



Professor William G. Hill
Mendel Medal 2019

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Comments from Colleagues



Carlos Lopez-Fanjul

It is very sad that Bill cannot give the talk at the Edinburgh meeting, but I am sure that you will present an excellent exposition of his work. I will not be able to attend but, if you find the occasion, please give him my deepest regards.

Susan Hayter and myself were the first Bill's PhD students, finishing in 1972. Sadly, Susie died a few years afterwards and Bill usually refers to me as his older student alive.

His work had always been a main source of inspiration of my research along 40 years and, to mark the permanence of this influence, I made an emotional point (so far unknown to him and to others) asking him to co-author what I thought it would be my last paper (Evolution 2014) as he has done with the first ones (Genetical Research 1973).

To this, I could add a number of personal notes but the following will suffice. Many years ago, I carried out an experimental check on Bill's predictions of the variability of the response to artificial selection. At the moment, I was unsure about Bill reaction and, hoping to skip that, I published my paper in French (Annales de Génétique et de Sélection Animale, 1982). A few months after I met Bill in a meeting and, in passing, he told me that he had refereed the paper and has been tempted to reject it: you have found a good agreement to a wrong formula (which was unknown to me at the time and was corrected by him in a later paper).

Bill has made a number of major contributions to quantitative genetics but, as you know, his theoretical treatment of the response to selection due to new mutations inspired a considerable part of my research.

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Mike Lynch

My involvement with Bill began when I was just starting to teach myself pop/quant gen, and I started corresponding with Bill via regular post (this was before email had been developed). I was interested in extending the neutral theory to quantitative traits, which required incorporating a lot of new complexities like dominance, inbreeding, and linkage disequilibrium. As you know, quant gen has a lengthy history of technical developments, and I did not yet know a lot of them, so I would spend hours and hours carefully deriving equations from first principles, and then sending the final results to Bill to get his take. He generally responded about as rapidly as possible with snail mail, with a few scribbled down steps, along with simple approximations, that reduced my dozen or so pages of derivations down to just a couple of lines that he probably pulled off in a few minutes. Unfortunately, his handwriting was very bad, so I would then have to spend hours more trying to decipher what he had done. He must have found this a bit hilarious, but never showed any loss of patience with me. These experiences had a huge effect on me, and helped ease my way further into quant gen.

As Walsh and Lynch literally developed over a period of three decades, we were subject to periodic ribbing by Bill, who was beginning to doubt that the thing would ever be completed, and justifiably so. He also provided very valuable feedback on a number of difficult subjects. I hope he did have some chance to glance at the final product, and wasn't too disappointed.

His lasting legacy seems to be the Hill-Robertson effect, but those who know the field of theoretical quantitative genetics will understand that there is hardly an area in which he didn't make seminal contributions. Many of these on experimental design and analysis have had a huge influence in applied areas of breeding.

Jack Dekkers

Bill has obviously made numerous important contributions to the field of animal breeding, which I'll focus on. From predicting response to selection and rates of inbreeding, to gene flow methodology, the impact of mutations, linkage disequilibrium, variance of relationships, etc. What has always struck me is that, on the one hand, Bill is obviously a genius when it comes to the theory of quantitative genetics, but on the other hand, he can relate extremely well to the application of that theory to practical animal breeding and has also made numerous contributions to that field. Apart from his scientific contributions, his legacy of course resides in all the students that he has trained over the decades.

My first interaction with Bill was towards the end of my PhD. I had of course read many of Bill's papers but had never met him. As part of my PhD I derived predictions of asymptotic rates of response to selection on BLUP EBV, accounting for the Bulmer effect. My results disagreed with results in a paper of one of Bill's students due to an oversight on their part. I presented my work at a WCGALP and remember how nervous I was because I assumed he would be in the audience. He was, however, extremely gracious and afterwards, took the time to write me a very nice personal letter, acknowledging their oversight and congratulating me on my work. That was the start of a very congenial relationship that has lasted through this time.

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Han Mulder

I visited Bill for the first time in spring 2005 as a PhD-student from Wageningen University to discuss with him opportunities for a sabbatical in autumn 2005. So I stayed from September until December in Edinburgh. He was already retired but with a great and sharp mind with respect to almost everything, but especially quantitative genetics. It was in the beginning still a bit of search for a topic that we both liked and were able to see the light. Finally, I started simulations about genetic variation in environmental variance. Step by step we were trying to understand the results and this led to what became my biggest contribution to quantitative genetics: prediction of breeding values and selection responses with genetic heterogeneity of environmental variance (*Genetics* 175:1895-1910) so far. I could not have done it without him. Later when I was back in Wageningen I continued with Bill on email distance and also that worked. Later I wrote with him the review Hill and Mulder 2010 (*Genet. Res.* 92:381-395), for which I stayed a couple of days with him in his house. He was so energetic, unbelievable. This review is now one of my most cited papers. When I became assistant professor and decided to develop my research line about genetics of environmental variance, I visited Bill regularly (2013, 2014, 2015, 2018), which resulted in one extra paper (Mulder, H. A., W. G. Hill, and E. F. Knol. 2015. Heritable environmental variance causes non-linear relationships between traits: application to birth weight and stillbirth of pigs. *Genetics* 199:1255-1269). He became a mentor for me and I enjoyed every minute speaking with him. Also in between we at least emailed a couple of times a year.

One of the things that we have in common is interest in farming, so he always talked with me about his farm as I did with respect to my father's farm.

Reading his papers is always inspiring, so his early papers on de novo mutations were a great inspiration for my recent work on de novo mutations and their impact on quantitative traits (H. A. Mulder, S. H. Lee, S. Clark, B. J. Hayes and J. H. van der Werf. 2019. The Impact of Genomic and Traditional Selection on the Contribution of Mutational Variance to Long-Term Selection Response and Genetic Variance. *Genetics* early online).

Bill's greatest contributions to animal breeding:

I think his greatest contributions are his research on maintenance of genetic and environmental variance, so this includes things like genetics of V_e , maintenance of genetic variance, e.g. contribution of DNM, but also the variability in relationships which is of great importance for predicting accuracy of genomic prediction.

Bill as a person:

- Very friendly and helpful
- Great and sharp mind
- Interest in family life
- Hard working, workaholic

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Robin Thompson

My collaboration with Bill mainly arose through the guise of helping with the statistical analysis of the order of 20 Ph.D. theses involved with the analysis of selection experiments and animal breeding schemes. It was exciting times with the ability for the first time to fit interesting and more relevant genetic models using the animal model. Most of this work used computer programs written by Karin Meyer, one of our first joint students.

Bill was a rigorous and exceptionally conscientious supervisor. The discussions with students I always found illuminating (sometimes more for me than the student). I quickly learnt not to immediately read a document a student gave me. Within a day Bill would send a corrected manuscript with scribbles for corrections and suggestions for improvement. One student had not got the self-confidence to write up their work and was reluctant to even come to work. Bill suggested a fellow student to go round and encourage the student to come to work. The student was still reluctant to complete her thesis. Bill showed the student a thesis with essentially each chapter based on a paper. The student had completed several papers so Bill suggested she could do something similar. The student then essentially pasted the papers complete with references in each chapter. When the external examiner read the thesis he asked if this format was acceptable. Bill replied that there was nothing in the university regulations to stop it. The student got their Ph. D. but Bill changed the university regulations the day after the student's oral.

A sample important paper is:

Hill, W. G. (1972). Estimation of genetic change. I. General theory and design of control populations. *Animal Breeding Abstracts*, 40, 1–16. This is one of a series of papers in the early seventies that enabled Bill to set the theoretical framework for the design, analysis and interpretation of selection experiments. (More personally I think these papers are crucial to Naomi Wray's thesis work on prediction of inbreeding in selected populations).

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Brian Charlesworth

Deborah and I first met Bill at the Population Genetics Group meeting in Bangor in December 1971, after I had started as a lecturer in the Liverpool Dept. of Genetics. He was very friendly to us, although of course was deservedly far better known than either of us. We have continued to be friends ever since, and Bill as Head of Biological Sciences was instrumental in getting us to move to Edinburgh in 1997. As you know, he is fiscally conservative, and was delighted that I was going to be supported on a Royal Society Research Professorship for up to 10 years, and Deborah on a NERC Senior Fellowship, thereby costing the University little in salary. But he did make sure that money was provided to give us well-renovated lab space.

Bill is certainly one of the most impressive people in population and quantitative genetics that I have known – and I have been well acquainted with many of the leaders of the field. I don't think I need to rattle off his numerous achievements, but I feel he is almost unique in having made fundamental contributions to theory in both population and quantitative genetics, as well as being deeply involved in practical applications to animal breeding (I don't know much about the latter, of course). Deborah and I remember staying a night on a dairy farm in Lancashire on our way up to Edinburgh on a pre-move visit, and the farmer had actually heard Bill talk at a meeting for breeders.

Alan Robertson is the only comparable person with this breadth of work, I think. Bill's early work on randomly generated linkage disequilibrium and selective interference has stood the test of time: not many scientists are still heavily cited for their PhD work 50 years later. He has also trained an outstanding group of PhD students and postdocs, including at least 2 FRSs. He is enormously respected by his peers. I remember John Maynard Smith in 1974 saying about a review of his famous hitchhiking paper that it must have been written by Alan or Bill, as they were the only two people in the country bright enough to understand it.

Bill is an extremely nice person, who is unduly modest about his own achievements (I had difficulty in getting him to let me nominate him for the Darwin Medal of the RS). I share his rather cynical views about human affairs (Rosemary once told me that I was the only person she'd met who was more cynical than Bill, but she may have overlooked Deborah), although we are at opposite ends of the political spectrum (I have the impression that he has moved a bit leftwards as result of Brexit, though). One of my favourite sayings of Bill's, after hearing an unsatisfactory seminar or reading a dodgy paper, is: *what is the question to which this is the answer?*

Until his recent decline, he was always able to ask pertinent, and sometimes devastating, questions at seminars and journal clubs, often after having apparently slept through much of the talks. He also gave excellent journal club presentations himself, avoiding too much detail and getting to the core of the topic. I remember one journal club presentation by him in which he pointed out a fatal statistical flaw in a *Nature* paper, which subsequently resulted in what amounted to a retraction.

Finally, Bill has been willing to act unselfishly as a good citizen, providing a lot of administrative service to the University, as an editor of journals (including *Proceedings B*), and of course as a consultant to the animal breeding industry. Remarkably, after serving as Dean of the Faculty of Science and Engineering and then taking early retirement (I think at 62), his research career really flourished again, with numerous important papers and a lot of collaborative work.

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Gene Eisen

Thank you for sending the note that Bill Hill has received the 2019 Genetics Society Medal. I was saddened to learn of his illness. I have always been a keen admirer of Bill's ability to zero in on a complex problem in quantitative genetics and then to come up with a, sometimes not so simple, solution. Bill and I never have collaborated, but we have remained good friends since he spent a sabbatical in Raleigh and I in Edinburgh.

Peter Visscher

My long-standing interaction with Bill starts in 1987, when I was enrolled in the MSc course in Animal Breeding (& where you gave the very first lecture that year!). I subsequently stayed for a PhD, supervised by Bill and by Robin Thompson. Bill has been a mentor to me ever since and we have only disagreed on one thing of importance, and that was when I decided to leave UoE and move to Australia in 2005. Bill didn't see the logic in that and he tried to persuade me to stay in Edinburgh. He later admitted that he was wrong, which was nice and typically Bill ("if the facts change then one can change one's opinion").

In the field of human genetics (and elsewhere), one of the major impacts of Bill's research has been the adoption of the correlation (r^2) measure of linkage disequilibrium, first proposed in Hill and Robertson 1968. It is of particular importance in genome-wide association studies, since the power of GWAS is proportional to the r^2 correlation between genotyped SNPs and unknown causal variants.

I have collaborated with Bill on a number of occasions since leaving Edinburgh. The most important paper from those collaborations is Hill et al. 2008 (PLOS Genetics), about the proportion of additive vs non-additive genetic variance.

For my own research, a brief communications paper by Bill in J Hered was influential (Hill WG 1993, Variation in Genetic Composition in Backcrossing Programs. Journal of Heredity). It is vintage Bill: apparently a horse breeder asked him the question about backcrossing and confidence in the actual proportion of 'pure' stock after multiple generations of backcrossing. Bill did the sums and provided the answers. So a nice bit of theory from a real practical question about upgrading animals via backcrossing. The theory is quite general and can also be used to quantify variation in realised relationships for pedigree relationships in outbred populations, and is relevant to the estimation of genetic variation using realised relationships. Bill later expanded the theory with Bruce (Weir) into a very nice and general paper (Hill & Weir 2011. Variation in actual relationship as a consequence of Mendelian sampling and linkage. Genetics Research).

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Peter Keightley

One thing I remember very well from doing my PhD with Bill was that he would come into the office pretty much every morning before the coffee break and ask the same question "What have you discovered?". This was not because he expected anyone to actually discover something every day, instead I think it was a nice way of opening the conversation about where we were with the project. He took an incredibly keen interest, but I never felt that it was too much and he was happy for me to go my own way.

I have a 15 min contributed talk at the meeting, and am planning to talk about inferring the distribution of effects of mutations for fitness and other quantitative traits. I intend to mention that Bill and Alan R. thought this was important, and briefly describe why. Over the years, I have worked a lot in this area and all of it was ultimately inspired by Bill.

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John Sved

Bill Hill, my guru.

I have been mostly a long distance collaborator of Bill's, and this account is limited to personal recollection of this part of his story. I first met Bill 50 years ago, not long after publication of the Hill and Robertson 1968 paper "Linkage disequilibrium in finite populations". I had stumbled across something similar, and so we had a lot to discuss. Bill was of course a master of population and quantitative genetics, whereas I had little background in quantitative genetics and hadn't even decided at the time whether I was trying to be a 'population geneticist'. So communication must have been difficult for him. Despite this, over the years he has been extremely supportive. After an initial foray, I published nothing on linkage disequilibrium for around 30 years, and would not have been able to get back into the field without his encouragement.

In one sense, the importance of his 1968 paper was the recognition that linkage disequilibrium had to be ubiquitous rather than rare. Last year I was privileged to co-write a Genetics Perspectives paper with Bill entitled "One hundred years of linkage disequilibrium", based on the coincidence of the initial description of the LD parameter by Robbins being in 1918. We had some discussion about calling the paper "Fifty years of linkage equilibrium and fifty years of linkage disequilibrium". But what really changed around the 1968 period was not so much the theory as the recognition by Lewontin, Hubby and Harris of how much closely linked polymorphism there must be. Under these circumstances, the idea of ubiquitous linkage equilibrium between closely linked loci in a finite population was clearly not possible. Bill once told me that he hesitated to write a paper making such an obvious point. The journal in which the paper was published, Theoretical and Applied Genetics, while a respectable journal, presumably does not have many papers with hundreds of citations.

The more lasting legacy from the paper was Bill's introduction of r^2 as a measure of linkage disequilibrium. He and Alan also suggested $1/4Nc$ as an approximate expectation for r^2 , a function of population size N and recombination frequency c . My contribution somewhat later was to add a 1 to the denominator. This used an obscure argument that essentially equates probability and frequency approaches. For a single locus, there is a clear relationship between the inbreeding as described using the correlation of frequencies and the probability of identity by descent. Bill and I tried to describe the two locus correlation in a similar way but ultimately were not able to come up with a rigorous approach.

I know from discussions with others how much broader Bill's influence has been. He managed this despite his time as Head of School, which obviously generated huge amounts of work. During a visit to Edinburgh during this period, I once tried to leave him some calculations for comment, and was bemoaning to a colleague about not hearing from him. He commented "You don't leave Bill such things on his desk, you leave it on his chair".

It is very pleasing to hear about the award of the Mendel Medal. I trust that the occasion will be a memorable one.

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Naomi Wray

I first met Bill on a farm field trip when I was an agriculture undergrad student. He explained to me the difference between “contemporary comparison” and “improved contemporary comparison”, I learned that day to say “can you say that again”, a phrase I have needed to use many times with Bill to understand all the nuance of the conversation!

Bill was my PhD supervisor 1986-89 and a mentor for many years to follow. With Bill as a PhD student I worked on prediction of responses to selection, and we have collaborated on a couple of papers more recently, where Bill’s depth of understanding of quantitative genetics was a critical crutch for me. Bill has been an incredible role model for mentorship. As a PhD supervisor Bill he came to check up on me every day without fail, I know I fall short of that role model.

A couple of snippets of advice have stuck with me.

“Use simulation to check theory...and indeed theory to check simulations, one without the other is unsatisfactory.”

“Each day work on the thing that is of most interest to you.” - I don’t manage to live up to that advice, but sometimes when I have a full to-do list of things needed by other people, I feel it is OK to focus on the thing I most want to do.

On the other hand, there is one piece of advice I have rejected! Bill advised to provide the first equation and the last equation and allow the reader to fill in the gaps. I have realised there are more people in the world like me, than like Bill (!), so I advise my mentees to provide all the steps along the way!

I might be able to find some old photos?

Raphael Mrode

I undertook my PHD studies under Bill as my supervisor.

He was very instrumental in the publication my first edition of my book on ‘Linear models for the prediction of Animal Breeding values’ and subsequent versions. He thoroughly went through the manuscript offering suggestions that completely transformed the outline of the book.

Over the past 30 years he has been a member of the Technical Committee that have guided and directed the Genetic Evaluation activities in the UK for dairy and beef cattle and sheep.

His valuable insights and keen eye for details has ensured the UK genetic evaluation systems keep abreast of advances in evaluation methodology while being very relevant for farmers.

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Karin Meyer

Bill Hill's contributions to quantitative genetics are enormous, spanning a great breadth from theoretical developments to the implementation of livestock improvement programmes.

A specific area of Bill's interest has been the estimation of genetic parameters. For instance, he made geneticist aware of the need for covariance matrices to be positive definite and the effects of sampling errors on response to selection on indices. Moreover, while he tended to stay clear of the computational side, he championed the uptake of maximum likelihood based estimation fitting linear mixed models. Edinburgh has been at the forefront of making REML the standard method for variance component estimation in quantitative genetics -- no doubt to a substantial extent due to Bill's involvement.

Bill is known for his unfailing dedication and rigorous approach to science. In addition to his own seminal contributions, he has had a profound impact through his numerous postgraduate students. Bill has had the uncanny knack of pushing his students to realms of genetics and statistics they would have never imagined or reached otherwise. In addition, his utmost interest in and emphasis on scientific papers instilled sound publication habits. Truly invaluable gifts which shaped the careers of many of us.

Bruce Weir

For over 30 years Bill and I spent at least a week each year working together: in Edinburgh, or Raleigh or Seattle. Over the years we developed a routine: we would each arrive at the other's airport with a bottle of duty-free scotch and some half-formed ideas about our next project. The first night we would crack the scotch and catch up on the family news. Then we would spend the week at work, often going home to Rosemary or Beth to moan about our lack of progress. We often managed to indulge our common interest in theatre, especially on those occasions when Beth or Rosemary made the transatlantic trip. Personal highlights in the early years were year-long sabbaticals for the whole Hill or Weir family in Raleigh or Edinburgh. Once the children had grown, we were able to explore new places together: Orkney one year and Alaska another.

In spite of our moaning, we did on occasion make some progress, bookended by "Effect of mating structure on variation in linkage disequilibrium" in 1980, and "Variation in actual relationship among descendants of inbred individuals" in 2012. Maybe not a great deal of variation in topic, but always immensely satisfying. Bill's deep intuition is well-known. Coupled with his superb computing and algebra skills, and long nights of hard work, some good papers came from our weeks together. A couple of them have even been well cited. I'm very proud of our work, but much prouder of a long period of friendship and collaboration with the leader of our field.

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Lutz Bungler

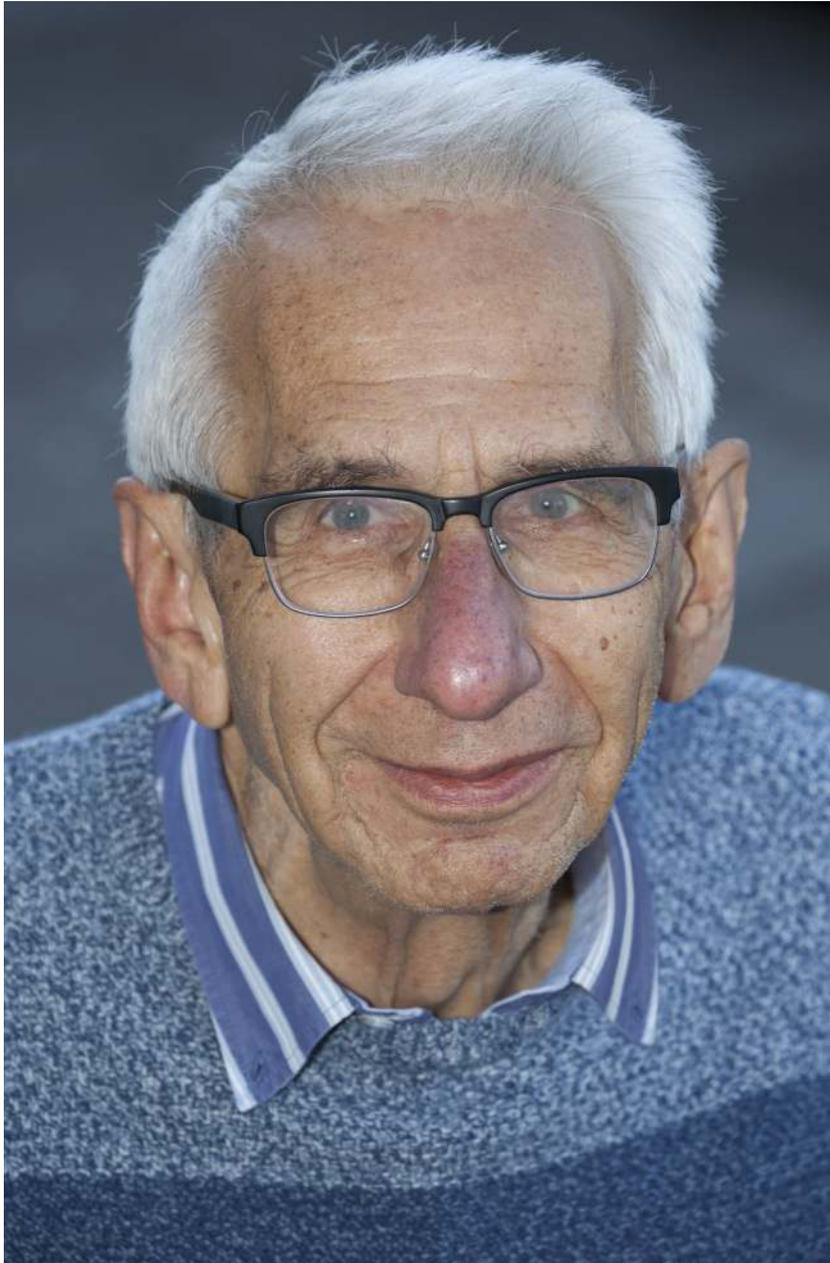
Lutz' story with Bill started actually in 1990; the wall came down in Nov 1989 and Lutz was afterwards able to attend his first WCGALP, organised by Bill and his team in Edinburgh; it was meanwhile the 8th WCGALP. He submitted his abstracts on the Dummerstorf long-term selected mouse lines, which he had printed using the only available printer at that time in his department, a needle printer (the older among you might remember these printers and their horrible print quality). Bill received the submitted abstracts and asked quickly his secretary (Anne Johnson) to retype them and to produce a decent looking print for the proceedings and subsequently Lutz' contributions were accepted. Two years later (1992) Lutz came with a German Grant again to Edinburgh for a few months to work with Bill and others.

At New Year's Eve 1993 (just the beginning of 1994) Bill sent Lutz a fax (some might remember that thing before emails kicked in), in which Bill offered Lutz the job of Ian Hasting who was about to leave the mice and turn to a Malaria project at the time. Lutz was impressed to have been asked and thought not for very long about it; to work with people like Hill, Falconer, Caballero, Roberts, Keightley and others made his knees trembling. The contract initially was for 3 years, which turned finally into over 25 years and if it were not Bill Lutz would not have come to Edinburgh and certainly he would/could not stay on "for good" and Lutz is very, very grateful.

Immediately after the 9th WCGALP in Guelph (1994) Lutz started his job as "ruler" of all Edinburgh and later all available international mouse selection lines".

It was mainly Bill who got substantial funding secured to enable also this mouse research and the construction of the Ann Walker building, the "New Mouse House" and possibly the only building on KB campus named after a technician. Anyhow, it took us a couple of years to transfer all mouse lines from the old to the new mouse house by embryo transfer; the special challenge was to produce scientific results simultaneously. This required long working hours: from 9.00 am till 9.00 pm, also on weekends was the norm for a long time. One of the stories Lutz contributed is the "Fat mice & Leptin" story, which goes like this: In 1994, Friedman's laboratory reported the identification of the ob-gene. Two years later Amgen who had acquired an exclusive licence from the Rockefeller University to develop and market products based on the discovery of the ob gene, started first leptin trials in humans. This was the test of a possible "wonder weapon" against the world-wide obesity epidemic. Reading the Friedman paper from 1994 we got the idea to test our "polygenic" mouse model, developed by long-term selection for its sensitivity to leptin, asking, is there a major gene/system involved in the fatness of our fat or lean line mice. After Bill corrected my draft letter to Amgen mainly for Grammar and English politeness (I was just one year in the UK), I sent it off to Amgen and received soon an invitation to visit them in Thousand Oaks and subsequently very soon the first ampullas with leptin, probably worth their weight in Gold at the time. Wow! Ready to go. Soon we were able to publish the natural leptin levels and the results of the sensitivity study. Today it's not so much about those results it's about Bill's involvement in this and other mouse work. By the way, 50 of his nearly 330 publications were "mouse papers". We are probably not too wrong to say, Bill has in all these years not seen much of any mouse house from inside or handled any mice himself, BUT this does not mean he was not interested or not influential. You bet he was!!! Lutz started the days of the leptin experiment with injecting and weighing mice from the fat and lean line very early in the morning and again late in the evening and this for 14 days, and guess who was in the door every morning and evening: Bill!!!! "What's new?!", was one of his standard questions. So, Lutz opened the freshly updated Excel sheet showing the weights over treatment time, and then they discussed what's going on, and what does it mean. I think one needs to mention that Bill probably "wasted" some of his best years in administration to the benefit of ICAPB and later the faculty/ school, but at the cost of science, he could have done at that time. Our Leptin experiment was in that period of time, so Bill did several marathons a week, running with large steps over the campus from meeting to meeting and to the ICAPB, to us, to ask "What's new?!", and this question was not rhetoric, it helped to continually push the boundaries. The other famous Bill question was "What's next?!", usually asked when a publication has been submitted. There was no way Bill would allow us "to rest on your laurels". Bill always believes that yesterday's success is like water under the bridge, but we think some stones put in by Bill stay forever like his milestone papers.

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Armando Caballero

I want to express in these lines my deep gratitude to Bill. He has been the person who taught me how science should be done based on quality and effort. I was very lucky to share with Bill numerous papers during my postdoc stay in Edinburgh in the 90s, when we developed many theoretical works on the prediction of effective population size, the estimation of mutational parameters and the response to artificial selection. Bill is the person I have met with the greatest scientific capacity and an example of human quality in personal treatment. He always made a pleasant working environment for his collaborators and students, and that is one of the most important things I learned from him. In these sad moments of his illness, the best way to honour him is to transmit his way of carrying out science and his human quality to our own students. I try to do so every day.

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Daniel Gianola

My first encounter with the name W. G. Hill was as a Ph.D. student, in 1973. Bill had published a series of papers in Biometrics on the estimation of realized heritability from experimental data. My major professor, Arthur B. Chapman had asked me to present this paper in a seminar. I did it, but then spent more than two years trying to understand and derive many of the formulae. It was not until mixed linear models surfaced that some of Bill's results made entire sense to me. Needless to say, I realized right away that he was intellectually formidable.

I met him personally in 1976 (First International Conference on Quantitative Genetics, Ames Iowa). I produced a bottle of scotch whisky (not a part of the Ames menu) and we had a good chat. Then, I saw him again in a livestock breeding conference in Madrid in 1982; his comments--together with those of Alan Robertson--electrified the audience, so we had additional chats, this time with Jamon pata negra and wine. A few months later, I visited Edinburgh in 1982 and gave a somewhat cryptic seminar, although Bill had nice things to say. He then took me to Alan Robertson's coffee hour (Falconer, Charlie Smith, Eric Reeve and Crad Roberts were there), where I was almost crucified by Alan Robertson when I attempted to explain BLUP in a blackboard containing some of Alan's *Drosophila* data, which I almost erased.

Subsequently, we corresponded frequently, and our friendship was reaffirmed when I learned that Bill had been the Ph.D. advisor of one of my best friends, Daniel Sorensen, who added views on "life with Bill from a student's perspective" to my knowledge.

In 1998, Bill invited Graciela (my wife) and I to spend a Summer (July in Scotland, wearing wool pull-overs in the Kings Buildings) in Edinburgh. Prior to moving to an apartment in Canongate, we stayed for a couple of days at his home in 4 Gordon Terrace. Laurie and Priscilla Piper (Australia) were also there on sabbatical, and we would go to pubs for pints with Bill and Rosemary. Bill was a Dean at that time, but made time for us, was a great and generous host, and allowed me to work in his office. I still have not published what I did during that Summer (BLUP of genetic value when a population is undergoing stabilizing selection), but I have retaken the subject from a genomics perspective.

My only paper with Bill as a co-author was published in *Genetics* (2009, "Additive genetic variability and the Bayesian alphabet"). Even though he agreed with the content, I was unable to make him a Bayesian. Now that I am (a bit) less fanatic about Bayesianism--Bill's views contributed to making me more moderate--everybody is doing it. He was also not very fond of the machine learning and neural network methodology I was developing because...there was no "breeding value". I was never able to convince him that the theory of quantitative genetics was useless to understand "genetic architecture", but that it is extremely effective for generating useful prediction machines. Time will tell, but I would not be surprised if Bill is right, as usual.

Bill is a brilliant scientist, an intellectual leader and a repository of common sense. His work, invariably rigorous, has had an important element of intuition. He could see quite clearly whether a theoretical result would make sense or not. Daniel Sorensen told me once that when he was a student, he gave Bill about twenty pages of algebra on some matter related to linkage disequilibrium. Bill examined the first page of the development, then moved to the last and concluded: "This is wrong, Daniel". Daniel replied "Why? How can you say that without reading my work carefully?". Bill replied "I feel it in my bones". Of course, he was right.

My main source of disagreement with Bill has been on football matters. Being an Uruguayan, I conveniently defended Luis Suarez's habit of biting rivals. Bill, being a gentleman, declared that Suarez was a ruffian, conveniently ignoring that Uruguay defeated England 2-1 in the 2014 World Cup, with Suarez scoring at minutes 39 and 85 of the game.

It is very fitting that William G. Hill is receiving the Mendel Medal in recognition of his formidable contributions to quantitative genetics, animal breeding, and science in general.

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Geoff Simm

I first met Bill in the early 1980s, when I was studying for a PhD at the University and the Animal Breeding Research Organisation (ABRO, later part of the Roslin Institute) on beef cattle breeding. My supervisor, Charlie Smith, encouraged me to attend the MSc in animal breeding in my first year. Most of the class struggled at times with the pace and complexity of Bill's lectures – sometimes not helped by the fact that he delivered them from a yoga-like position, behind curled limbs. I was elected class spokesperson to ask him regularly to slow down and repeat parts. So lectures often involved me doing that and him asking 'does anyone else apart from Geoff Simm not understand this', followed by complete silence from the class! This has scarred me for life! (PS Trudy – your lectures were great – we understood you!!)

On completing my PhD, I moved to the East of Scotland College of Agriculture (ESCA; later part of the Scottish Agricultural College (SAC), and now Scotland's Rural College (SRUC)). In ESCA, I assumed responsibility for the Langhill Dairy Cattle Breeding Project, initiated in the 1970s by ESCA, the University of Edinburgh and ABRO, and a newer selection project in Suffolk sheep. Over the next 15 years or so, Bill provided regular advice to me and a growing number of colleagues working on these and related projects - spanning biological and economic impact of selection, development of broader breeding goals and selection criteria addressing health, welfare and sustainability, and breeding programme design – and we jointly supervised many great MSc and PhD students, many now leaders in their fields.

It is notable that genetics in Edinburgh, under Bill's leadership and Alan Robertson's before him, has involved a two-way street between theory and practice. Both had farming interests and were passionate about application of science in livestock breeding – which has been to the great benefit of breeders and breeding organisations here & abroad. The challenges in application have often stimulated developments in theory. Bill has been very active in supporting what is now Holstein UK, Aviagen and pig breeding companies. (Trudy – if they are not already on your list, Mike Coffey (mike.coffey@sruc.ac.uk) could provide more on Bill's input to the Holstein UK, and Santiago Avendano on Aviagen (SAvendano@aviagen.com))

Around the turn of the millennium, UK levy bodies began to consider outsourcing livestock genetic evaluations. Many of us including Bill and colleagues in the University, Robin Thompson and Mike Coffey who had recently joined SAC, felt this was a threat to the 'route to market' for much local breeding research. So, we mounted a bid to create a research-led, UK-based evaluation service, which ultimately became EGENES, led by Mike Coffey. This continues to support the rapid uptake of new evaluation methods, breeding technologies and innovative use of data among users in the UK livestock breeding sector.

Lots of us in Edinburgh had fun (and much stress) organizing the 4th World Congress on Genetics Applied to Livestock production here in 1990, under his leadership – he made me responsible for the unusual combination of transport, press and toilet arrangements. Being in charge of 10 double decker buses remains the pinnacle of my career. I'll pass on the toilets next time...

Bill has been the principal flag bearer of Edinburgh's longstanding international reputation in genetics for over 30 years. Despite this he has always given very generously of his time, experience and considerable intellect to students and colleagues – something that is hugely appreciated by both groups! He wears his brilliance lightly, likes people (most of them anyway!) and sees the humorous side of many situations.

Rosemary and Bill have been fantastic hosts to generations of students and visiting scientists coming to Edinburgh.

It is a great honour to call Bill a colleague and friend and a delight to see him honoured in this way!

Professor William G. Hill, Mendel Medal 2019

Comments from Colleagues



Asko Mäki-Tanila, University of Helsinki

We all know Alan Robertson's 11 o'clock coffee sessions from old Genetics building. One morning the discussion rolled around finding new methods to old problems in quantitative genetics. Bill turned the floor upside down. 'When I see a new mathematical or statistical tool, it immediately strikes me where I could exploit it.' Probably a good example on this are the papers by Bill on order statistics in mid-1970s (*Biometrics* 32, 889-890 and 33, 703-712). A very practical implication from that work is the co-selection of relatives without own records. Bill is known for linkage disequilibrium. He took the area to extreme complexities dealing with concepts for several loci (*Theor Pop Biol* 5, 366-392 & 6, 184-198). Who knows, they may be useful one day.

In working with Bill, one never hits a wall. Either from his toolbox or in rare occasions from his bookshelf comes up a trick to go on. In these occasions, I have been encouraging him to write a manual revealing the contents of his plumber's toolbox. His obvious favourite is Taylor series. A beautiful example is the conclusion on the robustness of selection index to incorrect parameter values in the much quoted Sales & Hill paper (*Anim Prod* 22, 1-17). He can teach half quant genetics course around it – average effect, dominance deviation, variances, standard errors etc. Including the very general conclusion that most of the variation can be explain linear part. Again in the middle of discussion, with much sharpening of your ears you think you hear a phrase resembling words Heavy Going Vehicle. An explanation follows – HGV. Where are we? Hill, Goddard, Visscher 2008 Data and theory point to mainly additive genetic variance for complex traits. *PLoS Genetics* 4, e1000008.

If I were asked to name a single best paper by Bill, I can't do it. There are half a dozen of them.

I finish this by an extract from the preface Walsh & Lynch 2018: 'We especially want to acknowledge Bill Hill, who has been a major force throughout this process, and in many could be considered its third author.' This could be corrected for the 2nd edition of the book.