The Science of Genetics

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(Extracted from the Guernsey Breeders' Journal, Vol. 2 No. 4, Winter, 1948)

THE science of genetics, or the theory of inheritance, has had surprisingly little application in the field of applied breeding although the fundamental mechanism of inheritance has been well understood for many years. The main reason for this is that the characters most easily studied in the laboratory are those controlled by single genes (the unit of inheritance), and whose measurement is simple and clear-cut. Examples of such genes in cattle are those controlling red colour as against black, polled as opposed to horned, and also those controlling blood groups. Blood grouping in cattle has now reached the stage where cases of doubtful parentage can be settled with almost complete certainty and it is actually being used for that purpose by Guernsey breeders in America. Breeding for such characters as colour or lack of horns is comparatively simple, as it is fairly easy to decide which genes a given animal possesses. But when the scientist comes up against characters whose expression is controlled by more than two or three genes, the picture becomes entirely different. Almost all characters of economic importance in farm animals fall into this group—milk yield, fat percentage, rate of growth, and so on, and there is the additional complication that the measurement of the effects produced by the genes is no longer as clear-cut as deciding whether a cow is red or black. The 305-day yield is affected by many external factors that have nothing to do with a cow's breeding value—trouble at calving, infections, and so on. This leads to a situation far removed from that which the geneticist usually has to deal with in his laboratory. And it involves a completely different approach for him—one which often gets involved in complicated mathematics. However, the necessary techniques have been slowly built up and the stage has now been reached when some help may be given to the practical breeder. It is the intention of this article to show the geneticist's point of view and to indicate the application of the method to one or two breeding schemes.

Before the breeding method can be discussed, it must be made clear what we are breeding for; I would define this in dairy cattle as the economic production of milk and fat under commercial conditions. Included in this will be such characters as longevity, which influence the profitability of milk production. In this article, I shall be referring mostly to milk yield and fat percentage. It will be assumed from the beginning that all these characters are controlled by a large number of genes—the exact number being unimportant. The first step is to clear out of the way the variation caused by

external factors we know to affect milk yield—age, month of calving and preceding dry period. We will then correct for these factors, after determining their effect, and use the corrected yield for the genetic investigations. The next and most fundamental step in the geneticist's approach is to discover to what extent the corrected performance reflects breeding value. We can compare the breeding value of any two groups of cows by looking at the performance of their daughters by the same bull. Suppose we take all the daughters produced by a bull (all the daughters being in the same herd) and divide them into two groups according to the yield of their dams in the first lactation. Now the difference between the groups of daughters will be due to the genes contributed to the two groups by their mothers, since the sire will, on the average, contribute the same to the two groups. But this difference is only half the difference between the breeding value of the dams in the two groups, since they contribute only half their daughters' genes. In practice, we find that for 100 gallons difference between the groups of dams, there is 12 gallons difference between the daughters, i.e., 24 gallons difference in breeding value of the dam's groups. It means that, after correcting for the obvious external factors that affect yield, the difference in breeding value of any two cows is still only one-quarter of their difference in performance. In other words, only one-quarter of the variability of corrected yield is due to genetic causes and the remaining three-quarter is due to intangible differences in the surroundings of the cow, even though all cows have had the same treatment as far as the cowman is concerned. For fat percentage, the figure for the genetic variability is higher, probably accounting for about half of the total. This fraction, the proportion of total variability in corrected performance that is due to differences in breeding value, is of fundamental importance in the new approach and is called the "heritability" of the character in question. There are some breeders who, having realized that performance is a poor measure of breeding value, have gone the whole hog and denied any connection between the two at all. However, the above direct measurement of "heritability" in which the figures are drawn from actual results, contradicts this assertion.

So far, we have only discovered what happens inside a herd, in which, as far as the cowman is concerned, all cows get the same treatment. But nobody would dispute that, as far as concerns differences between herds, differences in management can play a very large part. For the comparison of records made in different herds, it is necessary to estimate the reliability of the herd average as a measure of the breeding value of the herd. As yet sufficient evidence is not available in this country to make a reasonable guess. However, the records from cows produced by artificial insemination by the same bull in different herds, now available from several A. I. stations, suggest that herd average is not a very accurate measure of the genetic level of the herd. Results from U. S. A. and New Zealand on progeny testing indicate that about one-quarter to one-third of the differences between herd averages is due to differences in genetic merit. The figure for fat is probably higher. It is well known that it is more difficult to put up fat by skilful management than it is to put up yield. In England and Wales, the picture is complicated by differences in local conditions which cause, roughly, high yield and low fat in the east and the reverse in the west. The whole question of the relation between the performance and breeding value of herds is one which needs

much further work. It is obviously of the greatest importance in evaluating pedigrees to get some method, even if only approximate, of allowing for the management level of a herd.

Within a herd, at least, the picture is fairly clear and it is possible to make use of the estimates of heritability to calculate the genetic gains possible by various methods of breeding. In this approach, we shall always be dealing, for instance, with the "average result" of a certain course of action or with the average yield of the progeny from a bull chosen in a certain manner. Even though the breeding value of the two parents is exactly known, it is impossible to predict the performance of any individual offspring with any certainty. One has only to look around to see the great differences there are between full brothers. This is partly due to the fact that all offspring do not receive the same genes from their parents and partly due to the large amount of variability from nongenetic causes. We will first consider a closed herd (i.e., one in which there is no importation of breeding stock) of sufficient size to avoid close inbreeding say 100 cows. The normal method of improvement can then be split into two—

(i) culling of low producers;
(ii) breeding of bulls from the best cows in the herd.

The possibility of the culling of low producers depends, of course, on the natural wastage rates in the herd. A distinction also arises between the breeder and the milk producers. It would seem profitable for the farmer to do all his culling early, say before the end of the second lactation, disposing also of all offspring of the culled animals and breeding from those retained, as long as they will live.

The producer, on the other hand, should cull entirely on the basis of the immediately previous lactation. In fact, the distinction between the two types of herd is far from rigid and most people carry out a mixture of the two policies. We will consider a breeder with a herd average of 800 gallons, who does all his culling on first lactation records and who feeds all available heifers into the herd. He would then dispose of about half his heifers after their first lactation, with the result (assuming that all his culling was for reasons of yield) that he would be breeding from cows which were about 100 gallons better in performance than the average of cows born in the same year, that is 25 gallons better in breeding value. He can breed bulls from the best cows in the herd, say the best 5 per cent. which means cows about 300 gallons better in performance than their contemporaries, giving a superiority of 80 gallons in breeding value. The offspring will receive half of these benefits—the heifers will be 12 gallons better and the bull calves 40 gallons better. So the animals born to be used for further breeding will be on the average $\frac{40+12}{2}=26$ gallons better than those born one generation before. As a generation in dairy cattle is 4–5 years, this means a genetic improvement of about 5–7 gallons a year. It must be emphasized again that this is an average value—it is what you would get if you carried out the same policy on several herds and took the average. Some would be lucky with bulls and some would not. Of this increase, about one quarter would

come from culling low producers—the rest would be from breeding bulls from good cows. Such closed herds are not very common, due to the inbreeding limitation on size and, as in buying a bull from outside one is presumably less informed about his probable worth than if he was homebred, this estimate is probably higher than the average rate of improvement over the whole country. The only herd that we have thoroughly analysed gave a probable improvement of 2–3 gallons per year although these low figures are partly due to much involuntary culling of reactors.

Some writers on animal breeding in reaction of the apparent lack of connection between performance and breeding value, have suggested that the progeny test may provide a possibility of rapid improvement. This is undoubtedly true, subject to certain conditions. From the genetic point of view, the progeny test is a method of increasing the accuracy of measurement of the breeding value of a bull, with the disadvantage of using him as a much older animal and thus increasing the generation length. Referring back to the calculation of the rate of gain in a closed herd, the total improvement is increased but it is now relative to those animals born 7 or 8 years back instead of 4 to 5. As the breeder is interested in rate of improvement per year, these two points are in conflict. It is roughly analogous to the dilemma of whether to take a stopping train leaving immediately or to wait two hours for the express. It is often assumed in discussions of progeny testing that the yield of 10 or 20 daughters gives sure measure of the bull's breeding value. But just as we can speak of the heritability of a cow's record, so we can speak of the heritability of a bull's performance. Suppose we pick out all bulls whose 10 daughters averaged 100 gallons better than their dams (and their dams were average for the breed) and use them again. Then their second lot of daughters will average 40 gallons better than their dams. In picking out those bulls with a good performance, we have chosen partly those whose daughters were fortunate in their environment and partly those really superior in breeding value. In other words, the difference in breeding value of bulls judged on 10 daughters is only 0·40 of the difference in performance. The corresponding figure for a judgement on 20 daughters is 0·57. These figures for the heritability of a bull's performance are derived directly from the figure of one quarter for the heritability of a cow's single record.

In the consideration of any scheme for progeny testing, we can vary a good may factors. We can list them as follows :—

(i) the size of the total unit;
(ii) the extent to which tested bulls are used;
(iii) the number of bulls tested;
(iv) the number of progeny tested per bull;
(v) the age of the bulls at testing.

The answer to the last question is obvious. Bulls must be tested at as early an age as possible to cut down the generation length and also to reduce losses between testing and further use, and increase the period of further use. The other questions require some thought. Some American workers have considered the value of progeny testing in a closed herd of similar size to that discussed above and have concluded that progeny testing was not economical there. In a small herd, the number of progeny required

to test a bull with any accuracy cuts down the number of bulls that can be tested (one may have to select one out of three) and also the proportion of the herd on which the tested bulls could be used. All in all, the testing does not pay for the increase in generation length.

It would seem obvious that if bulls are to be selected after considerable trouble, they must be used on the widest possible scale. This means artificial insemination and, if we are to avoid inbreeding and use at least two bulls per unit, a minimum size of 2,000 cows. Calculation shows that the best structure for such a unit would be somewhat as follows :—

(i) the usual culling of low producers ;
(ii) about 7 bulls out of the best cows in the unit, to be tested per year ;
(iii) each bull to settle 60 cows which may be expected to give 20 heifers in-milk in about 3 years ;
(iv) two tested bulls to be used on the rest of the unit (the testing will occupy about one-fifth of all cows). It is assumed that each tested bull will be good for three years further life. The wastage of bulls needs further investigation.

A Unit with this structure will give a probable improvement of around 10–12 gallons per year. Of this amount, about one-third comes from the first selection of bulls for testing from the best cows in the unit. Without this, progeny testing would apparently not be much more valuable than the normal selection outlined above. It seems probable therefore that progeny testing will be valuable if done on a sufficiently large scale and give improvements at about twice the rate expected by normal selection. However, progeny testing will not be valuable on small units of size around 100 cows. 2,000 cows would seem to be the minimum.

This argument has been built on what may appear to some to be a very shaky foundation. It is reasonable to ask what practical evidence there is as to the validity of such conclusions. Obviously, it is very difficult to test them in cattle because of time. However, similar calculations of the probable improvement have been made in pigs and poultry, where the generation length is much less, and in both cases the actual gains were very close to those expected.

This brief article has indicated the approach that geneticists are now using in connection with animal breeding and has shown its application to the question of progeny testing. There remain many topics with which there has not been time to deal, such as pedigree evaluation, nicking, and the different systems of mating such as inbreeding and line-breeding. Most of the examples used have been taken from American data. However, a large survey of the genetics of milk production is now under way in this organization, and the records of several of the leading Guernsey herds in the country have been kindly loaned to us by their owners and are included in this work. It is hoped that the results from this investigation, which at the present give the same general picture as the American results, will help in solving the problems which are arising in dairy cattle breeding in this country.