**The need for food: the history of the Animal Breeding Research Organisation, before Dolly.**

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ABSTRACT

The Animal Breeding Research Organisation (ABRO) was formed as a result of the recommendations of a joint Committee of the Agricultural Improvement Council and the Agricultural Research Council, set up in 1943, to consider the directions which research in animal genetics and breeding in Great Britain should take to advance scientific knowledge and assist animal production in the farming industry.

The organisation was formally started in 1945 with the appointment of a director and a chief geneticist, but did not begin to appoint other staff and to acquire experimental facilities until 1947 and onwards, when headquarters were set up in Edinburgh

This article places ABRO in its historical and scientific context and proceeds to chart its development over the years. Difficulties of acquiring experimental facilities are explained, but emphasis is placed on the projects that were undertaken, many of a long-term nature, the reasons for them, the problems that arose and the outcomes, many of which continue to be relevant to animal science and production now. The cloning that produced Dolly the sheep came after ABRO had been merged into the Roslin Institute, but the team involved derived from ABRO days. \_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_\_

This article is about an organisation that achieved world-wide recognition and renown but no longer exists in its original form having been merged into The Roslin Institute, now part of the University of Edinburgh. The organisation’s aim was to provide information, through research, that would be useful to farmers to improve their livestock in both current and future years. Improvement will mean different things to different people, but, as the organisation was conceived in wartime, with strict rationing of food, it seems certain that the future need for food was an important motivation. However, whatever the ultimate aim of improvement, the process will involve making use of genetic differences that may exist among the animals. This may involve selection of “the best” or crossbreeding. Something along these lines is likely to have existed from the time that mankind started to domesticate animals for use in transport or for meat, milk, wool or other animal products.

Scientific research normally progresses by small steps and technical advances open up new horizons. Occasionally there are big leaps forward. Much of the work of the Animal Breeding Research Organisation (ABRO) is still highly relevant today, but some of it has been overtaken by new techniques of assessing genetic merit (some of these arising directly from ABRO studies).

To improve productivity or efficiency in animal production by changing hereditary factors requires genetic variation to exist for the characteristics breeders may want to improve – be it lean meat production, more milk, increased prolificacy or disease resistance, to pick just some examples. The task of ABRO was to explore, by experimentation, the existence of genetic variation and how best to utilise it. The arrival of molecular genetics provided a whole new methodology for exploring genetic variation and for ABRO, in the 1980s, an additional direction for research.

The politics of that move in direction and the eventual outcome were dealt with by Myelnikov1 covering the last few years of ABRO’s independent existence. The present article concentrates on the scientific achievement in ABRO.

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It is appropriate to start with a direct quote from a report submitted to the Agricultural Research Council (but otherwise unpublished) by the late Professor R.G. White2 who was the first director of the Animal Breeding and Genetics Research Organisation (ABGRO) - as it was called in its early days.

“In the summer of 1943, a joint Committee of the Agricultural Improvement Council and the Agricultural Research Council appointed a small group with the following terms of reference: ‘To consider the directions which research in animal genetics and breeding in Great Britain as a whole should take in relation to: a. The advancement of general scientific knowledge of this subject which is still at an early stage of development; b. The major problems of the Industry.”

The Group recommended that a new research Organisation be established at an annual running cost estimated at £25,000 (equivalent to more than one £ 1million in today’s money).

The context, in the midst of the Second World War, with food shortages and food rationing, was to anticipate a time post-war when animal production would need to contribute more effectively and efficiently to the feeding and health of the Nation.

In the course of its deliberations the Group sought evidence from breeders, livestock officers and research workers (not named in Prof. White’s report). Five major problems were said to confront the industry and are quoted here from the report:

1. “The possibility of obtaining a greater degree of genetical homogeneity in agricultural stocks.
2. The inheritance of productivity and the fuller exploitation of data derived from performance and progeny tests.
3. The significance and value of crossbred, outbred and inbred stocks.
4. The inheritance of vigour and freedom from disease.
5. The relationship of genetical to environmental factors.”

The final report of the Group was submitted to the two Councils in the autumn of 1944 and they agreed to the recommendation that a new National Institute should be established to address these issues.

Professor R. G. White, himself a member of the Group and Professor of Agriculture at University College, Bangor, North Wales, was invited to become director of the new institute, named initially the ‘National Animal Breeding and Genetics Research Organisation (NABGRO). C.H. Waddington was invited and accepted the post of Chief Geneticist. Jumping ahead for a moment, it is amusing in retrospect to learn that when the headquarters of the organisation was set up in Edinburgh, the word ‘National’ was dropped from the title lest it were thought to be a Scottish organisation instead of a UK-wide one.

Professor White was a gentleman of the old school to the core. He was ever courteous and addressed his staff by their surname without any prefix. Christian names were not in his fashion – at least not in public.

White was experienced in agriculture and animal production but was not an animal geneticist. He accepted his appointment subject to being allowed to visit the USA and Canada where work in this field was ahead of that in the UK. He wanted to obtain ideas for potential experimentation in ABGRO.

Waddington meantime recruited a number of research workers, who, like himself, had been engaged in operational research during the war. He brought this group together in a laboratory in Hendon (London). Many of those in this group became well-known as geneticists in later years, some of them renowned.

**The place of the new Organisation in the historical context and that of its time**

Domestication of animals was started by hunter-gatherers thousands of years ago, but not all animals were suitable for domestication. They had to be tameable, provide products of direct use for man and not compete with man for food; basically, they needed to be grazing animals3. In a sense, this was the start of “animal breeding” – a term vague by itself. It could imply merely a decision by man to reproduce his animals. But, when people started to choose among animals which to reproduce and which not, it implied that livestock could be “improved” or changed for whatever purpose was thought important at the time. It is as a means of livestock improvement that the phrase “animal breeding” is used here and in the title of ABRO.

The pre-requisite for selection is the presence of variation in a characteristic of concern. The concept of genetic variation is readily understood by thinking about domestic dogs in comparison with domestic cats as species. In the dog, there is a huge variety of breeds differing greatly from each other. It indicates large genetic variation in the species. Though there are many breeds of domestic cat, the over-riding impression is the degree of similarity among them, indicating rather less genetic variation in that species.

Horses were probably the first species to be domesticated by humans. Their history stretches back over millennia from the Eurasian steppes through Bedouins, Egyptians and Romans to the present day. Horses are depicted in cave paintings and have been used for food and transport, in agriculture and in war, leading to the great number of breeds for the many different purposes. There are countless books on horses and most agree that the domestication started about six thousand years ago. Genetic selection and crossbreeding have led to the development of the diverse breeds.

Another mammalian species that displays the ingenuity of man in creating variety is the dog, as referred to earlier. All this happened without knowledge of the causes of genetic variation, or indeed a need for that knowledge.

Reliance on ingenuity and the ideas of individual breeders alone began to seem inadequate after the discovery of the basis of inherited differences. That must have been in the minds of those who mooted the establishment of an animal breeding and genetics research organisation – knowledge of the basis of inheritance would open new opportunities for the direction of livestock improvement.

Nonetheless, for domestic livestock, cattle and sheep in particular, there was an important period before this.

Thus, Lerner and Donald, 19664 provide a short but useful account of the historical background to livestock breeding practices before the time of the pioneer livestock improver Robert Bakewell (1725-1795). “From Aristotle onwards” they note “animal husbandmen have never been at a loss for theories on breeding.” Further, they quote G.L.L de Buffon who advocated systematic crossbreeding, and A.P. de Candolle, a botanist, who, in relation to animals, thought that some parts of the body were controlled by the dam and others by the sire.

Robert Bakewell of Dishley’s methods laid the foundations for all subsequent livestock breeding. He used selection and inbreeding as two of his tools, but did not reject crossbreeding when he found stock elsewhere to suit his purpose. His most talked-about achievement was the New Leicester breed of sheep which is prized to this day in its successor, the Border Leicester. The breed’s merits were earlier maturity and greater fleshiness, but for detractors its defect was an excess of fat. Most of his selection was based on eye judgement. Later refinements after Bakewell’s time would result in performance and progeny testing. Discovering further advances was one of tasks for ABRO.

A full account of the life and work of Bakewell was provided by Wykes5. It is said that Bakewell’s use of “artificial selection” (as it came to be called) inspired Charles Darwin to formulate his concept of Natural Selection as published in his famous work “on the Origin of Species by means of Natural Selection”6. The other great figure of nineteenth century genetics was Gregor Mendel whose studies with peas set the scene for the acceptance of particulate inheritance, i.e. the existence of genes as units for the inheritance of traits. His theory was little known in his own day but “re-discovered” at the start of the twentieth century. A book by Orel7 is regarded as a definitive biography of Mendel and his work. A later paper8  provides evidence of breeding practices in Central Europe, organised around the city of Brno, which highlighted the processes of heredity without, however, providing a satisfactory explanation for the process whereby change occurred. That is said to have given Mendel, when he came to Brno, a background for his experimentation and his ultimate conclusions on the workings of heredity.

One of the most lucid accounts of the history of animal breeding through to its application in modern times is given in the opening chapter of a textbook for students written by authors from the renowned Centre for Genetics and Breeding at Wageningen University in the Netherlands9. Although a very condensed exposition, it is well worth the effort of reading it, most particularly for non-specialists.

*The scientific environment into which ABRO was launched.*

In 1946 Edinburgh University made the smart move to appoint Waddington to the chair of animal genetics in Edinburgh vacated by F.A.E. Crew. As a result, Waddington brought his group of scientists from Hendon to join the University staff already at the Institute of Animal Genetics, situated at Kings Buildings, the science campus of the University. As a consequence, White chose Edinburgh as the headquarters for the new Organisation, against competition from Oxford. He set up his headquarters in the spring of 1947 in a large villa, “Glenbourne”, in South Oswald Road, about a mile from Kings Buildings.

The new Organisation entered an environment in Edinburgh with a long history of animal breeding and genetics. As described by Clare Button10 that history goes back to James Cossar Ewart, Professor of Natural History at Edinburgh from 1882 to 1927. He was succeeded by F.A.E. Crew under whose stewardship the Institute of Animal Genetics was established.

In the 1930’s and 40’s in Cambridge, at the Agricultural Research farm in Huntingdon Road, Micheal Pease conducted perhaps the last of the Mendelian-style projects to produce ‘auto-sexing’ breeds of poultry. The aim, which was achieved, allowed day-old chicks to be identified as either male or female from differences in the colour of their down. The breeds did not, however, attain commercial success and sexing of chicks remained the preserve of experts trained in methods developed in Japan.

 Of great importance for research in animal breeding and genetics is the ability to analyse the large amount of data derived from experiments usually involving a multitude of interacting factors. This analysis often requires complex statistical methods. It was fortunate, therefore, that many of these methods had been developed by R.A. Fisher in Cambridge including the all-important “analysis of variance” which allows the significance of the results (the degree to which the results are not due to chance) to be determined. Fisher alongside Sewall Wright in the USA and J.B.S. Haldane in the UK also developed the concept of population genetics which is important for the design of breeding plans. Fisher with Frank Yates (from Rothamsted Experiment Station) also published Statistical Tables for use in applying significance tests. David Finney set up an ARC Unit of Statistics, first located in Aberdeen and later moved to Edinburgh. All of this was to be important for ABGRO.

In the sphere of animal production, vocal advocates for genetic improvement were Professor Cooper at Newcastle and Professor Boutflour at the Royal Agricultural College at Cirencester. Later, former students of animal genetics at Edinburgh: John Bowman at Reading and Maurice Bichard at Newcastle became prominent advocates.

Special mention must be made of the role of John Hammond in Cambridge for creating an “atmosphere” conducive to livestock improvement, an atmosphere into which ABGRO was launched. Much of Hammond’s own significant research was related to the use of artificial insemination. But, he was also fond of dramatic “demonstrations” most obvious in his reciprocal cross of the very large Shire horse with the ultra-small Shetland pony. It demonstrated the large impact of the maternal environment on the foal. Of more immediate consequence for genetic selection were developments by Hammond’s colleagues Rowson and Polge in semen storage and delivery. These made possible the widespread use of artificial insemination, particularly for cattle.

AI centres were set up by the Milk Marketing Board (MMB) and at several independent centres. It revolutionised cattle breeding (dairy cattle in particular) by moving the system away from reliance on pedigree to greater reliance on performance and progeny test. A team within the MMB led by Joe Edwards provided much of the scientific input for that, but with some involvement from ABRO. Similarly, on the meat side of things the establishment of the Meat and Livestock Commission in 1966, whilst mostly concerned with marketing, provided advice on genetic improvement to farmers with help from ABRO.

Mention must be made of scientific societies that allowed the presentation of results of experimentation to a wider audience and fostered the exchange of ideas.

The British Society of Animal Production (later: British Society of Animal Science), started in 1944, became an annual conference event for many ABRO staff. ABRO staff had a particularly close relationship with the Society. Hugh Donald, director of ABRO served as one of BSAP’s presidents. Joe Read, another of ABRO’s staff was the Society’s treasurer for many years. I was the founding editor of its successful journal, *Animal Production* (later *Animal Science)*, that grew out of the Society’s former Proceedings. I remained in that role for many years and was joined, as editors, by distinguished scientists from various disciplines. For a while I was chairman of BSAP’s Publications committee. A number of those from ABRO who had served the Society, including me, were elected honorary members of BSAP/BSAS.

 The Cattle Breeders club and three so-called “Round Tables” one each for Poultry, Pigs and Sheep, gave ABRO staff opportunities to disseminate and receive ideas. Also popular was attendance at international conferences some of which were organised around species and others around discipline. All these events were appreciated by those attending for the informal opportunities to exchange knowledge, experience and emerging issues, as well as for the sumptuous conference dinner expected from the host country. However, funding for these events was limited and often had to be sought from outside sources.

*The role of the Agricultural Research Council*

Finally, the role of the Agricultural Research Council in monitoring the research programme of ABRO has to be recognized. A broad outline for the type of research to be undertaken, arising from the group that recommended the establishment of ABRO, was given above. Thereafter, ABRO, like all Institutes funded by the ARC, was subject to a review every four to five years by what was called a “Visiting Group”. That group appointed by the ARC, comprised distinguished animal geneticists and biologists (both theoretical and practical), representatives from Farming bodies (e.g. the Milk Marketing Board) at least one distinguished farmer and some administrators. The composition of the group might change, in part, from one visit to the next, but not necessarily so. As animal breeding experiments rely heavily on statistical treatment, some visiting groups included an expert in statistical methods.

 The task of the Visiting Group was to review the current research program, comment on successes and potential failures and interview each individual member of the scientific staff. They would comment on what they saw as strength or failings of each individual and would recommend support or “review” as they sought fit. They also visited the farms and laboratories of ABRO. Overall, the Group would give or withhold their approval for each research project or recommend changes. They would also, on occasion, make suggestions for future research. The Visiting Group reported to the ARC, but their report was also sent to the Director of ABRO and in later years passed on to me also. These reports clearly impacted on the program and finances of ABRO.

In between the five-yearly visitations, less formal visits were made to ABRO by ARC- appointed scientists for discussion with individual research workers on progress or problems with their research. The aim was to be helpful. No doubt these scientific visitors would report back to the senior scientific advisors in the ARC, but there was no formal follow-up to these visits.

*ABGRO in Edinburgh*

The accommodation in “Glenbourne” (the headquarters) became too small soon after numbers of science and support staff had been appointed by the mid 1950’s. An annexe was built in the garden of the villa to provide extra accommodation and some laboratories. As ABRO expanded further, these premises also became overcrowded and inadequate and Hugh Donald, by then the director (see later), received permission to build a new headquarters at a site on the Kings Buildings campus diagonally opposite the Institute of Animal Genetics. For the design he employed Basil Spence and Partners, based in Edinburgh, one of the foremost firms of architects in the UK. The same firm of architects was responsible for designing the greatly acclaimed new Coventry cathedral in the grounds of the old cathedral destroyed by bombing during the war.

The new ABRO headquarters building, occupied in 1964, lacked for nothing. Spacious rooms for staff, an even more spacious director’s suite, ample laboratories, a mouse house and a fine, well-stocked library run conjointly with the Commonwealth Bureau of Animal Breeding and Genetics – another occupant of the building. There was also a large lecture room for meetings and a comfortable Common room. The Common room played an important part in the life of ABRO, not just because morning coffee or afternoon tea was taken there (as well as many a lunchtime sandwich) but because Donald was wont to gather some of his research staff around him for often lengthy discussions on scientific matters. Sometimes new ideas for research would emerge.

Falconer11 has written an interesting overview of the work and staff of the Institute of Animal Genetics following Waddington’s appointment. It discusses both the ARC-funded and the University-funded staff. In part a eulogy of the place, the article nonetheless gives a noteworthy account of the research of that part of ABGRO not covered in the present article. The organisms used for research included mice, drosophila, paramecium and fungi. There were also a significant number of theoretical studies published to provide breeding plans for farm livestock – mostly for cattle.

The staff under Waddington worked effectively as a unit both in research and teaching – irrespective of whether they were ARC or University-funded. When Professor White retired from the directorship of ABGRO, Waddington’s ARC-funded group was split off from ABGRO and financed by the ARC as an independent unit. Hugh Donald was made director of the larger part of the Organisation which henceforth became ABRO, the “G” – genetics – being dropped from the previous name. In some respects that was misleading as ABRO continued to be concerned primarily with the genetic component of animal breeding and much of the research was at a fundamental level.

The decision to split ABGRO was taken largely for administrative reasons at the request of Waddington and his staff. It had the unfortunate consequence of separating statistical genetics at the Institute from the breeding research. As is apparent now, the statistical genetics approach is an important route for the implementation of breeding research.

***Prof. White’s visit to the USA and Canada***

White wrote an extensive report on his visit that was submitted to the Agricultural Research Council – the funding body for ABGRO. Unfortunately that report was not retained in the archives. As a result the only information about that visit comes from summaries in the later report2 already referred to.

White’s first stop was at the Bureau of Animal Industry which has a large experimental station at Beltsville, Maryland and a number of Regional stations catering for different species of livestock. It seems that White’s principal contact was Professor J.L. Lush – chief advisor to the Swine Laboratory but also Professor of Animal Breeding at Ames, Iowa. Lush’s fame rested in part on his book ‘Animal Breeding Plans’12. In that book, Lush adapted into his breeding plans much of the theoretical work of the renowned mathematical geneticist Sewall Wright. His book became required reading for students of animal breeding and genetics in the 1940’s and 50’s.

The main piece of advice that White brought back to the UK was the desirability of increasing the homozygocity (genetic uniformity) of livestock. He did this in spite of being advised against it in later visits to the Bureau of Dairy Industry and on visits in Canada. It was also strange advice coming from Lush as in his book he emphasises the difficulty of inbreeding with livestock, like cattle, with a low reproductive rate. In the event, Donald would have none of inbreeding, at least for cattle – as he explained in a later article13. Robertson14 came to a similar conclusion from a review of three inbreeding studies with cattle in the USA.

**The acquisition of the farms**

During his visit to the USA, White had been more impressed by the work at the regional centres catering for different species of livestock than by the centralised work at Beltsville. Thus, he resolved that ABGRO should follow the model of dispersed experiments. Accordingly, it was decided to acquire farms across the UK, each catering principally, though not exclusively, for one species: cattle, sheep or pigs.

It was fortunate that farms were being sold at prices within reach of the ABGRO budget – before land prices rocketed upwards in later years. Notwithstanding, and in keeping with White’s responsible stance in spending public money, there was a good bit of haggling over price.

*Stanhope*

This was one of the two hill sheep stations purchased with entry at the end of 1951. Stanhope is in the Tweed valley of Scotland. It extends to more than six thousand acres with four hirsels. The farm includes the highest hill in the Border country of Scotland rising to 2,500 ft. from the low ground beside the river at 700 ft. The farm environment was regarded as ‘hard’. Details of the farm were given by Beedie15.

*Rhydyglafes*

The second of the hill sheep stations, occupied in 1952 was located in North Wales. It comprised some 71 acres of low ground (550 ft above sea level) beside the river Dee, an intermediate, semi-improved grazing of 269 acres rising to 1300 ft, and 660 acres of mountain grazing rising to 2250 ft. It was typical of the area for Welsh Mountain sheep. Coutts16 has provided a fuller description of the farm and concentrated his article on the opportunities for improving the hill land for sheep production.

*Cold Norton*

This farm, intended primarily for dairy cattle – at least initially – is situated in Staffordshire in England – an area with a large cattle population. It was the first farm purchased by ABGRO and taken over in March 1948. Tavernor17 has described it in some detail. The farm extended to 450 acres of which 340 acres were suitable for cropping. Poor reproductive performance of the cattle of the previous owner of the farm had raised some doubts about its suitability for ABGRO, but these problems were put down largely to bad management. However, this point illustrates the kind of matters that needed to be investigated before any of the farms were acquired.

*Mountmarle*

Soon after the end of World War II, Edinburgh University purchased the Bush estate about eight miles south of Edinburgh (now a large biological sciences campus including the Roslin Institute). In 1947, White was able to negotiate land on the periphery of the estate - at Dryden Mains near the village of Roslin – for a pig station and an adjacent Field Laboratory (see later). As described by Bishop18, buildings for farrowing and housing large number of pigs were completed in 1952. Ian Will, the farm manager provided an update on Mountmarle19. It appears that what had been regarded as sophisticated and extensive facilities in the 1950’s no longer sufficed in the 1980’s for the increasing volume of research with pigs, prompting a substantial redevelopment.

*Blythbank (and Broughton Knowe)*

Both these farms, occupied in 1950, were classed as upland farms and lay between 800 and 1100 ft. Blythbank, some 22 miles south of Edinburgh, extended to 780 acres and the smaller Broughton Knowe (292 acres) another 6 miles further down the road. Blythbank became the venue for much cattle and sheep experimentation. Broughton Knowe was mostly for sheep. Harris20, the farm manager, wrote a retrospective article about the farm showing that with pasture improvements and ever increasing experimentation, stocking of sheep at Blythbank rose from an initial 300 to close to 3000 (including 1300 lambs) in 1981 and cattle from less than 200 to over 600. Moreover, neighbouring farmland of more than 400 acres was added to Blythbank when Broughton Knowe was sold in later years. It is useful to note these points as its relative proximity to Edinburgh made Blythbank a handy venue for scientists and their experiments – and a good place to take visitors.

*Skedsbush*

This farm of 184 acres was purchased in 1953. It lies below the foothills of the Lammermuirs and has a harsh winter climate. Faulkner21 gave a full description of the farm and its uses as a place for outdoor pigs – and some sheep. (In later years it was taken over by the Neuropathogenesis Unit of Alan Dickinson for studies on scrapie, a disease in sheep).

*Dryden field laboratory*

A field station within ready access from headquarters was intended for detailed experimental work under strictly controlled conditions. It included laboratories, an operating theatre, climate chambers, mouse house and accommodation for a limited number of farm animals – mostly sheep. The land for the station was occupied in 1951. Buildings were erected initially and substantially increased later. The station did not become operational until 1954. It was conveniently situated across the road from Mountmarle.

**The appointment of staff**

White’s first concern, apart from the need for administrative staff, was to appoint three Husbandry Officers, as they were called, one each for cattle, sheep and pigs. They were to have wide experience of farming practice and in particular of the species they were intended to support. They were also to have sufficient scientific background to be able to act as a liaison between the scientists designing experiments and the farm managers and support staff on the farms who might anticipate practical problems with implementing experiments. The sheep and pig posts were filled quickly, the cattle post not until a few years later.

Appointment of most of the scientific staff came later. Some of those appointed later were post-graduate students at Edinburgh University’s Genetics department. Two early appointments, however, were made in June 1947 when White and Waddington interviewed Hugh Donald for the senior position on the “applied” side, and me, the author of this article, in a junior scientific grade. Thus I started off, in some senses, as Donald’s assistant. That role had already been foreshadowed as Donald had offered me a post as his assistant in the University Genetics department – before ABGRO had come on the scene.

**ABRO’s projects**

A history of ABRO needs to consider, with at least some detail, the projects that were undertaken, the reasons for them and their outcomes, but importantly also, to provide an insight into the problems of designing and conducting the various livestock genetic experiments, many of a long-term nature. It is hoped that will be found informative and interesting.

**The first four long-term Experiments**

Long-term, in this context, means a duration of between ten and twenty-five years. ABRO was fortunate in having the privilege of receiving funding that took a long view.

 These long-term experiments are also the ones for which some theoretical geneticists have questioned the need - though with the benefit of hindsight. The doubters would probably not have questioned the need had post-war conditions been kept clearly in mind. The need then was to acquire new knowledge to improve UK animal production both in the immediate- and in the long-term. An unsatisfactory alternative would have been to extrapolate from experiments with different breeds in different conditions in far-off countries, or to rely solely on predictions from what theory existed.

In providing references to the experiments precedence will be given to publication in ABRO’s annual reports over scientific papers in peer-reviewed journals. By and large, the articles in the annual reports are more readable and generally provide a wider overview of the work – they are also available from some libraries. Some of the articles were published after 1980 but refer to the research undertaken prior to that.

Cattle crossbreeding- at Cold Norton

In dairy cattle breeding the two main genetic methods to improve yield, quality or efficiency of production are selection and crossbreeding. Crossbreeding can bring about rapid changes. For example, if payment for milk were to become based on quality e.g. fat percentage, a first cross between the Friesian and the Jersey breeds would achieve that in the short-term – the former breed with high milk yield and relatively low fat content, the latter with less milk but high in fat . In addition, crossbreeding may result in the offspring being better than the average of the parents. That is the definition of hybrid vigour (or heterosis as it is also called) as used here and as understood by the livestock breeding community.

Selection on the basis of an animal’s performance or that of its progeny became well established when bulls started to be selected for use in artificial insemination. Before that, individual breeders would undoubtedly make choices, particularly of bulls, based on their own ideas of what constituted merit. Occasionally it was based on expected financial reward if the breeder had purchased a pedigree show winner at an eye-watering price in the expectation of high prices for his sons in later years. Much less well established were the genetic consequences of crossbreeding, in particular whether hybrid vigour would have a significant role in the level of performance.

With such thoughts in mind a large-scale experiment was started at Cold Norton involving cyclical crossbreeding with the Ayrshire, Friesian and Jersey breeds. Purebreds were compared throughout with the various crosses – made reciprocally. Artificial Insemination from many bulls was used throughout. According to Donald, the experiment was carried out with the help of the Milk Marketing Board.

Two articles by Donald22 23 in ABRO annual reports provide some results albeit these are, for purposes of illustration, restricted to the Friesian x Jersey cross compared to the two pure breeds. For live-weight at 18 months of age the crossbreds exceeded the two-breed mean by five percent, but they were not as heavy as the pure Friesians.

 Milk yield showed a similar result and, as a consequence, so did total solids yield and butterfat yield. But solids and fat percentages gave no suggestion of hybrid vigour and none was expected as these are relatively highly heritable and hence can be altered more easily by selection.

Donald’s second article deals with mortality in this herd. There is a hint in the results that crossbreds were better than purebreds only in respect of fewer losses during the first twelve months of life and in respect of less barrenness in the period between first and second calving.

These results demonstrate that different characteristics provide different results depending on how they are inherited. They also demonstrate that experimentation is not straight forward, particularly as experiments related to fitness traits require larger numbers of animals to provide statistically significant results.

But what do the results mean for the dairy industry? So long as total quantity of milk is the objective the higher-yielding parent breed will win – as has indeed happened in the UK (and elsewhere) by the displacement of earlier breeds by the Friesian and more recently by its Holstein strain. Of course there should be other considerations – importantly the efficiency of producing the milk in relation to the feed input. Also important is the value of animals that are surplus to requirements, in particular the male calves. There would be general agreement that Friesian calves have a higher value than, for example, Jersey calves, which are smaller and less good for rearing for “beef”. With females that are surplus to requirements for the milking herd, farmers often meet the desire for meatiness by mating these cows to beef bulls. As referred to earlier, if payment for milk were based on criteria other than quantity new criteria would likely apply in the choice of breed and breeding policy.

McGuirk24 has written a well-documented history of the Dairy Cattle breeding industry and provides little evidence of crossbreeding in the industry. But there are situations that make crossbreeding necessary 1. In order to change the breed composition of the national herd (e.g. Friesians displacing the Dairy Shorthorn in England by repeated backcrossing to the Friesian and later being displaced itself by the Holstein) 2. To use beef breeds on surplus heifers and cows, as referred to above, and 3. To produce a different type of cow if highly specialised dairy cows, which may lack other important factors, were to lose favour. One might conceive of a return to a more dual-purpose type, or to cows able to cope with poorer feed or harsher environments.

This experiment stopped being quoted as an ongoing project in 1971 which suggests duration for the experiment little short of twenty years, whilst seemingly long is barely three generations of a rapidly changing dairy cattle population.

Selection in Scottish Blackface hill sheep – at Stanhope

*Selection for cannon-bone length*

There was some evidence from much earlier experimentation elsewhere, as well as popular perception in the agricultural community, that cannon-bone size was related to carcass quality. This led ABRO to start an experiment in 1954 of selecting for cannon-bone length in both directions. In addition, a control line of unselected sheep was maintained.

Stanhope, as referred to earlier, was a large hill farm, more appropriately regarded as mountainous, though not atypical of other farms in the area. The 1600 or so ewes all lambed on the hill in April and May. Lambs were identified when they were born and suitably tagged with their identity (the identity of the dam could be seen from some distance printed on a large, specially designed plaque carried around the ewe’s neck). All this was required great dedication from the shepherds and the technical staff.

In June the ewes and their lambs were brought down from the hill to paddocks where the measurements of cannon-bone length took place. Extra staff came out from ABRO’s headquarters in Edinburgh to assist in this process and in the recording. When the records were being processed, due adjustment was made for differences in the age of the lambs when measured, as age clearly affects the bone length. Ram lambs were then selected as the future sires in their respective lines. Some precautions were taken to avoid inbreeding when these rams were later used for mating.

From this description it will be apparent that the process of carrying out this experiment was complex and labour-intensive. No wonder then that prior to the start of the experiment there were doubts as to whether, logistically, it could be carried out. So, although this experiment became a good demonstration of the ability to select under difficult conditions and provided much useful genetic information for the traits involved, it did not become a model that many hill-sheep farmers would or could follow.

As noted by Purser25, cannon-bone length is quite highly heritable but not very variable among sheep. As a consequence the rate of divergence between short and long cannon-bone lines was slow. After more than twenty years of selection, the cannon-bone length of the two lines diverged from each other by twenty-five percent in length. This difference was quite obvious to the eye.

An unpredicted and interesting part of the results was that the sheep of the long cannon-bone line, compared to the short, had a higher lambing percentage and lower lamb mortality – and hence a larger percentage of lambs weaned. The long cannon-bone lambs also had a higher weaning weight and consequently more meat was produced per lamb under the hill conditions. When these factors were taken into account the overall meat production from the long-cannon-bone line was almost twice that of the short cannon-bone line – a divergence of twenty-five percent each, in opposite directions, from the control line.

 When older ewes from the short and long cannon-bone lines were transferred to another farm with milder conditions and better feed, the differences between the two lines were greatly magnified – the only negative view expressed was that the long cannon-bone line lambs and older sheep looked a bit ungainly.

As a final comment, carcass analysis on a limited number of the short cannon-bone sheep at slaughter appeared to confirm a long-standing presumption that short cannon- bone sheep – as represented by Down breeds like the Southdown – would be fatter at the same carcass weight than long cannon- bone sheep.

*Selection for hairiness*

A second experiment at Stanhope involved selection for increased or decreased hairiness in lambs. This was considered as potentially useful in understanding the role of the birth-coat in lamb survival. The logistics for carrying out this experiment were the same as for the cannon-bone length selection experiment described above.

Ryder, largely responsible for this experiment, was, however, more concerned with the effect of the selection on fibre types. Ryder was an expert on all aspects of “wool” and saw that as his main role. He26 reported that the birth-coats in the Hairy line were longer than those in the Fine line, had significantly more halo hairs and hairy-tip curly-tip fibres, but significantly fewer histerotrichs. The Hairy and Control groups also had a consistently higher percentage of primary medullation than the fine group.

A fuller explanation of the development of birth-coats in lambs and the effect on hardiness is found in another article by Ryder27

Pilkington and Purser28 described how medullation, as found in this experiment, was assessed in fleece samples of various fibre types.

Selection for birth-coat type in Welsh Mountain sheep – at Rhydyglafes

Hardiness is something of a blunderbuss term which can have many components. Most sheep farmers will take it to mean that hardy sheep are those with better survival and productivity than those less hardy – particularly under harsh conditions.

One of the components of hardiness is thought to be the type of birth-coat of the lamb. Thus, compared to the selection for hairiness at Stanhope, the experiment with the Welsh Mountain sheep adopted the more direct approach of concentrating on the birth-coat itself.

The birth-coat type can vary from very fine with almost no kemp (halo hairs, so called) on the body, to birth-coats that have a dense coat of halo hairs all over the body.

Starting in 1952, two lines were selected in opposite directions towards these two types (Purser29). At the start there was a lot of variation in birth-coat types (they were graded from 1 [fine] to 6 [hairy]). Accordingly, the heritability of the trait - the proportion of the total variation that is useful in selection - was very high (65-70per cent). The lambs at the extremes in birth-coat type displayed much less variation.

The biggest difference between the lines, based on thousands of lambs born over thirteen years, was the significantly higher mortality (13%) among the fine birth-coat lambs compared to all the rest – in fact the intermediate types had, for the most part, a slightly lower mortality rate (hovering around 3-4 percent) than those of the hairy line (5.1 per cent). Differences were even more apparent when lambs with different birth-coats were compared under bad or good weather conditions. In the bad weather conditions mortality of fine birth-coat lambs during the first four days of life was as high as 41.7 per cent compared to 9.8 per cent among the hairy lambs. In better weather, mortality was much lower but the fine birth-coat lambs still had a higher mortality rate (6.2 per cent) than the hairy ones (2.7 per cent). In both sets of conditions the intermediate birth-coat type lambs had slightly better survival rates than the hairy.

So what is a farmer, as distinct from a geneticist, to make of all this? He may say “do nothing” as extremes are worse than the intermediates. Or he may say “the less fine the better the survival and the total meat production from the flock”. He might even say, albeit foolishly, “fine birth-coats lead to finer and more valuable fleeces”. But it is a very long time since wool has been a more profitable product from sheep than meat. If a farmer has multiple objectives, as is commonly the case, he should call on the research geneticist who will construct a selection index to meet the multiple objectives in the best way.

Studies with cattle twins – at Blythbank

There are different methods for studying the relative importance of heredity and environment in their effect on different traits. Some of these studies require very large numbers of animals (or humans). Using twins is a useful method of achieving a similar end with much smaller numbers. The method has been widely used in humans. One-egg twins (also called identical or monozygotic twins) share all their genes, while two-egg twins (fraternal or dizygotic twins) share only fifty percent of their genes. Comparing the two types of twin under the same conditions, as in the experiment at Blythbank, thus helps to provide evidence for any discussion of “Nature vs. Nurture”. However, unlike in the cattle studies, in the studies with humans the identical twin pairs are not normally reared in the same environment as the fraternal ones - and that adds a complication.

The study at Blythbank added a third category of pair, half sisters (HZ) which share twenty-five percent of their genes) to the monozygotic (MZ) and dizygotic (DZ) twins. The members of each HZ pair were born on the same farm, around the same time and kept together under the same conditions. These three types of pair were purchased as newborn or very young calves. The offer to buy such calves was made by advertisement in the agricultural press and through word of mouth, mostly by livestock officers. The purchases were co-ordinated from Cold Norton – which, as referred to earlier, is located in the midst of a large cattle population.

Twins were considered to be monozygotic if they could not readily be distinguished from one another by visual appraisal. If they differed from one another in important respects they would be regarded as dizygotic. There were no absolute criteria available in those days. Muzzle prints in cattle (thought of analogous to fingerprints in humans)30, also provided mainly “negative” information. If the muzzle prints of a pair differed greatly they were unlikely to be from monozygotic twins.

Professor Medawar, of skin graft and organ transplant fame, thought that skin transplants might differentiate between the monozygotic and dizygotic pairs. The expectation was that monozygotic twins would tolerate each other’s grafts but dizygotic twins would not. A trial26 using large numbers of pairs of both types, then still at Cold Norton, gave the disappointing result that the dizygotic twins also, for the most part, tolerated each other’s grafts and that this technology was therefore not useful in the diagnosis of monozygocity . There was much speculation in their published paper31 as to why DZ twins showed this tolerance.

Soon after purchase, the pairs of calves were transferred from Cold Norton to Blythbank where all three types of pair (MZ, DZ and HZ) were reared and kept under the same conditions of feeding and management.

Comparison was made for various traits of the within-pair variation of each of the three types of pair. As noted earlier, the three different types of pair differ in their degree of genetic relationship. Accordingly, if a particular trait is sufficiently heritable, the expectation will be that variation within MZ pairs (i.e. the differences between the members of a pair averaged over all pairs) will be less than that within DZ pairs and variation within HZ pairs will be greatest.

A number of papers and reports31-36 provide some results (not as many as might have been hoped). In respect of fertility there were no statistically significant differences in variance within pairs of the three types of pair, although that within MZ pairs was least. In respect of growth and body size (live-weight and several body dimensions) the measure of variation within pairs was least for MZ pairs, followed by DZ, and greatest in HZ. Similarly for butterfat percentage in milk and slightly less so for solid-not fat in milk the MZ twins showed by far the least variation within pairs. This shows that these traits are heritable to a significant extent – unlike for the aspects of fertility.

The cattle twin studies started to wind down in the early 1970’s about twenty years after they had started.

Cattle twins were used in similar studies notably in Sweden and New Zealand, but not on the same large scale as in ABRO.

Taylor and Young37 used twins on constant feeding over a period of seven years to study growth and the efficiency of growth – a subject that became Taylor’s over-riding interest. The use of twins was coincidental to the study of efficiency of growth, but it was noted that the MZ twins showed less variability within pairs than the DZ twins.

Twins were also used in an offshoot from the main studies by placing one member of each pair (starting with 65 pairs) in a high-yielding dairy herd and the other in a low yielding herd of co-operating dairy farmers in the West-midlands of England (Wiener38). If the average difference in yield (and other traits like growth| was less for the twins than the corresponding difference between the herds it would suggest that part of the herd difference was genetic in origin. Conversely, if the twin and herd differences were similar to each other it would suggest that most or all the herd differences were due to differences in environment and management. Only 24 of the original 65 pairs completed one lactation. That was too few to make the difference in yield of 163 gallons of milk for twins and 213 gallons for the herds statistically significant. Members of twin pairs in high-yielding herds grew faster and became larger in the first year of life, suggesting that management during rearing was somehow associated with herd level of milk yield. The main point to take away from this experiment is how useful a contribution cattle twins can make to studies of the relative importance of heredity and environment, in its broadest sense.

**Later long-term experiments conducted by the staff who designed them**

Selection in a Hereford herd - at Cold Norton

There was a dramatic shift at Cold Norton in 1977 from dairying to beef production with the establishment of a herd of Hereford cattle (Simm and Smith39). The impetus for this experiment derived from an estimate, by the Meat and Livestock Commission, that more than two hundred thousand tons of waste fat were produced from beef, sheep and pigs each year. The aim of the experiment was to increase lean content of the meat at the expense of fat and to relate this to the feed intake by the animals.

The experiment had two selection lines – the bulls for one line were selected for lean growth rate (LGR – the product of growth rate, killing-out percentage and lean in the carcass estimated by ultrasonic means in the live animal). Bulls for the other line were selected for lean food conversion efficiency (LFCE – the product of food conversion efficiency – in place of growth rate - and the other two factors).

The article by Simm and Smith does not say how much lean content of the carcass changed as a result of the selection. Perhaps progress in that regard could be assumed – depending how heritable these traits are. But the authors made an important finding. The results they report would have been almost the same had selection been on growth rate alone instead of LGR or on food conversion efficiency alone instead of LFCE. The practical importance is that those are much simpler traits to measure, influencing, among others, recording schemes and inferences from breed comparisons.

This experiment continued past 1980 – the chosen end-point for this article.

Multi -breed studies with cattle – at Blythbank

Breed comparisons are often needed to find out if one breed of cattle will give better financial returns than another in specific situations. The question becomes most pressing when imports of foreign breeds are contemplated – as has happened over recent years particularly in respect of beef breeds. Such “comparisons” are often based on information of breeds kept in different environments (for example the breed performance in other countries prior to importation to the UK). Such comparisons are not genuine breed comparisons in the genetic sense.

 Taylor came up with a new concept – that of a multi-breed design whereby many breeds can be compared using only a minimal number of sires per breed, but all under the same feeding and management regime. He gives an example39 of testing facilities for one hundred animals which would allow 25 breeds to be compared with four sires per breed each with only one offspring. All the animals have to be compared using a complete pelletted diet as feed. This prevents animals from choosing among the different components that are included in conventional feeding.

A further article40reports on the first multi-breed experiment set up at Blythbank in 1972. It ends on the optimistic note: “some very interesting results are emerging on the inter-breed relationships between absolute growth rate, relative growth rate and food efficiency.” Further experiments followed41- 44 in relation to growth, milk yield and efficiency of maintenance feed requirements.

This trial is now internationally recognised as one that informs the global community of the importance of breed variation in the total genetic variation within a species. As such it is a key reference point for managing livestock genetic resources.

Studies on crossbreeding and inbreeding in sheep – at Blythbank

Around the year 1954 I persuaded my colleagues Clair Taylor (interested in growth) and Alan Dickinson (interested at that time in maternal effects) to join me in the design of a long-term (twenty years) crossbreeding and inbreeding experiment in sheep. This proposal to use inbreeding had nothing to do with the idea brought back by Prof. White from the USA that inbreeding should be used to promote uniformity of type. We did not even know at the time of that recommendation. The wish to use of crossbreeding and intense inbreeding had everything to do with the fact that this procedure can tell a great deal about the genetic make-up of the breeds – particularly the non-additive genetic variation (the variation contributing to hybrid vigour in crossbreds and to inbreeding depression).

The Scottish Blackface (B), South-country Cheviot (C) and Welsh Mountain (W) breeds of sheep, differing in body size and many other characteristics, and their reciprocal crosses, were used through all the stages of the experiment. As the experiment stretched over twenty years it was important to ensure that comparisons between the different stages of the breeding programme should overlap in order to be able, by statistical methods, to eliminate as far as possible the effects of year (seasonal differences) on the performance of the sheep. Thus, for example, after producing the first cross (F1) half of the dams producing that cross were mated to unrelated F1 rams to create a second cross (F2), and the other half of the dams were mated to their fathers (or their F2 sons) to create the first generation of inbreds (I1). In this fashion the breeding continued to produce three overlapping generations of inbred ewes – mostly by parent x offspring mating – and four generations of inbred lamb. This is the closest rate of inbreeding possible in sheep.

These inbreeding stages represent inbreeding coefficients of 25% (I1) 37.5% (I2) 50% (I3) and 59% (I4) (in percentage terms, the proportion of heterozygocity that is lost, or conversely the proportion to which homozygocity is gained).

For the first few years three other breeds were added to the mix to add even more variation: the large Lincoln Longwool (L) (about twice the weight of the Welsh Mountain sheep) the blocky Southdown (S) and the fine-wool Merino (M). A group of 12 females of each of these breeds were bred pure and rams of these breeds were also used for crossbreeding with the hill breeds.

Observations were made on body size and growth rate, reproductive and maternal performance, wool growth and components of the fleece and, importantly on health and survival.

(Wiener and Hayter)45 provided an overview of the results. For illustration the findings for one “composite” trait are given here: the total weight of lamb weaned per ewe mated. That depends on the proportion of ewes mated conceiving, the number of lambs that survived to weaning and their growth rate. For all three hill breeds, their crosses exceeded the parental breed mean – most for the B x C cross and least for the C x W. B x C and B x W crosses exceeded in this composite trait the production from the larger parent breed – hybrid vigour by any definition.

Effects of inbreeding, calculated independently for dam and lamb were even more dramatic. Litter weight of lamb weaned per ewe mated fell from 82 lb of lamb when F1 ewes produced F2 lambs to 36 lb of lamb when 50% inbred ewes produced 59% inbred lambs.

Some crosses of inbred lines (LC) were also made when other rams (fathers or sons of ewes) were not available. To some extent this must disadvantage the line crosses (LC) as they are from the lines in which fathers or sons had not survived. However, at all stages the LC performance exceeded the inbred and most dramatically when LC lambs were produced by LC dams. The article quoted above45 has a delightful photograph showing a 10-month-old 59% inbred hogg standing alongside its half-sib by the same father but from a line-cross mother. The inbred one had attained only 40% of the weight of its LC half-sib. This may not be typical of all such comparisons but it is a good illustration of the effect that intense inbreeding without selection can have. It also shows that there must have been a lot of variation for this trait in the initial breed population. For those who would strive for uniformity of breed type, the experiment highlights that continuing rapid inbreeding is unlikely to be a good route along which to proceed. However, as noted much earlier in this article, breeders like Bakewell in the 18th century used inbreeding as one of their tools in creating new breeds.

 The mating of Lincoln, Southdown or Merino breeds of ram to each of the three hill breeds in the first few years of the experiment provided additional evidence on the effects of crossbreeding and hybrid vigour.

One side-study involving embryo transfer deserves special mention46. Its purpose was to gauge the relative importance of the lamb’s own genotype and that of the maternal environment on birth-weight. Eggs from Lincoln or Welsh donor ewes were transferred to 4th parity Lincoln or Welsh recipient ewes and also to first parity Blackface recipient ewes. The breed of lamb turned out to be the most important factor influencing birth weight, but the maternal breed had some effect. This was shown by the difference in birth-weight between Lincoln and Welsh lambs of 5.8 lb in the Lincoln maternal environment, 3.8 lb in the Welsh maternal environment and 3.0 lb in that of the Blackface – all compared to 6.5 lb. when each of the two breeds (L and W) were born in their normal maternal environment. That suggests in turn that in the transferred groups the Lincoln provided a maternal environment least restrictive to the developing foetus and the first parity Blackface the most constraining.

For those who want to delve deeper into the results from this crossbreeding and inbreeding experiment, results from a small selection of the twenty-four published papers from this experiment must suffice to provide a flavour of the results. A second overview was provided by Wiener and Wooliams47who, with the inclusion of later results, concluded that breed was, as expected, an important source of variation – breeds had been chosen to differ greatly from each other (Wiener48) - hybrid vigour was variable in expression depending on the trait, and inbreeding depression was considerable especially for lamb survival49 and lamb weight50.

Conception rate51 declined almost linearly from 0.71 with zero inbreeding to 0.44 at 59% inbreeding and other aspects of reproduction had similarly large effects from inbreeding. An interesting finding emerged from a trial in which 6-month-old inbred and matching outbred sheep were given either ad lib feeding or a restricted plane of nutrition. Though the inbred sheep were substantially smaller than the outbred the two groups grew in parallel and with the same efficiency of food conversion52.

By way of a summary of the overall effects of inbreeding in this flock, a study53 translated the changes with inbreeding into financial returns (at 1992 prices). It showed that income declined almost linearly from the non-inbred level to 0.50 inbreeding followed by a small improvement at 0.59.

Studies on the genetics of mineral metabolism – at Blythbank

Occasionally in science as in medicine a discovery is set off by an unexpected event. So it was with the discovery that the absorption of dietary copper – and possibly of other trace- elements and minerals – is under a measure of genetic control.

The investigations were triggered by the occurrence, in one particular year, of “swayback” in the lambs of the crossbreeding and inbreeding flock described above. Swayback is caused by a copper deficiency during pregnancy. It is either fatal or greatly debilitating to the lamb. The condition can be avoided by giving supplementary copper to the pregnant ewes, but the need for such administration has to be known in advance. In the case of Blythbank farm there had been no earlier outbreaks of swayback and thus no prior warning of such a possibility.

In the event, forty percent of the Blackface lambs were affected by swayback, eleven percent of the Cheviots and none of the Welsh. To put icing on the cake for geneticists, so to speak, the incidences in crossbred lambs between these breeds were close to midway between the incidences in the pure breeds. All this was good additional evidence that heredity was involved.

The investigations that followed stretched over ten years before the conclusion was reached and confirmed that there was a significantly large genetic control of copper absorption from the diet. Some of the evidence for that is given below.

 Support in the investigations was received from the Moredun Research Institute (Dr A.C. Field in particular) to meet the large requirement for biochemical analysis and veterinary procedures.

Suttle54 provided a comprehensive account of the role of copper and its function in the metabolism of animals. Copper is essential for life in plants and animals. Sheep need adequate amounts – though “adequate” is a tiny in absolute terms.

The research was directed primarily at copper but there was preliminary evidence of wider associations of heredity with mineral metabolism in general for both sheep and cattle (Wiener55).

This was essentially a long-term project with many shorter-term experiments to progress it with many of the results summarised in an annual report56. In relation to copper, successive stages showed first that the breed and crossbred differences in swayback incidence were matched by copper concentrations in blood and liver tissue. There followed controlled feeding trials in a specially designed sheep house using a complete pelletted diet for the sheep. In one such trial the Blackface breed was compared with sheep of the Orkney breed from the island of North Ronaldsay (off the north coast of Scotland). On the island, this breed is kept for most of the year in the sea-shore where seaweed is the only feed available. There was evidence from the island that when these sheep are brought inland onto other grazing during the lambing period cases of copper poisoning occur among the sheep. North Ronaldsay sheep were purchased for the trials.

In a feeding trial, the Blackface sheep showed signs of copper deficiency whereas the North Ronaldsay sheep on the same diet, over the same period of time, would have died of copper poisoning (as judged by accumulation of copper in the liver) had the trial not been stopped. This showed clearly a large breed difference in copper absorption from the diet and that the previous findings in the Blythbank flock could not have been attributed to differences in grazing habits.

Further trials showed that incorporation of seaweed into the diet inhibited copper absorption. It follows that the North Ronaldsay sheep, which feed predominantly on seaweed, must have developed a highly efficient system for absorbing copper in order to get enough of it for their vital functions.

Other trials showed that following copper depletion of sheep, the provision of dietary copper led to different rates of increase in plasma-copper levels in different breeds, but injected copper resulted in no such breed differences57. This is further confirmation that absorption of copper through the gut is the operative mechanism for the genetic differences in copper uptake.

Several other breeds were included in trials which suggested a probability that the Suffolk and Texel breeds, which are used widely in crosses for intensive sheep production, could become susceptible to copper poisoning.

A final experiment involved selection for high or low plasma-copper levels58. There was an immediate divergence in the plasma copper levels of lambs after only one year of selection and this divergence between the two lines had increased by year three. One major outcome from this trial was the recognition that Cu deficiency led not only to swayback but also to an increased susceptibility to infection. Again a chance outcome, when the pastures in one year had become unexpectedly low in Cu, the lamb mortality in the low Cu lines was many times higher than in the high Cu line. Investigation showed that the difference in mortality rate was due to a wide range of causes, not only infection.

The conclusion from the experiments with copper is that heredity was involved to a greater or lesser extent in the requirements for this constituent. Preliminary studies with other essential dietary minerals were less conclusive although breed was a significant source of variation59as was breed of sire in a crossbreeding trial60. Therefore in feeding and management terms one system does not fit all breeds. This knowledge is of special importance in those several areas of the world, for example Australia, where mineral deficiencies or imbalances are endemic in some of the natural grazing territories. As a result, these studies were well received by veterinarians and animal production people – and at conferences even by the medical fraternity because of equivalent conditions in humans.

More research should, in time, lead to greater efficiency of production, but a cost/benefit calculation would be difficult to produce when there are so many unknowns. It is unlikely that the companies providing mineral supplements would welcome a reduction in the need for supplementation or would fund for such investigations.

Research with pigs – at Mountmarle and Skedsbush

Pigs at Mountmarle farrowed and fattened indoors, those at Skedsbush were outdoors.

The team concerned pre-dominantly with research on pigs was led by John King, supported in earlier years by Gavin Strang (who later turned to politics and became a Member of Parliament) and later still by John Webb. John Bishop, the pig husbandry officer, played an active role and Charles Smith contributed greatly with theoretical studies. The group contributed prolifically to ABRO’s annual reports and significantly to the scientific literature. The pig research was organised around a central theme – the improvement of pig production through breeding and through trying to solve some specific problems on the way (e.g. the occurrence of pale, soft and exudative pig meat - PSE). There were no individual long-term experiments of the type described earlier.

The Reference list provides a selection of articles from the ABRO reports. The first of these describes how one of the aims in pig breeding is to reduce the amount of fat produced by the pig61. A big aid to achieving a reduction is to measure fat depth in the live, breeding animal – most acceptably by use of ultrasonics.

Further reports discuss crossbreeding. This confers advantages on pigs in terms of litter production62, but raises questions of how to proceed with a crossbreeding system after the first cross is produced63. This question is not unique to pigs and could be equally applied to cattle and sheep crossbreeding.

Strang643 analysed a mass of pig industry data and showed that the heritability of litter production was very low (not unexpected for a fertility trait) and that applying the same intensity of selection on reducing back-fat thickness as for litter size would result in seven times the progress and much greater economic benefit. Avalos and Smith65 however, came to a different conclusion. Working with a mixture of commercial and ABRO data they agreed that the heritability of litter size is very low, but they showed that it is a very variable trait thus providing good opportunities for choice among sows. They also calculated that by including litter performance of relatives in a selection index relatively fast progress could be made in increasing litter size by selection.

Webb66 dealt with the important issue of Porcine stress syndrome (PSS) which increases the liability of pigs to die suddenly in response to stress. Pigs with that syndrome are also prone to develop pale, soft and exudative meat (PSE). The condition can now be identified in piglets at eight weeks of age by their reaction to a short exposure of the anaesthetic halothane. That reaction is inherited by a single recessive gene. Piglets having both copies of the recessive gene (homozygous for the recessive) react to the test, the heterozygotes and the normals (no copies of the gene) do not react. Thus selection can be used to alter the frequency of the gene and hence the frequency of PSE in the pig herd. There is a conundrum, because there are both advantages and disadvantages from PSE in pigs. PSE pigs are leaner and have a larger eye muscle area but are more liable to die from stress and they have a lower litter-size at weaning. It is therefore the relative economic value placed on these different traits in different herds and times that will decide whether the halothane gene should be eliminated or treasured.

The final article67 quoted here on pigs sums up the thinking in ABRO in1986 on genetic research for pig improvement. To quote the conclusions in full:

“As fat cover approaches an optimum, the emphasis in genetic improvement will swing towards efficiency of the production system and quality of the end product. The immediate priorities for research are therefore the rate of protein deposition, the number of pigs per sow per year and eating quality.

Perhaps the two greatest biological advantages of the pig are its high ovulation rate and daily food intake. The challenge for genetics will be to harness this biological potential in order to maximise the output of high quality lean meat per animal.”

Much of this would still be valid in 2021. But public attitudes can also change not only in relation to eating meat but to what the animals themselves eat. Pigs for fattening are predominantly fed crop-produced feeds from areas that could equally well produce crops for direct consumption by humans. Changes in attitude come slowly and are not easy to predict far in advance. That poses a problem for animal production improvement by genetic means - because genetic change needs a long time horizon.

Research at the Field Laboratory

The start of research at this out-station commenced with the appointment of H.B. Carter in 1954. An Australian, he recognized early in his career, and with practical experience on Merino stud farms, the importance of Merino wool to the Australian economy. More importantly, he found that there was substantial variation in the quality of the wool product. As scientist he noted the dearth of biological knowledge to rectify the economically important problem of variability in quality. Rectifying that dearth became his life ambition. He was renowned in Australia for his studies on wool and the development of the fleece and he was responsible for the design of a “Sheep Biology Laboratory”. However, in 1953 he resigned his post in Australia for personal reasons and accepted a post in ABRO.

Carter received special dispensation from Australia to import a small flock of fine-wool Merino sheep to ABRO, strictly for experimental purposes. He intended to continue his research where he had left off.

In 1955 he was joined by John Slee who had worked on the developmental morphology of the skin and hair follicles in mice and now pursued detailed studies in sheep of follicle development and the pathways involved. His article on moulting68 is an account of fleece shedding but also provides an insight into follicle development and the factors that initiate hair loss.

Michael Ryder was the next to be appointed. He became simply “Mr Wool” not just within ABRO but in the entire agricultural research service. His book with Stephenson on wool growth69 is a classic piece of work.

Unfortunately, things did not go well for Carter as his relationship with Donald, the director, soured to the point where they would not speak to each other. To me, looking in from the outside, but knowing the people involved, I deduced that the cause for the breakdown was Carter’s apparent hope to re-create at the Field Laboratory the former glories of his wool research in Australia and to expand the facilities for that. Donald, however, would not give him the necessary support. Wool in the UK is a by-product from the sheep industry and economically unimportant except in a small niche market. Carter resigned from ABRO in 1963 and took up a post at Leeds University. In fairness, it should be added that not all of ABRO’s scientific staff felt comfortable under Donald as director. Hugh Donald, an outspoken New Zealander, could be very demanding and blunt about it.

Slee’s main research veered to problems of lamb survival using climate chambers for his experiments70 71. Ryder continued with a variety of studies on wool.

J. Hancock and G. Hovell were important appointments in the early 1960’s. They were veterinarians skilled in many techniques including embryo transfer and in all aspects of the fertilization process. They also attempted hybridization of sheep and goats. A few of their publications on these subjects are listed72-76.

Two other members of staff were Marjory Fordyce in charge of the operating theatre and Bill Ritchie lending technical support and brilliant at manipulative techniques. Many years later, then under the auspices of the Roslin Institute, he undertook all the delicate work with sheep ova leading to the cloning of Dolly the sheep.

It is necessary to interrupt the story of the Field Laboratory to write about the importation of Finnish Landrace sheep which gave an added direction to the research at the Field station.

In June 1961 ABRO received a visit from Kalle Maijala, an animal geneticist from Finland. I had the privilege of being asked to host him. He told me, amongst other things, of the high prolificacy of his country’s Landrace sheep. Twins were normal, triplet births common and quad births not uncommon. Sheep of this breed also started to lamb at one- year-old. This information also excited others in ABRO including the Director who charged me with writing to Maijala for more detailed information. As a consequence Donald sent Joe Read, the sheep husbandry officer, to Finland to negotiate an importation of a flock to ABRO for experimental purposes. Later importations were to serve the commercial sheep sector. Barker77 has given an account of the Finnish Landrace breed in Great Britain and how it was used in the sheep industry.

The importation of the Finnish sheep led directly to the appointment of Roger Land to the scientific staff, of William Carr, a biochemist, and a few years later of Ian Wilmut.

Land set about with zest with the appointed task of researching the factors underlying differences in fertility. For example, ovulation rate sets an upper limit to the number of sheep eggs that can be fertilized and come to term. However, many other factors are involved in the reproductive efficiency of a ewe. Properties of the testis in males may be found to contribute to fertilisation rates. The two reports78 79 listed from Land’s prolific output of publications deal with these issues. Land developed and pursued the ideas of genetic differences in the system of negative endocrine feedback in the regulation of ovulation to explain breed differences such as between the high-litter size Finnish Landrace breed and others with much lower litter sizes.

As the aim at the Field laboratory turned towards study and understanding of physiological pathways underlying differences in performance, Carr80 provided an insight into opportunities for biochemical selection by discussing biochemical polymorphisms, variants in metabolic pathways and hormone assays among the approaches.

Wilmut’s initial research targeted embryo loss during pregnancy81. Embryo transfer82 was among the investigational tools he used. He also carried out important work demonstrating the importance of progesterone in preventing early embryo loss, work that the ARC then moved to Nottingham University. In much later years when he was on the staff of the Roslin Institute – into which ABRO had merged, Wilmut’s name became better known for being the leader of the team that produced the first cloned sheep, Dolly.

I was a relative late-comer to the staff at the field laboratory. When King became director in succession to Donald in January 1974 he created departments within ABRO. The departments replaced the benign autocracy that had existed until then. The work at the field laboratory became the Department of Physiological Genetics with me as its head.

**Short-term experiments in ABRO**

The term is relative to “long-term” discussed earlier. In genetic experiments with livestock species even “short” can often, not always, extend over a couple of years or even longer as replication is often needed to confirm a “result”. The short-term research can be grouped under a number of headings:

Applied studies

Operational research and theoretical studies: Charles Smith83-85 was the chief contributor to theoretical studies for the design of breeding schemes. Hinks86 87 had some input especially concerning issues in the dairy industry. Taylor designed the multi-breed approach for breed comparisons referred to earlier.

Many of the trials with pigs belong to the applied category such as the evaluation of foreign breeds, the effects of crossbreeding, the work on the porcine stress syndrome and the selection of a specially created pig sire- line for food conversion efficiency.

For sheep, the testing of terminal sire breeds and for cattle the Hereford project can be regarded as “applied” research.

 A flashback is needed here. When I was appointed in 1947 there were no experimental facilities. Donald suggested that I study of the population dynamics of the pedigree Ayrshire Cattle population – then still the foremost dairy cattle breed in Scotland and well represented in England. That study was classed as operational research and was to lead to a PhD. Among the many findings was that of herd structure. A small number of herds were at top of what could be represented as a pyramid of herds88. This top group tended to be self-contained as far as their own breeding stock was concerned. The top group also provided the bulls to the next tier down (the pyramid widening), often referred to as the multiplier herds (multiplying the genes from the top herds). They in turn provided breeding stock, mostly bulls, to the bottom tier, the broad mass of pedigree herds which obtain the bulk of their income from the sale of milk and surplus stock.

It was apparent from the study that livestock improvement was affected by the structure within breeds – both in cattle and sheep. As the use of artificial insemination in cattle expanded, the use of semen from bulls of the top tier began to give way to the use of semen from performance- and progeny-tested bulls, hence breed structure assumed much less importance.

Disease studies

Dickinson and his immediate colleagues provided most of these studies in relation to the sheep disease, Scrapie. To this day one can hear Dickinson say “it’s more complicated than that” - so the only safe option is to paraphrase from his reports89 90.

 “Most affected sheep scratch themselves until their flesh is raw and they become uncoordinated in behaviour. The sheep’s brain is damaged progressively by a virus-like agent (prion) which it has ‘caught’ years before. No way has yet been found to prevent the brain damage and the affected sheep die.” “The infective agent is very resistant to physical and chemical inactivation – which normally destroy viruses. It is not inactivated by irradiation or boiling but destroyed by autoclaving”.

 Clearly, scrapie is a formidable foe to sheep. Dickinson was appointed to head a Neuro-pathogenesis unit financed by the Research Council and independent from ABRO for the study of Scrapie and related conditions.

Some disease studies, mostly from animal industry data, were undertaken by Gilbert Young, a veterinarian trained in genetics. In a reportYoung91 wrote about a range of congenital and hereditary defects in cattle and sheep such as some skin diseases, malformations inherited as recessives and the dominant inheritance of the Dexter bulldog calf.

Immunology and the Blood Typing Service

This has been an important component of ABRO’s research from early on in its existence. The studies of this Service have long-term aims but progress by successions of relatively short-term experiments. Some observations in respect of immunology were derived from cattle, but most from sheep, on ABRO farms. In addition there was collaboration with other centres engaged in this type of work in other countries. The hope of the department was to identify genetic variation in active and passive immunity to disease and to other limitations on reproduction and survival. Some useful signposts of genetic influence have been found in differences among sheep breeds in the amounts of immunoglobulin transferred from colostrum to the newborn lamb. Efforts were also being made to understand a possible role of the ‘Major Histocompatibility Complex (MHC)’, which is a cluster of genes, on the genetic control of immunity.

Anyone reading this in the 2021’s may be tempted to ask “is that all?” But this article is an historical account. The work described was carried out with the technology available at the time – but a technology that was greatly advanced by the research of this group. Greater advances in the genetic control of disease may well come with the age of molecular genetics which was introduced to ABRO in the mid 1980’s.

The principal researchers in this field in ABRO, as described above, were John Hall, Ron Halliday and Roger Spooner.

A Cattle Blood Typing Service, initially led by Spooner and then by Hall and located in ABRO, was set up to assist the cattle breeding industry. The Service was self financing as users were charged a fee. Main users were the Artificial Insemination services of the Milk Marketing Board and Breed Societies. They used the Service to detect and eliminate errors in identity and parentage. For example, a cow might be served by more than one bull or inseminated with mixed semen from two or more males. Blood typing will then identify the correct sire of the calf. Data from this Service also provided opportunities for research into associations of blood groups with disease conditions and potentially other traits.

ABRO’s Mice

As referred to earlier there was a mouse house at the field laboratory and another at the headquarters building. John Slee conducted studies on the developmental morphology of the skin and hair follicles in normal and mutant mice. This provided a model for his corresponding studies on the skin and on fleece development in sheep.

Nigel Bateman92 started and continued for most of his career to use mice as a genetic model for traits important in livestock, such as the responses to selection of growth or components of fertility. Years later, Bateman took over, for analysis, data from the hill sheep experiments left behind following Purser’s untimely death. It was obvious to his colleagues that Bateman thoroughly enjoyed this career change – in fact his friends thought he revelled in it.

Support services

*Statistics and Computing.* From the start of ABRO it was realised that the data from the experiments would need sophisticated statistical analysis. Many factors contribute to differences in the expression of the traits that would be under study apart from the genetic component. Say, for example, that the trait under investigation is growth rate from birth to weaning in sheep. Then, factors such as year (where an experiment stretches over more than one), time or even week of the year, the parity of the ewe and the number of offspring born to her would need to be taken account of before effects of heredity could be identified. In the early days this was done with the aid of calculating machines that would now be regarded as antiquated. It was a cumbersome process as the effect of each of the factors involved had to be calculated separately. It was not until the advent of computers that different factors could be included simultaneously by appropriate programming.

Towards the end of the period considered here, the computation was done through the Northumbrian Universities Multiple Access Computer (NUMAC). Hollerith cards were used to code and hold the data. The cards were then transported from Edinburgh to Newcastle to be run overnight. The results were delivered back the next day, provided the cards had been prepared correctly and the job had run successfully: a slow process. Eventually the BIG (Prime) computer arrived. It needed its own air-conditioned room and its own full-time staff to program and run it. It was accessed from remote terminals in the ABRO building – ‘big’ of course is relative, as the continually increasing power of computers has meant that the computing power of the Prime was only a tiny fraction of today’s laptop.

Not all the geneticists and other scientific staff from different disciplines were skilled in statistical analysis. Accordingly three or four statisticians and statistically-literate staff were appointed. They assisted in the design of some of the experiments and in analysis. They also contributed occasional papers to journals in their own field of expertise.

The principal statistical and computing staff at the time comprised David Sales, Robert Findlay, Doug Maxwell, David Nicholson and Bill Russell.

*Record keeping.* ABRO’s long-term experiments, as well as many of the shorter term ones, generated a huge volume of data. In 1979 Maxwell93 wrote that the accumulated volume of records at ABRO amounted to50 million items which were added to at the rate of 10,000 a day.

The handling of data was also supported by a Records Section – latterly under the auspices of the Statistics and Computing Department but for many years before that under my watchful eye – as requested by Donald, the director. As he knew that I was neither a statistician nor skilled in any form of computing he must have decided I would be good at organising and at hiring and looking after the staff that made up the Records Section.

For perhaps the first twenty years all observations and measurements were recorded manually on paper and then transferred to the Records Section to align the new records with previous ones for each of the many experiments. For years, that also was done by hand. It was not until several years later that Hollerith punched cards were introduced. That made storing, sorting and tabulating of data much faster – but transferring written records to punched cards was a major undertaking. At its height, the section was staffed by ten highly motivated young women with Helen Kelly the senior one. The Records staff also assisted scientific staff with the analysis of data.

*The Typing Pool.*  The production of papers was a very different affair in the early days of ABRO. Papers were produced by typists from hand-written scripts, re-typed from scrawled previous drafts, or literally from cut and stapled bits of paper. So, the work of ABRO’s pool of typists was vital for the scientific and administrative staff, as all letters, scientific papers and reports were typed for them and even telephone calls connected for them.

Publications

Over a period of thirty years, over one thousand papers were published in scientific Journals and some in the Proceedings of scientific meetings. The bulk of the papers emanated from the so-called “short-term” experiments. That number must be regarded as very creditable coming, as it does, from a discipline where even so-called “short-term” experiments can stretch over years. This is particularly the case, when both the pressures on scientists and, as mentioned above, the preparation (analysis and writing) were very different from what they are today.

**Afterthoughts**

The great majority of the scientists working in ABRO would have said that theirs was a privileged existence. Few other professions, apart perhaps from artists, musicians and professional writers, are allowed the freedom, within limits, to follow their own ideas and insights in their work– a freedom that depends on self-motivation.

A criticism that has been directed at the four long-term experiments, which were designed when ABRO first started, is that the results from them were allegedly underused. This criticism has some merit (though this problem is not unique to ABRO). These experiments were largely designed by Hugh Donald and Professor White, no doubt with advice from others, but, importantly, not the scientific staff appointed subsequently. That staff, whilst concerned with analysing the results, had had no stake in the experimental design. One might ask whether such research staff, having no real ownership of the experiment to which they were assigned, albeit with good intentions, might have given greater emphasis to their own prior scientific interests. This is, of course, speculation, but is based on noting a far greater output of publications from experiments that were designed and carried out by the same person or team than from the four initial long-term projects.

 In the 1980’s ABRO entered some troubled times as reported by Myelnikov1 (see earlier). The Research Council, the main funding body for ABRO, had become concerned that the emphasis of ABRO’s research had shifted too far towards “applied” work intended to solve current problems of animal breeding rather than pursue more fundamental animal genetics. The then director, John King, was blamed for this in some quarters as his sympathies lay in the “applied” sphere. Perhaps that may have been a bit unfair as for many years prior to this there had been something of a tussle between the approach of the Research Council to pursue the more fundamental questions and anticipate future needs, and the wish of the Ministry of Agriculture to be involved by commissioning applied research in ABRO and elsewhere to solve today’s problems. That kind of “tussle” is not unique to this situation.

The Ministry of Agriculture had become the beneficiary of research funding transferred to them from the Agricultural Research Council, in order to commission applied research. It followed the government’s acceptance of the recommendations of the Rothchild Report in 1971. For some of the scientists in ABRO this must have seemed like a new opportunity. Thus, a significant proportion of ABRO’s research became of the commissioned, applied type. In some quarters this was perceived as a change of direction in ABRO’s research programme in spite of the fact that most of the core fundamental research continued, apart from the fundamental scrapie work. That had already been split off some years earlier into another independent unit under Alan Dickinson’s direction but ultimately became part of the Institute of Animal Disease managed from Compton. However, the Research Council took a harsher view of the change of balance between fundamental and applied research. Accordingly they undertook a massive reorganisation of ABRO leading to many redundancies of staff, the sale of some farm facilities and a merger with the neighbouring Poultry Research Centre to form the Edinburgh Research Station. The ABRO legacy within that Station was in turn forced, a few years later, into an arranged marriage with the Institute of Animal Physiology in Cambridge. When that marriage was dissolved, as it suited neither party fully, the Edinburgh Research Station was renamed, in 1993, the Roslin Institute under the directorship of Grahame Bulfield from the former Poultry Institute.

Since then, the Roslin Institute has become a part of Edinburgh University, was reunited with the scapie work, has greatly increased staff and expanded its research in novel and diverse directions. It is highly acclaimed as an animal science and biotechnology Institute.

It is, however, worth noting that Dolly the sheep, the first cloned mammal, which brought the Roslin Institute to wide popular notice in 1996, emanated from the work of an ABRO team all of whom, with the important exception of Keith Campbell, had been former members of ABRO’s department of Physiological Genetics. They were Ian Wilmut, the team leader, Bill Ritchie who did most of the intricate micro-manipulation of the embryos, Marjorie Fordyce with surgical skills and John Bracken and Dougie McGavin who provided technical and farm support. Keith Campbell, formerly at Nottingham University, had a long-standing interest in mammalian cloning and was credited by Wilmut with a major role in the achievements. The Roslin Institute nurtured this project after ABRO had become part of it.

Finally, the article by Myelnikov, referred to at the start of this article, left the impression that the introduction of molecular genetics to ABRO was the organisation’s salvation and only *raison d’être* for its continued existence*.* In fact most of the other research continued for some years, albeit with a declining budget. Moreover, the initial “molecular” project chosen, to produce a transgenic sheep that would produce a pharmaceutically useful product in its milk succeeded in that aim (the animal was named Tracey) but was commercially a dead end. It was not until later that gene mapping was introduced to ABRO by far-sighted members of its staff. This led, in turn, to the important tool of genomics in livestock breeding, now widely used

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