

A STUDY OF GENE ACTION IN CROSS-BRED CATTLE

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(Received : October, 1985)

SUMMARY

This paper derives the expected means of various crossbred generations utilising the relationships between the levels of exotic inheritance and the coefficients of the parameters $[h]$ and $[d]$, representing respectively the dominance and additive effects of genes involved. The estimates of these parameters have been obtained and tested for the economic traits of crossbred cows belonging to different grades, originated from Holstein Friesian \times Sahiwal cross, maintained at the Military Dairy Farms. It is inferred that the polygenes controlling the milk yield traits and age at first calving have probably significant additive and dominance effects, while dry period and calving interval have significant dominance effect only.

Keywords : Gene action; Exotic inheritance; Crossbreds.

Introduction

The knowledge of gene action operating in a population is of vital importance in deciding the breeding policy. Hill [3] studied this in plants using recurrent back cross generations. Jain [4] gave a procedure to estimate the parameters concerning the gene action by fitting genetic model which leaves no degree of freedom for testing the goodness of fit. It appears, however, that no systematic work to investigate the nature of gene action by fitting the genetic model has been undertaken in crossbred cattle. Accordingly this aspect is investigated in this paper utilising the data obtained from a number of Military dairy farms in India. In the process a general procedure to work out the expected generation means is also given.

Material and Methods

Most of the cross-breeding programmes for cattle in India, at the Military dairy farms or elsewhere, consist of crossing cows of indigenous breeds with promising exotic bulls. When the cross-bred cows are crossed with exotic and indigenous bulls alternately, the method is called criss-cross breeding. Prior to 1952 criss-cross breeding was followed at Military dairy farms. But, later, the undesirability of a high proportion of exotic inheritance prompted the Military farm authorities to go for back crossing with bulls of indigenous breeds to reduce the proportion of exotic inheritance. The use of Holstein Friesian (male) and Sahiwal (both male and female) as exotic and indigenous breed respectively was however more frequent. As the F_1 generation obtained by crossing indigenous cows with exotic bulls has 50% genes of exotic breed, this generation possesses $\frac{1}{2}$ of exotic inheritance. The crossings of F_1 with Holstein Friesian (H.F.) and Sahiwal (Sah.) bulls produce B_1 and B_2 back cross generations with exotic inheritance of $\frac{3}{4}$ and $\frac{1}{4}$ respectively. In our notation the back cross generation contains the suffix 1 if the crossbreds are crossed with superior parent (H.F.) and 2 if crossed with inferior parent (Sah.). Further, if cows of B_1 generation are crossed with bulls of H.F. and Sahiwal breeds, we get B_{11} and B_{12} generations with exotic inheritance of $\frac{7}{8}$ and $\frac{3}{8}$ respectively. The breeding policies adopted at the Military dairy farms from time to time, thus led to a large number of backcross generations. The proportions of exotic inheritance (grade) in respect of these generations can be obtained by making use of the obvious one to one correspondence between the backcross generations and the proportion of exotic inheritance as follows :

Let B_{ijklmn} be a backcross generation obtained by crossing first, the cows of F_1 generation with bulls belonging to breed i , then the cows of the resultant backcross generation, B_i with breed j to get the generation B_{ij} and so on and finally B_{ijklm} with breed n . The suffixes i, j, k, l, m, n assume the value of 1 or 2 according to whether they represent superior parent or otherwise. Then to obtain the proportion of exotic inheritance in any of the back-cross generation, we half either the proportion of exotic inheritance of the previous generation as it is or after incrementing it by 1 according to whether the suffix of B is 2 or 1. For example the proportion of exotic inheritance in generation B_1 is equal to $(\frac{1}{2} + 1) \times \frac{1}{2} = 3/4$, in B_{12} it is $3/4 \times \frac{1}{2} = 3/8$. . . and in B_{12121} it is

$$[\{(\frac{1}{2} + 1) \times \frac{1}{2}\} \times \frac{1}{2} + 1] \times \frac{1}{2} \times \frac{1}{2} + 1] \frac{1}{2} = 43/64.$$

The generation means expressed in terms of the mid-parent value m , the overall additive effect $[d]$ and the overall dominance effect $[h]$, assum-

ing, of course, the absence of interactions and linkage between non-allelic genes as well as other disturbing factors like differential viability and fertility, are in fact the expected generation means. The expected means of Sahiwal breed is taken as $m - [d]$ while that of F_1 generation $m + [h]$. The expected mean of any backcross generation is obtained by using the relationships between the proportion of exotic inheritance, and the coefficients of $[h]$ and $[d]$ in the expression for expected generation means established by the authors.

If we denote the proportion of exotic inheritance (grade) by g , the coefficient of $[h]$ by H and the coefficient of $[d]$ by D , the following relationships hold :

$$H = 2g \quad , \quad \text{for } g \leq \frac{1}{2}$$

$$H = 2(1 - g) \quad , \quad \text{for } g \geq \frac{1}{2}$$

$$D = -(1 - H) \quad , \quad \text{for } g \leq \frac{1}{2}$$

$$\text{and } D = (1 - H) \quad , \quad \text{for } g \geq \frac{1}{2}$$

As an example consider the determination of H and D for the generation B_{12121} . Since g of this generation is $43/64$ which is $\geq \frac{1}{2}$, the coefficient of $[h]$ which is $2(1 - g)$ is equal to $21/32$ and $D = (1 - H) = 11/32$. The coefficient of m is always one. Following this procedure the expected means of the commonly occurring generations (grades) at the Military dairy farms were obtained and are presented in Table 1.

The data pertaining to first lactation of crossbred cows of seven Military dairy farms located at Dehradun, Jabalpur, Lucknow, Meerut, Ambala, Jullundur and Pimpri for the period 1945 to 1979 on the characters lactation yield (kg), 300-day yield, yield per day of lactation length, yield per day of calving interval, lactation length (days), first dry period, first calving interval, weight at calving were utilised for the estimation of m , $[d]$ and $[h]$ parameters. The cows, whose performance records were available, belonged to 32 generations (grades) (generation defined as per Mather and Jinks, [5]). Though the data should be from animals subjected to uniform environmental conditions, this is not practicable in case of large animals. As such it was decided to adjust and thus render the data free from the influences of external factors such as farms, periods and seasons of calving or birth by using suitable statistical technique. The appropriate linear model with farm, period, season and generation or grade as fixed effects was fitted by the least squares technique as per Harvey [2]. Dropping the non-significant non-genetic effects the linear model was again fitted for the various characters. The original observations on individual cows were adjusted for significant non-genetic effects. The means and standard errors of the available generations were obtain-

TABLE 1—EXPECTED GENERATION MEANS

Generation	Proportion of exotic inheritance or grade	Coefficient of the parameter		
		<i>m</i>	[<i>d</i>]	[<i>h</i>]
Sahiwal	0	1	-1	0
<i>F</i> ₁	1/2	1	0	1
<i>B</i> ₁	3/4	1	1/2	1/2
<i>B</i> ₂	1/4	1	-1/2	1/2
<i>B</i> ₂₂	1/8	1	-3/4	1/4
<i>B</i> ₁₂	3/8	1	-1/4	3/4
<i>B</i> ₂₁	5/8	1	1/4	3/4
<i>B</i> ₁₂₂	3/16	1	-5/8	3/8
<i>B</i> ₁₁₂	7/16	1	-1/8	7/8
<i>B</i> ₂₂₁	9/16	1	1/8	7/8
<i>B</i> ₁₂₁	11/16	1	3/8	5/8
<i>B</i> ₂₁₁	13/16	1	5/8	3/8
<i>B</i> ₁₂₂₂	3/32	1	-13/16	3/16
<i>B</i> ₁₁₂₃	7/32	1	-9/16	7/16
<i>B</i> ₁₂₁₂	11/32	1	-5/16	11/16
<i>B</i> ₁₁₁₂	15/32	1	-1/16	15/16
<i>B</i> ₁₂₂₁	19/32	1	3/16	13/16
<i>B</i> ₂₁₂₁	21/32	1	5/16	11/16
<i>B</i> ₁₁₂₁	23/32	1	7/16	9/16
<i>B</i> ₁₂₁₁	27/32	1	11/16	5/16
<i>B</i> ₁₁₂₂₂	7/64	1	-25/32	7/32
<i>B</i> ₁₁₁₂₂	15/64	1	-17/32	15/32
<i>B</i> ₁₁₂₁₂	23/64	1	-9/32	23/32
<i>B</i> ₁₂₂₂₁	35/64	1	3/32	19/32
<i>B</i> ₁₁₂₂₁	39/64	1	7/32	25/32
<i>B</i> ₁₂₁₂₁	43/64	1	11/32	21/32
<i>B</i> ₁₂₂₁₁	51/64	1	19/32	13/32
<i>B</i> ₁₁₁₂₁₂	47/128	1	-17/64	47/64
<i>B</i> ₁₁₂₂₂₁	71/128	1	7/64	57/64
<i>B</i> ₁₁₁₂₂₁	79/128	1	15/64	49/64
<i>B</i> ₁₁₂₁₂₁	87/128	1	23/64	41/64
<i>B</i> ₁₁₂₂₁₁	103/128	1	39/64	25/64

ed for all the nine traits using the adjusted individual records. Equating the observed generation means obtained from the adjusted data to the corresponding expected generation means in terms of m , $[d]$ and $[h]$ parameters (Table 1), we obtain 32 equations which have been used to estimate these parameters. As generation means were not based on equal variances, the weighted least squares technique (Bulmer [1]), was used to estimate these parameters, taking inverse of the squares of standard errors of generation means as weights. For completeness the expression for the estimates of the parameters using weighted least squares technique is given below :

$$\hat{g} = (X' W X)^{-1} (X' W y)$$

Where y is a vector of observed generation means obtained using the adjusted data, \hat{g} is a column vector of the estimates of the parameters m , $[d]$ and $[h]$, X is a matrix of the coefficients of the parameters m , $[d]$ and $[h]$ in the expected generation means, $W = V^{-1}$, the matrix of weights, is the inverse of a diagonal matrix of variances of generation means on the assumption of zero covariances between them. The standard errors of m , $[\hat{d}]$ and $[\hat{h}]$ are $\sqrt{j^{11}}$, $\sqrt{j^{22}}$, and $\sqrt{j^{33}}$ respectively, where j^{11} , j^{22} , and j^{33} are first, second and third diagonal elements respectively of the matrix $(X' W X)^{-1}$. The test of significance of the estimates of the parameters is done by t test. The adequacy of the additive dominance model can be assessed by calculating the weighted deviation sum of squares $y' W y - \hat{g}' X' W y$, which is distributed as chi-square with $(n - p)$ degrees of freedom, where n and p are respectively number of generations available and the number of parameters estimated.

Results and Discussion

The estimates of the parameters m , $[d]$ and $[h]$ alongwith their standard errors are presented for each of the nine traits in Table 2. The estimate of the parameter $[d]$ representing the additive effect of genes was found to be significant for first lactation yield, 300-day yield, yield per day of lactation length, yield per day of calving interval and age at first calving, while the parameter $[h]$ representing dominance effect was significant not only for these traits but also for first dry period and first calving interval. On the basis of these findings it seems that effects of polygenes controlling the production traits first lactation yield, 300-day yield, yield per day of lactation length and yield per day of calving interval and the reproduction trait age at first calving are additive in nature. The presence of dominance effect of genes is also supported in the present study in the case of the traits dry period and calving interval in addition to the above

TABLE 2—ESTIMATES OF m , $[d]$ AND $[h]$ PARAMETERS OF COMPONENTS OF GENERATION MEAN

Traits	$\hat{m} \pm S.E.$	$[\hat{d}] \pm S.E.$	$[\hat{h}] \pm S.E.$	χ^2 with 29 d.f.
1st lactation yield (kg)	2134.4** \pm 50.1	381.0** \pm 47.0	339.4** \pm 75.0	79.9**
300-day yield	2183.6** \pm 57.1	343.1** \pm 50.9	331.6** \pm 83.5	83.5**
Yield/L.L.	7.10** \pm 0.14	1.20** \pm 0.13	1.31** \pm 0.20	125.0**
Yield/C.I.	4.92** \pm 0.13	0.88** \pm 0.13	1.06** \pm 0.19	92.8**
Lactation length (days)	293.6** \pm 3.9	4.3 \pm 3.6	5.0 \pm 5.8	30.5
Dry period	155.2** \pm 6.0	-6.5 \pm 5.5	-43.2** \pm 8.6	50.0**
Calving interval	449.5** \pm 7.3	0.7 \pm 6.7	-36.6** \pm 1.1	53.2**
Weight at first calving	374.6** \pm 3.2	-2.6 \pm 2.9	2.6 \pm 4.9	39.0
Age at first calving	1112.0** \pm 8.6	-53.3** \pm 7.9	-85.2** \pm 12.9	39.6

** : $p < 0.01$

five traits. The positive and significant estimates of the parameter $[h]$ in case of the characters first lactation yield, 300-day yield, yield per day lactation period, yield per day of calving interval indicate that the dominance effects of the genes controlling these characters are preponderantly in the direction of the superior parent (H.F.). Similarly negative and significant estimates of $[h]$ for the characters dry period, calving interval and age at first calving indicate that the dominance effect of the individual genes controlling these characters are also preponderantly in the direction of the superior parent as the values of these characters were higher in inferior parent (Sahiwal). The non-significance of $[h]$ in case of lactation length and weight at first calving does not necessarily indicate the absence of dominance. As expected the estimate of the parameter $[d]$

in case of age at first calving is negative in addition to being it significant. This is because the value of this trait is higher in inferior parent (Sahiwal) than that in superior parent (H.F.). Depending on the significance of the estimates of the parameters $[d]$ and $[h]$, it can be said that the genes controlling the characters first lactation yield, 300 day yield, yield per day of lactation period, yield per day of calving interval and age at first calving have significant additive-dominance effects. It can be further stated that the chi-square values (Table 2) measuring the adequacy of additive-dominance model could confirm the adequacy of additive-dominance model only in the case of age at first calving, lactation length and weight at first calving.

ACKNOWLEDGEMENTS

The authors are grateful to the Director of Military Farms, Army Headquarters, New Delhi, for providing the necessary data from the military farms.

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