s, when he reports being rebuked by the chairman, Lord Florey FRS, for suggesting that the group should study interracial differences in reproductive rate in relation to warfare ((27), page xxxvi). It was the final five chapters of *The genetical theory* that Hamilton enthused over in a postcard to his sister Mary, written on the very day that he discovered the book.

It has to be said that the scientific basis of Hamilton's eugenic views is not established, although he provided interesting possible hypotheses. In principle, the selective forces he identified could be at work, but there are no measurements, and modern conditions might for all we know have introduced other counteracting forces. A start on an intellectual engagement with Hamilton's views has been made in considered remarks of Haig (2003).

A fitting memorial to Hamilton would be a collaborative effort between evolutionary and medical sciences keeping a watchful eye on the selective effects of modern medicine. The evolutionary as opposed to medical perspective emphasizes a long timespan, so that we should be concerned about 10 and 100 and more generations into the future, and simultaneously about the possibility that new challenges will emerge, such as a return to stone-age conditions for one reason or another. It goes without saying that those engaged in the collaboration will need to employ more political sensitivity than Bill possessed if they are to do their job effectively.

It is interesting also to view this line of Bill's thinking in a second context, that of his autobiographical work. Two of his brothers died young, one soon after birth because of a handicap, and the other at the age of 19 years in a mountaineering accident. In a remarkable passage in *Narrow roads of gene land*, vol. 2 ((27), pp. 477–483), the first death is compared to that of a dog belonging to his own family many years later, and Bill reflects on what makes creatures morally deserving, pursuing the logic through to its difficult conclusion in his own personal case. Bill cycled helmetless at high speed through Oxford traffic on the bike belonging to the second brother who died, maintaining decades later a memorial love of thrill and disdain for danger. His eugenic views might have been a way to make sense of these two deaths, of his own near-fatal childhood accident, and his and his family's reactions to them. These views were the public face of private convictions. Bill often said he did not want to grow old, and he took many risks. Risks such as those in his brother's mountaineering accident, and in his own expedition to the Congo, were all part of the Hamilton family ethos. Bill's distinguished achievements, along with those of his siblings, must be put on the positive side of that balance.

Perhaps his most extraordinary autobiographical piece is concerned with his death, or rather 'My intended burial and why', published in English in 2000 (25) after originally appearing in 1991 in the Japanese entomological journal *The Insectarium* (30). In this romantic flight of fantasy, Bill sweeps far and wide over his childhood, his intellectual development, the Amazon and, finally, the habits of beetles.

A worthy successor to Darwin and Fisher

Hamilton's great contributions to biology relied on an essential admixture of mathematics and modelling. Darwin's original arguments were purely verbal, and mathematics was first brought in by the heroic figures of population genetics: Haldane, Fisher and Wright. Among these it was Fisher who paid particular attention to Darwinian aspects of population genetics, most notably in his microscope argument, his use of reproductive value and optimization ideas particularly in his sex ratio argument, and the encapsulation of natural selection in his fundamental theorem. Hamilton pursued this line in a way that was too mathematical for a Darwin, and too biological for a Fisher. His contributions have enormously enhanced Darwinian areas of biology, influencing its practitioners as well as those in the increasing spread of subjects in which Darwinism has an important role, such as demography, economics and anthropology. The widespread assumption that organisms maximize their inclusive fitness, valuing the reproduction of relatives according to coefficients of relatedness, is of far-reaching importance, and close enough to the truth.

The combination of intelligence, dedication and grit that Hamilton brought to bear on his work was truly outstanding, and it is futile to plan for more 'Hamiltons'. However, the nature of his achievements leaves no doubt how valuable is the combination in one individual of deep biological knowledge and commitment with mathematical skills.

When the history of natural selection comes to be written, Darwin will take pride of place. The first half of the twentieth century will see Fisher reconciling Darwinism with Mendelism, and representing in mathematical terms the force of natural selection within the maelstrom of population genetics. Hamilton will emerge as the major figure of the second half of the twentieth century, the first to extend the principle of natural selection, and the architect of the biological theory of social behaviour.

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