

Introduction: population genetics, quantitative genetics and animal improvement: papers in honour of William (Bill) Hill

William (Bill) Hill FRS is probably the world's most eminent quantitative geneticist, with a distinguished research career spanning 40 years (mostly at the University of Edinburgh) reflected in over 200 refereed publications in major journals. Quantitative genetics is concerned with the analysis of variability in complex traits that is caused by the joint effects of variant alleles at several genetic loci, as well as non-genetic factors. Most traits of evolutionary and economic importance are of this type. While long regarded as a poor sister of molecular genetics, the revolution in genetic mapping technology and the advent of whole genome sequences have turned quantitative genetics into one of the fastest growing areas of biology. This development is critically dependent on the foundation of knowledge laid down by Bill's generation of quantitative geneticists.

Understanding quantitative variability involves a combination of breeding experiments, statistical analysis and mathematical modelling of genes in populations. Bill is a master of all three and has maintained the high standards set by the original members of the Edinburgh group, notably the late Alan Robertson FRS and Douglas Falconer FRS. In addition to his purely scientific work, he has made many important contributions through the application of genetics to animal (livestock) improvement. These have had a major impact on the UK and worldwide livestock breeding industry. His contribution to the UK animal breeding industry was one reason for his OBE award in 2004. He also served with distinction in several academic administrative posts at the University of Edinburgh, culminating in the Deanship of the Faculty of Science and Engineering. During his Deanship, Bill somehow kept up with science, reading draft manuscripts of students, postdoctoral fellows and other colleagues (with barely legible comments usually given the next day). He even managed to publish single-author papers, often written on a plane to or from the USA. Since his formal retirement at the age of 62, he has continued an active research programme as well as several important editorships and committee memberships.

We felt it appropriate to celebrate Bill's 65th birthday by bringing together a set of papers from his former students, postdoctoral fellows and colleagues in the field. We hope that the breadth of these papers, and the global span of the contributors, will convey some idea of the extraordinary scope of his work and influence.

Much of his research has been theoretical, using mathematical and computer models of the behaviour of

genes in populations to understand the genetic basis of quantitatively varying traits, the maintenance of quantitative genetic variation and the responses of traits to artificial and natural selection (Felsenstein 2005; Mackay & Lyman 2005; Meyer & Kirkpatrick 2005; Toro & Caballero 2005). He also contributed to methods for estimating effective population size (Liu & Weir 2005; Wang 2005) and marker-based methods for estimating relationships among individuals in a population (Thomas 2005). He has made some very influential contributions to our understanding of the effects of finite population size and mutation on variability and selection responses (Johnson & Barton 2005). He has conducted experiments on the effects of artificial selection, using the mouse as a model system, to test the predictions of his theories (Bürger *et al.* 2005). He developed methods for estimating the genetic parameters of quantitative traits in livestock populations for the purpose of designing improvement programmes for economically important traits (Brotherton & Goddard 2005; Hospital 2005; Nicholas 2005; Thompson *et al.* 2005). Of especial importance has been his work on linkage disequilibrium, non-random associations between genetic variants at different sites in the genome (McVean & Cardin 2005). Such associations now provide an immensely important tool for human (and other) geneticists seeking to map and identify disease-causing genes. Bill's work has provided a basic framework for modelling and analysing linkage disequilibrium, which he went on to apply to the genetic mapping problem (Knott 2005). Interestingly, Bill never jumped on to the 'QTL (quantitative trait loci) bandwagon'. This was not because he believed that genetic loci with large effects on quantitative traits did not exist but, presumably, because he realized the limitations of their use for artificial selection programmes. Nevertheless, he has been highly supportive of research in this area by his colleagues (including P.K., P.V. and Knott).

We did not seek a contribution related to his seminal PhD work, which showed how linked sites subject to selection interfere with each other in a way that reduces the effectiveness of selection (Hill & Robertson 1966), now known as the Hill–Robertson effect. This is simply because this idea plays such a major role in our understanding of genome evolution and the evolution of sex that it is all-pervasive. For example, almost any paper which discusses the relation between recombination and other features of the genome cites this effect (e.g. the recent paper on the chicken genome sequence; International Chicken Genome Sequencing Consortium 2004).

One contribution of 16 to a Theme Issue 'Population genetics, quantitative genetics and animal improvement: papers in honour of William (Bill) Hill'.

Bill always has been modest about his own achievements: 'the last thing I want to be known for is a paper that I wrote 30 years ago'; from what we have just said, he may be disappointed in this. His focus and dedication has been on the science (rather than personal gain, building a large group or publishing in high profile journals. How times have changed...) and a typical comment is 'what is the scientific question you are addressing' or 'to what question is this paper the answer?' Perhaps the best example of his dedication 'to the laboratory' is that when one of us phoned him at home to congratulate him with his OBE on New Year's Eve 2003, he got a message to phone the laboratory instead.

Brian Charlesworth¹
Peter Keightley¹
Peter Visscher^{1,2}

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¹*Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh EH9 3JT, UK*
(brain.charlesworth@ed.ac.uk;
peter.keightley@ed.ac.uk; peter.visscher@ed.ac.uk)
²*Queensland Institute of Medical Research,
Royal Brisbane Hospital, 300 Herston Road,
Brisbane 4029, Australia*

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