

George Christopher Williams (1926 – 2010): Gene's-eye view of evolution

Professor George C. Williams, one of the most influential evolutionary biologists of modern time, died on September 8, 2010 at the age of 84. Professor Williams finished his doctorate at University of California in Los Angeles and his career path led him to State University of New York at Stony Brook where he remained for the rest of his academic life and taught the courses in marine vertebrate zoology. He was the last of the 1999 Crafoord Prize-winning trio, which included the famous Ernst Mayr (1904-2005) and John Maynard Smith (1920-2004). I have had some retrospective thoughts about E. Mayr and J. Maynard Smith and their works in the pages of this journal. Therefore, it is not only enlightening



Figure 1. In 1999, Ernst Mayr (left, in front), George C. Williams (standing), and John Maynard Smith were awarded with the Crafoord Prize in Biological Sciences from the Royal Swedish Academy of Sciences. They were honored for their "pioneering contributions to broadening, deepening and refining our understanding of biological evolution and related phenomena." (Photo © Royal Swedish Academy of Sciences)

and enlivening, but also fitting to reminisce about the penetrating thinking of this great evolutionary biologist.

Professor Williams was the most outspoken critic of group selection theory. Along with William D. Hamilton and J. Maynard Smith, he pioneered the development of the gene's eye-view of evolution in 1960s. Professor Williams became known for his 1957 paper *Pleiotropy, Natural Selection, and the Evolution of Senescence*, which introduced several fundamental ideas into evolutionary biology. This work was what put Williams at the center of attention. The central idea of *antagonistic pleiotropy*, which still remains the prevailing evolutionary theory of senescence, really was a more fully developed version of Peter Medawar's 1952 idea. Medawar (1952) suggested that lethal mutations that affect later in life accumulate in populations more rapidly than those expressed earlier in life because selection against them is weak. Williams (1957) proposed antagonistic pleiotropy (or *genetic trade-offs*) which states that, because of the greater reproductive value of earlier age classes, an allele that is advantageous early in life has a selective advantage even if it is deleterious later in life (i.e., having genetic trade-offs or pleiotropy). Therefore, senescence follows as it may be one of the costs of reproduction. The 1957 paper also outlined the basics of so-called "*grandmother hypothesis*" that states natural selection might select for post-reproductive life span in females. One of the outgrowths of Williams' 1957 theory of aging is *Darwinian medicine*, which Williams in collaboration with Randolph Nesse (1994) basically founded while exploring so-called diseases of aging in a book *Why We Get Sick: The New Science of Darwinian Medicine*.

His first and best known book was *Adaptation and Natural Selection*, published in 1966. In this book, he criticized the theory of *group selection*, which in layman's terms can be stated as the idea that traits evolve 'for the good of the species.' Williams emphasized that selection can only act on individuals. These differences in thinking about the nature of natural selection coalesce at the time of Charles Darwin and Alfred Wallace.

Darwin thought that natural selection acts on individuals and only indirectly on the group. On the other hand, Wallace thought that selection could work for the good of the group even against the interests of individuals. The theory of group selection was disposed of, as it was shown that mutation manifesting a cheater strategy would spread in a population of altruists. The anthology *Group Selection* published in 1971 under the editorship of Williams provides a nice overview of the shifts in biological thinking and he revisits the idea of group selection in his 1992 book. *Adaptation and Natural Selection* was one of the foundations on which the formulation of the gene's-eye view of natural selection was founded in the 1960s and effectively changed the landscape of evolutionary theory. At that time, adaptations were used to explain very much everything without clear understanding what it is. Williams memorably argues that "The ground rule- or perhaps *doctrine* would be a better term- is that *adaptation* is a special and onerous concept that should be used only where it is really necessary" and that when it is necessary, selection among genes or individuals would in general be the preferable explanation for it. This idea was significantly built upon by Richard Dawkins in *The Selfish Gene* (Dawkins, 1976).

Williams was also well known for his work on the evolution of sex, in which he tackles the issue of "*the two-fold cost of sex*". This idea was further developed by John Maynard Smith (1978). Evolution of sexual reproduction is arguably the most important question in evolutionary biology and Williams was pioneer of the challenge to elucidate the seemingly

obvious question (Williams, 1975).

To conclude, Professor G.C. Williams was a pioneer who helped shape our current way of thinking in many areas of evolutionary biology with his penetrating thoughts and clear writings. This retrospective was put together not only to reminisce about these great achievements in evolutionary biology, but also to encourage Mongolian biologists to study the original works of this and other great evolutionary theorists.

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