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ABSTRACT

GENETIC TRENDS OF DAUGHTERS OF

BULLS SELECTED FOR MILK YIELD

By

Gurdas Singh Dass

The experiment was designed to measure the phenotypic and genetic trends and correlations in a selected trait (milk) and non-selected traits (milk fat, body weight, and wither height). Method of least square procedure was used to analyze 179 first lactation records adjusted to mature equivalent, 2X and 305 days. Two lines, best and worst, were created from one herd using best and worst bulls selected on first evaluation of their daughters' milk production in Michigan. The best line produced 1082 kg and 13.6 kg more milk and milk fat than the worst line. Control line was produced by 13 bulls which were active in AI when the experiment was started; this was a base for comparison with other lines.

There were 1,142 repeated measurements on each trait (body weight and wither height) recorded on the daughters of best, worst and control bulls. From the least square analysis of variance lines had no detectable difference for body weight and wither height when the lines were significantly different for milk and milk fat.

The bull group constants ($\hat{B}_{(ij)k}$) indicated genetic differences among bull groups. The weighted constant of each bull group within

line was plotted to make comparison of classes of bull groups for each trait. The response of bull groups for milk fat was similar to milk yield, indicating a positive correlation of milk fat and milk whereas response of bull groups for body weight and wither height was irregular under different age groups and with the whole data.

A comparison of sire's mean deviation for milk from herd average was made with the initial basis of selection (daughter's deviation from herd average in Michigan) and with the latest predicted differences calculated by USDA sire summary of November 1974. The rank correlations of USDA sire summary and MSU data was .72. The rank correlations of USDA sire summary with initial basis of selection was higher (.92) due to larger number of daughters. Sires could have been ranked more accurately if there had been more daughters per sire.

Average genetic progress in kilograms per year was 46.7 ± 32.5 , -9.4 ± 59.4 for milk and 1.2 ± 2.3 , 7.7 ± 3.7 for milk fat in best and worst line, respectively, calculated by regressing the average genetic values on years. The two lines were, therefore, spreading apart by 56 kg and 6.5 kg per year for milk and milk fat. On the other hand, the average genetic change for body weight and wither height remained almost unchanged between the two lines. This indicated little influence of milk yield on body weight and wither height.

Genetic correlations were simple product moment correlations from average genetic values estimated per year for each trait. There was a positive genetic correlation of $.71 \pm .41$ between milk and milk fat. Body weight and wither height were correlated negatively genetically ($-.004$ to $-.82$) in both the lines with milk yield. The genetic correlations of body weight and wither height with milk

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production between the line differences were small (.004 to .24), although positive. Body size had little influence on milk production. Since body size has been studied as an indirect response to selection for milk production, it requires a large amount of data for precise estimate of correlated response in body size. In conclusion, selection of bulls in AI for milk produced significant changes in yield of milk and fat. There was little change in body size as an indirect response to selection on milk production and the effects were clouded by sampling of small numbers. Trends were short and unstable and, as the experiment progresses, they will stabilize enough to measure the relation of body size with milk production.

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INTRODUCTION

Improvement in milk production of dairy cattle is beneficial to both consumer and producer. Improvement in the trait can be achieved temporarily by improving management such as better feeding, proper housing, and efficient herd health program. Change can be permanent in what is heritable by increasing frequencies of desirable genes. Selection of genetically superior animals is, therefore, of great importance to genetic improvement. The problem is that observed superior performance of the animal is a confounded combination of genetic superiority and management or environment.

In small animals, methods to measure the efficiency of selection which remove systematic environmental bias and reduce error from uncontrolled random influence have been developed. In large animals (dairy cattle), large space is required for much longer due to long generation interval which makes difficult control of the environment, thereby diminishing applicability of these methods. Therefore, a method has to be developed which can control successfully the environment of large animals for effective genetic evaluation of the animal.

Selection for individual traits can be more effective where the number of traits is limited. Selection for a single trait may change the population far from the original mean and may affect general fitness for economic production. Prediction formulae based upon the heritabilities and genetic correlations have been developed to

estimate the change in correlated traits. However, the actual correlated response in single trait selection needs to be evaluated.

The purpose of this study was to measure the phenotypic and genetic trends in a selected trait (milk) and unselected traits (milk fat, body weight, and wither height) and phenotypic and genetic correlations among these traits. This would estimate the effectiveness of selection for milk production and also could measure the ability of sire selection to obtain superior sires. Such results should be of interest to dairymen and artificial insemination (AI) units which provide the genetic base for most dairy cattle.

REVIEW OF LITERATURE

One of the major tasks of the dairy husbandman is to develop and institute procedures which lead to increased production of milk and milk fat by dairy cattle. He may choose to achieve his goal either by improving the breeding value of the population or by improving the management or by a combination of both. The improvement in the mean breeding value may be achieved by careful selection of the individuals of higher genetic merit. Measure of response to selection is difficult due to confounding of genetic and environmental changes. An accurate comparison of the actual and expected response to selection depends upon valid separation of genetic and environmental trends.

Laboratory animals including poultry have been subjects of the largest number of experimental investigations relating to accurate measure of genetic response to selection. In poultry, selection for increased egg production on the basis of family records appeared to follow predictions from selection differentials in the early generations of selection (42). After a few generations of selection, there was complete cessation of increase in egg production in spite of the fact that selection differentials still remained high. In another experiment in poultry (40), mass selection for longer shanks was unusually effective until a plateau was reached. Again the plateau was not due to exhaustion of genetic variability of longer shanks, but to correlated response of other traits of reproduction. Suspension

of selection under these circumstances might have resulted in a full or partial return of the selected character to an unimproved state and in restoration of reproductive fitness. The conditions under which it may occur and phenomenon of genetic homeostasis have been discussed (41,55).

The asymmetry of response to selection in opposite directions has appeared in many two-way selection experiments. Falconer (17) did two-way selection with mice for body weight at 6 wk. Selection was carried through 30 generations in the upward direction and 24 generations in the downward direction. Two distinct lines were created from the foundation stock by selection. In these lines, asymmetrical response also was marked. Asymmetrical response to selection for 6-wk body weight of chickens (42) resulted in approximate doubling of body weight in the high line whereas the low line remained unchanged. Thus, there was marked difference in the amount of response to selection pressure in the two lines. Lerner (42) has discussed in detail the various causes of asymmetrical response to selection.

Control strains have been used in laboratory animals through which the genetic mean would remain more nearly constant in successive generations and would provide estimates of purely environmental changes. The function of control populations (21) is to assess the magnitude of short term fluctuations, to maintain genetic constancy over time, and to serve as a gene pool with known genetic parameters for use as base material in selection experiments. Control lines, however, are not always available. It is, therefore, difficult to assess the effectiveness of selection in the improvement of

domesticated animals because in the absence of a control there is no sure way of deciding how much of the improvement is due to selection and how much to progressive change in the conditions of management. Lush (44) has assembled a number of graphs showing the improvement of farm animals during the present century. It is difficult to avoid the conclusion that much of the improvement is the result of selection, but in the absence of any standard of comparison it is difficult also to decide how much is due to selection and how much to changed methods of feeding and management. The control population, which provides a base, also is subject to change in gene frequency by random drift and natural selection, and changes in gene expression caused by inbreeding are possible sources of change in genetic merit (18). Random mating has been successful (65) in minimizing genetic changes in a large control population. The test for significance of changes in phenotypic frequency from one generation to the next was Chi-square analysis. At the same time possibility of genetic drift at particular loci could not be ruled out (39) though the effect may be averaged out because of the many loci for traits of economic importance. The value of the random bred control strain was demonstrated (21) in separating the genetic and environmental effects. Also, the results (22) justified the extra labor of pedigreed matings compared to random bred control strains.

The extensive material available to laboratory geneticists, to plant breeders, and even to workers with poultry has not been available to geneticists interested in larger animals. The number of controlled selection experiments on livestock on a sufficiently large scale to permit accurate comparison of the results obtained

and the results expected is small. As a rule there are no special forms of inheritance peculiar to livestock, and the genetic theory derived from other organisms seems equally applicable to cattle, pigs, and sheep. In swine, Dettmers *et al.* (12) reported a successful 11-yr program of developing in Minnesota a strain of miniature pigs for medical research. Body weight at 140 days was reduced by at least 29%. There was neither control nor selection in opposite direction. In another experiment Craig *et al.* (9) did include two-way selection for heavy weight (10 generations) and light weight (8 generations). The two lines derived from Hampshire swine became more and more distinct for 154 and 180 day weight as selection continued. Analysis of swine data (10) indicated that selection was effective in bringing about a substantial increase in number of pigs farrowed and in average weaning weight. Since these traits have low heritabilities, it takes many generations before the ultimate benefits of selection would be realized. One-way selection for less backfat thickness in Danish Landrace pigs from 1952 to 1960 (58) showed a decline from 34.2 mm to 28.5 mm, a change of two standard deviations. Estimates of genetic change ($-.15 \pm .10$ mm per year) in backfat thickness were from progenies of sires and of dams which represented 1/5 of the observed change.

Methods of Estimating Genetic and Environmental Trends

A simple genetic model may be adequate in the early stages of a selection program, but genetic and environmental relationships become more complicated after prolonged selection. Dickerson and Hazel (14) suggested that the two factors, in addition to heritability, which

determine the annual improvement from selection are average genetic superiority of those animals selected to become the parents and the average age at which parents bear offspring, the generation interval.

Nelson (49) used two methods to determine the amount of genetic change in a herd of cows. The first method involved computation of the average difference in production for all cows that had records in consecutive years and use of the results as an estimate of environmental change between 2 yr. Differences were summed to estimate the average differences between nonconsecutive years in environment.

Dickerson (14) suggested two methods of determining selection response. Measurement of genetic divergence as experimental mean minus control mean may eliminate any systematic difference in environmental influences. In concept, the use of a control strain would keep the genetic mean constant in successive generations and would provide estimates of purely environmental change. Hickman and Freeman (33) described the following experimental designs that measure direct and indirect response to selection from measurements on progeny of successive bull groups.

In this design young bulls were selected each year on pedigree performance and progeny tested in the closed herd. These young bulls were used for 2 yr and mated at random across all females except the nominated cows selected every year to be the dams of young bulls. Randomness was determined by sex of the last calf produced. Heifers or cows whose calf could not be sexed (abortions) were divided at random into 2 groups by random number or order of date of breeding to obtain representative mates each year for each bull group. This proposed criterion measured the total genetic effect of cow culling.

The (I) after bull group N in the design indicates an alternate plan in which bull group I replaces the bull group that would otherwise be used (N+I). Designs B and C are similar to Design A and are self-explanatory.

The analysis proposed for all designs shown below is a statistical estimate of the consequences of selection operations measured within time since the selection is based on phenotype which is assumed to be an unbiased estimate of genotype in one herd where environments are averaged out. Therefore, the average difference in phenotype between daughters of successive bull or cow selections is, consequently, an unbiased estimate of differences in genotype created by operation of selection. If bulls are selected in the same direction each year, the average difference between successive bull groups is estimated efficiently by the regression of daughter's performance on bull group number. The following model can be used to estimate effect of year or time and effects of bull group. There is also possibility of estimating simultaneously the effect of female culling on genetic progress. The model is

$$Y_{ijkl} = Y_i + b_{B_j} + b_{C_k} + E_{ijkl}$$

where Y_i is an overall mean plus year effect, b_{B_j} = the regression of daughter's performance on bull group number, b_{C_k} is the regression of daughter's performance on "culled" or "kept" codes, and E_{ijkl} is the portion of Y_{ijkl} unexplained by the model and is normally and independently distributed.

Accurate appraisals of the results of breeding programs and most efficient estimates of breeding values of individuals where own records

Arrangement of progeny by sire and dam group over years (Hickman and Freeman [33])

	<u>Bull group by number and sequence of use</u>						
	Year						
	1	2	3	4	5	6	N
<hr/>							
<u>Design A</u>							
Dam group 1	I	III	III	V	V	VII...N+1(I)	^b
Kept ^a	II	II	IV	IV	VI	VI...N	
Dam group 2	I	III	III	V	V	VII...N+1(I)	
Culled ^a	II	II	IV	IV	VI	VI...N	
 <u>Design B</u>							
Divided	I	II	III	IV	V	VI...N	
by dam	II	III	IV	V	VI	VII...N+1(I)	
groups as	III	IV	V	VI	VII	VIII...N+1(I)+2(II)	
above.						(N+2)	
 <u>Design C</u>							
Divided	I	I	V	V	V	V...I	
by dam	III	III	III	III	VII	VII...N+I	
groups as							
above.							

^aKept or culled determined by presence in the herd throughout the year daughter's record is started.

^bNumbers in brackets indicate alternate bull group.

and relative's records were made in several different years require quantitative measures of the effects of changing herd environment. Least square method for obtaining such measures would give biased estimates when records of cows culled from the herd are either above or below the herd average. This bias results from the lack of perfect repeatability of records because there might be some genes affecting milk yield which become active in later lactations. Method of maximum likelihood described by Henderson (32) is preferred over least square method since it takes into account incomplete repeatability and annual culling levels and utilizes all of the records in such a way as to obtain more precise estimates of yearly environmental effects than least square method.

Maximum likelihood method was used (2) in estimating the genetic change in fat-corrected milk (FCM) in a population of 11,993 lactation records of 3,900 Jersey cows in 12 herds over 30 yr. Annual genetic change was linear regression of FCM yield on year of records adjusted for yearly environmental effects. The average genetic change for all herds was 33.64 kg FCM annually, and within individual herds the genetic change ranged from -23 ± 23 to 65.9 ± 9.54 kg FCM per year. A pooled intrasire regression of the progeny's most probable producing ability (MPPA) on generation number within the largest herd yielded an estimate of genetic change which agreed closely with the maximum likelihood estimate.

Qureshi (53) used least square procedure since there were no repeated records to study the genetic trends in first lactation milk and milk fat production records of Holstein and Jersey cows of Texas. There was an upward trend in average genetic merit in terms of milk

and milk fat yield in each progeny group during the study, except for milk yield of registered Holstein sire progeny. The results were not compared with any other method.

VanVleck and Henderson (60) published annual estimates of the genetic difference between the progeny of artificial insemination (AI) and natural service (NS) sires. First lactation records of 24,995 AI progeny and 32,831 NS progeny were compared by contemporary comparisons within herd-year-season. Artificially sired progeny were superior in genetic differences for each of 9 yr. Trends of genetic differences in the last 7 yr were about .5% of the mean. Using the same data, VanVleck and Henderson (61) estimated the genetic change in NS population by absorbing AI sire effects, then solved AI sire effects corrected for the genetic change in the NS population. This procedure to estimate the genetic trends was adopted according to Robertson and Rendel (54). The model was $Y_{ijkp} = U + h_i + S_j + M_k + E_{ijkp}$, where Y_{ijkp} was the record in i th herd in the k th year - season of freshning of the p th first-lactation cow sired by the j th sire, and U was a population constant. The sire effect (S_j) was fixed and the herd effect (h_i) and year-season of freshning (M_k) were either fixed or random effects. Comparisons were within herd-year-season groups. Annual genetic trends were 20 kg of milk and .8 kg of fat in the NS group compared with 25 kg and 1.2 kg in the AI group.

Three basic estimators suggested by Smith (57) are used in the literature, as described in equations 1, 2 and 3.

$$\hat{G} = 2(b_{P.T.} - b_{P.T/S}) \quad (1)$$

$$\hat{G} = b_{P.T} - b_{P.T/S.D.} \quad (2)$$

$$\hat{G} = -2(b_{(P-\bar{P}).T/S}) \quad (3)$$

where \hat{G} is the estimate of genetic contribution and regression estimates are represented by b . The regression of performance (P) on time of calving (T), $b_{P.T}$ represents the total trend (E+G) while the regression within sires ($b_{P.T/S}$) is only E+1/2G, because sires are held constant and only the dams contribute the genetic progress. The expected value of the regression within sire on time of deviations from the population mean (\bar{P}), $b_{(P-\bar{P}).T/S}$, could be written as -(1/2)G. The regression of performance on time within sire and dam (D), $b_{P.T/S.D}$, contains only the environmental trend because subjects within a subclass have the same parents and are expected to have the same breeding value.

Simulated data were used (16) to test the method of Smith (57) with slight modifications. In this simulation study the genetic and environmental trends calculated from the parameters were 61.2 and -1.9 kg per year, respectively. When trends were estimated by pooling the regressions within sires by the inverse of the variance of each regression, the estimated genetic and environmental trends were 67.7 and -8.4 kg of production per year, respectively. This method appears to provide reasonably accurate estimates of the trends. Effect of age and culling of dams was an important consideration to obtain accurate estimates of the trends. The term Δc was estimated in simulation which is defined as the bias due to culling dams over time and

calculated as $b_{P.T} - b_{D.P.T./S}$, where $b_{P.T}$ is the regression of performance on time and $b_{D.P.T./S}$ is the regression of dam's production on time within sire. Since dam contributes one-half of the genotype of their offspring, therefore $\Delta c/2$ was subtracted from the regression of daughter's production on time, pooled within sires, to give an unbiased estimate of the genetic trend.

According to Powell and Freeman (52), the term Δc is a phenotypic trend and should be regressed by heritability. Further, it should be added rather than subtracted. They compared five estimators of intra-herd genetic trend in 13,615 Holstein first lactations from 220 progeny test herds. The method which estimated the genetic trend as minus twice the regression within sire-herd subclass of deviated production on time of freshening described in equation 3 was preferred over other estimators because of less bias involved in this method. They also reported that methods involving deviated records substantially overestimated genetic trend if the mean from which the records are deviated excludes the sire's progeny. The genetic progress in milk production by Acharya and Lush (1) estimated as $-2b_{(S-P)T}$ (Twice the pooled intrasire regressions of the sire's progeny on time, the records being deviated from contemporary average) was 10 kg or 1.5% of the average first lactation yield per year, which is lower as compared to expected progress from direct selection per year. Weighted regression analysis of year constants from least squares was used with sires included or omitted from the model which estimated annual phenotypic and genetic trends in data collected at the Florida experimental station (50,63).

A knowledge of environmental and genetic trends is necessary (31) for the comparison of AI sires when differences exist among the sires in average freshening dates of daughters. Ideally, a method of sire proving should eliminate differences among estimates of sires' breeding values attributable to environmental trends and should retain those differences caused by genetic trends in sire breeding value. The ranking of 38 sires used in New York from 1951 to 1959 was altered (62) only slightly by adjustment of the sire proofs for effects of genetic trends. Miller *et al.* (47) estimated sire merit by averaging all direct and indirect comparisons among sires. Each comparison was weighted by the inverse of the variance. This procedure considered the sire of each herd mate and was free from bias due to genetic trend. These unbiased estimates of sire merit were used to obtain an average breeding value of the sires of cows in each of 21 year seasons. Twice the regression of these averages on time produced estimates of genetic trend of 48 kg of milk for daughters of proven bulls and 18 kg for daughters of sires being sampled.

Burnside and Legates (7) compared two methods to estimate genetic trends in the data comprised of one-third paternal half-sister families and one-seventh of full-sister families. Full sisters were analyzed to obtain least square constants for years adjusted for sire's and dam's effects and corrected for selection. Weighted regression of these constants on years indicated the environmental trend in the population and comparisons with the environmental and genetic trend (45 ± 16 kg for milk and $.018 \pm .003$ for fat percent). A second estimate of annual genetic trends (55 ± 26 kg for

milk and $.016 \pm .005$ for fat percent) was obtained by comparing the overall trend with one-half the genetic plus environmental trend estimated from records of paternal half-sisters adjusted for sire effects. There was a close agreement in results of the two methods.

Records from DHIA from 1956 to 1962 were used to determine the effects of trends on New York State sire evaluation procedures. The total intraherd trend was estimated to be 176 ± 8 kg of milk and $6.4 \pm .3$ kg of milk fat per year (31). Intraherd environmental and genetic trends indicated an environmental trend of 128 ± 17 kg of milk and $4.9 \pm .7$ kg of milk fat per year and a genetic trend of 47 ± 17 kg of milk and $1.5 \pm .6$ kg of milk fat per year. The authors concluded that modifying the New York sire proving procedures to account for effects of genetic trends would not alter significantly estimates of a majority of sire breeding values. However, the estimated breeding values of certain of the sires might be altered enough to make such modifications worthwhile.

Body Size in Relation to Milk and Milk Fat Production

Body weight and wither height, which are measures of skeletal size, have been in use by various judges as indicators of milk secreting ability of the cow for a long time (25).

An ideal cow which is known for higher milk and milk fat production should be of good wedge shaped and better than average weight for her breed and age. (Gowen, 27)

For a clear concept of body size, normal growth of dairy cattle has been studied in detail (15,43). In most of the studies results have been reported (3,8,23,24,26,34) which show a positive association of body size with milk and milk fat production. All body measurements

under study (26) showed a linear relationship with 7-day milk production in Jersey cows, and the most important element in predicting the milk yield was the body weight of the animal. The average body weight of the animal in a herd might be a useful tool in evaluating the environmental differences between herds (38). There is a general agreement that milk yield increases as body weight increases, but controversy regarding the nature and degree of relationship exists. There are some papers (28,29) which indicate that body size on the whole is an inferior means of predicting future milk production, contrary to the previous reports. In addition, there was a negative relationship of live weight at 180 days after freshning with first lactation milk production (35) when age at freshning and freshning weight were held constant. From these results, body size at freshning and weight loss during lactation are equally as important as actual weight in determining milk production. Differences in results may be because the body measurements were at different ages which gave different results when correlated at different stages of lactation. For example, Brum and Ludwick (6) found a positive phenotypic correlation (.09 to .14) of body weight, wither height, chest depth, and body length at 12 mo or older with milk production in first lactation in Holstein cows. At the same time the same data gave negative association ranging from -.03 to -.15 between precalving body measurements and milk production in first lactation. Similarly, precalving body measurements gave no significant correlations with average milk fat production of life time (56), but gain in chest depth from 10 to 12 mo of age had significant intrabreed correlation of .31 with fiducial limit of .16 and .46 with average lifetime production of

milk fat. Davis and Willet (11) found no significant correlation indicated by gain in weight, increase in height at withers, and by increase in chest girth from birth to 2 yr with milk and milk fat production for the first lactation and for the lifetime average of lactations. Since these results were from 76 Holstein females, the possibility is nonsignificance of results may be due to small sample size. However, a similar study (36) supports the above findings that it is unlikely the rate of body weight gain from birth to 6 mo of age can be used to predict subsequent milk yield of dairy cows.

Analysis of data within sire collected at Iowa State University Holstein herd from 1932 to 1958 (20) gave phenotypic and genetic correlations of wither height, paunch girth, heart girth, and ratio of the latter two with mature equivalent milk production in the range of .5 or larger. Harville and Henderson (30) reported a small intra-herd phenotypic correlation of (ME) milk production and body weight ranged from .08 to .17 in Holstein, Guernsey, and Jersey breeds. In addition to milk production, most probable producing ability has been used which gave a positive correlation of .34 with heart girth measured between 10 and 12 mo of age (51). It was indicated that knowledge of growth at this age may be of help in evaluating future butter fat production of the individual.

Cows continue to grow from their first lactation up to the age of 5 yr. Age and weight during this period are correlated. Milk production adjusted for age indirectly removes some of the correlations of body size with milk production because of positive correlation between age and body size (59). To separate the combined effects of age and weight, the effect of one of these factors should be

determined independently. The expected change in milk production associated with a change in weight at first calving is dependent on the size at which a change in weight occurs, and production reaches a maximum at weight 136.4 to 181.8 kg above the breed average for the age (46).

Using multiple regression analysis to determine the independent influence of age and weight on milk produced in 180 days of first lactation in Holstein cows, Clark and Touchberry (8) reported an increase of 60.9 kg of milk and 3.5 kg of fat for each 45.5 kg increase in body weight over a constant age and for a constant weight; increase of 1 mo of age was accompanied by an increase of 20.9 kg of milk and .55 kg of fat. Probably similar variation in milk production is associated with body weight as with age. However, other workers (5,26,38,46) considered body weight as an important source of variation in production records than age. Linear and quadratic effects of age and weight within cow (19) showed that age is more effective than weight in accounting for variance in actual milk production. Through partial linear regression coefficients the direct effect of age was responsible for 41.4% of the variance within sire in weight although the actual relationship was curvilinear (48). Also, effects of age were the most important source of variation in body weights and changes in weight.

Knowing the role of genotype in the relationship of body size with milk and milk fat production is essential to assess the genetic progress made in the herd due to selection. Baily and Broster (3) found no genetic correlation between the live weights at calving with milk production in 47 daughter-dam pairs. They concluded that a herd

breeding policy which selected animals according to their body size would fail, except by chance, to improve the production of the herd. Although the conclusion of this study was based on only 47 daughter-dam pairs, similar types of results also have been reported by other workers (59,64). A negative genetic correlation between milk production and body size (4,45) suggested that selection for milk yield would increase skeletal size but decrease fleshing. Also, live weight of young heifers up to 2 yr of age has little value for prediction of future milk production (37).

Genetic correlations from paternal half-sister data in Holstein cows tended to be higher for measurements taken earlier than first lactation, and chest depth was most strongly genetically related to milk production (6). Genetic correlations between precalving body weight or chest depth with milk production ranged from $.34 \pm .27$ to $.90 \pm .34$, and heritabilities for body weight, wither height, chest depth, and body length at 3, 6, and 12 mo of age ranged from .10 to .52. Genetic correlations of wither height and body length with milk production were smaller and frequently negative. From these results precalving body measurements along with milk production in selection index would result in 25% greater genetic progress in milk production of first lactation as compared with selection on yield of first lactation alone. Selection for milk production might reduce skeletal size because of negative association with wither height and body length, which is opposite to results of others (4,45). There was a positive genetic correlation of body length, chest depth, heart girth, paunch girth, body weight, and wither height measured at 3, 6, 12, and 18 mo of age and at 3 mo postpartum,

but none was significantly different from zero except the genetic correlation ($.43 \pm .19$) between 12-mo body weight and milk production in first lactation (64).

Brum and Ludwick (6) gave a wide range of genetic correlation ($-.45$ to $.31$) from regression of daughter on dam of precalving body measurements and milk production in first lactation, and heritabilities ranged from $.06$ to $.61$ for the body measurements at 3, 6, and 12 mo of age. Heritabilities of measures at 2 yr of age from daughter-dam regression for wither height, chest depth, paunch girth, heart girth, and milk production (ME) were $.84$, $.74$, $.44$, $.54$, and $.20$ in the Iowa State University Holstein herd (20). Clark and Touchberry (8) reported heritabilities from 385 daughter-dam pairs for body weight, milk in first lactation, and fat production were $.29$, $.44$, and $.00$, and were $.19$, $.43$, and $.41$ for all lactations one through fourth lactation combined. Genetic correlations ranged near zero in first lactation, $-.53$ in second lactation, and the genetic correlation between body weight and milk and body weight and fat production were $-.12$ and $-.23$ when the first four lactations were combined. These negative genetic correlations indicate that less progress would be expected in selecting for both increased body weight and milk production. From these studies body measurements at later age are more heritable than at an early age. Also heritabilities from daughter-dam regression are expected to be higher as compared with estimates from paternal half-sib data because of maternal influences of the dam.

Different breeds of cattle give different correlated response to selection. There was an indication of genetic trend during the course of selection towards a presumably optimum body weight and

with height with Holstein decreasing and Ayrshire increasing (34). Since the correlated response is a function of heritability and genetic correlations of traits, the differences in results can be explained by differences in heritabilities in different breeds. There was a wide range of intraherd heritability estimates (30) based upon 22,767 Holsteins, 2,174 Guernseys, and 1,036 Jerseys for first lactation DHIA (ME) records which were .37, .25, and .00, and heritabilities adjusted for age or taped body weights were .16, .40, and .24 for Holstein, Guernsey, and Jersey cattle. There were also positive genetic correlations of .45 and .40 between ME milk records and body weights adjusted for age for Holstein and Guernsey breeds. Because of these positive genetic correlations between body weight and milk production, body weight could be used to select for milk production when no other information is in hand.

SOURCE AND DESCRIPTION OF DATA

Data pertain to the Michigan State University Holstein herd from 1967 through 1973.

Design of Experiment

Selection of Bulls

The plan was to select the two highest ranking and the two lowest ranking bulls for milk production from the class of young bulls on test whose daughters were distributed through AI and whose summaries first became available in that year. First available tests were to include at least 35 daughters. In the beginning of the experiment, selection of highest and lowest ranking bulls was not very effective because of availability of few bulls until Select Sires started testing young bulls in Michigan. Also, the goal of having a minimum of 35 daughters on the first test for selection of bulls was seldom achieved. Each bull was used for two years and two new bulls were introduced every year in each line; thus, except for the first year there were four bulls in each year for best and worst line.

Every year these bulls were randomly arranged in the block of four. The assignment of matings to individual bulls in the block was arranged according to the expected date of calving, such that the cow freshening first is mated with the first bull in the block and so on in each line. Mating of sire with its daughter was prohibited

to avoid inbreeding, and in such cases mates of adjacent cows were switched. The schematic diagram of use of bulls in each line is presented as follows.

Lines	Year 1	Year 2	Year 3	...	Year N
Best	B_{11}	B_{12}	B_{23}	...	$B_{(i-1)N}$
		B_{22}	B_{33}	...	$B_{(i)N}$
Worst	W_{11}	W_{12}	W_{23}	...	$W_{(i-1)N}$
		W_{22}	W_{33}	...	$W_{(i)N}$
Control		C_{12}	C_{13}	...	$C_{(1)N}$

B_{ij} = the i th class of best bulls used in the j th year.

W_{ij} = the i th class of worst bulls used in the j th year.

$C_{(1)N}$ = there was only one class of 13 bulls used over all the years.

There were 13 tested bulls active at M.A.B.C. (Michigan Animal Breeders Cooperative) in early 1967 when the experiment was started. These bulls were control bulls. Every year these bulls were arranged randomly within blocks of 13, and matings were assigned to the best and worst cows whose first calf was a female. This procedure continued until there were sufficient females in the control line produced as maternal sisters of daughters of best and worst bulls to provide a control line; then the system was switched to continuous mating of control females to control bulls. The semen of 80 vials was collected from each bull to be used for 10 yr.

Division of Foundation Females

The herd was divided at the start of the project into best and worst lines from the foundation cows. All the cows in the herd were arranged according to their age and assigned to each line alternately by date of birth. Thus, each line had equal numbers of young and old cows. The mating was done with bulls of like group. All the male calves born in each line were culled, and cows having female calves from selected bulls from both the lines were mated with control bulls. Therefore, the control line was formed by the maternal sisters of daughters of best and worst bulls. The mating for first calving was to be at the earlier of heat nearest 15 mo of age or 120 cm wither height. The cows were to be bred after the first calving at first heat after 50 days following calving. When space was needed for heifers, cows with three lactations sired by control bulls were to be removed first, and then oldest females were to be removed keeping nearly equal numbers of cows in best and worst lines. Hope was expressed to get all females into milk before culling.

Information on each animal consisted of its date of birth, dam number, sire number, line, date of body measurement, body weight, wither height, age in days, date of freshening, parity, milk and milk fat records. In my study only the first lactation milk and fat records adjusted to 2X, 305 days mature equivalent were analyzed. The records short of 305 days of cows removed from the herd with at least one test period were extended to 2X, 305 days mature equivalent. The data for body weights and wither heights were recorded on the first test day after freshening in lactating cows, and measurements in young heifers were in April and May before they were let out for

grazing and again in October and November before the start of winter season. Therefore, body measurements varied because of measurements taken at different ages. Body weights were measured in pounds on the scale. Wither height was the vertical distance in centimeters from the highest point over the withers to the ground with the heifer standing squarely on a level surface.

METHODS

There were 179 first lactation records of daughters of best, worst, and control lines adjusted to 2X, 305 days mature equivalent for analysis. The following full model describes each record.

$$\begin{aligned}
 Y_{ijklmn} = & U + y_i + L_j + (yL)_{ij} + B_{(j)k} + (By)_{i(j)k} + D_l + \\
 & (LD)_{jl} + (BD)_{(j)kl} + (yD)_{il} + (LyD)_{ijl} + (ByD)_{i(j)kl} \\
 & + S_{(jk)m} + (yS)_{i(jk)m} + (DS)_{l(jk)m} + (yDS)_{il(jk)m} \\
 & + E_{(ijklm)n}
 \end{aligned}$$

where Y_{ijklmn} is the first lactation milk record of nth cow belonging to the mth sire within kth bull group of jth line made in ith year with lth code of culling of its dam;

U = the constant common to all observations;

y_i = the mean effect common to all cows in ith year;

L_j = the mean effect common to all cows in the jth line;

$(yL)_{ij}$ = the mean effect common to the cows in ijth year line subclass;

$B_{(j)k}$ = the mean effect common to cows of kth bull group in jth line;

$(By)_{i(j)k}$ = the mean effect common to cows of kth bull group of jth line in ith year;

- $D_{\underline{l}}$ = the mean effect common to the cows of \underline{l} th code of culling of their dam (the dam kept or culled from the herd at the time of measurement on its daughter);
- $(LD)_{j\underline{l}}$ = the mean effect common to the cows of \underline{j} th line and code of culling of dam subclass;
- $(BD)_{(j)\underline{k}\underline{l}}$ = the mean effect common to the daughters of \underline{k} th bull group with \underline{l} th code of culling of dam in \underline{j} th line;
- $(yD)_{i\underline{l}}$ = the mean effect common to the \underline{i} th subclass;
- $(LyD)_{ij\underline{l}}$ = the mean effect common to the \underline{ij} th subclass;
- $(ByD)_{i(j)\underline{k}\underline{l}}$ = the mean effect in the daughters of \underline{k} th bull group in \underline{j} th line of \underline{i} th year with \underline{l} th code of culling of dam;
- $S_{(jk)\underline{m}}$ = the mean effect common to the daughters of \underline{m} th sire in \underline{jk} th bull group and line subclass;
- $(yS)_{i(jk)\underline{m}}$ = the mean effect common to the daughters of \underline{m} th sire in \underline{jk} th line and bull group subclass;
- $(DS)_{1(jk)\underline{m}}$ = the mean effect common to the daughters of \underline{m} th sire with \underline{l} th code of culling of its dams in \underline{jk} th line and bull group subclass;
- $(yDS)_{i1(jk)\underline{m}}$ = the mean effect common to the daughters of \underline{m} th sire in \underline{jk} th line and bull group subclass belonging to \underline{l} th code of culling of dam in \underline{i} th year;
- and $E_{(ijklm)\underline{n}}$ = the random error associated with each observation, which is normally and independently distributed with zero mean and σ_e^2 variance.

Due to vastness of computation difficulties and to many two-way and three-way interactions in the model probably being unimportant to the objectives and design of the experiment, from the model two

final models were proposed to separate environmental and genetic trends.

Model 1:

$$Y_{ijklm} = U + y_i + L_j + (yL)_{ij} + B_{(ij)k} + D_l + (LD)_{jl} + E_{(ijkl)m}$$

In this model bull groups (B) were nested within years since their daughters were not distributed over all the years. Also, daughters of bull groups within years compare contemporarily to each other, thus nullifying the effect of years in bull groups. In this model Y_{ijklm} is the record of m th cow with l th code of culling of its dam belonging to the k th bull group in j th line and i th year;

U = a constant common to all records;

y_i = the mean effect common to all cows in i th year;

L_j = the mean effect common to all cows in j th line;

$(yL)_{ij}$ = the mean effect common to the cows in ij th year and line subclass;

$B_{(ij)k}$ = the mean effect common to the daughters of k th bull group in i th year and j th line;

D_l = the mean effect common to the cows with l th code of culling of its dam;

$(LD)_{jl}$ = the mean effect common to the cows in jl th subclass;

and $E_{(ijkl)m}$ = the random error associated with each measurement and distributed independently with mean zero and variance σ_e^2 .

All factors in the model were fixed except residual error since interest centers on genetic trends. The machine method of fitting constants (Harvey, 1960) was used for each effect in the model.

Assumptions Underlying the Model

Eisenhart (1947) has described the necessary conditions underlying the analysis of variance, and Cochran (1947) has discussed some of the consequences when these conditions are not fulfilled. Effects of different factors in the model are additive and errors are normally and independently distributed with a common variance and zero mean are necessary if tests of significance are precise.

Method of Estimation of Constants

To minimize the sum of squares of deviations of the observed values from the fitted plane in estimation of parameters, it is necessary to take the partial derivatives of

$$\sum e_{ijklmn}^2 = \sum (Y_{ijklmn} - U - y_i - L_j - (yL)_{ij} - B_{(ij)k} - D_l - (LD)_{jl})^2$$

with respect to each of the unknown parameters and then to set the resulting derivatives equal to zero. These give rise to a series of simultaneous equations which can be arranged in the form of a matrix ($\underline{X}'\underline{X}$). Since this matrix is not a matrix of full rank, its inverse does not exist. For a unique solution of the subsequent equations, the following restrictions were imposed.

$$\sum_i y_i = \sum_j L_j = \sum_i (yL)_{ij} = \sum_j (yL)_{ij} = \sum_k B_{(ij)k} = \sum_l D_l = \sum_l (LD)_{jl} = \sum_j (LD)_{jl} = 0$$

The reduced matrix is transposed (\underline{X}') and the transposed \underline{X}' matrix multiplied with \underline{X} matrix to get $\underline{X}'\underline{X}$ matrix. Normal equations can be written in this form:

$$\underline{X}'\underline{X}\underline{b} = \underline{X}'\underline{y}$$

where \underline{b} is a column vector of unknown parameters and $\underline{X}'\underline{y}$ is the element of the right hand side containing sums corresponding to the elements in \underline{b} . Obtain the inverse of $X'X$ matrix and multiply with the right hand side to provide a solution of \underline{b} .

$$\underline{b} = (\underline{X}'\underline{X})^{-1} \underline{X}'\underline{y}$$

Now obtain the reduction sum of squares due to fitting the whole model; multiply each constant so obtained with its right hand side and sum these products. Similarly, to calculate the sum of squares for each effect, a reduced model is fitted and calculate the regression sum of squares from the reduced model and the difference from the regression sum of squares due to fitting the whole model will give sum of squares for that effect. The sum of squares for each effect is represented as follows:

Regression sum of squares due to fitting the whole model =

$$U Y_{....} + y_i Y_{i...} + L_j Y_{.j..} + (yL)_{ij} Y_{ij..} +$$

$$B_{(ij)k} Y_{ijk.} + D_l Y_{...l} + (LD)_{jl} Y_{.j.l} = A$$

Reduction due to years:

$$R(U, y_i, L_j, B_{(ij)k}, D_l, (LD)_{jl}) - R(U, L_j, B_{(ij)k}, D_l, (LD)_{jl})$$

Reduction due to lines:

$$R(U, y_i, L_j, B_{(ij)k}, D_l, (LD)_{jl}) - R(U, y_i, (yL)_{ij}, B_{(ij)k}, D_l, (LD)_{jl})$$

Reduction due to year x line:

$$A - R(U, y_i, L_j, B_{(ij)k}, D_1, (LD)_{j1})$$

Reduction due to dam:

$$R(U, y_i, L_j, (yL)_{ij}, B_{(ij)k}, D_1) - R(U, y_i, L_j, (yL)_{ij}, B_{(ij)k})$$

Reduction due to line x dam:

$$A - R(U, y_i, L_j, (yL)_{ij}, B_{(ij)k}, D_1)$$

Reduction due to bull groups:

$$A - R(U, y_i, L_j, (yL)_{ij}, D_1, (LD)_{j1})$$

The year constants (\hat{y}_i) estimated from this model will reflect environmental changes associated with different years if each cell had an equal number of observations. Since the data are unbalanced due to unequal numbers of observations, the constants for years will also include other effects. The constants for bull groups ($\hat{B}_{(ij)k}$) will indicate the genetic change from one bull group to another in each line. Since the daughters of each bull group are distributed over some of the years, a weighted constant for each bull group will be estimated over the years to make comparisons among bull groups within each line. The weighted constant will be calculated by multiplying the inverse of variance with each bull group constant over all the years, summing the products, then dividing the sum of the products with the sum of the inverse of the variances.

To estimate the effect of each sire in milk and milk fat data, a separate model was used.

Model 2:

$$Y_{ijkl} = U + L_i + B_{(i)j} + S_{(ij)k} + E_{ijkl}$$

where Y_{ijkl} is the l th record of k th sire belonging to j th bull group in i th line. The least square analysis was used to estimate the constants for each sire in ij th line and bull group subclass. The detailed procedure of estimating the constants and conditions are similar to model 1 already discussed.

The data for body measurements had variation because of the measurements taken at different ages. The adjustment for effects of age is important to have a precise estimate of genetic effects. There were 1,142 records of body weight and wither height up to the age of 3 yr. Two of the possible ways of adjusting the body weights and wither heights for the effects of age were:

1. By fitting regression of body size (body weight and wither height) on age to the whole data and making adjustments towards the mean age.

2. Another possible way is to make separate adjustments for each age group. The main difficulty which arises using separate adjustments is that the comparison of means of different age groups becomes impossible. The adjustment of data by fitting one regression line was, therefore, preferred because of the following reasons:

- A. By fitting one regression line to the whole data there will be only one variable instead of different variables for adjustments for each age group separately.

- B. When data are adjusted towards one mean, the comparisons among age groups are possible.

Different regression equations were fitted to find the best fitted regression of body weight and wither height on age. A three degree polynomial curve was the fitted regression on age.

$$\hat{Y} = \hat{b}_0 + \hat{b}_1 x_1 + \hat{b}_2 x_1^2 + \hat{b}_3 x_1^3$$

where \hat{b}_0 is constant and \hat{b}_1 , \hat{b}_2 , and \hat{b}_3 are the estimated partial regression coefficients, and x_1 , x_1^2 , and x_1^3 are the age polynomials.

The equation for the adjusted body weight or wither height can be written:

$$(\text{Adjusted})Y = Y_{(\text{observed})} - \sum b_i (x_i - \bar{x}_i) \text{ or}$$

$$Y(\text{Adjusted}) = Y_{(\text{observed})} - [\hat{b}_1 (x_1 - \bar{x}_1) + \hat{b}_2 (x_1^2 - \bar{x}_1^2) + \hat{b}_3 (x_1^3 - \bar{x}_1^3)]$$

After the data were adjusted for effects of age the model 1 described earlier was used to estimate the effects of each year and bull group for the whole data and under different age groups. The estimates for the sire effects were for body weight and wither height from model 2 as for milk and milk fat data. The least square means and standard errors for different effects were calculated as described by Harvey (1960). The comparison among sires within bull groups and lines will reflect the genetic response on body measurements in the daughters of sires selected for milk production.

Phenotypic and Genetic Correlations and Trends

Average phenotypic effect per year was calculated within line by adding the following constants which can be written in the form of an equation:

$$\hat{P} = \hat{Y}_i + \hat{L}_j + (\hat{Y}L)_{ij} + \hat{B}_{(ij)k} + \hat{S}_{(jk)l}$$

where \hat{P} is the estimated average phenotypic effect;

\hat{Y}_i is the year constant reflecting environmental differences among years;

\hat{L}_j is the line constant representing the average genetic differences between the lines;

$\hat{Y}L_{(ij)}$ is the constant for year x line interaction;

$\hat{B}_{(ij)k}$ is the average genetic contribution of bull groups, since each bull group had constants for each year because of distribution of their daughters over years. Also, the number of daughters per year were not equal. Therefore, one weighted constant for the bull groups was calculated by the inverse of the variance of bull group constants in each year. The weighted constant of bull groups was further adjusted for the unequal number of daughters per year; and

$\hat{S}_{(jk)l}$ is the sire constant within bull group and line estimated by model 2. This estimate gave genetic differences among sires peculiar to a particular bull group and line subclass. The sire constants also were adjusted for the unequal number of daughters.

The average genetic effect per year was calculated within line by adding the line constant, sire constant and average bull group effect. It can be written in the form:

$$\hat{G} = \hat{L}_j + \hat{B}_{(ij)k} + \hat{S}_{(jk)l}$$

where \hat{G} is the average estimated genotypic effect per year in each

line. The line constant (\hat{L}_j), bull group effect ($\hat{B}_{(ij)k}$) and sire constant ($\hat{S}_{(jk)l}$) have already been described.

Phenotypic and Genetic Correlations

The phenotypic and genetic correlations were simple product moment correlations among traits from average phenotypic and genetic effects per year. The standard error for the correlations is given:

$$SE = [1 - (r_{12})^2] / (n-2)$$

where r_{12} is the correlation of trait 1 and trait 2 and n is the number of observations on which this correlation is based.

RESULTS AND DISCUSSION

The least square means for 179 records of first lactation milk and milk fat are in Table 1. The best line produced 1082 kg more milk and 13.6 kg more milk fat per lactation (ME) than the worst line. Controls exceeded best and worst lines in milk and milk fat. This may be because of random chance due to few cows in the control line. Secondly, the control bulls were selected for milk production and were being used in the herd at the time this project was started. The least square means were close to the arithmetic averages in Table 2. Since both the means are within a range of one standard deviation, the differences can be ascertained by looking at the simple averages in this design.

Effect of Management and Selection of Bull Group on Milk and Milk Fat

The least square analysis of fitting constants was run to test the significance of each factor according to model 1. The results are shown in Table 3. There was no significant difference between years for milk yield whereas in milk fat the differences between years were significant. The year constants (\hat{y}_i) estimated from model 1 (Table 4) reflect mostly the environmental changes associated with different years. On the whole, year 1971 provided the best environment for milk and milk fat production with a tendency to decline in later years. In 1972 a new farm manager was appointed, and feeding

Table 1. Least square means (M)^a and standard errors (SE) for lines, years, and year x line interaction for milk and milk fat adjusted for different factors

Lines	Years				
	1969	1970	1971	1972	1973
MILK					
<u>Line 1 (best)</u>					
M 7661	7554	7935	7436	7710	7838
SE 826 (86) ^b	928	893	875	1087	998
<u>Line 2 (worst)</u>					
M 6579	7039	5205	6864	6927	7027
SE 826 (69)	1431	1196	882	1094	904
<u>Line 3 (control)</u>					
M 7899	8075	8275	8854	7564	6894
SE 846 (24)	1038	1377	1116	956	1068
M	7409	6991	7571	7253	7106
SE	974 (15)	910 (39)	842 (57)	867 (26)	861 (42)
MILK FAT					
<u>Line 1 (best)</u>					
M 247	266	279	260	240	252
SE 41 (86)	46	45	44	54	50
<u>Line 2 (worst)</u>					
M 234	273	195	257	248	256
SE 41 (69)	71	60	44	55	45
<u>Line 3 (control)</u>					
M 273	302	299	319	260	244
SE 42 (24)	52	69	56	48	53
M	274	251	272	243	245
SE	49 (15)	45 (39)	42 (57)	43 (26)	43 (42)

^aUnits in kilograms.

^bNo. of records in parentheses.

Table 2. Arithmetic averages (M)^a and standard deviations (SD) for lines, years, and year x line interaction for first lactation records adjusted to mature equivalent

Lines	Years				
	1969	1970	1971	1972	1973
MILK					
<u>Line 1 (best)</u>					
M 7507	7520	7644	7372	7273	7635
SD 1425 (86) ^b	1737	1032	1536	2202	1110
<u>Line 2 (worst)</u>					
M 6824	7039	6547	6742	7167	6983
SD 1158 (69)	1360	1294	1231	1629	823
<u>Line 3 (control)</u>					
M 7749	--	8372	8834	7591	6927
SD 1214 (24)	--	1030	1187	1120	858
M	7456	7288	7213	7379	7223
SD	1617(15)	1248(39)	1476(57)	1591(26)	981(42)
MILK FAT					
<u>Line 1 (best)</u>					
M 260	265	270	259	232	253
SD 46 (86)	47	43	48	52	41
<u>Line 2 (worst)</u>					
M 249	273	236	248	263	253
SD 46 (69)	21	46	47	71	34
<u>Line 3 (control)</u>					
M 274	--	305	318	262	246
SD 40 (24)	--	15	10	29	23
M	266	260	259	253	252
SD	44(15)	47(39)	49(57)	50(26)	35(42)

^aUnits in kilograms.

^bNo. of records in parentheses.

Table 3. Analysis of variance to test the null hypothesis of years, lines, year by line, dams, line by dam, and bull groups for milk and milk fat

Source	DF	Mean squares	F
MILK			
Years	4	5008835	<1
Lines	2	57899993	7.5**
Y X L	7	17085747	2.2*
Dam	1	1161789	<1
L X D	2	28478156	3.7*
B group/ _{Y/L}	13	11772367	1.5
Error	149	7708519	
Total	178		$R^2 = .2623$ or 26%
MILK FAT			
Years	4	19449	2.4*
Lines	2	36167	4.5**
Y X L	7	22734	2.8**
Dam	1	46	<1
L X D	2	26981	3.4*
B group/ _{Y/L}	13	22882	2.9**
Error	149	9258	
Total			$R^2 = .3195$ or 32%

* $P < .05$.

** $P < .01$.

Table 4. Least square estimates of years, lines, year x line interaction, bull groups, dams, and line x dam interaction in kilograms for milk and milk fat

	Milk	Milk Fat		Milk	Milk Fat
μ	7413.6	263.8	G2Y73L2	+514	+16
Y69	+155	+16	G3Y73L2	-229	+2
Y70	-275	-5	G4Y73L2	-285	-19
Y71	+305	+15	Y69L1	-283	-10
Y72	-12	-13	Y69L2	+283	+10
Y73	-159	-12	Y70L1	+515	+25
Line 1 (best)	+281	-3	Y70L2	-1132	-44
Line 2 (worst)	-800	-17	Y70L3	+617	-19
Line 3 (control)	+519	+21	Y71L1	-563	-14
G1Y70L2	+1532	+46	Y71L2	-52	-4
G2Y70L2	-1532	-46	Y71L3	+616	+19
G1Y71L1	+53	+13	Y72L1	+28	-5
G2Y71L1	-53	-13	Y72L2	+327	+16
G1Y71L2	-498	-32	Y72L3	-355	-10
G2Y71L2	+498	+32	Y73L1	+303	+5
G1Y72L1	+761	+19	Y73L2	+574	+22
G2Y72L1	-823	-11	Y73L3	-878	-28
G3Y72L1	-1405	-40	Dam 1 (live)	+48	+3
G4Y72L1	+1467	+32	Dam 2 (dead)	-48	-3
G1Y72L2	-535	-42	L1D1	+396	+12
G2Y72L2	+1092	+61	L1D0	-396	-12
G3Y72L2	-557	-18	L2D1	-251	-6
G1Y73L1	-531	-35	L2D0	+251	+6
G2Y73L1	-314	-9	L3D1	-145	-6
G3Y73L1	-46	+7	L3D0	+145	+6
G4Y73L1	+892	+37			

G indicates bull group.

of concentrates to the cows also was modified, which might be responsible for this decline. Selection of dams had no effect on milk and milk fat, indicating that the cows were not culled because of milk production. The interaction of lines by selection of dams was significant in both the traits. There was a significant difference between the lines for milk and milk fat production. The best line was expected to produce more milk as compared to worst line since the bulls used in the lines were selected on milk production of their daughters. The best line also produced more milk fat as a correlated response to selection for milk yield than the worst line and the differences between lines were highly significant.

The constants for bull groups ($\hat{B}_{(ij)k}$) within year and line subclass indicate the genetic differences from one bull group to another. There was a separate bull group constant for each year within line, because the daughters of each bull group were distributed over many years. A single constant for each bull group was weighted within line by the inverse of the variance of bull group constant in each year. The weighted constants for each bull group within line are plotted for milk and milk fat in Figure 1. There was only one group of control bulls; therefore, a straight line for controls indicates the base for comparisons with other lines. Differences between classes of bull groups within and between lines reflect the selection of bull groups. In the beginning there were few bulls available from which to select best and worst bulls. The differences between the first class of bull groups of best and worst line are large. The top bulls selected in this class happened to be the best as compared to the bulls in worst line. In the second class

Figure 1. Weighted constants of bull groups over years within each line for milk and milk fat.

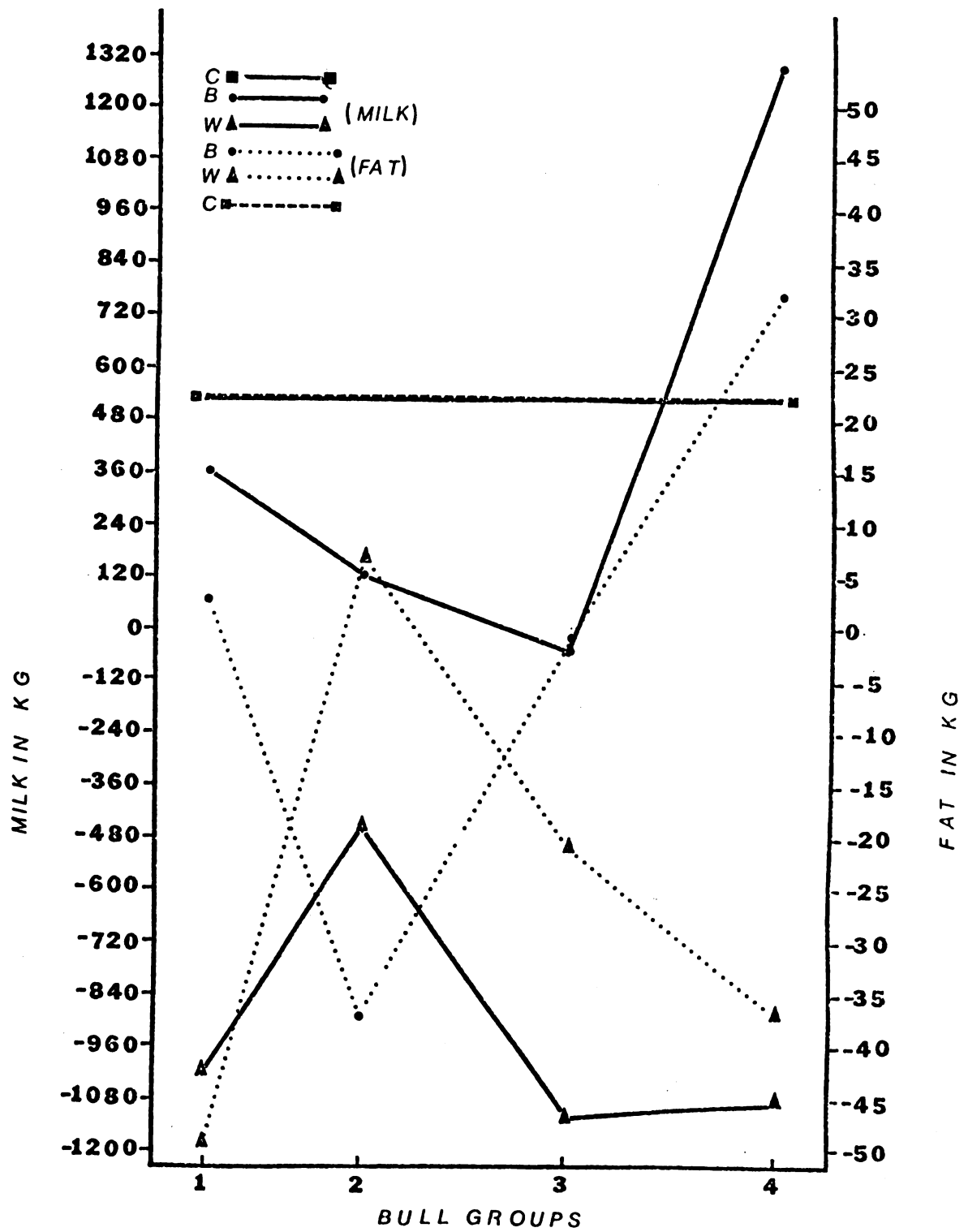


Figure 1

of bull groups the best bull selected turned out to be worst bull and vice versa. This resulted in decline in the best line. There was further decline in the third class of bull group in best line. For this class of bull groups there were six bulls available and one bull died at the age of 1-1/2 years. No semen from this bull was available. Therefore, there were only five bulls left out of which four bulls had to be selected as two best bulls and two worst bulls. Moreover, the differences in their daughters' milk production was not great. The fourth class of bull group happened to be really top bulls, which pushed the best line upward. On the whole, two separate lines were created from one herd by using the selected bulls. Since the selection of bull groups was only on milk production, a graph for milk fat shows a correlated response to milk yield.

Comparison in Ranking of Sires in Milk Production

Table 5 gives the analysis of variance to test the differences between sires within bull groups and line subclass for milk and milk fat by model 2. This model was decided on because it was not possible to take the inverse of a large matrix on the computer for one model only. Sires within bull groups and lines were not significantly different for milk, but the differences for milk fat were highly significant. It is possible that the best sires which were chosen on their daughters' milk production may not necessarily be best for milk fat or vice versa. The sires were ranked to compare the efficiency of selection with the initial basis of selection and with the latest predicted differences published by USDA (United States Department of Agriculture) Sire Summary, November, 1974, in Table 6.

Table 5. Analysis of variance to test the null hypothesis of sire effects for milk and milk fat

Source	DF	MS	F
MILK			
Lines	2	42544557	5.5**
Bull groups (G)/ _L	6	5415726	<1
Sires/ _{G/L}	18	12237018	1.6
Sires/ _{G/L₁+L₂}	8	7451572	<1
Sires/ _{G/L₃}	10	11010111	1.4
Error	152	7716456	
Total	178		$R^2 = 25\%$
MILK FAT			
Lines	2	21833	2.6
Bull groups (G)/ _L	6	15485	1.9
Sires/ _{G/L}	18	19129	2.3**
Sires/ _{G/L₁+L₂}	8	17327	2.1*
Sires/ _{G/L₃}	10	16943	2.1*
Error	152	8265	
Total	178		$R^2 = 28\%$

*
P<.05_{L₁} = best line_{L₃} = control line**
P<.001_{L₂} = worst line

Table 6. Ranking of sires on milk production (kg) based upon initial basis of selection, USDA sire summary and MSU data

USDA Sire Summary													
Class of bull groups	Bull no.	Initial basis of selection		Nov. 1974		MSU		Ranks					
		No. of daughters	Milk ^a mean dev.	No. of daughters	Milk P.D.	No. of daughters	Milk ^b mean dev.	Initial			USDA	MSU	
1	B11 ^c	55	+524	2112	+287	31	+676	8	5	2			
	B12	62	+305	516	-109	22	+339	10	9	7			
	W12 ^d	386	-344	4510	-707	17	-1390	13	15	14			
	W11	5	-333	232	+14	16	-1275	12	8	13			
2	B21	65	+836	1067	+564	13	+474	4	4	4			
	B22	28	+492	125	-113	5	-488	9	10	10			
	W21	49	-682	183	-1081	9	-121	16	16	9			
	W22	48	-401	109	-374	7	-49	14	13	8			
3	B31	48	+695	448	+695	6	+646	6	3	3			
	B32	58	+683	96	-131	2	-778	7	11	12			
	W31	61	-585	186	-605	3	-1913	15	14	16			
	W32	58	+44	124	-298	7	-701	11	12	11			

Table 6 (continued)

Class of bull groups	Bull no.	USDA Sire Summary									
		Initial				Nov. 1974				MSU	
		basis of selection		No. of daughters	Milk ^a mean dev.	No. of daughters	Milk P.D.	No. of daughters	Milk ^b mean dev.	Ranks	
		No. of daughters	Milk ^a mean dev.							Initial	USDA MSU
4	B41	24	+2657	671	+1217	3	+425	1	1	5.5	
	B42	15	+1627	56	+740	4	+425	2	2	5.5	
	W41	19	+1306	94	+24	3	+1119	3	7	1	
	W42	90	+807	247	+128	7	-1571	5	6	15	

^aIn initial basis of selection, daughter's average was deviated from breed average in Michigan.

^bIn MSU data, daughter's average was deviated from the herd average.

^c B_{ij} is the j th best bull in i th class.

^d W_{ij} is the j th worst bull in i th class.

Predicted differences calculated by USDA are the most accurate estimate of transmitting ability of the sire because of large numbers of daughters distributed over many herds. Moreover, adjustments are made for the number of daughters, distribution of daughters over herds, environmental correlation, adjustment for herd environment, number of herd mates, and contemporaries and herd genetic average. The correlations of ranks were computed (Table 7) to compare how efficiently sires can be selected in one herd under this design.

Table 7. Rank correlations of sires for milk

	Initial selection	USDA	MSU
USDA	.92	1	.72
MSU	.69	.72	1

The rank correlation between USDA sire summary and MSU data was .72. As the number of daughters per sire increased, the rank correlation also increased (.92) between USDA sire summary and initial basis of selection. From the rank correlations the sires could be ranked more accurately if there had been more daughters per sire.

Phenotypic and Genetic Trends in Milk
and Milk Fat Production

Phenotypic Trends

The average phenotypic effect per year within each line was estimated by combining the year effect, line effect, year by line effect, bull group effect and sire effect. The contribution of selection of dams was not included because of their insignificant effect on milk yield. The estimates for the sire constants were computed using model 2 where years, dams and line by dam interactions were not considered. These effects might have introduced a bias in the estimates of sire effects. The detailed description of calculating the average phenotypic effects is described in the methods section, page 34.

Table 8 gives the average phenotypic effects and Figure 2 gives the phenotypic trends for milk and milk fat. Average phenotypic progress in kilograms per year was 78.6 ± 86.5 , 108.5 ± 280 for milk and -5.5 ± 5.3 , 9.8 ± 11.9 for milk fat in best and worst line from regressing the average phenotypic values on years. The phenotypic trend reflects a combination of genotypic and environmental effect. Since all cows were in one herd under the same management, the environment is assumed to be the same for all the lines. In the control line the same bulls were used over all the years; therefore, no genetic change was expected. The variation in the control line was due to environmental changes from one year to another and sampling. The worst line improved phenotypically more than the best line, which may be due to chance. There was a negative phenotypic trend in best line for milk fat and a positive phenotypic trend in worst line. The

Table 8. Estimates of average phenotypic and genetic effects (kg) in each year for milk and milk fat within each line

Y Years	Phenotypic Effects			Genetic Effects		
	X ₁ Best (L ₁)	X ₂ Worst (L ₂)	X ₃ Control (L ₃)	X ₁ Best (L ₁)	X ₂ Worst (L ₂)	X ₃ Control (L ₃)
MILK (kg)						
69	+237	-581	675	365	-1020	519
70	589	-2391	862	350	-983	
71	85	-576	1441	344	-829	
72	351	-1069	151	335	-701	
73	750	-700	-519	606	-1114	
MILK FAT (kg)						
69	14	-23	38	8	-50	22
70	26	-97	36	7	-46	
71	3	-20	56	3	-31	
72	-20	-7	-3	-.4	-10	
73	10	-19	-19	17	-29	
MILK (kg)			MILK FAT (kg)			
Genetic		Phenotypic	Genetic		Phenotypic	
$b_{x_{1,Y}}$	$= 46.7 \pm 32.5$	78.6 ± 86.5	$b_{x_{1,Y}}$	$= 1.2 \pm 2.3$	-5.5 ± 5.3	
$b_{x_{2,Y}}$	$= 9.4 \pm 59.4$	108.5 ± 280	$b_{x_{2,Y}}$	$= 7.7 \pm 3.7$	9.8 ± 11.9	

Figure 2. Average phenotypic trends for milk and milk fat.

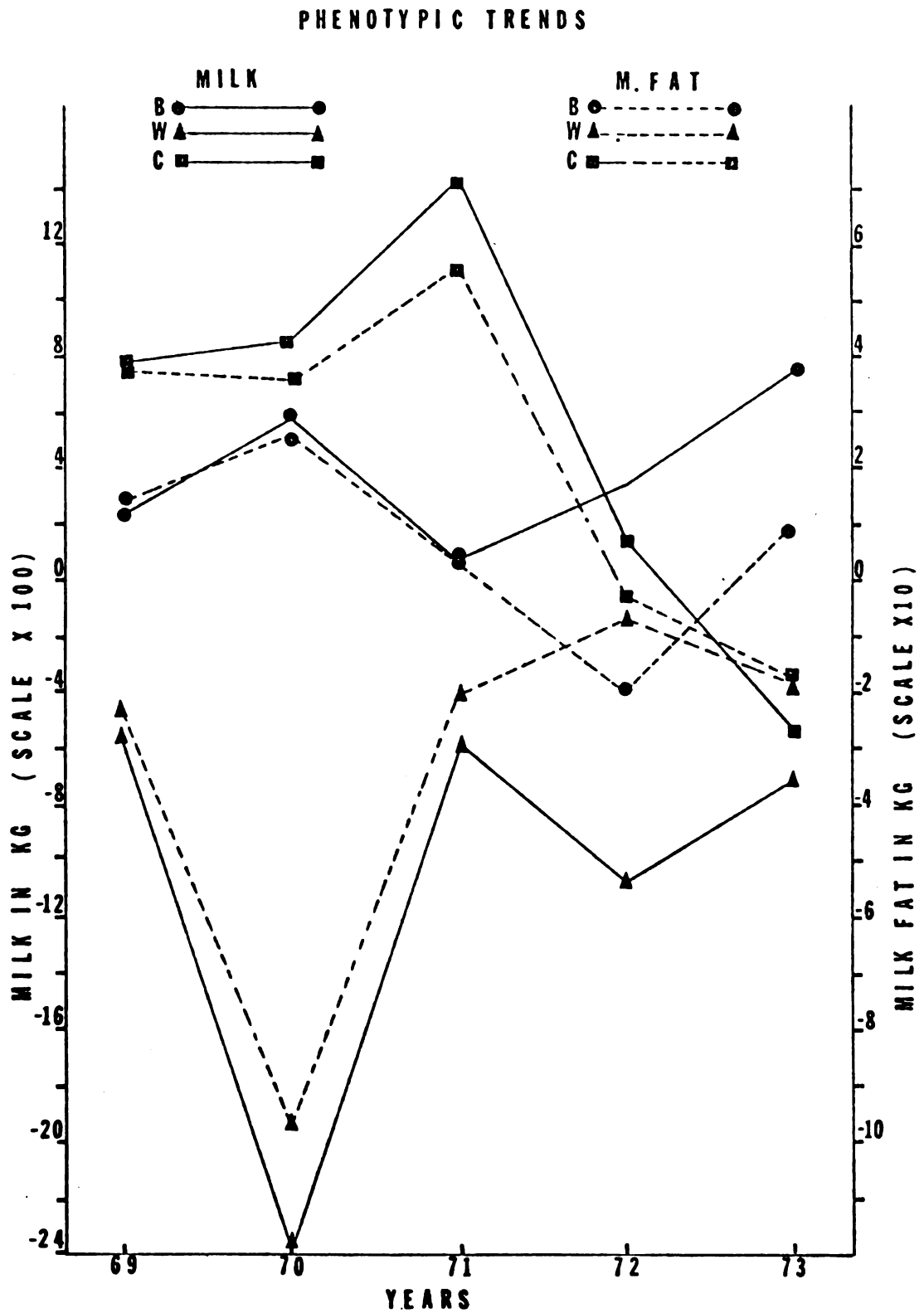


Figure 2

Figure 2. Average phenotypic trends for milk and milk fat.

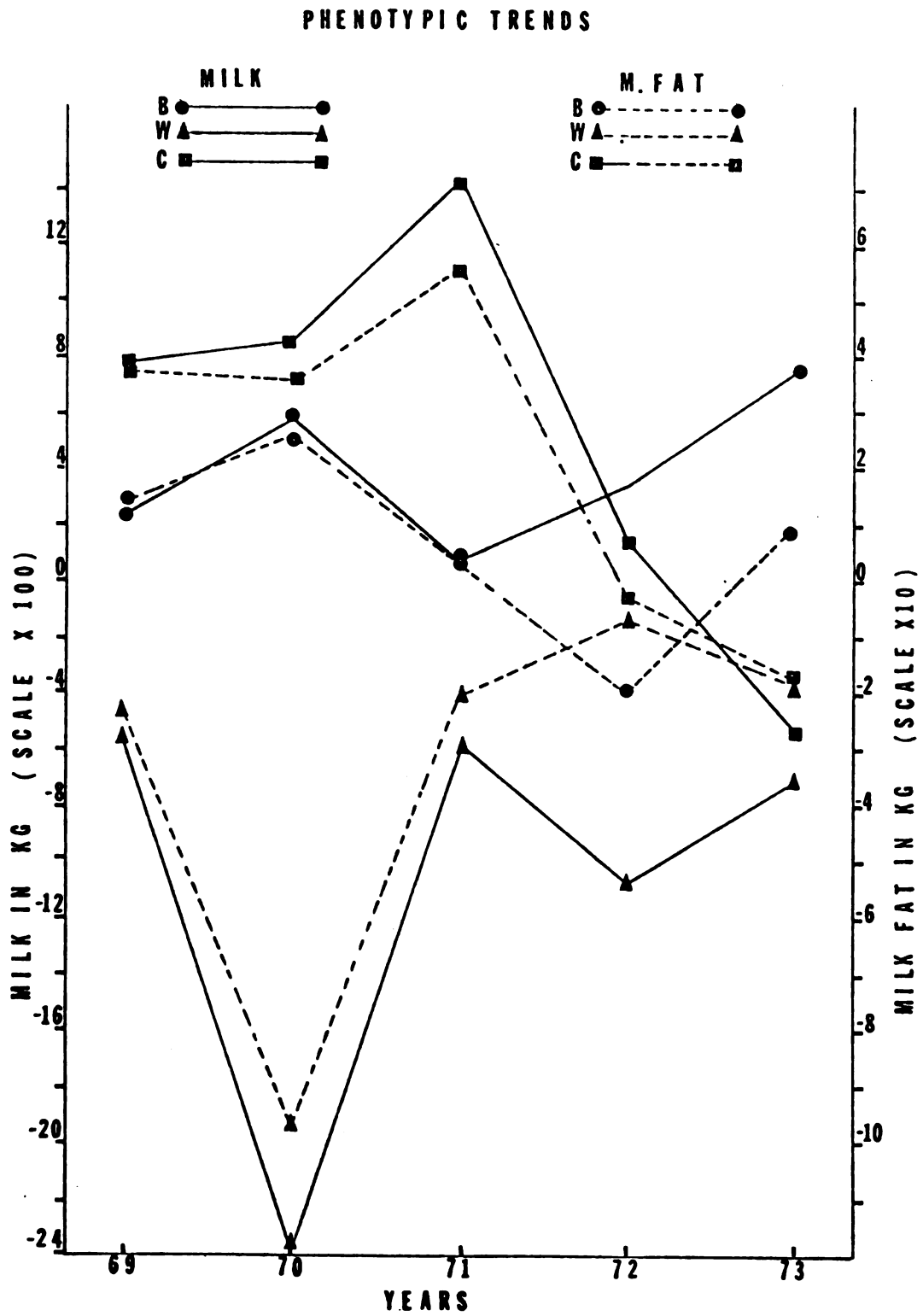


Figure 2

phenotypic trend in milk fat indicates a correlated response to milk yield.

Genetic Trends

Average genetic effects per year are presented in Table 8 and genetic trends for milk and milk fat are in Figure 3. The best line shows a slightly downward trend and worst line gives an upward trend with a big difference in two lines in the last year. This reflects the genetic differences in each year between the two lines. Average genetic progress in kilograms per year was estimated 46.7 ± 32.5 , -9.4 ± 59.4 for milk and 1.2 ± 2.3 , 7.7 ± 3.7 for milk fat in best and worst line. This indicates that on the average the two lines are spreading apart by 56 kg and 6.5 kg per year for milk and milk fat. In the literature genetic trends have been estimated by various regression techniques which are discussed in detail by Smith (57) and the estimates of genetic progress per year have been reported to vary from 20 to 55 kg and .8 to 6.4 kg for milk and milk fat (7,47, 60,61). The estimates of genetic progress per year in this study closely resemble the above-mentioned reports, although the design of the experiment and method of computing genetic trends was different. The genetic progress in milk fat per year is a result of correlated response to selection for milk production, thus indicating a positive genetic correlation between the two traits.

Correlated Response on Body Measurements

Body size (measure of body weight and wither height) is a factor often considered important in both inter- and intrabreed evaluation of dairy cattle. Such evaluation usually is based on the theory that

Figure 3. Average genotypic trends for milk and milk fat.

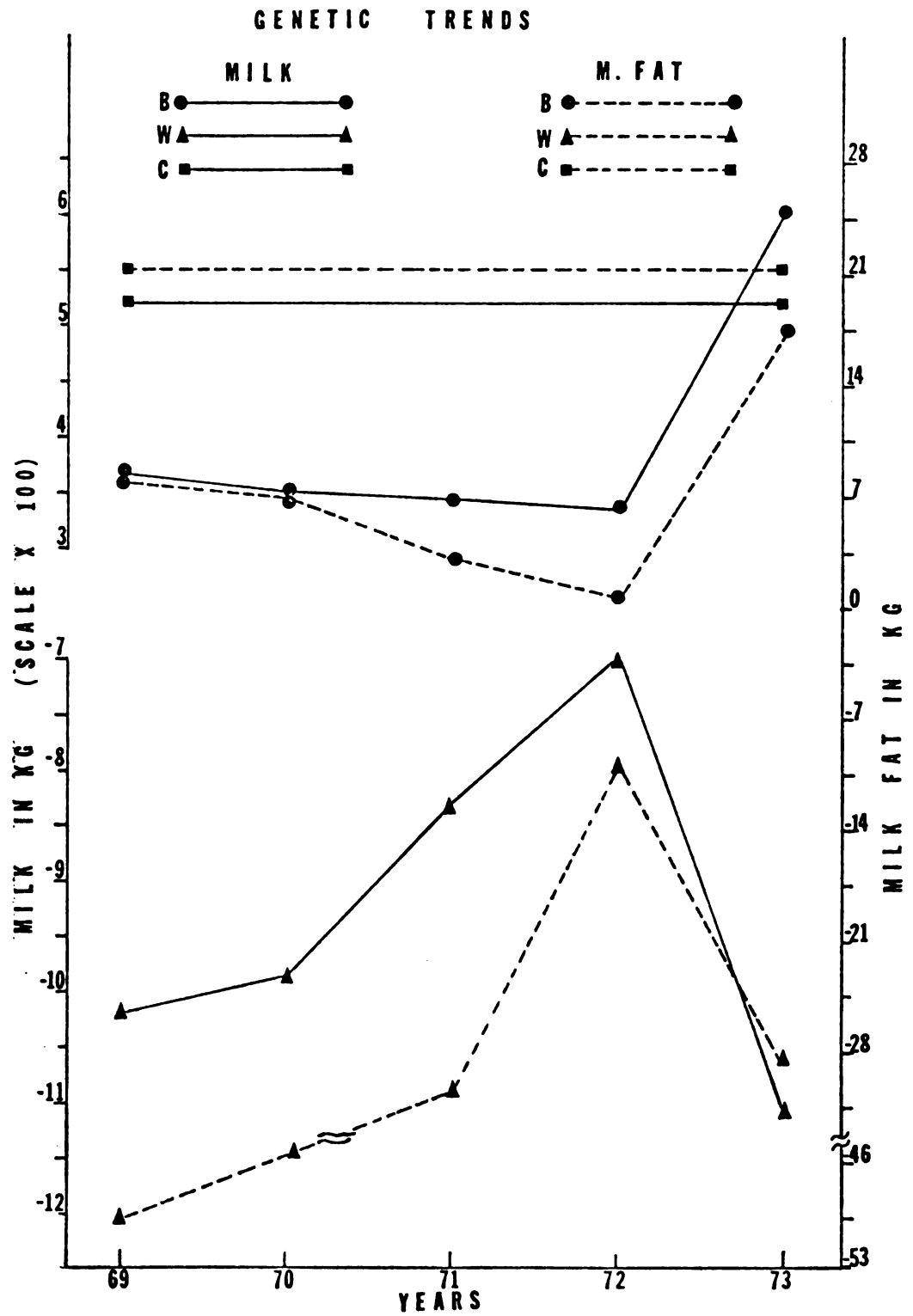


Figure 3

a deficiency in size is to a large extent reflected in a deficiency in the capacity for the consumption and storage of nutrients. A positive association of body size with milk and milk fat has been reported (3,8,23,24,26,34). In these studies basis of selection was not only one trait. It was of interest to measure the relationship in body weight and wither height as a correlated response to establish the association of body size with single trait selection (milk).

There were 1,142 repeated measurements on each trait (body weight and wither height) up to the age of 3 yr on 179 daughters of bulls selected on milk production. The data for body measurement had a lot of variation due to age. If the records were not corrected for age, some of the changes due to age could be interpreted as genetic effects which would bias the estimates of genetic correlations. Figures 4 and 5 are the graphs of three degree polynomial regression of body weight and wither height, on age of measurement. The regression coefficients of three degree polynomial regression are in Table 9. This regression removed 82% of the variation due to age for body weight and wither height.

Correlated Response of Bull Group Differences for Body Size

The whole data were adjusted towards the mean age by three degree polynomial regression coefficients. Table 10 gives the analysis of variance for body weight and wither height to test the significance of each factor. The least square constants estimated from the analysis for each factor are in Table 11. There was no detectable difference between years for body weight, but years were highly significantly different for wither height. Effect of lines, year by

Figure 4. Three degree polynomial regression of body weight on age in days fitting the whole data.

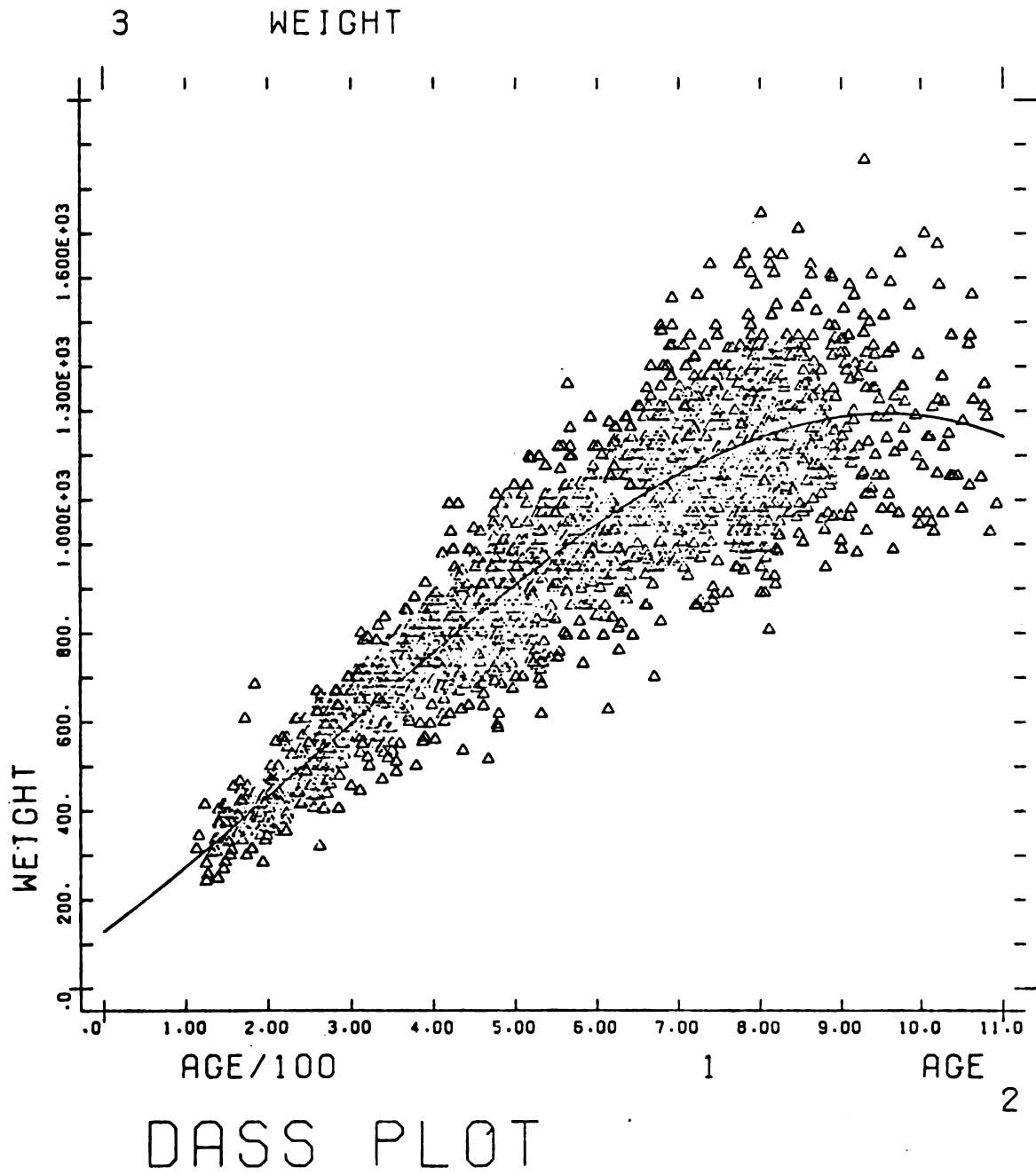


Figure 4

Figure 5. Three degree polynomial regression of wither height on age in days fitting the whole data.

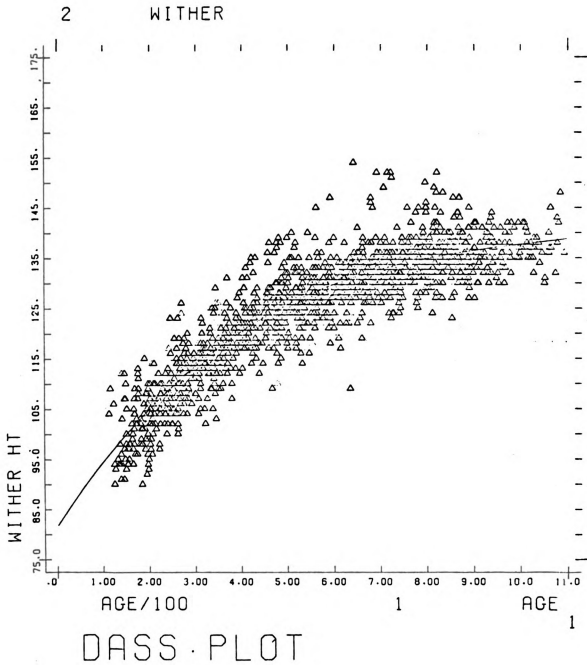


Figure 5

Table 9. Estimates of three degree polynomial regression of body weight and wither height on age in days to adjust for effects of age

Regression coefficients		Mean age/ 100 days
BODY WEIGHT		$R^2 = 82\%$
Constant	128	
Age 1	139	5.5574
(Age 1) ²	9	36.2614
(Age 1) ³	-1	262.0871
WITHER HEIGHT		$R^2 = 83\%$
Constant	81	
Age 1	13	5.5574
(Age 1) ²	-1	36.2614
(Age 1) ³	.0389	262.0871

Table 10. Analysis of variance of body weight and wither height to test the null hypothesis of years, lines, year by line, dam, dam by line, and bull groups

Source	Body weight			Wither height	
	DF	MS	F	MS	F
Years	6	29212	1.83	202	9.3**
Line	2	40867	2.56	38	1.74
Y X L	9	26074	1.63	5	<1
Dam	1	16034	1.0	<1	<1
L X D	2	10724	<1	9	<1
Bull group/ _{Y/L}	27	34307	2.15**	49	2.26**
Error	1094	15969		21	
Total	1141				
		$R^2 = .09$		$R^2 = .18$	

** P<.01.

Table 11. Least square estimates of years, lines, year x line interaction, bull groups, dams, and line x dam interaction for body weight and wither height

Constants	Body weight	Wither height	Constants	Body weight	Wither height
μ	429	124	Y73L3	+1	+.28
Y67	-6	-.9	Dam 0 (dead)	-2	+.01
Y68	-14	-1	Dam 1 (live)	+2	-.01
Y69	-5	-1	L1D1	-1	+.12
Y70	-4	3	L1D0	+1	-.12
Y71	+3	.11	L2D1	-2	-.18
Y72	+7	.78	L2D0	+2	+.18
Y73	+19	-1	L3D1	+4	.06
Line 1 (best)	-7	-.60	L3D0	-4	-.06
Line 2 (worst)	-2	.14	G1Y69L1	-2	+.81
Line 3 (control)	+9	.46	G2Y69L1	+2	-.81
Y68L1	-.54	-.10	G1Y69L2	-2	+.93
Y68L2	+.54	+.10	G2Y69L2	+2	-.93
Y69L1	+5	.23	G1Y70L1	+2	+.98
Y69L2	+5	.04	G2Y70L1	-13	-2.02
Y69L3	-11	-.27	G3Y70L1	+11	+1.04
Y70L1	+13	.18	G1Y70L2	+5	.28
Y70L2	+.78	.15	G2Y70L2	-7	-1.76
Y70L3	-14	-.34	G3Y70L2	+2	1.47
Y71L1	+2	-.50	G1Y71L1	+40	2.66
Y71L2	-13	-.04	G2Y71L1	-20	-1.10
Y71L3	+10	.54	G3Y71L1	-28	-1.70
Y72L1	-2	-.09	G4Y71L1	+7	.14
Y72L2	-11	.31	G2Y71L2	+11	-1.24
Y72L3	+13	-.21	G3Y71L2	-20	-1.26
Y73L1	-19	+.29	G4Y71L2	+3	1.72
Y73L2	+18	-.57	G1Y72L1	+45	-.27
			G2Y72L1	-13	-.53

Table 11 (continued)

Constants	Body weight	Wither height	Constants	Body weight	Wither height
G3Y72L1	-5	-.95	G2Y73L1	-7	1
G4Y72L1	+13	-.40	G3Y73L1	+30	.64
G5Y72L1	-40	+2	G4Y73L1	+12	-.66
G1Y72L2	-53	-2	G5Y73L1	+7	-1.76
G2Y72L2	+17	-1	G2Y73L2	+50	1.65
G3Y72L2	+3	-1	G3Y73L2	+3	2.42
G4Y72L2	+22	1	G4Y73L2	-25	.40
G5Y72L2	+9	3	G5Y73L2	-29	-4
G1Y73L1	-42	.05	G1Y71L2	-	+.78

G indicates bull group.

line interaction, selection of dam and line by dam interaction were insignificant for both the traits. The main contributors to the total variation for body weight and wither height were year and bull group effects. The least square means between lines for body weight and wither height (Table 12) represented no difference when the lines were distinctly apart on milk and milk fat. This reflects the indirect response of selection for milk on body size. The least square means were compared with the arithmetic averages (Table 13), which were within the range of one standard deviation. Differences in body weight and wither height could be visualized simply in the arithmetic averages.

The constants for bull groups ($\hat{B}_{(ij)k}$) reflect the correlated response in genetic differences from one bull group to another for body weight and wither height for each year line subclass. The weighted constants for each bull group were calculated as described for milk and milk fat and the graph is in Figure 6. The bull groups for body weight follow almost the same trend as that for milk production in Figure 1 for both the lines whereas response in wither height was irregular. Since there was one group of control bulls, a straight line was drawn for body weight and wither height for the control to indicate the base line for comparison. The response by bull groups for body weight and wither height reflects a correlated response to selection for milk production. Since the study is based on four bull groups and a small sample of data, these estimates must be used with caution in general.

Table 12. Least square means (M) and standard errors (SE) for lines, years, and year x line interaction for body weight and wither height adjusted for different factors

Lines	Years				
	1969	1970	1971	1972	1973
BODY WEIGHT (kg)					
<u>Line 1 (best)</u>					
M 424	422	432	429	427	422
SE 9 (538) ^a	20	20	15	16	23
<u>Line 2 (worst)</u>					
M 430	428	424	418	424	465
SE 9 (459)	18	17	16	22	19
<u>Line 3 (control)</u>					
M 442	423	421	454	461	460
SE 10 (145)	33	17	15	18	25
M	422	423	431	435	447
SE	15(180)	13(268)	12(297)	13(204)	20(116)
WITHER HEIGHT (cm)					
<u>Line 1 (best)</u>					
M 124.2	122.5	127.3	123.2	124.2	122.7
SE .51 (538)	1.1	1.1	.79	.89	1.28
<u>Line 2 (worst)</u>					
M 124.9	123.1	128.0	124.4	125.4	122.6
SE .51 (459)	.98	.93	.86	1.22	1.05
<u>Line 3 (control)</u>					
M 125.2	123.1	127.8	125.3	125.2	123.8
SE .56 (145)	1.8	.93	.83	.99	1.37
M	122.7	127.5	124.1	124.8	122.9
SE	.84 (180)	.71 (268)	.65 (297)	.73 (204)	1.10 (116)

^aNo. of records in parentheses.

Table 13. Arithmetic averages (M) and standard deviations (SD) for lines, years and year x line interactions for body weight and wither height

Lines	Years				
	1969	1970	1971	1972	1973
BODY WEIGHT (kg)					
<u>Line 1 (best)</u>					
M 425	420	430	426	425	437
SD 58 (538) ^a	52	62	78	49	42
<u>Line 2 (worst)</u>					
M 428	426	426	418	438	448
SD 63 (459)	52	56	83	55	50
<u>Line 3 (control)</u>					
M 447	430	423	457	455	454
SD 45 (145)	20	32	47	49	41
M	422	427	429	435	443
SD	51(180)	56(268)	76(297)	52(204)	46(116)
WITHER HEIGHT (cm)					
<u>Line 1 (best)</u>					
M 124.1	123.3	127.4	123.2	123.7	122.4
SD 5.04 (538)	4.03	6.53	4.51	3.88	3.41
<u>Line 2 (worst)</u>					
M 124.9	123.7	127.7	123.9	125.5	122.7
SD 5.18 (459)	3.74	7.0	4.46	3.25	4.52
<u>Line 3 (control)</u>					
M 125.6	123.1	127.8	125.3	125.2	123.8
SD 4.51 (145)	2.41	6.37	3.24	4.49	2.67
M	123.4	127.6	123.9	124.7	122.7
SD	3.86 (180)	6.67 (268)	4.33 (297)	3.84 (204)	3.88 (116)

^aNo. of records in parentheses.

Figure 6. Weighted constants for bull groups over years within line for body weight (kg) and wither height (cm).

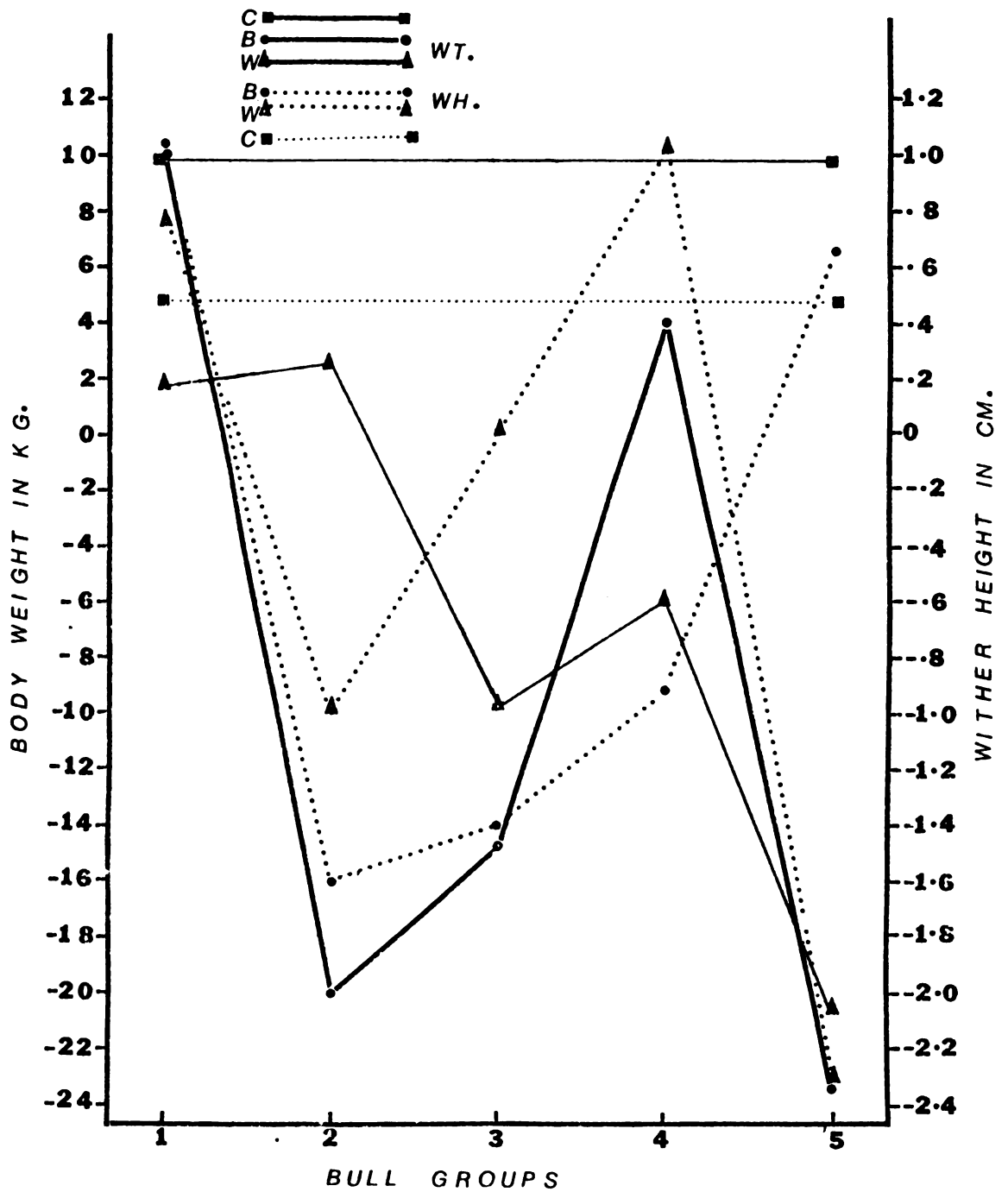


Figure 6

Bull Group Differences Under Different Age Groups

There are some genes which express themselves at a certain age; therefore, I decided to look into bull group differences under different age groups for body size within each line. The least square analysis of fitted constants for each age group from model 1 for each factor is in Tables 14 to 18 to test the significance of bull group differences, and Tables 19 and 20 give the least square constants for each factor for body weight and wither height. Differences among bull groups were not significant at the earlier age for both the traits. However, there was no significant difference between the lines in all age groups except for body weight under age group 1. To have a more clear picture of bull group differences, weighted constants of bull groups were plotted in Figures 7 to 11 for body weight and wither height under different age groups. From the graphs growth pattern of daughters of bull groups was irregular in both the lines.

Phenotypic and Genetic Correlated Response on Body Size

The idea of correlated response has always been of great importance in the minds of both evolutionists and breeders. In simple words, correlated response is an indirect response on the unselected traits when selection pressure is applied to some single trait. In my study the selection pressure was applied to a single trait (milk) and it measured the change in the unselected traits (body weight and wither height) which would reflect the relationship of selected and unselected traits.

Table 14. Analysis of variance of body weight and wither height to test the null hypothesis of each factor under age group 1 (0 to 180 days)

Source	DF	Body Weight		Wither Height	
		MS	F	MS	F
Years	4	2477	1.2	173	11.2**
Lines	2	10528	5.1**	19	1.2
Y X L	6	6893	3.3**	20	1.3
Dam	1	6129	3.0	103	6.7**
L X D	2	1824	<1	57	3.7*
Bull group/ _{Y/L}	7	2073	<1	25	1.6
Error	34	2077		15	
Total	56				

* $P < .05$.

** $P < .01$.

Table 15. Analysis of variance of body weight and wither height to test the null hypothesis of each factor under age group 2 (181 to 365 days)

Source	DF	Body Weight		Wither Height	
		MS	F	MS	F
Years	6	10873	2.7**	70	3.7**
Line	2	623	<1	21	1.1
Y X L	9	7807	1.9*	26	1.4
Dam	1	591	<1	1	
L X D	2	10062	2.5	2	1
Bull group/ _{Y/L}	17	5526	1.4	19	1.0
Error	252	4059		19	
Total	289				

* $P < .05$.

** $P < .01$.

Table 16. Analysis of variance of body weight and wither height under age group 3 (366 to 545 days) to test the null hypothesis of each factor

Source	DF	<u>Body Weight</u>		<u>Wither Height</u>	
		MS	F	MS	F
Years	5	17051	1.5	246	10.7**
Line	2	24182	2.2	11	<1
Y X L	9	23350	2.1*	13	<1
Dams	1	1183	<1	12	<1
L X D	2	4153	<1	8	<1
Bull groups/ _{Y/L}	13	20006	1.8*	32	1.4
Error	250	11133		22	
Total	282				

* P<.05.

** P<.01.

Table 17. Analysis of variance of body weight and wither height under age group 4 (546 to 730 days) to test the null hypothesis of each factor

Source	DF	Body Weight		Wither Height	
		MS	F	MS	F
Years	5	17017	<1	39	1.5
Lines	2	60776	2.8	67	2.5
Y X L	7	4241	<1	3	<1
Dam	1	87087	4.1*	12	<1
L X D	2	11819	<1	9	<1
Bull groups/ _{Y/L}	13	26563	1.2	56	2.1**
Error	225	21528		26	
Total	255				

* $P < .05$.

** $P < .01$.

Table 18. Analysis of variance of body weight and wither height under age group 5 (731 to 1096 days) to test the null hypothesis of each factor

Source	DF	<u>Body Weight</u>		<u>Wither Height</u>	
		MS	F	MS	F
Years	4	40019	1.2	4	<1
Lines	2	8138	<1	9	<1
Y X L	7	38875	1.2	7	<1
Dam	1	99	<1	5	<1
L X D	2	29004	<1	15	<1
Bull group/ _{Y/L}	10	38924	1.2	36	2.1*
Error	229	32161		17	
Total	255				

* P<.05.

Table 19. Least square estimates of years, lines, year x line interaction, bull groups, dams, and line x dam interaction for body weight under different age groups

Constants	Body Weight				
	0-180 days Age 1	181-365 days Age 2	366-545 days Age 3	546-730 days Age 4	731-1096 days Age 5
μ	437.71	424.37	430.16	434.92	432.12
Y69	-8.03	+3.82	-11.90	5.38	-20.27
Y70	+5.33	-5.28	+6.96	0	-19.84
Y71	-1.08	+4.63	-10.92	7.36	+4.85
Y72	--	+7.68	+7.53	17.58	+2.66
Y73	+14.10	+7.94	+20.53	17.87	+32.50
Line 1 (best)	-13.04	.73	-11.26	-18.69	-3.57
Line 2 (worst)	+14.00	-1.63	6.16	-10.23	-7.71
Line 3 (control)	-.96	.89	5.10	+28.92	+11.28
Y69L1	11.29	1.81	15.15	1.07	-12.19
Y69L2	-14.63	1.57	.87	-1.07	+12.19
Y69L3	3.34	-3.38	-16.02		
Y70L1	+26.04	10.95	+21.15	6.49	8.77
Y70L2	-11.94	3.40	-20.36	-6.34	24.08
Y70L3	-14.10	-14.36	-.79	-.15	-32.84
Y71L1	+3.19	-7.44	-20.37	-8.34	19.15
Y71L2	-13.95	-2.21	-5.55	-5.26	-13.70

Table 19 (continued)

Constants	Body Weight				
	0-180 days Age 1	181-365 days Age 2	366-545 days Age 3	546-730 days Age 4	731-1096 days Age 5
Y71L3	10.76	9.65	25.93	13.60	-5.45
Y72L1	--	-13.20	-16.44	-8.7	14.63
Y72L2	--	16.23	7.00	-3.43	-33.00
Y72L3	--	-3.03	9.43	4.30	18.37
Y73L1	-45.56	5.37	-4.15	1.65	-30.36
Y73L2	+45.56	-16.50	22.70	16.10	10.44
Y73L3	--	11.13	-18.55	-17.75	19.93
Dam 1 (live)	-8.01	1.07	-1.27	12.16	+47
Dam 0 (dead)	+8.01	-1.07	+1.27	-12.16	-47
GLY69L1	--	-1.50			
G2Y69L1	--	1.50			
GLY69L2	25.36	-3.59			
G2Y69L2	-25.36	3.59			
GLY70L1	-15.20	10.21	20.35	18.01	
G2Y70L1	--	-7.26	-20.35	-18.01	
G3Y70L1	+15.20	-2.95			
GLY70L2	+18.17	+14.71	-.92	13.93	
G2Y70L2	-17.93	-8.05	+9.2	-13.93	

Table 19 (continued)

Constants	Body Weight				
	0-180 days Age 1	181-365 days Age 2	366-545 days Age 3	546-730 days Age 4	731-1096 days Age 5
G3Y70L2	.24	-6.66			
G1Y71L1				34.47	25.72
G2Y71L1		-10.31	+16.26	-28.90	-25.72
G3Y71L1	-5.48	-8.83	-16.26	-8.58	
G4Y71L1	+5.48	19.14			
G1Y71L2			36.29	25.97	1.05
G2Y71L2		5.23	5.49	11.85	-1.05
G3Y71L2	5.73	-.65	-41.78	-37.82	
G4Y71L2	-5.73	-4.58			
G1Y72L1	--	7.21	-.50		74.71
G2Y72L1			-34.01	-6.25	-48.03
G3Y72L1	--	12.10	+3.17	-14.48	-26.68
G4Y72L1	--	9.03	+31.34	+20.73	
G5Y72L1	--	-28.34			
G1Y72L2					-35.70
G2Y72L2			10.36	+3.65	47.26
G3Y72L2		17.04	-4.90	-13.00	-11.56
G4Y72L2		-3.25	-5.46	9.35	

Table 19 (continued)

Constants	Body Weight				
	0-180 days Age 1	181-365 days Age 2	366-545 days Age 3	546-730 days Age 4	731-1096 days Age 5
G5Y72L2		-13.79			
G1Y73L1				-52.09	
G3Y73L1			16.01	9.20	30.27
G4Y73L1	8.56	-2.34	-5.59	42.89	-13.45
G5Y73L1	-8.56	2.34	-10.42		
G2Y73L2					36.24
G3Y73L2				.16	-.44
G4Y73L2	-13.75		+26.02	-.16	-35.80
G5Y73L2	13.75		26.02		
G2Y73L1					-16.82

G indicates bull group.

Table 20. Least square estimates of years, lines, year x line, bull groups, dams, and line x dam interaction for wither height (cm) under different age groups

Constants	Wither Height (cm)				
	0-180 days Age 1	181-365 days Age 2	366-545 days Age 3	546-730 days Age 4	731-1096 days Age 5
μ	125.11	123.72	124.35	124.07	124.98
Y69	-2.95	-.53	-1.31	-.036	.078
Y70	7.58	2.92	5.46	2.38	.519
Y71	-2.48	.79	-.87	-.39	.224
Y72	--	.93	.24	.99	-.607
Y73	-2.45	-2.92	-2.51	-.526	-.214
Line 1 (best)	-1.77	-.73	-.59	-1.43	-.517
Line 2 (worst)	.015	.24	-.03	.233	-.363
Line 3 (control)	1.75	.48	.62	1.199	.879
Y69L1	1.08	.25	1.58	.097	-.837
Y69L2	-2.99	-.77	1.88	-.097	.837
Y69L3	1.91	.53	-3.46	--	
Y70L1	2.85	1.03	.05	-.264	.955
Y70L2	1.01	-.31	-1.52	-.209	.778
Y70L3	-3.86	-.72	1.47	.474	-1.733
Y71L1	-2.17	-1.42	-.95	+.341	-.331
Y71L2	.22	.90	.51	-.685	-.954

Table 20 (continued)

Constants	Wither Height				
	0-180 days Age 1	181-365 days Age 2	366-545 days Age 3	546-730 days Age 4	731-1096 days Age 5
Y71L3	1.95	.52	.44	+.344	1.285
Y72L1	--	-1.27	-1.07	-.377	+.73
Y72L2	--	2.58	.40	.157	-.69
Y72L3	--	-1.32	.67	.220	-.04
Y73L1	-1.01	.80	.39	.203	-.52
Y73L2	1.01	-1.80	-1.27	.834	.034
Y73L3	--	1.00	.88	-1.037	.484
Dam 1 (live)	-2.29	.07	-.29	.324	.239
Dam 2 (dead)	2.29	-.07	.29	-.324	-.239
GLY69L1	--	.86			
G2Y69L1	--	-.86			
GLY69L2	+3.22	.36			
G2Y69L2	-3.22	-.36			
GLY70L1	-.57	1.65	3.30	3.71	
G2Y70L1	--	-.07	-3.30	-3.71	
G3Y70L1	+5.7	-1.58			
GLY70L2	3.55	2.60	.65	3.15	
G2Y70L2	-6.57	-.45	-.65	-3.15	

Table 20 (continued)

Constants	Wither Height (cm)				
	0-180 days Age 1	181-365 days Age 2	366-545 days Age 3	546-730 days Age 4	731-1096 days Age 5
G3Y70L2	3.02	-2.14			
G1Y71L1				2.24	2.17
G2Y71L1	--	-2.00	.93	-.29	-2.17
G3Y71L1	.13	.18	-.93	-1.95	
G4Y71L1	-.13	1.82			
G1Y71L2			2.40	1.87	1.18
G2Y71L2		-1.38	-.90	.40	-1.18
G3Y71L2	-1.16	.06	-1.50	-2.27	
G4Y71L2	+1.16	1.32			
G1Y72L1	--	-7.19	-1.71		4.76
G2Y72L1			1.18	.333	-1.20
G3Y72L1	--	2.03	.34	-1.65	-3.56
G4Y72L1	--	1.34	.19	1.32	
G5Y72L1		3.82			
G1Y72L2					-.153
G2Y72L2			.42	-1.13	.443
G3Y72L2		-1.19	-.88	-.606	-.290
G4Y72L2		.32	.45	1.73	

Table 20 (continued)

Constants	Wither Height (cm)			
	0-180 days Age 1	181-365 days Age 2	366-545 days Age 3	546-730 days Age 4
				731-1096 days Age 5
G5Y72L2		.87		
G1Y73L1			.355	
G2Y73L1				.788
G3Y73L1			-1.04	2.29
G4Y73L1	-.45	-.78	2.22	-2.65
G5Y73L1	.45	.78	-1.18	-.490
G2Y73L2				-.389
G3Y73L2				1.03
G4Y73L2		1.89	-.03	-.637
G5Y73L2		-1.89	.03	

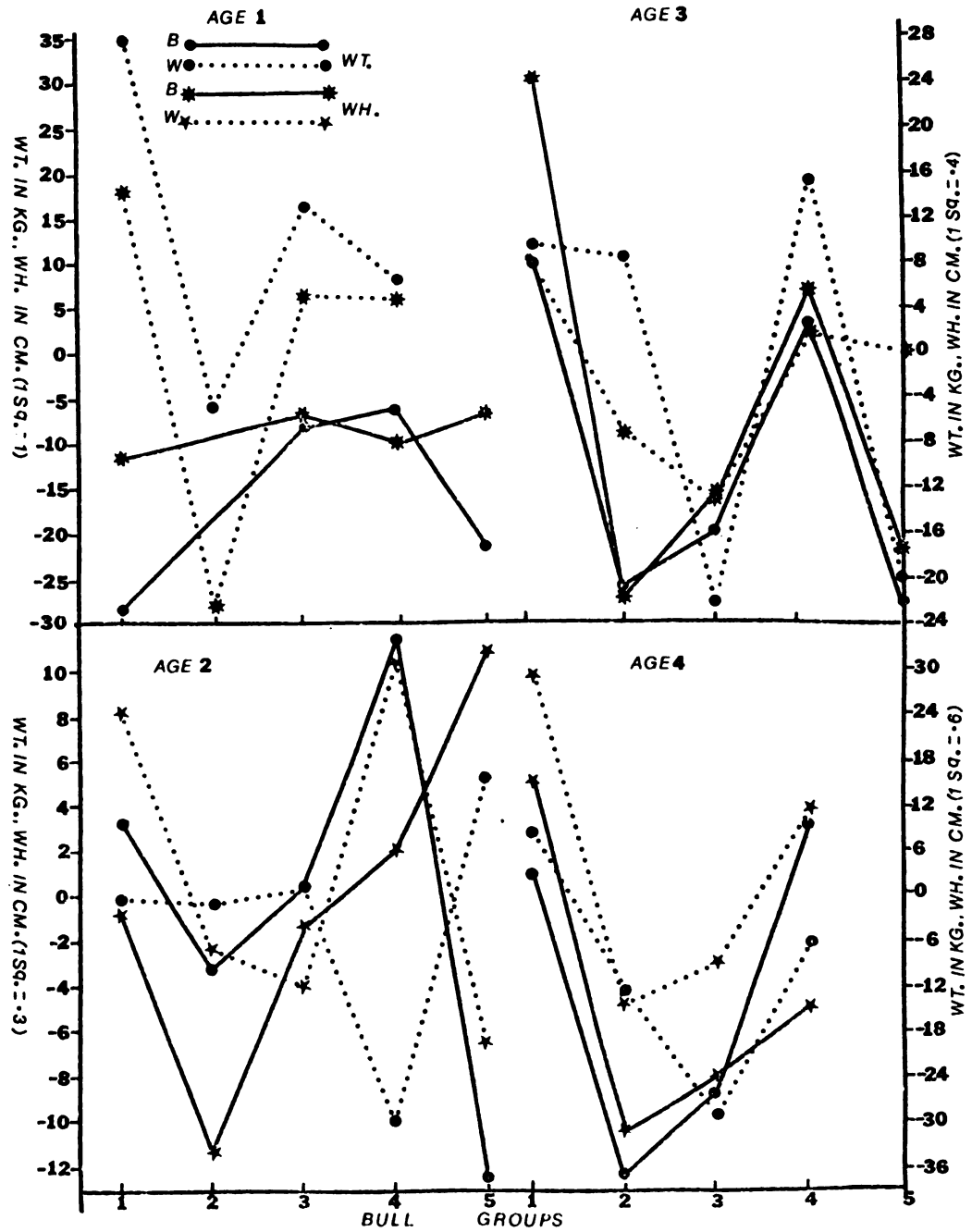
G indicates bull group.

Figure 7. Weighted constants of bull groups adjusted over years for body weight (kg) and wither height (cm) within each line for age group 1 (0 to 180 days).

Figure 8. Weighted constants of bull groups adjusted over years for body weight (kg) and wither height (cm) within each line for age group 2 (181 to 365 days).

Figure 9. Weighted constants of bull groups adjusted over years for body weight (kg) and wither height (cm) within each line for age group 3 (366 to 545 days).

Figure 10. Weighted constants of bull groups adjusted over years for body weight (kg) and wither height (cm) within each line for age group 4 (546 to 730 days).



Figures 7, 8, 9, and 10

Figure 11. Weighted constants of bull groups adjusted over years for body weight (kg) and wither height (cm) within each line for age group 5 (731 to 1096 days).

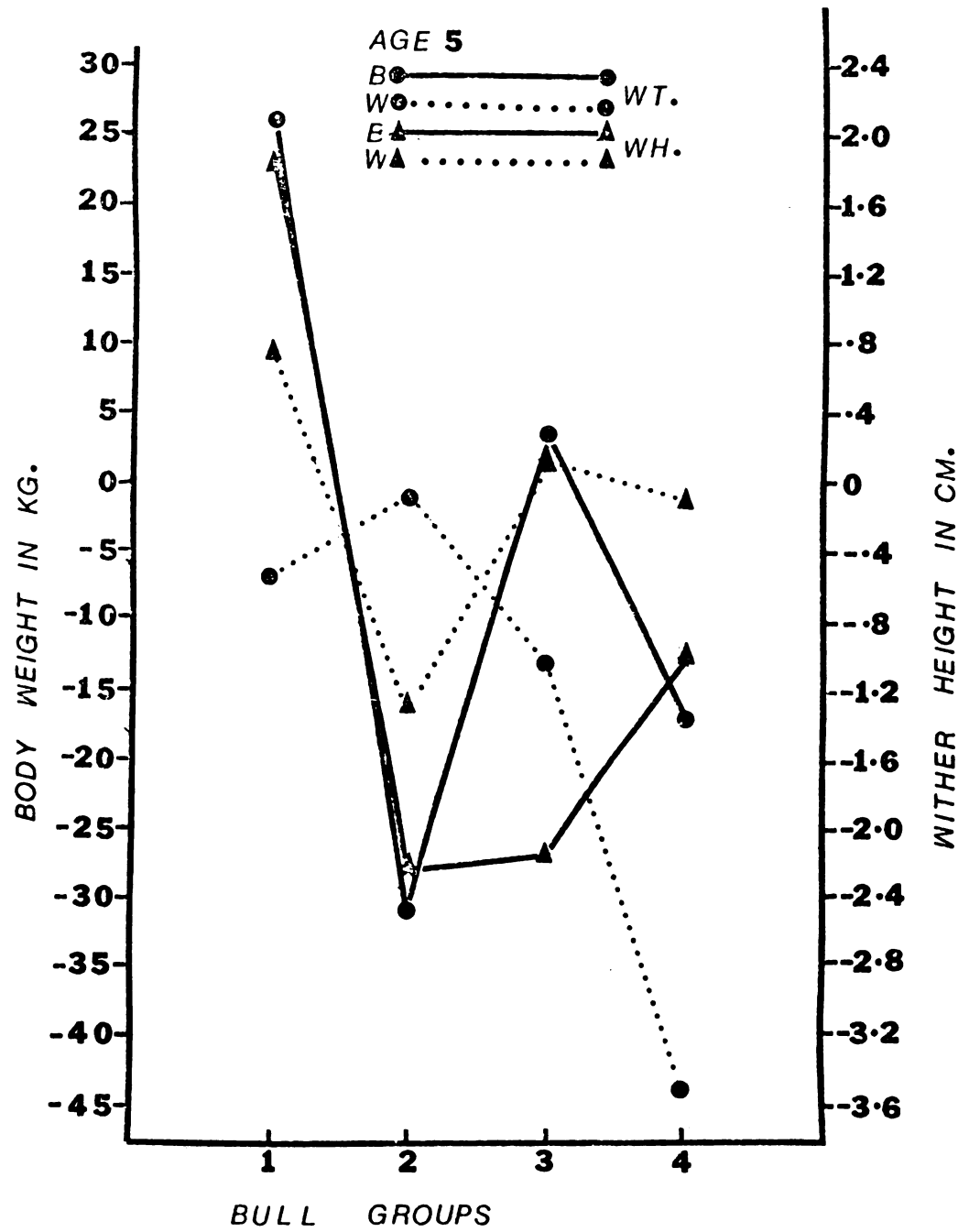


Figure 11

Phenotypic Correlated Response

The phenotypic correlated response in body weight and wither height were estimated from the average phenotypic effects for each line. The average phenotypic effects per year for each line were calculated by the sum of the estimates for years, lines, year by line interaction, bull groups, and sire constants. The estimates for the sire effects were calculated for body weight and wither height by model 2 as described earlier. Table 21 gives the analysis of variance to test the differences among sires within line and bull group subclass and the estimates of least square constants for each factor are in Table 22. Sires were highly significantly different for both the traits.

The average phenotypic trends of body weight and wither height are shown in Figure 12 for best, worst, and control lines. The average phenotypic trend is a combination of genotypic effect and environmental effect. In the control line the genotype is assumed to be the same in all the years. Therefore, fluctuation in control line reflects the environmental changes and influence of some sampling effect. Table 23 presents the average phenotypic change per year in each line calculated by regressing the average phenotypic effects on years. There was hardly any difference in phenotypic trends for wither height, and the trend was negative in all the lines. The best line showed a negative phenotypic trend of $3.32 \text{ kg} \pm 1.9$ whereas a positive phenotypic trend was $4.5 \text{ kg} \pm 5.9$ in the worst line per year for body weight. The two lines were, therefore, spreading apart by 7.8 kg per year. From the phenotypic responses as milk production increased, the body weight decreased. These results

Table 21. Analysis of variance of body weight and wither height to test the differences among sires within bull groups and lines

Source	DF	Body Weight		Wither Height	
		MS	F	MS	F
Lines	2	92315	5.7**	141	5.8**
Bull groups/ lines	8	29871	1.8	98	4.1**
Sires/ groups/lines	22	30809	1.9**	48	2.0**
Error	1109	16222		24	
Total	1141				

**
P<.01.

Table 22. Least square estimates of lines, bull groups and sires for body weight and wither height

Constants	Body weight	Wither height	Constants	Body weight	Wither height
μ	432.35	124.36	S2G2L1	5.259	1.4656
Line 1 (best)	-9.517	-.7569	S1G3L1	10.326	-.6696
Line 2 (worst)	-3.645	-.4145	S2G3L1	-10.326	.6696
Line 3 (control)	13.162	1.1714	S1G4L1	1.201	.6045
G1L1 ^a	3.831	1.3864	S2G4L1	-1.201	-.6045
G2L1	-8.023	.1453	S1G5L1	-16.50	-.2223
G3L1	-3.038	-.446	S2G5L1	16.50	.2223
G4L1	14.965	-.3917	S1G1L2	7.714	-.5121
G5L1	-7.735	-.6940	S2G1L2	-7.714	.5121
G1L2	-3.173	1.7478	S1G2L2	21.368	1.9838
G2L2	-4.917	-.0424	S1G3L2	-11.120	.2651
G3L2	-12.70	.3530	S2G3L2	11.120	-.2651
G4L2	13.762	1.0463	S1G4L2	.8397	.0539
G5L2	7.03	-3.1047	S2G4L2	-.8397	-.0539
S1G1L1	8.074	.2278	S1G5L2	10.233	.5548
S2G1L1	-8.074	-.2278	S2G5L2	-10.233	-.5548
S1G2L1	-5.259	-1.4656	S2G2L2	-21.368	-1.9838

^aG indicates bull groups.

Figure 12. Average phenotypic trends for body weight and
wither height.

PHENOTYPIC TRENDS

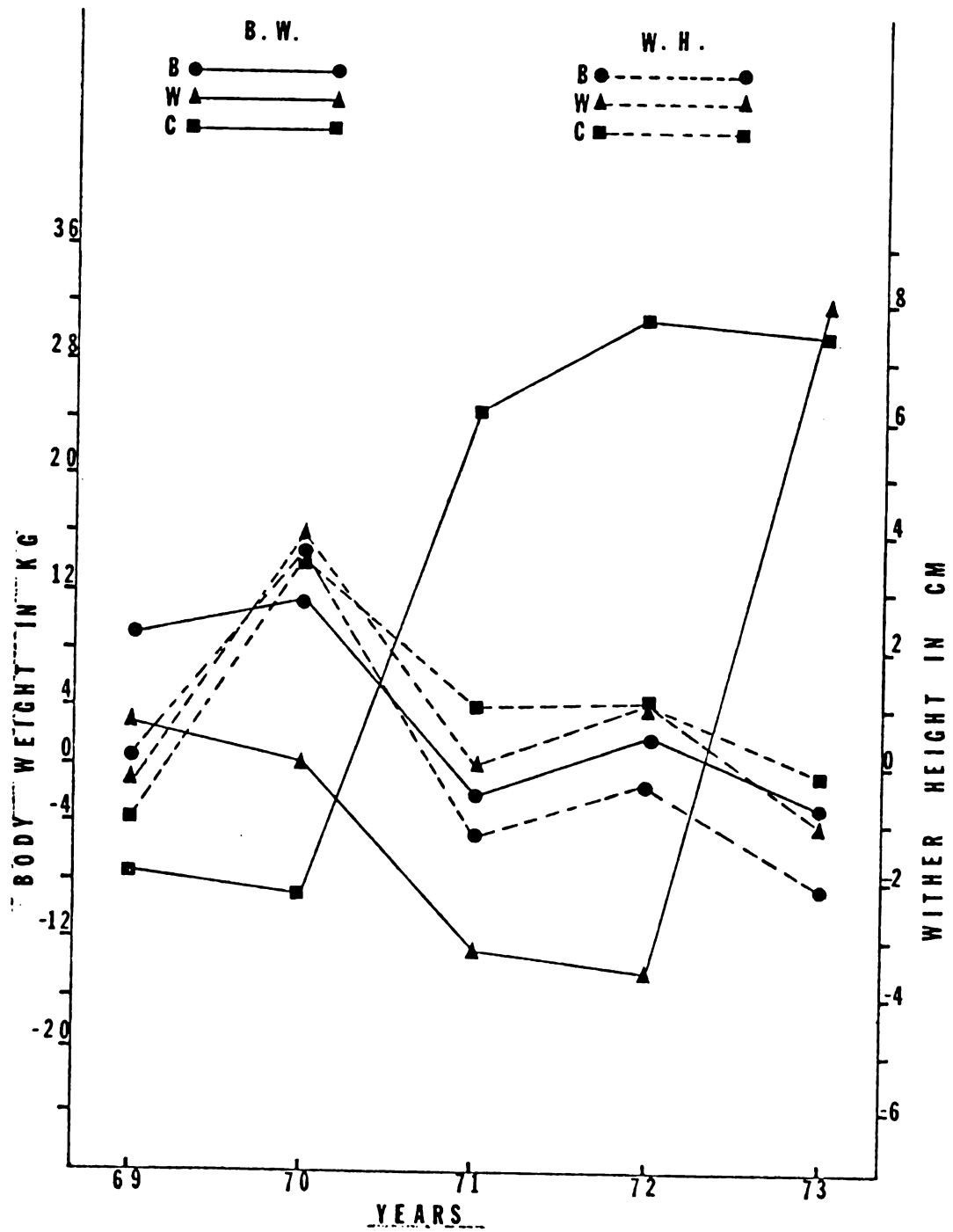


Figure 12

Table 23. Average phenotypic and genetic effects in each year for body weight (kg) and wither height (cm) within each line

Y Years	Phenotypic Effects			Genetic Effects		
	X ₁ Best (L ₁)	X ₂ Worst (L ₂)	X ₃ Control (L ₃)	X ₁ Best (L ₁)	X ₂ Worst (L ₂)	X ₃ Control (L ₃)
BODY WEIGHT (kg)						
69	9.17	3.72	-7.21	8.82	3.48	+9.87
70	11.61	.13	-8.65	1.90	3.37	
71	-1.91	-10.65	+24.52	-8.46	-.64	
72	2.28	-11.91	+31.13	-7.28	-7.82	
73	-2.75	+32.07	+30.60	-2.71	-5.51	
WITHER HEIGHT (cm)						
69	-.19	-.68	-1.09	.86	.56	+.46
70	3.84	3.93	+3.63	.15	.27	
71	-1.40	.04	+1.11	-1.01	-.03	
72	-.65	1.25	+1.03	-1.34	-1.34	
73	-2.18	-1.06	-.39	-1.34	.64	
REGRESSION COEFFICIENTS						
BODY WEIGHT (kg)			WITHER HEIGHT (cm)			
	Phenotypic	Genetic	Phenotypic	Genetic		
b _{x₁.Y}	-3.32 ± 1.9	-3.22 ± 1.8	-.85 ± .7	-.589 ± .12		
b _{x₂.Y}	+4.5 ± 5.9	-2.92 ± .82	-.34 ± .7	+0.005 ± .10		

are not in agreement with Clark and Touchberry (8), who studied the independent influence of age and body weight on milk and milk fat production. These differences in results may be due to the fact that selection pressure in the present study was milk production, but the phenotypic trends in body weight and wither height represent correlated response instead of direct response.

Genetic Correlated Response

The average genetic contribution of each line per year was calculated from constants for effects of line, bull groups, and sires. The details of calculating the average genetic effects are given in the methods section, page 34. Table 23 exhibits the average genetic effects per year and the genetic trends are in Figure 13 for body weight and wither height. The control line was plotted for comparisons with other lines. The average genetic change for body weight per year was lowered by $3.2 \text{ kg} \pm 1.9$ and $2.9 \text{ kg} \pm .82$ in best and worst line, and decline in wither height per year was $.59 \text{ cm} \pm .12$ in best line with almost no change ($.005 \text{ cm}$) in worst line. By comparing the average genetic change in body size which reflects the correlated genetic response to selection on the trait of interest (milk), it appears that the differences in body weight and wither height between the best and worst line are hardly detectable when the two lines differed in milk production by 56 kg per year. Since the correlated response is a combination of heritabilities of the traits and genetic correlations of selected and unselected traits, phenotypic and genetic correlations should be able to throw more light on the relationship of selected and unselected traits.

Figure 13. Average genetic trends for body weight and
withers height.

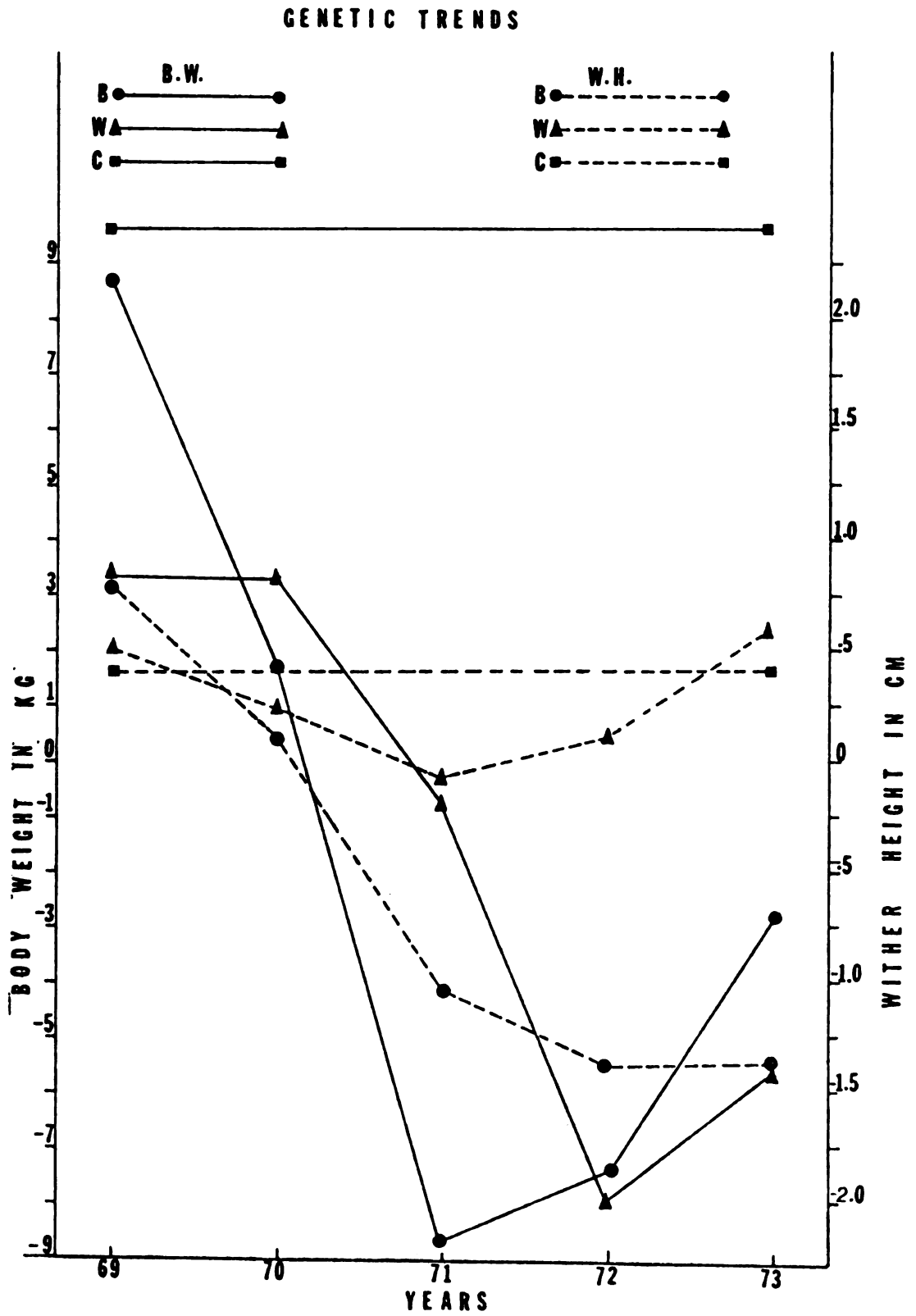


Figure 13

Phenotypic and Genetic Correlations

Phenotypic Correlations

Phenotypic correlations were calculated by simple product moment correlations of the average phenotypic deviation per year (5 yr) for each line. Table 24 presents the phenotypic correlations within each line and between line differences for milk, milk fat, body weight, and wither height. The phenotypic correlation of body weight was .03 and .37 and of wither height was .19 and -.96 with milk in best and worst lines, respectively. Phenotypic correlations among all traits in the best line were expected to be nearly the same as in worst line, but, in fact, there were big differences between lines in phenotypic correlations. These differences are due to small sample size with larger standard errors. There was a positive phenotypic correlation (.87) of milk and milk fat from differences between the lines. Phenotypic correlations of differences between lines for body weight and wither height were +.13 and -.54 with milk production. Phenotypic correlations of differences between lines measure the relationship of spread for one trait with the spread of another trait between the two lines. The negative phenotypic correlation of milk with wither height indicates that the differences between the two lines for wither height are undetectable when there is a big spread between the two lines for milk. At the same time, small positive correlation of body weight and milk appears to show some difference between the lines for body weight. These results agree with Harville and Henderson (30), who reported low (.08 to .17) but positive phenotypic correlation of (ME) milk production and body weight

Table 24. Phenotypic product moment correlations of the average estimated phenotypic effects per year (5 yr) for milk, milk fat, body weight, and wither height within best and worst line and differences between lines

	Milk	Milk fat	Body weight	Wither height
		<u>BEST (L₁)</u>		
Milk		+.33	+.03	+.19
SE		.55	.58	.57
Milk fat	+.91		+.52	+.56
SE	.24		.49	.48
Body weight	+.37	+.011		+.89
SE	.54	.58		.26
Wither height	-.96	-.82	-.42	
SE	.16	.33	.52	
Milk		+.87	+.13	-.54
SE		.28	.57	.49
Milk fat			-.17	-.84
SE			.57	.31
Body weight				+.025
SE				.58
Wither height				
SE				

in Holstein, Guernsey and Jersey breeds. The report from the Iowa State University Holstein herd (20) gave phenotypic and genetic correlations of wither height, paunch girth, heart girth and the ratio of the latter two with mature equivalent milk production in the range of .5 or larger. Phenotypic correlations in my study reflect mostly genetic correlations among traits because the data pertain to one herd where all lines were treated alike.

Genetic Correlations

Genetic correlations suggest the degree and direction of correlated change in a trait when selection pressure is placed upon a second trait. Generally genetic correlations are calculated from daughter-dam relationship and paternal half-sib variances and covariances. In this study genetic correlations (Table 25) were calculated by simple product moment correlations of average genetic values per year for all the traits within each line and differences between lines. There was a positive genetic correlation of .71 between milk and milk fat, indicating that there are common genes which influence both milk and milk fat. Therefore, selection for milk production indirectly selects for milk fat at the same time. It agrees with results in the literature. Body weight and wither height were negatively genetically correlated, ranging from -.004 to -.82 in both the lines with milk yield, and the genetic correlations of body weight and wither height between the line differences were small (.004 to .24). It appears from the results that body size had little influence on milk production. This is in contrast to most of the studies (3,8,23,24,26,34) which reported a positive association of

Table 25. Genetic product moment correlations of the average estimated genetic effects per year (5 yr) for milk, milk fat, body weight, and wither height within best and worst line and differences between lines

		Milk	Milk fat	Body weight	Wither height
		<u>BEST (L_1)</u>			
WORST (L_2)	Milk		+.91	-.0035	-.37
	SE		.24	.58	.54
	Milk fat	+.68		+.35	+.02
	SE	.42		.54	.58
	Body weight	-.40	-.94		+.91
	SE	.53	.20		.24
	Wither height	-.82	-.38	+.07	
	SE	.33	.54	.58	
	Milk		+.71	+.004	+.24
	SE		.41	.58	.56
	Milk fat			+.27	-.53
	SE			.56	.49
	Body weight				-.19
	SE				.57
	Wither height				

body size with milk and milk fat production. Body size on the whole has been an inferior means of predicting future milk production (27,28,29). Davis and Willet (11) also found no significant correlation indicated by gain in weight, increase in height at withers for the first lactation and lifetime averages of lactations. From present information it is difficult to arrive at any conclusion regarding the relationship of body size with milk production. My results are based upon a small sample of data which had standard errors and the data may not be sufficient to separate the lines on body size. Secondly, body size has been studied as an indirect response to selection on milk production, which requires the experiment to be continued for a few more years to collect sufficient data for a precise estimate of correlated response in body size.

SUMMARY AND CONCLUSIONS

Data collected over a 5 yr period from Michigan State University's Holstein herd were used to measure the phenotypic and genetic trends in a selected trait (milk) and nonselected traits (milk fat, body weight, and wither height). Two lines (best and worst) were created from one herd using best and worst bulls selected on first evaluation of their daughters' milk production in Michigan. From the analysis of 179 first lactation records adjusted to mature equivalent, 2X and 305 days, best line produced 1802 kg and 13.6 kg of more milk and milk fat than the worst line. Control line was produced by 13 bulls which were active AI when the experiment was started; this was a base for comparison with other lines.

There were 1142 repeated measurements on each trait (body weight and wither height) recorded on 179 cows at different ages to measure genetic and phenotypic correlated responses and their relationship with milk and milk fat production. The least square means of all the traits when compared with arithmetic averages were within one standard deviation; thus, the differences could be ascertained by looking at the arithmetic averages.

From the least square analysis of variance lines were found to have had no detectable difference for body weight and wither height when these lines were significantly different for milk and milk fat. Least square constants were estimated for each trait by model 1.

Constants for years (G_i) reflected the environmental changes. There was a decline in environment from 1971 to 1973. This decline could be due to appointment of a new farm manager and modification in the amount of feeding concentrates to the cows. Because selection of dams had little influence on milk and milk fat, it appears that the cows were not culled from the herd by milk production.

The bull group constants ($\hat{B}_{(ij)k}$) indicated genetic differences among bull groups. The weighted constant of each bull group within line was plotted to make comparison of classes of bull groups for each trait. The differences between bull groups reflected the selection of bull groups for milk. The graphs of bull group constants for milk fat, body weight, and wither height indicated a correlated response to selection on milk yield. The response of bull groups for milk fat was similar to milk yield, indicating a positive correlation of milk fat and milk whereas response of bull groups for body weight and wither height was irregular under different age groups and with the whole data.

The constants for the individual sire effects were estimated by a separate model because of computational difficulties on the computer. A comparison of sires' mean deviation for milk from herd average was made with the initial basis of selection (daughters' deviation from breed average in Michigan) and with the latest predicted differences calculated by USDA sire summary of November 1974. The rank correlation between USDA sire summary and MSU data was .72. The rank correlation of USDA sire summary with initial basis of selection was higher (.92) due to larger number of daughters. Sires could have been ranked more accurately if there had been more daughters per sire.

Average genetic progress in kilograms per year was 46.7, -9.4 for milk and 1.2, -7.7 for milk fat in best and worst line, respectively, calculated by regressing the average genetic values on years. The two lines were, therefore, spreading apart by 56 kg and 9 kg per year for milk and milk fat. On the other hand, the average genetic change for body weight and wither height remained almost unchanged between the two lines. This indicated little influence of milk yield on body weight and wither height.

Phenotypic and genetic correlations among all the traits were to establish the relationship among the traits. The phenotypic correlations reflected mostly the genetic correlations among traits because of measurements in one herd and all the lines were treated alike. Genetic correlations were calculated by simple product moment correlations from average genetic values estimated per year for each trait. There was a positive genetic correlation of .71 between milk and milk fat. Body weight and wither height were negatively genetically correlated (-.004 to -.82) in both the lines with milk yield. The genetic correlations of body weight and wither height with milk production between the line differences were small (.004 to .24), although positive. Body size had little influence on milk production. Since body size has been studied as an indirect response to selection for milk production, it requires a larger amount of data for precise estimate of correlated response in body size. In conclusion, selection of bulls in AI for milk produced significant changes in yield of milk and fat. There was little change in body size as an indirect response to selection on milk production and the effects were clouded by sampling of small numbers. Trends were short and unstable and, as

the experiment progresses, they will stabilize enough to measure the relation of body size with milk production.

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