

DEATH OF AN ALTRUIST

WAS THE MAN WHO FOUND THE SELFLESS GENE TOO GOOD FOR THIS WORLD?

BY JAMES SCHWARTZ

IN A RUTHLESS, Darwinian world, human heartlessness is easy to explain. After all, natural selection eliminates the weak and rewards the strong. Unselfish behavior, on the other hand, is baffling. Compassion, kindness, and loyalty ought to be weeded out almost as soon as they arise.

To explain the evolution of altruism, Charles Darwin suggested that natural selection could act on groups as well as individuals -- an idea known as group selection. Within a tribe, it could hardly be doubted that "selfish and treacherous parents" would have the most children, he wrote in his 1871 classic, *The Descent of Man*. On the other hand, he explained, tribes including many members "ready to give aid to each other and sacrifice themselves for the common good would be victorious over other tribes."

But Darwin never fully developed his ideas about group selection, and his heirs continue to argue over it. The late William D. Hamilton, widely regarded as the most important evolutionary thinker since Darwin, proposed an enormously influential alternative to group selection called the theory of nepotistic altruism. This is the idea that all apparently altruistic behavior is directed exclusively toward genetic relatives. True selflessness, in Hamilton's opinion, almost never happened. Among human beings, the two examples that came most readily to Hamilton's mind were Mother Teresa and his friend the brilliant, iconoclastic American scientist George Price.

Despite his remarkable scientific achievements and the intense drama of his personal life, George Price has remained a relatively obscure figure in the history of science. And yet he played a key role in shaping the conceptual basis of sociobiology and its offshoot, evolutionary psychology. He was the first to apply the principles of game theory to the analysis of animal conflicts, and he discovered an elegant formula to describe evolutionary change that both simplified and improved Hamilton's theory of nepotistic altruism. Furthermore, Price's formula provides a rigorous mathematical framework in which to understand group selection.

In his last years, even Price himself lost interest in securing recognition for his scientific achievement. Altruism, which had begun as an intellectual problem, became an all-consuming personal concern. In the midst of an extraordinary burst of scientific creativity in the summer of 1970, Price abruptly converted from militant atheist to fundamentalist Christian. After his conversion, he combined his work in genetics with a passionate interest in biblical exegesis. Later, he decided that the mission of a true Christian was to help his fellow man, and he spent increasing amounts of time aiding homeless alcoholics and the elderly in his adopted city of London. As he ministered to others, his own life disintegrated into chaos. He died in 1975.

In the years before his own untimely death this past spring, William Hamilton often wrote and spoke about Price in an effort to

draw attention to his old friend's ideas. Earlier this year, Hamilton shared with me his lengthy correspondence with Price. With the help of these unpublished letters and Hamilton's recollections, as well as additional aid from Price's two daughters and many friends and colleagues, I have tried to piece together the tumultuous story of this extraordinary man.

A PHYSICAL chemist and a journalist before he studied genetics, George Price took a circuitous path to evolutionary biology. Born in 1922, he was only four years old when his father died. His mother, a former opera singer and actress, struggled to keep the family's lighting company afloat through the Depression, and it was difficult for her to support George and his older brother, Edison. After attending public school in New York City, George went to the University of Chicago, where he earned a Ph.D. in chemistry, and later worked on the Manhattan Project. In 1947, he married Julia Madigan, and they had two daughters. Three years later, the family moved to Minneapolis, where Price worked as a medical researcher at the University of Minnesota. Because George was a fire-spitting atheist and Julia a devout Christian, their relationship was contentious from the beginning. After eight years, the marriage ended in acrimony.

In 1955, the year of his divorce, Price published his first magazine piece, a long article in *Science* in which he questioned the quality of the evidence used to demonstrate ESP. It was the first of several highly visible, and often farsighted, forays into journalism. The following year Price published "How to Speed Up Invention" in *Fortune* magazine. In the age of punched cards and Teletypes, the article described in detail a hypothetical "design machine," which would feature a graphic display, a cursor-like light pen, and a mouselike device to rotate, shrink, and enlarge shapes.

In 1957, Price sent Senator Hubert Humphrey an early draft of an essay he was writing for *Life* titled "Arguing the Case for Being Panicky." The article warned that a decline in U.S. military strength could lead to catastrophe, and it so impressed Humphrey that the two men went on to exchange dozens of letters. Price told Humphrey about several novel foreign policy ideas he had derived from game theory. He suggested, for example, that the United States offer to buy every Russian citizen two pairs of high-quality shoes (at a cost of \$2 billion) in exchange for the liberation of Hungary. The same year, Price began to write a book on the Soviet threat for Doubleday, which he abandoned in 1959 when he concluded that the Soviet position on disarmament was more commendable than the U.S. position. He returned to scientific research by accepting a post at IBM, where he worked on the development of mainframe computers and the mathematical modeling of free markets.

But Price's career soon took a dramatic turn. In 1966, he was treated for thyroid cancer. Price believed that the doctor, an old friend of his from Chicago, badly mishandled the operation. The surgery, added to earlier nerve damage caused by polio, left

Price's shoulder partially paralyzed. The misfortune earned Price a generous insurance settlement, and he decided to use the money to finance one final career shift.

IN NOVEMBER 1967, Price sailed on the *Queen Elizabeth*, pleased to be the sole occupant of a stateroom meant for two. In England, bankrolled by his insurance settlement, he rented a large flat in an affluent section of London near Oxford Circus. In his first letter to his grown daughters, he reports humorously about his exploration of the city: "Dear Babies, I have seen quite a lot of London so far, including the British Museum library, the Museum of Natural History library, the University of London library, the University College library, the Wellcome Historical Medical library, and *Science* and Technology library. Soon I hope to visit the Royal College of Surgeons library and Royal Zoological Society library."

Among the articles Price read in his library visits was William D. Hamilton's now-classic study "The Genetical Evolution of Social Behavior." A watershed in the history of evolutionary biology, it would be Price's point of entry into the field.

According to traditional Darwinism, natural selection is the survival of the fittest -- with "the fittest" defined as those organisms who leave the most descendants. It was easy for Darwin to account for the evolution of traits that directly benefit individuals, such as good eyesight. However, it was harder to explain the evolution of behavior that benefits fellow organisms while lowering an individual's own fitness. In the early 1960s, the most common explanation was the theory of group selection. It was believed that natural selection acted on two levels, favoring better adapted individuals (who left more progeny), on the one hand, and better adapted groups, on the other. A selfish individual would tend to leave more offspring than an altruist, but a group that contained many altruists would tend to grow faster than a group that didn't.

Hamilton rejected this notion altogether. He insisted that the natural selection of individuals was responsible for all significant evolutionary adaptations, including self-sacrificing behavior. The problem, as Hamilton saw it, was that evolutionary biologists had been defining fitness too narrowly. What mattered was not merely the number of offspring an individual had but his "inclusive fitness." In addition to an individual's own progeny, you had to consider the progeny of his relatives, fractionally weighted according to how closely they were related. Hamilton's argument depended on the "gene's eye" point of view -- the idea that it was the survival of particular genes, rather than the survival of the individuals who carried them, that was crucial. This was the argument that Richard Dawkins would develop with dazzling lucidity in his 1976 book, *The Selfish Gene*.

In March 1968, Price wrote Hamilton requesting a reprint of the paper. "The mathematics in it is a bit formidable to absorb in library reading," he explained. Price's initial observations were nonetheless so perceptive that Hamilton was inspired to write two dense, handwritten pages in return. Hamilton described his recent work and disappointed Price with the news that he would be unavailable for further discussion: He was about to depart for a nine-month research trip in Brazil.

Left to his own devices, Price set out to find a simpler, more direct way of achieving Hamilton's results. That summer, he wrote Hamilton in Brazil to report that he had found "a more transparent (though less rigorous) derivation and formulation of the main result of your paper." This was an understatement. He hadn't merely simplified Hamilton's math. He had reconcep-

tualized the mathematics of how genes flourish or fade under natural selection, and he had done it with a startlingly simple equation. The equation was so pared down that it could apply to any form of selection, "from selecting a book or a radio station to genetic selection," as Price later put it in a letter to a friend.

AT THE HEART of Price's equation is the mathematical concept of covariance -- a statistical measure of the relationship between any two sets of data. Take, for example, the rainfall and temperature in a given place over thirty days. If rainfall is independent of temperature, then the covariance of rainfall and temperature will be close to zero. If days with more than average rain also tend to have higher-than-average temperatures, then the covariance will be positive. But if days with more rain than usual tend to have lower temperatures than usual, then the covariance will be negative.

How can a covariance measure natural selection? Price's equation describes the change in a gene's frequency from one generation to the next. Specifically, it relates that change to the covariance between an individual's possession of the gene and the number of children he or she has. If having the gene leads to having more offspring, the frequency of the gene will increase in the next generation.

It sounds so straightforward as to be almost tautological. But Price's mathematics was strikingly original. Furthermore, in the process of inventing a new algebra of natural selection, Price also devised a more sophisticated and accurate way of understanding relatedness. In his own work, Hamilton had assumed a population that was infinitely large. But Price saw that calculations of relatedness turn out differently in a small population of closely related individuals. In a finite population, individual A can be *negatively* related to individual B, in the sense of sharing fewer genes with B than with the members of the group on average. Negative relatedness changed the predictions of Hamilton's theory in subtle but significant ways. First, it made clear that if you have a gene that benefits your group, that gene will survive only if it is of more benefit to your close relatives than to your distant ones. More disturbingly, it implied that it could be adaptive for animals to harm themselves in order to harm others more. Price called this "spiteful behavior": It might pay for an animal to take the life of a "negatively related" neighbor even at some cost to itself.

Price's approach bore no relation to previous work. At first, even Price was convinced that his equation was too simple to be new, so he decided to check it with an expert at the Galton Laboratory at University College, London, the famous department of human genetics named in honor of Darwin's cousin Sir Francis Galton. When he visited the Galton Labs in June 1968, Price asked to speak with a mathematical geneticist and was taken to Cedric Smith, a respected biostatistician. "Smith said it was very interesting, very pretty, and he had never seen anything like it before," Price later wrote to his mother. After quizzing him about his work, Smith brought Price to the department chairman. Eighty minutes later, Price had an honorary appointment, an office, and keys. He left walking on air.

WITH A TITLE, an office, and the support of certified experts, Price set off with new confidence to write up his results. He believed that university backing would help him get funding and make it easier to publish his work. But outside of work, it was a difficult period for Price. His shoulder was troubling him again, and he was anxious over money, since he had spent most of his insurance settlement. To top it off, his mother had fallen seriously ill.

In March 1969, his mother's health took a precipitous downturn, and he flew to New York to see her once more before she died. During his visit, he met Richard Lewontin, a young and highly regarded population geneticist. If anyone was in a position to understand Price's new selection mathematics, it was Lewontin, the most mathematical of the young geneticists. But the meeting did not go well; and Price blamed himself for failing to convey his new approach. After he returned to England in early May, however, things started to look up. He learned that he had become a grandfather, and in July he received a grant from Great Britain's *Science Research Council*.

Hamilton meanwhile had returned from Brazil, and in late July 1969, Price contacted him again. Nearly a year had elapsed since their last communication. In his letter, Price gently explained that Hamilton's formulation of nepotistic altruism did not work quite the way Hamilton thought it did. He generously offered to spare Hamilton the awkwardness of being corrected publicly. "I did want -- in view of your friendly correspondence, because I respected your work, and because everyone makes a mistake now and then -- to publish in a way that would not embarrass you," Price wrote. He left a telephone number and the times he could be reached.

In his 1996 book, *Narrow Roads of Gene Land*, Hamilton recalled his first telephone conversation with Price. "His voice was squeaky and condescending, rather guarded, on the phone," Hamilton wrote. In the conversation, Price described his covariance equations as "surprising for me too -- quite a miracle." Price also asked if Hamilton had noticed that the equation could describe group selection as well as individual selection. Hamilton was skeptical. After all, it was through his rejection of group selection that he had arrived at the theory of nepotistic altruism in the first place.

But Price would eventually cause Hamilton to rethink his position. To understand why, we have to back up for a moment. Price's equation was in fact slightly more complex than the rendition of it above. In order to assess the fortunes of a particular gene, it's not enough to know whether having that gene correlates with having more children. It's also important to know how likely it is that your children will actually inherit that gene. And so there was a second term in Price's equation, assessing the likelihood of a particular gene's transmission. In most cases, children inherit a parent's genes at random -- that is, the gene does not affect the viability of the sperm or egg -- and the second term can be safely ignored.

But it is thanks to this second term that Price's equation sheds such powerful light on group selection. As Price hinted to Hamilton on the phone, it is possible to redefine the two terms in his equation by shifting them one notch up the population structure. Instead of applying to *individuals and their sperm or eggs*, the equation would apply to *groups and the individuals they contain*. The forces of selection acting at both the group and the individual level appear side by side in the revamped formula, making it possible to compare their relative strengths. A century after Darwin first wrote about group selection, Price's equation spelled out the precise conditions under which the interests of the group could trump the interests of the individual.

As it happened, one of the first well-documented examples of group selection had recently been reported. In Australia, scientists had introduced a disease virus in an attempt to control the native rabbit population. Although the virus was at first an extremely effective rabbit killer, over time it became considerably less virulent. Within any given rabbit, viruses that multiplied

faster had the advantage over viruses that multiplied more slowly. In other words, on the individual level -- in this case, the virus level -- natural selection favored faster-multiplying (therefore more lethal) viruses. But when a rabbit died, the viruses inside died with it. (The virus was spread by mosquito, and mosquitoes do not bite dead rabbits.) Thus the faster a group of viruses multiplied, the more likely it was that their rabbit host would die before the virus could be transmitted to another rabbit. At the group level -- at the level of the rabbit host -- natural selection favored less lethal, slower-multiplying viruses. Price's equation could explain this evolution of an "altruistic" virus -- a virus that multiplied less greedily so that its rabbit host could live longer.

Despite the strain in their first conversation, Hamilton quickly grasped the significance of Price's covariance equation and soon found himself won over. "I am enchanted with the formula derived in your manuscript," he wrote to Price in December 1969. A month later he'd begun to rethink the issue of group selection. "In its general form, I can see how one might use your formula to investigate \bar{w} group selection," he wrote.

Although Price's equation was strikingly original, its publication, which would be Price's first in his new field, was by no means assured. Hamilton, who had felt isolated and unappreciated while working out his theory of nepotistic altruism, was anxious to help his friend avoid a similar fate. Together they devised a clever strategy to break into *Nature*, one of the premier science journals. Price would submit his paper on the mathematics of natural selection first. One week later, Hamilton would submit a paper that depended on Price's formula to re-derive his theory of inclusive fitness.

It came as no surprise when Price's paper was returned immediately. The editors had not seen fit to send it out for review. No less surprising, the paper by Hamilton, a well-established name, was accepted without delay. According to plan, Hamilton wrote *Nature* to withdraw his paper. He explained that he had made use of a "powerful new method," and he could not in good conscience publish his results until the method he used was published. The plan went off without a hitch; *Nature* promptly reconsidered. Price's "Selection and Covariance" was received on November 12, 1969, and published on August 1, 1970. Befitting its entirely original approach, the paper appeared without citations.

EARLY IN THE summer of 1970, at the age of forty-seven, Price underwent a sudden religious conversion. "On June 7th I gave in and admitted that God existed," he explained to friends. He viewed his conversion as a logical necessity, the result of a series of coincidences that had befallen him. After calculating the odds of their occurrence and finding them to be "astronomically low," he was convinced that there had been supernatural manipulation. One week later, he attended his first service at All Souls at Langham, a particularly evangelical branch of the Church of England, located around the corner from his apartment.

Over the course of the next year, Price's scientific work was accompanied by a new passion -- biblical exegesis. Adopting a highly literal approach to the Bible, Price set out to reconcile discrepancies among the four Gospels. Nearly a year after his conversion, he completed a fifty-page article, "The Twelve Days of Easter," which proposed to replace the traditional eight-day Holy Week with a new chronology. He believed he had resolved several of the long-standing puzzles of biblical scholarship.

He sent the article to Hamilton, who was impressed by Price's reconstruction of the events of Easter week and encouraged him to publish it. But he did not accept Price's arguments for the existence of God, nor did he convert, as Price had hoped he would. In a letter, Hamilton likened his resistance to Christianity to "the Irishman who was asked whether he liked oysters and he replied, no, he didn't like oysters and he was glad he didn't like them because if he did he'd be eating them all the time when he hated the damned things."

Hamilton also attempted a more serious response to Price's new thinking about Christianity, prophecy, and free will. "Why should we respect Moses if he was just a puppet carrying out maneuvers to foreshadow the crucifixion, and why respect Jesus for following a canon that he was bound to follow anyway? A plot so elaborate would make life meaningless if one believed in it -- and ugly too."

Price waited four months before replying. "The question is not whether you like it but whether it is true," he wrote. "What difference does it make whether you approve of it or not? Do you think that is something that I wanted to believe in?"

MEANWHILE, Price's second major breakthrough in evolutionary biology was at last about to see the light of day. Back in 1968, the same summer he happened upon his covariance equation, Price had become intrigued by the fact that male animals of the same species rarely fight to the death. In July of that year, anxious that his windfall insurance payment was running out, Price had worked night and day to complete an article setting forth a new idea, namely, that game theory might help evolutionary biologists understand animal conflict. At the time, Price hoped that a quick and dazzling academic paper would pave the way for profitable magazine sales.

Price's key insight had been to see that the genetically optimal behavior for an animal could depend on the behavior of other animals. In a population made up of animals genetically programmed to make war, for example, an animal programmed to retreat from a threat might actually be at an advantage. On the other hand, in a population of less aggressive males, a confrontational male would have the advantage. Price had titled his paper "Antlers, Intraspecific Combat, and Altruism" and sent it off to *Nature* on the last day of July 1968. The following February, he learned that *Nature* had accepted the article, provided it was shortened. But several years passed, and Price never bothered to undertake the revision.

As it happened, the reviewer of Price's paper had been John Maynard Smith, the head of the biology department at the newly created University of Sussex. Maynard Smith saw the potential of Price's unpublished idea, and he wanted to use it in a paper he was writing. In 1971, he wrote a letter asking for permission to thank Price for showing him an "unpublished manuscript." Price wrote back that he would rather Maynard Smith referred to a discussion between them and not a manuscript. "If one mentions an unpublished manuscript," Price explained, somewhat mysteriously, "then someone might wonder whether it was used with permission."

Price's concern was a delicate reference to a long-running, acrimonious dispute between Maynard Smith and Hamilton, whose paper on nepotistic altruism Maynard Smith had reviewed for the *Journal of Theoretical Biology* a few years earlier. It was Hamilton's belief that Maynard Smith had in effect stolen his idea. "His account of the matter," Price explained to Maynard Smith in the fall of 1972, "is that you refereed his 1964 paper for the

Journal of Theoretical Biology, and required a major revision...that caused a nine-month delay in publication and meanwhile you sent *Nature* a letter with the term 'kin selection' that has received much of the credit for the idea."

"I seem to have this fate of getting ideas from other people's manuscripts when I referee them," the genial, white-haired Maynard Smith explains today. Asked about Hamilton in particular, he is somewhat more defensive: "I wasn't trying to steal his idea, or I don't think I was, so it wasn't conscious." At first, Price doubted Maynard Smith's integrity and suspected him of delaying the "Antlers" paper as he had Hamilton's. But he changed his mind after meeting Maynard Smith. In fact, Maynard Smith was scrupulous about crediting Price -- he offered to make Price a co-author of the paper he was writing.

In the fall of 1972, "The Logic of Animal Conflict," co-written by John Maynard Smith and George Price, was accepted by *Nature*. On receiving this news, Price wrote to Maynard Smith that "I think this is the happiest and best outcome of refereeing I've ever had: to become co-author with the referee of a much better paper than I could have written by myself." The paper was one of the first to set forth the ideas of evolutionary game theory, ideas that in the years since have been used to analyze everything from reciprocal grooming in African antelopes to egg swapping among hermaphroditic fish.

IN JUNE 1972, the three-year grant that Price had obtained from the *Science* Research Council came to an end, and he chose not to seek to renew it. He preferred to give more time to his Christian work and less to mathematical genetics. By the fall, Price had decided to live according to his literal interpretation of the teaching of Jesus. Inspired by Jesus' advice in the Sermon on the Mount to take no heed of the morrow, Price was pushing himself to the brink of disaster. He was almost joyous in anticipation of the extreme deprivation that his faith had brought upon him. "I am now down to exactly fifteen pence," he wrote to Maynard Smith that October. "I look forward eagerly to when that fifteen pence will be gone."

A month later, Price's diet consisted of one pint of milk a day, and he was weak from malnutrition. He stopped taking the thyroxine pills that his thyroid cancer had rendered necessary to his survival. Price believed that if God wanted him to continue living, He would provide the missing hormone. In early December, Price seems to have attempted suicide; in any case, he ended up in a hospital. An alert doctor noticed that he was suffering from myxedema, a result of his thyroxine deficiency, and provided the missing hormone without informing the patient. Taking this as a sign that he was meant to go on living, Price followed the doctor's orders and started taking his pills again.

Price made his final revisions to "The Logic of Animal Conflict" the following February. In a cover letter, he explained to Maynard Smith that he had made a few changes to accommodate his newfound belief in creationism. "I think I found wordings that you won't object to, and that won't shock *Nature's* readers by making them suspect what I believe," he wrote.

Later that month, Price's religious crisis deepened. In what he described as "an encounter with Jesus," he saw that he had misunderstood the real nature of Christianity and that his true duty was the care and love of people rather than biblical study. He began to devote himself to the needy. He helped out at various old people's homes and gave away all his money to homeless alcoholics on the street, often inviting them to stay in his flat. He also set out to make amends for the failures in his private life,

apologizing to his elder daughter, Annamarie, for deserting her and being a poor father. For a short period, he hoped to remarry his former wife, Julia, and reunite the family in London.

Toward the end of June 1973, Price gave up his comfortable flat and lived as an itinerant. Once the model IBM employee, short-haired and suited, Price now let his hair grow out and dressed in sneakers and colorful shirts with an aluminum cross around his neck. He gave away the last of his possessions, including his watch and coat, and lived hand to mouth. In a letter to Hamilton, he explained that he was living according to Luke 6:30: "Give to every man that asketh of thee; and of him that taketh away thy goods ask not again."

Elizabeth Mansell, who worked as a manager of an old people's home where Price volunteered, recalls his arriving on Christmas Eve 1973 "like an angel coming in." She and Price stayed up past midnight wrapping Christmas presents for the old people, and she overslept the next morning. Rushing down in a panic, she found Price had fed and dressed all twenty-one residents.

In the little time that remained after doing his Christian work, Price continued his genetics research at the Galton Labs, where Cedric Smith, his first sponsor, had procured him a one-year Medical Research Council stipend. But by the end of the year, he was forced to avoid the lab because his charity cases were causing disturbances there. In one incident, a belligerent alcoholic (whose abused wife Price had been protecting) pissed publicly on the front steps of the genetics building, smashed a bike lamp, and scattered the contents of a student's satchel while shouting obscenities. Fortunately, Price's recent paper with Maynard Smith in *Nature* had earned him credit with the lab authorities. As he wrote to his daughter Annamarie, "I expect that one cover-illustrated lead article in *Nature* compensates for one urination at the front entrance to the building."

In March 1974, Price took up temporary residence in the home of an elderly woman whom he'd helped. By keeping his whereabouts secret from his charity cases, he hoped to get some work done on a joint project on sexual selection with Hamilton. In June, he took a job as a night office cleaner. In a letter to Hamilton, he wrote, "I thought it was about the first honest work I'd done in my life -- working for others rather than for my own amusement or advance." In August, Price gave up his night job and moved into a commune located in six deserted buildings a mile north of his first flat.

This move would mark the last major transition in his life. He wrote to his daughter Kathleen that after the summer's low in money and social prestige, he was "heading back up" and had started acquiring possessions again, which he was now slower to give away. He wrote to Hamilton that he believed "Jesus wants me to do less about helping others and give more attention to sorting out my own problems." To another friend he wrote that honesty perhaps meant confessing to "one's deepest selfish desires." He had fallen in love with a woman in his commune, and he hoped to move back to the States. In November, he confided to his brother, Edison, that he had given up his social work, returned to a more conventional Christianity, and was considering marriage.

Meanwhile, Price was beginning to receive some long-overdue recognition. Five years after their New York meeting, Richard

Lewontin wrote Price: "It has taken me a long time to come around to understanding the work you have been doing, which I was too stupid to appreciate when you first showed it to me." In October, Price also received a long and detailed letter from the eminent American population geneticist James Crow. Like Lewontin, Crow expressed chagrin at having been so slow to appreciate the significance of Price's work.

Just before Christmas, Price visited the Hamilton family for a little more than a week at their home outside London. When he left on December 19, he seemed to have recovered much of his good spirits, and Hamilton had almost persuaded him to resume full-time work in genetics. The Hamiltons were going to spend Christmas in Ireland, but it was agreed that Price would stay with them again after the New Year. However, on his return to London, Price's spirits dropped precipitously. On January 2, one of his Christian acquaintances wrote to urge him to contact the Samaritans. But Price's life had spun out of control. He was found dead in his squatter's tenement on January 6, 1975. The nail scissors he had used to cut his throat were on the floor beside him.

THE SCIENTIFIC community has been slow to appreciate Price's contributions, perhaps because he never pursued academic recognition strenuously. The application of Price's covariance formula to group selection, for example, has far-reaching implications, but Price never drew attention to them. Before his own death this spring, Hamilton said, "It's as if you've discovered the calculus and put it into one of your obscure papers but never explained to people how useful it was." In a 1975 paper, Hamilton tried to popularize Price's cryptic treatment of the subject. But Hamilton's paper got little attention, and Price's genuinely novel approach remained largely overlooked.

That may be changing. In 1995, twenty years after Price's death, the theoretical biologist Steven Frank of the University of California at Irvine wrote a paper reviewing Price's remarkable contributions to evolutionary theory in the *Journal of Theoretical Biology*. The journal also presented a previously unpublished manuscript by Price giving a complete account of his unified theory of selection mathematics. (Two other complete Price manuscripts remain to be published.) Price's equation also played a prominent role in *Unto Others*, an important new book on altruism by David Sober and David Sloan Wilson.

For his groundbreaking insight into the evolution of altruism, Price merits a special place in the history of evolutionary biology. The painful irony is that his struggle to extinguish all selfish motives in his own life nearly prevented him from achieving it. In *Narrow Roads of Gene Land*, Hamilton recalled a conversation between them that took place when Hamilton was first beginning to appreciate how Price's discovery might change the understanding of group selection. "I thought you would see that," Price said.

"Then why aren't you working on it yourself, George?" Hamilton asked.

"Oh, yes. Cedric wants me to also.... But I have so many other things to do," Price replied. "Population genetics is not my main work, as you know. But perhaps I should pray, see if I am mistaken."

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