

## ON GENE INTERACTION IN INDIAN DAIRY CATTLE

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(Received : May, 1988)

### SUMMARY

Considering thirty two Holstein Friesian-Shahiwal grade (generation) means obtained from the adjusted data of seven Military Farms (pertaining to the period 1945-79) as dependent variable ( $y$ ) and the coefficients of the parameters of components of mean in the corresponding expected means as independent variable ( $x$ ), the digenic, trigenic and quadrigenic interaction models were fitted by the weighted least square method for characters lactation yield, dry period and calving interval.

Although digenic interaction model is inadequate for all the three traits, the trigenic interaction model is adequate for dry period and quadrigenic interaction model for lactation yield and calving interval. Thus non-allelic interaction of one kind or other is present in all the traits considered. As such these characters having mainly non-additive gene action can be improved through corssbreeding.

*Keywords* : Gene interaction; Quadrigenic interaction; Grade.

### Introduction

The type of breeding policy to be adopted in plants or animals depends on gene action and interaction. Hill [2] studied the gene action in plants using recurrent backcross generations. Sharma and Narain [5] studied gene action for quantitative characters in dairy cattle by fitting additive-dominance model, which however failed to fit well in six of the nine characters considered. An attempt is made in this paper to examine the influence of non-allelic interactions on the production and reproduction

traits in dairy cattle by fitting digenic, trigenic and quadrigenic interaction models.

### 1. Material and Methods

The data from seven Military Dairy Farms for the period 1945 to 1979 pertaining to first lactation of Sahiwal cows and 31 backcross generations (grades) originated from an initial Holstein Friesian  $\times$  Sahiwal cross on characters lactation yield (LY), dry period (DP) and calving interval (CI) adjusted for farm, period and season effects (Harvey [1]) were utilised in the present study. The means and standard errors for the various grades were obtained for all the traits considered and means are presented in Table 1. Further details of the data are as given in Sharma and Narain [5]. Generations were defined as per Mather and Jinks [4]. Because of the one to one correspondence between grades and generations (Sharma and Narain [5]) these are used as synonymous terms in this paper. The present work will be confined to the fitting of digenic, trigenic and quadrigenic interaction models for those characters for which additive-dominance model was shown to be inadequate by Sharma and Narain [5]. The derived characters studied in the earlier paper are also dropped.

The presence of digenic interactions introduces three additional parameters  $[i]$ ,  $[j]$  and  $[l]$ , which are respectively additive  $\times$  additive, additive  $\times$  dominance and dominance  $\times$  dominance interactions. The coefficients of  $[i]$ ,  $[l]$  in the expected mean of any generation can be obtained by squaring the coefficients of  $[d]$  and  $[h]$  respectively and that of the parameter  $[j]$  by multiplying the coefficients of  $[d]$  and  $[h]$ . Thus it is clear that the expectation of any generation mean in the presence of digenic interactions can be written for any arbitrary number of pairs of genes with arbitrary distribution of genes between parents by using the parameters  $m$ ,  $[d]$ ,  $[h]$ ,  $[i]$ ,  $[j]$  and  $[l]$  if the expected generation (grade) mean is available in terms of  $m$ ,  $[d]$  and  $[h]$  parameters.

The presence of trigenic interactions introduces four additional parameters :

$[n] = [i_{abc}]$ , denoting the sum of all trigenic interactions among the homozygous combinations,

$[o] = [j_{abc}]$ , denoting the sum of all trigenic interactions among the pairs of homozygous combinations and each heterozygous combination in turn,

TABLE 1 — TRAITWISE MEANS OF VARIOUS HOLSTEIN FRIESIAN  
 × SAHIWAL GRADES (GENERATIONS) OBTAINED FROM  
 THE ADJUSTED DATA

<i>Grades</i>	<i>Generations</i>	<i>Lactation yield (kg)</i>	<i>D. P. (days)</i>	<i>C. L. (days)</i>
0	Sahiwal	1760	160	456
1/2	F <sub>1</sub>	2742	119	418
1/4	B <sub>2</sub>	2181	161	482
3/4	B <sub>1</sub>	2699	154	445
1/8	B <sub>22</sub>	1864	169	450
3/8	B <sub>12</sub>	2028	145	447
5/8	B <sub>21</sub>	2642	114	425
3/16	B <sub>122</sub>	1979	161	446
7/16	B <sub>112</sub>	2229	123	400
9/16	B <sub>221</sub>	2343	105	400
11/16	B <sub>121</sub>	2423	136	425
13/16	B <sub>211</sub>	2542	145	448
3/32	B <sub>1222</sub>	2020	112	401
7/32	B <sub>1122</sub>	2125	132	435
11/32	B <sub>1212</sub>	2037	143	437
15/32	B <sub>1112</sub>	2224	129	418
19/32	B <sub>1221</sub>	2481	135	444
21/32	B <sub>2121</sub>	2637	179	402
23/32	B <sub>1121</sub>	2610	136	432
27/32	B <sub>1211</sub>	2499	122	457
7/64	B <sub>11222</sub>	1995	125	380
15/64	B <sub>11122</sub>	2253	143	439
23/64	B <sub>11212</sub>	2187	128	444
35/64	B <sub>12221</sub>	2749	92	394
39/64	B <sub>11221</sub>	2570	126	437
43/64	B <sub>12121</sub>	2546	117	432
51/64	B <sub>12211</sub>	2020	129	418
47/128	B <sub>111212</sub>	1995	113	438
71/128	B <sub>112221</sub>	2595	93	391
79/128	B <sub>111221</sub>	2592	120	413
87/128	B <sub>112121</sub>	2538	104	387
103/128	B <sub>112212</sub>	2365	112	412

$[p] = [j_{a/bc}]$ , denoting the sum of all trigenic interactions among the pairs of heterozygous combinations with each homozygous combination in turn, and

$[q] = [l_{abc}]$ , denoting the sum of all trigenic interactions among the heterozygous combinations.

The above parameters take into account the signs of the interactions and the distribution of the interacting genes between the two parents except the parameter  $[z]$  which takes only sign into account and is independent of the distribution of the genes in the parents. As in case of digenic interactions the coefficients of trigenic interactions in the expression of the expected generation (grade) mean can be obtained using the coefficients of  $[d]$  and  $[h]$ . The coefficients of  $[n]$  and  $[q]$  are cubes of the coefficients of  $[d]$  and  $[h]$  respectively, the coefficient of  $[o]$  is the product of the square of the coefficient of  $[d]$  and the coefficient of  $[h]$ ; and the coefficient of  $[p]$  is the product of the square of the coefficient of  $[h]$  and coefficient of  $[d]$ . Thus using the coefficients of the parameters  $[d]$  and  $[h]$  as derived by Sharma and Narain [5], the expected means of the grades (generations) can be obtained assuming the presence of digenic and trigenic interactions as per the procedure outlined above.

Further to specify the contribution of quadrigenic interactions to the generation means five parameters are required in addition to ten parameters necessary to accommodate the contribution of additive, dominance, digenic interaction and trigenic interaction effects. To estimate these parameters a minimum of 15 generations with a different expectation in terms of the parameters of the model are required.

The five parameters required to specify quadrigenic interactions are described below as an extension of the notation of Jinks and Perkins [3].

$[r] = [i_{abcd}]$ , denoting the sum of all quadrigenic interactions among the homozygous combinations,

$[s] = [j_{abc/d}]$ , denoting the sum of all quadrigenic interactions among the triplets of homozygous combinations and each heterozygous combination in turn,

$[t] = [j_{ab/cd}]$ , denoting the sum of all quadrigenic interactions among the pairs of homozygous combinations with each pair of heterozygous combination in turn,

$[u] = [a/bcd]$ , denoting the sum of all quadrigenic interactions among the triplets of heterozygous combinations and each homozygous combination, and

$[v] = [1_{abcd}]$ , denoting the sum of all quadrigenic interactions among the heterozygous combinations

The above parameters take into account the signs of the interactions and distribution of the interacting genes between the parents except the parameter  $[v]$  which takes only sign into account and is independent of the distribution of genes in the parents.

As in case of digenic and trigenic interactions the coefficients of quadrigenic interactions in the expression of an expected generation (grade) mean can be obtained using the coefficients of  $[d]$  and  $[h]$ . The coefficients of the parameters  $[r]$  and  $[v]$  are the fourth power of coefficient of  $[h]$  and  $[d]$  respectively, the coefficient of  $[s]$  is the product of cube of the coefficient of  $[d]$  and the coefficient of  $[h]$ , the coefficient of  $[t]$  is the product of the square of the coefficient of  $[d]$  and square of the coefficient of  $[h]$  and the coefficient of  $[u]$  is the product of cube of the coefficient of  $[d]$  and coefficient of  $[h]$ . Thus as per the procedure explained above the generation (grade) means can be expressed in terms of 15 parameters of quadrigenic interaction model.

In this paper attempt is made to fit digenic, trigenic and quadrigenic interaction models for each of the three traits considered by the method of weighted least squares minimising the weighted error sum of squares with respect to the parameters of the particular model. This resulted in the normal equation  $(\underline{x}' \underline{w} \underline{x}) \underline{g} = \underline{x}' \underline{w} \underline{y}$  where  $\underline{x}$  denotes a matrix of the coefficients of the parameters in the expected means of generations,  $\underline{w}$  is a diagonal matrix of inverse of the squares of standard error of generation means on the assumption of zero covariance between them;  $\underline{g}$  is a vector of parameters and  $\underline{y}$  is a vector of generation (grade) means obtained from adjusted data. The solution of the above normal equations could not be obtained due to singularity of the matrix  $(\underline{x}' \underline{w} \underline{x})$ . While searching the possible reasons for the singularity of the matrix it was found that the sum of the coefficient of  $[h]$  and the absolute value of the coefficient of  $[d]$  is always one. This has probably caused the singularity of the matrix. The ranks of the matrices for the digenic, trigenic and quadrigenic interaction models were found to be five, eight and eleven respectively. As no inverse was possible for these singular matrices the  $g$ -inverse was found by obtaining their non-zero eigen roots and eigen vectors. Let  $\lambda_1, \dots, \lambda_r$  be the non zero roots and  $\xi_1, \xi_2, \dots, \xi_r$  be the column vectors corresponding to the non-zero roots of one of the three matrices. Thus the  $g$ -inverse of the matrix  $(\underline{x}' \underline{w} \underline{x})$  is given by

$$(\underline{x}' \underline{w} \underline{x})^- = \sum_{i=1}^r \lambda_i^{-1} \xi_i \xi_i'$$

The solution of the normal equations for the

parameters was obtained by the usual method of the weighted least squares by replacing unique inverse by the  $g$ -inverse. The solution of the above normal equations is given by  $\underline{g}^{\circ} = (\underline{x}' \underline{w} \underline{x})^{-1} (\underline{x}' \underline{w} \underline{y})$ .

The estimates of the parameters are not unique and will depend on a particular  $g$ -inverse of the matrix  $(\underline{x}' \underline{w} \underline{x})$ . However, the adequacy of the model can be assessed by calculating the weighted deviation sum of squares:  $(\underline{y}' \underline{w} \underline{y}) - \underline{g}'^{\circ} (\underline{x}' \underline{w} \underline{y})$ . This is distributed as a chi-square with degrees of freedom equal to  $n - r$ , where  $n$  and  $r$  are respectively number of generations (grades) available and the rank of the matrix  $(\underline{x}' \underline{w} \underline{x})$ . Thus the chi-square measuring adequacy of the model is given by  $\chi^2_{n-r} = (\underline{y}' \underline{w} \underline{y}) - \underline{g}'^{\circ} (\underline{x}' \underline{w} \underline{y}) = \sum_{i=1}^n w_i (y_i - \hat{y}_i)^2$ , where  $y_i$  and  $\hat{y}_i$  are respectively observed and expected means of  $i$ th generation. This expression of chi-square is unique and does not depend on the solution of the normal equations.

## 2. Results and Discussion

As explained above the digenic, trigenic and quadrigenic interaction models were fitted and the calculated values of chi-square measuring adequacy of additive-dominance, digenic, trigenic and quadrigenic interaction models are presented in Table 2, where the chi-square values for additive-dominance model have been taken for completeness from Sharma and Narain [5].

TABLE 2—CHI-SQUARE VALUES MEASURING ADEQUACY OF THE VARIOUS MODELS

Traits	Models	Chi-square value for			
		Additive-dominance model	Digenic interaction model	Trigenic interaction model	Quadrigenic interaction model
	D. F.	29	27	24	21
Lactation yield		79.9**	70.3**	40.6*	32.0
Dry period		50.5**	46.9*	32.2	—
Calving interval		53.2**	52.6**	41.9*	39.0

\* :  $p < 0.05$ ; \*\* :  $p < 0.01$ .

The chi-square values measuring adequacy of the digenic interaction model turned out to be significant ( $p \leq 0.01$ ) for all the characters

considered indicating the inadequacy of digenic interaction model for these characters [Table 2]. The trigenic interaction is adequate for dry period and quadrigenic interaction models for lactation yield and calving interval.

On the basis of these findings it is observed that non-allelic interactions are present in all the traits considered, viz. lactation yield, dry period and calving interval. Accordingly, these traits can be improved through suitable crossbreeding programme.

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