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PROSPECTS IN ANIMAL IMPROVEMENT THROUGH BREEDING

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SUMMARY

In this paper some ways of speeding up progress in improvement of livestock by genetic means are discussed. Attention is drawn to the need to clarify the objectives of an improvement programme under a grassland system of farming, and to the need for the development of services to assist breeders in making selection decisions. Other topics considered are early recognition, the association of simply-inherited characters with production, and manipulation of the environment to display genetic variation.

IN CONSIDERING METHODS whereby progress in livestock improvement can be speeded up by genetic means, it is convenient to divide the topics to be discussed into two groups:

(1) Methods which can be adopted within the framework of existing breeding systems.

(2) Approaches which modern genetic knowledge, based largely on laboratory organisms, suggests as being worthy of experimental investigation with livestock.

The discussion will necessarily be brief and will omit reference to a number of questions such as corrections for environmental effects and the use of artificial breeding.

PRESENT BREEDING METHODS

In the larger domestic animals, selection and cross-breeding are the main, if not the only, methods used at present to produce genetic change. In this paper attention will be focused on selection.

The theory of selection which is actually used in animal breeding work at present is comparatively simple. It is convenient for present purposes to write the genetic gain per year achieved by selection in the following way:

$$\text{Genetic Gain per year} = \left\{ \frac{\text{Heritability} \times \text{Selection Differential}}{\text{Generation Interval}} \right.$$

In general, speeding up the genetic gain per year can be achieved by either increasing the accuracy of selection (heritability), increasing the amount of selection (selection differential) or decreasing the generation interval—or a combination of these three factors.

The above description of the response to selection is based on the assumption that the character is controlled by many genes, each with individually small and additive effects. The main developments of this simple theory, at least in breeding most animals, have been towards increasing the accuracy of selection by using progeny tests, family tests and repeated measurements on the individual—*i.e.*, sources of information which have generally a higher heritability than just a single observation on the phenotype of the individual animal.

The immediate objection which can be raised at this stage is that the selection theory outlined above is too simple to describe the genetic situation. For example, it omits the possibility that dominance, gene interaction, interaction between heredity and environment, linkage, maternal effects, etc., may be causes of variation in the character being selected. This is true. The main reasons why they were neglected are, first, that very little is yet known of their importance in livestock and, secondly, that, with perhaps the exception of cross-breeding, the methods required to utilize this non-additive genetic variance are difficult, time-consuming and expensive. Hence, the cost of achieving genetic gain would be much higher than at present. Thus, it is of great importance to investigate all possibilities of making the simple additive theory work as well as possible.

Objectives in Livestock Improvement

Clarification of the objective in an improvement programme is still a major consideration in speeding up progress from breeding. Most attempts to assess the relative economic value of traits in farm animals, such as those of Rae (1954) and Dunlop and Young (1960), have been based on prices which the market is prepared to pay for differing qualities and quantities of the product concerned. However, even if all the data required to use this approach are available, it still suffers from disadvantages, some of which have been pointed out (Rae 1958). In particular, it will always rank the highest-producing animal (where production is measured as a combination of the various characters weighted by their relative economic value) as "best". It takes no account of the possibility that the highest-producing animal may not in fact be the most "efficient".

A concept of animal efficiency which is useful for animal breeding within a grassland system of farming is by no means easy to define. Probably the simplest measure of animal-grassland efficiency is production per acre. If one is prepared to neglect the animal-pasture interactions and possible heredity-environment interactions, then the more traditional animal measure of efficiency, such as production per unit of feed consumed, should be related to production per acre. Even this is not sufficiently easily measurable under grassland conditions to act as a suitable yardstick. Consequently, in practice, one is forced to measure efficiency by expressing production as a ratio to some function of body weight. Such a measure of efficiency has been suggested by Wallace (1956) for butterfat production and by Ferguson (1956) for wool production.

Although the information is not available to reach any conclusion, it seems worth analysing further the question of selection for efficiency in the Romney Marsh breed. Considering first, selection for efficiency of wool production measured following Ferguson (1956) as the ratio of fleece weight/body weight. It is possible to estimate the heritability of this compound trait and the consequences of its use. Taking the heritability of fleece weight and body weight as 0.17 and 0.40 respectively, the phenotypic correlation between the two as 0.40, and the genetic correlation as 0.20, then the heritability of efficiency is found to be 0.38. Selection for fleece weight alone would tend to increase efficiency but at less than a third of the rate achieved by direct selection for efficiency. On the other hand, selection for efficiency would produce only little increase in fleece weight. Hence it would be necessary to achieve an accurate balance between pasture production and stocking rate in order to reap the benefits of using the more efficient animals.

A very important consideration is that the genetic correlation between this measure of efficiency and body weight is negative and quite large (−0.79). Thus, in use, such a measure would lead to a consistent reduction in body weight. The importance of such a reduction cannot be assessed until more information is available. If the genetic correlation between body weight and lamb production is positive, then a reduction in body weight would be undesirable.

Although no conclusion can be drawn, enough has been said to emphasize the fact that adequate definition of the objective in animal improvement is of major importance.

Early Recognition

The length of the interval between generations has a very substantial effect on the rate of genetic progress. Basically the length of the generation interval is a property of the typical age composition and reproductive properties of the species. But to some extent it is also under the control of the breeder. For example, there is evidence to suggest that, in breeding Romney Marsh sheep, increased rate of progress can be obtained by using selected sires for only one season and then replacing them by sires selected from the next crop of two-tooth rams. In effect, the selection differential is slightly lower by the use of this procedure but this is more than compensated for by the lowering in the generation interval.

In many circumstances, the length of the generation interval is controlled by the length of time the breeder has to wait to obtain the information on which to make his selection decisions. For example, progeny test information on a dairy bull is not available until a sufficient number of his daughters have had at least one lactation. If the productive merit of the daughters can be recognized earlier, then it may be possible to reduce the generation interval. In poultry breeding, basing selection on a part egg production record of 4 to 5 months' duration, has allowed flocks to be composed, if needed, entirely of pullets and cockerels, whereas selection on a full record necessitates using only older birds for breeding. By so doing, the generation interval is reduced from two or more years to one year.

In sheep breeding, one of the most economically important problems where an earlier assessment of a character is required concerns selection for lamb production. Selection for fleece and carcass characters can be adequately carried out before the ewe enters the flock. But the earliest assessment of the ewe's phenotype for fertility and milk production can be made only after she has had the opportunity to lamb as a two-tooth. At present, there are at least four characters under investigation which could be used in normal stud or flock conditions to predict the likely performance of a ewe before she has had a lambing. These are face cover, body weight, occurrence of and number of oestrous cycles as a ewe lamb, and whether the ewe was born as a single or a twin. It is perhaps worth outlining the information which is required for a final assessment of the usefulness of these techniques:

(a) The phenotypic relationship between each character and subsequent lamb production. There is now quite extensive information available for all of these traits.

(b) The genetic correlations between each character and lamb production. No information is yet available in New Zealand on this aspect. It is, however, necessary to determine these correlations since they decide both the direction and the amount of the genetic change in lamb production which would result from selecting on any one or a combination of the suggested bases.

(c) The heritabilities of each of the traits. Some information is available on face cover and body weight.

This information also determines to what extent the various traits contribute independent information about lamb production and whether combined use of two or more of them is justified. Generally, in problems of this sort, the question is whether the often decreased accuracy of selection is more than compensated for by the decrease in the generation interval.

ORGANIZATION

Before closing this discussion of methods of speeding genetic improvement within the present structure of breeding systems, it is pertinent to ask the question whether the knowledge currently available on how to achieve maximum gains from selection is being used efficiently in breed improvement. In the dairy industry, the answer is in the affirmative. In the sheep, beef cattle, and the poultry industries, the answer is negative. The reasons for this state of affairs are complex. One basic problem, however, is the lack of any organization to supply the necessary services to these industries.

Basically, a system of organization is required which achieves three purposes:

(a) Increased size of breeding unit where this is necessary.

(b) Technical advice and operational research on breeding matters.

(c) Record keeping and analysis of information for selection decisions.

There seem to be three ways in which this can be accomplished:

(a) By industry organization with Government support as has been achieved in the dairy industry.

(b) By individual breeders grouping together to form either public or private companies in order to have units which are of sufficient size to make it economic to cover the costs involved in the services mentioned above.

(c) By establishment of co-operative societies whereby a number of breeders pool their resources to organize the services which they require for their breeding work and integrate their breeding operations to obtain the advantage of adequate size.

There is, however, insufficient experience available to choose between the three possibilities. It may well be that, in the variety of circumstances which exist in the various industries, all methods of organization may play their part.

GENETIC PHENOMENA OF INTEREST IN ANIMAL IMPROVEMENT

In recent years, not only have a number of new genetic phenomena been described, but also new knowledge has given a better understanding of phenomena which have been known for many years. From this vast accumulation of information, it is difficult to choose aspects which are likely to have significance in animal improvement. The present selection is not exhaustive and many important possibilities such as the induction of mutation and the physiological analysis of complex traits are not considered.

The Nature of the Gene

In reviewing progress in genetics, the most striking advance has been in knowledge of the nature of the gene. The classical concept of the gene as a single indivisible entity, defined in terms of mutation, recombination and function, has been vastly altered by detailed studies of complex loci in many organisms. The question must then be raised as to whether the modern concept of the gene requires some re-formulation of the theory of quantitative inheritance.

Briefly, it appears that the chromosome may be divided into regions or loci, each of which has a specific function in controlling a biological activity. Each locus probably contains a number of sites at which mutation and recombination can occur. In addition, within a locus, position effects may occur between alleles at different sub-loci. No attempt has yet been made to study a model for quantitative inheritance which takes into account intra-locus position effect. Griffing (1960), however, has pointed out that, if the locus is still regarded as the basic entity, then the possible gene states at the sub-loci can be looked on as different alleles of the locus. This by-passes the need to consider position effects. This approach requires a broadening of the definition of mutation to include both change at a mutational site and recombination within the locus. However, since both of these are of low frequency, they can well be neglected in animal breeding studies.

Thus, at present, there still seems to be no compelling reason for changing basic genetic models of quantitative inheritance (provided they are broad enough to encompass multiple alleles at a locus). Yet one cannot entirely avoid the suspicion that deepening knowledge of gene structure will produce information of significance to population genetics.

Association of Simply-inherited Characters with Production

In the past 15 years, there has been considerable interest in the study of simply-inherited biochemical systems in domestic animals. A number of such systems are known—the blood groups, serium β-globulins, haemoglobin types, β-lactoglobulins, α-lacto-albumins of milk, potassium blood levels, etc. A major incentive in the investigation of these factors is that they may be of assistance in speeding up livestock improvement.

From the genetic viewpoint, there are two aspects which need to be taken into account in considering the usefulness of simply-inherited characters such as the blood groups. First, there may be a consistent average difference between those animals which carry a particular gene or show a reaction with a specific serum and those animals which do not. Secondly, heterozygotes at the marked locus may be superior in production characters to homozygotes.

Evidence for the existence of the first phenomenon—an average difference in a trait due to a particular allele—has recently come to hand. Ashton (1960) in a study of the serum β-globulin types of bulls at cattle breeding centres in England concluded that the β-globulin locus was concerned in genetic control of milk yield. Rendel (1959) found significant associations between some blood group genes and fat percentage in Swedish cattle, while Mitscherlich, *et al.* (1959) gave evidence of a depression of milk yield associated with the blood factor *M*. Neimann-Soerensen and Robertson (1961), working with the Red Danish dairy cattle, found that cows with one of the *B* system alleles had higher fat percentage.

There are two possible genetic explanations for this direct effect:

(a) The locus controlling the blood group antigen may be linked with a locus which affects the productive trait.

(b) The blood group gene may have a phenotypic effect on the productive trait—*i.e.*, the blood group gene plays a direct part in the physiological processes regulating the trait. In the limit, of course, these two processes are operationally undistinguishable, since, if no crossing-over occurs between the two loci, their effects can never be separated.

It has been recognized for a long time that linkage between a marker gene and genes for production is unlikely to be helpful in animal improvement. This arises simply because, if crossing-over occurs, the genes can exist in either the repulsion or the coupling phase. These two phases in time reach an equilibrium condition at which stage selection for the marker gene will not alter the frequency of the gene concerned with production. Temporary advantage could possibly be taken of linkage where the equilibrium has been disturbed for the time-being as a result of a recent cross. The statistical difficulties of establishing the existence of linkage between a marker gene and metric traits are also important and have been reviewed by Lowry and Schultz (1959). Neimann-Soerensen and Robertson (1961) found no evidence for linkage in their data. The efficiency of the test, however, was of a low order.

The usefulness of a direct pleiotropic effect of the marker gene in improving the efficiency of individual selection depends primarily on the proportion of the total additive genetic variance which it controls. Ashton (1960) reported that the β-globulin locus controls about one-sixth of the additive genetic variance in milk yield. This would appear to be an overestimate, and Robertson (1961) considers that only four per cent. of the variation between sires in their progeny test results is controlled by this locus. Neimann-Soerensen and Robertson (1961) estimated that about eight per cent. of the additive genetic variance in fat percentage was controlled by blood group loci. It is clear that this proportion is too low to have much value in selection of individuals in most circumstances. At the same time, the value of information on a marker gene will depend on what other information is available. It is relatively more useful in prediction of production where no measure of the productive worth of the individual is available, *e.g.*, choosing young bulls for progeny test.

So far, evidence for the second aspect—superiority of the heterozygote—comes only from studies of the blood groups in poultry. In this species it has been found that highly inbred lines of chickens show greater heterozygosity in the A and B blood group systems than would be expected from the degree of inbreeding reached. This observation suggests that artificial and natural selection tends to favour birds which are heterozygous for the blood group alleles. It has also been found that productive characters such as hatchability, viability, growth rate and egg production were better in heterozygotes than homozygotes. This information, supplied by blood grouping techniques, seems to have found successful application in poultry improvement. Little information is available on the larger domestic animals. Neimann-Soerensen and Robertson (1961) failed to find any superiority of heterozygotes for blood groups in their study of Danish dairy cattle.

Disruption of Canalization

Waddington (1957) has discussed the importance of the phenomenon which he has called "canalization"—*i.e.*, the tendency for a developmental process to be retained within its normal course in the face of both genetic and environmental forces tending to deflect it into other pathways. Since canalization of a character confers regularity and precision on its development, natural selection will operate in favour of its development in characters which are important to the fitness of the individual. Moreover, the result of the development of strong canalization will be to mask both genetic and environmental variability and, in the limit, to make the character invariant and, therefore, in normal circumstances, unresponsive to selection. In contrast, disruption of, or avoidance of, canalization by either genetic or environmental means, may uncover hidden genetic variability and make it available to selection.

Work to elucidate this phenomenon has been done largely with laboratory animals (*e.g.*, Dun and Fraser, 1959; Rendel, 1959; Fraser and Kindred, 1960; Rendel and Sheldon, 1960). The implications for animal improvement are that it may be possible to manipulate the environment, or specific components of it, to display more clearly the hereditary potentialities of an animal. For example, use of nutritional stress may well be a useful tool in breeding animals for a grassland system of farming where normal methods of pasture management lead to such a stress at certain times of the year.

Alternatively, genetic means may be used to uncover hidden variability. It is generally true that mutant genes have a greater phenotypic variability than their normal alleles. In effect, they act as a stress on the organism carrying them. In general, the availability of such mutants in domestic animals is a factor which limits their usefulness in this sphere.

In conclusion, it should be noted that one of the important contributions which genetics has made to the problems of animal improvement is in giving a better appreciation of the types of genetic variation which control productive characters of livestock. In addition, genetics has given a better understanding of how this variation has been moulded by the previous history of the species. Information of this type is always useful in tackling the basic operational problem of livestock improvement.

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