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A SUGGESTED APPROACH TO THE SELECTION OF DOMESTIC ANIMALS ON PHYSIOLOGICAL CHARACTERS

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SUMMARY

Selection methods are discussed in relation to current theories of gene action. The investigation of the inheritance of simple physiological characters in farm animals is suggested, and evidence is presented which indicates that such investigation would be worth while.

INTRODUCTION

This paper discusses the use of recent advances in knowledge of gene action and animal physiology in speeding up the genetic improvement of farm animals.

The discussion is in three main sections:

(1) The relationship of current theories of gene action to present research on, and practice of selection methods.

(2) Some preliminary evidence that investigation of the genetic aspects of some of the more easily measured physiological variables would be profitable.

(3) Some suggestions for an approach to the study of the inheritance of some physiological characters which may underlie productivity in farm animals.

CURRENT GENETIC THEORY AND ANIMAL BREEDING

In recent years there have been rapid advances in knowledge of the possible structure of genetic material, desoxyribonucleic acid (DNA), and of the possible ways whereby it can control those characters of an animal which are inherited. While it is likely to be many years before an animal's genotype can be specified chemically and the results of such specification used to predict its phenotype, present ideas of gene action can be used to determine possible approaches to more rapid selection techniques. (Although the definition of a gene is at present in a state of flux, it is used here in the sense of a portion of the chromosome which in inheritance acts as a unit.)

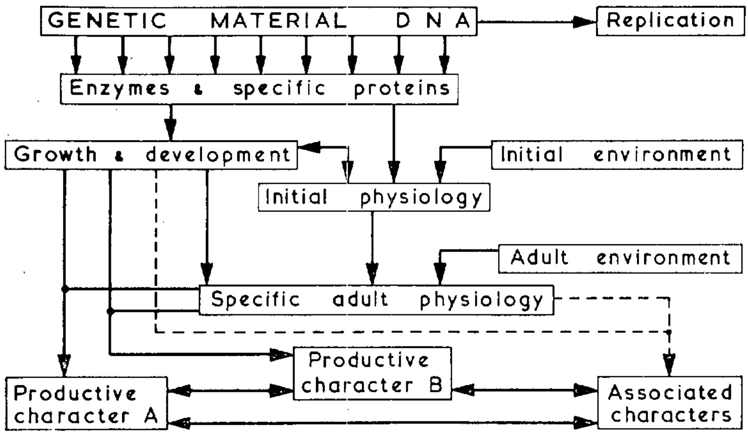

Fig. 1: A generalized scheme of gene action.

Figure 1 shows a generalized scheme of gene action in relation to two productive characters of a domestic animal. On current theory the particular structure of the DNA will determine the production of specific enzymes or other protein molecules, such as the haemoglobins. The presence or absence of these enzymes will determine the reactions that take place in a cell or within the body. The process will not be entirely one of biochemical systems as the action of these will depend on the developing anatomical features. For example, a mouse may be without a tail from the action of a gene acting initially through a biochemical system, or its failure, in the embyro. However, as the animal develops, the lack of a tail may lead to difficulty in heat loss, which in turn could affect other reactions which are temperature dependent. A further point is that one series of biochemical reactions will depend on the substrate from another series, and the interactions can become very complex. Therefore, even if all the genes were known, prediction of the final phenotype would still be a very difficult task, in particular when this phenotype is not a simple presence or absence effect but has to be assessed in quantitative terms.

In the next stage removed from the initial gene action, at least for most characters, the animal grows to an adult which will have a specific anatomy dependent on its initial development, and on its early physiology and environment. These effects of early physiology and environment can be seen for example in N-type lambs which in some years show poor early growth as lambs (Cockrem and Rae, 1959). This is in some way related to the size of the primary wool follicles and in turn results in a smaller adult sheep. This small size is essentially an anatomical feature which, however, is likely to both affect, and be related to, the adult physiology.

Finally, the anatomical and physiological characteristics of the adult animal will interact with its environment to determine the productive characters.

This general scheme is by no means new, a very similar one having been suggested by Wright (1941); however, recent advances have tended to confirm it and to expand many details and, possibly more important, knowledge of domestic animals has now increased to a point where use can be made of this type of concept.

In making use of these ideas there are two main points to consider:

(1) In general, the nearer to the initial gene action a character can be measured, the higher will be the heritability. Thus, in the extreme case, direct selection for the presence or absence of particular enzymes (as probably happens in many cases of flower colour) would be selection for the presence or absence of individual genes.

(2) The definition of breeding aims. Before going as near to the basic gene action as possible, the object of the selection must be clear, both in terms of the characters required and, as far as possible, the biological factors underlying these characters. For, as selection is made more effective, so will narrow or ill-defined aims be more likely to result in an imbalance which in the long run defeats the objective of breeding a more productive animal.

In practice, breeding aims are variable and not always clearly defined. With sheep, the stud breeders' aims appear to be to select an animal which will show well (by their criteria), and, more important, sell well. The farmer is probably more in line with the research worker in aiming for maximum production in a particular environment, although the maximum production may not itself be clearly defined.

In general the stud breeder selects for characters which originally were thought to be associated with productivity—that is, for characters seen rather than measured, which since Roman times (Varro, B.C. 37, quoted by Turner, 1956) were believed to reflect an animal of high productivity. In biological terms, they are selecting for certain physiological factors underlying these breed points with the implied assumption that these physiological factors are the ones associated with higher production.

If this were in fact so, their methods would have much to recommend them. Unfortunately, those associated characters which have been investigated in sheep or dairy cows show little association with production or, as with face cover, the relationship is a negative one.

However, the animals produced in this way are the genetic raw material which is available, so the underlying physiology and the relationships of these associated characters have to be considered in animal breeding research.

Because of the general lack of prospects of further advances using associated characters as used at present, the main alternative investigated has been that of direct selection for the productive characters themselves. Successful selection of this kind implies that the appropriate, underlying system of physiological and developmental factors have also been selected for. If these depend on the environment in which the animal is to produce, then selection in this environment should result in a suitable animal. In this way the productive character or characters may be obtained without any detailed knowledge of the underlying factors contributing to them.

However, the very presence of these interacting factors in the determination of the required trait, together with selection at the point farthest from the initial gene action, means that progress is likely to be slow. Furthermore, there are likely to be inter-relationships between the productive characters themselves and, as in the case of fleece weight and fertility, these relationships may be negative. This can be allowed for by the appropriate selection methods and progress can still be made (*e.g.*, Cockrem, 1959a) but it may be slow, and methods could become difficult to apply if many characters were concerned. In addition, there may be several possible combinations of physiological factors which can lead to a more productive animal. Selection for a productive character itself may not result in the best possible combination of physiological factors, particularly when other characters are being selected for at the same time.

A further method of selection which has been investigated extensively is that of correlating characters in the young animal with the required productive traits in the adult. If a reasonable correlation exists, then selection can be made on the earlier character, which method is more economical and also likely to be closer to the original gene action.

An extension of this method is by a more detailed analysis of the development of a character, such as has been done with the carpet-type fleece of the N-type sheep (Cockrem, 1959b). The inter-relationships of various characters can then be determined and the effects of selection and of some environmental components predicted.

In the case of the N-type investigation it was found that the production of the carpet-type fleece was associated in some years with poor body growth of the lamb in the first six weeks after birth. In the ordinary Romney a genetic correlation indicates that a similar relationship may exist (Rae, 1958), so that selection for coarser fleeces could result in lamb growth problems in some as yet undetermined environments. This is as much as this work can predict at this stage. A more precise prediction, and hence a possible method of overcoming the potential problem, can come only by determining the physiological causes of this relationship—that is, a shifting of the breeding aims and investigations from the end point of the physiological relationship to the physiological relationship itself.

With the N-type example, the use of the single gene, N, in comparative studies would make such an investigation quite feasible if the facilities were made available. However, characters based on a large number of genes, while still open to physiological investigation, would be more difficult to study because of the lack of clear-cut differences. Therefore, it is suggested that it would be worth while to investigate possible genetic differences of the more important physiological characters which can be measured on a reasonable number of sheep.

The type of characteristic worth investigating is best explained by examples and the remainder of this paper presents some results already obtained and a suggested future approach which these results indicate.

EVIDENCE FOR THE POSSIBLE GENETIC CONTROL OF A PHYSIOLOGICAL CHARACTER

In a previous paper (Cockrem, 1960) it was suggested that some of the face cover relationships might be explained if greater wool growth on the face were associated with a greater blood supply to this region. This might then be part of a syndrome of which the important aspect was a failure of the woolly-faced sheep to respond adequately to stress situations. Blood supply has been investigated by means of skin temperatures and, as these were likely to be dependent on deep body temperature, rectal temperatures were measured at the same time.

Measurements were taken of these variables for nine sheep, three each of the open, intermediate and woolly grades of face cover. For each sheep two measurements were made daily for three days, using a randomized block plan allowing for the time of day and the pen the animal was in. There were three sheep to a pen. These six measurements of each temperature for each sheep were made in March (when they were seven months of age), June, October (twice, with a fortnightly interval), and in January. The animals were shorn immediately before the first October set of readings. Rectal temperatures only will be discussed here.

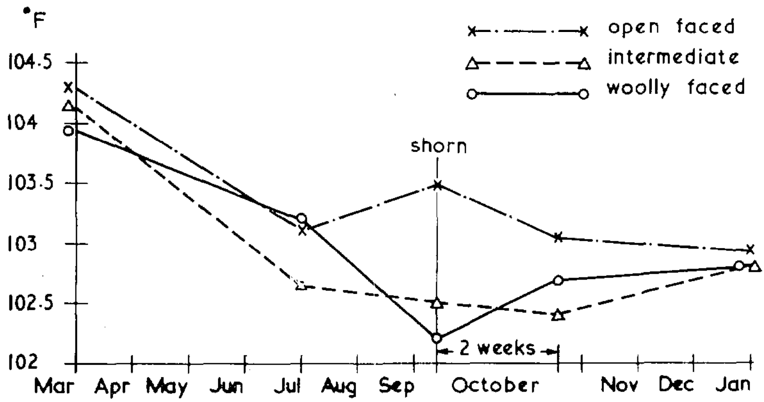

Fig. 2: Mean rectal temperatures (°F) of ewe hoggets (3 sheep per group) of different face cover.

Figure 2 shows the mean values of rectal temperature for each face cover grade for each measurement time. Thus each mean is based on 18 observations. Analysis of variance showed that there were significant differences between the face cover groups ($P < 0.05$). These differences were largely the result of the drop in rectal temperature of the more woolly groups after shearing. For differences among sheep, ignoring face cover, the main interest lay in a significant interaction ($P < 0.01$) between sheep and the time of year, although there were also differences between sheep. Again this interaction came mainly from a differential response to shearing.

This drop in rectal temperature after shearing occurred although the animals were housed and the ambient temperature was not low (59° F). Raising the ambient temperature to 78° F reduced the differences between groups—*i.e.*, the woolly-faced sheep then increased their rectal temperatures by a greater amount.

Thus it appears that the woolly-faced animals were less able to adjust to this particular environment resulting from shearing.

It seemed possible that this observation on rectal temperature response to shearing might be related to one on lamb growth a few years previously. In this case the lambs were exposed to a severe cold southerly storm immediately after being shorn. There was little effect on the body weight growth of open-faced lambs but a marked slowing of the growth of the woolly-faced ones.

Therefore relationships between body weight, body weight changes, and rectal temperatures were examined in the present nine sheep. Body weight and rectal temperatures measured at the same time of the year were not related, but average rectal temperatures and weight gains over the period March to January showed a correlation of $+0.4$ which is suggestive but not significant. However, weight gains from weaning to shearing showed a significant correlation of $+0.72$ with the rectal temperatures immediately after shearing—that is, the animals showing the lowest temperatures after shearing were those that had gained the least over the critical period of hogget growth. That these were not necessarily the smallest animals was shown by the lack of correlation with actual body weights—*i.e.*, these results are not a simple heat loss—body size phenomenon, but evidence of the possibility of a relationship between a physiological trait, response to cold, and an economic trait, body growth. Furthermore, the association with face cover, itself strongly inherited, suggests that investigation in genetic terms would be worth while.

Evidence for genetic differences in body temperature variation has also been found for mice (McLaren, 1961). More constant temperatures were found for C_3H mice over short periods but there were greater long-term effects of lactation and age than for C57 mice. Lactation increased body temperatures in the C_3H mice.

Thus it appears that genetic differences in rectal or body temperature *variation* and their importance to productive traits would be a field well worth investigation.

AN APPROACH TO THE STUDY OF THE INHERITANCE OF SOME MORE EASILY MEASURED PHYSIOLOGICAL CHARACTERS

In the sheep, amount and type of wool, body growth and

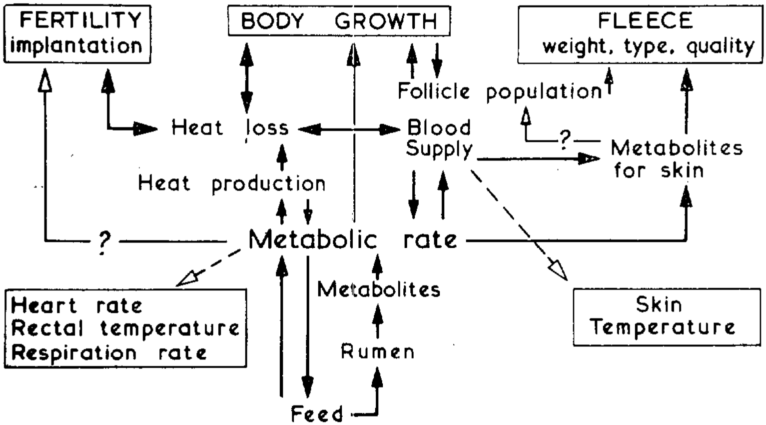

Fig. 3: Some of the possible inter-relationships of productive characters in sheep.

tility, possibly through effects on implantation of the egg (Inkster, 1959). The question arises, are there common factors, genetic and physiological, which underlie the most productive sheep under particular environments?

Figure 3 shows, in a very simplified form, the type of system which could result in an underlying common factor, in this case metabolic rate. This would, of course, vary as the other factors vary, but it would be this variation as well as the absolute values which would be of interest. For example, an animal with a high fleece weight per unit of body weight must have a good supply of metabolites to the wool follicles. If, in a particular hypothetical case, this was dependent on blood supply rather than on a high metabolic rate, then wool growth might be at the expense of the efficiency of the prevention of heat loss, particularly after shearing.

The details of such systems are not known; however, the emphasis in this paper is on the possibility of genetic differences in such systems and in their control. The systems are likely to work in a similar way between sheep, but slight differences in their balance could be of great importance to the animal's productive performance.

In more general terms, this could be considered as suggesting an investigation of the genetics of the physiological homeostasis of the animal in relation to production. If successful, it could lead to further investigation of possible differences in the endocrine and sympathetic nervous control of the systems concerned. This would then be a further step towards the initial gene action.

Figure 3 also shows some suggested methods of measurement. These are not methods which give complete information of the metabolism of an animal. More detailed methods are also required to assist the interpretation of the less precise results. The reason for suggesting these measurements is that they could be used on a reasonable number of animals, which is essential if genetic differences are to be investigated.

The key point in this type of investigation would be the differences in reactions of animals or groups of animals to changes in their environment, in particular in temperature, feed, and in the imposition of stress situations.

While it would be possible to take skin temperatures and rectal temperatures in the field of up to 20 sheep an hour, such a method has severe limitations as it leaves to chance the appropriate conditions of temperature and to some extent nutrition. Treatments such as shearing are likely to give variable results according to the weather over which there is no control.

Thus, with present facilities, groundwork can be done on measurement methods and on possible breed differences under field conditions. Fortunately, the N-type sheep and also the Cheviot are available for contrast with the Romney for this type of field study. However, the proof of this type of approach for animal breeding, and in particular for sheep and wool problems, must await individual pen feeding and temperature control facilities. Until then it is hoped to use various special stocks of mice to investigate the possibilities of measuring and selecting for genetic differences in simple physiological traits.

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