

The Importance of Genetic Correlations in Selection

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IN studies on the breeding of farm animals, considerable emphasis has been placed on the investigation of correlated variation in order to make selection both easier and more effective. It was hoped that improvement of a trait difficult to measure could be carried out quite successfully by finding another character closely correlated with it and using the latter as a basis of selection. As a result, the early literature on animal breeding abounds in reported correlations between the various characters affecting productivity. It is to be noted that a similar approach was adopted in plant breeding (Jenkins, 1929) but it was soon realised that the results did not justify the hopes that had been placed in correlation between characters as a help in breeding for improvement. It is worthwhile to review briefly the change in thinking which led to an appreciation of the role of correlation in breeding practice.

The application of the principles of genetics to problems arising in animal breeding is based on the theoretical considerations of Wright, Fisher and Haldane. The details of this approach are given by Lush (1945). The basic concept, that of heritability, recognises that the observed variation in a character may be divided into two main parts—an additively genetic component and a component due to variation caused by the environment. The heritability of a trait can be used to predict the genetic gain expected from selecting for this trait alone and thus to decide the best breeding plan to adopt for the improvement of this trait. Consequently, to the present time, most work on investigating the statistical properties of livestock populations has been concerned with estimating, one by one, the heritability for each trait comprising productivity.

It was not until the work of Hazel (1943) and Smith (1936) that it was clearly realised, that for predictions based on heritability alone to be reasonably accurate, it is necessary that selection be for this one trait only or that the trait be uncorrelated genetically with any of the others affecting productivity or fitness of the animal. In considering the nature of the phenotypic correlation between two traits, Hazel pointed out that such a correlation may occur for two reasons. First, some of the genes affecting one character may also affect the other character. Secondly, the two traits may be correlated because some of the external and internal environmental influences affecting one may also affect the other. That is, just as in the concept of heritability where the total variation is divided into a genetic and an environmental component, so also in the case of a phenotypic correlation, we partition it into a genetic correlation and an environmental correlation. Unless the phenotypic correlation is thus separated into these two parts, it is impossible to forecast the genetic effects which selection will have on the population.

A positive genetic correlation between two traits presents no difficulties since it helps in the improvement of the two traits simultaneously. A negative genetic correlation, however, implies that selection for one trait will by itself cause some deterioration of the other. If both traits are important from the standpoint of productivity, selection for one of them cannot be maintained for long, but will need to be relaxed while efforts are directed toward repairing the damage done to the other trait. Basing selection on a properly balanced combination of the two traits avoids wide fluctuations in either one of them, but the net effect is still that progress will be slower than that which could be achieved

if the traits were independent. These aspects may be clarified by noting that, as a result of selecting for character X alone, the change in a character Y which is correlated genetically with X is given by the following relation:

Genetic change in Y equals genetic correlation between X and Y multiplied by ratio of genetic standard deviation of Y to that of X multiplied by genetic change in X. Since the last two terms of the right hand side are positive, the sign of the genetic correlation (whether positive or negative) decides whether the genetic change in Y is towards improvement or towards deterioration. Moreover, the size of the genetic correlation is important in deciding the extent of the change towards higher or lower values.

It is important to realise that a phenotypic correlation between two traits does not necessarily mean that they have a common genetic basis, i.e. selection for one character does not always bring about an increase in other characters positively correlated with it phenotypically. In fact, the opposite may occur if the genetic correlation is negative even though the phenotypic correlation is positive. For this to be the case, the environmental covariance between the two traits would have to be positive and larger in absolute value than the negative genetic covariance between the traits.

The estimation of genetic correlations presents some difficulties. It is obvious that whenever the traits are measured on the same individuals the common environment to which they are subjected will conceal the true nature of their relationship. One method of overcoming this difficulty is to compute the correlation between traits in different individuals who bear a known relationship to each other. For example, considering parent and offspring a correlation between character "A" of the parent with character "B" of the offspring would provide us with a measure of the association between "A" and "B", uncomplicated by the common environment to which they have been subjected. The specific methods of calculation have been developed by Hazel (1943), using the relationship between parent and offspring, and Hazel et al (1943) where the relationship is between paternal half-sibs. It is worth noting that the estimates of genetic correlations obtained from actual data are subject to large sampling errors. This happens because a genetic correlation is computed as a function of the four covariances between the measurements of the two characters on the parent and on the offspring. Each one of these covariances naturally has its own sampling error. Analyses carried out so far on Romney sheep (Rae, 1950) suggest that about 2000 parent-offspring pairs are required to reduce the standard error of a genetic correlation to the order of 0.05 to 0.10.

Preliminary analyses of the genetic correlations occurring between traits in the New Zealand Romney Marsh (to be published elsewhere) indicate the following pattern of relationships: selection for increased greasy fleece weight will produce correlated responses in the direction of coarser wool, slightly greater staple length, no change in fleece quality and body type and an increase in hairiness. Selection for greater staple length will be accompanied by coarser, heavier and more hairy fleeces with no alteration in fleece quality and body type. Selection against hairiness will result in fleeces being finer, shorter in staple length and lighter but slightly better in fleece quality. Some improvement in body type is to be expected with decreased hairiness. The principal genetic antagonisms are between count and staple length, count and fleece weight, hairiness and fleece weight.

Present knowledge of the genetics and physiology of wool growth is insufficient to give an explanation of the pattern of genetic correlations found. In general, however, genetic correlations are produced if some genes affect more than one character. Since hereditary differences between individuals are produced by the effects of genes

on developmental and metabolic processes, a gene which alters a particular developmental or metabolic process will have an effect on any character or organ which is influenced by this process. Even though the gene has but a single primary action, the varied subsequent effects of that may cause it to show pleiotropic action on many features of the animal. One example of a gene having more than one effect is the N gene in the Romney Marsh (Dry, 1946). The most obvious effect of this gene is to produce a high abundance of halo hairs in the birth coat of the lamb. It is now well substantiated that the same gene leads to the growth of horns in rams (Dry et al, 1947).

Lush (1948) has suggested that, if past selection has been effective, it may be instrumental in producing negative genetic correlations. The frequencies of genes which have favourable effects on both characters, and of genes which affect on character favourably but have no effect on the other, will have been raised to a sufficiently high level that they contribute little to the additively genetic variance. Genes which have a beneficial effect on one character and a deleterious effect on the other will have had their frequencies brought to intermediate levels by continued selection for both characters. This class of genes will contribute more to the additively genetic variance. At the same time, the genetic correlation between the two characters will be negative.

Linkage between genes has also been suggested as a cause of genetic correlations. It will usually be a minor effect, since crossing-over in a freely interbreeding population leads to the coupling and repulsion heterozygotes becoming equally frequent in the population. Linkage is likely to be a detectable cause of genetic correlations in the first few generations after a cross between previously separate strains or varieties.

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