

like the worm-fly choice the decision will affect the progress of academic biology. One of the most disturbing aspects of the history of the worm-fly genome decision is John Sulston's claim that they went ahead with worm partly because the clones were already available. It was the challenge of scaling up, of developing the large scale sequencing methodologies on easily available DNA that excited them more than the choice of biological target.

LIAM KEEGAN

Hyde Park, Killucan, MRC Human Genetics Unit,  
Co. Westmeath, Western General Hospital,  
Ireland Edinburgh, EH4 2EH

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Population genetics, quantitative genetics and animal improvement: papers in honour of William (Bill) Hill. *Philosophical Transactions of the Royal Society B* (2005) **360**. Edited by B. Charlesworth, P. Keightley & P. Visscher

This volume was published as a (surprise, I believe) tribute to Bill Hill<sup>1</sup> on the occasion of his 65th birthday. As anyone in quantitative or population genetics should know, Bill has made numerous important contributions to the subjects in the title of this volume over the last 40 years. Bill must now be considered the "eminence grise" of quantitative genetics – a term he is bound to object to due to its connotations of established and unquestioned expert (and age!). Bill would never like to be unquestioned and still relishes a good debate; nevertheless, this collection reflects the breadth and depth of his contributions to these areas. Written by experts in their own right, the contributors include former students and current collaborators. Many of the contributors have worked or passed through the Department in Edinburgh where Bill has spent the majority of his time and a few have not.

The collection displays the vigour in quantitative genetics and related areas today. As the editors point out in their introduction, quantitative traits, influenced by a number of genes and environmental factors, include most of the important traits of evolutionary, economic and medical importance. For a while the molecular genetic revolution put quantitative genetics in the shade. However, in recent years it has become obvious that it is only possible to dissect complex traits, to understand how gene action and other factors control trait variation, to utilise quantitative traits in artificial breeding or disease prediction and to predict the outcome of selection or other interventions on such traits by combining the tools of

genomics and molecular genetics with sophisticated models of quantitative genetics. The papers gathered here represent just some of the most important areas of development in genetics and all relate in some way to contributions of Bill Hill.

I assume the contributors were given relatively loose guidelines on the nature of their contributions as the structure varies from paper to paper. However, the papers fall broadly into two categories: authoritative overviews of a particular subject or more focussed novel contributions. All the papers are worth reading and it is unfair to pick out only a few for mention – however, I'll do it to give a flavour of the content of this volume. The collection opens with an excellent review by Toro and Caballero (2005) of genetic diversity in subdivided populations. The major focus and relevance of this contribution is to species under domestication or conservation and the authors review estimation of molecular and phenotypic diversity, the balance of within and between population diversity in the context of conservation and the genetic management of subdivided populations. This paper should really be obligatory reading for all those involved in conservation – it is both scholarly and comprehensive (within the limits of the space allowed it) and sets the tone for the remainder of the volume. In a similar vein of the scholarly overview are the contributions of Wang (2005) on the use of marker data to estimate effective population sizes and that of Thomas (2005) who reviews use of marker data to infer relationships between individuals.

The nature and maintenance of quantitative variance is another fascinating subject that attracts the attention of experts in this volume. Johnson and Barton (2005) review the apparent incompatibility between the existence of substantial genetic variation for most quantitative traits and the fact that such traits can often be shown to be under stabilising selection that under simple models should act to purge the population of variation. They look at attempts, as yet not fully successful, to reconcile the facts, again providing a scholarly and readable review. Mackay and Lyman (2005) review understanding of the genetic control of *Drosophila* bristle numbers, archetypal quantitative traits, once thought of as simple traits under additive genetic control and subject to stabilising selection. Not only does this review reaffirm the value of studying this apparently simple model, but it also demonstrates that these traits are anything but simple. Amongst other things, the work summarised demonstrates the importance of pleiotropy (also a conclusion reached by Johnson and Barton), and the major roles played by complex interactions: gene by gene (i.e. epistasis), gene by sex and gene by environment. Thus theoretical and other studies of the maintenance of genetic variation need

<sup>1</sup> I have never heard anyone refer to him as William except in jest or at one of those daft formal occasions. Perhaps he has a maiden aunt who still refers to him as William?

to consider further the impact of these potential complexities on the conclusions reached.

Several of the papers deal with another of Bill Hill's long term interests – that of animal breeding. This area is of some considerable economic, social and environmental interest, sitting as it does at the top of a production pyramid that encompasses a major part of world agriculture. Work in Edinburgh over the last 50 years has made a substantial contribution to the development of this technology. Bill Hill, working alongside others such as the late Alan Robertson has had a significant input. Animal breeding often imposes high selection intensity in relatively small populations and so imposes a severe challenge for quantitative genetic theory. Nonetheless, Brotherstone and Goddard (2005) in their review on selection in dairy cattle echo the point made by Johnson and Barton in pointing out that intense selection with rapid genetic progress is not accompanied by an observable decline in the heritability and noting that work is required to fully reconcile these observations.

The last contribution in the volume from Frank Nicholas (2005) also focuses on animal breeding, this time in relation to disease. Nicholas reviews evidence on single gene and multifactorial susceptibility to both infectious and inherited disorders, information he has been involved in painstakingly cataloguing online (<http://www.angis.org.au/omia>). Nicholas points out that Bill Hill's first publication was also the first to identify a single gene disorder in Japanese quail and that he has since made contributions to the debate on the relationship between breeding, inbreeding and the occurrence of inherited disorders in livestock. Nicholas puts in a plea for Bill Hill to write the definitive paper on the occurrence and control of single-locus disorders in animal breeding programmes. Whether Bill chooses to take up this challenge in a retirement in which he remains as sharp and as active as ever remains to be seen. In the meantime we have this volume to remind us that the fields of quantitative and population genetics are as relevant and as full of new challenges as they have been at any time during the last fifty years.

Brotherstone, S. and Goddard, M. (2005) Artificial selection and maintenance of genetic variance in the global dairy cow population. In “*Population genetics, quantitative genetics and animal improvement: papers in honour of William (Bill) Hill*” (Edited by B. Charlesworth, P. Keightley and P. Visscher). *Philosophical Transactions of the Royal Society B* **360**: 1479–1488.

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P. Keightley and P. Visscher). *Philosophical Transactions of the Royal Society B* **360**: 1411–1426.

Mackay, T. F. C. and Lyman, R. F. (2005) *Drosophila* bristles and the nature of quantitative genetic variation. In “*Population genetics, quantitative genetics and animal improvement: papers in honour of William (Bill) Hill*” (Edited by B. Charlesworth, P. Keightley and P. Visscher). *Philosophical Transactions of the Royal Society B* **360**: 1513–1528.

Nicholas, F. (2005) Animal breeding and disease. In “*Population genetics, quantitative genetics and animal improvement: papers in honour of William (Bill) Hill*” (Edited by B. Charlesworth, P. Keightley and P. Visscher). *Philosophical Transactions of the Royal Society B* **360**: 1529–1536.

Thomas, S. C. (2005) The estimation of genetic relationships using molecular markers and their efficiency in estimating heritability in natural populations. In “*Population genetics, quantitative genetics and animal improvement: papers in honour of William (Bill) Hill*” (Edited by B. Charlesworth, P. Keightley and P. Visscher). *Philosophical Transactions of the Royal Society B* **360**: 1457–1468.

Toro, M. A. and Caballero, A. (2005) Characterization and conservation of genetic diversity in subdivided populations. In “*Population genetics, quantitative genetics and animal improvement: papers in honour of William (Bill) Hill*” (Edited by B. Charlesworth, P. Keightley and P. Visscher). *Philosophical Transactions of the Royal Society B* **360**: 1367–1378.

Wang, J. (2005) Estimation of effective population sizes from data on genetic markers. In “*Population genetics, quantitative genetics and animal improvement: papers in honour of William (Bill) Hill*” (Edited by B. Charlesworth, P. Keightley and P. Visscher). *Philosophical Transactions of the Royal Society B* **360**: 1395–1410.

CHRIS HALEY  
Roslin Institute

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*Proteomics for Biological Discovery*. T. D. Veenstra & J. R. Yates III. Wiley-Liss. 2006. 307 pages. ISBN 0 471 16005 9. Price £41.50. (paperback)

### The rise of the proteome

In days gone by the analysis of proteins was very much the provenance of Biochemistry Departments with the focus on isolating and characterising individual polypeptides. In the post-genome era, where we have the genetic blueprints of hundreds of organisms readily available, the focus has changed to a