Douglas Scott Falconer
FRS, FRSE

Professor Douglas Falconer was Emeritus Professor of Genetics, and formerly Professor of Genetics, Head of the Department of Genetics and Director of the AFRC Unit of Animal Genetics at the University of Edinburgh. He made major contributions to the understanding of the genetics of quantitative traits through his research, teaching and writing, notably his book 'Introduction to Quantitative Genetics', and was elected FRSE in 1972 and FRS in 1973. He was born in Old Meldrum, Aberdeenshire on 10 March 1913, and died in Edinburgh on 23 February, 2004, aged 90.

Falconer's parents were from Edinburgh, neither coming from a scientific background. His father was a minister of the United Free Church, whose first parish was where Douglas was born, but the family returned to Edinburgh soon after. He attended Edinburgh Academy where he developed an interest in science, although biology was not taught. His university education was delayed for five years as he contracted tuberculosis, and he did not start at St Andrews University until 1936. There he was particularly influenced by D'Arcy Thompson, graduating with first class honours in Zoology in 1940. Apparently Thompson would have awarded the degree without an exam, but the Dean prevailed, and a nominal oral was held. From there Falconer went to Cambridge and took a PhD under James Gray, working on the behaviour of wireworms. From 1943-5 he held a temporary lectureship at Queen Mary College, London, then based in Cambridge.

Falconer developed an interest in genetics, giving a course at QMC. To further this he took an opportunity for a research assistant position at Cambridge with Sir Ronald Fisher, the leading statistician and geneticist. There Falconer started work with the mouse, the animal that he used so successfully for the rest of his career, to study the genetics of both individual mutant genes and quantitative traits. Falconer concluded that one of Fisher's experiments was flawed; but his criticism was ill-received, Fisher telling him the next day that he had better arrange to go to Edinburgh soon, where he had obtained a research post.

Falconer was appointed to the ARC's new Animal Genetics and Breeding Research Organisation in Edinburgh in 1947. He was based in the University in the Institute of Animal Genetics under C H Waddington, Buchanan Professor of Genetics. This comprised an illustrious group indeed, including many Fellows of the RSE, among whom in the 1940s/50s on the quantitative genetic side were Eric Reeve, Jim Rendel, Alan Robertson, Forbes Robertson and Falconer; in mouse genetics were Mary Lyon and Toby Carter; and in other areas Charlotte Auerbach, Geoffrey Beale, Alan Beatty and Mick Callan. Here Falconer's research on genetics of relevance to animal improvement using the mouse flourished and in due course he obtained funds for a large new animal house.

The group saw a need to train people in genetics for research and the animal breeding industry. A postgraduate Diploma in Animal Genetics, including courses in quantitative genetics, was established, taught by University and non-University staff. This led to Falconer's *'Introduction to Quantitative Genetics*', first published in 1960 and going through four editions, the last in 1996 co-authored by his former colleague Trudy Mackay, with translations into at least nine languages. The Introduction to the first edition defines the subject:

'Quantitative genetics is concerned with the inheritance of those differences between individuals that are of degree rather than of kind, quantitative rather than qualitative. These are the individual differences which, as Darwin wrote, "afford materials for natural selection to act on and accumulate, in the same manner as man accumulates in any given direction individual differences in his domestic productions." An understanding of the inheritance of the difference is thus of fundamental significance in the study of evolution and in the application of genetics to animal and plant breeding; and it is from these two fields of enquiry that the subject has received the chief impetus to its growth.'

The Preface outlines Falconer's objectives:

'My aim in writing this book has been to provide an introductory textbook of quantitative genetics, with the emphasis on general principles rather than on practical application, and one moreover that can be understood by biologists of no more than ordinary mathematical ability…

‘I have had no particular class of reader in mind, but have tried to make the book useful to as wide a range of readers as possible.’

He certainly succeeded, for me and numerous others. The book has had a great and continuing influence on the development of quantitative genetics, as a class text and a reference for evolutionary biologists, for breeders, and for investigators of natural, domestic animal and human populations. Its clarity is matched only by Falconer’s other writing and teaching.

Falconer’s earlier publications in genetics were on mutant genes in the mouse, which he identified and mapped into linkage groups, including a neurological mutant ‘reeler’ and the first useful sex-linked mutant ‘Tabby’. He also undertook theoretical studies on estimation of mutation rates and linkage. The quantitative genetic work had a longer gestation, for he used selection experiments where the heaviest or most prolific animals were selected as parents of the next generation. This provided a route both to estimate parameters such as heritability of the traits and to investigate how much change could be achieved. Although his experiments could last five or more years, the twenty generations in mice represented a century of cattle breeding.

His first published selection experiment was important. There was then a dogma, espoused by Hammond, that rate of improvement was maximised by rearing breeding animals in a high quality environment, regardless of how well commercial stock were managed. By selecting lines for high body weight on both full and restricted feeding, Falconer showed, however, that most response on each was made on their own environment, but when transferred to the other diet, those reared on the poorer diet did relatively better. He also had an important insight, that growth on the two environments could be regarded as two traits and analysis could be in terms of the genetic correlation, previously defined only for traits on the same individual.

He worked extensively on the inheritance of litter size. Although closely related to fitness and thus previously subject to natural selection, Falconer showed it could be increased by artificial selection. With students, including his subsequent colleague Crad Roberts, he demonstrated the expected deleterious effects of inbreeding, but that the best inbred lines could reach the outbred level. Based on his analysis of litter size he developed an inciteful model to describe maternal effects in terms of a regression of offspring on mother’s performance.

He further demonstrated the power of selection experiments by increasing the susceptibility to urethane induced lung tumours, nicely illustrating genetic variability in susceptibility to cancer.

Falconer’s last major experiment involved selection for high and low body weight in replicated lines to provide material for subsequent evaluation of its genetic basis. He designed an elegant experiment, in which chimaeric embryos were made from high and low lines. These differ randomly in the proportions of tissue from each parent, so by using a genetic marker, growth rate could be related to the proportion of high/low genotype in each organ of each individual. No single organ was found to ‘control’ growth: gene action was both systemic and more dispersed, as might be expected with polygenic inheritance.

Stimulated by an enquiry on how to analyse the inheritance in humans of common diseases with all-or-none expression but not due to single genes, such as susceptibility to diabetes or renal stones, Falconer made a major contribution to human genetics. Based on just two quantities, the incidences in the population and in the relatives of affected individuals, he showed how to estimate the heritability of liability to the disease and that in many cases values were high.

Falconer became deputy director of the ARC Unit of Animal Genetics and, following appointment in 1968 by the University of Edinburgh to a Personal Chair in Genetics, Director of the Unit until his retirement in 1980. He also was head of the Department of Genetics from 1969-1977, which was an onerous task, for it was in effect a large group of semi-autonomous but high quality research fiefdoms. It continued to thrive under Falconer’s direction. He was a quiet spoken and extremely polite individual, most effusive in his thanks, notwithstanding any reservations about the quality of the advice he received.

Douglas Falconer married Margaret Duke, a classics teacher and daughter of a classics don at Cambridge, in 1942. She and their two sons survive him. Douglas and Margaret were a close couple, including a shared interest in walking, gardening and music, Douglas playing the flute well into his 80s. He was also a keen bird-watcher and sailor. He developed diabetes in mid life, which he controlled, but in his last years he became increasingly blind. On his retirement, he ceased experimental work, but maintained an office and continued writing. Indeed the 4th edition of his book was published when he was 83, and he still came into the lab for discussions about science.

He is remembered with affection by me and his other colleagues and former students, and by many who knew him only through his writing.

William G Hill

Douglas Scott Falconer, FRS, FRSE. Born 10 March 1913. Elected FRSE 1972. Died 23 February 2004.