Back to article page

London Review of Books

Reasons for Being Nice and Having Sex

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Narrow Roads of Gene Land: The Collected Papers of W.D. Hamilton. Vol. II: The Evolution of Sex by W.D. Hamilton
Oxford, 872 pp, £50.00, January 2001, ISBN 0 19 850336 9

Early in the first volume of his collected papers, the evolutionary biologist W.D. Hamilton retells a Victorian joke. Two ladies are conversing, and one says: 'Have you heard that Mr Darwin says we are all descended from an ape?' The other replies: 'Oh, my dear – that surely cannot be true! ... But, if it should be true, let us pray that at least it will not become generally *known*!' Hamilton sees this response as being as relevant today as it was then: people have 'an instant, automatic wish for both the evidence and the idea to go away' because evolutionary notions 'have the unfortunate property of being solvents of a vital societal glue'. Whereas the Victorian ladies were concerned about evolution's challenge to conventional religion, their equivalents today are worried about its impact on the egalitarian premise on which democracy is based. Perhaps, Hamilton suggests, Darwin's lesson, put simply, is that all men are not born equal. He considers the current academic enthusiasm for political correctness – an 'escape route for less able minds' – an institutionalised form of denial.

The two volumes of *Narrow Roads of Gene Land* (the title is a reference to Basho's *Narrow Roads of Oku*: 'my presumptuous and vague idea is that my introductions may simulate his diary and my papers, his poems') are a compilation of Hamilton's scientific publications from the first two-thirds of his career (1964-91). Each article is prefaced by an autobiographical account of its genesis and by other retrospective thoughts. In the first volume (1964-80), these prefaces are brief scene-setting essays; in the second, they have evolved into lengthy free-association sermons. Hamilton died unexpectedly three years ago, before the editing of the second volume was complete, so maybe this self-indulgence was never intended for public consumption. Perhaps, too, some of the more extreme statements in the second volume about the dissolution of that societal glue were similarly not supposed to see the light of day. I doubt it, though. Self-censorship, as Hamilton occasionally learned to his cost, was not his strong suit.

Hamilton's obituarists were not timid in their assessment: Richard Dawkins called him 'a good candidate for the title of most distinguished Darwinian since Darwin'. His most important contribution was a Darwinian explanation of altruism, a problem over which Darwin himself admitted to having had sleepless nights. Why, in a naturally selected world in which reproduction counts for everything, would a worker bee forego reproduction in order to assist her mother, the queen, in producing more offspring? In Darwinian terms, giving up the chance to breed is the most extreme form of altruism conceivable. Hamilton realised, however, that since we share genes with our relatives, having offspring of our own is only one of several ways of ensuring that our genes are passed on to the next generation. Given the unusual patterns of relatedness within a bee colony, it makes sense – from the point of view of passing on genes – for a worker bee to assist the queen in producing more offspring instead of producing them herself. Alluding to the classical Darwinian idea of 'fitness' (originally an indication of an individual's fit to its environment but subsequently simply a measure of its evolutionary success), Hamilton coined the term 'inclusive fitness' for this notion that genes can be passed on indirectly via relatives, and his prediction that altruism is preferentially directed in this way became the lynchpin of many evolutionary analyses of human behaviour. It also generated a whole new perspective in evolutionary biology. What matters is that genes are being passed on: the details of who is doing the passing on is secondary. The resulting 'gene's-eye view' of the evolutionary process, a direct outgrowth of Hamilton's insight, was most famously articulated by Dawkins in *The Selfish Gene*.

Hamilton was an obsessive. He had become interested in the evolution of social behaviour as an undergraduate at Cambridge, and had approached University College London with a view to doing postgraduate work on the topic. UCL wasn't keen: Hamilton's embryonic ideas seemed to bear the taint of eugenics. He found a more sympathetic institutional ear at the London School of Economics and enrolled there. After first one supervisor and then another decided that Hamilton's work was becoming too esoterically genetic, he found himself back at UCL, where a geneticist was supplied to provide some guidance. This meant that Hamilton's postgraduate career was effectively unsupervised. Since he didn't have a desk at the LSE or at UCL, he did most of his work in his Chiswick bedsit, in libraries, or in the gardens of Chiswick House or Kew (with 'the wind scattering the reams of my wretched and erroneous algebra across the grass'). He was so lonely that he occasionally ventured out at night with his books and equations to Waterloo Station, where 'the human pageant' provided some distraction. He planned to become 'a carpenter, in case my theory, as I was now calling it in my hopeful moments, proved in the end to be unpublishable'. His main worry, however, was that he was a 'crank'. 'How could it be that respected academics around me, and many manifestly clever contemporary graduate students that I talked to, would not see the interest of studying altruism along my lines unless it were true that my enterprise were bogus in some way that was obvious to all of them but not to me?'

The key to Hamilton's biological insight was his skill as a naturalist. Whether on the North Downs of his native Kent or in seasonally flooded regions of the Amazon rainforest (another favourite), he could name every species and tell of each one's peculiarities. His main interest was insects, especially those dwelling in dark, damp places – under the bark of rotting trees, for example. The side of biology that deals with whole organisms (as opposed to the molecules they are composed of) is inhabited in approximately equal measure by naturalists and applied mathematicians. Naturalists supply myopic, parochial analyses of their chosen domains, while mathematicians, building on the models underpinning ecology and population genetics, produce grand generalisations that cavalierly overlook critical biological details. Too often, the naturalists lack the mathematical skills to evaluate their colleagues' models; and the mathematicians, incapable of distinguishing a winkle from a whelk, are correspondingly ill-equipped to appreciate naturalists' contributions. Hamilton was no mathematician – 'I had little talent in mathematics, and even less training in it' – but, critically, he was not intimidated by a page of algebra, even if digesting it was a long and painful process. His ability to straddle the naturalist-mathematician divide enabled him to produce plenty of original ideas.

Take, for instance, his work on what he called 'extraordinary sex ratios'. A hero of Hamilton's, R.A. Fisher, who laid the mathematical foundations of the modern theory of evolution, had argued that sex ratios should always evolve to an equal number of males and females in a given species. In his thought experiment, a male born into a species with a female-biased sex ratio is at an advantage, as he has more mating opportunities than a female. In this case, a gene that results in the production of an excess of males will be favoured by natural selection. However, the frequency of the gene will eventually reach a point where the sex ratio of the species is now male-biased, whereupon the alternative, a gene promoting the production of females, will be favoured, and so on. This process results in the species sex ratio converging on 1:1. Hamilton's familiarity with obscure corners of the insect world (knowledge that Fisher, a mathematician to the core, was singularly lacking) alerted him to many exceptions to this rule, and he developed an influential theory showing that under certain conditions (typically involving a healthy dose of incest) Fisher's rule could be broken. In the case of parasitic wasps, whose larvae gruesomely consume the insides of a living caterpillar, a single female inserts a batch of eggs into a caterpillar. These may yield a whole fleet of females, but just one male. The male inseminates all his sisters (the genetic costs associated with inbreeding in species such as ours do not apply). The females then fly off to seek new hosts in which to insert their eggs while their brother-cum-husband expires, oversexed but flightless. From the mother wasp's perspective such an arrangement represents optimal use of her hapless caterpillar victim: why produce more than one male when one will suffice to fertilise all the females?

Despite the stream of innovative articles Hamilton poured out during the first ten years of his career, recognition was slow in coming. Perennially unpromoted from his lowly position as a junior lecturer at Imperial College (he had been one of only two applicants for the position, and been offered it only after the other candidate turned it down), he moved in 1978 to the University of Michigan. His lack of progress was due partly to his failings as a public speaker: he was a mumbler. Dawkins, in his introduction to the second volume, recounts a typical Hamilton performance.

> There was a blackboard that completely covered one wall. And Bill made the most of it. By the end of the seminar, there wasn't a square inch of wall that was not smothered in equations. Since the blackboard went all the way down to the floor, he had to get on his hands and knees in order to write down there, and this made his murmuring voice even more inaudible. Finally he stood up and surveyed his handiwork with a slight smile. After a long pause, he pointed to a particular equation . . . and said: 'I really like that one.'

Imperial College undergraduates were understandably unenthusiastic about his teaching. 'During the classes most students would be good-humouredly chatting or perhaps deep in their morning newspapers,' he recalled. 'And towards the end of the course I knew they would have another topic: they would be discussing who would lead this year's delegation to the professor to complain about the irrelevance and incomprehensibility of the lectures I was giving.' Hamilton salvaged some pride from remembering that the 'world's greatest-ever scientist', Isaac Newton, occasionally found himself addressing 'ye bare walls' of a deserted lecture theatre.

In spite of Hamilton's failings as a self-publicist, his work eventually received the recognition it deserved. The catalyst was the publication in 1975 of the Harvard ant expert E.O. Wilson's *Sociobiology*. Although it was primarily about animals (especially social insects such as ants), Wilson had also ventured boldly into human territory, settling firmly for nature in the face of the nature-nurture divide. The heated debate that followed turned the spotlight on Hamilton's evolutionary analysis of altruism. The impact of Wilson's book on Hamilton's career is quantifiable, since Wilson mis-cited Hamilton's original paper, and a large proportion of post-1975 citations perpetuated his error. As a result, it is possible to identify those occasions when the paper is being cited by way of *Sociobiology* rather than by direct reference to Hamilton's original text. The appearance in 1976 of *The Selfish Gene*, in which Dawkins, too, mis-cited the paper, further enhanced Hamilton's reputation. When, in 1984, he returned to England, he came as a Royal Society research professor.

With the acceptance of his theory of altruism – proof, apparently, that he was no crank –

Hamilton turned his obsessive gaze on a major evolutionary problem he had touched on already: sex. Surprisingly, it is not at all clear why sex exists. Requiring the contribution of two parents in the production of offspring is remarkably inefficient. Think of a mutant female – a hermaphrodite – who can reproduce without male input, and whose offspring have the same ability. All the other females in the population are splitting their reproductive effort between males and females even though it is only the females, primed by a few sperm, who go on to contribute offspring to the next generation. Effectively, only 50 per cent of a female's output will contribute to that generation. Each one of the hermaphroditic offspring of our original hermaphrodite is capable of reproducing by itself, however, so that in this case 100 per cent of the original reproductive effort will contribute offspring to the next generation. In evolutionary terms, hermaphroditism is thus twice as efficient a reproductive strategy as sex. Why, then, isn't the natural world dominated by male-less species?

Because sex is so prevalent, it must have an evolutionary advantage powerful enough to counteract the impulse to eliminate it. Hamilton suggested that disease – carried by parasites – may be the critical factor. When a population of sexless clones is attacked by a parasite that has breached their immune defences, the population is devastated. Imagine, however, a pair of like-minded sexual individuals among the clones. Instead of foisting the same (clonal) version of the immune system on their offspring, they will pass on new versions of the system courtesy of the reshuffling of genes that is part of the sexual process. Maybe one of these new variants holds the key to overcoming the parasite. Thus for Hamilton, sex was all about reconfiguring genetic variation to combat the latest challenge to the immune system. Because the interaction between parasite and host is essentially an arms race – as soon as the host population has cracked the puzzle posed by the parasite, the onus is on the parasite to evolve a new and more devious means of defeating the host's immunity – the evolutionary interplay between parasite and host is a non-stop cycle of evolutionary thrust and parry. This has been called a 'Red Queen' process – 'it takes all the running you can do,' she explains to Alice, 'to stay in the same place.'

Ever the obsessive, Hamilton developed a parasite-dominated vision of the natural world. He suggested that even the bright colours of birds were produced by parasite pressure. A female bird choosing her mate among males is keen to pick an individual with good genes (because some of them will be passed on to her offspring). How does she pick a male whose genetic complement confers protection against disease? By picking the one with the brightest colours, Hamilton claimed: the flashiest crest, the glossiest plumage. These characteristics are all readily (and detrimentally) affected by disease: if I'm an unhealthy male, my crest isn't flashy and my plumage is dull. Hamilton demonstrated that the males of those bird species which are more prone to parasitic infections – those, in other words, in which this way of assessing immunity is most pertinent – tend to be brighter and flashier than the males of less disease-

prone species. It seems that male display characteristics have indeed evolved in response to the female need to assess the male's state of health.

It was the parasites that got Hamilton himself in the end. In keeping with his new world-view, he had become interested in the origins of Aids, and was a keen supporter of the conspiracy theory championed by Edward Hooper, which suggested that an early polio vaccine programme in the Congo had inadvertently introduced HIV from chimps into the human population on a massive scale. Hamilton had written a preface for Hooper's book, *The River*, and, perhaps recalling his own early days on Waterloo Station, had backed Hooper in his lonely campaign against the medical establishment (which did not take kindly to being accused of having initiated the pandemic).[*] In December 1999, Hamilton went to an area in the east of the Congo to obtain DNA samples from the local chimps. It was from here, according to Hooper's theory, that the culprit chimps came, and in their DNA that Hamilton hoped to find the smoking gun – HIV. That this region (near Kisangani) was embroiled in an ongoing war was of no consequence to him. He survived the war, but got malaria, and died in London in March 2000, of complications. Subsequent evidence has failed to support Hooper's theory, but Hamilton died doing what he liked to do best: trying, in what was for him the damp magic of the tropical rainforest, to find support for a theory that the establishment wanted nothing to do with.

Despite his hard-won mathematical competence, Hamilton was most at home in the field. I spent time with him in the rainforests of the Far East and was taken aback at first by his boyish exuberance. Every time I turned round, he would be climbing a tree, wading up an inviting river, or digging into a fallen tree with his penknife. The mumbling professor had turned into Indiana Jones. He made regular trips to remote parts of the Amazon rainforest, where seasonal floods produce a bizarre drowned world in which fish feed in the submerged crowns of trees. On one occasion, his boat started sinking: a naked Royal Society research professor repaired the leak in the course of several lengthy underwater explorations.

Some of the most beguiling interstitial passages in *Narrow Roads of Gene Land* are accounts of life in the field. Hamilton was studying wasps in Brazil when his (ultimately) famous paper on altruism was published:

> I was travelling up mainly overland from São Paulo towards Canada on my way home to Britain. Very probably the sun of the day that witnessed my paper going into the post from the offices of the *Journal of Theoretical Biology* would have seen me weaving my old American jeep between the corrugations, stones and potholes of the Belém-Brasília road (first of Brazil's transcontinentals, just two years old). At midday it would have blazed near vertically on the top of my head as I stopped at the roadside and collected wasps from some nest; later at sunset,

> if still able to pierce the haze, it would have seen me and my Brazilian companion, Sebastião Laroca, slinging our hammocks between low cerrado trees not far back from the stony or sandy piste where occasional lorries still groaned on into the night. For sure, both that day and that night I was blissfully untroubled about the finer points of measuring [genetic] relatedness.

Hamilton unflinchingly viewed human beings with the same Darwinian lens through which he saw the natural world. The result was a set of opinions often at odds with conventional notions. It also seemed to be at odds with Hamilton himself. In person, he was about as far removed as possible from the aggressive, self-seeking brute predicted by a literal reading of Darwin. Rather, he was an unrelenting champion of the underdog, and given to quoting poetry at great length. Japanese scientists treating their august visitor to an evening of karaoke found themselves subjected to twenty minutes of A.E. Housman.

Ultimately, however, biological considerations, not cultural ones, were paramount. One reason for his leaving the US after a profitable seven-year stay was the criticism levelled at him for writing a letter of reference in support of a woman graduate student whose theoretical and statistical abilities he praised as 'especially remarkable in view of her sex'. For Hamilton, it was an evolutionary fact of life that males and females have different sets of skills: 'Even in rats females have been shown to be less good at spatial and route-finding tasks than males.' Even by sociobiological standards, Hamilton's line connecting the behaviour of animals to that of humans was short and straight, the evolution of the human brain having done little to warp or extend it. His biologisation of our species accordingly pervades the two volumes, but is more prominent in the second. It's as though he had tested the waters with the first, and finding the response not unfavourable, let loose every politically dubious thought in the second. Inter-racial tension is inevitable because races represent extended family groups and we have evolved to treat kin preferentially. Eugenics – selective breeding – is the best way to ensure that the future of our species is a happy one. Selective elimination of genetically flawed newborns is necessary if we are to prevent their inferior genes from entering the gene pool. Throughout, Hamilton seems obstinately oblivious of the horrific past of the eugenics movement. He would, I think, have justified his lopsided perspective on the grounds that he was a biologist, not a historian.

The biology-is-all perspective has more to say about the future than the past. Hamilton was concerned about the high proportion of births by Caesarean section in modern hospitals (the figure he gives is 15 per cent) and worried that this represents the relaxation of a longstanding constraint imposed on human populations by natural selection. Women must have a birth canal wide enough to deliver a baby, and the baby's head must not to be so large as to cause complications. Hamilton sees the present era of drop-of-a-hat Caesareans as undoing eons of

natural selection. Come some natural disaster that causes a suspension of medical services, a species-wide crisis will occur as too-narrow women try to deliver too-big babies. Sad to say, Hamilton's final publication is a rich source of similarly wild speculations. Some evolutionary truths may indeed threaten our 'societal glue', but his scattershot application of Darwinian thinking neither reveals precisely where he supposes the ungluing will occur nor supplies a prescription for responding to it.

Brilliant field biologist that he was, Hamilton was at his best when focusing not on people but on the bizarre insects he loved. In an article written for a Japanese entomological magazine entitled 'My Preferred Burial and Why', he provided both an epitaph and, characteristically, a macabre insight into the life-cycle of beetles that lay their eggs in animal corpses they have buried.

> I will leave a sum in my last will for my body to be carried to Brazil and to these forests. It will be laid out in a manner secure against the possums and the vultures just as we make our chickens secure; and this great *Coprophanaeus* beetle will bury me. They will enter, will bury, will live on my flesh; and in the shape of their children and mine, I will escape death. No worm for me nor sordid fly, I will buzz in the dusk like a huge bumble bee. I will be many, buzz even as a swarm of motorbikes, be borne, body by flying body out into the Brazilian wilderness beneath the stars, lofted under those beautiful and un-fused elytra which we will all hold over our backs. So finally I too will shine like a violet ground beetle under a stone.

Regrettably, convention (and practicalities) intervened and Hamilton was buried in the usual way in Oxfordshire.

[*] *The River* was reviewed in the *LRB* by Roy Porter (2 March 2000).

Vol. 25 No. 3 · 6 February 2003 » Andrew Berry » Reasons for Being Nice and Having Sex
pages 35-36 | 3852 words

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^ Top