George C. Williams
(1926–2010)

Incisive thinker who influenced a generation of evolutionary biologists.

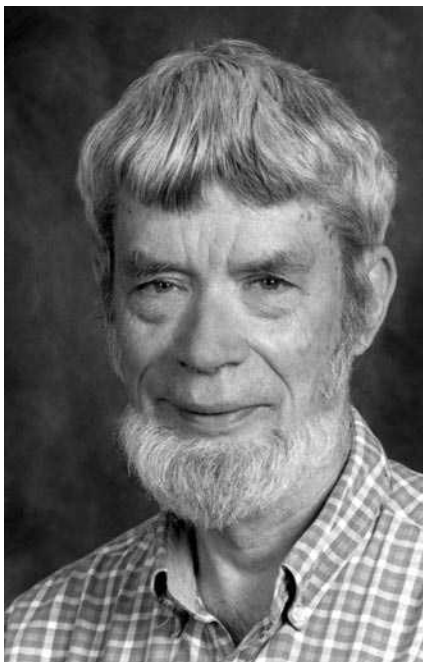
In 1978, at the age of 52, the great evolutionary theorist George C. Williams began to chronicle his own senescence, recording once a year how long it took to run 1,700 metres round a track in Stony Brook, New York. Williams presented the graph of his 12 years of slowing speed at his acceptance speech for the Crafoord Prize in Bioscience that he shared with Ernst Mayr and John Maynard Smith in 1999. He later published it in *The Quarterly Review of Biology*, with which he was involved for 32 years. The plot encapsulated his lifelong fascination: why do we decline with age?

Williams died on 8 September, aged 84. Little known to the public, this tall, reserved man with an Abraham Lincoln beard will be remembered by evolutionary biologists as one of the most incisive thinkers of the twentieth century. His major contribution, the theory of gene-level natural selection, left a profound and enduring stamp on fields from sociobiology and evolutionary psychology to behavioural ecology. He spoke slowly and little, but when he spoke, you listened: his words were full of insight and flashes of dry wit.

GENE-LEVEL SELECTION

After a stint in the US Army, working on a water purification plant in Italy during the Second World War, Williams finished his BA in zoology at the University of California, Berkeley in 1949. He got his PhD from the University of California, Los Angeles in 1955 for work on the ecology of the blenny — a type of fish. There followed a postdoc at the University of Chicago and an assistant professorship at Michigan State University. In 1960, Williams moved to the State University of New York at Stony Brook. He later became one of the first professors in its newly formed Department of Ecology and Evolution. There he remained until his retirement in 1990 — the year I arrived as assistant professor and inherited his freezer of Icelandic eel samples. He had spent two sabbaticals in Iceland, was fluent in Icelandic and published on the European and American species of eels and their potential hybrids on Iceland.

In 1957, he published his seminal paper 'Pleiotropy, Natural Selection, and the Evolution of Senescence' in the journal *Evolution*. He argued that genes that enhance fitness early in life but have detrimental effects later in life — genes with 'antagonistic pleiotropic effects' — would



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be expected to persist and even increase in abundance as long as, on balance, they boost an individual's fitness. He also pointed out that selection should be weaker in older age because fewer individuals are alive to be subject to it — an idea for which Williams shares credit with Peter Medawar.

The dominant narrative of early 1960s evolutionary biology was that natural selection acts at the level of the group or even for 'the good of the species'. Even death was explained in a group-selectionist light — as creating space for the next generation. Williams skewered this thinking, which he felt was "sloppy" and "anti-Darwinian", in his most influential book, *Adaptation and Natural Selection* (1966). In it he proposed that natural selection almost always acts more directly, swiftly and strongly at the level of the gene or the individual than at the level of the group or even species. He also railed against 'pan-adaptationism' — the idea that every feature is adaptive: he showed that adaptations have to have fitness-enhancing effects at the level of the individual rather than at the level of the species.

Adaptation and Natural Selection was way ahead of its time; its impact was felt for decades. Following Williams, E. O. Wilson extended gene-level and individual selection in *Sociobiology: The New Synthesis* — his controversial 1975 book on the role of genetics in social behaviour, even of humans. And Richard Dawkins's 1976 book *The Selfish Gene* popularized some of Williams's ideas. That said, gene-level selection and inclusive fitness were not universally accepted then, and still meet with occasional criticism — notably from researchers trying to explain altruism and eusociality, for example. These ideas remain, nonetheless, cornerstones of modern biological theory.

COMPETITION NOT COOPERATION

Williams made further influential contributions. With his 1975 book *Sex and Evolution*, he was among the first to offer explanations for the puzzling prevalence of sexual reproduction. He pointed out that it is yet another example of competition, not cooperation, being the dominant force in evolution — with genes from each parent battling for influence within the same genome. (He saw a bright future for the fields of genetic imprinting and epigenetics.)

Williams went even further with his reductionist view of natural selection in *Natural Selection: Domains, Levels and Challenges*, his 1992 book about information and matter. He pointed out that what is of importance in evolution is the information that is contained in genes, genotypes and gene pools, not the physical objects — a position reminiscent of Dawkins's 'meme' concept.

Williams returned late in life to his abiding concern — ageing. In 1994 he wrote the book *Why We Get Sick: the New Science of Darwinian Medicine* with the physician Randolph Nesse. Williams and Nesse proposed that disease symptoms should be understood, and treatment informed, by the long evolutionary history that shaped immune responses. Their work has spawned a new field of study, evolutionary medicine.

"He spoke slowly and little, but when he spoke, you listened: his words were full of insight and flashes of dry wit."

It is a cruel irony that this brilliant man who first explained senescence died of Alzheimer's disease. ■

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