Genetic improvement in milk yield due to selection in a herd of Sinhala Cattle

BY

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IT is well recognized that the main object of any breeding programme is to change the genetic composition of a given population so as to increase the proportion of the more desirable genotypes in it at the expense of the less desirable ones. In consequence, the degree of success attained would depend firstly, on the accuracy with which the breeder decides on the animals that should be permitted to reproduce themselves. If no restriction of any sort is imposed on the animals in a given population and if all of them are allowed to leave progeny in equal numbers in the herd, then it is obvious that there would be no genetic improvement at all. Ordinarily, however, in dairy cattle breeding a certain amount of selection does go on at least through limitations on the size of the herd that could be maintained in a given unit. On the accuracy of such selection, which involves the estimation of the true genotypic values of the individuals comprising the population, would depend the actual genetic improvement achieved. But the appraisal of genotypic values is rendered difficult for most quantitative characteristics such as milk production in dairy cattle by the apparent lack of connection between phenotype and genotype. Since the production performance of a cow depends partly on the enviroment to which she is exposed and partly on her innate potentialities, any attempt to estimate the latter would be subject to some errors from mistaking the effects of enviroment for the effects of genes. The greater the non-genetic sources of variation affecting the character, the greater would be the errors in a phenotypic estimation of genetic merit. In other words, the accuracy of selection of genotypes on the basis of phenotypes is proportional to the heritability of the character.

A second factor which affects the genetic gain due to selection is the intensity of the selection practised. It can readily be seen that in a herd where a relatively small percentage of animals is selected for breeding, the average superiority of the selected group over the original herd would be greater than where a large percentage is retained if the accuracy of selection is the same in both cases. But there is a natural limitation to the selection intensity that could be practised, because if the population is to be maintained at a constant or expanding size the selection intensity would be dependent on the reproductive rates prevailing. The most useful measure of the intensity of selection in a given population is the average superiority of the selected parents over the mean of the group from which they were selected with respect to the trait considered. This is termed the selection differential.

With a knowledge of the accuracy and the intensity of selection it should be possible to compute the changes in the genetic worth of a population in each generation within limits of sampling errors. But such an expression will be useful only where the animals belong to non-overlapping generations and where the inter-generation span remains constant. This is never attained in practice, and in consequence what is really needed is the genetic gain per year rather than per generation.

The interval between generations is therefore a third factor which affects the efficiency of selection. It is measured in terms of the average age of the parents when the offspring are born. Where the inter-generation span is long, other factors being constant, the rate of improvement per year would be small, and vice versa.

The probable annual change in average genetic worth of a population can then be calculated on the basis of these three factors, *i.e.*, the accuracy of selection, the intensity of selection and the interval between generations. A method involving the use of these factors has been employed in the present work to estimate the rate of improvement actually achieved by selection in a closed herd of black Sinhala cattle in Ceylon.

SOURCE OF DATA

The herd used for this study was founded in 1938, and is still in existence. No breeding stock has been introduced during this time and all the animals up to about the end of 1950 have been sired by home-bred bulls, thereby making it possible to calculate the selection actually practised in breeding both cows and bulls.

COMPUTATIONAL METHODS AND RESULTS

Dickerson and Hazel (1944) have shown that, if $\triangle G_g$ is the rate of change per generation in the average value of the genotypes in a population, i the intensity of selection in terms of selection differentials and h^2 the heritability of the trait, then

$$\triangle G_g = ih^2$$

In other words, the multiplication of intensity by accuracy of selection gives the average gain per generation.

But, the whole process of selection is really composed of four parts, namely the contribution of male and female parents to male offspring and of male and female parents to female offspring respectively (Rendel and Robertson 1950). These must therefore be computed separately, the total improvement being the sum of the individual components. The four components may be designated I_{BB}, I_{CB}, I_{BC}, and I_{CC}, where I_{BB} is the mean genetic superiority of bulls from which bull calves are bred over their male contemporaries, I_{CB} is the mean genetic superiority of cows from which bull calves are bred over their heifer contemporaries, and so on. In the present herd I_{BB} and I_{BC} are zero, since there was no selection amongst bulls in the absence of progeny testing. Therefore, only I_{CC} and I_{CB} need to be computed.

A calculation was made in terms of selection differentials of the intensity of the selection (I_{CC}) practised in the present herd. Since selection was not all done at a given age (there being a continual selection at all ages), it was first decided to compute the selection differential on the basis of the first lactation only. This was done by weighting the first lactation record of each cow according to the number of daughters she left in the herd and comparing the average yield obtained by this process with the average of all first lactations in the group. This gave the " apparent" phenotypic selection differential as measured on the first lactation, and it was converted to a genetic measure by multiplying it by the appropriate figure for the heritability of milk yield.

There is a fair amount of evidence that within herds the heritability of milk yield is in the region of 0·25 (Lush 1940, Johansson 1947, Tyler and Hyatt 1947, Mahadevan 1950), and it is this value that was used here. The statement that the heritability of milk yield is one quarter means, in non-statistical language, that the difference in the breeding value of any two cows is, on the average, only one quarter of the difference between their records.

The " apparent " genotypic selection differential calculated above had a value 0·4 gallons. In other words, the average genetic superiority of the dams of cows based on the first lactation was 0·4 gallons. If all the culling were done on the first lactation, this figure would represent the true genotypic selection differential. The actual amount of culling on first lactation can, in fact, be calculated by comparing the first lactation yields of cows that also had a second lactation, with the average first lactation yield for the whole group. It was found, however, that in this particular herd there was no culling on first lactation, and that whatever selection was practised took place at later ages.

It was therefore evident that the genetic superiority of the cows chosen as parents, should be calculated on the basis of all available records. The figures for heritability used in such a computation would then be dependent on the number of available records for each cow. The genetic superiority, as shown by Rendel and Robertson (1950), would be given by $I_{CC}=\Sigma n h_l^2 (Y_l - \overline{Y})$ where h_l^2 is the heritability based on l lactations, $\overline{Y}$ is the mean of the first lactations of the whole group, Y_l is the mean of the lactations (standardised to first lactation) and n the number of daughters, for each cow. The values of I_{CC} thus calculated gave an average genetic superiority of dams of cows of 1·2 gallons (Table I). This is a threefold increase over that calculated on first lactations only.

The same method of calculation was applied to estimate the improvement (I_{CB}) achieved through the selection of dams of bulls as well. In this case each dam was weighted according to the number of daughters which her son had in the herd. The results obtained showed that the average genetic superiority of dams of bulls was 14·0 gallons (Table I). Combining this figure with the value of I_{CC} found above, we have $I_{CC} + I'_{CB} = 15{\cdot}2$ gallons.

TABLE I

Estimation of selection differential from culling practised

	Genetic superiority based on the 1st to 4th lactations (gallons)	Number of daughters in herd
Dams of cows (I_{CC})	1·2 ..	63
Dams of bulls (I_{CB})	14.0 ..	133
Total (ΣI)	15.2 ..	

It has, however, been pointed out earlier in this paper that the best criterion of the efficiency of any breeding programme is the genetic improvement per year rather than per generation. Therefore, the figure 15·2 obtained above, must be divided by the total generation length in order to obtain the annual improvement. The total generation length (ΣL) itself can be calculated quite simply as the sum of the four components, L_{CC}, L_{CB}, L_{BC} and L_{BB}, where L_{CC} is the mean age of the dams when the heifer calves are born, L_{CB} is the mean age of the dams when the bull calves are born, and so on. The generation lengths for the Sinhala herd used in the present study are set out in Table II, and show a total generation length of 24·0 years. The total genetic improvement per year due to selection is therefore given by $\frac{15\cdot2}{24\cdot0} = 0\cdot6$ gallons. Since the average yield per cow in the whole population studied was 94 gallons, this means a rate of genetic improvement of 0·64 per cent. per year.

The generation interval for this herd is exceptionally long. Lush (1945) has estimated the mean generation interval (*i.e.* $\frac{\Sigma L}{4}$) in dairy cattle at 4-4½ years, and Mahadevan (1950) obtained a value of 4·9 years for Ayrshire herds in Scotland.

TABLE II

Generation Lengths

L_{CC}	=	78 months
L_{CB}	=	77 months
L_{BC}	=	65 months
L_{BB}	=	68 months
ΣL	=	24·0 years

The value of the above method for estimating the genetic gain due to selection lies not so much in the absolute value of the rate of advance calculated, but in the comparison of it with the rate of gain in other populations. The method employed may, however, be criticised on the grounds of the applicability of heritability figures derived from other herds and breeds of cattle to this particular herd. Although a reliable estimate of heritability within the herd itself could not be arrived at owing to the standard error of the estimate being large, the figures for repeatability (*i.e.*, the average correlation between different records of the same cow) indicate that the assumed values of heritability are probably applicable to this herd.

DISCUSSION

These results for Sinhala cattle are in general agreement with those obtained by Robertson (1951) for Fulani (private communication), and lead to the unavoidable conclusion that improvement by mass selection is a very slow business. Nevertheless, we would incline to the view that it is worth persevering with to some extent, provided it is carried out systematically. Proper selection entails a regular culling of animals on the basis of production performance. Merely increasing the number of animals in a herd would certainly not lead to any genetic improvement at all. The fact that, in the present herd, barely one sixteenth of the total improvement came from the selection of dams of cows shows that a large percentage of the cows which should really have been culled for low production, were allowed to remain in the herd and procreate. Moreover, whatever selection was practised was not all directed towards milk yield. Selection for other characteristics such as colour, type and conformation, without reference to milk yield, would naturally have lowered the selection differential on yield. It is no doubt true that these other characteristics must not be forgotten. For example, a point of conformation of particular interest to dairy farmers might be the shape of the hind leg. But, selection for these characteristics should not be at the expense of milk yield if the ultimate aim is to increase the milking potentialities of the herd. In this connection, the suggestion that draught might have been an additional criterion of selection in the Sinhala herd, and might have been a contributory factor to the low selection differential on yield, cannot be taken seriously because no attempt has hitherto been made to measure the draught propensities of any of these animals.

Other reasons for the low genetic gain in this herd are —

(*a*) Selection has often been incomplete, in that the offspring of cows which were themselves culled for low milk production were frequently incorporated into the herd. In consequence, what was effectively a cull became part of the breeding stock in the next generation.

(*b*) The interval between generations has been exceptionally long, resulting in a proportionately low rate of annual advance. This is mainly attributable in the present herd to the late age at first calving.

It has been suggested by different observers that progeny testing provides a useful method of increasing the rate of improvement. By progeny testing is meant the estimation of an individual's genotype by studying its offspring. Tyler and Hyatt (1948) have, however, shown by an analysis of Ayrshire records that a single record of a dam is a more accurate guide to the yield of her subsequent daughters than the average of her first three daughters. It is therefore evident that the use of progeny testing on the female side is highly limited. On the male side, it can be extremely useful, but the extra information provided by a progeny test about a sire's genotype must be weighed against the increase in generation length resulting from his use. Dickerson and Hazel (1944) have concluded that in breeding for butter fat production in a closed herd of 120 cows, the genetic improvement will actually be faster without progeny testing. The main reasons for the ineffectiveness of progeny testing in small herds are that (*a*) when a sufficient number of cows have been used to provide an adequate test of young bulls, there are few cows left on which to use the tested bulls, and (*b*) the number of young bulls that can be tested is small and hence the value of the selection is limited.

Progeny testing therefore does not seem to provide a solution for increasing the rate of selection in a herd of the present size. In consequence, there are only two possible alternative tools at the breeder's disposal for bringing about any genetic improvement. One consists of the adoption of a more rigorous culling based on production performance, and the other involves the introduction of 'foreign blood'. As regards the first alternative, it may be worth noting that it is possible to show by a theoretical method of estimation that the maximum possible genetic gain under the best conditions of selection would be about twice the rate of advance actually achieved in this herd. The second alternative of introducing 'foreign blood' may be a gamble, but nevertheless, if it is carried out scientifically, one may expect a rapid advance in productivity. It is our contention that these two alternative methods should go hand in hand, so that comparative data would be available from which a definite decision on breeding policy for Sinhala cattle could be arrived at.

Finally, a word of warning is required. Whatever breeding policy is adopted, one cannot expect great overall progress in dairy-cattle improvement if the level of feeding and management remains at a very low level. It is probably true to say that at the present time, the greatest advance could be made if the nutritional level of cattle in Ceylon is given serious consideration and substantial measures adopted for its improvement—though this does not necessarily mean that we should now concentrate entirely on environmental measures. Genetic differences between individuals are present on a sufficiently large scale to provide a basis for considerable increases in production over and above any which may be brought about by improved environment. It is only by a successful dovetailing of environmental and genetical methods that we can hope to derive the greatest benefits for our labours.

SUMMARY

The method used for the estimation of genetic gain due to selection in dairy cattle is outlined. An estimated gain of milk of 0·6 per cent. per year is given for a Black Sinhala herd in Ceylon. The reasons for the low rate of advance due to selection are discussed in relation to the rate of advance expected with other breeding methods.

ACKNOWLEDGMENT

Sincere thanks are due to Mr. F. I. Bagot for his conscientious help with the computations.

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