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GENETICS AND LIVESTOCK IMPROVEMENT

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The choice of a topic for a Presidential Address should entail little difficulty for an animal breeder since it involves selection, a process on which he should be well informed. I am forced to admit, however, that experience of selection has proved of little value in this connection, except perhaps to exemplify further one of the recurrent problems facing the breeder—that of defining his objective. Perhaps it is worth a minute or two to detail the selection process and the reasons for culling. The problems of dairy cattle improvement have been ably dealt with by our President of last year. Pig improvement, we hope, will be the purview of our President for next year. Poultry improvement by breeding has never been the subject of discourse at these meetings and although there is a wealth of overseas information of interest and importance, there are few data on our local problems. Breeding for better wool, while it would be an interesting topic, is a little specialized and narrow for present purposes. The possibilities thus being limited, it seemed a favourable opportunity to talk about genetics in relation to modern animal breeding, to define the scope of the problems the geneticist considers to be in his field, to review our present state of knowledge on the concepts involved, and finally to see their application to my own current interest in breeding more prolific sheep. The first aspect is an obligation which has to be discharged because of the frequent misunderstanding, evident in many recent statements, of the role of the geneticist interested in animal production. The second is a concession to the need to talk about a problem of more than passing local interest.

THE FIRST CONCERN of the animal breeder is to define the goal for improvement in the particular breed to which he is devoting his efforts. Any discussion of objectives in animal improvement requires consideration of two questions. First, what do we wish to do? Should we, for example, strive towards producing a single champion performer—the ideal animal—in the hope that it will propagate its kind? Discussion with most sheep

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stud breeders suggests that this would be their wish. Our increasing awareness of the properties of animal populations has, however, allowed us to define more rationally, if perhaps more conservatively, what can be done. Essentially, the aim must be to increase the average productivity of the flock or herd. No longer do we regard the single outstanding performer as our goal, since we can be sure, in most cases, that its outstanding performance is due more to a happy quirk of the environment than to exceptional inherent ability. Our concern is with the superior population, not with the superior individual. It can be argued that we would like to have a greater control over variability—that genetic homogeneity would be desirable as Hagedoorn has claimed. It is open to doubt whether this objective is desirable even if it could be attained. Genetic homogeneity implies adaptation of the breed or strain to only a small range of environments, and, in lowly heritable characters, accomplishes only little reduction in phenotypic variability. Moreover, it now appears unlikely that a homozygous genotype giving optimum productivity exists.

The second problem in defining objectives arises from the fact that it is seldom that total productivity of the animal is dependent on only one characteristic. In these circumstances, it is necessary to decide on an order of importance of the various characters so that selection can be most effective in improving total productivity. This problem occurs in its most acute form in the sheep, where wool, lambs and meat, each with its own details of quality, are part of the total production from the animal.

One approach to this difficulty has been to determine a 'relative economic value' for each character—*i.e.*, to find the amount by which the net financial return from the animal is increased by improving each trait by one unit. This involves a study of prices, costs and returns for products of differing quality and quantity and, as such, is a problem which can be placed fairly in the lap of the economist. The fact is, however, that the economists have evinced little interest in this approach and it has been left to the animal breeder to attempt to assemble the information required to make initial approximations in order to define his objectives. At the same time, one must concede that little attempt has been made to formulate the problem in a way which can be best understood by the economist.

This approach of determining the economic importance of each character is defensible on the grounds that it is directly

related to the financial return which the commercial producer receives. It thus spells the death knell of breed standards and breed points as the criteria of the worth of an animal. It substitutes an operational principle for the traditional belief in the importance of the hallmarks of a breed. Its acceptance in the long run relegates the maintenance of breed fancy points to the sportsmen or devotees of the 'fancy' where their efforts should in time involve little hinderance to the course of breed improvement. It does involve problems, some of them not simple. How, for example, does one distinguish the true and long-term changes in market price from short-term fluctuations? Moreover, one is usually required, because of the long-term nature of breed improvement, to predict what the future structure of prices will be. Also the approach is one-sided in that it defines only the economic environment within which the breed is expected to produce. It takes no account of any limitations imposed by the physical environment and thus gives no measure of the importance of a characteristic such as "hardiness" or adaptation to the environment. Furthermore, it does not take into account the more fundamental conception of the efficiency of the animal in the productive process of converting fodder to meat, milk and wool. Its present justification lies in the fact that it gives immediately useful information to act as a guide while more basic information is coming to hand.

Another approach to the elaboration of objectives is worthy of mention because of its particular pertinence to wool, a product in which assigning a direction of improvement is difficult. The question can be posed in this form: To what extent are the characteristics of the fleece important to the manufacturer in deciding the quality of the finished fabric and the efficiency of the manufacturing process? To what extent do differences in handle, lustre, length, fibre diameter, variations in fibre diameter, crimp etc., affect the performance of the fibre in manufacture? If this question—or rather, series of questions—can be answered, then we have an independent basis for deciding on the relative importance of these characteristics in wool improvement.

It is indeed remarkable that the last 25 years of wool research has produced very little factual information in this field. The great physical distances separating the research workers interested in production problems from those interested in manufacturing research is partly the cause of this state of affairs. The difficulties in organizing this type of work are exemplified by the most important current project in which

wool from experimental sheep in Australia is being put through manufacturing trials at the Textile Research Institute, Princeton, U.S.A. A good local example is the work of McMahon and Henderson on the effects of varying degrees of hairiness on the manufacturing properties of the wool fibre. Prosecution of work on this type will be welcomed by the animal breeder as a useful addition to his knowledge of the required direction of wool improvement. It is perhaps not too naive to suggest that this knowledge will prove equally enlightening to the manufacturer and his wool buyer.

The Concept of Heritability

The next consideration must be the ideas which are contained in the modern theory of animal breeding. The main integrating concept is that of the additive genetic variance between individuals and its related parameter, the heritability. Heritability is a figure which describes the proportion of the total variance in the characteristic which is controlled by the strictly additive effects of the genes affecting that characteristic. It is of use in predicting the rate at which different selection techniques can produce change in the character, the estimation of the breeding value of individuals from their performance, in considerations of the accuracy of progeny and sib tests and in evolving selection indices. The approach adopted is essentially statistical in nature and because of the widespread opprobrium accorded most statistical and mathematical formulations of biological problems, it is worth spending a little time in arguing why it is necessary.

It has long been recognized that most of the productive traits with which we have to deal are controlled in their inheritance by many genes and are often greatly affected by many non-genetic factors. This statement has, of course, become a platitude. Its implication may be regained, however, if it is realized that a character controlled by as few as 16 pairs of genes would give rise to more separate genotypes than there are pounds in New Zealand's overseas trade deficit. Enumerating individually those genotypes is about as meaningful as the ancient philosophers' question as to how many angels can be balanced on the point of a pin. We are nevertheless presented with a situation which is bewildering in its complexity and in which traditional genetic methods fail completely. Even if it were possible to identify each and every gene, which certainly cannot be done, the situation would still be unbelievably complex and the accuracy of prediction still limited by the random segregation of genes in each generation.

In circumstances such as these, it is a common method of science to attempt to abstract the essential elements of the problem, to build a statistical model on the basis of this abstraction in the hope that individual unpredictability may nevertheless show regularity in the mass. This process is exemplified in the words of Bell when he said; "The world that impinges on the sense of all but the most introverted solipsist is too intricate for any exact description yet imagined by human beings. By abstracting and simplifying the evidence of the senses, mathematics brings the worlds of science and daily life into focus with our myopic comprehension, and makes possible a rational description of our experiences."

Many people are opposed to such abstraction because it often fails to predict individual behaviour even though it gives useful results on a population basis. The writer is inclined to agree with Rudolf Carnap that acceptance or rejection of the process of abstraction has a psychological basis. People of the one type are attentive to and have a liking for nature with all its complexity and dislike seeing these qualities overlooked. People of the other persuasion like the neatness and exactness of formal structure and are given to oversimplification to achieve this. However, whatever may be the cause, the history of science abounds with controversy between the two and makes it clear that progress depends on the co-operation of both types.

The particular abstraction with which geneticists are concerned and upon which the concept of heritability depends contains the following assumptions:

- (1) Quantitative inheritance is particulate and duplicate—*i.e.*, it is by genes which occur in pairs.
- (2) The Mendelian laws of segregation hold.
- (3) All genes have small and additive effects—*i.e.*, a gene always has the same effect irrespective of what other genes are present.

There is no doubt that this is a drastic simplification and it is the writer's intention to see how well it describes the situation in practice.

Selection Experiments

Over the last 10 to 15 years, many papers have been published giving estimates of heritability for characters of importance in animal production; so many in fact that one wonders if further addition to this literature is not superfluous. It must be remembered, of course, that the concept of heritability and the methods used to determine it yield results which are ap-

plicable strictly only to the particular population from which it was derived—to the particular breed in its own set of environmental conditions. Thus there is reason for a multiplicity of estimates and the fact that it appears that heritability estimates for different breeds and different locations do not differ greatly can be established only by the availability of many estimates from many sources. Their similarity can be regarded as a fortunate coincidence rather than a necessity.

Nevertheless, an examination of the value of the use of heritability as an approach to the improvement of productive traits in farm livestock is worth while. Any such examination must at present be based on limited evidence. The major difficulty is that of distinguishing in non-experimental populations those changes which are genetic in origin from those which result from the improvement of the environment. The only attempt to develop methods for separating the change in the mean of a group into its genetic and environmental components is that of Henderson. This method, which seems sound in its essentials, has yet had only limited trial and only in cases where the conclusions derived from its use cannot be checked against independent evidence on the rate of genetic change.

Hence to find out to what extent the predictions of "heritability" analysis are borne out in practice, research workers must fall back to actually applying selection to a population under experimental conditions so that an estimate of the rate of genetic change can be made. The objectives of such selection experiments are to answer some or all of the following questions:

To what extent are the gains predicted from knowledge of heritability actually achieved in practice?

How long does progress from selection continue and is there an upper limit to the response?

Does the method of selection influence the result?

Are there correlated responses in characters other than the main one to which selection is applied?

Does selection in opposite directions give similar rates of change?

What happens in the selected population if selection is relaxed, or reversed in direction?

To what extent are the results of selection repeatable in different experiments?

A few experiments to answer some of these questions have been set up using domestic animals, notably the sheep, the

techniques usually being selection from the same base population in opposite directions or of selecting in one direction only with a randomly selected group to act as a control. Examples of work already under way with sheep include the following characters: Body size, skinfolds, clean fleece weight, fibre numbers, fibre diameter, yield and wool produced per unit area, carried out by C.S.I.R.O.; skinfolds, weaning weight and fleece weight at Trangie Agricultural Experiment Station; twinning ability at Ruakura Animal Research Station; fleece weight, face cover and lamb production at Massey Agricultural College. Most of these experiments have not yet advanced far enough to give adequate results and no final interpretations are available. With few exceptions, however, there is little doubt that useful responses to selection have been obtained.

Experiments of this type involve several difficulties and uncertainties. In the first place, large numbers of animals are required for an adequate analysis, especially when the character under selection is only lowly heritable. Secondly, the time required can be considerable, especially where the interval between generations is long. Moreover, when the results are obtained, there is still an element of subjectivity in deciding whether they agree with prediction. Finally, there is the difficulty that the very fact of applying selection itself leads to a change in the heritability. Selection changes the frequencies of the genes in the population. This change in gene frequency in turn alters the amount of genetic variability and thus alters heritability. Hence, although heritability can be used to predict the change in the mean due to a generation of selection, it cannot be used adequately to predict changes in itself.

These difficulties, particularly the length of time required and the high cost, have resulted in the use of laboratory animals for checking the response of populations to selection. Most of this information comes from work on *Drosophila*, and the mouse, carried out particularly at the Institute of Animal Genetics, Edinburgh.

Naturally, it cannot be concluded that what happens in these laboratory animals will necessarily happen in the larger domestic animals. Rather, the intention behind selection experiments with small animals is to increase the understanding of quantitative inheritance. By studying a large number of characters in different species, it may be possible to find some consistency of response which can be related to the nature of the trait or the biological properties of the species and thus

serve as a basis for generalization. The results of a number of experiments to date do suggest that a pattern is emerging although it can still be discerned only sketchily.

Responses to Selection

A wide variety of responses to selection have been found. There are cases in which selection was not effective, cases where the change continued over a large number of generations, and cases where the initial response has been followed by a plateau which in turn was succeeded by a further response. In most cases, there appears to be a reasonably satisfactory agreement between the observed change and that expected from heritability over the first five to ten generations. Thereafter the response becomes attenuated and finally ceases altogether. The actual cessation of response to selection is, however, quite different from what is expected in simple theory. Instead of a gradual exhaustion of genetic variation as the frequency of the desirable genes is increased and with this a gradually diminishing response till the final plateau is reached, it is found that the endpoint is one of unstable equilibrium with much genetic variation still present. Moreover, asymmetry in the response to selection in the sense that the rate and extent of change were different depending on the direction of selection was a phenomenon which was often found. Whatever the nature of the response, however, all populations have in the end run into difficulties which cannot be encompassed within the simple theory expounded above.

What then are the causes of the lack of response to selection in populations where genetic variability still exists? It is a major advantage of the use of *Drosophila* that the special techniques available in this species can be used to analyse the situation. One such cause is the breakdown of the assumption that the genes are acting additively. Analyses of the selected populations in which responses have ceased show a wide variety of gene and chromosome interaction. In other words, it is the gene combination rather than individual gene action that produces the desired result. These gene combinations as such are not transmitted intact to the offspring but are broken up by Mendelian segregation in each generation. That which is built up in one generation is broken down in the next. In other cases, it has been found that selection is for heterozygotes of genes which are lethal when homozygous and the lack of response and the maintenance of variability can be attributed to the fact that the frequencies of these genes are maintained at an

intermediate level. This situation is described as involving overdominance in the sense that the heterozygote has an advantage over both of the homozygotes. Here, as Robertson has stressed, it is necessary to distinguish between two situations which are superficially alike. In one case, the gene has no effect on the natural fitness of the animal but the heterozygote is more extreme for the selected character than is either homozygote. In the other, the gene is additive in its effects on the selected character but the homozygote is inferior in natural fitness. The consequence of either situation is that the population will remain in equilibrium with no response to selection but with genetic variation being maintained.

Genetic Homeostasis

This ultimate resistance of the population to change is obviously an important feature. Its frequent occurrence in selection experiments suggests that it is, in fact, a basic biological property. There are two essential requirements that a population must satisfy to carry on a successful existence. First, a large proportion of its members must exhibit a total phenotype near the optimum adapted type for the conditions in which the population finds itself. A second requirement is that the population must carry within itself genetic reserves to be able to withstand fluctuating environmental conditions. The first requirement is measurable in the sense that the characteristic of the group may be expressed as an average of the characteristics of its members. The second prerequisite, on the other hand, is not manifested in any single individual but in the population as a whole. It can be uncovered only by subjecting the population to stress, either by environmental change, a change in the breeding system, or by selection. In other words, a feature of both populations and individuals is their ability to maintain a steady state. Although this property of homeostasis has long been recognized by physiologists in the development and response to stress of the individual organism, it is only recently that the concept as applied to populations has been clearly formulated, largely as a result of the interpretation of selection responses, heterosis and inbreeding depression by Lerner.

An example of the manifestation of homeostasis at the population level is provided by work on selection for shank length in chickens by Lerner and Dempster. For seven successive generations progress was obtained, but gradually the reproductive capacity of the population decreased and a plateau was

reached. After four more generations a partial recovery occurred, accompanied by a resumption of gains. Suspension of selection in the twelfth generation resulted in a partial return of average shank length towards the unselected control, and in an improvement of reproductive ability. The changes in the trait under selection were thus apparently obtained at the cost of a reduction in fitness. Furthermore, the decrease in fitness was found to be differential—in the plateaued population, the extreme genotypes for shank length did not leave as many offspring as those closer to the mean.

These results may be explained by assuming that the previous evolutionary history of the population has led to an average genotype integrated in such a way that the various morphological and physiological characters were in balance with each other so as to produce maximum fitness. Selection for specific genes which produce a marked departure from this optimum in one character destroys the balance. As a result, fitness is reduced, particularly in the extreme individuals and an antagonistic relationship between artificial and natural selection induced. The maintenance of the balance is the phenomenon which has been called genetic homeostasis. Application of sufficiently strong selection pressure may lead to the extinction of the population. Relaxation or suspension of artificial selection brings about recovery of balance. Resumptions of gains after plateaus indicates that, under a combination of natural and artificial selection pressures, new genotypic combinations are produced, in which a different level of expression of the selected trait is in balance with the rest of the genotype. Lerner has reviewed much evidence to show that the maintenance of this stable genetic situation is a result of the superior fitness of the heterozygote. Whatever may be the explanation, the evidence for the existence of genetic homeostatic mechanisms is very strong.

It is thus important to take into consideration the relationship between the character under selection and "natural fitness". It must be remembered that selection, whether it be based on criteria useful to man or "natural" selection, is the result of differential mortality, differential fertility, and differential rate of attaining maturity which combine so that different genotypes contribute differing numbers of offspring to the next generation. Conceptually, characters can be imagined which have little or no direct connection with fitness—*i.e.*, they are not "useful" to the animal. Fleece style or character in the sheep might be cited as an example. At the opposite end of the scale would be

a relationship where the highest development of the character gives highest fitness. Such a character, of course, would be fitness itself, although it is hard to identify any other character with this relationship. Then between these two extremes is the case where an intermediate is the optimum, with fitness declining as the character departs from the optimum in either direction. It is this last case which is of particular interest in the present context. Where the optimum from the viewpoint of fitness is an intermediate, natural selection opposes artificial selection. Extreme individuals fail to reproduce themselves as effectively as those nearer to the original average of the population and consequently the response to artificial selection grinds to a halt.

Selection Limits

It will be seen that, although predictions of selection gains are usually reasonably satisfactory in the short term, they are unreliable in the long run. Thus, there is a limited justification for the use of the heritability concept in animal improvement, and in an enthusiasm for precision it would be definitely wrong to throw overboard this approach. It still gives the most accurate prediction of breeding value which is available at present, and the gains to be made from its use are still tremendous. It must be recalled that, while consideration has been given to the reasons why the selection response has ceased and great complexity of the genetic situation has been found at that stage, nevertheless selection has often shifted the mean by two or three standard deviations from its original position and the response has continued for 10 to 20 generations. At the same time, the greater effectiveness of selection based on the concept of population genetics, together with the simplification and clear definition of the objectives of improvement, means that this limit point is reached more rapidly. It is thus of value to consider what can be done when the limit is reached.

Here, some suggestions are offered as means of attack on the problem. First, it is to be noted that the limits imposed on the power of selection have been genetic in nature. They do not seem to involve a physiological ceiling which cannot be surpassed. This is confirmed by the fact that crossing of selected strains followed by further selection leads, in most cases, to a resumption of gains. Thus it is obvious that potentialities for genetic change still exist at these limits, but considerable work will be required to discover how best to manipulate these potentialities. Secondly, much assistance is to be gained from

expanded knowledge of the physiology of the development and control of the character under consideration. For population genetics deals essentially with genes and final phenotypes, but has little as yet to say about the vast developmental gap between the two. It has been common to regard the two approaches as antagonistic; that either one or the other, but not both, is the only true approach to animal breeding problems. This belief is manifestly unsound. After all, most of the interactions considered, dominance and epistasis, are essentially developmental concepts and not statistical. The union between the two approaches, however, can be very fruitful, as is shown by Cockrem's analysis of the manifold effects of the *N* gene. In this partnership the geneticist's function is to identify and produce the genetically differentiated strains for the physiologist to work on.

In considering other forms of attack, there seems to be a proneness to neglect the possibilities of single identifiable gene differences as a further method of leverage on these problems. It is undeniable that the assumption is often made of multiple gene inheritance and the absence of genes with major effects on very slight evidence. Dry's discovery of the *N* gene affecting the abundance of halo hairs in the Romney lamb should be a warning against the too facile acceptance of the assumption of polygenic inheritance. As an example of the advantage of an identifiable gene difference affecting a productive trait, and to those who are sceptical about the value of investigating such cases, it is no exaggeration to say that a very large proportion of present knowledge of the physiology of the wool follicle has stemmed from research on the mode of action of the *N* gene. Similarly, great increments in knowledge in this field can be expected from the collection of mutant fleece types made in Australia.

In this regard, the genetics of blood differences deserves further effort. Early work on blood group differences had suggested that the genes controlling them had no selective advantage and that their distribution in different populations was determined by the random processes affecting gene frequency. However, there is growing evidence that some of them may have other effects. Of the cases available only two shall be mentioned.

Briles and his co-workers at Texas have found that poultry heterozygous for a particular blood group tended to grow faster, had greater viability, and produced more eggs with a

better hatching rate than did the homozygotes. In sheep it has been known for some time that the potassium content of the red blood cells varies about two or more distinct mean values. It has recently been shown by Evans and King that the difference is controlled by a single gene, the low potassium type being dominant.

More recently, Evans and Mounib have surveyed the incidence of the two types in a number of British breeds. The results suggest that there is a predominance of "high potassium" types in mountain and upland breeds, and raise the possibility that this factor may have some bearing on survival under rigorous conditions. A similar suggestion is raised by an analysis of blood potassium levels of Romney and Cheviot sheep at Massey Agricultural College by Cresswell. These possibilities are tantalizing enough to emphasize the need for keeping a weather eye open for simple genetic situations which may help to improve the accuracy of selection.

Increasing Lamb Production

In turning attention now to the problem of increasing lamb production in sheep and particularly Romney sheep under New Zealand conditions, it would seem worth while to review briefly existing knowledge which has a bearing on the problem. First, it is known that lamb production of the ewe is the character to which most importance should be attached in breed improvement. Evidence for this comes not only from study of the relative economic value of the productive characters of sheep under New Zealand conditions but also from Lambourne's studies of the efficiency of pasture conversion by the ewe and from breed cross comparisons, as for example with the Cheviot and Border Leicester. Secondly, it is known that there is considerable variability between sheep and between flocks not only in the final lamb production but also in the components of the sequence which leads to that final result. Thirdly, there is evidence that heritability of lamb production by the ewe is low and that its repeatability is only little higher. Fourthly, there is some suggestion of genetic antagonisms with other traits, notably fleece weight, although more evidence is required on this point. Fifthly, there is the evidence already mentioned of the advantage of crossing with the Cheviot or Border Leicester although there is no definite evidence that heterosis or hybrid vigour is involved. Sixthly, it is known that face cover, and possibly vagina classification, have an effect on lamb production of the ewe.

At this stage, information ceases and much of what follows must be frankly speculative. Its basis rests in the ideas that have been reviewed earlier; its justification lies in the hypotheses which it suggests which can be subjected to experimental attack.

Problems for Investigation

The first point concerns the relationship of the number of lambs reared to fitness. The two features must obviously be closely related, the closeness depending on how fecundity is actually measured. If it is measured as the number of offspring per ewe which, in turn, survive to breeding age, the relationship to fitness must be very close. On the other hand, if it is measured at earlier ages, possible associations between later deaths and genotype could make the relationship less direct. There is evidence to suggest that the relationship is not perfect; for example, the higher mortality rate of triplets and possibly twins would imply that there is an optimum number of young which is adjusted by the genetic properties of the population and the environment in which it lives. Hence, fitness and reproductive behaviour cannot be exactly identified. There is a largely untouched field of study here in attempting to define by survey and experiment the variation in reproductive rate and in fitness for different types of environment. The implication, however, is that it will be found that there is much interaction both of the gene-gene, and the gene-environment type.

There are many isolated pieces of evidence to support this possibility. For example, there are indications that large single lambs tend to come to grief during the birth process, while small twin lambs, although surviving the hazards of birth, are often too weak to live. Vita has shown another case in which flushing (an environmental agency) depended for its effect on the genetic potentiality of the ewe to produce twins or triplets.

In this regard it becomes important to examine the question posed by the localization of most stud stocks of the Romney breed to good lowland conditions. If the breeding aim is for high lamb production under good conditions, does the array of genotypes thus obtained represent those which will give best results under somewhat more severe conditions of commercial hill farming? As has been seen, the nature of the trait concerned suggests that to assume that this is so represents a considerable act of faith. This question is subject to experimental attack by several methods, the most expeditious being the

rearing and recording of the performance of samples of daughters of the same sires under the two contrasting environments.

The problem of possible genetic antagonisms between lamb production and other characteristics must also be considered. For example, the genes which cause wool to grow on the face must also have an effect on some developmental processes which, in turn, affect reproductive rate. It is probable, too, that some genes which have the effect of increasing fleece weight also tend to reduce the efficiency of the ewe from the viewpoint of lamb production. One aspect which has not been investigated is the possible genetic relationships existing between body size, lactation and reproductive rate. There are indications from other species that these relationships may be very important, and, on occasion, quite complex. For example, the number of offspring reared by the dam may influence the growth of the daughters. If their size has an effect in determining their fecundity, then those reared as twins, being smaller, will have fewer offspring. This results in a negative correlation between the dam's and daughter's fecundity, which cancels out in part the positive correlation obtained by the genetic transmission from dam to daughter. In sheep the strength of the non-genetic pathway would appear to be determined by the level of the environment. For example, in Cheviots bred on poor, untopped hill country, the above mechanism seems to operate at the two-tooth lambing, whereas at higher planes of nutrition any differential in growth between twins and singles seems to have disappeared by the first lambing.

It is clear that extended knowledge of the physiology of growth and reproduction will aid in elucidating these relationships, but it is beyond the scope of this discussion to consider this in detail.

In this regard it seems important to develop lines of sheep by selection which differ as much as possible in fertility levels, because to a large extent it is only when these lines are available that it is possible to investigate efficiently many of the points raised here. They are valuable from the viewpoint of analysing the physiological differences which have been established by the genetic separation of the two types. They thus make it possible to bring to bear on the problem the full power of our accumulated knowledge of reproductive physiology.

Thus research workers are presented with the possibility of a rather complex array of interactions. What, then, is the likely advance that can be made by selecting for fecundity in

the ewe? The results of selection experiments for this trait to date do suggest that a gain can be made and there is no reason to believe that this gain will not continue for a number of generations before a plateau is reached where the various balancing mechanisms which have been discussed come into play. The study of what has actually happened with regard to selection for fertility in some stud flocks suggests that, in fact, selection for this trait has been more or less random, because in most cases it has not been taken into account. The present genetic potentiality has, therefore, been balanced by natural forces, and the changes which have resulted are likely to be the consequence of correlated responses to other characters such as face cover, or to environmental changes. Hence there is likely to be a reserve of genetic variability which can be attacked by selection.

In drawing this discussion to a close, it can be seen that the geneticist's immediate contribution to animal improvement is in the clear definition of objectives and the most effective use of selection. There is evidence that these attributes can contribute steadily and, in the long run, greatly to increasing production. At the same time, the fact that there are genetic limits to selection emphasizes that there is no cause for complacency. Their existence highlights the fact that in many ways our herds and flocks will have to be considered as populations which have genetic properties and mechanisms which are manifest at the population level but not in the individual. It must also be realized that the integration of these mechanisms has been the task of Nature over countless thousands of years. Her method of trial and error is slow and wasteful, but it is painstakingly accurate in suiting genotype to environment. Man, in attempting to modify this finely balanced relation, must above all recognize its existence. The geneticists' task in the future is to direct their efforts to understanding it more fully in order to use it for their own ends.