

QUANTITATIVE GENETIC THEORY AND LIVESTOCK IMPROVEMENT

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As in many areas of science, so also in the field of genetics, there has been an explosion of knowledge in recent times. Despite the pioneering work of Mendel and Darwin over a century ago, it was not until the early decades of this century that we could claim to have a generally accepted and verified theory of how inheritance works. It is less than 25 years since Watson and Crick discovered the biochemical nature of the genes which link the generations. The study of the biochemical basis of genetics has since expanded to become the field of "molecular biology", which holds tremendous promise for eventual applications in agriculture, medicine and industry.

While we still have much to learn, therefore, we have the substantial advantage over previous generations of livestock breeders that we can approach the subject with a comprehensive and proven theory of inheritance, which works all the way from the level of the molecule to the level of the population. How can this theory add to the effectiveness of breeding programs? After all, it can, with considerable validity, be claimed that previous generations of livestock breeders achieved remarkable changes and improvements in their livestock without the benefit of any knowledge of genetics. The answer is that the theory has two uses. In the first place, it provides a rational explanation of the way things work, and enables us to clear away much of the mystery and magic which in the past obscured the field. Thus, for example, we know why the genetic contribution of the male and female parents to the offspring are generally equal, why reproductive and survival traits are usually more difficult to improve than things like growth and carcass composition, how and why inherited defects can be reduced to negligible frequency in the population, but not completely eradicated, and why inbreeding is usually a practice to be avoided.

Secondly, our knowledge of genetic theory gives us a rational basis for planning and decision-making in livestock improvement programs. Parallel developments have taken place in other fields: a knowledge of the nature of disease has replaced empiricism in medicine; physics and metallurgy have become the basis of engineering practice. So in genetics, we are now able to calculate, with reasonable precision, the probable consequences of an inbreeding structure, the likely rate of improvement in a dairy breeding program, the limits to productivity in laying hens, and the appropriate balance to strike between different sources of information in selecting breeding animals. Furthermore, we are now able to link these physical consequences of the breeding program into their financial effects, and to develop a whole framework by which we can treat investment in livestock improvement as we would any other investment with a technological base.

HOW RELIABLE IS THE THEORY?

One might reasonably ask two important questions about this body of theory. The first is how reliable it is as a basis for action, in other words as a basis on which we can be expected to commit our time and resources. Secondly, if the theory is good, and well understood, why has it not been more widely used?

The physical reality which genetic theory seeks to explain is extremely complicated. Each individual (in mammals at least) receives an approximately equal complement of DNA molecules from each parent. There are thousands, perhaps millions of these units involved in developing and controlling the physiology of the animal. In addition to the active ones, there is an even higher proportion which appears to have no direct function. These molecules, which for convenience we call genes, are organized in packages, which we call chromosomes. The genes in general do not have direct effects themselves, but simply activate chemical networks, which are of great complexity, and are constantly shifting as the animal develops, and as the environment changes. A small part of this array of genes determines the sex of the animal, and thus switches the whole complex into either a male or a female development path. Furthermore, the genes which an individual receives from its two parents are not just thrown together in a common pool, but are arrayed in pairs which interact with each other in all kinds of ways. Sometimes the genes from both sides appear to co-operate, sometimes one masks the effect of the other, and sometimes their effects are antagonistic to each other. As a further, but by no means final, element of complexity, each year discloses new levels of variation and structural detail even within our convenient "genes".

Except in rare cases (e.g. horns in cattle) we cannot expect to link the performance of our livestock back to individual, and traceable, genes. The models we use effectively treat the basic chemistry of genetics as a "black-box". However, this is not so much a statement of ignorance, but an accommodation to practical needs. In building a bridge, an engineer does not need to refer to the basic chemistry of steel. He works instead with working models at a higher level, where the molecular properties of the material are represented by notions such as tensile strength and coefficient of expansion. In precisely the same way, the chemical processes of heredity underly the working models which we use in building breeding programs, and which use the concepts of heritability, genetic correlation, variance, heterosis, coefficient of inbreeding and so on.

The question of the reliability of our models is therefore not so much concerned with the basic chemistry of heredity, but with how well these working versions of it perform in practice. I have gone into the evidence which we have on the reliability of these models in somewhat more detail elsewhere (Cunningham, 1979). The present state of affairs can be summarized as follows:

1. For most traits of economic interest in livestock (growth, carcass composition, shape, milk production, temperament, disease resistance), heritability is in the range 0.2 to 0.6, and is quite a good predictor of response to selection for at least half a dozen generations into the future.
2. For many traits, the prediction may be good even beyond that. However the mere exercise of selection changes the genetic architecture of the population, and so we are much less sure about long-term predictability. In general, laboratory animal populations continue to respond for between 10 and 20 generations, though in large populations, response can last much longer than this.

3. For reproductive and fitness traits, heritability tends to be low (under 0.2) and is also a much less accurate guide to selection response. Often, this is simply because the expected response is low, and any deviation from it therefore appears proportionally larger. More importantly, it is probably because in these traits we do not act alone: nature is playing a simultaneous hand.
4. Where we get an advantage in crossbreds, this may be due to complementarity, or to heterosis, or to both. The heterosis effect appears to be linearly dependent on the amount of heterozygosity, that is on just how "crossbred" the animals are.

While some uncertainty always remains, therefore, the situation is that this working version of heredity enables us to launch a breeding program with reasonable confidence.

Why has this theory not been put to more use? First, because it is very new. If we were to ask these questions about the reliability of the models twenty years ago, the available evidence would have been extremely limited. Even today, much more testing and evaluation is needed. Furthermore, in the short time during which we have had enough understanding of genetics to apply it to breeding programs, it has found significant application in several species. In animal production, the most notable applications have been in poultry, where almost all layer and broiler strains in use in the western world are now the product of scientifically designed programs. Testing and selection schemes in pigs, and to a lesser extent in dairy cattle, have within the past two decades been set up to use the theory. In populations where it has not been used, it has largely been a matter of structure and organization. In order to apply the theory, some minimal degree of formal decision-making is required. Populations therefore which lacked a production recording system, and which had no objectively defined breeding goals have not been able to exploit the theory, at least in any coherent way. Furthermore, the mechanics of assembling data and refining it to the point where theoretically correct decisions could be made about breeding animals was extremely difficult until computers became better and more widely available. This, as we know, has been a very recent development. While we may sometimes complain at the long time lag between theoretical and actual realization of the gains which scientific breeding programs can bring, I think that people in a generation's time will be quite impressed with the speed with which theory was brought to bear on many domestic animal populations in our time.

WHAT OPTIONS DOES THIS THEORY PROVIDE?

Quantitative genetic theory presents us with three broad strategic options in the improvement of livestock populations. These are

1. *Selection within the population.* The selection may be based on individual performance, on information from relatives, on correlated or indicator traits, or on combinations of these. The success of selection depends on three factors: the accuracy with which genotypic values can be estimated, the intensity of selection, and the rate at which superior genotypes replace inferior ones in the population. This last factor involves many aspects of population structure, and it is only within the past decade that its importance has been fully realized.
2. *Population replacement.* It is probably true to say that most of the genetic change in our livestock populations in recent times has resulted from population replacement. Our experience in Ireland in the last two

decades has been a typical one. The replacement of the Shorthorn by the Friesian as the basic breed type in our cattle population began in 1949 with the introduction of the first Friesian bull in AI. By 1973, 70% of dairy cattle were classified as Friesian or Friesian cross, and this figure is approximately 90% today.

Most breed replacements which have taken place in the past have happened in an unplanned way. That is to say that they were not preceded by any systematic comparisons of the old and the new populations. In our case, analyses carried out when the change was about half completed showed a breed difference in milk production of the order of 20%, and for growth rate of about 8%, in both cases in favour of the Friesian. It is fairly clear in retrospect that this breed substitution was well advised, and that there would have been considerable advantages from speeding up the process.

In a cattle situation, where breed replacement is normally carried out by crossing with imported bulls, it is possible to quantify the potential benefits. I have attempted to do this (Cunningham, 1974) for the dairy situation.

TABLE 1: Expected frequency of occurrence of bulls of given breeding merit from populations differing in mean genetic value. (from Cunningham, 1974).

Breeding Merit of Bull*	Native Population	Population Exceeding Native by		
		8%	16%	24%
Number of bulls which must be tested to find one bull with merit specified in first column				
100	2			
102	3			
104	6	2		
106	15	3		
108	44	6	2	
110	160	15	3	
112	740	44	6	2
114	4,300	160	15	3
116	32,000	740	44	6
118	1,000,000	4,300	160	15
120	3,500,000	32,000	740	44

* Defined as percent of the average merit of tested bulls of the native population.

We can use this table to compare the benefits from importation with those from a within-population selection program. Thus, in the native population, a bull whose progeny exceeds the population mean by 10% is found once for every 160 bulls tested. If the exotic population exceeds the native one by 16% on average, then one bull in every three tested from the new population should have progeny of that merit. We can thus say that the expense incurred in acquiring and testing 160 bulls in the native population gives the same result

as the expense of acquiring and testing three bulls from the imported population. This is obviously an over-simplified picture, since other traits will be involved, and some of superiority may be due to heterosis. However, it does indicate that where substantial breed differences can be demonstrated, there is likely to be great, even irresistible, pressure for a wave of breed substitution.

There is great need for a more systematic approach to the exploitation of inter-population genetic differences than we have had in the past. In essence, this means a greater input to well planned, and internationally co-ordinated breed comparisons. In recent years, we have seen the beginnings of this in cattle populations. The growing interest in North American Holsteins in many Friesian populations stimulated the establishment of a large FAO sponsored comparison of black and white strains, which is currently underway in Poland. Similarly, the spread of Charolais and other European beef breeds had led to the establishment of beef breed comparisons in many countries, of which the largest is that in Clay Center, USA.

3. *Stable crossbreeding systems.* Crossbreeding systems are designed to exploit heterosis or complementarity or both. If the preservation of heterosis is the main interest, then systematic crossing between pure breeds or strains is the normal solution. In species with a high reproductive rate, like pigs, this can be achieved by continuous production of F_1 breeding animals. In cattle, this is normally not feasible, and the alternative usually is a reciprocal back-crossing (or criss-cross) system. Where the aim is to maximize complementarity, that is to simply combine the separate merits of the strains, then the formation of a new synthetic or gene pool population may be the alternative. A large number of breeding systems are available which meet these requirements. The following are six of the more likely structures to be of interest in a cattle population.

- * Two breed criss-cross. Pure-bred bulls of the two breeds are used in alternate generations. Offspring have 67% genes from the first breed, 33% from the second, or vice-versa. This is the main disadvantage, that these two levels of breed mix are always present in the population. On average, 67% of maximum heterozygosity is achieved.
- * Two breed gene pool. This is simply a synthetic, in which two breeds are crossed and *inter se* mating together with selection proceeds from the F_1 generation. This system maintains 50% of maximum heterozygosity, and on average a 50% mixture of the two breeds. However, individuals can vary in their composition from a predominance of genes from one breed to a predominance from the other.
- * Grading up to F_1 . This is a system in which F_1 bulls are continuously used on the population. The first generation contains a 75/25 gene composition, which rises over about three generations to a 50/50 mixture. The system maintains 25% of maximum heterozygosity.
- * Two breed gene pool with 75/25 mixture. This can be established by generating an F_1 between two breeds, and backcrossing this to one of the breeds, followed by selection from the offspring of this cross. A 75/25 breed mixture is maintained on average, but with individual animals deviating from this. Twenty-five percent of maximum heterozygosity is maintained.
- * Three breed gene pool. A cross between two breeds produces an F_1 , which is mated to a third breed, giving a 50/25/25 mixture, from which selection proceeds. Individual animals vary in their genetic constitution about this average. Fifty percent of maximum heterozygosity is maintained.

- * Criss-cross between pure breed and F_1 . In this system, an F_1 is produced by mating two pure breeds. The offspring are backcrossed to one breed. F_1 bulls are used in the next generation, and their offspring are again mated to the purebred. Purebred bulls of one strain, and F_1 bulls are used in alternate generations. The system maintains, on average, a 75/25 breed mixture and 50% of maximum heterozygosity.

SOME CURRENT BREEDING PROGRAMS IN DIFFERENT COUNTRIES

In the preceding section, I have discussed selection programs very briefly, because this structure is well-known. I have dealt in rather more detail with breed replacement and stable crossbreeding structures, because these are less well understood, because there has been considerable recent interest in crossbreeding in many populations, and because this is likely to be a more prominent feature of genetic improvement programs in the future.

I would like to follow this by commenting on some of the more progressive, successful or notable examples of breeding programs in current use in cattle populations in different countries.

Dairy Cattle

In most developed countries, dairy cattle populations are normally served by centralized AI systems, backed by intensive bull screening and selection programs and massive herd recording. The scale of these programs is perhaps best exemplified by the Norwegian scheme. This relates to a single population of approximately 400,000 cows, 97% of which are bred by AI, and 70% of which are milk recorded. Average production is over 12,000 lbs of milk at 4.55% butterfat. The breeding program involves computer preselection, and inspection of 1,500 bull dams, which are mated to a small number of bull sires, to produce 400 calves which go on station performance test for growth and feed efficiency. One hundred and fifty of these are selected for entry into AI, where they are used on sufficient cows to generate approximately 100 recorded progeny. After this, the semen is banked from each bull, until a total of 25,000 doses are frozen, after which the bull is slaughtered. Bulls which have had a high thyroxine value are retained until 50,000 doses have been stored. (Research has shown this measure to be related to the eventual milk production of their daughters). When the progeny test is complete after several years, 12 of these bulls are selected for widespread use, and the semen of the remainder is discarded. From among the 12, three are selected as bull sires for the next generation. Comparable, though less intense, programs are to be found in most European dairy cattle populations, and are in general delivering rates of genetic gain in excess of 1% per annum for milk production, together with maintenance or improvement of a wide range of parallel traits.

While this demonstrates a selection program, many European populations are simultaneously engaged in a breed replacement movement. The changing economics of dairy production, and in particular the improvement in the milk/concentrate price ratio in recent years has led to a great intensification of dairy production in European countries. This in turn has led to considerable interest in the more specialized north American Holstein strains of Friesian, which are now widely used in most European countries. In France, Germany, Denmark and Italy, Holstein use is now at a level which will effectively convert those populations to north American genotypes in less than a decade.

At the same time, we have in eastern Europe an example of the formation of a new dairy synthetic population, on a very large scale. In East Germany, the cattle population in 1970 contained 80% of Friesian types. Since then,

the authorities in that country have begun a program to produce a new strain which will have 50% Holstein-Friesian genes, 25% German Friesian, and 25% Danish Jersey. I understand that by 1980, one million out of the two million dairy cows in that country will have this breed constitution, and the expectation is that within a decade, over 90% of the population will consist of this new "SMR" synthetic dairy breed.

Beef Cattle

In beef cattle populations, the degree of organization of breeding programs is usually considerably less than in dairy cattle. The biggest single-purpose beef populations to be found in Europe are those in France, where approximately 1.5 million breeding cows make up the Charolais population, with about 400,000 in Limousin, and about 200,000 in the Blonde d'Aquitaine population. Each of these populations is served by a centralized breeding scheme. The bull selection cycle includes planned matings, preselection of young bulls at three months of age, testing in central performance test stations for growth, conformation and feed efficiency to one year of age, followed by progeny testing through artificial insemination. The progeny test is concerned with both the production characters of slaughter progeny and the maternal performance of the bulls' daughters as suckler dams. The progeny test for maternal characters is carried out in special testing stations, where the bulls' daughters are maintained from insemination through to weaning of their calf. All the heifers in the station in any one year are mated to a single bull to equalize the paternal effect.

In addition to purebred beef bull testing, in several countries, notably Britain, Ireland and Sweden, extensive testing of beef breed bulls is done for their value as crossing sires in dairy populations. In Ireland, for example, beef bulls recruited to AI after a station performance test are subsequently tested on approximately 300 calvings for ease of calving, and a sample of 20 steer progeny are reared through for growth and carcass assessment. The principal purpose of this testing is to select bulls which will then be widely used to produce commercial slaughter offspring from the dairy population. However, they also breed cows in their own purebred population (Hereford, Charolais, Angus or Simmental), and these breeds therefore benefit greatly from the testing and selection carried out.

In addition to pure selection schemes and systematic crossbreeding structures, we have had in recent years a number of synthetic beef breeds developed usually to combine the attributes of several strains. The Australian Belmont Red is an outstanding example. In Europe the only comparable enterprise is the Coopelso 93 strain, developed from the Charolais, Limousin and Blonde d'Aquitaine breeds by the French Midatest AI Organization.

FUTURE DEVELOPMENTS

What are the likely future developments of animal breeding structures and practices? Apart from the natural progression, development and intensification of selection schemes in most populations, I would expect to see much greater use of systematic crossbreeding in the long term. In cattle populations in which AI is feasible, crossbreeding is very easily implemented, and I would therefore expect to see crossing of some kind in most of our purebred dairy populations in the future. This will most likely take the form of criss-crossing between two separate, but approximately equal, strains. The black and white populations will probably constitute one strain, and the north European red populations may well provide the other. This judgement is based, firstly, on the growing evidence that while there is not much heterosis

for milk yield *per se*, there is considerable heterosis for total economic performance in dairy cattle. Secondly, as production levels increase, secondary characters connected with ease of management are likely to become more important, and in these, crossbreeding is likely to give a benefit. I would like to make two further important points about crossbreeding. The first is that to be useful, it must be systematic, and planned to meet precisely defined needs. The second is that whatever crossbreeding structure is adopted, long-term gains are still dependent on continued selection, whether in the parent strains or in a synthetic population.

The movement of genetic material is now a great deal easier than it was years ago. In particular, shipment of semen can make available overnight genotypes from the other side of the world. One consequence of this is the universal, and growing, swing to extreme Holstein-Friesian dairy types of cattle in all parts of the world. This concentration, world-wide, on a single, though large, pool of genotypes seems to me dangerous in the long run, and some kind of corrective action will be needed. However, it is difficult to know how we can at reasonable cost go about the preservation of genetic material on such a scale.

We will probably see the development of much more extreme genotypes and production systems than we can now imagine, to serve particular economic opportunities. Perhaps the best current example is the evolution of the Belgian Blue-White breed from a dairy population 20 years ago, to the point where half of the population, comprising a quarter of a million cows, are now engaged in purebred beef production in a highly specialized form. The selection emphasis is on the double muscle character, which gives carcasses of extremely high value (2,000 to 2,500 Australian dollars). However, this entails an incidence of Caesarian delivery of calves of approximately 50% in heifers, and over 20% in cows.

If control of the sex ratio became feasible, then the breeding structure of populations would change greatly. It would have the immediate effect of driving all dairy populations into a highly specialized dairy role, coupled with extensive crossing with highly specialized beef sires to produce male calves for slaughter. However, on present evidence, this is still some decades away. Other developments in reproductive physiology are closer at hand. Bovine and ovine egg transfer is now common. Its primary benefit seems to have been to permit the rapid expansion of small nuclei of animals. Its use in a beef population can permit a doubling of the rate of genetic change for a character like weight gain. However, this is only in ideal situations, and is likely to be worthwhile only in rare cases. On the dairy side, while egg transplantation is routinely used in, for example, Germany, to produce young bulls for AI testing, it is difficult to justify this operation on the genetic gains which it brings, and the practice is therefore not likely to become widespread. Now that freezing of embryos is becoming a practical proposition, ovum transfer in commercial conditions may become feasible. This can be used to bring about a high rate of twinning, and could give an increase of 60% in the net revenue of a suckler calf operation.

Another area in which I can see significant development in the years ahead is in the development of selection programs geared to disease resistance. There is substantial evidence that, at least in mice, selection can be effective for immunological reaction to sheep leucocytes, and also that phagocytotic activity, as measured by carbon clearance rate, is responsive to selection.

The structure of the organizations that serve animal populations has changed dramatically in some countries in recent years. In most European countries, the breed societies, which formerly limited their activities to maintenance of a herdbook and organization of shows, have now generally come

together with the AI industry, largely co-operative in structure, and the recording and data processing organizations, to operate planned breed improvement programs. This growth in co-operation has taken time, and much discussion, but I think you would find it difficult to persuade cattle breeders and producers that it has been other than worthwhile. This kind of collaboration has of course been most rapid on the dairy and beef scene, where the need to pool interests in a program linked to AI was obvious. It is also happening in sheep and pig populations, usually to exploit the benefits of centrally organized testing and recording schemes. It is notable that these developments have in many cases brought a new level of importance to the traditional purebred seed-stock producers, who can now benefit from a much more objective selection base, and a good network for the propagation of superior stock. One of the significant developments for the future will be the spread of this kind of co-operative breeding structure to other areas.

The one confident prediction that I can make is that the task of managing the future evolution of our domestic livestock populations holds plenty of challenge for both breeder and geneticist.

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