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GENETIC ANALYSIS OF A CLOSED

HERD OF INDIAN CATTLE

by

Radha Mohan Acharya

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DOCTOR OF PHILOSOPHY

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I. INTRODUCTION

India is predominantly an agricultural country with more than three-fourths of her population depending on agriculture for their living. Livestock, especially cattle, supply an important source of power for agricultural operations. They are also an important means of transporting agricultural produce from village to the market and they supply motor power for irrigating land from wells in dry regions of the country. They are also the chief source of manure for the field. It does not seem possible or even feasible for some reasons that mechanization in agricultural operations in India will entirely replace the animal power in the near future, although some change is apparent. In India where the great majority of the people are vegetarian, milk provides a vital source of animal protein in human nutrition.

Cattle in India are reared for two main purposes, draught and milk. There is practically no slaughter of cattle for meat, except of buffaloes, and little attention has been paid to that purpose. Because of the poor financial status of an Indian farmer, he is not in a position to maintain two different types of cattle; one for producing milk for his family needs and the other for producing male calves to be used as oxen. Most of the Indian breeds of cattle are of draught type, except for the Red Sindhi and Sahiwal which are of milk type. However, a few draught breeds have shown a reasonably good milking potential. On these breeds (designated as dual purpose breeds) great efforts for improvement of draught and milk producing ability have been made.

The Indian Council of Agricultural Research, in collaboration with the Punjab Government, established a herd of Hariana cattle in the Punjab state in the year 1945 at the Government Livestock Farm at Hissar for studying whether through selective breeding draught ability and milk yield could be combined suitably to evolve a dual purpose type which would best serve the economic needs of the country. No great progress in the study of this objective has been made because no suitable measure of draught ability has been established so far. The selection of the stock in this herd has therefore been based mainly on milk production with a little attention paid to the breed characteristics.

The problems of breeding dual purpose cattle relate to improving both the draught ability and milk production of these animals. The draught ability of Hariana cattle is well established. The main components of low productivity are a late age at first calving, long calving intervals, and low daily milk production. Attempting to increase the productivity of these cattle may therefore be viewed as being concerned mainly with these components.

The present investigation was aimed at assessing the genetic gains made in milk yield through selection over a twenty-year period in this closed Hariana herd and also at evaluating the genetic changes made in other traits of economic importance towards which no great direct attention was paid. It was also desired to estimate genetic and phenotypic parameters for four important economic traits: milk yield, butterfat per cent, age at first calving and interval between calvings, and to combine them in a manner to maximize genetic gains through selection.

the time when progeny test information becomes available is so late that most sires are too old to be used for service or are even dead.

Some idea about age at first calving in different Indian breeds of cattle can be had from Table 1. The average age at first calving ranges from 39 to 58 months; with most averages falling in the 40-50 months range. The average age at first calving in the Hariana breed has been reported to range from 39 to 51 months in the data from four government farms in Uttar Pradesh (U. P.) (Singh and Desai, 1961a). The average age at first calving in the present study was 57.7 $\pm$ .4 months, based on 561 records. This is higher than in any other report reviewed.

a. Environmental factors affecting age at first calving Tandon (1951) reported from his work on Sahiwal x Holstein and Sindhi x Holstein crossbred cows maintained at Military Dairy Farms in India that age at first calving was not significantly affected by the season of calving.

b. Relationship between age at first calving and milk production in the first lactation Relationship between these two traits has been studied by different workers using the correlation, regression and analysis of variance techniques. The estimates of phenotypic correlations between these traits found in the literature are presented in Table 2. Some of these estimates are low and non-significant whereas others are large positive or large negative and highly significant.

In addition to the estimates reported in Table 2, Lecky (1951) observed a low correlation between these traits in Sahiwal cows. Amble et al. (1958) using the analysis of variance found that the variation in

II. LITERATURE REVIEW

A. Estimates of Genetic and Phenotypic Parameters

Numerous reports on Indian cattle have been published concerning the effects of environmental and physiological factors on the phenotypic expression of some traits of economic importance and on the phenotypic relationships among these traits. However, little has been done with respect to estimating genetic parameters. The failure to attempt the latter may have been due partly to the non-availability of large volumes of data and the lack of facilities for their analyses. Recently a few estimates of heritability and repeatability of some economic traits have appeared. Most of these are based on small numbers of observations and consequently have large sampling errors. Here the literature on Indian cattle, pertinent to the problem under investigation, has been reviewed.

1. Age at first calving

Late first calving is common in most tropical breeds of cattle. This, along with the long calving interval is the most important contributor to the unproductive life of these cattle. To improve the economic prospects of dairying in the tropics where the milk yield of most breeds is low, decrease in age at first calving is highly desirable. Reducing age at first calving would, in addition to decreasing the unproductive life, reduce the generation interval, making progeny testing of sires more feasible and thus would permit more rapid genetic progress. With the present age at first calving and the present calving intervals,

Table 1. Age of some Indian breeds of cattle at first calving

Breed	Number of records	Average (months)	Reference
Red Sindhi	350	41.7± .4	Amble et al. (1958a)
Red Sindhi	289	41.7± .4	Amble et al. (1958a)
Red Sindhi	82	42 ±1.0	Sundaresan et al. (1954)
Red Sindhi	59	40.5	Stonaker (1953)
Red Sindhi	216	42.9	Venkayya and Anantakrishnan (1956)
Tharparkar	422	49.4± .4	Amble et al. (1958a)
Tharparkar	209	48.7	Singh (1957)
Tharparkar	90	43.2± .9	Singh and Choudhury (1961)
Sahiwal	118	41.1± .6	Singh and Choudhury (1961)
Gir	80	47.3	Venkayya and Anantakrishnan (1956)
Gir	88	47.0± .8	Amble et al. (1958a)
Kangayam	477	44.1± .4	Amble et al. (1958a)
Kankrej	98	47.4± .8	Amble et al. (1958a)
Hariana	689	45.0± .5	Indian Veterinary Research Institute (1955)
Hariana	417	46.7 ± .4 [38.92±1.0 to 50.87± .6]	Singh and Desai (1961a)
Hariana	561	57.7 ± .4	Present study

age at first calving had significant effect on milk production in the Red Sindhi and Kangayam herds at Hosur and the Tharparkar herd at Patna. Production in different classes of age at first calving in different herds

Table 2. Estimates of phenotypic correlations

Breed	d.f.	Estimate	Reference
Age at first calving and milk production in the first lactation			
Red Sindhi	80	.06	Sundaresan et al. (1954)
Murrah (Buffalo)	60	.11	Sundaresan et al. (1954)
Sahiwal	116	.09	Singh and Choudhury (1961)
Tharparkar	88	.05	Singh and Choudhury (1961)
Red Sindhi	214	.44	Venkayya and Anantakrishnan (1956)
Gir	78	.34	Venkayya and Anantakrishnan (1956)
Ayrshire x Sindhi	239	.19	Venkayya and Anantakrishnan (1956)
Red Sindhi	62	.78	Venkayya and Anantakrishnan (1957)
Ayrshire x Sindhi	63	.41	Venkayya and Anantakrishnan (1957)
Tharparkar	38	-.42	Puri and Sharma (1965)
Sahiwal	22	-.42	Puri and Sharma (1965)
Red Sindhi	14	-.18	Puri and Sharma (1965)
Hariana		.18	Tandon (1961)
Age at first calving and first calving interval			
Red Sindhi	68	-.15	Sundaresan et al. (1954)
Murrah (Buffalo)	44	-.25	Sundaresan et al. (1954)
Red Sindhi	214	.56	Venkayya and Anantakrishnan (1956)
Gir	78	.20	Venkayya and Anantakrishnan (1956)
Ayrshire x Sindhi	239	.28	Venkayya and Anantakrishnan (1956)
Tharparkar	207	.025	Singh (1957)
Sahiwal	116	.12	Singh and Choudhury (1961)

Table 2 (Continued)

Breed	d.f.	Estimate	Reference
Age at first calving and first calving interval			
Tharparkar	88	.04	Singh and Choudury (1961)
Tharparkar	38	.10	Puri and Sharma (1965)
Sahiwal	22	-.14	Puri and Sharma (1965)
Red Sindhi	14	-.19	Puri and Sharma (1965)
Hariana		.11	Tandon (1961)

given in this report was plotted and an almost linear relationship was observed between these two traits in the Tharparkar herd and the Sahiwal herd at Hosur. In the Kangayam herd on the contrary production dropped up to the age of 49-52 months and then showed an increase. In the Red Sindhi herd at Bangalore, the effect of the variation in age on production was not significant and no relationship was observed between these two traits.

Significant effect of the variation in age at first calving on milk production in 150 days of the first lactation was also observed by Singh and Sinha (1960); the effect on milk production in 300 days of the first lactation was, however, not significant. The relationship between age and production in 150 days was curvilinear.

In most studies on the European and American cattle the relationship between these two characters has been observed to be curvilinear. Most

of the workers who estimated correlations between these characters reported in Table 2 did not discuss the nature of this relationship except to make inferences from the statistical significance of the estimate of correlation. If the true relationship in these cases was curvilinear the coefficient of linear correlation or regression would not measure the true relationship. With a very late first calving in most Indian breeds hardly any relationship between production in the first lactation and the age at first calving may be expected. The variation in production in different classes of the age at first calving may be mostly random.

Tandon (1961) reported a negative genetic correlation (-.19) between these two characters in Hariana cattle maintained at the Indian Veterinary Research Institute at Izatnagar (I.V.R.I.).

c. Relationship with milk production in subsequent lactations and lifetime production Sundaresan et al. (1954) found a significant negative correlation between age at first calving and various measures of lifetime production in purebred Sindhi and 1/4 Jersey x 3/4 Sindhi crossbred cows. The coefficients of regression of milk production up to 10 years of age on age at first calving in months, based on only 17 and 14 animals, were -513 lbs. and -377 lbs. in the two cases. Recently Puri and Sharma (1965) also have observed a highly significant and negative relationship between first calving age and lifetime production (yield up to 10 years of life) in Tharparkar, Sahiwal, Red Sindhi and Jersey x 1/2 Thari crossbred cows.

Table 3. Estimates of heritability of age at first calving for some Indian breeds of cattle

Breed	d.f.	Method of estimation	Estimate	Reference
Red Sindhi	192	Intra-sire regression of daughter on dam	- .09 ±.17	Amble et al. (1958a)
Red Sindhi	134	Intra-sire regression of daughter on dam	.16 ±.29	Amble et al. (1958a)
Red Sindhi	90	Intra-sire regression of daughter on dam	.39 ±.16	Stonaker (1953)
Tharparkar	215	Intra-sire regression of daughter on dam	.48 ±.16	Amble et al. (1958a)
Tharparkar	140 daughter-dam pairs of 16 sires	Intra-sire regression of daughter on dam	- .361±.10	Singh (1957)
Tharparkar	140 daughter-dam pairs of 16 sires	Intra-sire correlation	- .305±.08	Singh (1957)
Tharparkar	140 daughter-dam pairs of 16 sires	Half-sib correlation	.048±.09	Singh (1957)
Kangayam	281	Intra-sire regression of daughter on dam	- .08 ±.16	Amble et al. (1958a)
Gir	29	Intra-sire regression of daughter on dam	-1.24 ±.58	Amble et al. (1958a)
Kankrej	41	Intra-sire regression of daughter on dam	.66 ±.24	Amble et al. (1958a)

Venkayya and Anantakrishnan (1957) found no influence of age at first calving on milk production in subsequent lactations. Similar results were obtained by Singh and Sinha (1960), who however found the cows freshening for the first time at a later age to be retained in the herd for a longer period, thus having longer productive life.

A highly significant negative correlation (-.27) between age at first calving and production in the first four lactations was estimated by Sidhu (1964) in cows maintained at Karnal.

d. Relationship with calving interval The estimates of phenotypic correlation between age at first calving and first calving interval found in the literature are reported in Table 2. Most of these estimates are small and non-significant except those reported by Venkayya and Anantakrishnan in Sindhis and Sindhi x Ayrshire crossbreds. The low correlation between these traits indicates little apparent effect of age at first calving on the subsequent breeding efficiency.

A positive genetic correlation (.27) was observed between these two characters in Hariana cows by Tandon (1961).

e. Heritability estimates In Table 3 are presented the estimates of heritability of age at first calving in some Indian breeds of cattle, along with the volume of data and the method of estimation. These estimates range from -1.24 to +.66. The estimates based on more than 200 daughter-dam pairs are generally positive and sufficiently large (.30), except in the case of Kangayam breed where the estimate is -.08. The estimates of heritability of this trait in the Hariana breed both at

four government farms in U. P. and at I.V.R.I. at Izatnagar are larger than .30.

2. Milk yield

Indian cattle and cattle in the tropics in general are known for their low production. The average production of different Indian breeds of cattle in their first lactation can be viewed from Table 4. The average

Table 4. First lactation milk production of some Indian breeds of cattle

Breed	Number of records	Average (lbs.)	Reference
Red Sindhi	328	3595±83	Amble et al. (1958b)
Red Sindhi	390	2674±75	Amble et al. (1958b)
Red Sindhi	216	3323	Venkayya and Anantakrishnan (1956)
Red Sindhi	82	2600±151	Sundaresan et al. (1954)
Sahiwal	118	3283±142	Singh and Choudhury (1961)
Tharparkar	90	3228±139	Singh and Choudhury (1961)
Hariana	434	2115.6 [1538 to 2580]	Singh and Desai (1961b)
Hariana	561	1501±29	Present study

for the first lactation can give a fair idea of the production in general because the increase from first lactation to the lactation of maximum production in these cattle is small. The averages in most breeds range from 1500 to 3600 pounds. The averages for the Hariana breed reported by

Table 3 (Continued)

Breed	d.f.	Method of estimation	Estimate	Reference
Hariana			.375	Tandon (1961)
Hariana	244 daughter-dam pairs of 24 sires	Intra-sire regression of daughter on dam	.34 ±.12	Singh and Desai (1961a)
Hariana	244 paternal half sibs of 24 sires	Half-sib correlation	.34 ±.20	Singh and Desai (1961a)
Hariana	322 paternal half sibs	Half-sib correlation	.40 ±.02[a]	Singh and Desai (1961a)

[a]Standard error is extremely small but is cited here as reported in the reference.

Singh and Desai (1961b) from four Government farms in U. P. ranged from 1538 to 2579 pounds with an overall average of 2116 pounds. The average first lactation milk production of 1501 ± 29 pounds in the herd under the present study was the lowest of all reported.

a. Environmental factors affecting the first lactation milk production Year of freshening, when grouped into 5-year periods and adjusted for generation differences, had a significant effect on the first lactation milk production of Sahiwal cows maintained at the Hosur and the Bangalore herds. There was no difference in the milk yield of animals freshening for the first time in different months (Amble et al., 1958b). Sikka (1931) and Tandon (1951) also did not observe any differences in production of animals freshening in different seasons of the year in Sahiwal, Sahiwal x Holstein, and Sindhi x Holsteain crossbred cows, respectively.

Similar non-significant effects of month or season of freshening on the milk yield were recorded by Venkayya and Anantakrishnan (1958) in Red Sindhi cows; by Tomar and Mittal (1960) in Hariana cows and by Sidhu (1964) in cows at the National Dairy Research Institute at Karnal. However, Dutt and Singh (1961) and Agarwala (1962) recorded the season of freshening to have significant effect in Hariana and purebred Sindhi cows, respectively. In most cases the winter calvers had higher yield than animals calving in other seasons, except in the case of Red Sindhi cattle studied by Agarwala who found summer calvers to produce the highest.

b. Heritability estimates Estimates of heritability of the first lactation milk production of some Indian breeds of dairy cattle are

presented in Table 5. These estimates range from .13 to .43. The estimates obtained from intra-sire regressions of daughter on dam for the Red Sindhi breed and based on a relatively large volume of data are greater than .30. The estimates for the Hariana and Tharparkar breeds are, however, low and range from .13 to .26. Most of these estimates are well within the range of those reported for European breeds. The estimates for the Hariana seem to be low, especially for first lactation records. Heritability estimates based on first lactation records are generally expected to be a little higher than those based on later records (Rendel et al., 1957 and Freeman, 1960).

c. Relationship between first lactation milk production and milk production in later lactations and lifetime production Sikka (1933) was the first to study the reliability of different lactation yields (standardized to an 85-day service period) as an indicator of a cow's milking capability in the Indian cattle, using the correlation coefficients between successive lactation yields and the highest lactation yield as a measure of reliability. The values of these correlation coefficients increased with successive lactation yields and from this Sikka concluded that the mean of several records was more reliable than an individual record as a measure of a cow's milking capability.

Sundaresan et al. (1954) reported that milk production in the first lactation was highly significantly correlated (r = .77 to .85) with the different measures of lifetime production in Red Sindhi cows. These measures were production in 5 years following first calving, the

Table 5. Estimates of the heritability of first lactation milk yield for some breeds of Indian cattle

Breed	d.f.	Method of estimation	Estimate	Reference
Red Sindhi	91 daughter-dam pairs	Regression of daughter on dam	.2 [based on b = .14 and repeatability estimate of .41]	Mahadevan (1955)
Red Sindhi	182 [intra-sire]	Intra-sire regression of daughter on dam	.34±.18	Amble et al., (1958b)
Red Sindhi	143 [intra-sire]	Intra-sire regression of daughter on dam	.37±.14	Amble et al., (1958b)
Indian breed crosses with European cattle	1102 daughter-dam pairs	Intra-sire regression of daughter on dam	.38	Mahadevan (1954)
Sahiwal			.26	Patel (1956)
Sahiwal	127 daughter-dam pairs of 10 sires	Intra-sire regression of daughter on dam	.44±.32	Kooner (1963)
Sahiwal	127 daughter-dam pairs of 10 sires	Half-sib correlation	.37±.37	Kooner (1963)
Kankrej			.20	Patel (1956)
Malvi	44 daughter-dam pairs	Regression of daughter on dam	.43±.20 [based on 1st and 2nd lactation records]	Taneja and Bhatnagar (1959)
Hariana	80 daughter-dam pairs	Intra-sire regression of daughter on dam	.18±.22	Annual Report., I.V.R.I. (1955-1956)
Hariana			.26	Tandon (1961)
Hariana	178 daughter-dam pairs of 18 sires	Intra-sire regression of daughter on dam	.15±.04[a]	Singh and Desai (1961b)

[a]Standard error is extremely small but is cited here as reported in the reference.

Table 5 (Continued)

Breed	d.f.	Method of estimation	Estimate	Reference
Hariana	211 daughter-dam pairs	Intra-sire regression [based on average of all lactations and adjusted to one lactation basis]	.13±.09[a]	Singh and Desai (1961b)
Hariana	178 half-sibs of 18 sires	Half-sib correlation	.20±.01[a]	Singh and Desai (1961b)
Hariana	322 half-sibs of 22 sires	Half-sib correlation	.13±.12	Singh and Desai (1961b)
Tharparkar	335 daughter-dam pairs of 21 sires [only sires with six daughter-dam pairs]	Intra-sire regression of daughter on dam	.22±.02[a]	Kooner (1963)
Tharparkar	335 daughter-dam pairs of 21 sires [only sires with six daughter-dam pairs]	Half-sib correlation	.47±.34	Kooner (1963)

Table 6. Calving interval of some Indian breeds of cattle

Breed	Number of records	Average (months)		Reference
Red Sindhi	261	18.0 ±.3	(first calving interval)	Amble et al. (1958a)
Red Sindhi	237	14.7 ±.3	(first calving interval)	Amble et al. (1958a)
Red Sindhi	794	17.4 ±.2	(all calving intervals)	Amble et al. (1958a)
Red Sindhi	775	14.8 ±.2	(all calving intervals)	Amble et al. (1958a)
Red Sindhi	216	15.4	(first calving interval)	Venkayya and Anantakrishnan (1956)
Red Sindhi	70	16.0	(first calving interval)	Sundaresan et al. (1954)
Red Sindhi	22	15.4	(first calving interval)	Stonaker (1953)
Sahiwal	118	16.2 ±.34	(first calving interval)	Singh and Choudhury (1961)
Tharparkar	90	16.02±.38	(first calving interval)	Singh and Choudhury (1961)
Tharparkar	376	14.8 ±.2	(first calving interval)	Amble et al. (1958a)
Gir	69	15.7 ±.5	(first calving interval)	Amble et al. (1958a)
Gir	80	15.5	(first calving interval)	Venkayya and Anantakrishnan (1956)
Hariana	484	16.63	(first calving interval)	Singh et al. (1958)
Hariana	738	16.13±.16	(all calving intervals)	Singh et al. (1958)
Hariana	1258	18.9 ±.15	(all calving intervals)	Present study
Hariana	344	20.75±.26	(first calving interval)	Present study

production up to 7 years of age, and production up to 10 years of age with and without excluding milk production in the first lactation. Automaticity would have been responsible for these high correlations except between production in the first lactation and production up to 10 years of age excluding production in the first lactation. There was a part-whole relationship between production in the first lactation and different measures of lifetime production as the production in the first lactation was included in these measures of lifetime production. However, the difference in the correlations between production in the first lactation and production up to 10 years with and without excluding production in the first lactation was not large. Similar highly significant correlations were observed by Puri and Sharma (1965) in Tharparker, Sindhi, Sahiwal and crossbred cows.

3. First calving interval

Averages of first and subsequent calving intervals of some Indian breeds of cattle are presented in Table 6. The first calving intervals in the reports cited range from 15 to 21 months; most of the estimates being between 15 and 18 months. The average first calving interval of 20.75 ± .26 months for the herd under study was largest among those reported.

Calving interval can be considered as consisting of two parts, one from calving to next conception (service period) and the other the period of gestation. Gestation length has much smaller standard deviation than the service period. That the small differences generally observed in

gestation length are partly genetic is evidenced by significant breed differences in gestation length; however, Singh et al. (1958) estimated heritability of gestation length at .002 ± .084 based on 126 d.f. from intra-sire regressions, and of .3 ± .8 based on paternal half-sib correlations in Tharparkar cows. These authors also did not find any effect of sex on calf, age of dam, season and year of freshening on the gestation length. On the contrary, Chaudhuri and Sinha (1951), Lazarus and Anantakrishnan (1952) found most of these effects to be significant. Kohli and Suri (1957) in data from the herd under the present investigation found sex of calf, sequence of calving, month of freshening and sire to have significant effect on the length of gestation period.

Service period and calving interval should automatically bear a high correlation for biological reasons and the effect of both on milk production should be similar, especially where the average service period is long.

a. Environmental factors affecting calving interval Significant effects of year of calving and calving sequence on the calving interval of Tharparkar cows were reported by Singh (1958), who however did not find any significant effect of season of calving. Singh et al. (1958) on the contrary found rather large differences in the length of calving interval in different seasons in Hariana cows. Animals freshening from July to November had shorter calving intervals.

b. Heritability estimates Estimates of heritability of first calving interval of some Indian breeds of cattle are presented in Table 7.

Table 7. Estimates of the heritability of first calving interval for some Indian breeds of cattle

Breed	d.f.	Method of estimation	Estimate	Reference
Red Sindhi	155	Intra-sire regression of daughter on dam	-.08 ±.20	Amble et al. (1958a)
Red Sindhi	125	Intra-sire regression of daughter on dam	.13 ±.20	Amble et al. (1958a)
Red Sindhi and their crosses with European cattle	41	Intra-sire regression of daughter on dam	.88	Stonaker (1953)
Kangayam	223	Intra-sire regression of daughter on dam	.11 ±.19	Amble et al. (1958a)
Gir	23	Intra-sire regression of daughter on dam	-.37 ±.48	Amble et al. (1958a)
Kankrej	25	Intra-sire regression of daughter on dam	-.31 ±.40	Amble et al. (1958a)
Tharparkar	204	Intra-sire regression of daughter on dam	-.01 ±.16	Amble et al. (1958a)
Tharparkar	59	Intra-sire regression of daughter on dam	-.18 ±.14	Singh (1958)
Tharparkar	59	Intra-sire correlation between daughter and dam	-.16 ±.13	Singh (1958)

Table 7 (Continued)

Breed	d.f.	Method of estimation	Estimate	Reference
Hariana				
Hariana			.224	Tandon (1961)
Hariana	68 daughter dam pairs of 9 sires	Intra-sire regression	.198±.119	Indian Veterinary Research Institute (1955)

These estimates range from -.37 to +.88. The only two estimates based on over 200 d.f. are -.01 and .11, and have rather large standard errors.

c. Effect on milk production Sikka (1931) found a correlation of .33 between service period and lactation yield in Sahiwal cattle; the relationship between these characters was not linear, however. Similar correlation (.31) between these two characters was reported by Venkayya and Anantakrishnan (1958) in Red Sindhi cows. In contrast to these observations Kohli and Acharya (1961) found a non-significant correlation (.13) between these two characters in the herd under study.

Tandon (1961) reported .11 and .27 as the estimates of phenotypic and genetic correlations respectively between first calving interval and milk production in the first lactation.

4. Butterfat per cent

In India, except for legal standards, fat per cent in milk does not carry any significance, especially from the point of view of market price. There is however a large difference in the price of cow and buffalo milk, primarily because the latter has a higher percentage of fat and total solids. Table 8 shows the butterfat per cent in the milk of some Indian breeds of cattle. These averages range from 4.0 to 5.3. The mean butterfat per cent in first lactations was 4.34 in the present study.

a. Environmental factors affecting butterfat per cent Differences in butterfat per cent due to time of milking, month of the year, month of freshening, and lactation sequence have been reported in the

Table 8. Butterfat per cent of some Indian breeds of cattle

Breed	Number of records	Average (per cent)	Reference
Sahiwal	—	5.2	Mahadevan (1958)
Sahiwal	—	5.3	Mahadevan (1958)
Red Sindhi	—	5.0	Mahadevan (1958)
Red Sindhi	—	4.6	Mahadevan (1958)
Hariana	—	4.9	Mahadevan (1958)
Tharparkar	—	4–4.5	Mahadevan (1958)
Hariana	404	4.34±.02 (first lactation)	Present study
Hariana	979	4.27±.01 (all lactations)	Present study

literature. Kohli and Lohia (1959) working on the data from 331 cows of the herd in the present study reported the following observations:

(1) fat per cent was higher in the morning milk;

(2) the fat per cent declined up to the fourth lactation;

(3) the fat per cent was highest in the month of November and lowest in March, June and July and

(4) cows freshening from April to August had the highest fat test for the lactation, while the cows freshening in December had the lowest.

Kothawala and Doctor (1939) and Ahuja and Gautam (1956) found the evening milk to be richer in fat than the morning milk in the Hariana

breed. This is contrary to the finding in the present herd. Kohli and Lohia explained these differences as possibly due to extreme differences in night and day temperature at the location of this herd.

Ahuja and Gautam report that fat per cent was highest in the month of December and lowest in the month of May in the Hariana breed. Kothawala and Doctor, however, did not find any effect of the season of freshening on butterfat per cent.

b. Heritability estimates Stonaker (1953) estimated heritability of first lactation butterfat per cent in Red Sindhis and their crosses from intra-sire regressions based on 82 d.f. to be .09. A rather high estimate of .67 for the first lactation butterfat per cent was reported by Tandon (1961) in Hariana cattle maintained at I.V.R.I. He did not, however, report the method of estimation and volume of data. No other reports on the heritability of butterfat per cent of Indian cattle were found.

Mahadevan (1958), reviewing the composition of milk of dairy cattle breeds in tropics, has commented that the high fat content which is characteristic of the milk of Zebu cattle appears to be strongly inherited.

c. Relationship with other characters The only report found on the phenotypic and genetic relationship between fat per cent and other characters was that by Tandon (1961). These correlations along with others are presented in Table 9. The genetic correlations are all negative, whereas the phenotypic correlations with age at first calving and

Table 9. Estimates of genetic and phenotypic parameters[a] in Hariana cattle of the Indian Veterinary Research Institute herd at Izatnagar (Tandon, 1961)

Trait	(X_1)	(X_2)	(X_3)	(X_4)
Age at first calving (X_1)	.375	-.187	-.129	.272
First lactation 300 day milk yield (X_2)	.183	.259	-.102	-.132
First lactation butter-fat per cent (X_3)	-.464	-.119	.674	-.375
First calving interval (X_4)	.109	.233	.048	.224

[a]On the diagonal are heritability estimates; below the diagonal are phenotypic correlations and above the diagonal are genetic correlations.

and with first lactation milk yield are negative and the one with first calving interval is positive but very small.

B. Effect of Age on Production

Records of milk production of purebred Sahiwal cows and Ayrshire x Sahiwal crossbred cows maintained at Lahore, Ferozepore and Pusa, were subjected to statistical analysis by Sikka (1931), who observed the curve describing the function of variation in milk yield with age to be logarithmic. The age of maximum production was attained by the third to fourth lactation in purebred Sahiwals as against about the sixth of foreign cows and approximately the eight for Pusa crossbreds. The increase in milk yield from first lactation to the lactation of maximum production in purebred Indian cattle was approximately 10 per cent against 30 to 40 per cent in the foreign and Pusa crossbred cows.

Stonaker (1953) working with data on Red Sindhis and their crosses and backcrosses with Jerseys observed the maximum production in crossbreds and backcrosses to be attained by the third lactation with a little change up to the fifth lactation. The purebred Sindhis showed highest production in their first lactation; the first lactation continued to be the highest in these animals even after correction for incomplete repeatability.

Animals in a Red Sindhi herd in Ceylon studied by Mahadevan (1955) showed an increase of only 6 per cent from their first to their fourth lactation (the lactation of highest production).

Venkayya and Anantakrishnan (1957) found on paired lactation comparisons that the maximum yield in Red Sindhis maintained at the

Southern Regional Station of National Dairy Research Institute was attained by the third lactation and the increase in the yield was only 8 per cent. Amble et al. (1958b), using part of the data used by Venkayya and Anantakrishnan and also data from the Hosur herd, found that Red Sindhi cows reached their maximum production by the third and fourth lactation with an increase of 7.6 and 11.2 per cent.

In Hariana cows maintained at I.V.R.I. the maximum yield was reached by 7.5 years (approximately the fourth lactation). Dutt and Singh (1961) reported maximum production in Harianas to be attained by the fifth lactation.

Mahadevan and Hutchinson (1964), studying East African Zebus and Zebu x European crossbreds from coastal regions of Tanganyika, found an increase of 17 to 18 per cent in milk production with age in both purebreds and crossbreds and that the maximum production was reached by the second lactation in purebred Zebus and by the third lactation in crossbreds.

The increase in production with age and the age or lactation when the maximum production is reached differ in different breeds and even in the same breed at different places. The effect of age on production is to a great extent a function of management and feeding in the early life of the animal and the age at first calving (Kay and M'Candlish, 1929 and Bonnier et al., 1948).

Most of the studies reviewed above indicate that animals in the tropics reach maturity or maximum production one or more lactations earlier

than animals in temperate regions and the increase in milk yield of the former is much less than in the latter. This may be due to delayed age at first calving and the generally long calving intervals of the animals in tropics. Animals freshening for the first time at 3 1/2 to 4 1/2 years should have completed their growth with respect to body size, weight and associated growth in the active secretory tissue of the udder. The increase in milk production of these animals from the first to the second or a later lactation would probably be due to the increased functional activity of the secretory tissue during the first and second gestation and the first and second lactations.

Most of the age correction factors developed for Indian cattle are lactation correction factors; age being expressed in terms of lactation number. Though the correlation between the lactation number and the age in years at which that lactation is initiated will be quite high for biological reasons, yet it will not be perfect, especially in animals where the age at different calvings is quite variable. But, as explained above, the effect of age on production in these animals which calve for the first time very late may be due primarily to functional development of the udder secretory tissue from the first to the second or third lactation rather than to the general growth and development of the body. If so, the lactation correction factors may be expected to remove most of the age differences, if any.

Age correction factors for Hariana cattle have been developed at the I.V.R.I., age being expressed in years and by Dutt and Singh (1961) for

cows in four government farms in U. P. expressing age in lactations. The use of correction factors developed for other herds may not be feasible because of differences in the climatic conditions, management, culling and breeding policy of these herds.

C. Repeatability Estimates

Estimates of repeatability of milk production and calving interval of some Indian breeds of cattle are presented in Tables 10 and 11. Most of the estimates for milk yield range between .37 and .60. The estimates for most of the breeds other than Hariana are above .4.

Sikka (1933) reported the following correlations between different lactation and highest lactation yield from his study of reliability of different records for predicting cow's producing ability. On the basis

Lactation	Correlation with highest lactation yield
1	.50±.04
2	.66±.03
3	.67±.03
4	.77±.02

of these correlations Sikka concluded that the reliability of an individual record is low compared to the mean of larger number of records. These correlations reflect also some importance of adjacency or proximity. The correlations tend to become large as the lactation is nearer to the lactation of highest production.

A correlation of .5 between first and second, and second and third lactations in Red Sindhi cows was reported by Stonaker (1953).

Mahadevan (1954) using 3,000 records of crossbreds of Indian and European cattle, whose last production record exceeded 2,000 pounds, obtained the following intra-herd correlations between different lactations.

Lactations correlated	Proportion of European blood			
	1/4	1/2	5/8	3/4
1 : 2	.63	.60	.75	.48
2 : 3	.66	.59	.74	.42
3 : 4	.70	.63	.49	.30
1 : 3	.37	.52	.71	.32
2 : 4	.67	.53	.50	.49
1 : 4	.44	.41	.40	.34
Average	.58	.55	.65	.41
No. of animals	299	630	260	309

The average intra-herd repeatability from these data was .534.

Kooner (1963) reported the following coefficients of correlation between different lactation records in the Tharparkar, Sahiwal and Sindhi herds of the National Dairy Research Institute at Karnal:

Tharparkar

Lact. no.	2	3
1	.54±.08 (323)	.46±.14 (224)
2		.43±.11 (222)

Table 10. Estimates of repeatability of milk production of some Indian breeds of cattle

Breed	d.f.	Method of estimation	Estimate	Reference
Red Sindhi	922 records of 305 animals	Intraclass correlation	.61 [.56-.67][a]	Amble et al. (1958b)
Red Sindhi	959 records of 270 animals	Intraclass correlation	.54 [.38-.67][a]	Amble et al. (1958b)
Red Sindhi		Intraclass correlation	.41	Mahadevan (1955)
Red Sindhi		Intraclass correlation	.37±.12	Kooner (1963)
Sahiwal		Intraclass correlation	.48	Lecky (1951)
Sahiwal		Intraclass correlation	.40	Patel (1956)
Sahiwal		Intraclass correlation	.52±.06	Kooner (1963)
Kankrej		Intraclass correlation	.60	Patel (1956)
Indian breeds and their crosses with European cattle	5992 records of 1498 animals [1st to 4th records only]	Correlations between different records	.534	Mahadevan (1955)

[a]Ninety-five per cent confidence interval.

Table 10 (Continued)

Breed	d.f.	Method of estimation	Estimate	Reference
Hariana	188 cows with 3 records each	Intra-herd Intra-cow correlation	.39	Singh and Desai (1961b)
	with two and 3 records each	Intra-cow correlation	.37-.65	Singh and Desai (1961b)
Tharparkar		Intraclass correlation	.49±.06	Kooner (1963)

Table 11. Estimates of repeatability of calving interval of some Indian breeds of cattle

Breed	d.f.	Method of estimation	Estimate	95% Confidence interval	Reference
Red Sindhi	729 records of 275 animals	Intraclass correlation	.21	[.13-.28]	Amble et al. (1958a)
Red Sindhi	854 records of 244 animals	Intraclass correlation	.08	[.00-.22]	Amble et al. (1958a)
Kangayam	1013 records of 322 animals	Intraclass correlation	.08	[.01-.14]	Amble et al. (1958a)
Gir	130 records of 44 animals	Intraclass correlation	.17	[.00-.37]	Amble et al. (1958a)
Kankrej	100 records of 34 animals	Intraclass correlation	.17	[.00-.39]	Amble et al. (1958a)
Tharparkar	1582 records of 408 animals	Intraclass correlation	.19	[.14-.24]	Amble et al. (1958a)
Tharparkar	194 animals with 3 intervals each	Intraclass correlation	.23±.05		Singh (1958)
Tharparkar		Interclass correlation (Corrected for effect of year and calving sequence)	.28±.05		Singh (1958)
Hariana	102 first, 99 second and 60 third calving intervals		.75±.02		Indian Veterinary Research Institute, (1955)

Sahiwal

Lact. no.	2	3
1	.56±.17 (210)	.53±.21 (169)
2		.48±.12 (168)

Sindhi

Lact. no.	2	3
1	.40±.18 (88)	.26±.24 (65)
2		.46±.22 (64)

Within parentheses are presented degrees of freedom for each estimate.

The author did not report any combined estimate using these correlation coefficients. These correlation coefficients are quite comparable to the repeatability estimates of .49 ± .06, .52 ± .06 and .37 ± .12 for the Tharparkar, Sahiwal and Red Sindhi breeds respectively, derived as intra-class correlations.

The estimates of repeatability of calving interval reported in Table 6 range from .08 to .75. The highest estimates of .75 was reported in Hariana cattle and was based on a rather small set of data.

Singh (1958) from data on 1149 records of Tharparkar cows, corrected for effect of year and calving sequence, reported a repeatability of .28. Most of the estimates of repeatability of calving interval in European cattle reviewed by Bohlder (1957) range from .03 to .19.

D. Estimates of Genetic Progress

In India where tremendous amounts of money and resources are being and will be spent on schemes relating to livestock improvement through breeding in order to overcome the menace of the ever-growing food problem, it is desirable to assess the genetic gains made through selection and improved breeding methods in the herds or other livestock populations under these schemes.

There have been only a few attempts at evaluating genetic improvement through selection in dairy cattle herds in India. Stonaker (1953) reported an annual genetic gain of .5 pounds of butterfat per year or .3 per cent of the average butterfat production per year in an Indian herd of Red Sindhi cattle. The increase though relatively small was not considered discouragingly low in view of the small herd size and long generation interval (6.65 years, approximately). The estimate of genetic improvement was based on the genetic superiority of the cows retained for an additional lactation and the genetic superiority of the bulls used in the herd.

A genetic advance per year of .02 per cent and 1.1 per cent of average lactation yield in the Red Sindhi herds at Hosur and at Bangalore in India was reported by Amble et al. (1958b) based on the genetic superiority of cows and sires used in the herd. They found a genetic increase of 1.2 and 1.4 per cent of the average yield for the Hosur and Bangalore herds, respectively, based on the method suggested by Rendel and Robertson (1950). These authors also studied the genetic change in milk production by comparing the production in different generations adjusted for environmental

changes from period to period. Periods were composed of consecutive five years. Adjustment for periods was expected to remove the environmental changes over the time the data were available. The results from this analysis indicated little overall progress in the Hosur herd but a progressive improvement of about 170 pounds per generation in the Bangalore herd.

Mahadevan (1953) reported, from the analyses of the genetic gain in milk yield due to selection in a herd of Sinhala cattle in Ceylon over a period of fourteen years, a probable genetic gain of .64 per cent of the average yield per year due largely to more stringent selection of dams of bulls than dams of cows. In another study of genetic gain in milk through selection over 12 years in a Red Sindhi herd in Ceylon, Mahadevan (1955) however found no genetic advance; what had really been achieved was an overall negative selection pressure for the yield. The generation intervals in the two herds studied by Mahadevan were reported to be 6 years and 6.5 years.

Recently Sundaresan (1961) has reported an estimated genetic gain of 80 pounds of milk per generation in a closed herd of Tharparkar cattle over a period of forty years. The maximum expected genetic improvement per generation in a herd of the size used is reported to be 200 pounds.

Robertson (1950) observed a probable annual genetic gain of 2.5 gallons or 1.4 per cent of the average yield in the first lactation in a White Fulani herd in Nigeria during the first 13 years of its existence.

III. SOURCE OF DATA

The data for the present investigation pertain to a herd of Hariana cattle, a dual purpose breed (milk and draught) belonging to the scheme to supplement livestock investigation, located at the Government Livestock Farm, Hissar.

A. Farm and the Breeding Stock

The area of the Government Livestock Farm, Hissar, where the herd was located, is a continuation of the Rajasthan desert. The soil is soft loam interspersed with sand and clay. The climate is relatively dry and rains usually occur during the months of July, August and September. During the summer months, day temperature may go as high as 115° F and sand storms are common. During winter the minimum temperature recorded is 36.9° F. The monthly average of some meteorological observations at Hissar is presented in Table 12.

The experimental herd was established in the year 1945 with 230 females (150 heifers and 80 cows) and 12 bulls. The female stock was selected on basis of conformity to the breed characteristics and no attention was paid to the udder development, other dairy characters or milk production in their selection. The bulls were selected on the same basis as the female stock. Twenty animals out of the female stock were removed from the herd during 1945-46 because of death, positive reaction to tuberculosis and bad conformation. These were replaced by 20 heifers about 3 years old from the general herd of the farm in June, 1946. Six

Table 12. Monthly average of some meteorological observations at Hissar[a]

Months	Temperatures		Av. humidity		Av. rainfall (inches)
	Av. maximum (°F)	Av. minimum (°F)	8.30 hr. (per cent)	17.30 hr. (per cent)	
January	71.4	41.8	77	41	.61
February	77.7	46.0	69	35	.71
March	88.3	58.4	63	30	.41
April	99.0	65.7	46	23	.18
May	107.4	76.8	44	22	.48
June	106.8	82.4	52	30	1.27
July	98.9	81.2	73	53	4.84
August	95.4	78.6	79	63	6.09
September	96.7	75.1	74	51	1.44
October	93.4	63.4	66	39	1.02
November	85.2	49.1	65	34	.04
December	75.6	42.6	74	39	.05

[a]Kohli et al. (1961, p. 326).

of the 12 bulls were purchased from outside the farm to provide greater genetic heterogeneity; the other six came from the farm-bred stock.

The whole stock was divided into ten groups at random, each with 23 animals, and 10 out of the 12 bulls were randomly assigned to these groups.

B. Feeding and Management

The animals were maintained in open enclosures throughout the year except during severe winter when they were moved into roofed enclosures.

The cows in milk, dry cows, young calves and bulls were kept in separate enclosures. Up to the end of the year 1952, both the cows in milk and the dry cows were let out for grazing on farm (natural) pastures from 8:00 A.M. to 2:00 P.M. After 1952 the cows in milk were no longer grazed on pastures and were stall fed.

Weaning was not practiced in the herd. At the start of daily milkings calves were allowed to suckle their dams a little to stimulate letting down of milk. After a part of milk was drawn the rest was allowed for the calves to suckle. On weekly record days, however, the calves were used only to stimulate letting down of milk; all the milk was drawn and recorded. The milk yield was recorded until the animal went dry up to the year 1953, when the lactation length was restricted to 300 days.

Male calves were transferred after weaning to another area of the farm where they were maintained in semi-wild conditions along with other male stock of the general herd.

Dry stock was grazed on farm pastures throughout the year. When the pastures were sparse, grazing was supplemented with roughages and some concentrates.

The young heifers under the semi-ranch conditions were domesticated at the age of two years for a period of about six weeks to make them docile and manageable. During this period they were tied and stall fed.

The breeding bulls were sent for grazing on farm pastures from 8:00 A.M. to 2:00 P.M. daily but in different paddocks where they had no access to the female stock. Concentrates were fed at a flat rate of 4 lbs. per

head per day in the evening. The dry or green fodder was also fed in the afternoon. The promising young males were selected and retained in the herd for individual care and feeding.

For identification, the calves were tattoed with the brand number of their dams in the left ear. At the age of 3 months, they were branded on the left thigh for the age indicating the quarter and year of birth. At the age of 9 months they were branded on the right thigh for serial number.

Records of the pedigree and performance of each animal were maintained regularly.

The animals were milked twice daily at 3:30 A.M. and 3:30 P.M. The milk was recorded once a week. Individual homogenous samples of two ounces of milk for butterfat test were taken both morning and evening every 10 days after complete milking. Gerber's method was used for determining the fat per cent. The fat testing was started on the animals of the first generation.

Periodic testing of the herd against brucellosis and tuberculosis was carried out every year by the Disease Investigation Officer of the farm. The animals found positive to these infections were segregated to a separate area of the farm. These animals, if subsequently declared negative on two or three later tests, were returned to the herd.

The prophylactic vaccination was carried out against black-quarter at the time of serial branding of calves and every year against haemorraghic septicemia and rinderpest.

The female stock was fed ration computed on the basis of Morrison standards. The composition of feed varied according to the availability of crops during the year. Green jowar (Andropogon sorghum) was fed during the months of June to October, and green berseem (Trifolium alexanderinum) and rape mixture (Brassica napus) during November to March. Dry fodder consisted of Karbi bajra (stover of Pennisetum typhoideum) and bhoosa of wheat (straw of Triticum vulgare). The concentrate mixture fed to an animal was composed of 2 lbs. crushed gram (Cicer ariatum), 1 lb. of barley (Hordeum vulgare) or oats (Avena sativa) or bran, 1 lb. of oil cake (til, toria, Sesame, etc.) and two ounces of common salt (Sodium chloride). The standars of feeding were maintained to the best of the capacity and resources of the farm, although the feeding may have fallen short of the standard when there was a shortage of concentrates and fodder.

C. Selection of Breeding Stock and Breeding Policy

Up to the year 1949 there was no culling of any male stock. It was then decided to retain as replacement only the males whose dams yielded 2,000 lbs. or over in 300 days, limited to one-third of the total number of males in each sire family. The males retained had to conform to the draught type. In families where the dam's performance had not reached 2,000 lbs. or in sufficient numbers, a minimum of 3 males of the best performing dams and conforming to draught type within a family were to be retained and the rest were culled.

In 1954 after progeny test information was available on the foundation bulls, all foundation bulls were culled except the bull no. 13HP/144.

The female stock were not culled prior to the year 1952-53. Later only such cows as yielded 800 lbs. or more of milk in a standard (300 day) first lactation were retained, provided they also had in addition the desired conformation. All heifers except those not conforming to breed characteristics had to be maintained for at least one lactation.

The cows were culled heavily in 1952-53 and 1953-54; a majority of these culls were from the parent generation. In 1954, the retained females were divided into six groups. Each group contained at least 25 animals. The assignment of the bulls and cows to these groups was at random. The bulls assigned to these reorganized groups were the progeny of the foundation bulls nos. 2HP/44, 13HP/44 and 1631/40 and 13HP/44 himself. Care was taken to avoid matings between close relatives.

Out of the total of 2248 records of some 716 animals, 373 records were excluded from the study for being incomplete due to various recorded reasons such as death of the calf; the lactation followed a stillbirth, abortion or premature birth; the cow was culled or died during lactation; being vicious and not allowing milking or suckling of the calf; segregated due to positive reaction to brucellosis, tuberculosis or being victim of mastitis or other udder diseases. This left 1875 records of 680 animals.

Table 13 presents the frequency of animals culled due to various recorded reasons, along with the average age at disposal.

Table 13. Causes of disposal of animals from the herd[a]

Cause	Number of animals disposed	Percentage	Average age at disposal (months)
1. Low production	247	50.3	103
2. Debility and weakness	10	2.0	129
3. Old age & infertility	26	5.3	181
4. Brucellosis	18	3.7	120
5. Tuberculosis	74	15.1	137
6. Mastitis and other udder diseases	2	.4	105
7. Death	114	23.2	119
Totals	491	100.0	106

[a]Table does not include the number of animals disposed of due to non-conformity to breed type and other reasons before freshening for the first time.

IV. STATISTICAL METHODS

The age at first calving, milk production in the first 300 days of the first lactation, first lactation butterfat per cent and first calving interval were the traits of interest for which the phenotypic and genetic parameters were desired. These characters, as explained earlier, are important components of productivity in dairy cattle. The inclusion of only the first records in the analyses for computing the genetic and phenotypic parameters was based on the following reasons:

(1) Since all heifers, except a very few who did not conform to the breed characteristics, were maintained to complete their first lactation in the herd, voluntary selection could make scarcely any bias in the estimates obtained from first lactations.

(2) Since it was decided to express the later lactation production in terms of the first to correct for age differences, including only the first lactation records in the analyses would permit little bias from errors in age correction factors.

(3) The largest volume of data pertained to the first lactation.

(4) The first lactation records are expected to be affected less by environmental and physiological factors than later records, thus requiring corrections for the effects of fewer of these factors and indirectly introducing lesser bias in the estimates of genetic and phenotypic parameters.

A. Effects of Environmental Factors

Since the data were collected over a 20-year period during which selection was operative and changes in nutritional and managemental practices might have been introduced intentionally or unintentionally, it was considered necessary to study the effect of the year of freshening on these traits. The month or season of freshening is also expected to affect the production and reproduction, therefore the effect of the month of freshening on these traits was also studied. Analysis of variance techniques were used in evaluating the effects of the year and month of freshening.

B. Estimation of Genetic and Phenotypic Parameters

1. Heritability

A knowledge of the heritability of an economic character is necessary for devising an efficient selection and breeding plan.

All the ways frequently used for estimating heritability are based on phenotypic resemblance between relatives. Lush (1940, 1948, 1949) has described the different methods of estimating heritability along with their advantages and limitations. Heritability is often used in animal breeding in the narrow sense, i.e., the transmissibility or the fraction of the total observed or phenotypic variance which is due to the additive effects of genes, in contrast to the broader sense which Lush has termed genetic determination.

The regression of offspring on parent and the correlation between full sibs or half sibs are the two common methods used for estimating heritability.

The estimation of genetic parameters requires correcting for the environmental factors affecting the traits on which these estimates are desired. A convenient method of correcting for the environmental factors is to express the record of performance as a deviation from the contemporary average (average based on the records of the animals in the same environmental class as the individual). Van Vleck et al. (1961) reported the expectations of various sums of squares and sums of cross-products for four different types of deviations from contemporary averages. Freeman (1964) considered the effect of expressing records as deviations from contemporary averages in estimating heritability and genetic correlations by regression of offspring on parent.

As the year of freshening affected significantly all the traits on which estimates of genetic parameters were desired, it was decided to express the records as deviations from the mean of the year of freshening. In the case of butterfat per cent, however, the month of freshening also had a significant effect and, as discussed under environmental effects, it was decided to compute means of each year-season combining December of the previous year and January to April of the current year as one year-season and May to November of the current year as the other year-season. Estimates for butterfat per cent were also computed expressing records as deviations from the mean of the year of freshening.

Records of all individuals in a particular year or year-season were used in computing the mean. The individuals that were genetically related to the individual whose record was being deviated were not excluded from the mean of the contemporaries. The individual's own record was also included in the year or year-season mean.

The production record of an individual can be described by the following model:

$$Y_{ij} = \mu + a_i + g_{ij} + e_{ij}$$

μ is the over-all mean

a_i is effect of the ith year or year-season of freshening.

g_{ij} is the breeding value of the ij^{th} individual.

e_{ij} is the random error associated with the ij^{th} record.

The mean of the year or year-season can be expressed as follows, in terms of the above model:

$$YA = \mu + a_i + \frac{g_{ij} + \sum_{r=1}^{n_{(ij)}} g_{ir}}{n_{(ij)} + 1} + \frac{e_{ij} + \sum_{r=1}^{n_{(ij)}} e_{ir}}{n_{(ij)} + 1}$$

r refers to the contemporaries of the jth individual in the ith year or year-season and goes from 1 to $n_{(ij)}$.

Let d_{ij} be the deviation of ij^{th} record from the contemporary mean (YA).

$$\text{Then } d_{ij} = \frac{1}{n_{(ij)} + 1}\left[n_{(ij)} g_{ij} - \sum_{r=1}^{n_{(ij)}} g_{ir} + n_{(ij)}\, e_{ij} - \sum_{r=1}^{n_{(ij)}} e_{ir}\right]$$

Expressing the record as a deviation from the mean of the respective year or year-season will remove the year or year-season effect.

a. Regression of daughter on dam Using these deviations for computing the regression of daughter on dam, the variance and covariance will be:

$$\hat{\sigma}_{\left(d_{(ij)} d_{(ij)}\right)} = \frac{1}{N-1}\left[\sum_{(ij)} d_{(ij)}\, d'_{(ij)} - \frac{\sum_{(ij)} d_{(ij)} \sum_{(ij)} d'_{(ij)}}{N}\right]$$

$$\hat{\sigma}^2_{d_{(ij)}} = \frac{1}{N-1}\left[\sum_{(ij)} d_{(ij)}^2 - \frac{\left(\sum_{(ij)} d_{(ij)}\right)^2}{N}\right]$$

In the above expressions $d_{(ij)}$ is the deviation of $(ij)^{th}$ dam's record from her contemporary mean and $d'_{(ij)}$ is the deviation of $(ij)^{th}$ daughter's record from her contemporary mean; (ij) = 1, 2, $\cdots$N. The presence of the same subscript on daughters and dams indicates the relationship and is not intended to imply that daughters and dams are in the same environmental group. Since only the first record of daughter and dams is being considered, it is not possible for a daughter and her dam to be included in the same environmental group.

$$E\,\hat{\sigma}^2_{d_{(ij)}} = \frac{1}{N-1} E\left[\sum_{(ij)} d_{(ij)}^2 - \frac{\left(\sum_{(ij)} d_{(ij)}\right)^2}{N}\right]$$

$$= \frac{1}{N-1}\left[E \sum_{(ij)} d_{(ij)}^2 - \frac{1}{N} E \sum_{(ij)} d_{(ij)}^2 + E \sum_{(ij)} \sum_{(ij)'} d_{(ij)}\, d_{(ij)'}\right], \quad (ij) \neq (ij)'$$

$$= \frac{1}{N} E \sum_{(ij)} d_{(ij)}^2 - \frac{1}{N(N-1)} E \sum_{(ij)} \sum_{(ij)'} d_{(ij)} d_{(ij)'}$$

Let $E(g_{ij})^2 = E(g_{ir})^2 = \sigma_g^2$

$E(e_{ij})^2 = E(e_{ir})^2 = \sigma_e^2$

$E(g_{ij}) = E(e_{ij}) = E(g_{ir}) = E(e_{ir}) = 0$

$E(g_{ij}, g_{ir}) = \sigma_{g_{ij} g_{ir}}$

$E(g_{ir}, g_{ir'}) = \sigma_{g_{ir} g_{ir'}}$

$E(e_{ij}, e_{ir}) = E(e_{ir} e_{ir'}) = 0$

Then

$$E \sum_{(ij)} d_{(ij)}^2 = \sum_{(ij)} \left[\left(\frac{n_{(ij)}}{n_{(ij)} + 1} \right)^2 \sigma_g^2 + \frac{n_{(ij)}}{\left(n_{(ij)} + 1\right)^2} \sigma_g^2 - 2 \left(\frac{n_{(ij)}}{n_{(ij)} + 1} \right)^2 \sigma_{g_{ij} g_{ir}} - 2 \frac{n_{(ij)}\left(n_{(ij)} - 1\right)}{\left(n_{(ij)} + 1\right)^2} \sigma_{g_{ir} g_{ir'}} + \frac{n_{(ij)}}{\left(n_{(ij)} + 1\right)^2} \sigma_e^2 + \left(\frac{n_{(ij)}}{n_{(ij)} + 1} \right)^2 \sigma_e^2 \right]$$

$\sigma_{g_{ij} g_{ir}}$ is the genetic covariance between an individual and her contemporaries while $\sigma_{g_{ir} g_{ir'}}$ is the genetic covariance among contemporaries of the individual.

Assuming these covariances to be zero, which is not true in the present case because including in the mean all animals making a record in

a particular environmental group will make that mean contain some animals genetically related to the individual,

the $E\left(\sum_{(ij)} d_{ij}^2\right)$ would reduce to

$$\frac{1}{N} \sum_{(ij)} \left(\frac{n_{(ij)}}{n_{(ij)} + 1} \right) \left(\sigma_g^2 + \sigma_e^2 \right)$$

and $$E\, \hat{\sigma}_{d_{(ij)}}^2 = \frac{1}{N} \sum_{(ij)} \left(\frac{n_{(ij)}}{n_{(ij)} + 1} \right) \left(\sigma_g^2 + \sigma_e^2 \right) - \frac{1}{N(N-1)} E \sum_{(ij)} \sum_{(ij)'} d_{(ij)} d_{(ij)'}$$

Freeman (1964) has discussed the nature and source of the last term in the variance of $d_{(ij)}$ and has shown that for same kinds of data it can probably be assumed to be zero without introducing any large error.

$$E\, \hat{\sigma}_{\left(d_{(ij)} d'_{(ij)}\right)} = E\left[\frac{1}{N-1} \left(\sum_{(ij)} d_{(ij)} d'_{(ij)} - \frac{1}{N} \left(\sum_{(ij)} d_{(ij)} \sum_{(ij)} d'_{(ij)} \right) \right) \right]$$

$$= \frac{1}{N} E \sum_{(ij)} d_{(ij)} d'_{(ij)} - \frac{1}{N(N-1)} E \sum_{(ij)} \sum_{(ij)'} d_{(ij)} d'_{(ij)'}$$

$$E \sum_{(ij)} d_{(ij)} d'_{(ij)} = \sum_{(ij)} \left[\frac{n_{(ij)} n'_{(ij)}}{\left(n_{(ij)} + 1\right)\left(n'_{(ij)} + 1\right)} \sigma_{g_{ij} g'_{ij}} - \frac{n_{(ij)} n'_{(ij)'}}{\left(n_{(ij)} + 1\right)\left(n'_{(ij)'} + 1\right)} \sigma_{g_{ij} g'_{ir}} - \frac{n'_{(ij)} n_{(ij)'}}{\left(n_{(ij)} + 1\right)\left(n_{(ij)'} + 1\right)} \right.$$

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$$\sigma_{g'_{ij}\, g_{ir}} + \frac{n_{(ij)'}\, n'_{(ij)'}}{\left[n_{(ij)'} + 1\right]\left[n'_{(ij)'} + 1\right]}\, \sigma_{g_{ir}} \sigma_{g'_{ir}} \Bigg]$$

Environmental covariances between daughter and dam, between daughter and contemporaries of dam, between dam and contemporaries of daughter and among contemporaries of dam and contemporaries of daughter have been assumed to be zero. The environmental covariance between daughter and dam will not be truly zero if the daughters of high producers are given differential treatment compared to the daughters of low producers.

$\sigma_{g_{ij}\, g'_{ij}}$ is the genetic covariance between a dam and her daughter.

$\sigma_{g_{ij}\, g'_{ir}}$ is the genetic covariance between a dam and contemporaries of her daughter.

$\sigma_{g'_{ij}\, g_{ir}}$ is the genetic covariance between a daughter and contemporaries of her dam.

$\sigma_{g_{ir}\, g'_{ir}}$ is the genetic covariance among contemporaries of a dam and contemporaries of her daughter.

The last three of these covariance may not be far from zero. Considering these to be zero, the expectation reduces to:

$$\sum_{(ij)} \frac{n_{(ij)}\, n'_{(ij)}}{\left[n_{(ij)} + 1\right]\left[n'_{(ij)} + 1\right]}\, \sigma_{g_{ij}\, g'_{ij}}$$

and the $E\,\hat{\sigma}_{\left(d_{(ij)}\, d'_{(ij)}\right)}$ $= \frac{1}{N} \sum_{(ij)} \frac{n_{(ij)}\, n'_{(ij)}}{\left[n_{(ij)} + 1\right]\left[n'_{(ij)} + 1\right]}\, \sigma_{g_{ij}\, g'_{ij}}$

$$- \frac{1}{N(N-1)} \sum_{(ij)} \sum_{(ij)'} d_{(ij)}\, d'_{(ij)'}$$

The second term can be assumed to be zero without any large error, leaving

$$E\,\hat{\sigma}_{\left(d_{(ij)}\, d'_{(ij)}\right)} = \frac{1}{N} \sum_{(ij)} \frac{n_{(ij)}\, n'_{(ij)}}{\left[n_{(ij)} + 1\right]\left[n'_{(ij)} + 1\right]}\, \sigma_{g_{ij}\, g'_{ij}}$$

The true value of the regression can then be written as

$$b_{dd'} = \frac{\sum_{(ij)} \frac{n_{(ij)}\, n'_{(ij)}}{\left[n_{(ij)} + 1\right]\left[n'_{(ij)} + 1\right]}\, \sigma_{g_{ij}\, g'_{ij}}}{\sum_{(ij)} \left(\frac{n_{(ij)}}{n_{(ij)} + 1}\right)\left(\sigma_g^2 + \sigma_e^2\right)}$$

$\sigma_{g_{ij}\, g'_{ij}} = 1/2\ \sigma_g^2$ under the assumptions of no non-allelic gene interaction and no maternal effects.

$$b_{dd'} = \frac{\sum_{(ij)} \frac{n_{(ij)}\, n'_{(ij)}}{\left[n_{(ij)} + 1\right]\left[n'_{(ij)} + 1\right]}\, 1/2\ \sigma_g^2}{\sum_{(ij)} \left(\frac{n_{(ij)}}{n_{(ij)} + 1}\right)\left(\sigma_g^2 + \sigma_e^2\right)}$$

If $n_{(ij)} = n'_{(ij)} = n_{(ij)'} = n'_{(ij)'}$, the coefficient in the numerator will become $\frac{N}{2} \frac{n_{(ij)}^2}{\left[n_{(ij)} + 1\right]^2}$ and that in the denominator will become

$N \frac{n_{(ij)}}{\left[n_{(ij)} + 1\right]}$ reducing $b_{dd'} = \frac{n_{(ij)}}{\left[n_{(ij)} + 1\right]}\ \frac{1/2\ \sigma_g^2}{\sigma_g^2 + \sigma_e^2}$.

Because $\frac{n_{(ij)}}{\left[n_{(ij)} + 1\right]}$ will always be less than 1.0, this will tend to bias the regression downward. With an increase in $n_{(ij)}$ the bias will tend

to become small. If $n_{(ij)}$'s were all the same this bias could be removed by multiplying the estimated regression by inverse of this bias. Since $n_{(ij)} \neq n'_{(ij)} \neq n_{(ij)'} \neq n'_{(ij)'}$; the correction for this bias will be rather difficult.

In computing the intra-sire regression, the variances and covariances were pooled over all sires. The heritability estimate was obtained by doubling the computed regression. This estimate of heritability would contain some contribution from the interactions between non-allelic genes ($1/2\ \sigma_{AA}^2 + 1/4\ \sigma_{AAA}^2 + \cdots$), from genetic variation in direct maternal effects, and covariance between total genetic deviations in the transmitted and the direct maternal effects (Dickerson, 1960). In computing regression, the dam's record was repeated for the record of each of her daughters. This is entirely valid if the correlation among offspring of a parent is zero. This correlation is however a function of the square of the regression parameter and the correlation between deviations from regression of any two offspring of the same parent. The other method, in which the arithmetic average of records of all offspring of a given parent is regressed on the parent's record to take account of variable number of offspring per perent, would be entirely valid if the correlation among the offspring of a parent were 1.0. Kempthorne and Tandon (1953) have derived a weighted regression technique for estimating the regression of single offspring on parent with a minimum variance when the number of progeny per parent is variable. These authors, using the data from the Iowa State University Holstein herd found little difference in the

estimates using their weighted regression technique or the method in which the dam's record was repeated with the record of each of her offspring, presumably because the estimated correlation among the offspring of a parent was small and also because only a few dams had more than one daughter. Similar conclusions have been reached by Bohren *et al.* (1961) using poultry data.

b. Half-sib correlation For computing heritability estimates from half-sib correlations the record of the individual could be expressed as:

$Y_{ijk} = \mu + a_i + s_j + e_{ijk}$

μ is the over-all mean.

a_i is the effect peculiar to individuals freshening in the ith environmental group.

s_j is the effect common to the daughters of the jth sire.

e_{ijk} is random error.

a_i, s_j and e_{ijk} are independent and have expectation of zero and variances σ_a^2, σ_s^2 and σ_e^2 respectively.

The year or year-season average in terms of the above model will be equal to:

$$\mu + a_i + \frac{s_j + \sum_{r=1}^{n_{(jk)}} s_r}{n_{(jk)} + 1} + \frac{e_{ijk} + \sum_{r=1}^{n_{(jk)}} e_{irm}}{n_{(jk)} + 1}$$

$n_{(jk)}$ is the number of contemporaries of individuals included in the contemporary mean.

Let d_{jk} be the deviation of a record from the contemporary mean.

Then

$$d_{jk} = \frac{1}{n_{(jk)} + 1} \left[n_{(jk)}\, s_j - \sum_{r=1}^{n_{(jk)}} s_r + n_{(jk)}\, e_{ijk} - \sum_{r=1}^{n_{(jk)}} e_{irm} \right]$$

$$\text{and } \sigma_{d_{jk}}^2 = \left(\frac{n_{(jk)}}{n_{(jk)} + 1} \right) \left(\sigma_s^2 + \sigma_e^2 \right)$$

Deviation records in the analysis of variance can be described as:

$$d_{jk} = \mu + s_j + e_{jk}$$

The analysis of variance using deviation records will be as follows:

Source	d.f.	Sum of squares	Mean squares	Expected mean squares (assumed)
Total	N-1	$\sum_{j=1}^{s} \sum_{k=1}^{n_j} d_{jk}^2 - \frac{d_{..}^2}{N}$		
Among sires	(s-1)	$\sum_{j=1}^{s} \frac{d_{j.}^2}{n_j} - \frac{d_{..}^2}{N}$	A	$\sigma_e^2 + n_o \sigma_s^2$
Within sires	$s(n_j-1)$	By substraction	B	σ_e^2

The sire component will be

$$\hat{\sigma}_s^2 = \frac{A-B}{n_o}$$

$$n_o = \frac{1}{s-1} \left[N - \frac{\sum_{j=1}^{s} n_j^2}{N} \right]$$ where s is the number of sires and n_j is the number of observations in the jth sire group and N is the total number of observations.

The analysis assumes homogeneity of variances within sires and independence of s_j and e_{jk}.

Van Vleck et al. (1961) have worked out the expected values of the variance components using the same model used here and the following simplifying assumptions:

(1) Each observation is from a different environmental group.

(2) No sire included as a sire group appears as a sire of any stablemate; that is, the sire of an individual is not the sire of any of her stablemates.

(3) No sire is the sire of more than one stablemate, i.e., n_{jk} different sires are sires of the contemporaries of an observation.

They considered these assumptions to be not strictly true in practice but that the error involved by making them would be small.

As a further simplification in obtaining the expected values they considered equal numbers: all $n_j = p$ and all $n_{jk} = n$.

The expected values are:

$$E\, \hat{\sigma}_e^2 = \frac{n}{(n+1)^2} \sigma_s^2 + \frac{n}{n+1} \sigma_e^2$$

$$E\, \hat{\sigma}_s^2 = \left(\frac{n}{n+1} \right)^2 \sigma_s^2$$

With these expected values, the true value of half-sib correlation (t) can be written as

$$t = \frac{\left(\frac{n}{n+1}\right)^2 \sigma_s^2}{\left(\frac{n}{n+1}\right)^2 \sigma_s^2 + \frac{n}{(n+1)^2} \sigma_s^2 + \frac{n}{n+1} \sigma_e^2} = \left(\frac{n}{n+1}\right) \frac{\sigma_s^2}{\sigma_s^2 + \sigma_e^2}$$

$$\text{then } h^2 = 4 \left(\frac{n}{n+1}\right) \frac{\sigma_s^2}{\sigma_s^2 + \sigma_e^2}$$

Because $\frac{n}{n+1}$ will always be less than 1.0, this will tend to bias the estimate of heritability downwards. With an increase in n the bias will tend to become small and t will tend to approach $\frac{\sigma_s^2}{\sigma_s^2 + \sigma_e^2}$.

σ_s^2 equals 1/4 σ_A^2 (one-fourth of the additive genetic or genic variance) under the assumptions of no interaction among non-allelic genes, no genotype-environment interaction, no effects due to sex-linkage and random mating. However, σ_s^2 will contain some variance due to the interaction among the additive effects of non-allelic genes (1/16 σ_{AA}^2 + 1/64 σ_{AAA}^2 + ···) and also the variance due to any other factor correlated with the sires. In case of partially inbred population the coefficient of σ_A^2 will be $\frac{1}{4} \frac{1+F'+6F}{1+F}$, where F' and F are coefficients of inbreeding of the parents and the sibs, respectively.

In computing estimates of heritability from the sire component most of the sires with only one daughter were removed from the analyses. Swiger et al. (1964) have examined the gain or loss in precision of the intraclass correlation from adding information from groups with only one observation. They used both an approximate formula for the variance of the intraclass correlation, and some results obtained by empirically generating data on a computer. The results from both procedures indicated an increase in the variance of the intraclass correlation in many cases on adding single observation groups. The empirical results in this study suggested further that the increase in variance is even more important than indicated by the approximate formula, especially when the intraclass correlation is large. This study showed that an approximate formula for the variance of the intraclass correlation, $V(t) = \frac{2\,(N-1)(1-t)^2[1+(K-1)t]^2}{K^2\,(N-s)(s-1)}$, where t is the intraclass correlation, s = the number of sires, N = total number of observations and $K = \frac{1}{(s-1)}\left[N - \frac{\Sigma n_i^2}{N}\right]$, was satisfactory.

The variances of the heritability estimates computed for half-sib correlations were derived by multiplying by sixteen the variance of the observed intraclass correlations.

2. Genetic correlation

A genetic correlation is a description of the relationship between the sets of genes which are responsible for the genic part of the variance in the corresponding traits.

Genetic correlations can be caused by linkage of genes affecting different characters, pleiotropy (manifold effects of genes) and different intensities or directions of selection in the non-interbreeding subgroups

of a population. Pleiotropy would be the most important cause of the genetic correlations between different characters in the same animal. Linkage is usually a minor cause for genetic correlations because crossing over in a freely interbreeding population will tend to equalize the frequency of the coupling and repulsion double heterozygotes. However, the approach to equilibrium is asymptotic and if the linkage is close, traces of correlation from this cause may be detectable for several generations after a cross (Lush, 1948).

The genetic correlation between two traits (X, Y) is desired for evaluating correlated response in a trait X when selection is based on a related trait Y, for constructing selection indexes, and for evaluating net genetic gain when selection is based on more than one character.

The most feasible way to estimate genetic correlation is from the correlations or regressions of trait X in one individual on trait Y in a close relative. The more closely the two individuals are related, the smaller the sampling error of the estimate, provided care is taken that the environments of the two individuals are not correlated also.

In using correlations between parent and offspring the parents are likely to have been selected. Since such selection when based only on the independent variable would not bias the regression on that variable, it is expedient to use the corresponding regression of offspring on parent. Hazel (1943) used the regression of offspring on parent for estimating genetic correlations among three production traits in swine.

The genetic correlation using parent-offspring relationship can be estimated by the following formula:

$$r_{G_X G_Y} = \left[\frac{b_{Y_2 X_1} \cdot b_{X_2 Y_1}}{b_{X_2 X_1} \cdot b_{Y_2 Y_1}} \right]^{1/2}$$

This can also be expressed in terms of covariances.

Then

$$r_{G_X G_Y} = \left[\frac{\text{cov. } Y_2 X_1 \cdot \text{cov.} X_2 Y_1}{\text{cov. } X_2 X_1 \cdot \text{cov.} Y_2 Y_1} \right]^{1/2}$$

The subscripts 1 and 2 indicate the parent and offspring, respectively.

The genetic correlation between trait X and Y using deviations from the contemporary averages may be estimated as:

$$r_{G_X G_Y} = \left[\frac{\hat{\sigma} d_{X_{(ij)}} d'_{Y_{(ij)}} \cdot \hat{\sigma} d_{Y_{(ij)}} d'_{X_{(ij)}}}{\hat{\sigma} d_{X_{(ij)}} d'_{X_{(ij)}} \cdot \hat{\sigma} d_{Y_{(ij)}} d'_{Y_{(ij)}}} \right]^{1/2}$$

As shown earlier

$$E\, \hat{\sigma} \left(d_{X_{(ij)}} d'_{X_{(ij)}} \right) = \sum_{(ij)} \frac{n_{(ij)} n'_{(ij)}}{\left[n_{(ij)} + 1 \right] \left[n'_{(ij)} + 1 \right]} \sigma_{g_{X_{(ij)}} g'_{X_{(ij)}}}$$

and similarly

$$E\, \hat{\sigma} \left(d_{X_{(ij)}} d'_{Y_{(ij)}} \right) = \sum_{(ij)} \frac{n_{(ij)} n'_{(ij)}}{\left[n_{(ij)} + 1 \right] \left[n'_{(ij)} + 1 \right]} \sigma_{g_{X_{(ij)}} g'_{Y_{(ij)}}}$$

Because the coefficients in the numerator and denominator of the $r_{G_X G_Y}$ are the same they will cancel leaving

$$r_{G_Y G_Y} = \left\{ \frac{\sigma_{g_{X_{(ij)}} g'_{Y_{(ij)}}} \cdot \sigma_{g_{Y_{(ij)}} g'_{X_{(ij)}}}}{\sigma_{g_{X_{(ij)}} g'_{X_{(ij)}}} \cdot \sigma_{g_{Y_{(ij)}} g'_{Y_{(ij)}}}} \right\}^{1/2}$$

The geometric means of the two covariance in the numerator and of the two in the denominator will be $\sigma_{g_X g_Y}$ and $\sigma_{g_X} \sigma_{g_Y}$, under the assumptions of no interactions among the non-allelic genes and no maternal effects.

$$r_{G_X G_Y} = \frac{\sigma_{g_X g_Y}}{\sigma_{g_X} \sigma_{g_Y}}$$

Genetic correlation can also be calculated from the analysis of variance and covariance, using half-sib data. Genetic correlation between traits X and Y obtained from such an analysis will be:

$$r_{G_X G_Y} = \frac{\sigma_{S_{XY}}}{\sqrt{\sigma^2_{S_X} \sigma^2_{S_Y}}}$$

whereas $\sigma_{S_{XY}}$ is the sire component of covariance between traits X and Y and $\sigma^2_{S_X}$ and $\sigma^2_{S_Y}$ are sire components of variance for traits X and Y.

Estimates of genetic correlations were calculated from computed intra-sire regressions of daughter on dam and analysis of variance and covariance using half-sib data.

Standard errors of the estimates of genetic correlations were calculated using an approximate formula suggested by Robertson (1959).

$$V(r_g) = \left(1 - r_g^2\right)^2 \frac{\left[V\left(\hat{h}_X^2\right) \; V\left(\hat{h}_Y^2\right)\right]^{1/2}}{2 \, h_X^2 \, h_Y^2}$$

3. Phenotypic correlation

Two causative forces, of genetic and environmental origin, are responsible for observed relationship among different traits. The phenotypic correlation between two traits (X and Y) can be written in terms of its genetic and environmental components as shown in Fig. 1.

$$r_{P_X P_Y} = h_X \, r_{G_X G_Y} \, h_Y + e_X \, r_{E_X E_Y} \, e_Y$$

where h is the square root of heritability, e is equal to $\left(1-h^2\right)^{1/2}$ and $r_{G_X G_Y}$ and $r_{E_X E_Y}$ are genetic and environmental correlation between trait X and Y.

The phenotypic correlation between two traits can be computed as a simple (linear or product moment) correlation between their observed values (Snedecor, 1956). The mean squares for different traits and mean cross-products among them were obtained using deviation records.

Sampling error for the lower values of the correlation coefficient (r) can be calculated as $\left(\frac{1-r^2}{n-2}\right)^{1/2}$. For values of r close to the end of the range (-1 or +1) the curve of sampling error distribution of the

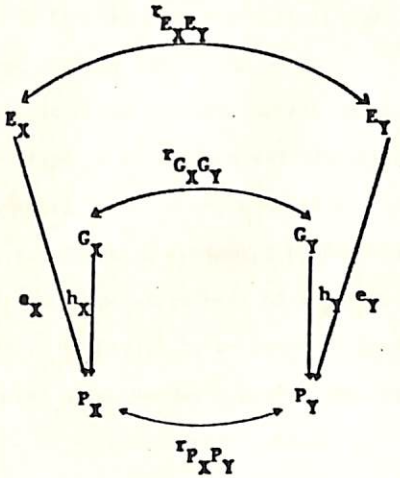

Fig. 1. Path diagram illustrating the components of phenotypic correlation between traits X and Y under the assumption, $P_i = G_i + E_i$

correlation coefficient is extremely skewed and the formula $\left(\frac{1-r^2}{n-2}\right)^{1/2}$ for the sampling error does not hold true. Fisher (1921) showed that this group of curves of sampling errors could be reduced both to normality and approximate constancy by transforming r to Z where $Z = .5 (\log \overline{1+r} - \log \overline{1-r})$. Z is normally distributed with a variance $\frac{1}{n-3}$. The variance of Z is independent of the value of r.

Since most of the estimates of phenotypic correlations in the present study were small, the sampling errors were computed as $\left(\frac{1-r^2}{n-2}\right)^{1/2}$.

C. Age Correction Factors

It is often necessary to compare production of animals of different ages and, because age influences production, it is desirable to make age corrections in such comparisons. The objective of the age correction is to measure what a young cow under the same set of environmental conditions would have produced if she were mature. The age correction factors must not remove any other differences which may really be due to things inherent in the animals themselves. The inherent and the environmental or physiological factors, such as age, are often confounded and it is difficult or even impossible to separate the effects of these factors clearly. The apparent effect of age will often reflect some effects of selection because at each age some cows with low production are culled. This leaves in the older cows a larger fraction with inherently high production and a smaller fraction with inherently low production than are among the cows who made records at a younger age. An opposite bias is introduced if the

average producing ability is rising, because then the averages for the older ages will not include records of cows in the most recent years when the average productivity of the population was higher. The effect of genetic time trends in the inherent productivity are thus confounded with age effects (Lush and Shrode, 1950).

Gowen (1920) compared the averages of all records made at different ages (the gross comparison method) to study the effects of age on production. Its weakness, that of not necessarily comparing the lactations of the same animal, was first circumvented by Sanders (1928) by making comparison between each consecutive pair of records of the same group of cows (paired comparison method). Selection introduces a bias in the opposite direction when using Sander's paired comparison method, because lactation records are only incompletely repeatable.

Lush and Shrode have discussed the biases that selection introduces in these two methods. If the culling were entirely based on the individual performance, and was only due to low production, and if the repeatability of individual records is t, then the ratio of the two biases would be $-(1-t)/t$. The negative sign merely indicates that the two biases are in the opposite direction. If t is less than .5, the bias in the paired comparison method is actually larger than the bias in the gross comparison method. But the culling is never based wholly on the individual's production and not all the animals failing to make records at a later age are culls. Basing culling partly on other characters or on records of relatives close enough to have any practical influence on

predictive value, would have the same effect as making t larger. These authors have also shown that the gross comparison curve lies beneath the paired curve at immature ages. Assuming the true curve to be intermediate, gross age factors tend to over-estimate the production at immature ages while under-estimating the mature equivalent yield of aged cows. The paired correction factors are in error in the opposite direction. Miller (1964) using 405,330 lactations records of registered DHIA Holstein cows for studying the effect of biases in estimating the regression of milk production on age, also obtained a similar difference in the two age-correction methods.

Rendel and Robertson (1950) have argued that age-correction factors which are worked out from the data provided by the herd on which they are to be used will be complicated by changes due to genetic and environmental trends. Correction factors taken from estimates made in other herds have the same drawbacks; that is, of the confounding of environmental and genetic trends and also the doubt as to their suitability for use in a different herd, due to differences in the managemental practices. The effect of the age is not independent of the management; animals raised on a high plane of nutrition will show less age effect than ones reared on a low plane of nutrition (Bonnier et al., 1948). This would mean that age correction factors should be fitted for each herd separately.

In considering the effect of age on production, age is generally regarded as a measure of maturity. According to Kay and M'Candlish (1929) two factors viz: growth and development appear to be intimately associated with maturity of the cow and with variations in milk production. Growth

includes changes in body size and weight and probably an increase in the active secretory tissue in the udder; development means the increased functional activity of the secretory tissue of the udder, and also other parts of the body through use especially in a first few lactations. In part the increase in the functional activity of the secretory tissue occurs concurrently with age, so that, to the extent that age is confounded with lactation number, age effects include effects due to both growth and development of the udder and other body systems. This growth and development is governed to some extent by herd environment and management, particularly methods of raising the calf and age at first calving. This suggests that herd differences are important when computing age correction factors. (Searle and Henderson (1959) have, however, shown that the multiplicative factors do take care of the differences between herds in age effects.)

Searle and Henderson (1960) have studied different means for judging the effectiveness of different age correction factors for estimating the cow's record at one age from her record at the other under exactly the same environmental conditions. They found no single criterion wholly satisfactory for this purpose.

The errors in age correction factors, though small, may introduce relatively large biases because the age effect is large compared to other effects and the errors in age-correction factors are cumulative.

Henderson (1958), using records from 11 New York herds and applying the maximum likelihood method for estimating environmental trends, showed the

effect of biases in estimates of age factors and repeatability. For each extra pound by which first lactation records were built up, the environmental trend was biased downwards by .22 pounds of butterfat per cow per year. For each .01 by which the repeatability actually used exceeded true repeatability, the downward bias is .08 pound butterfat per cow per year.

Kempthorne and von Krosigk in Henderson et al. (1959) have illustrated the importance of the assumption of perfectness of the age correction factors when the maximum likelihood method is used. Considering only first and second records made in successive years in the Iowa Board of Control herd at Woodward for the period 1940 to 1954, they found that using the factor 1.25 instead of 1.28 as a correction for the first record would increase the estimate of total environmental change by approximately 120 pounds of butterfat.

The effect of age on production was studied in the present investigation by gross and paired lactation comparison methods and by expressing the later records as a percentage of the first records of the same cows. The effect of variation in age at first calving on milk production in different lactations and the effect of variations in age at each subsequent calving on the production in the lactation immediately following these calvings was also studied using the correlation and regression techniques.

D. Repeatability Estimation

Repeatability is needed (1) in predicting the most probable producing ability of a cow or her breeding value from repeated observations, (2) in

selection indexes and (3) in estimating the environmental and genetic trends when the method of maximum likelihood is used (Henderson et al., 1959). Repeatability expresses the importance of permanent differences among cows. It is a ratio of the genetic variance and the variance due to permanent environmental effects to the total variance.

Repeatability is estimated as an intraclass correlation obtained from the analysis of variance or as a regression or correlation among different records of the same cow. Kempthorne and von Krosigk in Henderson et al. and Curnow (1961) have suggested the use of maximum likelihood method to estimate repeatability from records subject to culling. Repeatability in the former method is estimated as a weighted average of the simple regression coefficients. This method is expected to circumvent the effects of selection if the selection is based solely on the previous records. The validity of this method also requires equality of the partial regressions of subsequent records on preceding ones and homogeneity of variance of different records in an unselected population.

Wadell (1959) examined two methods (intraclass correlation computed from variance components and a combined estimate computed from regression of the next record on the sum of all earlier records) of computing repeatability for bias due to the possible existence of curvilinearity, incompleteness in USDA age correction factors, and selection. He found little evidence for any curvilinearity important enough to make any material difference in the estimate. Inequality of age corrected records at various ages caused a decrease in the intraclass correlation of the

order of .02. The combined regression estimates were consistently higher than the estimates obtained from intraclass correlation by four times their approximate standard errors. Failure to correct for differences between means might have played a major role in causing the differences in the estimate from the two methods. When no account was taken of the differences which selection caused between the means of first records and of second records of cows who had both, the intraclass correlation decreased by .02 for each increase of 5 per cent in truncation selection. Correcting for inequality of means of the first and second lactations eliminated almost all this decline in the computed intraclass correlations even when selection as severe as 50 per cent truncation selection was practiced. From this study, the author recommended that if the variance component method were used for computing repeatability, some correction should be made for inequality in the means of different records; otherwise the regression method should be used. The author, however, neglected the requirement that the variances of different records should essentially be the same if unselected records were used.

Butcher (1965) used five different methods for estimating relationship between various pairs of lactations expressed as deviations from herd-year-season averages. These methods were: (1) analysis of variance using only cows with both records of a pair, (2) analysis of variance using all cows with the first record of a pair even if the second record of the pair was missing, (3) a maximum likelihood procedure obtained by Curnow (1961), (4) simple regressions of the second record of a pair on

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the first record of that pair and (5) simple correlations using estimates of variances and covariances free of the effects of selection obtained from regression technique. All these methods gave similar results as long as the analyses of variance were used on data with equal means and equal variances. The author contended that the regression or the intraclass correlation estimates when all records of a pair are included are much easier to compute and give essentially the same results as the more complicated procedures of maximum likelihood and correlation free of the effects of selection.

The following model will describe a production record deviated from the contemporary average:

$Y_{ij} = \mu + c_i + e_{ij}$

where Y_{ij} is the jth record of the ith cow,

μ is the overall population mean,

c_i is the effect common to all lactations of the ith cow. It is assumed that $E(c_i) = 0$ and $E(c_i)^2 = \sigma_c^2$,

e_{ij} is the random error associated with the jth record of the ith cow. It is assumed that $E(e_{ij}) = 0$ and $E(e_{ij})^2 = \sigma_e^2$.

Repeatability as an intraclass correlation obtained from among and within cow analysis can be defined as:

$$r = \frac{\sigma_c^2}{\sigma_c^2 + \sigma_e^2}$$

Since the assumption of the equality of lactation means will not often be fulfilled, adjustment of the intraclass correlation for the inequality in lactation means will be required.

Adjustment of the intraclass correlation for the inequality in lactation means.

The model for the analysis of variance for repeatability as an intraclass correlation when lactation means are unequal may be represented as:

$Y_{ij} = \mu + c_i + l_j + e_{ij}$

where Y_{ij} is the jth lactation of the ith cow,

μ, c_i and e_{ij} are the same elements as in the model on page 71 and have the same assumptions.

l_j is the effect common to j^{th} lactation of all animals. It is assumed that $\sum_j l_j = 0$ and $E(l_j)^2 = \sigma_l^2$.

The following analysis of variance will result when the effect of different lactations is considered in an among and within cow analysis.

Source	d.f.	Expected mean squares
Total	$(n_{..}-1)$	$\sigma_e^2 + \frac{1}{n_{..}-1}\left[n_{..} - \frac{\sum_j n_{.j}^2}{n_{..}}\right]\sigma_l^2 + \frac{1}{n_{..}-1}\left[n_{..} - \frac{\sum_i n_{i.}^2}{n_{..}}\right]\sigma_c^2$
Among cows	$(c-1)$	$\sigma_e^2 + \frac{1}{c-1}\left[c - \frac{\sum_j n_{.j}^2}{n_{..}}\right]\sigma_l^2 + \frac{1}{c-1}\left[n_{..} - \frac{\sum_i n_{i.}^2}{n_{..}}\right]\sigma_c^2$
Within cows	$(n_{..}-c)$	$\sigma_e^2 + \sigma_l^2$

The coefficient of σ_1^2 for between cows mean squares will be zero if the number of records in each lactation is the same. An estimate of σ_1^2 can be obtained from the between and within lactation analysis or as one half of the average squared differences between lactation means.

Repeatability estimates of milk yield in the present study were computed from intraclass correlations and from regression and correlation coefficients, using records corrected to a first lactation basis and deviated from their contemporary means. The standard errors of repeatability estimates obtained from intraclass correlations were computed using the approximate formula for the variance of an intraclass correlation, reported under heritability estimation.

E. Estimation of Genetic Progress

Different methods of measuring genetic change in livestock populations have been developed. The improvement in the performance of a herd or other livestock population can be caused by better management and feeding conditions, and also by selection of genetically superior stock. The changes in management, both the deliberate and the unintentional are mostly confounded with the effects of selection unless some effective control population is maintained along with the selected population to allow correction for the environmental changes. In most livestock species it may not be economically feasible to maintain a large control population to provide an effective measure of environmental changes. A control population would itself be subject to genetic changes as a result of (1) change in gene frequencies from random drift or natural

selection and (2) change in genetic expression from segregation and recombination of genes having dominant or epistatic effects on performance, including inbreeding effects. Any such change in a control population would bias the evaluation of genetic change (Dickerson, 1960).

The earliest attempt to measure the genetic changes in the herd performance were made by Lortscher (1937) and with somewhat more sophisticated statistics by Nelson (1943).

Evaluating the environmental changes by comparing the repeated records of the same animal made in successive years might be possible. After eliminating the environmental changes from year to year, the genetic changes can be calculated. In the least square approach used by earlier workers the errors in the age correction factors were confounded with the environmental changes from year to year. The least square method also tends to give biased results because of the effects of culling and of incomplete repeatability.

Rendel and Robertson (1950) have proposed estimating genetic gains directly from the selection applied as, according to them, the indirect estimates are biased for different reasons mentioned earlier. The genetic improvement in a population can be envisaged to occur, through four paths, through the selection of dams of bulls (I_{CB}), selection of dams of cows (I_{CC}), selection of sires of bulls (I_{BB}) and selection of sires of cows (I_{BC}). The genetic improvement per generation is the pooled genetic superiority of the four types of parents. To get the genetic

improvement per year, the genetic improvement per generation is divided by the pooled generation interval (ΣL).

$$\Delta G = \frac{\Sigma I}{\Sigma L}$$

This method requires valid estimates of heritability and repeatability (in case of the repeated records), the phenotypic selection differential for the traits under consideration and the generation interval. Selection must also be only for the trait in question. The method provides estimates of absolute genetic gain only in the populations such as a closed herd where records can be expressed relative to a similar genetic and environmental base.

This method, however, ignores any factor which contributes to the reduction of net response to selection (ΔG) below the predicted from phenotypic selection differential times heritability. Dickerson (1955) refers to this reduction in the predicted response to selection as "genetic slippage". He has offered the following expression for ΔG:

$$\Delta G = \frac{\bar{s} \cdot H - \Sigma a}{t}$$ (Dickerson, 1961)

where $\bar{s}$ = mean phenotypic superiority of the parents selected on a single quantitative trait.

t = mean age of parents, or generation interval.

H = fraction of $\bar{s}$ which represents superiority in average gene effects in a given complex of environmental influences or heritability in a narrow sense.

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Σa_i = summation of factors which contribute to reduction of net response to selection (ΔG) below that predicted from $\bar{s}$ x H for single traits.

It is, however, difficult to evaluate these factors causing reduction of net response to selection.

Henderson et al. (1959) have presented two methods for maximum likelihood estimation of genetic and environmental trends. Method I of Henderson uses the following linear model of a cow's record.

$$Y_{ikt} = \mu + d_k + g_t + c_{it} + e_{ikt}$$

where Y_{ikt} is the record made by the ith cow of the tth genetic group in the kth year. μ is the population average, d_k is the environmental effect due to the kth year, g_t is the mean real producting ability of the tth group of cows, c_{it} is the real producting ability of the ith cow of the tth group and e_{ikt} is the random environmental effect peculiar to Y_{ikt}. c_{it} and e_{ikt} are assumed to be normally and independently distributed with mean zero and variances σ_c^2 and σ_e^2 respectively and c's and e's are uncorrelated. The problem involves estimating the d's and g's, assuming that the repeatability is known. The method will provide unbiased estimates of genetic and environmental trends if the appropriate age correction factors and repeatabilities are known.

Method II of Kempthorne and von Krosigk uses Y_{ijkt} to describe the records of a cow where subscript j indicates the jth record of the ith cow and plays no part in terms of the elements of the model. However, inclusion of the subscript j in the model does make possible the estimation of repeatability as an integral part of the computation. In this

paper Searle has shown that when repeatability is assumed known the two methods give the same estimates of estimable linear functions of the fixed affects μ, d_k, and g_t.

Another method of measuring genetic improvement in a population is to compare the change in performance of successive progeny groups of individual sires with the change in the whole population. This has been described by Smith (1962). The method measures the genetic change due to changes in the array of dams and assumes that the same rate of change occurs in both sexes. Since the dams are daughters of sires of the previous generation, the rates of change in the two sexes over a period of time must be almost the same. The pooled intra-sire regression of the deviation of the population performance from the individual sire progeny performance on time $[b_{(P-S)T}]$ or the difference between the regression of population performance on time and the pooled intra-sire regression of individual sire progeny performance on time $[b_{PT} - b_{ST}]$ will measure one-half of the genetic improvement in a population per time unit. This requires assuming that the mates of sires are a random sample of those available. $b_{(P-S)T}$ provides a better estimate of genetic change than $[b_{PT} - b_{ST}]$, as it discounts year-to-year fluctuations in environment.

The genetic improvement measured by this method is the improvement in the female population if the dams mated to sires were random samples. The genetic improvement measured is due to direct selection or correlated response in the period under study. If the sires used in several years have been selected on the performance of their early progeny, there will

be some regression towards the mean in their subsequent progeny. This will bias the estimate of genetic change. If there is, however, a time of decision in selecting or culling sires, then the records of the progeny before and after culling can each be used separately to give an unbiased estimate of genetic change. This method provides a sound estimate of genetic change over a period if (1) each unit of time is well represented, (2) there is an over-lapping in time of progenies of different sires, and (3) the progenies of each sire are spread over time.

Walton (1961) studied the genetic improvement in milk and fat yield in the Iowa State University Holstein herd over a period of 24 years, using the Henderson's maximum likelihood method and the actual selection practiced. The estimates obtained from the method of maximum likelihood using repeatabilities of .3, .4, and .5 and USDA age correction factors were consistently higher than those computed from actual selection and assumed heritability and repeatability of .25 and .4 respectively. The use of additional age correction factors derived from the actual data, and the use of repeatability estimated from an intraclass correlation in the actual data in the method of maximum likelihood, brought the estimates from the two methods in a close agreement.

McDaniel et al. (1961) used both Henderson's maximum likelihood method and the least square method of fitting constants (intra-sire) for first records to study the environmental trends in a Holstein Friesian herd over a period of 8 years. The two methods gave similar environmental trends. The deviation of the least square constants from the maximum

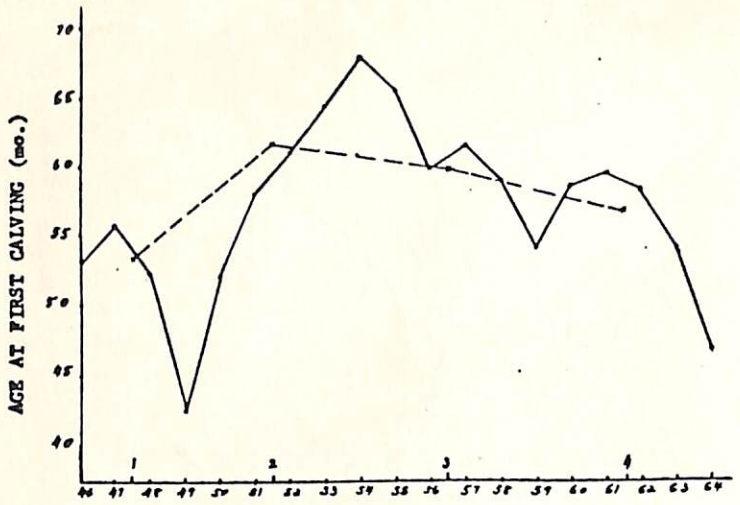
likelihood year estimates was smaller when the first records used in the least square procedure were corrected for regression on dam's production.

Henderson's maximum likelihood procedure and the pooled intra-sire regression of progeny yield (MPPA) on generation number were used on a large herd by Arave et al. (1964). They found the results from the two methods agree closely.

Estimates of genetic progress were obtained in the present study from the regression method as suggested by Smith (1962) and from direct selection using estimates of heritability and repeatability calculated from the actual data.

Fig. 2. Yearly average age at first calving. Broken line indicates averages in the four periods

Fig. 3. Yearly average milk production. Broken line indicates averages in the four periods



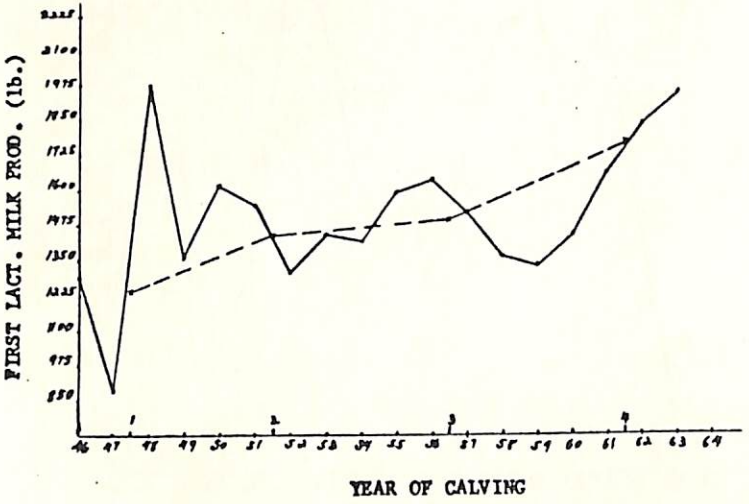
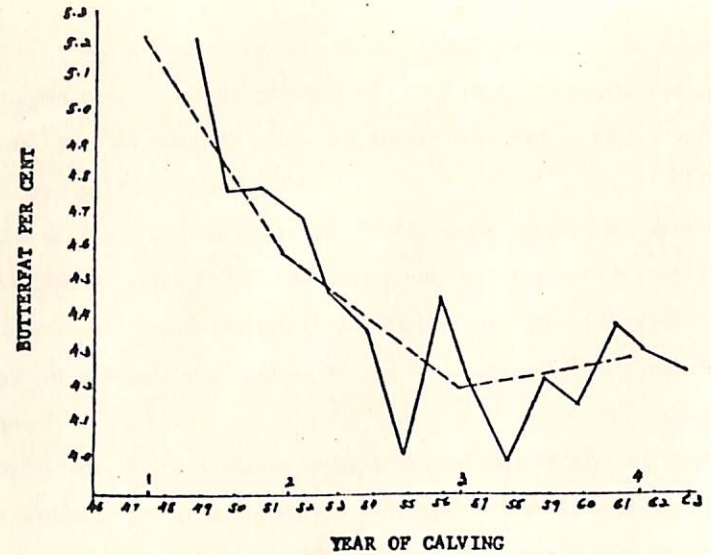
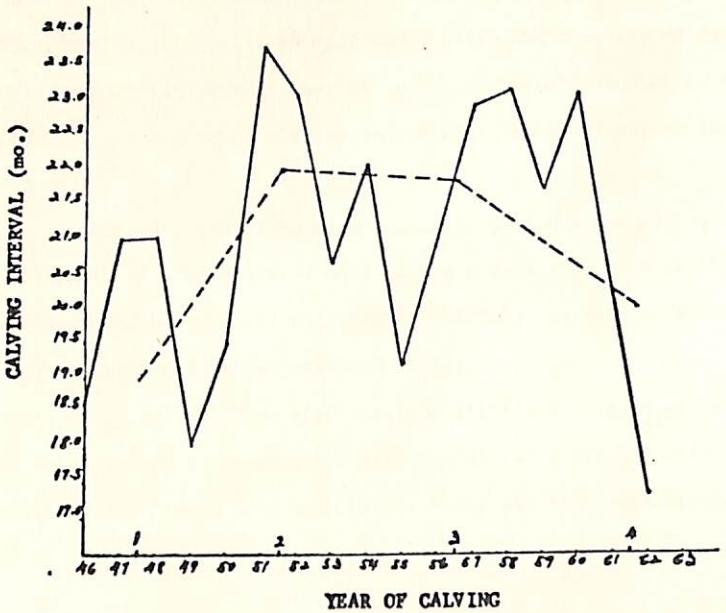


Fig. 4. Yearly average butterfat per cent. Broken line indicates averages in the four periods

Fig. 5. Yearly average first calving interval. Broken line indicates averages in the four periods





V. RESULTS AND DISCUSSION

A. Effect of the Year and Month of Calving

The effects of the year and month of calving on age at first calving, on first lactation 300-day milk production, on first lactation butterfat per cent, and on first calving interval was studied on 561 first lactation records.

The year effects, when plotted showed no distinct yearly trends except for milk production and butterfat per cent (Figs. 2-5). Milk production showed a rather large rise in the last five years. Probably this was mostly due to improved nutritional standards and care of the young heifers during these years. The trend in butterfat per cent was distinctly downwards. This occurred in the first seven years of recording of fat test. No biological reason of this decline is evident. However, there might have been some unrecorded or even unnoticed change in the techniques of testing or recording butterfat per cent or a change in the operators. As the milking was done by hand, the effectiveness of the manager in getting the milk completely or incompletely stripped might have influenced the butterfat test. The butterfat per cent, as used in the present study, was an average of trimonthly tests over the lactation. Any random errors such as might have been caused by the lack of vigilance or by the ineffectiveness of the milker in stripping the animal, should cancel out in the average. Those seemingly should not be responsible for such a continuous decline. Most cattle in the tropics are highly temperamental and a tendency suddenly to hold back or refuse to let down is rather common. The

practice of not allowing the calf to suckle on the day of the test might have caused some retention of milk; but this would have affected not only the test but also the milk yield and should have had an almost uniform effect over all the years.

The differences among periods of five consecutive years accounted for much of the variation in all the characters, ranging from 5-25 per cent. The highest was for the butterfat per cent. This high contribution in the case of fat per cent was because of the big decline in the first two periods.

Different analyses showed an important effect of year of freshening on all the four characters studied. The year effect is expected to include several environmental influences causing yearly mean production to fluctuate, either indirectly through the quality and quantity of feed available or directly through the influence of climatic conditions such as temperature and humidity or changes in managemental practices or genetic improvement.

The animals were grazed on farm (natural) pastures for most of the day (animals in milk were grazed only to the year 1952). The availability of grass depended on rainfall and that varied from one year to another and would have contributed to year-to-year variations.

Amble et al. (1958b) had also observed significant differences among periods (constituted of consecutive five years) for first lactation milk production in Red Sindhi cows both at the Hosur and the Bangalore farms.

Table 14 shows the frequency of first and all calvings in different months of the year. Though calvings are more frequent in the months from February to April in both cases, the larger frequency of first calvings is spread over the months from January to July whereas the higher frequency of all calvings is confined to the months of January to April.

Table 14. Frequency of calvings in different months

Month	First calving		All calvings	
	Number of calvings	Percentage	Number of calvings	Percentage
January	52	9.3	202	10.8
February	56	10.0	242	12.9
March	83	14.8	237	12.6
April	69	12.3	191	10.2
May	52	9.3	144	7.7
June	64	11.4	166	8.9
July	72	12.8	152	8.1
August	45	8.0	125	6.7
September	18	3.2	100	5.3
October	14	2.5	81	4.3
November	13	2.3	100	5.3
December	23	4.1	134	7.2
	561		1875	

Dave (1941) and Tandon (1951) found most calvings to occur in the months of January and February in Red Sindhi cows. Singh et al. (1958) found more calvings in four Hariana herds in U. P. to occur during February and March. A tendency for more calvings to occur during February to April was also observed by Singh et al. (1962) in Tharparkar cows. Amble et al. (1958b) and Tomar and Mittal (1960), however, found

no differences in frequency of calvings in these breeds. A tendency to calve more frequently in the months of February to April has been observed in cattle in the USA. Presumptive evidence that seasonal variations in hours of daylight affected fertility levels was offered by Mercier and Salisbury (1947). These authors observed a significant correlation between length of daylight and fertility level. Younger animals were more easily influenced by photoperiodicity than mature animals.

Yeates (1954) had pointed out that the breeding season in animals native to the temperate zones is almost invariably timed for the young to be born at a time of the year most favorable to their survival. Natural selection must have operated to develop reproductive photoperiodism.

Recently Goswami and Nair (1964) have shown that air temperature and relative humidity have an important effect on the conception and calving of buffaloes. Conception is most frequent in the months of October to January when relative humidity and air temperature are low.

Spring has been observed to be associated with highest fertility in cattle in the USA. Warm weather may favor the production of good quality semen but spermatogenesis is depressed when temperatures are very high. Occasionally a lag of about one month is noted before semen quality is reduced.

The largest frequency of all services and the highest per cent fertility in this herd occured in March to June. The number of all services and per cent fertility was lowest in the winter months. The herd is located approximately at a latitude of 30°N. The average hours of

daylight were obtained for different months of the year at this latitude from the Nautical Almanac, a publication issued by the Nautical Almanac Office of the U. S. Navy. The number of fertile services in different months follow almost a similar pattern as the hours of daylight (Table 15).

Table 15. Average hours of daylight and average number of fertile services in different months

Month	Average hours of daylight	Average number of fertile services[a]
January	10.4	3.7
February	11.1	4.5
March	12.0	7.9
April	12.9	10.0
May	13.7	11.5
June	14.0	8.5
July	13.8	6.7
August	13.2	5.9
September	12.3	5.5
October	11.4	4.5
November	10.6	3.6
December	10.2	3.4

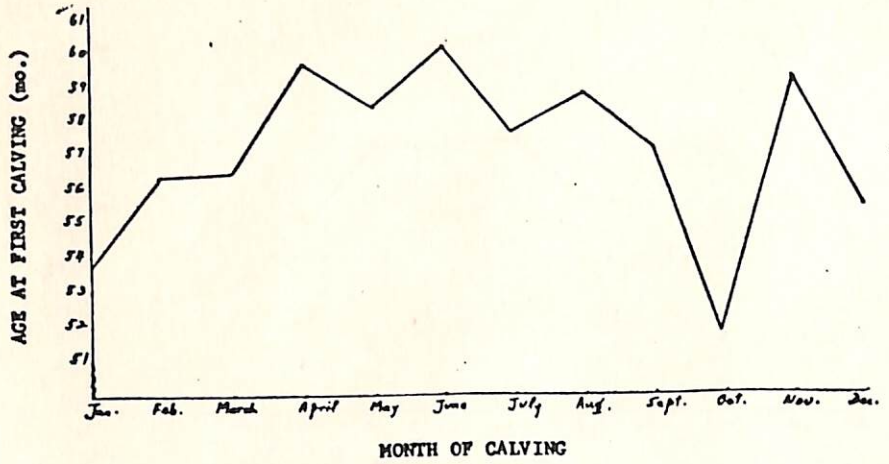
[a]Average based on data over 15 years.

A highly significant correlation ($r = .79$, $P < .01$) was found between the hours of daylight and the number of fertile services. Relative humidity and temperature were found to have a very small and non-significant effect on the number of fertile services. The seasonality of conception in this herd seems most likely to be associated with reproductive photoperiodicity.

Figs. 6-9 show monthly averages (pooled over years) for different first lactation traits studied. The month of freshening within a year showed a large contribution to the variation in all the four traits, ranging from 5-18 per cent, the highest being for butterfat per cent. The month of freshening within a year will determine under what nutritional and seasonal conditions the animal will make the important part of her record. Differences in the environmental conditions directly affecting production, or exerting their effects through feeds and pastures available, will account for differences among months of freshening. These effects should not be large until the weather conditions change drastically from one part of the year to the other. The months when pooled over all years did not show significant differences in those characters, except for the butterfat per cent. When consecutive months within a year were combined, the analyses showed little difference within pairs of consecutive months of freshening. Most of the variability was between the pairs of consecutive months, indicating no drastic month-to-month fluctuations within a year. The lack of agreement between effect of months within a year and the effect of months pooled over all years may indicate that the seasonal fluctuations within a year are not repeatable from one year to another and thus have a tendency to cancel when months are pooled over years. In spite of non-significant effect of months of freshening over all years, the milk production was consistently higher than average for animals freshening during the months of January to April. This tendency has also been observed by Dutt and Singh (1961), Singh *et al*.

Fig. 6. Monthly average age at first calving

Fig. 7. Monthly average milk production in the first lactation



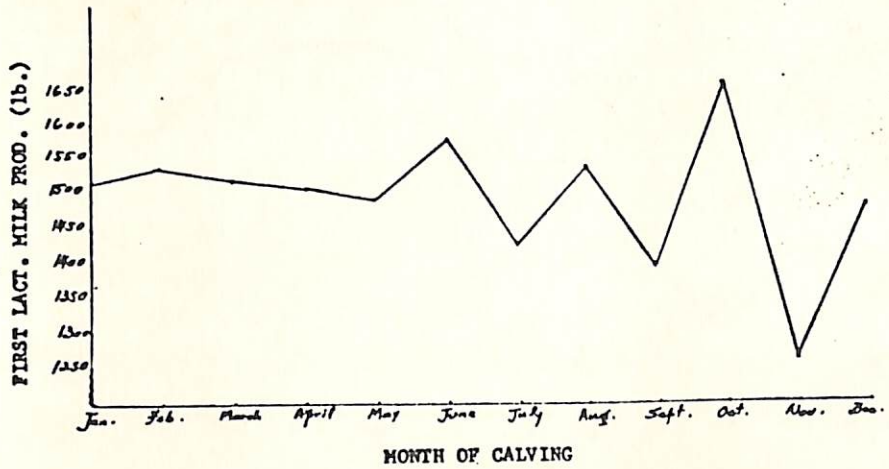
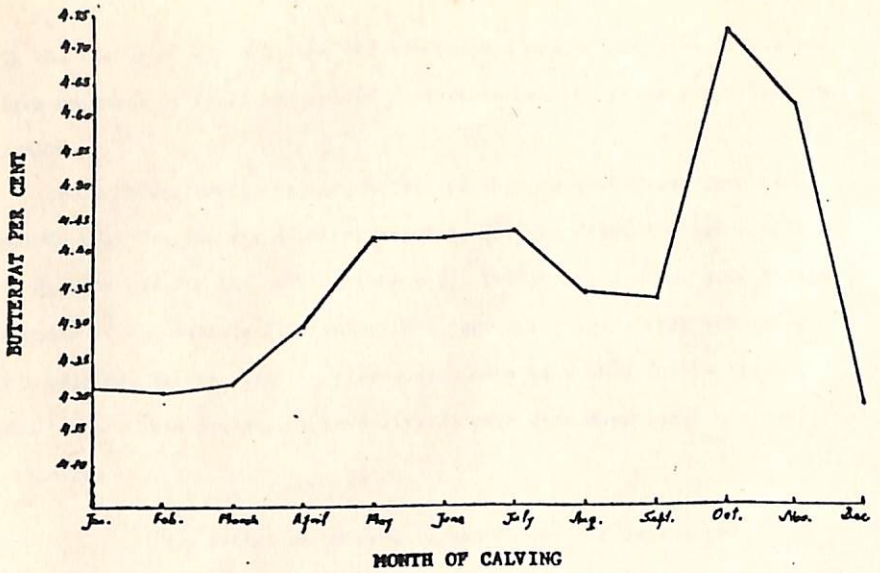
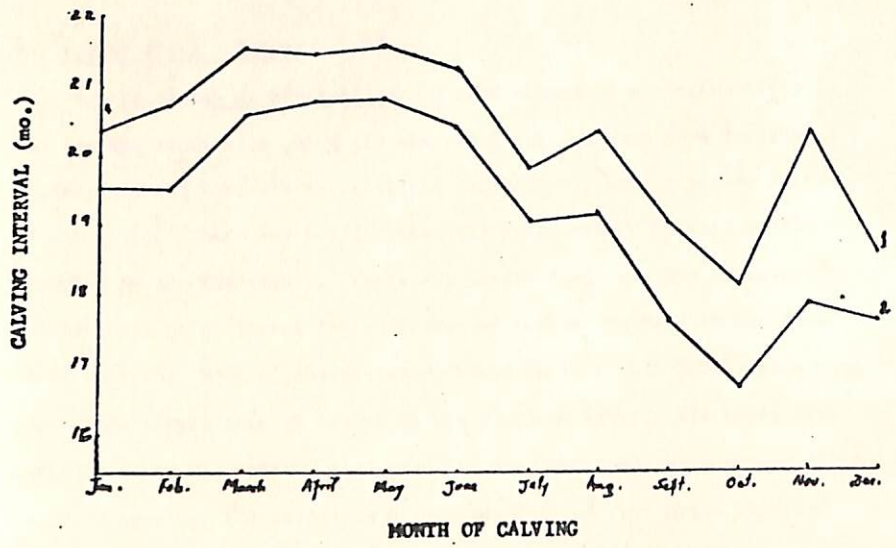


Fig. 8. Monthly average butterfat per cent in the first lactation

Fig. 9. Monthly average calving interval

1. First calving interval
2. All calving intervals

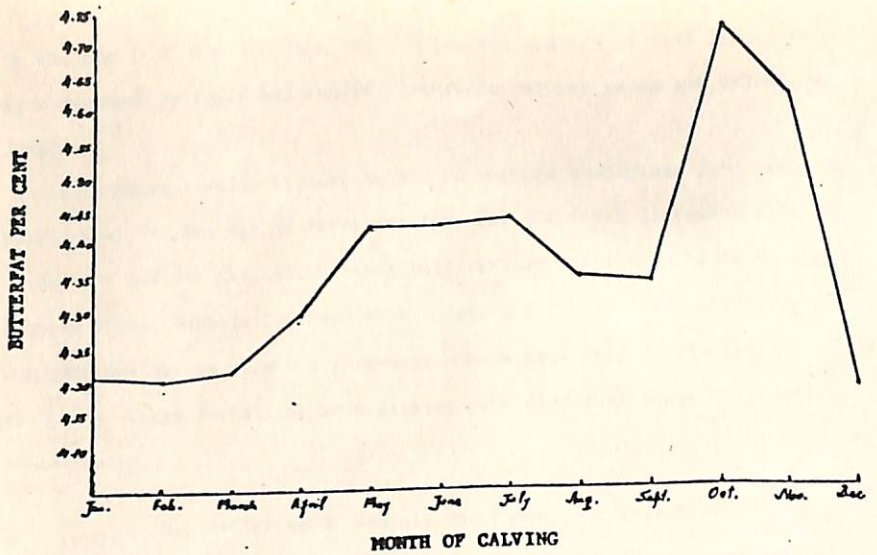


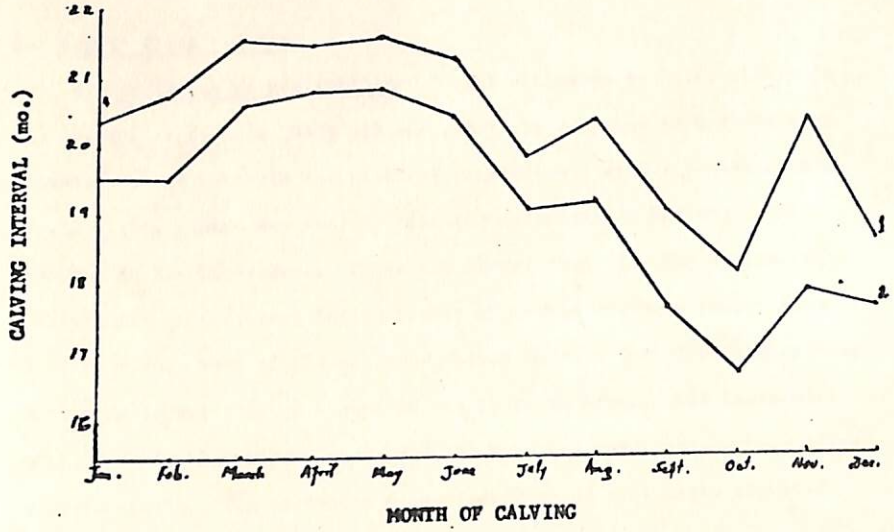


(1962), Batra and Desai (1964), and Sidhu (1964) regardless of whether the apparent effect of the month of freshening was significant or non-significant.

Animals freshening from April through August had a consistently higher than average age at first calving.

The animals freshening in the months of March to June had the highest calving interval. The animals tended to freshen subsequently during the popular season (January to April, the season when clavings were most frequent). This was reflected in the length of the calving interval of animals freshening in different months. Because the animals were allowed to suckle their calves, they were less likely to come in heat soon after calving and to conceive during the months of maximum conception (March to June). They might have to wait until next year before conceiving again. Subsequent calvings tended to happen sooner for the animals freshening during the months of July to December. This delaying or hastening of subsequent freshening is shown in Fig. 10 for first calvers and Fig. 11 for those calving for a first or later time. The upper and lower lines are displaced by enough to make their means coincide, i.e., by the average calving interval for the different months of first and all freshenings. This may further point to the possibility of some environmental factor, such as increasing daylight, influencing the breeding season in this herd. Singh et al. (1958) also found that animals freshening in the months of July to November had the shortest calving interval, the animals freshening





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in the months of May and June had the longest and the animals freshening from December to April had calving intervals between these two values in length.

From these results it was decided to compute deviations from each yearly mean for the age at first calving, for the first lactation milk production and for the calving interval. Yearly means were based on the records of all animals freshening in a particular year. For butterfat per cent deviations from the year-season mean were used in the later analyses. These deviations have already been discussed under heritability estimation.

B. Estimates of Genetic and Phenotypic Parameters

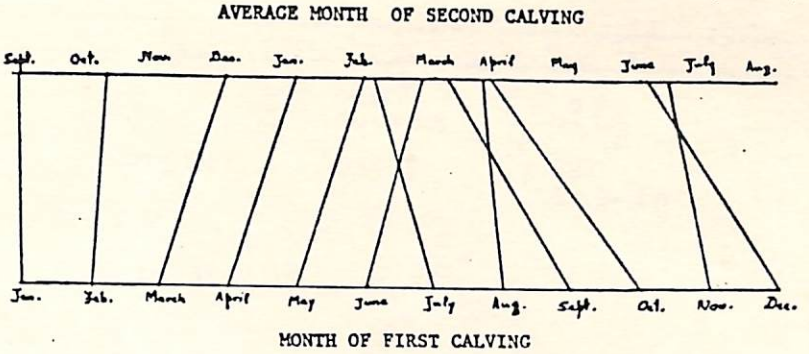
Estimates of heritabilities, and genetic and phenotypic correlations among the four first lactation traits are presented in Table 16 and 17.

1. Age at first calving

a. Estimates of heritability The estimates of heritability in the present study were .04 ± .18 and .14 ± .12 computed from intra-sire regressions and half-sib correlations respectively with a pooled figure of .11 ± .10. These are smaller than the estimates on Hariana cattle reported in the literature. Those are larger than .3. The estimates of heritability on different Indian breeds of cattle reviewed ranged from -1.24 to +.66. Most of the estimates based on more than 200 daughter-dam pairs were larger than .3 except in the Kangayam breed. All these estimates, both in the present study and the ones reviewed, have rather large standard errors. The estimates of heritability of this trait reported

Fig. 10. Tendency in subsequent calving of animals calving in different months, first calvers

Fig. 11. Tendency in subsequent calving of animals calving in different months, first and later calvers



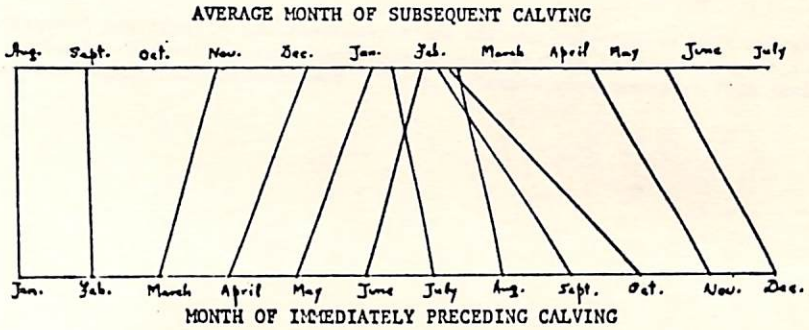


Table 16. Estimates of heritability

	From intra-sire regressions of daughter on dam				From regression of daughter on dam		From half-sib correlations	
	(a). Using actual records		(b). Using deviated records		Using deviated records		Using deviated records	
Trait	d.f.	Estimate	d.f.	Estimate	d.f.	Estimate	d.f.	Estimate
Age at first calving	223	-.17±.14	223	.04±.18	332	.14±.15	419	.14±.12
300-day first lact. milk production	223	.42±.12	223	.48±.13	332	.45±.11	419	.42±.15
Butterfat per cent	88	-.10±.12	88	-.08±.13	179	-.03±.09	323	.05±.10 .02±.11[a]
First calving interval			62	.24±.21	152	.18±.14	240	.40±.20

[a]Computed using deviations for year-season mean.

Table 17. Estimates of genetic and phenotypic correlations[a]

	X_1	X_2	X_3	X_4
Age at first calving (X_1)		-.16	0	0
		(-.46±.30)	(2.76)	0
300 day first lact. milk production (X_2)	-.007±.046		0	.41
			(.55±.43)	(-.20±.31)
First lact. butterfat per cent (X_3)	-. 16±.05[b]	.36±.05[b]		0
				(-.98±1.42)
First calving interval (X_4)	. 15±.06[c]	.09±.06	.13±.07	

[a]Above the diagonal are genetic correlations; those without parentheses were calculated from intra-sire regression and with parentheses were calculated from half-sib correlations. Below the diagonal are phenotypic correlations. These estimates were computed from deviated records.

[b]$P < 0.01$.

[c]$P < 0.05$.

for most European breeds are very low and in most cases not far from zero. Because of the large standard errors of most of the estimates on Indian cattle it is hard to reach a definite conclusion about the extent to which the variation in the age at first calving in Indian cattle is due to additive gene action. These estimates however, suggest that age at first calving is at least moderately heritable in Indian cattle.

b. Relationship of age at first calving with other characters

Phenotypically, age at first calving was correlated negatively with first lactation milk production and butterfat per cent, the correlation with the latter being highly significant. Age at first calving was also positively and significantly related to first calving interval phenotypically. Age at first calving had a negative genetic relationship with milk yield but hardly any relationship with butterfat per cent or with calving interval.

Non-significant phenotypic correlations between age at first calving and first lactation milk production have been reported by Lecky (1951), Sundaresan et al. (1954), Singh and Sinha (1960), Singh and Choudhury (1961), Mahadevan and Hutchinson (1964) and Sidhu (1964). Venkayya and Anantakrishnan (1956, 1957), however, found positive and statistically significant phenotypic correlations between these characters. Puri and Sharma (1965) recently reported a negative and highly significant correlation between these two traits.

Tandon (1961) found a negative genetic relationship of age at first calving with first lactation milk yield and with butterfat per cent in

Hariana cows. The correlation between the age and milk production was of the same magnitude as in the present study. Tandon also reported a large positive phenotypic and genetic correlation between age at first calving and first calving interval. Sundaresan et al. (1954) observed a negative and non-significant phenotypic correlation between these characters in Sindhi cows and in Murrah buffaloes. Singh (1957), Singh and Sinha (1960) and Singh and Choudhury (1961) reported non-significant but positive phenotypic correlations between these characters in different Indian breeds of cattle. Venkayya and Anantakrishnan (1956) also found positive phenotypic correlations between these two characters in Sindhi, Gir and in Sindhi x Ayrshire crossbred cows. The correlation was statistically significant in the case of Red Sindhi and crossbred cows only. The results of the present study and those reviewed indicate that age at first calving bears hardly any relationship phenotypically with milk production in the first lactation but the two traits are negatively correlated genetically. Age at first calving has a positive phenotypic and a low positive or no genetic relationship with first calving interval.

2. First lactation milk production

Heritability estimates of .48 ± .12 and .42 ± .15, computed from intra-sire regressions and half-sib correlations are considerably larger than most of the estimates on Indian breeds reported in the literature. The pooled figure was .46 ± .10. The two other estimates on Hariana cattle reported in the literature on a similar volume of data are comparatively low (.26 and .15). However, the estimates for the Red

Sindhi breed reported from the Hosur and Bangalore herds are larger than .3. The standard errors of the estimates in the present study and of the other estimates reported are large. The difference in the two estimates in the present study is small and non-significant.

3. First calving interval

a. Estimates of heritability Heritabilities of .24 ± .21 and .40 ± .20, based on intra-sire regressions and half-sib correlations, were found in the present investigation. The pooled figure was .32 ± .15. Estimates on other Indian breeds of cattle range from -.37 to .88. Most of these are small, except in the Red Sindhi and Hariana, and they all have large standard errors.

b. Relationship with other characters First calving interval was positively correlated phenotypically with other traits but significantly only with age at first calving. The genetic correlation between first calving interval and first lactation milk production, based on intra-sire regressions, was positive and large, but the one based on half-sib correlations was negative.

Tandon (1961) observed a positive phenotypic and a negative genetic correlation between calving interval and the other three characters.

4. First lactation butterfat per cent

a. Estimates of heritability The estimate of heritability for this trait, based on intra-sire regressions using deviations from the yearly mean, was small and negative. The estimates based on half-sib

correlations, using deviations from the yearly mean and from the year-season mean, were both extremely low (.051 ± .105 and .021 ± .112). Tandon (1961) reported a heritability of .67 for butterfat per cent in a herd of Hariana cattle; but did not describe the method of computing this estimate and the standard error. Stonaker (1953) on the contrary found a heritability of only .09 in Red Sindhi cows, based on 82 intra-sire degrees of freedom. All of these estimates necessarily have large standard errors, being based on very small sets of data. The estimates for the Red Sindhi reported by Stonaker and those for the Hariana in the present study are extremely low for a trait which is known in most European and tropical breeds of cattle to have a rather high heritability. Year and season of freshening accounted for a large proportion of the variation in butterfat per cent in the present study. This is contrary to what is biologically expected.

b. Relationship with other characters A positive and highly significant phenotypic correlation between butterfat per cent and first lactation milk production was observed in the present work. The genetic correlation based on intra-sire regressions was zero but when computed from half-sib correlations it was rather high and positive. The genetic and phenotypic correlations are contrary to those expected and to the ones reported in the literature. Tandon (1961) reported negative phenotypic and genetic correlations between these two characters.

C. Effect of Age on Milk Production

The effect of age on production was studied by using both gross and paired lactation comparison methods and by expressing the later records as a percentage of the first records of the same cows.

Though the correlation between the lactation number and the age in years at which that lactation is initiated would be quite high for biological reasons, yet it would not be perfect especially where the age at different calvings is quite variable. The effect of the variation in age at first calving on milk production in different lactations and the effect of variation in age at each subsequent calving on milk production in the lactation immediately following these calvings was studied using correlation and regression techniques.

Preliminary analyses involving 80 animals which each had records for five lactations (Table 18) showed that the correlations and regressions of milk production in different lactations on age at first calving were all statistically significant except in the third lactation. The correlations and regressions of milk production in different lactations on age at initiation of that lactation (age at subsequent calving) were also significant except in the fifth lactation. The relationship between age and production was not exactly linear and these correlations and regressions would explain only a linear part of this relationship.

When all records of animals having a first lactation were used (Table 19), age at first calving had no significant effect on production in any lactation except the fourth and fifth. However, the age at each subsequent

Table 18. Coefficients of correlation and regression of milk production on age at first and subsequent calvings (only 82 animals each with first five lactations)

Lactation no.	Average 300-day milk production (lbs.)	Average age at calving (months)	r_{YX_1} [a]	b_{YX_1} [a] (lbs.)	r_{YX_s} [b]	b_{YX_s} [b] (lbs.)
First	1810±72	57.8±1.0	.27[c]	18.2[c]		
Second	2071±80	76.4±1.2	.33[c]	24.3[c]	.39[c]	24.0[c]
Third	2147±72	94.8±1.4	.19	13.4	.32[c]	17.1[c]
Fourth	2049±79	112.9±1.5	.26[d]	19.9[d]	.41[c]	21.9[c]
Fifth	1988±88	133.3±1.8	.26[d]	22.2[d]	.13	6.44

[a] r_{YX_1} and b_{YX_1} are the correlations and regressions of milk production in different lactations on age at first calving.

[b] r_{YX_s} and b_{YX_s} are the correlations and regressions of milk production in different subsequent lactations on age at subsequent calving.

[c] $P < 0.01$.

[d] $P < 0.05$.

Table 19. Coefficients of correlation and regression and partial regression of milk production in different lactations on age at first and subsequent calvings

Lactation no.	Number of records	Age at first calving (months)	Age at subsequent calving (months)	300-day milk production (lbs.)	$r_{X_1X_s}$ [a]	r_{YX_1} [b]	r_{YX_s} [b]	$b_{YX_1 \cdot X_s}$ [c] (lbs.)	$b_{YX_s \cdot X_1}$ [d] (lbs.)
First	561	57.7±.4		1502±29		-.006			-.45
Second	343	57.8±.5	79.0±.7	1834±42	.73[e]	.05	.12[f]	-6.8	10.5[e]
Third	233	57.3±.6	96.7±.8	1902±52	.82[e]	.12	.13[f]	3.0	6.7
Fourth	181	56.9±.6	113.1±1.0	1821±60	.75[e]	.21[e]	.31[e]	3.8	20.6[e]
Fifth	109	57.3±.9	130.2±1.5	1838±87	.77[e]	.34[e]	.39[e]	10.1	17.5[f]
Sixth	53	56.7±1.2	147.6±2.3	2120±108	.60[e]	.09	.23	6.9	13.0

[a] $r_{X_1X_s}$ is the correlation between age at first calving and age at subsequent calving.

[b] r_{YX_1} and r_{YX_s} are the correlations of milk production with age at first and age at subsequent calvings.

[c] $b_{YX_1 \cdot X_s}$ is the regression of milk production in different lactations on age at first calving with constant age at subsequent calving.

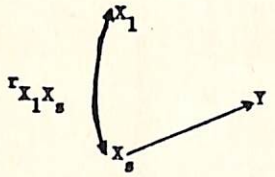
[d] $b_{YX_s \cdot X_1}$ is the regression of milk production in different lactations on age at subsequent calving with constant age at first calving.

[e] $P < 0.01$.

[f] $P < 0.05$.

calving had significant effect on production in the lactation immediately following these calvings except in the sixth. Regressions of production in different lactation on age at first calving with a constant age at subsequent calvings were all non-significant. On the contrary regressions of production in different lactations on the age at subsequent calving with a constant age at first calving were all significant.

The relationship among milk production in a lactation following a subsequent calving (Y), age at first calving (X_1) and age at subsequent calving (X_s) can be presented in the form of a path diagram given below:



Most of the influence of X_1 on Y will be expected through its relationship with X_s. $r_{X_1X_s}$ is very high in all lactations ranging from .60 to .82. This relationship must be very high for biological reasons. Animals calving late for the first time will have a late subsequent calving compared to animals calving early for the first time. There will be some effect of the variation in calving interval of different animals on age at subsequent calving but this variation will be much smaller than the variation in age at first calving.

A positive correlation between age at first calving and first calving interval observed in the present study would indicate that the

factors that caused the animal to calve late for the first time, possibly through retarding growth and development and thus delaying attaining sexual maturity, persist in the first lactation causing animals to have a late subsequent conception.

Fitting age at subsequent calving (X_s) alone, accounted for most of variation in production due to X_1 and X_s. The production in the second to sixth lactation was adjusted to an average age at these calvings to remove the effect of variation in the age at the initiation of different lactations.

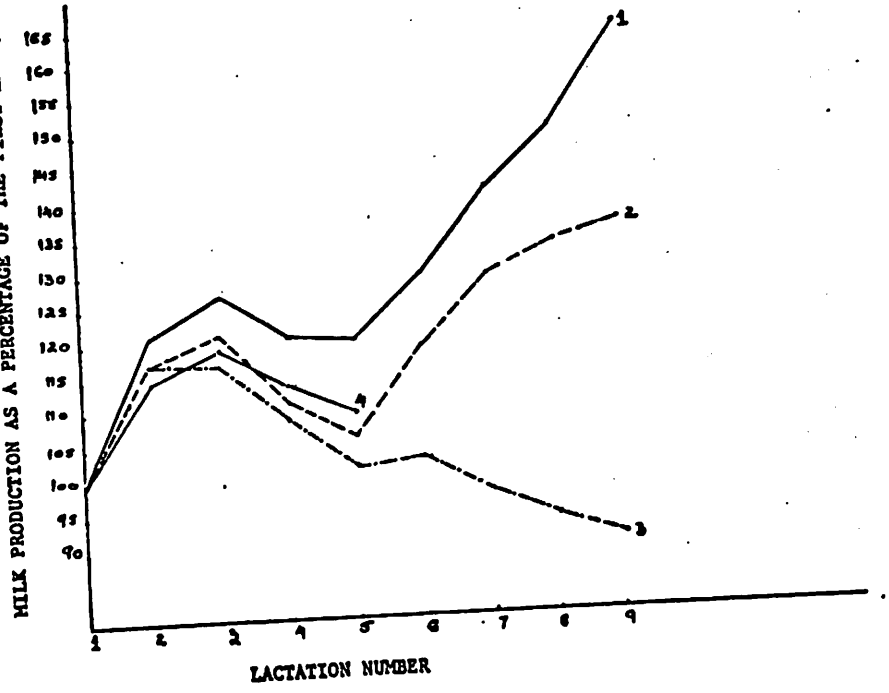
Fig. 12 shows the lactation curves using different lactation comparisons. The gross lactation comparison curve (1) is mostly on the top and the paired lactation comparison curve (3) is mostly at the bottom. The curve, when subsequent records are expressed as per cent of their first records (2), is intermediate. The true age curve is expected to lie in between the paired and gross comparison curves.

Table 20 presents the milk production in different lactations expressed as percentages of the first lactation milk production using different ways of comparison.

The gross comparison of the records in different lactations indicated that the peak was attained in the third lactation with an increase of about 27 per cent, followed by a decline in fourth and fifth lactations and then a continuous increase in all the other subsequent lactations. This differs much from the expected lactation curve based on the physiological expression of growth and senescence. That would lead one

Fig. 12. Production in successive lactations expressed in different ways relative to the production in the first lactation

1. Gross lactation comparison.
2. Expressing later records as a per cent of the first records of the same cows.
3. Paired lactation comparison.
4. Gross lactation comparison but using only the data on 82 cows which each had first five lactations.



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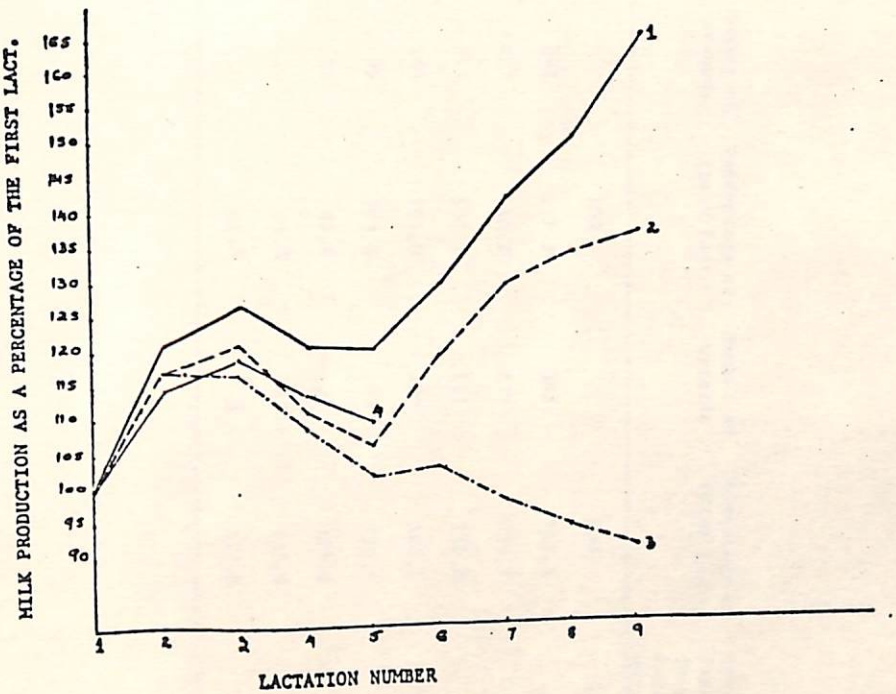

Table 20. Milk production in different lactations expressed as a percentage of production in the first lactation

	1. Gross comparison					2. Paired lactation comparison		3. Later records expressed as a percentage of the first record of the same cows		
	a. Using all records				b. Using records of 82 animals with 5 records each					
Lact. no.	Number of records	Actual (lb.)	Percentage of first lact.	Av. age at calving (mo.)	Percentage of first lact.	Number of records	Percentage of first lact.	Number of records	Percentage of first lact.	Correction factors (based on comparison no. 3)
1	561	1502	100	57.8	100		100		100	1.000
2	409	1816	120.9	76.4	114.4	343	117.3	343	117.3	.852
3	307	1906	126.9	94.8	118.6	257	116.7	233	120.7	.828
4	255	1821	121.3	112.9	113.2	218	108.2	181	110.8	.902
5	163	1810	120.5	133.3	109.8	140	101.8	109	106.1	.942
6	90	1942	129.3	142.4		77	103.4	53	119.4	.838
7	44	2137	142.3	156.2		39	97.8	27	129.4	.772
8	25	2258	150.4	165.0		20	94.0	15	133.9	.747
9	11	2482	165.2	177.4		10	91.3	8	137.0	.730

to expect a rise at an ever-decreasing rate until the age of maximum productivity and thereafter a decline at an ever-increasing rate as the animal advanced in age. Perhaps selection in the later lactations was intense, as compared to the earlier ones. The higher average performance in later lactations might also have been due to the contribution from animals which were already in their later lactations when introduced in the herd at the time of its establishment and therefore were not represented in the averages of the earlier lactations. Reportedly the foundation stock was not selected on the basis of milk production, yet some selection of these animals for higher production might have occurred, perhaps indirectly. Chance, along with small numbers and selection might have been responsible for the much higher production in the last three lactations.

The paired lactation comparison indicate that the peak was attained in the second lactation with an increase of about 17 per cent, followed by little change in the third lactation and then a gradual decline in all subsequent lactations. This contrast between the paired lactation comparison and the gross comparison has also been observed by Sikka (1931) in Sahiwal cattle and by Mahadevan (1955) in Sindhi cattle. In the paired lactation comparison subsequent records were first expressed as a per cent of their preceding records. Then to express them as a per cent of the first lactation production, these different percentages were multiplied. Any error in expressing one record as a per cent of another would have biased the other percentages when the records in different lactations were expressed as a per cent of the first lactation production. To the

extent that selection was being practiced, the paired lactation comparison is also biased by the incomplete repeatability of lactation records. To correct for this would require that repeatability be known. The estimates taken from other studies might not be suitable. Also in making such a correction repeatability would be assumed constant. This is not wholly true, as adjacency will cause a higher correlation between adjacent records than between records separated by one or more other lactations. The intensity of selection for the trait under study should also be known, since if all culling was for random reasons, having no relationship with the desired trait, there will be little bias due to culling as the mean of the animals retained will vary from the mean of all records only by chance. However, even though only a small percentage of culling is based on the desired trait, the other reasons of culling are not entirely random and may have some relationship with the desired trait. It may be difficult to know as to what extent the culling was based on the desired trait and on other reasons and to what extent the other reasons of culling are related to the desired trait. Most of the time the reasons of culling are not properly recorded. An animal is often culled for more than one reason but only one of these, considered most important, is recorded. Some of these other causes of culling such as udder diseases and certain types of hormonal imbalances leading to infertility (cystic ovarian degeneration) are related to high milk production. Elimination of animals for such reasons will tend to cause the mean of animals retained to be lower than if the same number of animals were culled

because of low production only. If on the contrary the animals culled for other reasons were low producers, their elimination may act in terms of the mean production of the animals retained similar to culling animals on production.

When selection is not based entirely on production and other reasons of culling are not correctly known, or their relationship with production is not clear, the correction of the mean production of the animals retained for incomplete repeatability, i.e., converting the observed mean production to the mean producing ability of the animals retained might introduce a larger bias than it would remove. No correction for incomplete repeatability was therefore made.

The error inherent in the paired lactation comparison because the different percentages are multiplied was avoided by expressing all records in different lactations as a per cent of their first lactation records. This did cause a slight loss of information but avoided any errors in one percentage affecting the other percentages, as in paired lactation comparison.

The age correction factors (age being measured by lactation order) used in the later analyses were developed by expressing the later records as percentages of the first records of the same cows.

D. Repeatability Estimates

Estimates of the repeatability of 300-day lactation milk production were computed as an intraclass correlation and as correlations and regressions of the subsequent records on each preceding one.

The use of an analysis of variance to estimate relationship among lactations requires the assumption of equal variances and equal means of the different lactations. All records from the first nine lactations were used in the analysis. The records in each lactation (second to sixth) were corrected to an average age at the initiation of the particular lactation and were then expressed on the first lactation basis using age correction factors derived from the present data. The age corrected records were then deviated from the yearly means. Bartlett's χ^2 test for homogeneity of variance gave no evidence of heterogeneity of variances of the different lactations. Since the means of different lactations were unequal, correction for this inequality in means was made as described under statistical methods. The analysis of variance for the repeatability of 300-day lactation milk production as an intraclass correlation is presented in Table 21. The standard error for the estimate was computed by the approximate formula for the variance of an intraclass correlation, described under heritability estimation.

This estimate is a little larger than the estimates reported on other breeds of Indian cattle, especially when compared with the intra-herd estimate on Hariana cattle reported by Singh and Desai (1961), who used data on 188 cows with three records each. Nothing was mentioned by these authors regarding the homogeneity of variances or the equality of the lactation means. Their value will also be expected to be smaller than the one in the present case because of including in the present analysis all cows, even those with just one record. Exclusion of such cows will

Table 21. Analysis of variance for the repeatability of 300-day lactation milk production

Source	d.f.	M.S.	E.M.S.
Total	1864		
Among cows	679	864,249	$\sigma_e^2 + .465\,\sigma_1^2 + 2.741\,\sigma_c^2$
Within cows	1185	164,643	$\sigma_e^2 + \sigma_1^2$

$\hat{\sigma}_1^2 = 13{,}090$

$\hat{\sigma}_c^2 = 258{,}155$

$$r = \frac{\hat{\sigma}_e^2}{\hat{\sigma}_c^2 + \hat{\sigma}_e^2} = .634 \pm .019$$

bias the mean squares between cows by deflation, yielding a smaller cow component and thus a smaller estimate of repeatability. Intra-herd intra-sire estimates in the study of Singh and Desai, however, ranged from .369 to .653.

The estimate of repeatability ignoring the differences in age at the initiation of a lactation, that is, making no correction of the records to an average age at the initiation of a lactation, was .699 ± .018. This is slightly higher than the estimate obtained by removing differences in the animals for age at the initiation of a lactation. This correction would tend to remove some of the differences among animals because of starting a particular lactation at slightly different ages. A

slightly higher estimate (.691 ± .017) was also obtained by analyzing the differences among cows within the genetic groups. The genetic groups in the present study were defined by the year of birth of the cows. All animals which entered the herd as foundation animals were put in one genetic group whereas the animals born in each subsequent two-year period were put into a separate group for each such period.

Table 22 presents correlations and regressions of subsequent lactations on each preceding lactation. The relationship between consecutive records is higher than the non-consecutive records in most cases. This shows the importance of adjacency in determining the relationship among lactations. Similar importance of adjacency in determining relationship among records is reflected from the results of Sikka (1933) and Mahadevan (1954). The variances of different lactations are presented in Table 23. On the diagonal in this table are the variances of different lactations including all records in each lactation. There is a significant difference in the variances of the first and second, and of the first and third lactations. A regression is not biased when the selection is solely based on the independent variable. In this case, however, for the regression to be an unbiased estimate of the relationship among lactations, the variances of the different pairs of records should not really differ. When the variances of the two lactations of a pair are not the same and/or the assumption of the selection having been made entirely on the basis of the previous record does not hold, the regression of the subsequent

Table 22. Correlations and regressions of subsequent lactations on each preceding lactation

Preceding lactation		Subsequent lactations 2	3	4	5	6
1	b	.75±.04	.66±.04	.69±.06	.63±.10	.69±.14
	r	.73	.69	.67	.53	.56
	d.f.	340	231	179	107	51
2	b		.74±.04	.77±.05	.88±.08	.90±.12
	r		.76	.73	.78	.69
	d.f.		255	196	122	65
3	b			.85±.05	.73±.07	.63±.10
	r			.75	.67	.62
	d.f.			216	125	65
4	b				.78±.06	.71±.10
	r				.73	.64
	d.f.				139	77
5	b					.66±.08
	r					.67
	d.f.					75

Table 23. Variance of a preceding lactation of cow having a subsequent lactation

Preceding lactation	Subsequent lactation 1	2	3	4	5	6
1	442,585	373,670	401,178	394,950	373,408	237,707
2		375,512	362,114	357,909	280,443	212,284
3			361,250	331,401	351,730	305,130
4				425,503	377,610	255,874
5					449,999	348,546
6						338,989

lactation on the preceding one does not provide an unbiased estimate of the relationship between the lactations of that pair.

Estimates of the repeatability were also obtained from $b_{3(1+2)}$ [regression of the third record on the sum of the first and second record] and $b_{4(1+2+3)}$ [regression of the fourth record on the sum of the first three records]. The regressions and the estimates of repeatability of single records obtained from these regressions were:

Type	Regression	Estimated repeatability of single records	d.f.
$b_{3(1+2)}$	.380±.022	.613±.057	212
$b_{4(1+2+3)}$	.317±.019	.869±.045	149

For the estimates of repeatability from $b_{3(1+2)}$ to be unbiased requires that the two partial regressions $b_{31.2}$ and $b_{32.1}$ shall not really differ. Similar assumptions about the equality of $b_{41.23}$, $b_{42.13}$ and $b_{43.12}$, must be fulfilled if the repeatability estimated from $b_{4(1+2+3)}$ is to be valid. These estimates to be valid also require the assumption of the equality of the variances of the records involved in the sum. The assumption regarding equality of $b_{31.2}$ and $b_{32.1}$ was tested by fitting two different models describing the third record as a function of the first two:

$$x_{3j} = b_{31.2}\, x_1 + b_{32.1}\, x_2 + e_{3j}$$

$$x_{3j} = b_{3(1+2)}(x_1+x_2) + e_{3j}$$

where $x_{3j} = (X_{3j} - \mu)$.

The test for the equality of the two partial regressions $b_{31.2}$ and $b_{32.1}$ indicated the differences to be highly significant. The F-test also showed that the variances of the first and the second records were significantly different. Because the assumptions of equality of the partial regressions and equality of the variances were not fulfilled, the estimate of repeatability obtained from $b_{3(1+2)}$ is biased. These assumptions for $b_{4(1+2+3)}$ were not tested.

Though the relationship among different lactations is not the same as indicated by the correlations and regressions of subsequent lactations on each preceding lactation, a single estimate of the repeatability of 300-day lactation milk production of .63, computed as an intraclass correlation, was used in the estimation of genetic progress.

Repeatability of calving interval was also estimated as an intraclass correlation. The analysis of variance for among and within cow differences for calving interval is presented in Table 24. The analysis involved records of the first five calving intervals deviated from the yearly mean.

The estimate of repeatability of calving interval found in the present study is larger than most other estimates reported on other breeds of Indian cattle. It is, however, only slightly larger than the estimate of .282 ± .046 reported by Singh (1958) in Tharparkar cows and based on 194 animals with 3 intervals each. This estimate was corrected for the effect of year and calving sequence. The slight difference may be because of including in the present analysis all cows, even those

Table 24. Analysis of variance for the repeatability of calving interval

Source	d.f.	M.S.	E.M.S.
Total	1034		
Among cows	447	33.33	$\sigma_e^2 + .447\,\sigma_1^2 + 2.31\,\sigma_c^2$
Within cows	587	16.32	$\sigma_e^2 + \sigma_1^2$
	$\hat{\sigma}_1^2 = .81$		
	$\hat{\sigma}_c^2 = 7.56$		
	$r = \frac{\hat{\sigma}_c^2}{\hat{\sigma}_c^2 + \hat{\sigma}_e^2} = .328 \pm .037$		

with one calving interval. Exclusion of such cows will tend to deflate the between cow mean squares, yielding a smaller cow component and thus a smaller estimate of repeatability. The only other estimate of the repeatability of calving interval in Hariana cattle found in the literature is more than twice the estimate obtained from the present data.

E. Estimates of Genetic Progress

1. Regression of production on time

The estimates of genetic progress were obtained for four first lactation traits viz: age at first calving, first lactation 300-day milk production, first calving interval, and first lactation butter fat per

cent, as $-2b_{(S-P)T}$ [twice the pooled intra-sire regression of sire progeny record deviated from contemporary average on time] and $2(b_{PT} - b_{ST})$ [twice the difference in the regression of population performance on time and pooled intra-sire regression of sire progeny performance on time]. The estimates were confined to first lactation records to avoid introducing any bias due to selection.

Standard errors of these regression estimates were large for all the traits.

The intra-sire regressions were pooled over all sires to give the estimate of $b_{(S-P)T}$ from which the genetic progress was finally calculated. A negative sign of this regression would indicate a positive change, while a positive sign would indicate a negative change. The genetic improvement measured from these regression estimates is the improvement accomplished in the female population. It represents one-half of the total genetic progress if the sires were mated to a random sample of dams. This assumption was tested on deviated first lactation milk records of the cows mated to different sires. The results in Table 25, indicate little evidence of non-randomness of females mated to different sires, so far as concerns their milk production.

Selection of sires to be retained on the basis of the production of their early progeny and a tendency of later sires to be mated to genetically better cows and/or older cows will tend to bias these estimates of genetic improvement. Some selection among the sires on the basis of their early progeny performance did occur. Four sires were

Table 25. Analysis of variance of mates of sires

Source	d.f.	M.S.
Total	261	
Between sires	36	364,570
Within	225	465,859

continued in the herd after information on their early progeny performance was available. Only one of these four sires was extensively used. No correction for this possible source of bias was made in the present study. The second source would have little possibility to cause bias in the present investigation.

The estimates of genetic progress worked out as $2(b_{PT} - b_{ST})$ and as $-2b_{(S-P)T}$ are presented in Table 26.

Table 26. Estimates of genetic progress per year

Trait	$2(b_{PT} - b_{ST})$	$-2b_{(S-P)T}$
Age at first calving	- 2.90 months	- 1.48 months
First lactation 300-day milk production	67.7 lbs.	22.7 lbs.
First lactation butterfat per cent	.071 per cent	- .010 per cent
First calving interval	- .66 months	- .29 months

The estimates worked out as $2(b_{PT} - b_{ST})$ are considerably larger than those worked out as $-2b_{(S-P)T}$. The latter seems more dependable as the method tends to eliminate any effect of year-to-year fluctuations in the environment. The estimates by the latter method indicate an annual genetic improvement of about 23 lbs. of milk or 1.5 per cent of the average first lactation yield. Age at first calving decreased about one and a half month per year, butterfat per cent decreased about .01 per cent per year, and calving interval decreased about .29 month per year.

2. Estimate from direct selection

The selection in this herd was primarily based on milk production with little attention paid to any other production or reproduction trait. The expected genetic change in milk production through direct selection was evaluated using the method suggested by Rendel and Robertson (1950).

a. Selection of dams of bulls Genetic superiority of each dam was estimated by the following formula:

$$\text{Genetic superiority} = \frac{nh^2}{1 + (n-1)r} \text{ [dam's average - herd average]}$$

where

n = number of lactations,

h^2 = heritability and was taken as .46, the pooled estimate found in this study,

r = repeatability and was taken as .63, the intraclass correlation estimate found in this study.

The herd average used was a composite of the production of all cows other than the dam herself in the year in which she had made her records. Only the first five lactations of dams were used to calculate genetic superiority. All records in a lactation (second to fifth) were corrected to an average age at the initiation of that lactation and were then expressed on the first lactation basis using age-correction factors reported earlier. The genetic superiority of each dam was expressed in pounds of milk and as a percentage of the herd average.

Nineteen of the male calves born in the herd during the period for which the data were available were used in the herd as sires. These were the sons of 15 dams; one of these dams left three sons, two left two sons each and the rest left only one son each. The average age of the dams when their sons were born was about 9 years or the fourth lactation. The genetic superiority of the dams of bulls ranged from -41 to 1496 pounds of milk or -2.5 to 102.7 per cent of the herd average. Each dam's genetic superiority was weighted by the number of the daughters her son sired, when computing the genetic superiority of dams of bulls. The number of daughters for the sons ranged from one to twenty with an average of about eight. The average estimated genetic superiority of dams of bulls was 564 pounds of milk or 39 per cent of the average production per generation.

Amble et al. (1958b) found corresponding values of 21 per cent and 18 per cent for the genetic superiority of dams of bulls in the two Red Sindhi herds.

Five hundred and thirty-two cows born in the herd before 1955 or introduced in the herd as the foundation stock were the potential dams of bulls. The number of cows which actually became dams of bulls was 15 or 2.8 per cent. The average selection attained was equivalent to keeping 10 per cent of the cows as potential dams of bulls.

Dam no. 357H441 left three sons in the breeding herd. Her genetic superiority was 1496 pounds or 103 per cent of the herd average and accounted for a large fraction of the genetic superiority of dams of bulls.

b. Selection of dams of cows The phenotypic superiority of cows retained for each subsequent lactation is presented in Table 27.

Table 27. Phenotypic selection differential for milk due to culling from one lactation to the next

Lactation number	Number of cows	Per cent culled	Phenotypic superiority	
			(a) Pounds of milk	(b) As a per cent of the mean
1	561	37.6	60	4.0
2	410	37.3	102	6.6
3	307	29.0	71	4.3
4	255	45.1	129	7.9
5	163	52.8	142	8.4
6	90	56.7	253	15.5
7	44	54.5	186	11.3
8	25	60.0	237	14.0
	Mean selection differential:		176	7.2

Only the first six lactations were used in claculating the mean selection differential because the records in the later lactations were few. The per cent culled and the culling differential increased in each successive lactation with the exception of the third. This increase in culling might have been the result of losses through disease and mortality in the older animals. The policy in the herd of bringing all heifers in milk at least for one lactation would also have made it necessary to cull more of the older cows.

The average age of dams when their daughters were born was about seven years or approximately the third lactation.

The selection of the dams of future heifers is the result of continuous culling in successive lactations. A cow is more likely to leave daughters in the milking herd if she survives for more lactations. However, the correspondence between culling and selection of dams of heifers is not perfect; for example, all the calves a cow has may be bulls, or the breeder may save the daughter of a cow that has been culled at an early age.

The effect of culling in terms of its contribution to genetic improvement can be calculated only by weighting the yields of the cows according to the number of their daughters, which came into the milking herd. The number of lactations on which the genetic superiority of the cow is based should also be considered.

The genetic superiority of dams of cows was calculated by using the same formula used earlier for estimating the genetic superiority of dams

of bulls. In calculating the average genetic superiority of dams of cows, the genetic superiority of each dam was weighted by the number of daughters she left in the milking herd.

c. Selection of sires of bulls Progeny testing appeared to have been of some importance in this herd. A few sires did continue in the herd on the basis of their early progeny performance. The progeny test information, whenever available, was considered in selecting the sons of sires for use in the herd. Progeny testing was, in fact, family selection, the selection of young bulls being considered on the basis of their paternal half-sisters' performance.

The selection of young bulls to be tested in the herd was primarily based on their dam's production and their conformity to the draught type. However, the decision about a young bull could have been delayed awaiting preliminary information on his paternal sisters' performance.

The genetic superiority of sires of bulls was calculated using the following formula:

$$\text{Genetic superiority} = \frac{2nh^2}{4+(n-1)h^2} \text{ (daughter average - herd average)}$$

where

Daughter average = average of the first lactation records of all daughters of a sire,

Herd average = average of the first lactation contemporaries (animals freshening in the same year) of the daughters, and

$\frac{2nh^2}{4+(n-1)h^2}$ = regression of sire's breeding value on the average production of n of his daughters. h^2 is the heritability and was taken as .46, the pooled estimate obtained in this study. This regression assumes no environmental and no non-genic correlations among the daughters of a sire.

The genetic superiority of a sire was expressed in pounds of milk and as a percentage of the herd average. In calculating the average genetic superiority of sires of bulls the genetic superiority of each bull was weighted by the number of his sons and the number of daughters of each son.

The genetic superiority of sires of bulls as calculated here is in retrospect, as not all the daughters used in the sire evaluation would have made their records in the herd at the time when the decision to continue a sire or select his sons was made.

The sire no. 13HP44 was used over eleven years, seven of these years were after his early progeny performance became available. This sire contributed nine out of the nineteen bulls used in the herd. His genetic superiority was 579 pounds or 40 per cent of the herd average and made a large part of the overall genetic superiority of sires of bulls.

The average age of the sires when their sons were born was 8.5 years.

d. Selection of sires of cows Progeny testing of sires of cows was negligible in this herd. Only four sires were selected to continue in the herd on the basis of their early progeny performance. The average production of these sires except sire no. 13HP44 was not noticeably different from most other sires that were not continued in the herd after their early progeny test information became available. There was little culling of the cows on the basis of their paternal-sibs performance.

Robertson and Rendel (1950) have indicated the I_{BC} (genetic superiority of sires of cows) to be equal to I_{BB} (genetic superiority of sires of bull) multiplied by the proportion of cows mated to the tested bulls. Most of the sires were too old or even dead when their progeny test information became available. Four tested sires were continued in the herd on the basis of their early progeny performance, only one of these was used extensively. The contribution from this source to the total genetic gain could not be expected to be large in this herd.

The genetic superiority of all the sires used in the herd was evaluated, using the same formula as for sires of bulls. The genetic superiority of sires of cows was 21 pounds or 1.24 per cent of the herd average. The average age of sires when their daughters were born was 6.8 years.

e. Summary of selection practiced The generation interval and the intensity of selection from the four paths through which the selection operated are presented in Table 28.

The genetic change per year using the figures of ΣI and ΣL given in Table 28 is 36 pounds or 2.5 per cent of the herd average.

Amble et al. (1958b) reported a genetic advance per year of 1.2 and 1.4 per cent of the herd average in the two Red Sindhi herds. The herd

Table 28. Summary of selection practiced

Path	Generation interval (years)	Genetic superiority of the parents	
		Pounds of milk	As a per cent of the herd average
I_{BB}	8.5	501	34.9
I_{BC}	6.8	21	1.2
I_{CC}	7.1	47	2.9
I_{CB}	9.0	564	39.0
	ΣL 31.4	ΣI 1134	ΣI 78.0

average in their study was based on production over all the years the data were available. The herd size was about 70 in both the herds. The genetic superiority of sires was calculated using weighted deviations of the sires' corrected indices (based on daughter-dam comparison) from the overall herd average. Only 30 per cent of the sires used had six daughter-dam pairs, a condition for inclusion in the calculations for the genetic superiority of sires. These estimates of genetic gain are smaller than the one in the present study. The differences could partly be explained on the basis of small herd size, of no definite culling policy, relatively smaller estimates of heritability and including a limited number of sires in calculating the genetic superiority of sires in the herds studied by these authors.

The rate of probable annual genetic gains (expressed as a percentage of the herd average) reported by Amble et al. (1958b) and in the present study are larger than most estimates reported on European and American

cattle; the absolute rates of genetic gain are much smaller, however. Rendel and Robertson (1950) have shown that in a closed herd of about 100 cows the expected genetic improvement is about 1.0 per cent of the herd average per year under the following assumptions:

(1) There is no progeny testing and the bulls are chosen solely on the milk records of their dams.

(2) The selection is being practiced only in choosing cows to breed from and is based only on the first lactation.

(3) The natural mortality rates are 1/6 in the first three lactations and 1/3 for the fourth and later.

(4) About 39 per cent of the females are culled on their production and the bulls are bred from the top 5 per cent of the cows in the herd.

(5) $\sigma_p = .20\ \bar{Y}$ and $\sigma_G = .10\ \bar{Y}$, where $\bar{Y}$ is the average yield of the herd.

(6) Sum of generation lengths in about 13 years.

Under the above conditions about one quarter of the expected genetic gain comes from the early culling of heifers and the rest comes from the selection of dams of bulls. These authors, however, observed a genetic improvement of .7 per cent per year against the maximum of 1.0 per cent from their study of a partially closed herd. The rate of expected genetic improvement can increase to 1.1 per cent per year in case of progeny testing in such a herd (Robertson and Rendel, 1950). Specht and McGilliard (1960) following the method suggested by Rendel and Robertson (1950), have

shown that in a herd of about 100 cows the genetic progress with progeny testing exceeds that expected without progeny testing by as much as 20 per cent when 60 per cent or more of the females are mated to three or four young sires and one of them is selected.

Genetic improvement of 2.5 gallons of milk or 1.38 per cent per year was observed by Robertson (1950) in a closed herd of Fulani cattle at Shika, Nigeria, over a period of 13 years. Rendel et al. (1951) reported a probable genetic improvement of .3 to .4 per cent per year due to selection of dams of cows and dams of bulls in 22 high-yielding British herds of seven breeds. A genetic selection differential of .6 per cent per year was reported in the Iowa State University Holstein herd by Walton (1961).

Higher values of heritability and repeatability and a larger variation in lactation yield (C.V. = 40 per cent to 55 per cent) observed in the Indian herds should be to a large extent responsible for higher rates of probable genetic improvement (expressed as a percentage of the herd average) in Indian cattle compared to European and American cattle.

The estimate of genetic progress in the present herd could have been biased if the heritability and repeatability and age correction factors used were incorrect. The heritability and repeatability and age correction factors used were estimated from the data used for estimating the genetic gain. These estimates, though more appropriate than those from other studies, must have been affected by the genetic and environmental trends and the limited amount of data. Most

other estimates of heritability and repeatability for Indian cattle available in the literature were based on much the same volume of data as in the present study, and must have been affected by similar genetic and environmental trends. Walton (1961) has shown that small errors in age correction factors have little effect on the estimates of genetic superiority of selected parents. He has also pointed out the merit in adjusting production to the first lactation equivalent instead of the mature equivalent, the important reason being that all cows have a first record, but only a few cows reach maturity. If the correction factors were in error, a small bias would be introduced into the data by adjusting the part of the distribution curve that contained the lowest frequency of observations. As records in the present study were adjusted to the first lactation equivalent, bias due to incorrectness of age correction factor, if any, would be small. The incorrectness of the estimates of heritability and repeatability, if any, would have affected the estimates of genetic selection more seriously. In spite of a number of limitations the estimate of probable genetic gain per year indicates a large genetic improvement in milk production in the herd since its establishment.

3. Comparison of the genetic progress expected from direct selection with the genetic progress calculated from the regression estimate

An estimate of annual genetic progress of the first lactation milk production obtained as $-2b_{(S-P)T}$ (twice the pooled intra-sire regression of sire progeny performance deviated from herd average on time) is lower than the expected annual genetic progress from selection of 36 pounds or

2.5 per cent of the herd average. The rate of genetic progress obtained from the regression estimate being based on the first lactation records is free from the possible bias due to the incorrectness in age correction factors but might have been affected a little by the differences in the age at first calving, for which these records were not adjusted. The effect of age at first calving on milk production in the first lactation was not important in this study, however. The rate of genetic progress worked out from the regression estimate is also free from any biases due to the use of inaccurate estimates of the heritability and repeatability. The sampling error of the regression estimate of genetic progress will, however, be large because the estimate is based on a limited amount of data.

4. Correlated response in age at first calving and first calving interval to the selection for milk production

Reportedly there was little selection on the basis of age at first calving and/or first calving interval in this herd. This is supported in the case of age at first calving by the evidence presented in Table 29. However, there seems to have been some selection for a short first calving interval as this interval is shorter for the animals retained for an additional lactation and this tendency shows a rather steady increase.

The estimate of genetic change in these two traits obtained as $-2b_{(S-P)T}$ were -1.48 and -.28 months per year. These genetic changes might represent mostly a correlated response to the selection for milk production although in the case of first calving interval there is a small

Table 29. Average age at first calving and first calving interval in each lactation before and after culling

Lactation number	Average age at first calving (months)		Average first calving interval	
	Before culling	After culling	Before culling	After culling
1	57.7	57.8		
2	57.8	57.2	20.7	20.4
3	57.3	57.0	20.4	20.0
4	56.7	57.4	20.2	19.0
5	57.3	56.3	20.3	19.2

but gradually increasing culling differential. Lush has proposed that this be called secondary selection differential (Magee, 1965). Since the selection was not reportedly made for short calving interval no calculation of the genetic gain through direct selection for calving interval was attempted. The negative genetic change in age at first calving in response to selection for milk production in the positive direction indicates a negative genetic relationship between age at first calving and milk production. The genetic correlation between these two traits estimated in the present study from intra-sire regressions and half-sib correlations was -.16 and -.46 respectively. The negative genetic change in first calving interval may be partly due to direct selection and partly as a correlated response to selection for higher milk. This would indicate a negative genetic relationship between first