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Implications of curvilinear response in dairy cows with increasing level of exotic inheritance in relation to a plausible breeding strategy for cattle development

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Abstract

Although the most of the crossbreeding experiments, in dairy cattle, have revealed a curvilinearity in relationship between production and level of exotic inheritance, very little effort has been made in studying the reasons behind this curvilinearity. The present investigation is aimed towards bridging this gap to a reasonable extent. The fitness reversal and G $\times$ E interaction hypotheses of curvilinearity are tested empirically, using military dairy farm data. In the light of the results it is concluded that the curvilinearity is the result of a negative correlation between production and adaptation induced by 'fitness reversal' and G $\times$ E interaction has nothing to do with it. A case for developing a synthetic breed with 2/3 inheritance from two exotic breeds is also mooted.

Key words : Crossbred dairy cows, curvilinear response, fitness-reversal model

Introduction

Considering the high yields of exotic breeds like Holstein Friesian, Jersey, etc. as compared to the indigenous stock, crossbreeding between the exotic and indigenous stock offers a quicker process for increasing milk production than selective breeding and improvement of the indigenous cows. This is the reason why crossbreeding is underway in many tropical countries including India. Crossbreeding, however, is not without its limitations since, the crossbred animals may not have the same degree of physiological adaptability, which provides them immunity against diseases and tolerance to withstand the extreme climatic conditions as the indigenous ones. Whenever a new breed/type is introduced in a certain environment natural selection will have its role in shaping adaptation of this stock against the stresses and strains of adverse environmental conditions. Such an adaptation also involves physiological adjustments/changes placing limit on production, probably, through the depression of thyroid activity leading to lowered metabolic rate or through increased adreno-cortical activity to help maintain homeostasis [1], all resulting in depression in growth and other production activities. Any decision, on the choice of the exotic and indigenous breeds and the exact breeding policy in a crossbreeding program, whether the program is for grading up of indigenous cows or is aimed at new breed formation, has to be based on information from past studies on the effectiveness of these breeds and the optimum level of exotic inheritance for higher productivity. Most of the investigations on production traits of crossbred dairy cattle have established curvilinearity in response to the level of exotic inheritance-for instance, milk yield increases up to 50 per cent of exotic inheritance beyond which there is little improvement or there is a decline [1]. As suggested by these authors, this curvilinear relationship is difficult to explain because, continued backcrossing to the superior breed of exotic origin is supposed to increase the frequency of desirable genes in their progeny which should show improvement in the mean performance.

The curvilinear relationship could possibly due to (i) the reversal of the effect (on production) of genes controlling fitness in the tropical environment, leading to a negative correlation between production and fitness traits; (ii) G $\times$ E interaction; (iii) the disintegration of co-adapted polygenic blocks determining the balanced genotype or (iv) higher survival of gametes carrying higher complements of chromosomes from the indigenous parent. No serious attempt has been made so far, either in India or abroad, in testing these hypotheses about the possible mechanisms behind curvilinearity. Any study on the higher survivability of gametes carrying higher complements from the indigenous parent or regarding the disintegration of co-adapted polygenic blocks can be carried out only in well-equipped genetic laboratories. But the 'reversal of fitness' hypothesis and the possible involvement of genotype-environment interaction are, however, amenable to statistical testing. The suggestion of

Acharya and Bhat [1], that, a negative correlation between production and adaptation to tropical environment is a more logical explanation has provided the initial motivation for taking up this investigation in this direction. The results of Jain and Prabhakaran [2], in confirmation of the 'fitness reversal model', gave some additional impetus to the study. The conclusions of these workers based on scanty data had needed corroboration through further studies with larger amount of data. The purpose of this paper, therefore, is to report the findings of this investigation and also to suggest a plausible breeding strategy for cattle improvement in India.

Materials and methods

The basic data utilized for this investigation were extracted from the collection of military farm data at the Indian Agricultural Statistics Research Institute, New Delhi and formed part of the cattle breeding records of Lucknow, Meerut, Agra, Allahabad, Jabalpur, Dehradun, Ambala, Jallundhar, Bangalore, Secunderabad, Mhow, Namkum and Pune farms over the 30 years period, 1947-1976. Although a large number of cross breeding schemes on dairy cattle have been in operation in India, the only source of data which can provide some definite answer to the breeder's problems is of the military farms located in different parts of the country [3]. Derived from the initial crosses between the exotic breed Holstein Friesian and the indigenous breeds, Sahiwal, Sindhi etc., a very large number of grades of animals (designated by the level of exotic inheritance present) have been raised at the above farms as the policy of criss-cross breeding continued. Of these only animals with proportions, 1/4, 3/8, 1/2, 5/8 and 3/4 of, exotic inheritance have been considered. For these animals the details like age at first calving (AFC), average inter-calving period (AICP), fitness index (FI) were worked out from the basic data and were considered along with lactation yield and other coded information (period, farm etc.) about the individual cows. For the AFC and FI, the period was decided according to the year of birth of the cows and the 30-year period was broken up into six 5-year periods, the first and last periods being 1947-51 and 1972-76 respectively. For lactation yield the division was, however, according to the period of calving and this gave six periods, 1949-53, 1954-58, 1959-63, 1964-68, 1969-73 and 1974-78. Each year was further divided into four seasons viz. summer (April to June), rainy (July to September), winter (October to January) and spring (February to March). The animals which were born in a summer month were considered as having born in summer, those born in a rainy month considered as born in rainy season and so on. The season of calving was also decided in a similar fashion, taking note of the month of calving. In the present investigation the production has been measured in terms of the first lactation yield of the animals.

It is ideal if the data used for the testing of fitness reversal model are from cows, which are fairly contemporary and are analysed farm wise. This could have avoided the need for adjustments for the effect of extraneous factors, farm, period, etc. But a preliminary examination of data revealed that no other farm-period combination except the Lucknow-sixth period combination had sufficient number of data points under different grade categories justifying separate, adjustment-free, analysis. Accordingly the data after adjusting for farm, period and season effects were pooled in order to have more observations under each grade category, of the Holstein Friesian $\times$ Sahiwal cross. For G $\times$ E interaction analysis the Harvey least squares analysis [4] for non-orthogonal data with interaction, can be applied straight to the unadjusted data. The essential details of the methods of data analysis are provided in the following.

The fitness reversal model and its testing

Under the native environment the performance of exotic breeds is considerably affected. It may be possible that the genes controlling fitness, which were favourable in temperate environment, have detrimental effects on production in the tropics and the amount of depression caused is more in higher grades. The half-breds by virtue of their superior homeostatic property [6] both at individual and population level are, however, not much affected. This phenomenon can explain the curvilinear response in production in the crossbred population. Let us assume that two pairs of genes having additive and dominance effects respectively control both production and fitness. Further, the fitness genes in the exotics have harmful effects on production in the native environment. With this model, hereinafter referred to as "fitness reversal model" it can be expected that higher aggregate genotypic value and hence, peak production in the crossbred is attained at 50% of exotic inheritance and production declines as the inheritance deviates from this level on either side. On closer look it will be seen that the effect of the new environment on the exotics is to magnify a negative correlation between production and fitness- related traits. In other words natural selection is antagonistic to artificial selection.

By weighting the selection differential the joint effects of natural and artificial selection are measured together, and comparing the effective (weighted) selection differential with the expected would reveal whether natural selection is of importance and if so, whether it operates synergistically or antagonostically to artificial selection [2]. The expected selection differential is the simple mean phenotypic deviation of the selected parents while the effective selection differential is the weighted mean deviation of parents, the weights being the values of a fitness trait. The number of offspring left behind by different animals (selected) during their life-span could have been the best weighting factor but this was not feasible due to the culling practices observed at the military dairy farms. Accordingly a Fitness Index (FI) defined as

$$FI = \frac{\text{Number of progeny born upto the last recorded calving}}{\text{Age of the animal in years at last calving}}$$

and closely related to fitness is considered as a useful weighting factor. Other weights considered are the age at first calving (AFC) and the average inter-calving period (AICP) both being indirectly related to fitness of individual animals. In the event of both artificial and natural selection favouring higher values of the respective traits, the effective selection differential must be higher than the expected selection differential, and consequently the ratio of the former to the latter will be greater than unity. On the other hand when natural selection is working against directional selection the ratio assumes a value less than unity. There is also a third possibility that natural selection is not at all operative in which case the effective and expected selection differentials will be more or less of the same magnitude and the ratio between the two will be very close to unity.

The validity of the 'fitness reversal' hypothesis (model) can, therefore, be verified by showing that the role of natural selection is less pronounced in half-breds than in higher grades. For this purpose a selection pressure is superimposed on the different sets of data (pertaining to different grades) by discarding a certain percentage of cows judged inferior based on their lactation performance. Both effective and expected selection differentials are worked out for different grades, using, in turn the three fitness related traits, FI, AFC, and AICP as weighting factors and compared to discover whether natural selection is operative with regard to a particular grade and if so in which direction. However, there arises the question whether a certain deviation of the observed ratio of the effective and expected selection differential from unit is significant or not. Since the author could not decide on any efficient test procedure suitable for this purpose, the inference here is based on the similarity or otherwise of results from multiple samples by considering 25%, 30%, 35% and finally 40% of the highest yielding cows. The number, of observations on some of the grades was so small that any size below 25% of the original size was not considered useful from the point of view of meaningful interpretation.

Genotype-environment interaction model

Another important biological phenomenon, which might contribute to the non-linear response in dairy cattle, is genotype- environment interaction by which we mean the interplay of genetic and non-genetic effects causing differential relative performance of different genotypes (here, the different grades) in different farm/period or management environments. To discover whether genotype-environment interaction has influenced the response of different, genotypes, it will be sufficient to carry out an appropriate analysis of variance providing the break up of the total variance into components attributable to the main effects and interactions. Harvey least squares analysis [4] for non- orthogonal data with interaction was, therefore, applied to the unadjusted data taking into account only the Grade × Farm interaction component in the model apart from main effects. The other components could not be considered due to the non- filling of a number of sub classes. For the same reason the study had to be confined to Holstein Friesian × Sahiwal cross, which alone provided sufficient number of data points. If the presence G × E interaction is confirmed, then this could be counted as a possible, but not a sure, reason for the observed curvilinearity. But when the analysis indicates the absence of G × E interaction, the curvilinearity can almost surely be the resultant effect of a negative correlation between production and fitness and this will be in keeping with the 'fitness reversal' model explained earlier.

Results and discussion

The ANOVA revealed that the Grade × Farm interaction contributed little to the variability in lactation yield. All the grade means were significantly different except 1/4 and 3/8 grades. Also, as evident from Table 1 the curvilinearity persist even when the response of different grades is averaged over other factors, suggesting that Grade × Farm and other similar interactions are independent of curvilinearity. In all farms there was a continuous increase in the lactation yield up to 62% of exotic inheritance. However, the 3/4 grade performed very badly in all the farms except Lucknow, where it may not be inferior to the 5/8 grade. From the above confirmation of G × E interaction it can be understood that the performance of higher grades will not be improved by considering some of these grades for specific adaptation in favourable environments. The ratio between, effective and expected selection differentials for different grades of Holstein Friesian × Sahiwal crossbred in different sample sizes are presented in Table 2. These have been worked out by considering FI as weight. From the magnitude of the values it is evident that the rankings are, almost, identical suggesting a very high degree of concordance. This means that all the five different samples carry the same message

Table 1. Farm-wise least square means for different grades of exotic inheritance, in respect of lactation yield (kg)

		Grade					
S. No.	Farm.	1/4	3/8	1/2	5/8	3/4	Overall
1.	Dehradun	2620	2615	2889	3427	2614	2833
2.	Lucknow	2380	2529	3568	3596	3686	3152
3.	Meerut	2142	3061	3208	3293	2238	2789
4.	Ambala	2208	2376	2470	3646	2683	2731
	Overall	2337 (26)*	2645 (58)	3102 (194)	3492 (61)	2805 (113)	2876 (452)

*Figures within parenthesis are the number of observations on which the means are based

Table 2. Ratio between effective and expected selection differentials for different grades of Friesian × Sahiwal cross considering FI weighting

	Sample size				
Grade	25%	30%	35%	40%	Overall
1/4-bred	0.92	0.95	0.96	0.96	0.95
3/8-bred	0.95	0.94	0.95	0.96	0.95
1/2-bred	1.00	0.99	0.99	0.98	0.99
5/8-bred	0.98	0.98	0.98	0.98	0.98
3/4-bred	0.97	0.96	0.96	0.95	0.96

in so far as the joint role of artificial and natural selection is concerned. In the case of 1/2 and 5/8 grades, the ratio is very close to unity suggesting that these grades are almost unaffected by natural selection. But in other grades below and above 50% of exotic inheritance the ratios are always below unity, suggesting that natural selection in these cases operate antagonistically to artificial selection. This, therefore, points to the validity of the 'fitness reversal model'. Table 2 also shows the homeostatic capability of 5/8 grade which is very much comparable with that of half-bred cows. This agrees with the earlier observation (Table 1) that the 5/8 grade excels other grades in almost all the farms. The ratio of effective and expected selection differentials worked out by using AFC and AICP as weights were not fit for drawing any general conclusions and so are not considered here.

The confirmation of the fitness reversal effect makes the development of new breeds from suitable crossbred bases, satisfying the requirements of the tropical conditions for better performance all the more relevant and important. This is worth considering along with earlier findings [5] wherein the superiority, of 2/3 exotic obtained through C-system of crossing over other grades, with regard to production and adaptability characteristics as well as index of lifetime production, has been reported. The formation of a synthetic effecting the amalgamation of desirable qualities of two exotic breeds and a promising indigenous breed seems to be a potential strategy for cattle improvement in India. The operational advantages of this system (C-system) and the genetic composition of the three-breed gene pool are sufficient to justify this. The system which ultimately leads to the formation of an interbreeding population becomes, in due course of time, operationally much simpler because, selective breeding can be practiced by the average farmer and unlike crisscross or rotational breeding programmes no manipulation of multiple types are involved. After the formation of 2/3 grades several fold increase in their number can be brought about through multiple ovulation and embryo transfer technology, which is picking up in our country.

The superior production efficiency of the population of 2/3 exotic created by the C-system is quite natural because under this system the level of exotic inheritance at the population level is maintained, in every member of the population, and at a desirable level. Dickerson [7] has observed that compared with the parental breeds the greater initial heterozygosity of a new synthetic breed unless lost through early inbreeding should mean both higher initial performance levels and greater genetic variability for possibly enhanced response to further selection. Thus new breed development is indicated even when heterosis is important, if unfavourable recombination effects are negligible. However for the success of the breeding programme the effective population size should remain reasonably large to avoid inbreeding.

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