William G. Hill (1940–2021)

Quantitative geneticist who made fundamental contributions to understanding the nature of genetic variation.

Studies of molecular genetic variation have shown that regions of the genome subject to low rates of recombination experience higher rates of accumulation of deleterious mutations and lower rates of adaptive substitutions. In 1966, William (Bill) Hill supplied the mechanism that explains this, as well as other related phenomena in evolutionary genetics (such as a lower frequency of optimal codons in regions of low crossing over). This mechanism became known as the Hill–Robertson effect, as Bill discovered it while a PhD student studying with Alan Robertson. The Hill–Robertson effect is the reduction in the effectiveness of selection against deleterious mutations and in favour of advantageous mutations that occurs when non-neutral, linked alleles interfere with one another. It can be understood in terms of the reduction in the effective population size that occurs as a consequence of selection reducing the long-term contribution of individuals carrying advantageous alleles.

Bill Hill died on 17 December 2021 in Edinburgh, UK. He was born in Hemel Hempstead, UK, on 7 August 1940, and studied at Wye College London (BSc, 1961) and at the University of California Davis (MS, 1963), before moving to the University of Edinburgh where he completed his PhD and spent almost his entire academic career.

Bill's name will be remembered for the Hill–Robertson effect, a fact that he accepted but about which I think he may not have been entirely comfortable. A major impact of his work on the joint effects of natural selection and recombination in finite populations is that it provides an evolutionary advantage of recombination — namely, that the hitchhiking of mutations that increase the rate of recombination mitigates Hill–Robertson effects, so fixation of recombination modifiers increases rates of adaptive substitution and elimination of deleterious mutations. In population genetics, Bill also carried out important work on the phenomenon of linkage disequilibrium, the non-random association of alleles at more than one locus. He developed the basic framework for quantifying non-random associations, and establishing that genetic drift can increase linkage disequilibrium. This has had wide applications for quantitative trait locus and association mapping of quantitative traits, and particularly for understanding the genetic basis of complex-disease trait variation in humans. The major practical implications of this work mainly occurred decades after his seminal papers were published.

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Bill's primary area of research was in quantitative genetics, the study of the inheritance of continuously variable traits such as growth rate, milk yield and fitness, and he was the preeminent quantitative geneticist of his generation. He made fundamental contributions to our understanding of the genetic basis of quantitative variation, such as the role of mutations in explaining long-term responses to artificial selection, which often continue in experimental populations as well as domesticated animals and plants. This work inspired a generation of experimental quantitative geneticists to carry out long-term selection and mutation accumulation experiments to quantify and characterize quantitative variation arising from new mutations. He also worked on the consequences of finite population size and its implications for sustaining long-term selection responses and the maintenance of variation. Bill had a long association with the animal-breeding industry, and his influence led to the application of advanced quantitative genetics methodologies, including the optimal use of information from related individuals for making selection decisions. He was also aware of the possible adverse effects of selection focused solely on production traits such as high growth rate, which can lead to undesirable correlated effects (an example being skeletal deformation in broiler chickens). He advocated that such unsustainable effects could be prevented by collecting data on fitness, disease, conformation and related traits and including them in a multi-trait selection scheme. His work was particularly impactful for increasing the rate of genetic progress in dairy cattle in the UK, which was recognized with his award of the OBE (Officer of the Order of the British Empire) honour in 2004.

Bill has a lasting impact via his scientific research, but his long-term influence has also come from his mentorship of students and research associates, many of whom have gone on to have successful careers in academia and industry. He supervised more than 50 research

students at the University of Edinburgh and its associated institutions. Bill was a tremendously supportive mentor. He would typically do a round of his group before the morning coffee break (which was in Alan Robertson's office along the corridor, when I was doing my PhD) and often started with the same question: "What have you discovered?". This was not because he expected anyone to actually discover something new every day; instead, I think it was a nice way of opening the conversation about where we were with the project. We would then talk about what the latest results meant and what might be done next. He took an incredibly keen interest, but this was never overbearing and he was happy for students to go their own way with their projects, which is vital for becoming an independent scientist. What mattered to Bill was doing good science. Bill was also incredibly efficient at reading and commenting on manuscripts, and would always give insightful comments — usually the next day, in spite of his extremely busy academic schedule.

Among Bill's long list of honours and awards, he was elected Fellow of the Royal Society of Edinburgh in 1979 and the Royal Society in 1985, and was awarded the Royal Society of Edinburgh Royal Medal in 2005, the Royal Society Darwin Medal in 2018 and the Genetics Society Medal in 2019. ❐

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Additional information

P.D.K. carried out his PhD under Bill Hill's supervision.