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Author for correspondence:
Oren Harman
e-mail: oren.harman@gmail.com

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When science mirrors life: on the origins of the Price equation

Oren Harman

Graduate Program in Science Technology and Society, Bar-Ilan University, Ramat Gan, Israel

OH, 0000-0001-5148-1391

The Price equation was a piece of abstract mathematics. What kind of a connection could it possibly have had to George Price's personal life and biography? Here, I will argue that the initial impetus for Price's foray into mathematical population genetics stemmed from a preoccupation with the origins of family, one that was born following a divorce from his wife and the abandonment of their two young girls. What is special about the Price equation is the way in which it associates statistically between two groups, a 'mother' and 'daughter' population. The association need not mean genetic relatedness in the narrow sense of direct descent, and it allows us to see selection working at different levels simultaneously, a fact that was not lost on William Hamilton. Hamilton was one of the few friends who desperately tried to save Price from falling into the abyss of depression and homelessness in the period following the publication of 'Selection and covariance' (Price 1928 *Nature* **227**, 520–521 (doi:10.1038/227520a0)). Viewed in this light, the Price equation assumes new meaning.

This article is part of the theme issue 'Fifty years of the Price equation'.

1. Introduction

It was a cold morning, 19 December 1974, when William Hamilton drove his friend George Price to the Maidenhead train station in Berkshire, UK. Two weeks earlier, in London, Price had contacted a Dr O. W. Hill at the Middlesex Hospital Department of Psychiatry, asking for an appointment, which was duly scheduled for 9 January.[1] Would he last that long? It was far from certain. Price's mood had been faltering. Hamilton saw him towards the end of November, and Price did not look good. He was living in a London squat on 164 Drummond Street, and a pot of boiling water had recently tipped over, badly burning his hands. Years later his fellow squat mates would remember a strangely reserved man, 'walking about like a ghost, down to skin and bones, reeking, gaze downcast', often depressed and constantly mumbling about Jesus.[2] 'The Hounds of Heaven are closing in on me', Price wrote to his daughter, Kathleen, back in the United States, referring to the English poet Francis Thompson's 1907 poem, of which J. R. R. Tolkien had written 'Like the hounds follow the hare…so does God follow the fleeing soul by His Divine grace'.[3] George Robert Price was waning.

Hamilton and his wife Chris had, therefore, invited George Price to their home in Berkshire, hoping the time away from London in the countryside might help to quell his troubles. There was a possible further collaboration mentioned, a paper on altruism. They would need to leave to visit Chris' parents in Ireland for Christmas, but wouldn't it be nice to spend some time together towards the holiday season, leaving all worries behind? Price took the bait and the week in Berkshire turned out to be rather successful. Hamilton even showed Price a draft of a paper he was working on in which he was applying Price's covariance equation to individuals and now finally to groups.[4] This made Price happy. Perhaps he would stay in the field, after all, he told them.

And yet, hugging George Price on the station platform at Maidenhead as they said goodbye that morning, Bill Hamilton was far from sanguine. When the train left, he hurried back home, and immediately penned a letter to a Dr Kelly, secretary of the British Teilhard Association, founded in 1963 to promote the works of the French Jesuit evolutionist Pierre Teilhard de Chardin. Hamilton inserted in his

envelope a copy of an article by Price titled 'Twelve days of Easter', in which Price had tried to prove that there must have elapsed twelve, not eight, days between Palm and Easter Sunday. This, of course, was contrary to many hundreds of years of tradition in Western Christianity, but might Kelly consider publishing the article in their journal, nonetheless? It was based on meticulous research, Hamilton could vouch, as Price had been working alternately on biblical exegesis and on highly original work on the theory of natural selection. Surely, seeing his Easter paper published would help carry him up again. And if this was not possible, might the Association consider hiring Mr Price in some capacity, perhaps as a janitor?[5]

Two weeks later, George Price was found dead in his room in the squat, his back stooped against the door, blood all around him, his carotid cut by his own hand with a pair of tailor's scissors. Despite his best intentions, and those of a few others who saw Price descending, Hamilton had failed to save his friend.

Fifty years have passed since the publication of 'Selection and covariance', in which appeared what has become known as the Price equation [5]. Considered by some to be one of the deepest formalizations of the dynamic of natural selection—a statistical partitioning between a 'mother' and 'daughter' population which allowed us, for the first time, to see selection working simultaneously at different levels of the biological hierarchy—the Price equation slowly gained a following among evolutionary thinkers, as well as researchers in other fields, such as economics and epidemiology, even as the man himself, and the story behind his equation, were forgotten. But who was George Robert Price, and how did he come to formulate his equation?[6] As I will argue, the motivation behind the Price equation had a lot to do with its author's personal biography and preoccupation with family. George Price presents to us most starkly the notion that science, however mathematically abstract, may also be a reflection of life.

2. Beginnings

George Price was born on 16 October 1922 in New York to William Edison Price, a stage lighting electrician, and Alice Avery, a minor actress on Broadway. His father died suddenly of pneumonia in the winter of 1927, bringing his mother's acting career to a halt and destroying the family's happiness.[7] As the Great Depression hit, Alice Price was forced to spend her days drafting half-threatening, half-desperate letters to theatres who did not pay dues to William's business, Display Stage Lighting Company, for services rendered, as well as keeping at bay furious suppliers who wanted their monies upfront. By the autumn of 1931, Display had gone bankrupt. Moving from a spacious apartment in Hartsdale to a leaky city tenement on West 94th Street, Manhattan, the family teetered on the brink of survival. Price's older brother Edison was sent away to live on a farm upstate, freeing up his room, which fetched $7 a week.[8] Young George could be lugged along to the office. 'The child and I', Alice wrote in anguish to the Transfer Tax Commission in the autumn of 1934, 'have nothing left in the world except each other'.[9]

Gritty and hardworking, Alice slowly recovered, buying back Display from the receivers, and winning over theatres again, one by one. Soon, the Price family moved to a larger apartment at 311 West 95th Street, and Edison was spending more time at home and in the office. He would be the one to take over the family business, already dealing at 15 with creditors and debtors, and taking out patents for his own lighting inventions.

Young George, meanwhile, showed early academic promise. It was likely his 'rare quality of intensity',[10] and his mathematical acuity that landed him a seat gratis in the 11th form at Stuyvesant, considered the high school for the best and brightest of the city's lower classes. 'Now we are a nation of manufacturers and traders', exclaimed the dean of New York University's School of Pedagogy, and public schools like Stuyvesant and Bronx Science that took in the sons of Jewish, Italian and Irish immigrants were 'the educational hope of democracy' [7].

George joined the Experimental Physics Lab, the American Rocket Society, and the Chess Club, and listed 'research physicist' in the yearbook under 'Ambition'. He graduated second in a class of 708, and took a train to Cambridge, MA. His hopes were high. Following a 40 min probe, his interviewers at Harvard concluded: 'Might go hay-wire but will never be humdrum', [8] and accepted him into the class of '44.

3. Chicago to Minnesota

It would be a short union. Cocksure, George had enrolled in advanced graduate classes in chemistry and biology, as well as in German, despite a patent lack of talent for foreign languages.[11] When it became apparent that his grades would not satisfy his scholarship conditions, disappointed and cowed, he packed up and went home. Luckily, owing to his strong Stuyvesant record and his Harvard credits, he was accepted on a scholarship as a Home Study sophomore at the University of Chicago. The following year he arrived on campus, exuding his old confidence. His friends remembered him as eccentric and unscripted, a whiz at maths. He had a strange, squeaky voice, and his speech started and stopped in spurts. He was a contrarian, titillated by attention, but nevertheless craving acceptance. 'It helps my morale', he wrote to a friend, 'to learn that everyone doesn't dislike me'.[12]

By 1943 he had graduated Phi Beta Kappa with a degree in Chemistry, and was invited to stay on for a PhD at the Metallurgical Laboratory. He would be joining the Manhattan Project, working on the biological effects of radiation, specifically on devising a sensitive method to detect small traces of uranium that might find their way into people's bodies if an atom bomb were ever used. At Chicago, this was particularly salient: unbeknownst to George, the physicists Enrico Fermi, Martin Whittaker and Walter Zinn had built an atomic pile in a squash court under abandoned stands in the west wing of Stagg Field. At 15.53 on 2 December 1942, it had gone critical. The atomic age had dawned [9,10].

In between chemical analyses and constructing sensitive photoelectric fluorophotometers, George met and fell in love with Julia Madigan, a zoology graduate of the University of Michigan. Julia was the daughter of immigrant German Jews who had converted on the boat, and on her father's side of Roman Catholic Irish who had fled the potato famine in the 1850s. Growing up in the small paper mill town of Munising, Michigan, she attended Sacred Heart with the nuns, and became a devout Catholic. George's friends rubbed their eyes in disbelief: she was mercurial, he a prankster. She was conservative, he revelled in the extreme. Most of all, George was an atheist, and she a believer. They did not seem to agree on anything, even the bomb (George was for, she against).[13] How would the union last?

Completing his doctorate, George took up an offer to become a Chemistry Instructor at Harvard. He was engaged, as well, as a consultant at his former 'Met Lab', now christened the Argonne National Laboratory, which took him on frequent trips to Chicago. It was on one of those that he came across a paper by Claude Shannon, a general theory using mathematics to quantify information [11,12]. He judged it elegant, simple and exacting, a brilliant way to break a problem into its starkest logical components. A daughter, Annamarie, was born in May 1948, and the family was blossoming. Still, his Chemistry colleagues found him 'wholly disengaged'.[14] The world was going in the direction of computing and telecommunications, and in August, the Prices packed up from Cambridge and moved to Morristown, New Jersey. George was going to work for Bell Labs.

His new bosses, the future Nobel Prize winners William Shockley and John Bardeen, wanted to know more about temperature effects on transistor properties, and turned to George to do the measurements. As he went about mapping germanium surfaces, a second daughter, Kathleen, arrived in late summer of 1949, but not all was well. 'Better the girls become prostitutes than nuns', he would snap at his religious wife, pushing her into a cocoon of silence.[15] Increasingly, the home grew glum. When he was offered a job at the Radioisotope Lab by his old Manhattan Project doctoral supervisor, he jumped at the opportunity. Perhaps the move would save the marriage. As America ushered in the 1950s, the Prices settled into a two-story cottage on Fortieth Avenue in St Paul, a short drive from the University of Minnesota's Veterans Administration Hospital.

Already the laboratory had discovered that by localizing the fluorescence of intravenously administered porphyrin in tumour tissues, surgeons could estimate the extent of the metastatic spread of cancer. Porphyrins could either enhance or protect against the effects of ionizing radiation. If they could figure out the right dose and pigment, controlled radiation combined with haematoporphyrin could be used to get rid of tumours. George went to work developing special equipment to better observe the exact location of the porphyrin and cell type. While his scientific exploits were successful, the marriage was faltering. In a limerick, he referred to himself as 'a certain young man with porphyria whose existence grew drearier and drearier'.[16] By the beginning of 1953, he said goodbye to his daughters and moved into a dingy student complex north of the university, ambivalently coddling letters from his doting and increasingly dotty mother, uncertain about his future.[17]

It might have been his mother's letters to herself, addressed from long-deceased husband William, or perhaps his lingering resentment towards Julia's religiosity, that prompted Price to produce a hard-nosed debunking of extra-sensory perception (ESP), published in *Science* in 1955 and becoming the journal's most popular article that decade.[18] Price was digging into his materialism and scientific world view. The essence of science was mechanism, that of magic animism. 'Where is the definitive experiment?', he wanted to know [14].

He was also increasingly preoccupied with the Cold War. It began with a demolition of a Marxist theory by a well-known economist, in which Price suggested that it would be worthwhile to examine possible contributions to theory-weak economics by the older and more well developed natural sciences; there were deeper natural laws pertaining to behaviour, he was sure, and 'Perhaps the time approaches for a new Boyle to produce a *Skeptical Economist*' [15, p. 336]. Then it was 'How to speed up invention' for *Fortune* magazine, introducing a 'Design Machine' that would allow engineers to manipulate an object three dimensionally on a computer screen, and then produce the part from metal [16]. And there was also 'Arguing the case for being panicky' for *Life* magazine, calling on America to take the Red Threat far more seriously and double her defence budget [17]. Reactions came from all quarters.

He had parachuted out of nowhere to the centre of a debate about the foundations of science, jumped into the fray over world economics, invented a 'Design Machine' to speed up invention, and warned against impending national disaster. Was he a cocky chemist? A sober economist? A restless engineer? A writer? A prophet? Somehow Price was none and all of these all at once. Finalizing his divorce, he moved from Minnesota to New York in the winter of 1957 to become a rather low-rung employee of the Stevens Engineering Company producing instruction manuals for IBM computers.

4. New York

It was in New York that IBM's director of research summoned him to the company's headquarters at 590 Madison Avenue to discuss the 'Design Machine'. Price would be welcome at Research and Development, the director told him. But George demurred, figuring the company would steal his ideas if he did not first take out a private patent. Drafting a 75 page technical memorandum showing how an IBM 704 computer might be incorporated into a Design Machine, how a complex part could be described to the machine and how the machine could display the part in 3D, he nevertheless failed to file a patent before the *Fortune* article turned public domain. He was living in the Village now, alone, and doing a lot of drugs.[19] Ultimately, he joined IBM as an editor of technical manuals in a dreary office in Poughkeepsie. The station was far below his talents, but George enjoyed the freedom. He was planning on writing a book titled *No easy way* that would combine his economic, technical and political ideas to help save the Western world.[20]

Off-beat, self-taught, desperate for recognition and megalomaniacal, Price remained determined to make a breakthrough at all costs. Working on a new type of mathematical optimization system stemming from the development of procedures for solving linear problems with variables limited to 0 and 1, he thought he might be onto something big. The initial impetus had been to solve a computer programming problem (he had been upgraded to IBM's Department 630) but the 0, 1 restriction resulted in models more helpful than the usual linear ones for understanding behaviour of price and profit-based economic systems. He immediately wrote to the MIT economics professor and future Nobel Laureate, Paul Samuelson, to test the waters. Concomitantly, he sent the Nobel Laureate Sir John Eccles a paper he had written on 'Structure and function in the invaginated synapses of retinal receptor cells' in which he claimed to have achieved 'a discovery of major importance'.[21] He had been communicating with the geneticist Herman J. Muller, too, and with his hero Claude Shannon, both Nobel Laureates. None of his co-workers knew what he was up to; he hardly showed up for work. Despite the hustle, and the titillating rubbing-of-shoulders with the greats, nothing came out of any of it: not the independent brain neural network research, nor optimization system, nor the book to save the world. IBM was now developing computer-aided design (CAD), his brainchild, stolen, he thought, in broad daylight. His daughters had moved back to Washtenaw County, Michigan, where their frustrated mother became a third grade teacher. He had not seen them in nearly 10 years.

It was then that Price discovered that he had thyroid cancer, and went under the knife back in Chicago. The operation was successful in terms of the cancer, but the recovery was slow, and had left the right side of his neck and his right arm and shoulder without sensation. His wife Julia was after him for alimony payments, his daughter Kathleen needed him to foot the bill for her final year at a private school in New York, and he could hardly feel his face. He fell into a deep depression. His brother, Edison, who had since taken over Display and renamed it the Edison Price Lighting Company, soon to invent track-lighting and become a partner of such architectural greats as Buckminster Fuller, admitted him for a short while in the winter of 1967 to the Payne Whitney Psychiatric Clinic; George had been neglecting to take his thyroid medicine and the family were afraid for his life.

Everyone thought he was over-reacting when he quit his job at IBM, but Price insisted that there had been 'a radical change in my purposes, attitudes, motivations'.[22] Family was increasingly on his mind. When he himself was a child, the Great Depression almost destroyed the social fabric of America. Privately funded mutual aid societies in New York City shrank in number from 6000 in the 1920s to only 2000 after the markets collapsed. More than 400 private social service institutions—a total of one-third of those in the city—had closed their doors by 1933, and abandonment of women and children by husbands and fathers had rose by 135% [18]. Had it not been for his mother's grit, his own family no doubt would have disintegrated. Now he himself had abandoned his wife and daughters. Why? What allowed some families to stick together while others collapsed? He was reading a lot on evolution now, and thinking about behaviour.

Guilt-ridden and lonely, George did what George was good at: turned a highly personal concern into an abstract intellectual problem. On 13 November 1967, he embarked on the *Queen Elizabeth* for London, where he hoped to make a great discovery at long last, to find a piece of truth, whatever it took.

5. The Price equation

In retrospect, all the components were already there: optimality thinking, the penchant to break problems into their components, the consideration of individual versus community, an interest in evolution, a search for a Boyle-like law of human nature. But family was the most important immediate driving force, or rather the family that Price had abandoned. He was trying to live on $5 a day, irate at the surgeon who had operated on his cancer, and at his well-married[23] brother for not paying back a loan. He was angry at the world for not recognizing his genius. He was lonely. His daughters Annamarie and Kathleen were now 19 and 18, respectively. Afraid he 'would not live for more than a small number of additional years', he was concerned about their future.[24]

Price began frequenting libraries—the Senate House at UCL, Camden Town, Highgate, the Zoological Society, the British and Natural History museums—and when these closed, the late-opening Holborn Public Library. He was reading widely in linguistics, anthropology, neurophysiology, psychology and behaviour. In early March he came across a two-part paper by William Hamilton, 'The genetical evolution of social behaviour' [19,20]. He had not yet mastered its mathematics, but when he wrote unsolicited to the author to request a reprint, he had already decided that this would serve as a basis for a paper of his own. Did Hamilton know of any evidence for genes that enable those who carry them to detect exact copies of themselves in other persons? Contemplating his daughters and the Depression era trio George–Alice–Edison, which was finally now unravelling following years of jealousy and neglect, he wondered: could genetic similarity be sensed?[25]

A few weeks passed and a reply from Hamilton arrived:

> 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… 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? I wonder whether this is the field in which you think you see some light[26].

Hamilton had penetrated Price's thoughts. For upon encountering Hamilton's inclusive fitness equation, $rB > C$, Price could not help but wonder whether nepotism was the best nature could muster. If this were the case, the future of humanity seemed bleak. The very disgust from the prospect of a kin-limited altruism, Hamilton seemed to be suggesting, might itself be a trick played by our genes and ensconced in us by natural selection to improve humanity's survival: by broadening altruism beyond the family, humans would themselves contribute to the genetic diversity that would strengthen their kind. It was all in the genes. Was his guilt over abandoning his family, therefore, and morality itself more broadly, nothing but a sham?

Price was working on half a dozen different papers, but wrote to his daughter Kathleen in America that his big one would be about 'the evolutionary origin of the human family'.[27] In most mammals, males simply mated with females and did not care for their young. In humans, preferential care towards offspring by fathers had become the norm. 'Problem: why did our species evolve in this way?', he asked, signing off, without a hint of irony, 'With love, Daddy'.

He was working on a second problem, one that Darwin himself had recognized in *The descent of man* [21]. Why did ornate antlers evolve for combat if they were highly ineffective weapons for inflicting injury? Suddenly, Hamilton's 'games' jumped at him. Just as in the Cold War, with its ballistic missile and nuclear stockpiles, large antlers would serve as a deterrent to combat rather than something to be used to inflict real harm. It was a classic von Neumann game, and he set out to calculate its consequences. What he discovered was the first evolutionarily stable strategy: over time, limited combat strategies would evolve.[28]

Price had written to Hamilton that the flip side of kin selection was malevolence to non-relatives, but he could now see that combat too had its flip side—altruism—and it was plain that kin selection could not account for all cases of 'good deeds' in nature. Reciprocity might evolve, short of genetic relatedness, if retaliatory behaviour evolved against non-cooperators. To Hamilton, in the jungles of Brazil, he now wrote that he was working on 'a more transparent (though less rigorous) derivation' of his kin-selection mathematics.[29]

Hamilton seemed to suggest that relatedness was necessary for the evolution of 'altruistic' genes, but Price now perceived that it might represent one path among many. In evolutionary terms, the problem was one of tracking the change in a character

over time. The simplest way to do this was also the most intuitive: if there were two groups of 10 people with different heights, and the second group was composed exclusively of heights that already existed in the first, though in a different ratio, the average height among individuals of the new group would be determined by the relationship between the height of each individual and the number of 'copies' made of that individual in the second group, divided by the average number of copies. Technically speaking, this relationship was a 'covariance', and Price wrote down the simple equation:

$$\Delta\bar{z} = \frac{\mathrm{Cov}(w, z)}{\bar{w}},$$

capturing how the number of copies made (w) of the different heights (z) determine the average height of the new group ($\bar{z}$).

This was a general selection equation, good for things like determining the preservation of fossils in the earth as much as the culling of chemical crystals is space. Instructively, it could be applied to biological traits, too, like baldness and crooked teeth, and of course—altruism. The approach was more abstract and more general than Hamilton's coefficients of relatedness, but that seemed an improvement since altruism was dependent on association rather than family. The reason for this seemed clear to Price: natural selection could not care less why people end up in groups; similarity of traits would work just as well as common genetic descent. And since a covariance treated relatedness as a statistical association rather than a measure of common ancestry, relatedness could actually be negative, leading to spite—harming oneself in order to harm one's enemy more. In fact, spite and altruism were two sides of the same coin. Both existed as possibilities within us, but depended on the environment: If the surrounding creatures were similar, altruism would evolve, if they were different, it would be spite. It was the social environment that shaped our behaviour.

On 24 September 1968, Price wrote to his mother that 'something wonderful and totally unexpected happened to me an hour or so ago'.[30] He had taken his equation, off the street and unsummoned, to the biostatistics professor at University College London, who happened to be Hamilton's PhD supervisor Cedric Smith. Within 90 min, Smith had offered him an office and an honorary appointment in what was then a leading department in human genetics. Price went to work, obsessed with the mystery of family, determined to make this a logical and tidy exercise, unlike the mess he had sown in his own life.

It was an optimization problem, not unlike those he had considered at IBM. How did our ancestors allocate food? One option would be complete sharing on the backdrop of noncompetitive, promiscuous mating and cooperative rearing of the young with no recognition of paternity or maternity. An alternative would be cooperation between males for hunting but individual, family action in all other areas. This second path would favour monogamy, he thought, since keeping meat to oneself rather than sharing with partner and kin would reduce filial fitness, whereas frequent partner swapping would translate into feeding the kin of other males. Discounting some anthropological exceptions, this second option was the path *Homo sapiens* had taken. 'Fatherhood', when all was said and done, had been an optimal solution to the challenges attending daily grub, and love—an invention to oil its wheels. After all, love does not always lead to happiness; something more powerful like genetic evolution must have been responsible.[31]

It was a blow to idealism, perhaps, but it was logical. Still, he needed more mathematics. Where had evolution placed its eggs: in the individual or the group, the gene or the family? Travelling to America to visit his dwindling mother, he came across Garret Hardin's 'The tragedy of the commons' at the New York Public Library [23]. To solve the inherent conflict between individual and collective interest, Hardin had advocated 'mutual coercion mutually agreed upon' and Price now wondered whether it might be possible that evolution had fallen upon the same kind of solution. Group selection was theoretically possible [24], and early humans undoubtedly lived in groups in which cultural inheritance could have helped preserve the kinds of genetic behavioural variations that might have been swamped by migration. Price familiarized himself with the writings of Fisher [25], Wynne-Edwards [26] and Williams [27], and studied the debates over the unit of selection. In Hamilton's recent paper on 'Extraordinary sex ratios' Price recognized that Hamilton had offered a perfect example of group selection, though Hamilton himself had not yet seen it [28]. Perhaps, as Darwin recognized looking at the ants [29] and then at humans [30], selection might work on different levels of the biological hierarchy simultaneously.

The question now became not whether selection can work at the level of the group instead of the level of the individual, but rather, in each and every case, at which level selection was at work with greater force. Returning to his covariance equation,[32] Price added a 'transmission bias' which allowed us to see not only whether a trait moving from a 'mother' to 'daughter' population helped to increase fitness, but also what the chances were that it would be inherited:

$$\Delta\bar{z} = \frac{\mathrm{Cov}(w, z)}{\bar{w}} + \frac{E(w\Delta z)}{\bar{w}}.$$

The equation partitioned trait change in evolution into selection (Cov) and transmission (E), but with simple substitutions it also partitioned two levels of selection simultaneously, showing how much each contributed to the overall change. From the gamete and individual (the transmission and selection terms, respectively), the level could be bumped up a notch to individual and group, even species and lineage. 'Have you seen how my formula works for group selection?' Price asked in a 'squeaky and condescending' voice over the phone, to which Hamilton replied 'of course not…So you actually believe in that do you?' [33, pp. 172–173]. The answer was, Yes. In reply to Hardin's scenario, if not to his own familial woes, Price's full equation could specify the conditions under which the good of the group triumphed over the good of the individual. Distinct from Hamilton's kin-selection mathematics, it need not constrain goodness nor write it off as apparent: when selection worked more strongly between groups than within them, genuine altruism could evolve.[33]

To Hamilton, Price described his own creation as 'a miracle' [33, p. 173].[34]

6. Conclusion

The story of how Bill Hamilton hoodwinked the editor of *Nature* so as to help Price publish 'Selection and covariance' in its pages has been told in detail, along with Price's rapid descent into homelessness, depression, and finally suicide after the publication of what became known as 'the Price equation' [6]. Following a surprising conversion to evangelical Christianity, George Price became preoccupied with biblical exegesis and set out on the streets of London to help the homeless in any

way possible—providing food, cash, legal representation, shelter—ultimately giving away his last penny and falling into the streets himself. It was as if he was trying to prove, to himself and perhaps to the world, that when humanity saw itself as one, true selflessness was possible, despite countervailing dictates of the genes and the pull of selection on the individual. I do not dwell on these developments here so as to put in focus more clearly how the events leading up to Price's working out of the equation provide an illustration of the intricate ways in which science may reflect life.

Philosophers of science argue over the extent to which non-scientific factors play a role in the various aspects of scientific production, from influencing problem choice all the way to insinuating themselves into the very bones of scientific theories. Many works have shown that specific political, social and ideological agenda, as well as 'zeitgeist' more broadly, frame both how scientific problems are recognized and the manner in which they are approached. Others have gone further to claim that scientific facts are the products of scientific inquiry, rather than direct descriptions of realities 'out there'; that they are 'networked', and considered either 'false' or 'true' not based on the strength of any inherent veracity but rather on the strength of the networks that produce them—the tools, practices, institutions, rhetoric that render them intelligible and present them to consensus [35–39].

The case of 'the Price equation' illustrates how a preoccupation with the Cold War arms race, computer-age 'optimization', and a form of historically situated mechanistic scientism paved a road upon which Price advanced towards his evolutionary formalization. It also shows how the motivation for attacking a particular problem, that of the evolution of the family, stemmed from highly personal circumstances in Price's own life. Preoccupied with abandoning his daughters, guilt-ridden and searching, Price turned an existential quandary into an abstract scientific pursuit, ultimately re-translating his science back into life as he morphed into a Christian and radical altruist. As this theme issue amply shows, 50-years on, what he left behind him is making a real impact on disparate fields.[35] The lesson we learn from this is that we need not insist on the 'purity' of scientific pursuits: the roads that lead to good science are as rich and varied as the human experience.

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Endnotes

[1]Dr O. W. Hill, letter to George Price, 2 December 1974, George Price Papers (GPP; in the possession of Price's family).
[2]Shmulik Atia and Asher Dahan, interviewed by O.H., 4 and 7 May 2008.
[3]George Price, letter to Kathleen Price, 5 November 1974, GPP; on Thompson see [1,2].
[4]It would eventually be published as [3]. Hamilton had already reformulated his inclusive fitness ideas based on Price's insights, in [4].
[5]Bill Hamilton, letter to Dr Kelly, undated (*ca* 19 December 1974), British Library William Hamilton Collection (BLWHC), Z1X102_1.1.18.
[6]For an extensive treatment of George Price's life and work see [6].
[7]'Willian E. Price dies: South Broadway resident had revolutionized theatrical lighting with his inventions', unidentified newspaper clipping, Edison Price Lighting Company Family Archive (EPFA, in the possession of Edison Price's family).
[8]Alice Avery, letter to Remco Real Estate, 26 December 1934, EPFA.
[9]Alice Avery, letter to Transfer Tax Commission, 14 September 1934, EPFA.
[10]*Birch Log* 1935, p. 16.
[11]George Price, transcript, Harvard College, 1940–1941, Harvard University Archive.
[12]George Price, letter to Bob Sheffield, 6 February 1945, GPP.
[13]Kathleen Price, interviewed by O.H., 12–13 April 2008; Al Somit, interviewed by O.H., 16 April 2008.
[14]Professor Gilbert Stork, 11 January 2008, and Professor Leonard K. Nash, 5 May 2008, private communications.
[15]Annamarie Price, interviewed by O.H., 15 and 17 April 2008.
[16]Box 1, Samuel Shwartz Papers, University of Minnesota, undated.
[17]Alice Avery Price, letter to George Price, 22 September 1953, GPP.
[18]Price's [13] attacks were levelled specifically at the claims of the parapsychologists Samuel Soal and Joseph Rhine. There were thousands of excited reactions to his article, including from Aldous Huxley, Upton Sinclair and his hero Claude Shannon.
[19]These included iproniazid, Dexedrine, ephedrine, Seconal, as revealed in communications with his psychiatrist: George Price, letter to Dr Nathan Kline, 28 October 1958, GPP.
[20]George Price, *No easy way*, draft, GPP.
[21]George Price, letter to Paul Samuelson, 17 December 1965, GPP; John C. Eccles, letter to George Price, 20 January 1965, British Library George Price Collection (BLGPC), BL:KPX1_3.2.
[22]George Price, letter to W. A. Brockner, 11 July 1967, GPP.
[23]Edison married the daughter of an original General Motors stockholder.
[24]George Price, letter to A. Boardman, 25 December 1967, GPP.
[25]George Price, letter to Bill Hamilton, 5 March 1968, GPP/BLGPC (in the British Library).
[26]Bill Hamilton, letter to George Price, 26 March 1968, BLWHC, BL: KPX1_4.5.5.
[27]George Price, letter to Kathleen Price, 11 April 1968, GPP.
[28]Price's collaboration with John Maynard Smith is a whole other story, which will not be addressed herein. See [22].
[29]George Price, letter to Bill Hamilton, 3 August 1968, GPP.
[30]George Price, letter to Alice Avery, 24 September 1968, GPP.
[31]George Price, letter to Ludwig Luft, 29 January 1969, GPP. Price asked his friend Luft for the lyrics to Schumann's *Dichterliebe* for a paper he was preparing on the evolution of love.
[32]Unbeknownst to Price the simple covariance equation had been derived earlier independently in [31,32].
[33]Hamilton interpreted this to mean that in man, group selection leads to fascism. See [34].
[34]The 'miracle' was published in *Nature*, with no footnotes.
[35]Besides the Price equation, George Price's lasting contributions include the introduction of the concept of the Evolutionary Stable Strategy (ESS), and the formalization of Fisher's Fundamental Theorem. See [40].

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