George Robert Price

(16 October 1922–5 January 1975)*

George Price was born in 1922, in Scarsdale, New York, to Alice Avery and William Edison Price. Alice, originally Clara Ermine Avery, was the daughter of Emma Adale Gage, a devoutly Methodist school teacher, and Frank Avery, a prominent jeweller in Bellevue, Michigan. Alice had worked for a while as principal of a high school in Michigan, but then moved to New York City to try her hand at an acting career on stage. William, originally named Isak Preis, was born in a Yiddish-speaking family of Russian Jews who had emigrated to Chicago. William Price, along with two partners, ran the Display Stage Lighting Company which claimed to bring scientific lighting practices to the Broadway stage. He held several patents for innovative lighting products and was a trained electrician. William and Alice had a chance meeting at the Belasco theatre in New York City and married in 1917. Their first son, Edison Price, was born in 1918, to be followed by George, four years later. The immigrant origins and religious background of their father was kept hidden from the two children.

William Price died rather suddenly after contracting pneumonia in 1927, leaving Alice to bring up the two young children alone. She had by that time despaired of a successful acting career and had been helping her husband run the company. She moved from Hartsdale to cheaper accommodation in New York City and began taking in lodgers to help with finances. In a few years, another shock disrupted her already difficult life – in 1929 the stock market collapsed, and in 1931 the Display Stage Lighting Company went bankrupt. In 1932, with some help from her brother, Alice restarted the company. Her elder son, Edison, had been sent to live with friends at their farm in the countryside while young George continued to attend Birch Nathan School on a full scholarship. At school, George, who had relatively poor eyesight and showed signs of what today would likely be diagnosed as autism, was doing very well academically and also at soccer, basketball and chess. His intellectual interests ranged from physics and mathematics to temple architecture in ancient Greece. In 1938, George had to change schools due to financial problems, and shifted to Stuyvesant, a school with greater emphasis on technical and vocational training than his older school. Nevertheless, many students from his batch, or a year above and below him, went on to excel as doctors, scientists and engineers, including Joshua Lederberg who shared the 1958 Nobel Prize in Physiology or Medicine with George Beadle and Edward Tatum, for his work on bacterial genetics. George also did well academically, though contemporaries recall him being somewhat nerdy, self-assured and with

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a tendency to be 'different'. He spent the summers by himself at a farm in upstate New York, where he worked a lot and also read voraciously. At this point, he wanted to be a researcher in physics.

In 1940, George got a scholarship to attend Harvard University. His interviewers at Harvard noted that he "might go hay-wire, but will never be humdrum", an assessment eventually proven to be absolutely spot on. World War II was already on, but the USA was not yet a belligerent, although it was helping Great Britain in its war effort. George was taking advanced courses in chemistry, biology and German but, not being too disciplined in his working style, was finding things a bit tough compared to high school where he had been able to excel academically without too much effort. He had also become seriously interested in wrestling, in addition to his continuing engagement with chess. In 1941, the USA entered World War II after the Japanese attack on Pearl Harbour and Germany's subsequent declaration of war on the USA, in solidarity with its Japanese ally. George was exempted from military service due to his poor eyesight, but had to leave Harvard as a result of losing his scholarship owing to bad grades. Nevertheless, he was able to obtain admission at Chicago University, along with a scholarship, in January 1942. Chicago University was fully engaged in the war effort, as were most other universities in the USA at the time, and housed a major activity in the Metallurgical Laboratory involving Glenn Seaborg, Enrico Fermi and Arthur Compton, focussed on utilizing plutonium for developing an atomic bomb under the Manhattan Project. George did well academically at Chicago, graduating in late 1943 with a major in chemistry. He was promptly offered an Eli Lilly Fellowship to join for a PhD in the same university. He initially worked in the Enzyme Laboratory but was very soon transferred to work on the Manhattan Project, and obtained a PhD in chemistry in 1946 for his thesis titled 'Fluorescence Studies of Uranium, Plutonium, Neptunium, and Americium'. His doctoral work involved developing fluorescence-based assays for the detection of very small amounts of radioactive elements from tissue or urine samples, and the technique he developed was determined in 1945 to be the most sensitive and efficacious among those developed in seven different laboratories nationwide.

During his period at Chicago University, George continued to be actively engaged with both wrestling and chess, and also continued to build up a reputation as one who was, in the words of his best friend Al Somit, "an oddball among oddballs". He was a contrarian, often seeming to delight in shocking his peers with outrageous remarks, sometimes ironically bordering on rabid anti-Semitism. He was also socially awkward, either seemingly flippantly unaware of social mores, or sometimes almost spitefully dismissive of accepted norms of behaviour. Increasingly, his friends were finding it hard to understand him, but he did not seem to be bothered by that. During his doctoral years at the Metallurgical Laboratory, George got to know Julia Madigan, a zoology graduate from Chicago, who had shifted to the Manhattan Project from

Medical School. In 1945, much to Al Somit's surprise, George and Julia became romantically involved despite being opposites in many ways. George was militantly atheistic and a contrarian, somewhat extremist, rebel, whereas Julia was a devout Catholic, and fairly conservative in her social views and behaviour. Nevertheless, the two seemed to hit it off and were married on 28 June 1947, though not before her parents had extracted from him a promise that their children would be raised as Catholics. Since finishing his PhD in 1946, George had been working at Harvard as a chemistry instructor and, after their marriage, the couple took up residence in a small house near the chemistry department.

Over the next few years, George's life slowly began to spiral downwards. He did not like the department at Harvard, and the routine of classes and exams stifled him. He remained aloof and isolated from the other chemistry faculty members. As a diversion, he took up consultancy at his old haunt, the Metallurgical Laboratory at Chicago, by then christened the Argonne Labs, but the work there had shifted away from his expertise in screening for radioactive contamination to reactor piles and was not very satisfying to him. In May 1948, their first daughter Annamarie was born, but George and Julia were not getting along too well by this point. In August 1948, excited in part by the new information revolution in the air following Claude Shannon's first article on a general mathematical theory of information, George left Harvard for Morristown, New Jersey, to start work at the Bell Labs. Many years later, in an article originally written around 1971, but only published posthumously in 1995, he wrote, echoing the effect Shannon's article had had on him: "A model that unifies all types of selection (chemical, sociological, genetical, and every other kind of selection) may open the way to develop a general 'Mathematical Theory of Selection' analogous to communication theory...Selection has been studied mainly in genetics, but of course there is much more to selection than just genetical selection...yet, despite the pervading importance of selection in science and life, there has been no abstraction and generalization from genetical selection to obtain a general selection theory and general selection mathematics".

George worked at the Bell Labs for close to two years, on Germanium-based transistors. Though his work was successful and well appreciated, he seemed to tire of it. A second daughter, Kathleen, was born in 1949, but his relationship with Julia continued to deteriorate. He became increasingly quirkier and the contradictions between his atheism and his wife's devoutly Catholic views began to cause ever more friction between them. In 1950, he was tired of the situation at Bell Labs and, when his former Chicago boss Sam Schwartz invited him to work with him once again, George jumped at the opportunity for a change and the whole family moved to St. Paul, Minnesota. George started working on porphyrin fluorescence-based methods for imaging and radiotherapy of cancer cells at the Radioisotope Laboratory at the Veterans Administration Hospital. The work went well, and in a few years, George had achieved

several breakthroughs in techniques for cancer cell detection and treatment, leading Schwarz to say that he was the only 'man of genius' he had ever worked with. Yet, his personal life was falling apart. Finally, his marriage floundering, and his interest in the porphyrin work also abating, George opted to live separately from his family, in student housing near the hospital, in 1953, just six years after he and Julia had gotten married (the two would get divorced in early 1955). Shortly thereafter, George contracted polio, the disease leaving him with a permanent limp and severe damage to his right shoulder, necessitating him to learn how to do many daily chores with his left hand. The polio attack, when he was living alone and already somewhat depressed, added to his unsteady frame of mind, in part because it required him to curtail his normally very active physical lifestyle.

The early 1950s were also a time of turmoil within the USA, with the cold war and scientific rivalry with the USSR in full flow. The hydrogen bomb had been invented, by both powers within nine months of one another, and game theory, pioneered by John von Neumann, was increasingly being deployed to make tricky strategic decisions. George was among many Americans worried that the USA might lose the scientific, and thereby, the political "war" against the USSR. Increasingly, he was thinking about how his country could boost the rate of technological innovation and invention, and how to economically sustain such developments and also outcompete the USSR. This led him to an increasing interest in both economics and game theory. Around the same time, Europe and the USA had been seeing a renewed interest in psychic and paranormal phenomena, perhaps another expression of the troubled and uncertain times. In particular, over the preceding ten to fifteen years, Samuel Soal in England, and Joseph Rhine in the USA, one a mathematician and earlier skeptic, the other a theologian turned skeptical science student, had made a sustained and articulate case that science could not explain the paranormal. This implied that there was a major lacuna in scientific understanding of otherwise natural (in the sense of not involving supernatural or spirit powers) phenomena. George was aghast and angered by this and, having examined their writings, concluded that both Soal and Rhine were frauds. For many years, fuelled in part by his mother's claims to be communicating directly with his long-dead father, George had been railing against superstitious beliefs in the occult, mystical and paranormal. The seemingly 'scientific' arguments marshalled by Soal and Rhine were the proverbial last straw. In a blistering response to Soal and Rhine, George rejected their notion that science and the paranormal were compatible, laid out several ways in which they could have cheated, and argued for one conclusive experiment that would aim at elucidating a mechanism for these paranormal phenomena. Titled "Science and the supernatural", George's 1955 paper, appearing in the respected journal *Science*, attracted a great deal of attention and provoked many angry and antagonistic responses, culminating in two pointed rebuttals by Soal and Rhine, respectively, in the January 1956 issue of *Science*. George reiterated

his views in another *Science* article later in 1956, titled 'Where is the definitive experiment?', but thereafter seemed to have lost interest in this particular battle.

A little before his broadside against Soal and Rhine, in 1953, George had published a paper on economics in *Science*, attacking both the Marxist theory of governmental control of economies and the view widespread among western economists that humans could be viewed as 'rational actors', and economic phenomena modelled accordingly. George advanced the view that human behaviour, including economic decision making, was neither that straightforward, nor particularly rational, and that the modelling of economic phenomena was still at a very primitive level compared to the natural sciences. He also suggested that a more sophisticated science of behaviour may be needed before economics could truly progress. Ironically, this is almost exactly where we stand today, after almost 70 years, with the rise of 'evolutionary economics'. In 1956, George published an amazingly prescient article in the *Fortune magazine*, entitled 'How to speed up invention'. In this article, written before CAD (Computer Aided Design) became an active area of research, George put forth the notion of the Design Machine. This was a machine into which an engineer could input a mechanical design, with the machine then translating the design into mathematical language, which would, in turn, permit the engineer to visualize the designed part, manipulate and modify it as required, and then command the machine to direct its manufacture. He next came up with a detailed document laying out how the machine, which would incorporate an IBM 704 computer into it, would function. He also wrote passionately about the need for the USA to double its defence budget and invest heavily in research and development if it was to stay ahead in the cold war. In late 1957, George moved once more, back to New York, working as a subcontractor for the Stevens Engineering Company which, among other things, did quite a lot of outsourced work for IBM. His ex-wife Julia, and their two daughters, had meanwhile moved from Minnesota to Michigan.

Initially, IBM seemed to be interested in the Design Machine idea, but no concrete offer was forthcoming beyond a general suggestion from IBM's director of research, Emanuel Piore, that George might want to join their research and development team. George, on the other hand was not willing to join IBM unless they seriously wanted to put his idea into production. He was also exploring the possibility of seeking a patent on his Design Machine. Consequently, he continued to work for various subcontractors for the next several years, while doing a lot of science-related writing on the side. He was also trying to write a book titled *No Easy Way*, but the publishers, Harper and Brothers, turned down the draft in 1958, deeming the book unsaleable. He managed to negotiate a contract with another publisher, Doubleday, but they wanted the book within a few months. That was not to be, but George kept persuading them to give him more time. By this time, George was also increasingly in financial troubles. On the one hand, he had no regular fixed income and, on the other, he was in the midst of a bitterly

contested legal struggle with Julia over alimony. Amidst all this turmoil, he had not seen his daughters for several years. Living in Greenwich Village in New York, just a few years before a young Bob Dylan would burst onto the avant-garde art and music scene, George began to take a variety of drugs to allay his anxieties. He was also seeing a psychiatrist. Unfortunately, although the drugs helped him stay relatively calm, they also made it difficult for him to do any serious work. Around this time, too, George started following the work of the psychologist and behaviourist B F Skinner, who, among other things, argued that there was no innate human nature, and that an individual's personality and psyche were entirely shaped by experience. George was himself thinking about human nature, human social structures and family, and why they were the way they were, lines of thought that would eventually lead to his profoundly imaginative contributions to the understanding of animal behaviour and apparent altruism a few years later, after he moved to England.

In March 1960, on top of his disabilities due to polio, came another unpleasant shock: George was diagnosed with a non-malignant tumour in his thyroid and had to undergo surgery to remove it. In April 1960, IBM invited him to join their research team working on CAD. For a while George hesitated, but his dire financial situation tipped the balance. In early 1961, he set aside plans for the book and joined IBM, working there for the next six years. On the side, he submitted two more papers to *Science*, both being rejected by the journal with fairly scathing comments from the referees. He also dislocated his shoulder twice, further adding to his depression. Feeling bitter, George rapidly lost interest in the CAD work. In 1962, he began to think about writing a book challenging Skinner's simplistic and very mechanistic view of psychology and human behaviour. He was continuing to think about innate aspects of human behaviour and how and why they had arisen evolutionarily, especially the traits of being self-centred and egoistical, in addition to parental, especially paternal, care. He also worked on two new problems, dealing with novel optimization algorithms and a neurophysiological coding for colour vision, respectively. The latter interest had arisen from practical problems in developing machine systems of visual recognition. As often, George's ideas were imaginative, original and ahead of the times. His optimization work eventually led to a new class of economic models of profit-based systems, but at that time elicited only a tepid response from leading economists like Paul Samuelson. His work on vision indicated for the first time a role for glial cells in vision, but the idea did not appeal to leading biologists at the time, since the glial cells were not neurons. These lines of work, too, thus led nowhere, though George had been very hopeful that they would constitute important breakthroughs. He badly wanted some scientific success, partly to feel good about what he was doing, and also because a 'big' paper would help him sell his popular science writing better. George was a great believer in the notion that a motivated and passionate outsider to a particular scientific field could contribute to major new and

profound scientific understanding, and the fact that he had not managed to do so was adding to his general sense of melancholic dissatisfaction with life.

In February 1966, he underwent another operation to remove his thyroid entirely and, unfortunately, the surgery did not go well, leaving him eventually with practically no sensation on the right side of his face, and his right shoulder and arm, and resulting in a partly paralyzed right arm. In deepening depression, he stopped taking his thyroxine supplements, compounding his mental health problems, eventually necessitating a short internment in a psychiatric care facility. He was nursing a furious hatred towards the surgeon, a friend of his from Chicago, and mused that he would like to be able to sue him under Mosaic (an eye for an eye) rather than civil law. He had received a 25,000 dollar insurance settlement and, fed up with his life, wanted a change. In November 1967, George Price, 45 years old, brilliant yet unemployed and, to his mind, unsuccessful scientifically, divorced, and partly handicapped due to polio and the botched surgery, set sail for London. This was to be the stage for both his great scientific breakthroughs in the field of evolutionary biology over the next few years, and his untimely death by suicide in just over seven years.

In London, George rented a flat near the University and began to frenetically read a wide variety of papers and books on animal behaviour and evolutionary biology. Seemingly oblivious to the cultural riches of London, and to its increasing anti-war and avant-garde scene, he spent most of his time in libraries at University College, the Zoological Society, the British Museum and the Natural History Museum, in addition to several excellent public libraries that, luckily, remained open till quite late in the night. He cast his net wide, reading up on anthropology, behaviour, psychology, medicine, linguistics, neurophysiology and evolutionary biology, while leading what he termed an "anti-social" life in a letter to a friend back in the USA. In March 1968, he wrote his first letter to the evolutionary biologist William Hamilton (see *Resonance*, April 2001), who had recently published two landmark papers in 1964, one on the evolution of altruism and one on the evolutionary explanation of ageing. "I have just been reading your very interesting paper on 'The genetical evolution of social behaviour,"' began George's letter, "and would very much like to have reprints if you still have any to spare." He also asked whether Hamilton had any ideas on how cultural and genetic evolution might interact in humans, and whether he had any empirical evidence for what were later to be termed 'greenbeard genes'. Hamilton wrote back, regretting that he had no reprints left but sending a reprint of a more recent paper on sex-ratio evolution. He also seemed to intuit George's dismay that nepotistic altruism (kindness towards kin) might be all that nature offered in the way of 'goodness', writing "So far I haven't arrived at any clear idea even as to what sort of "game" the genes are expected to be playing when operating together (on different chromosomes or linked on a particular pair). Something like socialism (or is it racialism—can't tell), admittedly, seems

indicated, but I have only vague ideas as to the mechanisms by which biological and cultural evolution interact. With man culture did once, in the form of primitive religions, reinforce socialism, but now what we take to be highest in culture has swung strongly against nepotism and the like. Can this be just a higher hypocrisy induced by the need which civilization creates for genetic diversity—and perhaps even racial diversity—in human groups?". George was, indeed, agonizing over the issue of whether altruistic behaviour would necessarily be directed only towards kin, as Hamilton's formulation suggested. He was also wondering whether the converse was also true, that natural selection would tend to favour the evolution of malevolent behaviour towards non-kin. He was also pricked by Hamilton's reference to games, especially of the Prisoner's Dilemma kind, that might be "played" by genes over evolutionary timescales. George himself was familiar with the use of these sorts of results from game theory through his earlier study of John von Neumann's work. Unfortunately, Hamilton had written that he would be in Brazil for field work for quite a few months and, consequently, George could not mail his reply to him, although he wrote one.

Instead, George turned to another problem, that of the function of deer antlers, triggered by a recent paper suggesting their role in heat dissipation and, therefore, thermoregulation. George clearly saw that the argument would not stand, and over the next few months wrote up a paper, submitted to *Nature* in August 1968, in which he analysed the potential role of antlers in ritualized combat between males within an explicitly game theoretic framework. In this highly original and path-breaking paper, titled 'Antlers, intraspecific combat, and altruism', George not only applied game theory to the evolution of animal behaviour for the first time, but also came up with the notion of the unbeatable strategy, now called the Evolutionarily Stable Strategy, or ESS. He wrote, "A sufficient condition for a genetic strategy to be stable against evolutionary perturbation is that no better strategy exists that is possible for the species without taking a major step in intelligence or physical endowment. Hence a fighting strategy can be tested for stability by introducing perturbations in the form of animals with deviant behaviour, and determining whether selection will automatically act against such animals". Though ostensibly about antlers in deer, the paper was in fact the first step towards a form of evolutionary analysis that would eventually blossom into an entire sub-discipline within the broad field of evolutionary ecology, and was full of novel conceptual insights about the nature of the evolutionary process and how one could model it using game theory. Around this time, George moved to a new house and managed to find, through contacts in Imperial College, an address in Brazil at which he could send his reply to Hamilton. In his letter, he thanked Hamilton for the insight that game theory might explain genetic dynamics in evolution, and asked whether Hamilton had considered the evolution of malevolence towards unrelated individuals as the flip-side of his theory of kin-selection as an explanation of the evolution of altruism. He also

mentioned that he was planning to develop "a more transparent (though less rigorous) derivation" of Hamilton's explanation for the evolution of altruism and was hoping to seek his advice when this task was done. This is the first mention of what would end up being eponymously known as the Price Equation (see General Article in this issue). In the course of a few months in his new home in London, George was well into providing extremely novel and original insights into fundamental issues at the very heart of evolutionary biology.

Shortly thereafter, while continuing to wonder whether relatedness would constitute the only mechanism by which selection could favour the increase within a population of genes for altruism, George decided to try and derive from brass tacks, a mathematical formulation for change in population composition via natural selection. He realized that the change in mean trait value (phenotype) over one round of selection ($\Delta\overline{z}$) would be given by the covariance between an individual's trait value (z) and the number of offspring it produced (w), scaled by the average number of offspring produced in the population.

He was, at this time, thinking in terms of offspring exactly duplicating the trait value(s) of their parent(s): a later modification was yet to come. More importantly, though, George realized that by sticking to trait value (phenotype) and number of copies produced, his relationship, $\Delta\overline{z} = \frac{Cov(w,z)}{\overline{w}}$ would express the outcome of one round of a selective process of any kind, where a subset of some ensemble of entities was to be selected. It mattered little whether it was a person selecting radio frequencies or differential survival and reproduction among individuals of a species that was effectively selecting trait variants. The covariance between the characteristic and copies produced would determine how the composition of the ensemble changed with regard to the relative abundance of characteristics exhibited by its constituent entities. This very general formulation could also be used to explain the evolution of all kinds of behavioural traits ranging from altruism to spite. A few decades earlier, the legendary evolutionary biologist and statistician R. A. Fisher (see *Resonance*, September 1997), an intellectual hero to Hamilton, had started the preface of his book *The Genetical Theory of Natural Selection* with the cryptic, almost oracular, statement: "Natural Selection is not Evolution". He went on to lament that, because natural selection had been invoked as the main mechanism of adaptive evolution by Darwin and Wallace, this inter-twining of the two "had the unfortunate consequence that the theory of Natural Selection itself has scarcely ever, if ever, received separate consideration". Yet, in his own work, Fisher rooted the theory of natural selection in the recently rediscovered principles of Mendelian inheritance. This was largely due to the fact that, prior to a general appreciation of Mendelian inheritance, it had been thought that heredity and selection were incompatible (see *Box* 2 in *Resonance*, June 2017, pp.531–532). It was left to the maverick outsider, George Price, peering in from the outside à la Jim Morrison of the Doors, to develop the first truly generic mathematical description of selection that would apply to any arbitrary

form of inheritance that could generate the necessary covariance. Fittingly, it was later shown that Fisher's Fundamental Theorem of Natural Selection, though preceding it by almost four decades, was a special case of the Price Equation under the assumption of Mendelian inheritance. It is also, therefore, not surprising that the first fully satisfying elucidation of what exactly Fisher's Fundamental Theorem meant was actually given by George Price, in a paper published in the *Annals of Human Genetics* in 1972.

On 24 September 1968, George showed his work on selection and covariance to Cedric A. B. Smith, a well known mathematical geneticist and Weldon Professor of Biometry in the Human Genetics Department at University College London, in part to find out whether someone had already come up with the covariance formulation. Smith was much impressed and, after a brief meeting with the departmental chair, George was appointed as an honorary fellow with a small office in the department. An hour or so after leaving the department, George excitedly wrote to his mother, "Something wonderful and totally unexpected happened to me...I obtained a mathematical result that looked very interesting...this morning I went to talk to a Professor Smith...He looked at my result and said it was interesting, very pretty, and he had never seen anything like it before". Things were finally looking up for George. Hamilton had replied to his second letter, saying that there was no point sending a manuscript to Brazil and that he would be back in England around the end of the year. Clearly, some of the world's best evolutionary biologists were taking his work seriously.

Buoyed up by these recent developments, and waiting for a response from *Nature*, George worked on applying game theory to understand what kinds of behavioural strategies in early human hunter-gatherer societies might maximize transmission of genes inducing them, in a continuation of his attempt to understand the evolution of human social and marital systems. In 1969, this work brought him back to the perennial question of individual versus group benefits, an issue that had occupied him from the 1950s, and to the debates about whether democracies were less efficient and, therefore, less competitive, than more authoritarian systems, like the USSR, because they valued the individual more than the collective. In February 1969, there was more good news—*Nature* informed him that the antlers paper was provisionally accepted, provided he could trim its length considerably. Unknown to George at the time, one of the reviewers who was much impressed with the manuscript was John Maynard Smith (see *Resonance*, November 2005), the other leading evolutionary biologist in England, along with Hamilton. Unfortunately, though, George's mother Alice was in poor health, and deteriorating fast. Funded by his otherwise estranged elder brother, George flew back to the USA to see his mother for a couple of months. During his stay in the USA, he also read a paper on the 'Tragedy of the Commons', analysing the arguments of the author Garrett Hardin in light of his own thoughts on how evolution would work if traits were differentially beneficial or harmful

to the individual and the group, respectively. In late April 1969, he was back at University College, London. His mother died a few days later, and around the same time he heard that the Science Research Council of UK had approved his application for a three-year grant to study conflict and cooperation in the context of selection acting on individuals versus groups.

In the summer of 1969, continuing to ponder upon selection acting simultaneously at the individual and group levels, and how to separate those two components, George hit upon the idea of adding one more term to his selection equation, writing it as $\Delta\bar{z} = \frac{Cov(w,z)}{\bar{w}} + \frac{E(w,\Delta z)}{\bar{w}}$ where E is the expectation (equivalent to a mean) and Δz is the difference between the trait value of a parent and the mean trait value of its offspring (please see the General Article in this issue for details). The second term on the right hand side of the equation, as applied to classic selection among entities at the level of the biological individual, incorporated the effects on total change in the population of how much the offspring of an individual differed from it in trait value, on an average. This is nowadays often referred to as the 'transmission bias' in inheritance and could reflect the manifold effects of genetic mutations and recombination. However, what George also realized was the fact that just as the equation could be used to split total phenotypic change into components due to selection and transmission bias, it could also be used to split up total change due to selection between groups of individuals and selection among individuals within groups (please see the General Article in this issue for details). What was particularly heartening to George, with his obsessive interest in the nature and scope of 'human goodness', was the corollary that if selection between groups was stronger than that among individuals within groups, then a true altruism could evolve, contrary to the suggestion from Hamilton's kin-selection theory that all altruism would essentially be nepotistic, i.e., directed solely towards relatives. He wrote once again to Hamilton, who was back from Brazil, sending him the expanded version of the equation and relating the whole story of how he had ended up at University College. He also pointed out a small mistake in Hamilton's original formulation of kin-selection, suggesting that they could perhaps talk about it on the phone. The next day, Hamilton and George Price spoke for the first time, over the telephone. Hamilton recollected later that his voice was strangely squeaky and a little condescending, and that he referred to his equation as "surprising to me, too—quite a miracle". Hamilton was even more surprised when George asked him whether he had seen how the equation worked for group selection. Hamilton had been, along with Maynard Smith and George C. Williams, one of the trenchant critics of group selection, and he had not noticed at all that the Price equation actually allowed the analysis of selection acting at multiple levels. Following the phone call, the two did not interact for almost a year.

That intervening year was again somewhat disappointing for George. He worked on computer simulations of animal conflict scenarios and, in November 1969, sent a brief paper on selection

and covariance to *Nature*. He followed it up a couple of months later with a longer paper to *Science* in which he explicitly made the connection to group selection. In February 1970, *Nature* rejected his paper, with the chief editor writing that it was too difficult to understand. The rejection from *Science* the next month was even harsher, condemning the paper as too abstract, full of hubris, and not applicable to any particular scientific problem. This, in particular, hurt because George had pitched the *Science* paper as a general mathematical theory of selection analogous to Shannon's information theory. Once again, George lapsed into depression, until in May 1970 he received an almost breathlessly excited letter from the normally dour Hamilton. "I am enchanted with your formula", wrote Hamilton, most uncharacteristically, "I really have a clearer picture of the selection process as a result. In its general form I can see how we might use your formula to investigate 'group selection"'. When apprised of the rejection of Price's paper by *Nature*, Hamilton came up with a strategy to ensure its publication. He would submit a paper to *Nature* himself, an analysis of the evolution of spite in which he used Price's equation as the foundation. Once his paper was accepted, he would write to the editors of *Nature* stating that since his work was based entirely on Price's mathematical work, it would be difficult for him to agree for his paper to be published unless he could cite Price's work. He would also politely remind them that they had recently rejected Price's paper. The strategy worked: Price was asked to resubmit, and the paper was accepted, appearing in *Nature* in August 1970.

The next three years constituted a strange and tragic interwoven tapestry of continued scientific work and a rapid unravelling of George's mind and life. To George, formerly an atheist, he had been led by the Lord to discover religion and the true purpose of why he had been put on the earth. To his few friends and sympathizers, it appeared that he was slowly going mad. Around the time that Hamilton had realized the full implications of the Price equation, George became a fiercely dedicated, fanatic and evangelizing Christian, with every bit the passion with which he had hitherto been an atheist. He had convinced himself that his life was full of meaningful coincidences that inexorably led him to the conclusion that the Lord was speaking to him and urging him on to a new calling. He began studying the Bible carefully, and also the historical background to the life of Jesus. Characteristically, he soon began to disagree with many of the positions taken by the Church and soon was deep in bitter theological arguments with some of the pastors who had initially welcomed his conversion. At the same time, his evolutionary researches continued. In 1971, a paper of his extending the Hardy-Weinberg Equilibrium (see *Resonance*, October 2008, pp. 951–970) to situations with assortative mating was published in the *Annals of Human Genetics*. The year 1972 saw three more papers appear in print. The longer covariance paper, including the discussion on group selection, rejected by *Science* the previous year, featured on the cover of the *Annals of Human Genetics* in early 1972.

George's superb exposition of what Fisher's Fundamental Theorem really meant also appeared in the same journal a few months later, as well as a paper co-authored with C. A. B. Smith on Fisher's Malthusian parameter and reproductive value. These were all solid contributions, with novel insights, to fundamental issues at the heart of the theory of adaptive evolution by natural selection. By mid-1972, George was working on a mathematical theory of genetic variation and polymorphisms, being dissatisfied with Kimura's neutral theory approach to the problem of the maintenance of genetic variation in populations. He had tried some computer simulations of game theoretic models of animal conflict but, not getting any startling results, had largely given up on that work. However, Maynard Smith, his imagination pricked by George's antlers paper that he had reviewed for *Nature*, had been working on applying game theory to the evolutionary analyses of animal conflict, and was trying to write up his results. Searching for George's paper in order to cite it in his own, he realized that the paper did not seem to have been subsequently published either in *Nature* or elsewhere. Having briefly met George once at London, he wrote to him in 1972, sending him details of his own computer simulations on the issue. George was quite excited to see Maynard Smith's progress on a problem he had largely abandoned after being the first to develop the approach. Eventually, the two decided to write a joint paper on the logic of animal conflict, which appeared on the cover of *Nature* in November 1973. This was to be George Price's last scientific paper, with the exception of a long-forgotten manuscript on 'The Nature of Selection', published posthumously in the *Journal of Theoretical Biology*, twenty years after his death, thanks to the efforts of the theoretical evolutionary biologist Steven E. Frank.

By 1971, smouldering in the passion of his newly found religiosity, George had begun to upset and alienate his few friends, including Hamilton, by his insistence that they follow his path to Jesus. He believed he had arrived at a better reconstruction than theologians had of Jesus's last days and of the ancestry of Mary, Jesus's mother. He had learnt, from visiting family friends from the USA, of his Jewish paternity, but it only served to convince him further of the inevitability of his being drawn to Jesus. He invited his daughters and grandson to visit him, and tried hard to convert them to evangelical Christianity while they were with him in London in the winter of 1971–72. His attempts failed, with his daughters having rebelled against organized religion long ago, when they were still living with Julia. He proposed to a friend, Rosemarie, but she turned him down. In 1972, he even published an apology in *Science* to Soal and Rhine, for having doubted them for their faith in extra-normal phenomena, and started up a correspondence with Rhine. It did not quite have the effect he intended, though, because Rhine was not religiously inclined to a belief in supernatural things and had genuinely believed that para-normal happenings were actually due to natural phenomena that contemporary science could not explain. He quickly got exasperated with George's fanatic religiosity, and their

exchanges became increasingly acrimonious before petering out altogether. In July 1972, the SRC grant ran out, and C. A. B. Smith was trying to get him one year's funding to stay on at University College and work on genetic polymorphisms. The work on genetic polymorphisms, however, did not really progress, and neither did some work George was hoping to do with Hamilton on sexual selection. By late 1972, George had more or less stopped eating, living on milk alone, and, far more disastrously, had stopped taking his thyroid medication. One day, he was found unconscious on the staircase of his block of flats by a neighbour, one Mr. Wood, who rushed him to hospital. He was close to being dead. Luckily, the doctor attending to him noticed his severe thyroxine deficiency and started giving him intravenous thyroxine, thereby saving his life. George spent many weeks recovering in hospital, being discharged in January 1973.

During his convalescence at the hospital, George had been deliberating about his activities since his conversion and was coming to the conclusion that his Christian beliefs had been a hypocrisy. The essence of Jesus's teachings, he now thought, was love for your fellow beings, and he now felt that he had been misguided in his more intellectual involvement with religious affairs like his Bible exegesis. By February 1973, George underwent a second conversion, abandoning his Bible studies and trying one again to reach out to people, both friends and strangers. In particular, he devoted himself to serving the needy, elderly and homeless. He began to spend a lot of time with derelicts and homeless people, many of whom were in and out of jail, and began to spend all his meagre finances on helping them. He was also smoking cannabis regularly. He sold many of his few belongings to fund his charitable work, and began inviting homeless people to stay at his flat, even giving them spare keys. He also wrote to his ex-wife Julia, asking her to come and visit in the summer with their daughters and grandson, and wistfully wondering if they might get married again. He also explained to her, in the same letter, that now that he was busy doing Christian charity pretty much full time, he may not make a much better husband than in the past but that she would assuredly find him "much kinder than before". Julia did, in fact visit him in London in August 1973, but left after a couple of weeks, worried and saddened at his general decline.

In April 1973, the one-year appointment of George as an Associate Research Fellow at University College came through, though by now there was little hope that he would see any serious work through to completion. Towards the end of June 1973, the lease on his flat ran out and George became homeless. For a while he took to sleeping in his office, occasionally working but still devoting all his time and money to the homeless derelicts he believed it to be his role on earth to serve. Many of these derelicts, roaring drunk, began to come to his office at University College, creating unpleasant and embarrassing situations, especially for C. A. B. Smith. For some weeks, George lived with various friends, and then even took to sleeping

in parks for a while. In November 1973, his old friend from Chicago, Al Somit, visited him and was deeply shocked by how old and haggard George looked. His few friends, and even his otherwise estranged brother, were now genuinely worried about George's state, though he himself seemed to be in some sort of state of inner peace. By now, the weather was cold and George had no place to stay in the evening and night, because University College authorities, fed up of his strange and undesirable companions, had decreed that he could not be in his office outside regular working hours. Finally, late in 1973, George started sharing a room at a squatters' commune at the Tolmers Village Association, a small student led movement aimed at protecting poor residents of the area around Drummond Street from eviction by big developers who wanted to remove the largely poor and immigrant population of the area, tear down their dilapidated houses, and build office blocks in their stead. The community of about 180 squatters was a shifting one, and very diverse, ranging from students and artists to anarchists, unemployed drifters and the homeless. There were a few communal kitchens, and no toilets, except for a few outhouses and the facilities at nearby train stations. George settled down in this community and continued his charitable work with the elderly and homeless, occasionally finding time to work on genetic polymorphisms or sexual selection. In February 1974, he visited Hamilton at his home in Berkshire for a couple of weeks. Hamilton and his wife were shocked at his emaciated appearance and suggested that he try applying for a job at Imperial College. George said he would think about it but also told them that population genetics was no more his main work.

At the end of April 1974, George's fellowship was over, and he had exactly ninety-five pounds to his name. He had already been avoiding going to University College, being fully involved in his new community. He was also in an intimate relationship with a nurse, Joan Jenkins, but, uncharacteristically, it was George who did not want to actually get married. He had been changing residence from one squat to another quite frequently and at one of these, in Tolmers Square, he became infatuated with, and proposed to, a young twenty-five-year-old American artist, Sylvia. Although she made it clear to him that she was merely fond of him as an interesting older friend, George fantasized about marrying her and moving back to the USA. Just after his fifty-second birthday, in October 1974, he moved to yet another squat, further down the road from Tolmers Square, partly to avoid running into Joan. He had also been trying to find a job and had written to friends that he was on an upswing. In November, he burnt both his hands badly when a pot of boiling water overturned, and he again fell into a depressed state. He was not eating regularly and often not taking his medicine. Those who saw him at the time remembered him as being gaunt and emaciated—all skin and bones. In late November, he wrote to his daughter Kathleen that he felt that "the Hounds of Heaven are closing in on me". By early December, he was trying to see a psychiatrist, but the earliest available appointment

was for 9 January 1975. Hamilton met George in London in late November and, shocked at his condition, invited him to come over to Berkshire, which George did in mid-December. Hamilton tried again to wean him away from his destructive lifestyle back into evolutionary biology research, and George seemed to be convinced, even wondering if he could still hope to get a job at Imperial College. As Hamilton and his wife were going to visit her parents in Ireland for Christmas, George left for London on 19 December 1974. The next time Hamilton would see George would be at his funeral.

On the morning of 6 January 1975, Shmulik Atia, an Israeli ex-army man who lived in the same squat as George, saw an envelope pushed under the door. He could not read English, and thinking it might be an eviction notice, he ran upstairs to ask George. When he knocked, the door opened slightly, and Shmulik found George dead on the floor with a wound in his neck, a sharp scissors in his hand, and blood everywhere. Evidently, George had killed himself sometime during the night. After an inquest, at which Hamilton testified, a funeral service was finally held at St. Pancras Cemetery Chapel on 22 January 1975. Five of his homeless friends were there, along with William Hamilton and John Maynard Smith, as strange an assemblage as one could possibly see at a funeral. By and large, George's death passed unnoticed, though Hamilton wrote to his family back in the USA. A student newspaper, the *Sennet*, recorded his passing thus: "A prominent genetics researcher at UC Hospital gave up everything, including his life, for his religious beliefs. Dr. George Price gave away all his money, clothes and possessions to homeless alcoholics and left his flat in Bloomsbury to live as a squatter in Drummond Street, Kentish Town. It was there that he was found dead. A respected scientific researcher, Dr. Price was convinced that he had a 'hot line to Jesus"'. George Robert Price was buried in an unmarked grave, to which his family later added a tombstone referring to him as "Father. Altruist. Friend. A Brilliant Scientist noted for the Price Equation for Evolution", and including the original version of his covariance equation: $w\Delta z = Cov(w_i, z_i)$.

Suggested Reading

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