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IN A HOLSTEIN HERD.

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RESULTS OF SELECTION FOR PRODUCTION
IN A HOLSTEIN HERD

by

Robert Eugene Walton

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I. INTRODUCTION

Improvement in the genetic capacity of a dairy herd to produce milk should be a major objective of a breeder of dairy cattle. Continued improvement results only from deliberate selection. Since selection in a dairy herd is a continuing process, both its practice and its measurement are difficult. Selection takes place among all ages within each generation and also between animals of different but overlapping generations. If the practical maximum improvement per year or per generation could be known, that would be a useful standard by which a breeder could compare the progress in his own herd.

Selection of cows who will produce the calves and of the sires who will sire them will not in general be equally accurate or equally intense or happen at the same stages in the life cycle. Also some cows will be thought worthy of producing daughters but not worthy to have their sons used as sires. These things make it convenient to consider separately selection as being exerted on any one or all of four places in the pedigree of the succeeding generation. Those are the choice of: (1) bulls whose sons will be used as sires; (2) bulls whose daughters will be saved but not their sons; (3) cows whose sons will be used as sires; and (4) cows whose daughters will be saved but not their sons. The relative contribution that each of these four paths can make to the total genetic improvement of a herd will not in general be equal. Obviously, the source that can make the largest contribution should receive the most emphasis, also taking account of the relative expensiveness, accuracy and timeliness of selection through each path.

The average production of a herd is likely to increase with time, for several non-genetic reasons. Foremost would be the increase in skill and experience of the dairyman. Also research is likely to find ways of improving the methods of feeding and management from time to time and these new findings or devices are likely to find their way into practice more or less steadily. Partially offsetting these positive trends might be the emphasis on more efficiency in the total dairy operation which tends to reduce the care and concern for the individual cow. The increase in size of the herd and the intensity of the dairy enterprise on an individual farm may have tended to intensify the troubles from parasitism and contagious diseases. Successful measurement of genetic trends is dependent upon accurate evaluation of and adjustment for the effects which these changes in environment have had on the production records of a herd.

The first requisite for evaluating genetic improvement was accessibility to records of a herd which had been subjected to deliberate selection for several generations. If, in addition, the herd was a closed breeding unit during that period, evaluating the selection intensity would not only be simpler but also more accurate. This desirable combination of requirements seemed to exist in the Iowa State University Holstein herd which had been nearly closed to outside breeding since 1930 and wholly so since 1937.

The initial purpose of this study was to determine the genetic progress that had been made in the herd. Age correction factors, repeatability values, and environmental trends had to be assumed or estimated before the genetic trends could be evaluated. A considerable portion of

the thesis thus deals with secondary purposes, which were to investigate how errors in these related factors might bias the estimates of genetic change.

II. REVIEW OF LITERATURE

A. Methods of Estimating Environmental and Genetic Trends

Measuring the environmental effect on a herd would seem to be simply a problem of comparing successive lactations of the same cow. After removing the environmental trend from the records, the genetic changes would remain. This approach was used by Lörtscher (15) and with more formal statistics by Nelson (23).

Rendel and Robertson (28) demonstrated the logical error in this approach which negates the conclusions drawn. Their argument was that records of the same cow in successive years will vary systematically for two reasons: first, changes in management and environment whose effect we wish to evaluate and discount, and secondly, increase in the age of the cow. Before comparison of records in successive years can be made, therefore, all yields must be adjusted to their equivalent at a standard age. To do this, correction factors must be used. If these are calculated from the data provided by the herd under review, they will include the changes due to both environmental and genetic trends. Correction factors taken from other data would have similar objections in addition to doubt of their suitability to the conditions which had affected the herd under study.

If the problem of determining age correction factors could be ignored, the approach used by Lörtscher (15) and Nelson (23) of fitting a least squares model still has the objection of leading to biased estimates due to the effects of culling and of incomplete repeatability. Henderson (8) pointed out that a least squares procedure in which cow

effects are regarded as fixed (i.e., repeatability = 1.0) leads to biased estimates. Lush and Shrode (18) gave an explanation of the biases arising in the estimation of age correction factors and the same argument applies to the estimation of year effects. Their hypothesis was that year effects estimated by comparing all records made in each of two successive years would be biased upward by an amount $r(\mu' - \mu)$ where r is repeatability, μ is the herd average for the first year, and μ' is the mean of the cows retained in the herd after the first record. However, year effects estimated by comparing records made by the same cow in successive years would be biased downward to the extent $(1-r)(\mu' - \mu)$.

Henderson et al. (10) presented two methods for maximum likelihood estimation of environmental and genetic trends. Method I used the linear model.

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

where y_{ikt} is the record in the k^{th} year made by the i^{th} cow of the t^{th} group of cows in a herd; μ is the population average; d_k is the environmental effect of the k^{th} year; g_t is the mean real producing ability of the t^{th} group; c_{it} is the real producing ability of the i^{th} cow of the t^{th} group; and e_{ikt} is a random environmental effect peculiar to the individual record. The problem is to estimate differences among the d 's and g 's assuming that repeatability is known.

This is the same method as originally presented by Henderson (8). If appropriate age correction factors and repeatability values are available, this method will give unbiased estimates of genetic and environmental effects, whereas the least squares method will not.

Method II of Henderson et al. (10) has the same model as Method I except for the use of four subscripts on Y , Y_{ijkl} being the record made in year k by the i^{th} cow of the group of cows whose first records were made in year t , it being the cows j^{th} record. Thus j is no more than an ordinal indication of which record of the cow Y_{ijkl} is and in terms of the elements of the model it plays no part. It does make possible the estimation of repeatability as an integral part of the computations. Searle (10) showed that the two methods were equivalent for a given repeatability.

Rendel and Robertson (28) concluded that indirect estimates such as least squares of the genetic gain under selection were useless. Their alternative was to estimate genetic gains directly from the selection applied. They considered the whole process of selection as really composed of four parts; namely, the contribution of male and female parents to male offspring and of male and female parents to female offspring, respectively. The total improvement would be the sum of the four individual components. The four components were designated I_{BB} , I_{CB} , I_{BC} and I_{CC} , where I_{BB} represented the mean genetic superiority of bulls from which bull calves were bred, I_{CB} the mean genetic superiority of cows from which bull calves were bred, etc. The mean age of each of the four groups was designated L_{BB} , L_{CB} , L_{BC} , and L_{CC} , respectively. The rate of genetic improvement from selection is then

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

The information necessary to compute this estimate includes heritability, selection differential, and generation length for the herd and trait

under consideration.

B. Age Correction Factors

Lush and Shrode (18) have pointed out that the primary purpose of correction factors is to remove phenotypic differences which occur because the environmental conditions were not uniformly those chosen as standard. The corrections ought not to remove from the records any differences really caused by things inherent in the cows themselves. However, the inherent and the environmental causes of differences are often confounded so that it is difficult or impossible to separate cleanly the effects of one from the effects of the other. For example, if at each age some cows with low records are culled, then the older cows will include a larger fraction of those with inherently high production than are among all cows which make records at the younger ages. If the regression of production on age is computed from the averages of all data available at each age, that curve will not show the effects of age alone but will show those effects combined with whatever effects such culling actually had. An opposite bias is introduced if the average inherent productivity of the dairy population is increasing. In that case, at any given date the averages for the older cows do not include records from the cows born in recent years when the average productivity of the population had become higher. In this way the effects of any genetic time trends in inherent productivity may be confounded with the effects of age.

Lush and Shrode (18) computed age correction factors using 43,573 records from the files of the Holstein-Friesian Association of America.

The change in production was measured by the ratio between production at one age and production by the very same cows in their next lactation. They concluded that the Kendrick (12) factors were a bit too large at ages under 35 months and a bit too low at ages around 45 to 66 months. They observed a discontinuity in the age curve at near 35 months which perhaps had resulted from cows calving unusually young, both the first and second time. Presumably these cows began their second lactations still very immature and in many cases somewhat depleted nutritionally. Consequently, their second lactations were much smaller than their third ones and this caused a larger correction factor to be necessary for them than for their contemporaries of the same age calving for the first time.

Madden et al. (20) reported from a study of relations between parts of lactations and producing ability of Holstein cows of the Iowa State University herd that in this case correction of 243 day records for age using the D.H.I.A. factors (13) failed to remove age effects wholly, especially when applied to records begun before 3 years of age. Using 305 day correction factors for 243 day records may have caused this effect since heifers are usually more persistent than mature cows.

The effect of age is not independent of management. Bonnier et al. (3), working with monozygous twins, found that cows which matured early from heavy feeding did not show as marked an age effect as cows reared on a lower plane of nutrition. Searle and Henderson (32) reported that additive corrections for age should be larger in high-producing herds than in low-producing herds. Multiplicative factors tended to take account of differences between herds in age effects. These reports would seem to be in conflict but can be resolved by considering that in the

data of Bonnier et al. both groups of cows were subjected to the same favorable environment after coming into production and the cow raised on a lower plane of nutrition would have an opportunity to recover from the limiting effects of her earlier environment. In the data studied by Searle and Henderson, each cow was apt to remain under the same management throughout her life. Cows in low-producing herds tended more nearly to reach the environmental maximum at an early age. Thus, both situations support the thesis that correction factors, to be wholly satisfactory, should be adjusted to the management of the herd in question. Adequate degrees of freedom may not be available for attainment of this ideal adjustment.

Rendel and Robertson (28) noted that though errors in age correction factors are small, the age effect is large compared with the other effects, and any errors in its estimation will be cumulative.

The effect of age factors was further illustrated by Kempthorne and Von Krosigk (10) using the maximum likelihood method. Considering only first and second records made in successive years over a 14-year period, they found that using the factor 1.25 instead of 1.28 as a correction for first records increased the estimate of the environmental change by approximately 120 pounds of butterfat.

Henderson (9a) applied the maximum likelihood method to 11 New York herds. Two different sets of age correction factors were used. For each extra pound by which first records were built up, the environmental trend was biased downward by 0.22 pound of butterfat per cow per year. He also reported that for each 0.01 by which repeatability used in the estimation procedure exceeded true repeatability, the downward bias was

0.08 pound of butterfat per cow per year.

C. Repeatability Estimates

Madden et al. (20) analyzed 599 records by 253 cows of the Iowa State University herd made from 1940 through 1952. They attempted to remove the additional age effects remaining after using the D.H.I.A. factors (13) by considering as separate ages the records begun by cows before and after 3 years of age as one source of variation in an analysis of variance. Repeatability was computed as an intraclass correlation expressed as

$$\frac{\sigma_c^2}{\sigma_c^2 + \sigma_e^2},$$

where σ_c^2 and σ_e^2 are cow and lactation mean squares, respectively. If the differences between means of different orders are first removed and the variances are homogeneous this would be the correlation between records by the same cow. Madden et al. obtained estimates of repeatability of .545 and .481 for 243 day lactations, and .510 and .434 for 305 day lactations, for milk and fat, respectively. Their investigation indicated that production during the later months of a lactation was determined more by temporary environmental influences and less by permanent differences between cows than was production during the early months. This seemed to indicate that persistency of production was determined primarily by extraneous environmental sources and was not affected much by the inherent qualities of the cow herself.

In a study of 454 Holstein H.I.R. cows which had completed 6 or

more lactations, Berry (2) obtained an estimate of 0.29 for intraherd repeatability for butterfat production. This lower than usual estimate was attributed to the selection that had occurred within the herds where these cows were kept. Discarding after each lactation some of the cows with low records would, on account of imperfect repeatability, cause the mean of the first records of the survivors to be at least a little higher than the mean of their later lactations. Proximity was a strong factor in determining the correlation between records. Adjacent lactations showed an average correlation of 0.35 while those with 3 lactations intervening had an average correlation of 0.22. This suggested a general tendency for records made close together in time to be more highly correlated than records separated by long time intervals. An overlapping of common environmental effects from one lactation to the next would contribute to this correlation. There was also some tendency for later records to be more closely correlated with each other than the earlier records were with each other.

Laben and Herman (14), using intraclass correlation, obtained estimates of 0.41 and 0.36 for repeatability of milk and fat, respectively, in the Missouri Station Holstein herd. They found that the repeatability estimates for milk increased from 0.29 to 0.44 as adjustments were made for age and environmental effects.

Wadell (38) examined two methods (intraclass correlation computed from variance components and a combined estimate computed from regression of the next record on the sum of all earlier records) of computing repeatability for bias because of the possible existence of curvilinear relations, incompleteness in U.S.D.A. age correction factors, and

selection. He found little evidence to show any curvilinearity important enough to influence the estimates materially. Inequality of age corrected records at various ages caused a decrease in the intraclass correlation of the order of 0.020 and in the regression estimate of only 0.004. His estimates of intraclass correlation ranged from .387 to .449 and from .355 to .422 for milk and fat production, respectively. The combined regression estimates ranged from .469 to .516 and from .456 to .497 for milk and fat production, respectively. Failure to correct for differences between means may have played a major role in causing the difference in the estimates from these two methods. When no account was taken of the differences which selection caused between the means of first records and of second records of cows who had both, the intraclass correlation decreased 0.020 for each increase of 5 percent in truncation selection. Correcting for inequality of means of the first and second lactations eliminated almost all of this decline in the computed intraclass correlations even when selection as severe as 50 percent truncation selection was practiced.

D. Extent of Selection Practiced

Rendel et al. (29) studied the records of 22 high yielding herds in Britain, some of which were well-known bull breeding herds, to measure the amount of selection being practiced. The mean selection differential was 3.14 percent of the average yield. As a result of culling, the average genetic superiority of the cows which left heifers in the herd was 1.55 percent above their contemporaries. Culling of cows alone was estimated to give an annual genetic improvement of about 0.15 percent.

The cows from which bull calves were kept for use in pedigree herds were on the average 3.2 percent superior in yield genetically to their contemporaries. Bulls used in the herd in which they were bred were from dams that averaged 6.2 percent superior to their contemporaries genetically. From both culling and the selection of dams of bulls, Rendel et al. estimated that the probable genetic improvement would have been 0.3-0.4 percent per year.

Seath (33) studied in considerable detail the culling in 186 D.H.I.A. herds in Iowa and Kansas. He found an average culling differential of 4.1 and 3.1 percent for yield in Iowa and Kansas, respectively. Low yield was the chief cause of culling, accounting for 30.5 percent of all cows culled. Included in the low yield group were cows sold for beef and low producers sold for dairy purposes. The latter group ranked below any other group in production. Good producers sold for dairy purposes represented 19.0 percent of those leaving the herds. Culling for low production generally took place in the early lactations. Seath's estimate of the probable annual genetic improvement in yield as a result of culling (considering the results from both states) ranged between 25 and 38 pounds of milk and 0.28 and 1.55 pounds of butterfat.

E. Studies on Genetic Progress in Dairy Cattle

Plum and Rumery (27) reported a genetic improvement of approximately 7 pounds of butterfat per generation as a result of selection in the North Platte, Nebraska, Experiment Station Holstein herd. The average generation interval was 5.2 years for cows and 4.2 years for bulls. An effective selection differential of about 20 pounds of butterfat was

maintained through a rigorous selection program.

Nelson and Lush (24) found an increase in genetic ability for butterfat production of 40 pounds from 1930 to 1942 in the Iowa State University Holstein herd. This net change included an estimated 4.5 pound decrease in butterfat for each percent increase in inbreeding. The rather high increase of over 3 pounds of butterfat per year was attributed to intensive selection of the dams of sires. Losses from disease during this period limited severely the selection among females.

Laben and Herman (14) found a significant upward time trend in milk and butterfat production and in butterfat percent in the Missouri Station herd from 1902 to 1950. Butterfat increased about $1\frac{1}{2}$ pounds per year. No attempt was made to differentiate between the effects of heredity and management.

In a study of the Holstein herd at the University of Illinois, Dillon et al. (6) found the regression of average producing ability on years to be 0.68 pounds of 4 percent-fat-corrected milk per year while the environmental effects improved about 54 pounds of fat-corrected milk per year. This would indicate that practically all the improvement which took place during the 54 years covered by the study was due to improvement in the environment.

Harvey (7) estimated an annual increase in genetic merit of 8.0 and 5.3 pounds of butterfat in the University of Idaho Holstein and Jersey herds, respectively. These estimates are considerably higher than any other reported estimates.

Rendel and Robertson (28) estimated that selection of cows contributed a genetic increase of 33 pounds of milk per year in a herd of British

Friesian cattle. This represented an annual increase in genetic merit of 0.7 percent of the herd mean. Most of the increase was attributed to the selection of cows whose sons were used in the herd.

In a study of 12 herds of Ayrshire cattle, Mahadevan (21) found a total improvement per generation of 25½ pounds of milk (2.5 percent of the herd average). Selection of dams of cows accounted for a genetic improvement of only .3 percent per year.

F. Effect of Inbreeding

Von Krosigk and Lush (37) estimated the effect of inbreeding on production, using data from the Iowa State University Holstein herd covering the period 1930 to 1955. This herd was essentially closed to outside breeding during these years and the average inbreeding had risen to 11.8 percent. They found intrasire regressions of -1.7½ pounds of butterfat, -5½ pounds of milk, and +0.003 percent butterfat, for each 1 percent increase in inbreeding. They hypothesized that inbreeding caused some of the decrease in production through its detrimental effect on body size but some of its effects came through other paths. The authors suggested that inbreeding may act more to lower the rate of development than it does to limit eventual size and production at maturity. They found no evidence to indicate that the regression on inbreeding was not linear within the moderate range of inbreeding values covered by this study.

Studies by Bartlett and Margolin (1), Davis et al. (4), Laben and Herman (14), Nelson and Lush (24), Plum (26), Robertson (30), and Tyler et al. (34) gave values for the inbreeding effect similar to those

reported by Von Krosigk and Lush.

G. Progeny Testing as an Aid to Selection

Dickerson and Hazel (5) have pointed out that the criterion by which any breeding program must be judged is the genetic improvement per year rather than per generation. The extra information about a sire's genotype which a progeny test provides must be weighed against the increase in generation length resulting from using progeny-tested sires. They concluded that when breeding for butterfat production in dairy cattle in a closed herd of 120 cows, the genetic improvement would actually be faster without progeny testing. The main reasons for ineffectiveness of progeny testing in small herds are that (a) when a sufficient number of cows have been used to test the young bulls adequately, few cows are left on which to use the tested bulls, and (b) the number of young bulls that can be tested is small and hence the selection possible after the test is known is limited in its intensity.

III. SOURCE AND ADJUSTMENT OF DATA

An experiment was inaugurated in 1930 with the Iowa State University Holstein herd to test the practicability of improving dairy cattle by moderate inbreeding accompanied by intense selection. The herd then consisted of 42 females, 29 of which were in milk. The amount of inbreeding at the beginning of the experiment was probably similar to that found in the average purebred Holstein herd. The general breeding system previously followed was that of outbreeding with occasionally a limited amount of linebreeding. When a new sire was needed, he was selected from a currently prominent herd. Johnson (11) described the foundation and early history of the herd.

The herd was essentially closed to outside breeding in 1930. Exceptions were three proved sires from other herds which were used in 1932, 1933, and 1934, some heifer calves in 1932, and the addition in 1937 of several cows and heifers when the University veterinary and experimental herds were consolidated. Since 1937 the herd has been completely isolated from outside breeding.

During the first decade of the experiment about 20 to 50 females of milking age were maintained in the herd. Since 1940 the milking herd has consisted of about 70 to 80 cows.

The breeding system followed was to use sons of the best producing cows and to keep them in service until sufficient cows (30 or more) were bred to each one to be fairly certain he would have at least 8 tested daughters. This resulted in most of the bulls being used for slightly over one year each. The bulls were then sold with the option of

repurchase. This option was exercised only twice. Consequently, progeny testing of sires played a minor role as an aid to selection.

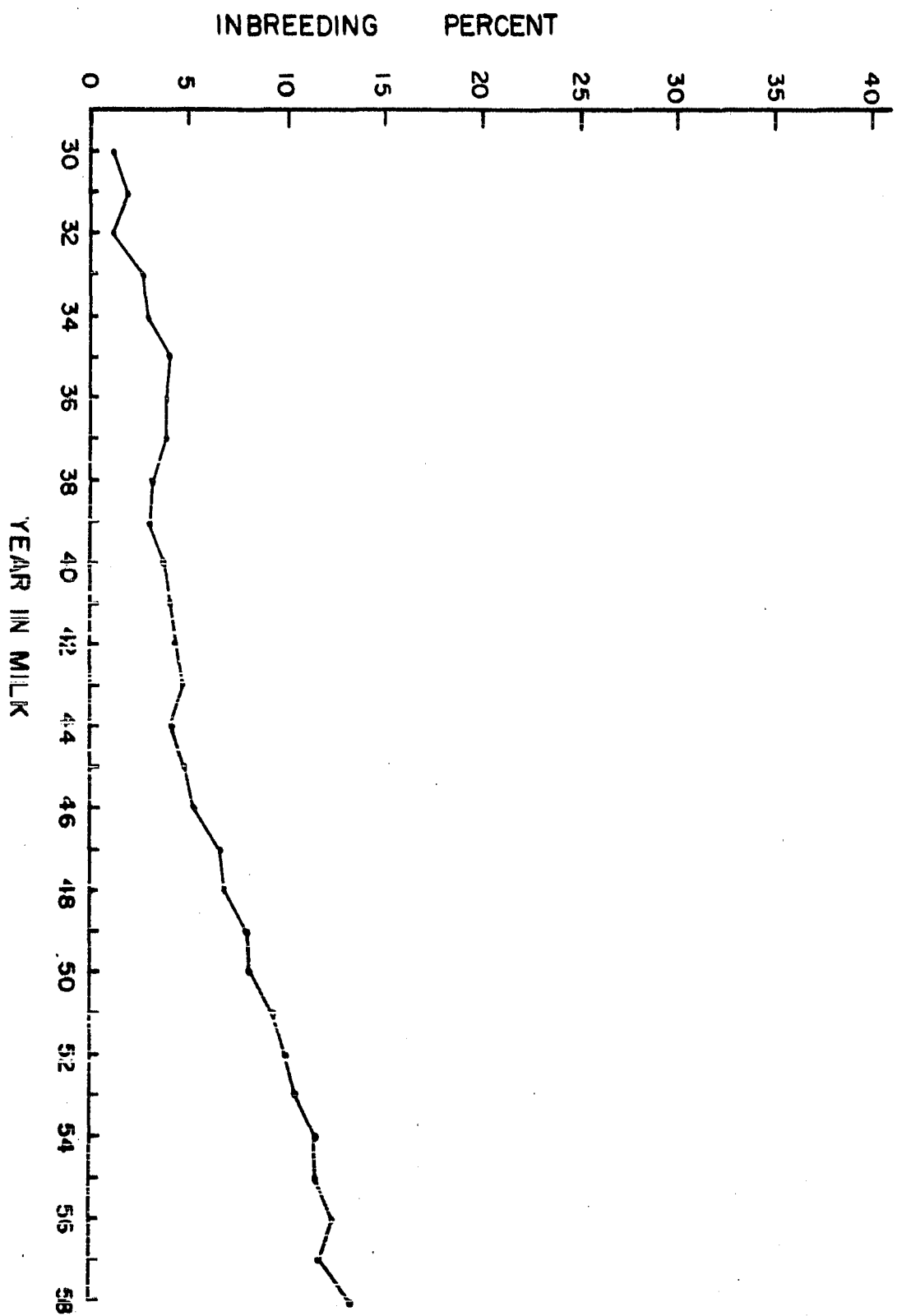
Inbreeding of animals in the herd during the period covered by this study ranged from zero to 35 percent with a mean of 7.1 and a standard deviation of 7.6. The average inbreeding of cows who calved in 1958 was 13.3 percent. Few cows in the early years were inbred as high as 12.5 percent. The inbreeding rose from an average of 1.1 percent in 1930 to 5.3 percent in 1946, i.e., and increase of 0.26 percent per year. Since 1946 the increase has averaged 0.67 percent per year. This may be compared with an increase of 0.08 percent per year in the Holstein breed from 1881 to 1931 as reported by Lush et al. (19). Figure 1 shows the average inbreeding of the herd for each of the years.

Relationship within the herd increased from an average of 11.7 percent in 1935 to 17.5 percent in 1946 and to 28.7 percent in 1958. Thus, the average relationship among cows currently in the herd exceeds that among paternal half sibs whose dams were unrelated. Lush et al. (19) found an average relationship within the Holstein breed in 1931 of 3.4 percent.

One cow, No. 2386, who was the hub of a linebreeding program through the use of 5 sons and 3 daughters in the herd, had an average relationship with the 1958 milking herd of 28.5 percent. In relationship she was slightly closer than a granddam to the herd. This relationship ranged from 10.8 to 65.8 percent. By careful planning of matings, it would still be possible to increase the relationship of the herd to this cow to an even higher level (toward a maximum of 65.8 percent, i.e., the highest

Figure 1. Average inbreeding percent of the Iowa State University Holstein herd (1930-1958).

FIG. 1



relationship any presently living descendant has to her).

A selection index, utilizing information on relatives as well as own performance and considering production roughly three times as important as type, has been used since about 1941. In the earlier years of the experiment selection among females was almost non-existent because of the high incidence of brucellosis, tuberculosis and pneumonia, as well as the need for more animals in an expanding herd. The selection index has been followed (when there were degrees of freedom for its use) except for rare vetoes based on serious objection to type or to color markings.

Management of the herd was maintained as nearly uniform as was consistent with practical conditions. The cows were fed a balanced ration of concentrates according to production, plus a hay and silage allowance according to body weight. Each cow was given a dry period of four to six weeks. The calves were fed liberally for full development and were bred first at 15 months or shortly thereafter. All heifers were kept until at least one lactation was completed unless they died or were barren (with the exception of 2 or 3 heifers consigned to state sales one year).

The herd was milked three times a day from 1930 to 1935 and from 1937 to 1941. Some few animals were milked four times daily in 1930 and 1931. The herd was milked twice daily from July 1935 (when fire destroyed the barns) until 1937 and from 1941 (when labor and management considerations made that seem the best long-time policy) to date.

Production records used in the present analysis were those made during the period 1930 to 1958, inclusive. To avoid corrections for

effects of pregnancy, only the first 243 days of each lactation were used. Evidence shown by Madden et al. (20) that 243 day records were a better indication of genetic ability for milk and butterfat production than 305 day records supported this decision. Every record was included unless evidence written in the herd books listed definitely an abnormality affecting the record. These exceptions were few. Records of less than 243 days were included as complete unless the cow was sold while milking. In that case the record was extrapolated to 243 days by the factors given in B.D.I.-D.H.I.A. 10, in the D.H.I.A. record book. All records were standardized to a 243 day, two-time milking, mature equivalent basis using U.S.D.A. age correction factors derived by Kendrick (13).

The 685 cows included in the analysis had 1,747 records which averaged 371 pounds of fat and 11,056 pounds of milk with a butterfat test of 3.35 percent. These 685 cows were daughters of 80 sires. However, only 48 sires were used in the herd during this period and these 48 sired 582 of the cows. The remaining 32 sires had a total of 103 daughters who were part of the original herd or were introduced during the first seven years.

Except for an increase from 3.03 to 3.37 percent during the first two years of the experiment, the butterfat percent has remained stable about a mean of 3.35. No further evaluation was made on the butterfat percent except to note that inbreeding seemed to have no effect upon it.

An adjustment was made to standardize the records to zero percent inbreeding. The corrections used were taken from the estimates made by Von Krosigk and Lush (37) of the regression of production on inbreeding. On a 243-day basis these corrections were to add 1.5 pounds of fat and

47 pounds of milk for each increase of one percent inbreeding. After this adjustment the 1,747 records averaged 382 pounds of butterfat and 11,366 pounds of milk with a butterfat test of 3.35 percent.

Table 1 gives the production, age, inbreeding and size of the herd for each of the 29 years included in this analysis.

Table 2 permits comparing, by inbreeding levels, the production before and after adjustment to zero inbreeding.

Table 1. Production, age, inbreeding and size of the herd (1930-1958)

Year	No. cows	Av. age	Av. inbr.	Av. 243 day ME 2x			Av. after inbr. adjustment	
				Milk	Fat	%	Milk	Fat
1930	24	51.1	1.08	10203	309	3.03	10254	311
1931	16	47.7	1.88	10490	335	3.19	10578	338
1932	17	48.6	1.06	10748	362	3.37	10798	364
1933	32	47.8	2.78	10666	363	3.40	10797	367
1934	36	46.0	2.92	10764	351	3.22	10901	356
1935	41	43.4	4.07	10948	371	3.39	11140	377
1936	36	48.1	3.78	11515	382	3.32	11692	388
1937	39	39.6	3.79	10882	371	3.41	11060	377
1938	49	43.7	3.29	10730	361	3.36	10884	366
1939	67	44.5	3.01	10507	354	3.37	10649	359
1940	68	46.2	3.74	10350	352	3.40	10526	358
1941	72	48.1	4.08	9895	335	3.37	10087	341
1942	72	48.8	4.43	10430	346	3.32	10638	353
1943	78	46.5	4.87	10504	358	3.41	10733	366
1944	67	47.5	4.09	10701	351	3.28	10893	357
1945	59	47.4	4.86	10656	365	3.42	10884	373
1946	65	43.2	5.34	11192	390	3.48	11443	398
1947	78	45.8	6.63	11918	403	3.38	12229	413
1948	72	46.1	6.94	12396	422	3.40	12722	432
1949	81	42.7	8.10	11358	389	3.42	11739	401
1950	82	46.3	8.40	11332	382	3.37	11726	394
1951	69	51.6	9.33	11826	400	3.38	12264	414
1952	87	48.2	9.93	11275	380	3.36	11742	395
1953	70	53.0	10.53	11184	360	3.22	11680	376
1954	72	47.2	11.51	11353	383	3.36	11894	400
1955	70	45.3	11.66	10982	376	3.41	11530	393
1956	80	44.3	12.49	11309	375	3.31	11896	394
1957	69	50.6	11.87	11271	363	3.22	11829	381
1958	79	46.7	13.34	11305	378	3.34	11923	398
Overall av.	60.2	46.7	7.08	11056	371	3.35	11388	382

Table 2. Production data, by inbreeding levels, before and after adjustment to zero inbreeding

Inbr. percent	No. cows	Av. lact. per cow	Av. inbr. percent	Av. 243 day ME 2x		Av. after inbr. adjustment	
				Milk	Fat	Milk	Fat
0	92	3.0	0	10939	369	10939	369
1-3	114	2.9	2.2	10626	361	10727	365
4-6	105	2.9	5.0	11369	378	11603	386
7-9	128	2.7	8.0	11211	378	11585	390
10-12	85	2.2	11.1	11276	372	11797	389
13-15	61	2.0	14.1	11238	375	11899	396
16-18	38	1.9	17.0	10987	369	11788	395
19-21	38	1.8	19.9	10668	362	11602	392
21-24	14	2.0	22.7	11358	366	12424	400
> 25	10	1.4	28.1	9772	339	11094	382

IV. METHODS OF INVESTIGATION

A. Consideration of Age Correction Factors

Since age correction factors are large in comparison with the genetic improvement possible in five or six generations, the data were examined to determine the suitability of the U.S.D.A. factors (13) (for 305 day lactations) to the 243 day lactations used in the present study.

Grouping by lactation number tends to ignore year to year differences. However, as pointed out by Lush and Shrode (18), if the average inherent productivity of a herd is increasing, the younger cows with the improved inheritance will contribute more heavily to the early lactations. Any selection practiced in the herd will introduce an opposite bias since the older cows will include a larger fraction of those with inherently high production.

These data also contained a bias in that the percentage of inbreeding increased throughout the experimental period. The assumption was made, however, that adjusting the data to zero percent inbreeding removed this bias.

The data were sorted by lactation number and were further subdivided depending on whether or not that cow had a succeeding lactation. Lactation means for selected and unselected groups are given in Table 3. (1958 records were not available when this portion of the analysis was being made.)

Cows which had a second lactation averaged in their first lactations on M.E. data corrected for inbreeding 14 pounds of butterfat above the average of all first lactations. However, their second lactations

Table 3. Means by lactation number of unselected, selected, and culled groups

Group	No.	Av. inbr.	ME basis		Inbr. corr. ME basis	
			Milk	Fat	Milk	Fat
A ₁ ^a	628	8.0	11043	373	11420	385
B ₁₀ ^b	219	9.9	10191	345	10654	360
C ₁₂ ^c	409	7.0	11500	388	11830	399
D ₂₁ ^{d,e}	409	7.0	11057	369	11387	380
A ₂	420	6.9	11035	368	11359	379
B ₂₀	171	8.3	10513	347	10902	360
C ₂₃	249	5.9	11394	383	11672	392
D ₃₂	249	5.9	10923	366	11201	375
A ₃	257	6.0	10870	366	11150	375
B ₃₀	108	6.3	10193	344	10487	353
C ₃₄	149	5.8	11362	382	11630	390
D ₄₃	149	5.8	11088	370	11361	379
A ₄	152	5.8	11122	371	11394	380
B ₄₀	60	6.8	10210	334	10530	344
C ₄₅	92	5.2	11716	395	11958	403
D ₅₄	92	5.2	11459	384	11702	392
A ₅	97	5.2	11429	383	11673	391
B ₅₀	15	5.8	10854	364	11125	372
C ₅₆	52	4.7	11927	400	12147	408
D ₆₅	52	4.7	11457	388	11678	395

^aA_i represents mean of all i^{th} lactations.

^bB _{i_0} represents mean of all i^{th} lactations that were terminal.

^cC _{$i, i+1$} represents mean of all i^{th} lactations that were not terminal.

^dD _{$i+1, i$} represents mean of $i+1^{\text{th}}$ lactations of cows which had an i^{th} lactation.

^eD _{$i+1, i$} differs from A _{$i+1$} primarily because of the few cows which entered the herd in early years after producing their 1st, 2nd, ..., i^{th} lactations in another herd. The few records rejected for abnormality also contributed to this difference.

Table 3. (Continued)

Group	No.	Av. inbr.	ME basis		Inbr. corr. ME basis	
			Milk	Fat	Milk	Fat
A6	54	4.5	11427	385	11640	392
B60	25	4.3	11109	369	11311	376
C67	29	4.8	11700	399	11924	406
D76	29	4.8	10951	369	11175	376
A7	31	4.6	10772	363	10985	370
B70	14	5.1	9940	320	10181	328
C78	17	4.1	11457	397	11648	404
D87	17	4.1	10754	363	10944	369
A8	17	4.1	10754	363	10944	369
B80	10	4.5	10145	345	10356	352
C89	7	3.4	11624	389	11785	395
D98	7	3.4	10170	354	10331	359
A9	7	3.4	10170	354	10331	359
B90	3	3.7	9297	328	9470	334
C9.10	4	3.2	10824	372	10977	378
D10.9	4	3.2	10077	343	10230	348
A10	4	3.2	10077	343	10230	348
B10.0	3	4.3	10581	365	10785	371
C10.11	1	0	8565	278	8565	278
D11.10	1	0	7705	271	7705	271

averaged 4 pounds less than the unselected first lactations. Thus, they regressed not only downward toward the mean but below it. The same tendency, to a lesser degree, was found when the second lactations of those cows which had third lactations were studied similarly. This regression below the means of the unselected preceding lactations indicated either that the age correction factors were overcorrecting the first and second lactations or that a negative correlation existed between first and second lactations of the same cows and between second and third lactations of the same cows which nullified the apparent progress obtained through selection.

It is conceivable that the few heifers with exceptionally high first lactations might have a physiological imbalance. Such a condition might overtax their body and lead to such things as sterility or broken udders at an early age and cause them to be culled for reasons other than productivity. Wadell (38) noted a slight deviation from normality in the distribution of cows with first lactations but without second lactations. These constituted an excess of only 0.5 percent in the number of cows beyond two standard deviations above or below the mean as compared with an entirely normal distribution. This was a maximum estimate since in Wadell's data some of these first lactation cows were still in the herd but had not completed second lactations when the study began. It was concluded that evidence was against the relationship between first and second lactations really being negative.

Discussion with those who worked with the project indicated that young animals which grew up in this herd were probably better fitted

and prepared for maximum milk production than heifers in an average D.H.I.A. herd. If this was correct, it would add credence to the suggestion that the standard U.S.D.A. age correction factors were slightly overcorrecting the records of young animals in this herd.

The relative magnitude of selected and unselected third, fourth, and fifth lactations agreed with values expected from data in which strong selection pressure had been applied. Since these records required little or no age correction this would cast further doubt on the suitability of the age corrections for the younger cows.

Lactations beyond the fifth (which include 114 of the 1,668 records used in this part of the study) present a situation similar to that found in the early lactations. The selected cows averaged less in their subsequent lactation than the average of all records in the current lactation. It is possible that the environment for older cows was deteriorating. Another partial explanation is that a few of the older cows were retained in the herd for the progeny they would leave even though they themselves were no longer profitable producers due to injury or disease. However, if that is so and if their records were to be included without adjustment, a strong downward bias in the estimate of the general environmental trend would result.

It was apparent that an attempt should be made to adjust the age correction factors to the conditions that existed in this particular herd.

Separating the inherent and environmental causes of age differences completely would seem to be impossible in almost any data. An empirical approach appeared to be the only alternative in the present case.

Objections of Rendel and Robertson (28) to using age correction factors derived from data under review were by-passed to some extent since the records have been at least partially age-corrected by U.S.D.A. factors which were independent of this herd.

If we let

\bar{y}_i = mean of all i^{th} lactations

y_i = mean of cows selected from all i^{th} lactations

y_{i+1} = mean of the subsequent lactations of cows selected
on the basis of i^{th} lactations

c_i = additional age correction for i^{th} lactations

r = repeatability

e_i = residual error

then $c_i \bar{y}_i$ represents the mean of all i^{th} lactations after being perfectly adjusted for age.

From a general regression model the following equations can be written:

$$c_2 \bar{y}_2 = c_1 \bar{y}_1 + r c_1 (y_1 - \bar{y}_1) + e_2$$

$$c_3 \bar{y}_3 = \left[\frac{c_1 \bar{y}_1 + c_2 \bar{y}_2}{2} \right] + \frac{r}{1+r} \left[c_1 (y_1 - \bar{y}_1) + c_2 (y_2 - \bar{y}_2) \right] + e_3$$

$$c_n \bar{y}_n = \left[\frac{\sum_i c_i \bar{y}_i}{n-1} \right] + \frac{r}{1+(n-2)r} \left[\sum_i c_i (y_k - \bar{y}_i) \right] + e_n$$

The e_i 's were assumed to be normally and independently distributed around zero with constant variance. Repeatability was assumed the same for all records. The latter assumption is not wholly correct as evidenced

by the effects of adjacency in estimating repeatability from regression.

Values of 0.40 and 0.50 were inserted for r and solutions were obtained for c_i using both milk and butterfat data on an inbreeding-corrected M.E. basis. Setting c_5 equal to 1.000 (i.e., assuming a cow to be mature at the beginning of her fifth lactation or 80 months of age in these data) and adjusting the other c_i values to this basis gave the values shown in Table 4. Since the estimates of repeatability obtained by Madden et al. (20) on a portion of these same data, after removing age differences by another method, were of the magnitude of 0.50, the corrections obtained using this value were used. Also influencing the decision to use these values in preference to those obtained with $r = 0.40$ was that they introduced a smaller correction and thus would be less apt to introduce biases opposite in nature to the ones being corrected.

The c_i values for milk and fat were averaged since they were quite similar. The U.S.D.A. factors are compared in Table 5 and in Figure 2 before and after adjustment by these corrections. The adjusted corrections for seventh and later lactations increased in magnitude faster than the U.S.D.A. factors and may reflect conditions quite peculiar to this herd. Since a total of only 60 cows are included in these age groups, these values are subject to large sampling errors and should not be taken as an indication that the U.S.D.A. factors were in error for the general population of cows older than eight years.

The disparity between the U.S.D.A. and the adjusted age correction factors was relatively small for the ages at which most of the records were made in this herd and would create minor or imperceptible differences

Table 4. Corrections computed by lactation number for adjusting U.S.D.A. (13) age correction factors

Lact. no.	No. records	r=0.40		r=0.50		Av. for milk and fat with r=0.50
		Milk	Fat	Milk	Fat	
1	628	.9490	.9515	.9661	.9610	.964 = c_1
2	420	.9780	.9780	.9793	.9914	.995 = c_2
3	257	1.0020	1.0020	1.0206	1.0186	1.020 = c_3
4	152	1.0047	1.0072	1.0194	1.0201	1.020 = c_4
5	97	1.0000	1.0000	1.0000	1.0000	1.000 = c_5
6	54	1.0127	1.0071	1.0094	1.0004	1.005 = c_6
7	31	1.0894	1.0661	1.0587	1.0560	1.057 = c_7
8	17	1.1325	1.1112	1.0869	1.0895	1.088 = c_8
9	7	1.1968	1.1744	1.1618	1.1256	1.144 = c_9
10	4	1.2608	1.2372	1.1812	1.1681	1.175 = c_{10}
11	1	1.4887	1.4609	1.5457	1.5280	1.537 = c_{11}

Table 5. Comparison of U.S.D.A. (13) and adjusted age correction factors.

Lact. no.	Av. age in mo.	U.S.D.A. (13) age correction factor	Correction factor (c_i)	Adjusted age correction factor
1	27.0	1.28	.964	1.234
2	40.4	1.14	.995	1.134
3	53.8	1.04	1.020	1.061
4	66.9	1.01	1.020	1.030
5	80.2	1.00	1.000	1.000
6	92.7	1.00	1.005	1.005
7 ^a	108.7	1.02	1.057	1.078
8 ^a	124.2	1.05	1.088	1.142
9 ^b	136.8	1.07	1.144	1.224
10 ^b	154.0	1.11	1.175	1.304
11 ^c	186.0	1.15	1.537	1.768

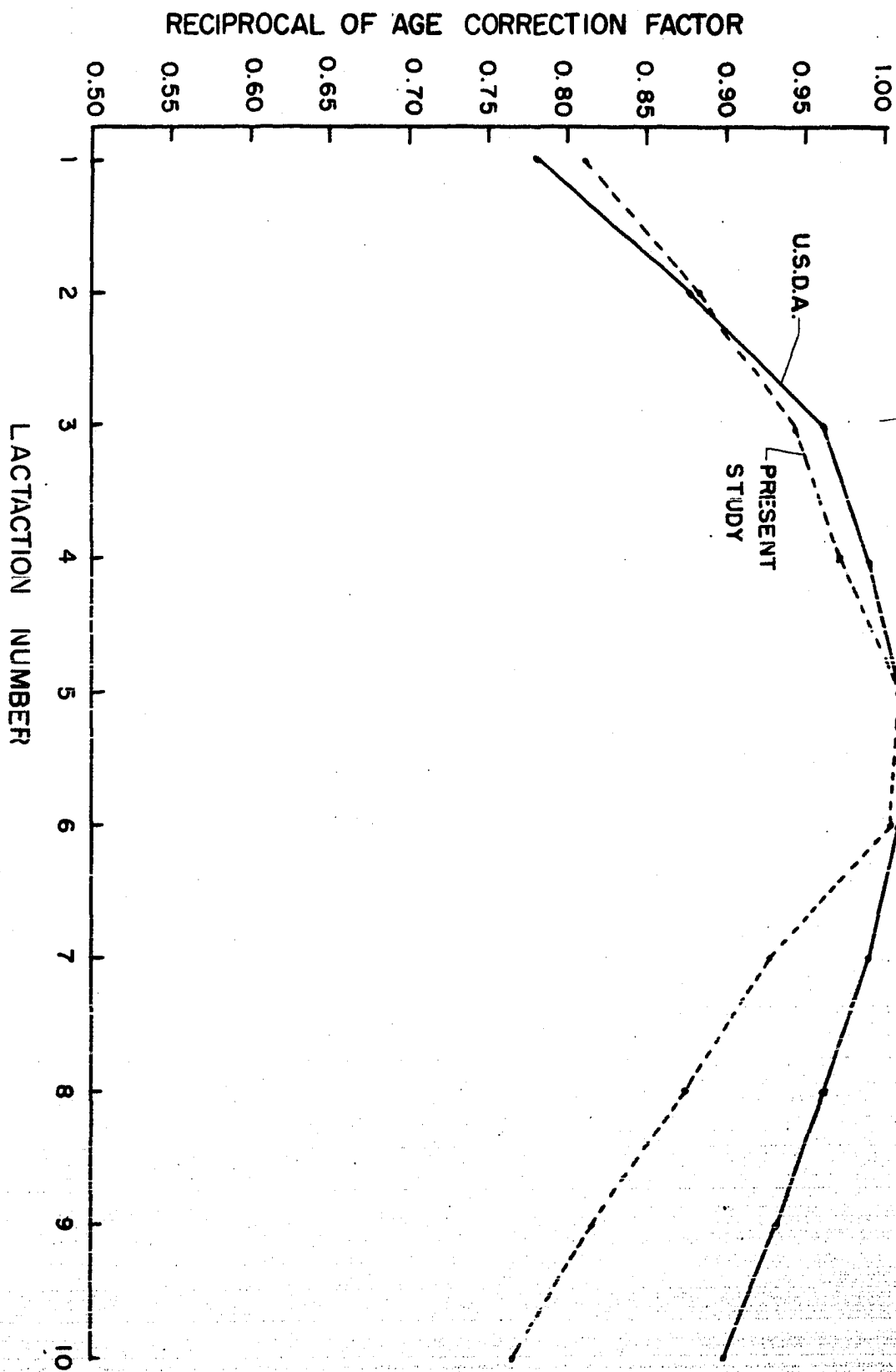
^a31 or fewer per group.

^b7 or fewer per group.

^c1 cow in group.

Figure 2. The regression of production on age, according to two sets of age correction factors.

FIG. 2



in the usual range of application of age correction factors. The major cause of the difference between the two sets of factors at the younger ages was probably that the increased persistency of first calf heifers was not fully taken into account when 305 day factors were applied to 243 day lactations. Nevertheless, for the purpose intended in the present study these minor differences were cumulative and soon would become major in relation to the genetic change.

The data were adjusted by the c values derived and the means thus obtained for selected and unselected groups are shown in Table 6.

To facilitate later discussion and reference the following designations will hereafter apply:

Method I. Records standardized to a two-time milking, 243 day, mature equivalent basis using the U.S.D.A. factors for age (13).

Method II. Same as Method I plus adjustment to zero percent of inbreeding.

Method III. Same as Method II plus additional adjustments for age using the factors derived from these data.

B. Estimation of Repeatability

1. Regression estimates of repeatability

In this portion of the analysis only Method II data were used since the age correction evaluation had not then been accomplished. Only cows which had records in successive lactations, beginning with the first, were included. Records beyond the 5th or begun in 1958 were also excluded. After these restrictions were met, there remained 409 cows which had both

Table 6. Means by lactation number of unselected, selected, and culled groups after adjustment by the derived age correction factors.

Group	No.	Av. inbr.	Means after adjustment	
			Milk	Fat
A ₁ ^a	628	8.0	11009	371
B ₁₀ ^b	219	9.9	10270	347
C ₁₂ ^c	409	7.0	11404	385
D ₂₁ ^{d,e}	409	7.0	11330	378
A ₂	420	6.9	11302	377
B ₂₀	171	8.3	10847	358
C ₂₃	249	5.9	11614	390
D ₃₂	249	5.9	11425	382
A ₃	257	6.0	11373	382
B ₃₀	108	6.3	10697	360
C ₃₄	149	5.8	11863	398
D ₄₃	149	5.8	11588	387
A ₄	152	5.8	11622	388
B ₄₀	60	6.8	10741	351
C ₄₅	92	5.2	12197	411
D ₅₄	92	5.2	11702	392
A ₅	97	5.2	11673	391
B ₅₀	45	5.8	11125	372
C ₅₆	52	4.7	12147	408
D ₆₅	52	4.7	11736	397

^aA_i represents mean of all ith lactations.

^bB₁₀ represents mean of all ith lactations that were terminal.

^cC_{i,i+1} represents mean of all ith lactations that were not terminal.

^dD_{i+1,i} represents mean of i+1th lactations of cows which had an ith lactation.

^eD_{i+1,i} differs from A_{i+1} primarily because of the few cows which entered the herd in early years after producing their 1st, 2nd, ..., ith lactations in another herd. The few records rejected for abnormality also contributed to this difference.

Table 6. (Continued)

Group	No.	Av. inbr.	Means after adjustment	
			Milk	Fat
A ₆	54	4.5	11698	394
B ₆₀	25	4.3	11368	378
C ₆₇	29	4.8	11984	408
D ₇₆	29	4.8	11812	397
A ₇	31	4.6	11611	391
B ₇₀	14	5.1	10761	347
C ₇₈	17	4.1	12312	427
D ₈₇	17	4.1	11907	401
A ₈	17	4.1	11907	401
B ₈₀	10	4.5	11267	383
C ₈₉	7	3.4	12822	430
D ₉₈	7	3.4	11819	411
A ₉	7	3.4	11819	411
B ₉₀	3	3.7	10834	382
C _{9.10}	4	3.2	12558	432
D _{10.9}	4	3.2	12020	409
A ₁₀	4	3.2	12020	409
B _{10.0}	3	3.2	12672	436
C _{10.11}	1	0	10064	327
D _{11.10}	1	0	11842	416

first and second records, 239 cows which had first, second and third records, 141 cows which had first, second, third, and fourth records, and 86 cows which had first, second, third, fourth and fifth records.

Regressing the second record on the first, the third on the sum of the first two, the fourth on the sum of the first three and the fifth on the sum of the first four gave four estimates of regression. They can best be represented in tabular form. Table 7 shows the regression estimates, the resulting estimates of repeatability, and the weights for

Table 7. Estimates of repeatability from regression

	Source	Estimate	\hat{r}	Weight
<u>Milk</u>	\hat{r}	0.616 ± 0.047	0.616 ± 0.047	461
	$\hat{r}/1+\hat{r}$	0.346 ± 0.032	0.528 ± 0.074	182
	$\hat{r}/1+2\hat{r}$	0.214 ± 0.031	0.375 ± 0.097	105
	$\hat{r}/1+3\hat{r}$	0.124 ± 0.037	0.199 ± 0.094	112
<u>Fat</u>	\hat{r}	0.605 ± 0.051	0.605 ± 0.051	389
	$\hat{r}/1+\hat{r}$	0.299 ± 0.039	0.426 ± 0.079	162
	$\hat{r}/1+2\hat{r}$	0.222 ± 0.036	0.399 ± 0.117	73
	$\hat{r}/1+3\hat{r}$	0.155 ± 0.037	0.291 ± 0.130	59

combining the estimates.

The weighted estimate of repeatability from the regression coefficients was 0.514 ± 0.034 for milk and 0.513 ± 0.036 for fat.

The pooled estimates as well as some of the separate estimates were higher than expected. Scrutiny of the data and of the method provided several plausible explanations. The estimate of regression of second on first lactations was apt to be strongly inflated by the effects of proximity. These effects would decline in intensity as the dependent variable became further removed by time from the independent variables. This would account, in part at least, for the steady decline in the estimate of regression as more independent variables, i.e., increased time intervals, were included. Since the regression of second on first

lactations received the most weight in the pooled estimate, the strongest proximity effect likewise received the most weight.

These estimates of repeatability were not entirely independent since many of the same lactations contributed to the variance and covariance terms of the separate estimates of regression. As a consequence of proximity and of lack of complete independence, the regression method would tend to overestimate repeatability.

2. Intraclass correlation estimates of repeatability

For this analysis the data were divided into 14 birth year groups as described in section IV-C-2. The intraclass correlations obtained by analyzing Method I and Method II data are shown in Tables 8 and 9, respectively.

The standard errors of the intraclass correlations were approximated by the method of Osborne and Paterson (25).

The estimates from Method II data were smaller than estimates from Method I data because the variation between cows was reduced by adjusting the data to zero percent inbreeding. The mean squares within cows in Tables 8 and 9 differ only because of rounding errors. In theory they should be exactly the same.

After the additional age corrections were made as described in section IV-A to produce Method III data, the intraclass correlations were again computed. These results are shown in Table 10.

The higher estimates from Method III data reflect the effect the additional age adjustments had upon removing the inequality between means of primarily first and second lactations. This supports Wadell's (38)

Table 8. Analysis of variance of Method I data

Source of variation	d.f.	Mean squares		Expected mean squares
		Milk	Fat	
Total	1746			
Between groups	13	24,826,237	32,473.15	$E + 3.649C + 124.145 G$
Between cows/groups	671	5,927,132	6,103.55	$E + 2.527C$
Within cows	1062	2,204,711	3,020.03	E
C		1,473,059	1,220.23	
C/C+E		0.400 ± 0.027	0.288 ± 0.028	

Table 9. Analysis of variance of Method II data

Source of variation	d.f.	Mean squares		Expected mean squares
		Milk	Fat	
Total	1746			
Between groups	13	42,056,611	49,723.85	$E + 3.649C + 124.145 G$
Between cows/groups	671	5,854,518	5,976.02	$E + 2.527C$
Within cows	1062	2,204,632	3,020.33	E
C		1,444,355	1,169.64	
C/C+E		0.396 ± 0.027	0.279 ± 0.028	

Table 10. Analysis of variance of Method III data

Source of variation	d.f.	Mean squares		Expected mean squares
		Milk	Fat	
Total	1746			
Between groups	13	37,693,506	46,095.27	$E + 3.649C + 124.145 C$
Between cows/groups	671	6,177,275	6,428.31	$E + 2.527C$
Within cows	1062	2,005,111	2,742.39	E
C		1,651,223	1,458.61	
C/C+E		0.441 ± 0.026	0.347 ± 0.028	

conclusion that correcting for inequality of means of different orders eliminated almost all of the decline in computed intraclass correlations.

The estimates of repeatability from intraclass correlation of 0.396 and 0.279 for milk and fat yield, respectively, were considerably lower than the corresponding estimates of 0.514 and 0.513 from regression using Method II data. Using Method III data, in which the inequality between means was partially corrected, increased the intraclass correlations to 0.441 and 0.347 for milk and fat, respectively.

In using the analysis of variance technique, it was necessary to assume a homogeneity of variance among the different orders. This assumption might not be valid in a population in which selection had occurred. Culling decreases the variance among cows by removing the lower segment of the distribution. This results in a decreased estimate of the cow effect and consequently a decrease in the numerator of the

intraclass correlation. The denominator would also be decreased but to a lesser extent since σ_c^2 is only one part of the denominator.

It was concluded that the intraclass correlation method underestimated the true repeatability in these data. As shown by the work of Madell (38), however, Method III data in which the inequality of means of different orders was at least partially corrected would be expected to provide the best estimates of repeatability. These were the repeatability estimates used later in this thesis for computing the final estimates of genetic and environmental trends by the maximum likelihood method.

C. Maximum Likelihood Estimation of Genetic and Environmental Trends

1. Model, assumptions and computational methods

The model for this analysis was the same as used by Henderson in his section of the paper by Henderson et al. (10). This model was

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

where

d_k refers to the environmental period in which a record was started ($k = 1, \dots, q$),

g_t refers to genetic group ($t = 1, \dots, p$),

c_{it} refers to individual within genetic group (m_t cows in the t^{th} group),

and

n_{ikt} = number of records made by the i^{th} cow in the k^{th} period.

μ , d , and g are regarded as fixed, while c and e are normally and independently distributed with means of zero and variances of

σ_c^2 and σ_e^2 , respectively. Repeatability was assumed known and equal to $r = \frac{\sigma_c^2}{\sigma_c^2 + \sigma_e^2}$.

The solution to the following equations provides values that can be used for the maximum likelihood estimation of estimable linear functions of the fixed elements of the model and for their sampling variances.

$$\begin{pmatrix} R & B & C \\ B' & D & E \\ C' & E' & F \end{pmatrix} \begin{pmatrix} G \\ Y \\ K \end{pmatrix} = \begin{pmatrix} U \\ V \\ M \end{pmatrix}$$

where

R is a p^2 diagonal matrix with elements $n_{i,t}$.

B' is a $(q-1) \times p$ matrix with elements n_{kt} , where

k refers to row and t to columns of this matrix and

$k = 1, \dots, (q-1)$.

C is a $p \times m$ matrix with elements $n_{i,t}$.

D is a $(q-1)^2$ diagonal matrix with diagonal elements $n_{k,k}$.

E' is an $m \times (q-1)$ matrix with elements n_{ikt} where i and

t refer to rows and k to columns of this matrix.

F is an m^2 diagonal matrix with diagonal elements

$$n_{i,t} + \frac{1-r}{r}.$$

G is a $p \times v$ matrix of unknowns.

Y is a $(q-1) \times v$ matrix of unknowns.

K is an $m \times v$ matrix of unknowns.

v refers to the number of different variates.

U is a $p \times v$ matrix with elements $y_{..t}$.

V is a $(q-1) \times v$ matrix with elements $y_{.k}$.

M is a $m \times v$ matrix with elements $y_{i,t}$.

Briefly, maximum likelihood is a method which estimates the parameters of the population which would be more likely than any other population to have yielded this supposed random sample. If an efficient estimator for small samples exists (i.e., has minimum variance), the then maximum likelihood estimators, adjusted for bias if necessary, will be efficient.

Solutions were obtained using an IBM 650 with a program written by Henderson (9b). For one complete run on the volume of data included in this analysis, approximately nine hours of machine time were required. Computations required for mean squares and sampling variance-covariance matrices (which were necessary only for computing the standard errors) were particularly slow. The standard errors obtained on the first run (see section 3a) were reasonably small. Consequently, standard errors were not computed for subsequent analyses.

2. Grouping and classification of data

To meet restrictions on the capacity of the program, the data were divided into 14 genetic groups (i.e., $t=1, \dots, 14$) and 24 environmental periods (i.e., $k=1, \dots, 24$) as indicated in Tables 11 and 12, respectively. The means for Methods I, II, and III data are also listed in these tables.

An inherent fault of any data on dairy cattle which includes several

Table 11. Means of genetic groups for Methods I, II and III data

Genetic group	Birth years included	Av. inbr.	No. cows	No. lact.	Method I		Method II		Method III	
					Milk	Fat	Milk	Fat	Milk	Fat
1	Before 1930	1.9	29	86	10775	350	10841	352	10947	356
2	1930-32	3.0	41	105	10933	368	11128	375	11031	371
3	1933-34	3.9	33	102	10596	361	10768	367	10877	371
4	1935-36	3.4	39	117	10394	346	10549	351	10468	349
5	1937-38	3.7	44	154	10435	351	10583	356	10543	355
6	1939-40	5.6	47	132	10605	361	10834	368	10757	366
7	1941-42	5.3	48	114	11027	366	11261	373	11166	370
8	1943-44	7.0	61	192	11380	393	11680	403	11659	402
9	1945-46	7.4	45	141	11764	392	12101	403	12104	403
10	1947-48	10.1	65	159	11530	388	11998	403	11919	400
11	1949-50	11.5	60	132	11353	377	11869	394	11730	389
12	1951-52	13.4	65	135	11013	369	11616	389	11432	382
13	1953-54	12.4	61	129	11344	377	11922	396	11740	390
14	1955-56	15.9	47	54	11326	375	12051	398	11661	385
Average		7.1	49	125	11056	371	11388	382	11311	379

Table 12. Means of environmental periods for Methods I, II and III data

Environmental period	Years included	Av. inbr.	No. lact.	Method I		Method II		Method III	
				Milk	Fat	Milk	Fat	Milk	Fat
1	1930-32	1.3	57	10446	332	10507	334	10435	332
2	1933-34	2.8	68	10718	357	10852	361	10721	357
3	1935-36	3.9	77	11213	376	11398	382	11313	379
4	1937-38	3.5	88	10797	365	10962	371	10818	366
5	1939	3.0	67	10507	354	10649	359	10557	356
6	1940	3.7	68	10351	352	10526	358	10472	356
7	1941	4.1	72	9895	335	10087	341	10054	340
8	1942	4.4	72	10430	346	10638	353	10599	351
9	1943	4.9	78	10504	358	10733	366	10651	363
10	1944	4.1	67	10701	351	10893	357	10836	355
11	1945	4.9	59	10556	365	10884	373	10854	371
12	1946	5.3	65	11192	390	11143	398	11293	393
13	1947	6.6	78	11918	403	12229	413	12125	410
14	1948	6.9	72	12396	422	12722	432	12718	432
15	1949	8.1	81	11358	389	11739	401	11647	398
16	1950	8.4	82	11332	382	11727	395	11631	392
17	1951	9.3	69	11826	400	12264	414	12183	412
18	1952	9.9	87	11275	380	11742	395	11631	391
19	1953	10.5	70	11184	360	11680	376	11671	376
20	1954	11.5	72	11353	383	11894	400	11858	399
21	1955	11.7	70	10982	376	11530	393	11420	390
22	1956	12.5	80	11309	375	11896	394	11764	390
23	1957	11.9	69	11271	363	11829	381	11830	381
24	1958	13.3	79	11305	378	11923	398	11857	396
Average		7.1	73	11056	371	11388	382	11311	379

generations is that all cows will not have lactations in all years. The available data will tend to cluster about the diagonal of a cow by year grouping, i.e., the older cows die before the later years are reached and the more recent cows obviously could not contribute lactations before they were born. This situation seems unavoidable and tends to confound environmental and genetic trends.

The grouping scheme outlined here can be criticized for failure to cleanly separate this confounding. However, the nature of the data make any such separation impossible.

3. Analyses considering all records

a. Effects of adjusting the data to zero percent inbreeding Cal-
culations were made using both Method I and Method II data on all but one of the following eight analyses. Since the results were so similar, only the estimates and standard errors using repeatability of 0.40 and including all records are listed herein. These are given in Tables 13 and 14 in terms of deviations from the overall mean for genetic and environmental trends, respectively, and in corresponding order in Tables 15 and 16 after being converted into actual means. The trends are illustrated in Figures 3 and 4 for milk and fat production, respectively. (The vertical scale for milk in Figure 3 had to be more concise in terms of standard deviations than the vertical scale for fat in Figure 4. This tended to make changes in fat trends appear larger than similar changes in milk trends. For consistency, however, these same vertical scales for milk and fat, respectively, were used in Tables 3-18.)

The genetic estimates from these sets of data differed by an amount

Table 13. Maximum likelihood estimates and standard errors of genetic deviations derived using a repeatability value of 0.40 and including all records

Group	Fat (lbs.)			Milk (lbs.)		
	Method I	Method II	Method III	Method I	Method II	Method III
1	-41+17	-50+17	18+17	-1099+492	-1384+491	618+486
2	-29+14	-35+14	18+13	-908+397	-1112+396	457+392
3	-42+12	-48+12	-3+11	-1250+338	-1437+337	-94+334
4	-49+11	-56+11	-19+11	-1140+316	-1352+315	-278+312
5	-34+10	-40+10	-12+10	-927+284	-1137+284	-304+281
6	-22+9	-26+9	-8+9	-688+274	-800+273	-279+271
7	-26+9	-30+9	-23+9	-484+272	-595+271	-395+268
8	-13+8	-14+8	-20+8	-476+242	-498+242	-676+239
9	-9+10	-9+10	-25+9	-52+280	-50+279	-502+276
10	7+9	11+9	-14+9	272+271	407+270	-322+267
11	34+10	40+10	4+10	957+292	1151+291	108+288
12	53+10	62+10	15+10	1299+303	1594+302	194+300
13	82+11	90+11	35+11	2085+329	2355+328	714+325
14	90+14	104+14	33+14	2412+400	2857+398	758+395

Table 14. Maximum likelihood estimates and standard errors of environmental deviations derived using a repeatability value of 0.40 and including all records

Group	Fat (lbs.)			Milk (lbs.)		
	Method I	Method II	Method III	Method I	Method II	Method III
1	11+17	11+17	-55+16	760+487	771+485	-1188+480
2	24+14	24+14	-36+14	835+417	846+416	-928+412
3	44+12	44+12	-34+12	1209+362	1233+360	-291+357
4	45+10	46+10	2+10	1072+286	1094+285	-203+283
5	30+10	31+10	-7+9	746+279	761+278	-339+276
6	23+9	24+9	-8+9	463+271	495+270	-456+268
7	3+9	4+9	-24+9	-118+258	-87+257	-894+255
8	7+9	8+9	-16+9	345+252	374+252	-325+249
9	15+8	16+8	-3+8	190+240	216+239	-337+237
10	6+8	6+8	-7+8	279+244	282+243	-116+241
11	15+8	15+8	9+8	200+240	201+239	18+237
12	34+8	34+8	34+8	683+230	670+230	589+227
13	42+7	42+7	45+7	1031+213	1038+212	1132+210
14	59+8	59+8	71+8	1468+232	1472+231	1831+229
15	24+8	24+8	40+8	382+235	377+234	845+232
16	7+8	7+8	25+8	121+238	109+237	641+235
17	6+8	6+8	28+8	79+246	74+245	717+242
18	-21+9	-21+8	6+8	-682+248	-585+247	113+245
19	-56+9	-57+9	-22+9	-1205+258	-1213+257	-180+254
20	-37+10	-38+9	3+9	-942+277	-961+276	250+274
21	-54+10	-55+10	-11+10	-1607+286	-1535+285	-345+282
22	-65+10	-66+10	-18+10	-1538+296	-1556+295	-148+292
23	-84+11	-85+11	-29+11	-1826+312	-1870+310	-214+308
24	-78+12	-79+11	-17+11	-1946+335	-2006+334	-172+331

Table 15. Maximum likelihood estimates of genetic means derived using a repeatability value of 0.40 and including all records

Group	Fat (lbs.)			Milk (to nearest 10 lbs.)		
	Method I	Method II	Method III	Method I	Method II	Method III
1	330	332	397	996	1001	1193
2	342	347	397	1015	1028	1177
3	328	334	376	981	995	1122
4	322	326	360	992	1004	1103
5	337	342	367	1013	1025	1101
6	349	356	371	1037	1059	1103
7	345	352	356	1058	1079	1092
8	358	368	359	1058	1089	1063
9	362	373	354	1101	1134	1081
10	378	393	365	1133	1180	1099
11	405	422	383	1202	1254	1142
12	424	444	394	1236	1298	1150
13	453	474	414	1314	1375	1202
14	461	486	412	1347	1425	1207

that reflected the increasingly larger inbreeding corrections applied to each successive group, as would be expected.

The environmental estimates were almost perfectly parallel throughout the years. They differed by a constant equal to the difference between the overall means of Method I and Method II data.

The standard errors were consistently larger, though the differences were barely perceptible, for the Method I estimates. This implied that adjusting the data to zero percent inbreeding decreased the variation among cows. Obviously such a result would be expected.

b. Effects of age correction factors Since age correction factors were important influences in similar studies (9,10) it seemed

Table 16. Maximum likelihood estimates of environmental means derived using a repeatability value of 0.40 and including all records

Group	Fat (lbs.)			Milk (to nearest 10 lbs.)		
	Method I	Method II	Method III	Method I	Method II	Method III
1	382	393	324	1182	1216	1012
2	395	406	343	1190	1224	1038
3	415	426	371	1227	1262	1102
4	416	428	381	1213	1248	1111
5	401	413	372	1181	1215	1097
6	394	406	371	1152	1189	1085
7	374	386	356	1094	1130	1042
8	378	390	363	1140	1176	1098
9	386	398	376	1125	1161	1097
10	377	388	372	1134	1167	1119
11	386	397	388	1126	1159	1133
12	406	416	410	1174	1206	1190
13	412	424	424	1209	1243	1244
14	430	441	450	1253	1286	1314
15	395	406	419	1144	1177	1216
16	378	389	404	1118	1150	1195
17	377	388	407	1114	1146	1203
18	350	361	385	1038	1071	1142
19	315	325	357	986	1018	1113
20	334	344	382	1012	1043	1156
21	317	327	368	945	975	1096
22	306	316	361	952	983	1116
23	288	297	350	923	952	1110
24	293	303	362	911	938	1114

Figure 3. Environmental and genetic trends estimated from Method I and Method II milk data by the maximum likelihood method using a repeatability value of 0.40 and including all records.

FIG. 3

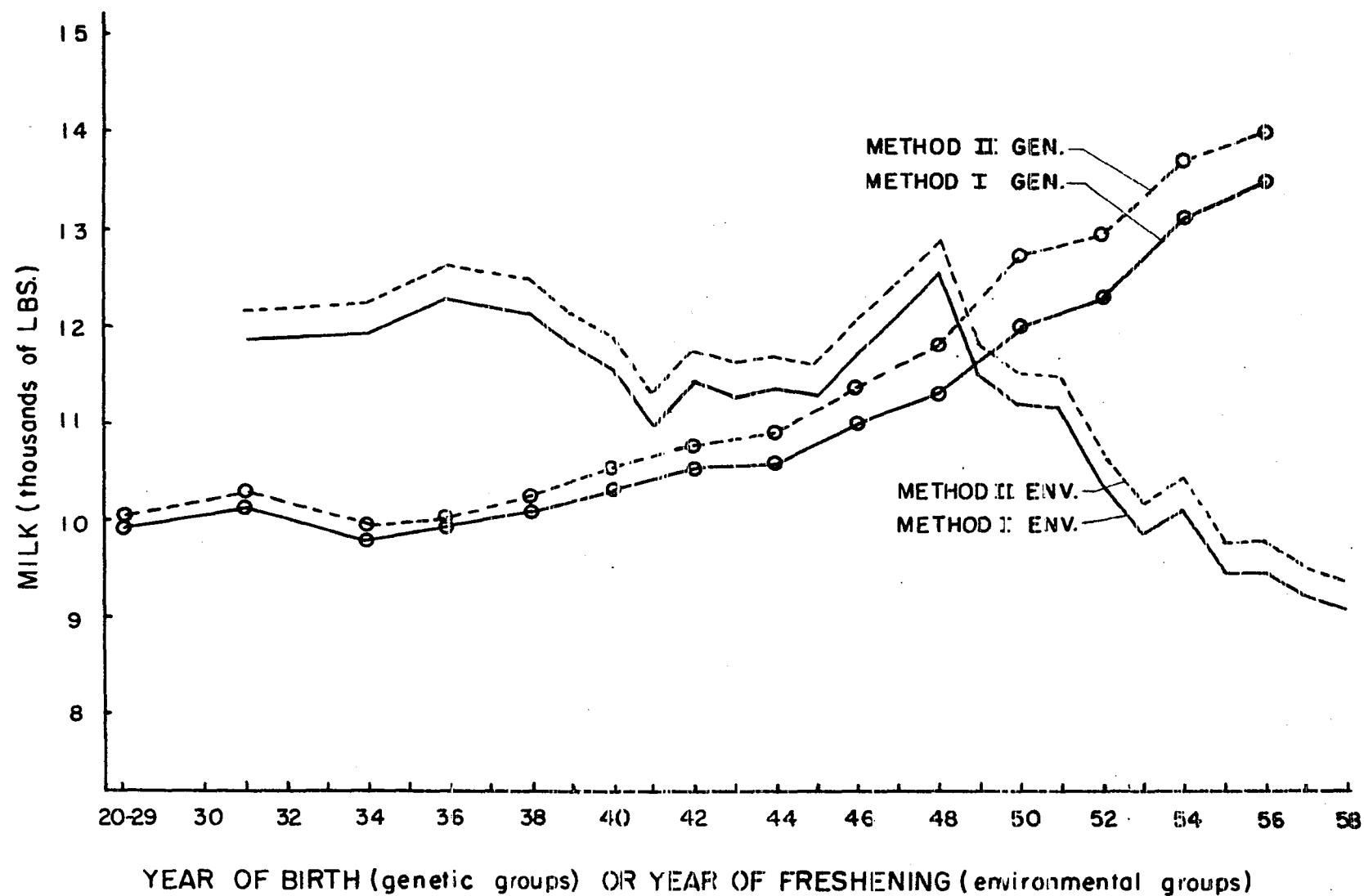
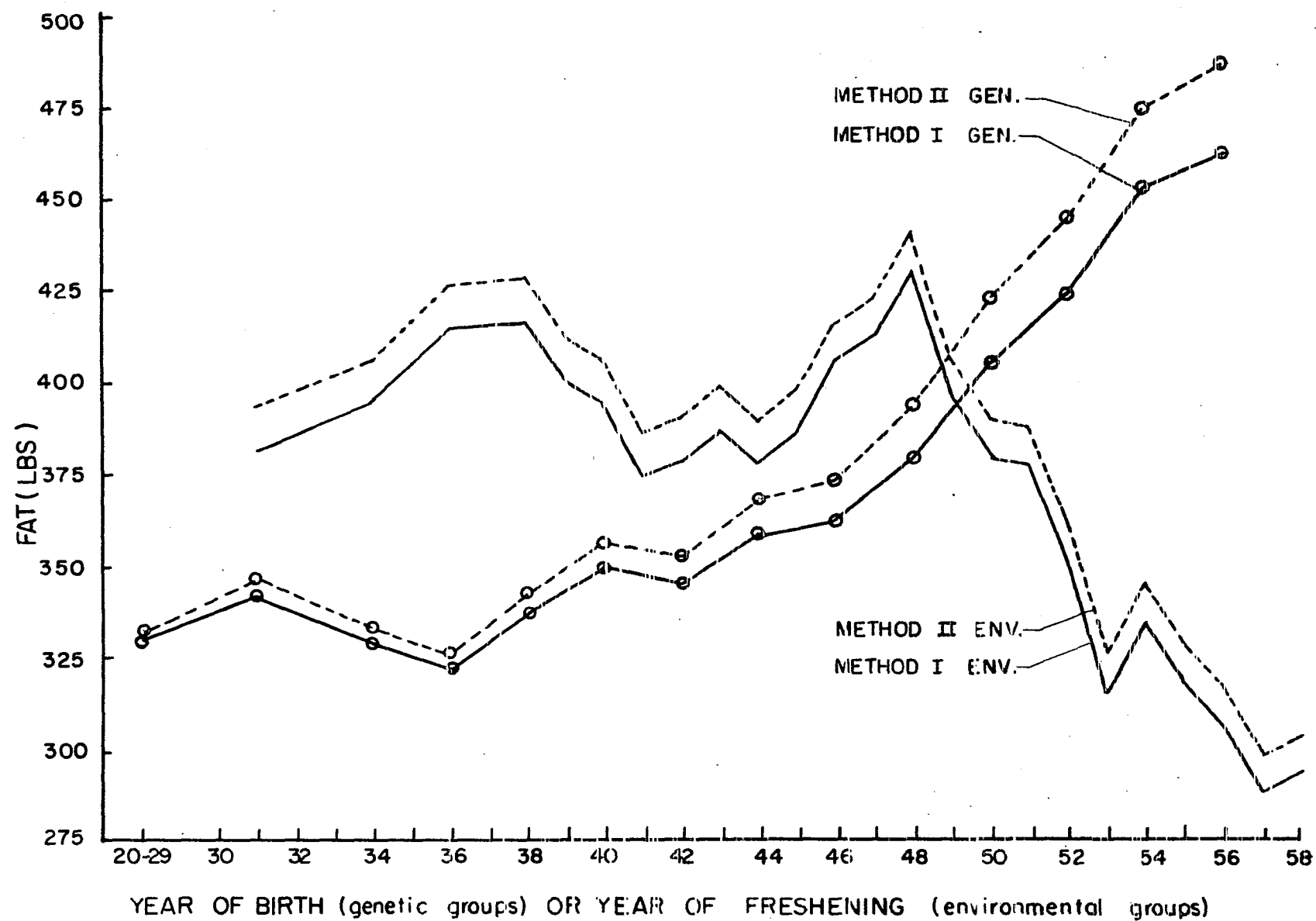


Figure 4. Environmental and genetic trends estimated from Method I and Method II fat data by the maximum likelihood method using a repeatability value of 0.40 and including all records.

FIG. 4



logical to examine their effect on these data, particularly in view of the results found in section IV-A. Estimates of genetic and environmental trends were obtained using a repeatability value of 0.40 and including all data from Methods II and III. The estimates, with their standard errors, are listed as deviations in Tables 10 and 11 for the genetic and environmental estimates, respectively. In Tables 12 and 13 the estimates were converted from deviations to means by adding the deviations to the overall mean of each variable. Figures 5 and 6 present the environmental and genetic trends for milk and fat production, respectively.

Comparing only the results from the fat data, Method II gave average annual values of +5.71 and -3.11 for genetic and environmental estimates, respectively, while Method III gave corresponding values of +0.57 and +1.31. These trends were opposite in direction for the environmental estimates and of quite different magnitude for the genetic estimates. A more extensive examination and discussion of these results will follow in a later section.

c. Effects of using different repeatability values Separate analyses using both Method II and Method III data were made using $r = 0.30$ and $r = 0.50$ to determine the effect that an incorrect or biased repeatability value might have on the estimation of genetic and environmental trends. The Method II results, converted to means, are illustrated in Figure 7 for milk production and in Figure 8 for fat production for genetic and environmental estimates. Corresponding estimates for Method III data are shown in Figures 9 and 10, respectively.

In general, increasing the repeatability value caused an increase

Figure 5. Environmental and genetic trends estimated from Method II and Method III milk data by the maximum likelihood method using a repeatability value of 0.40 and including all records.

FIG. 5

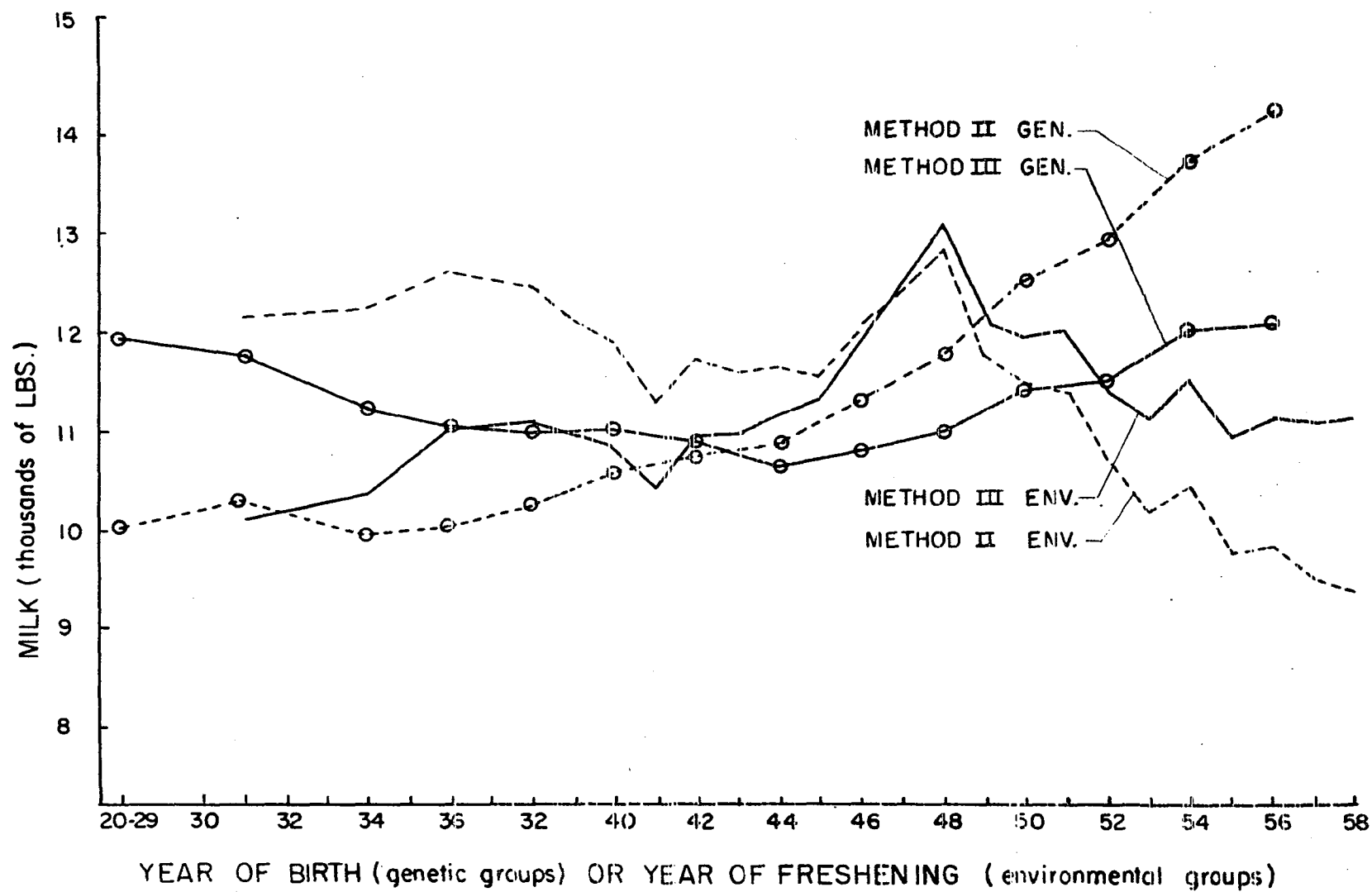


Figure 6. Environmental and genetic trends estimated from Method II and Method III fat data by the maximum likelihood method using a repeatability value of 0.40 and including all records.

FIG. 6

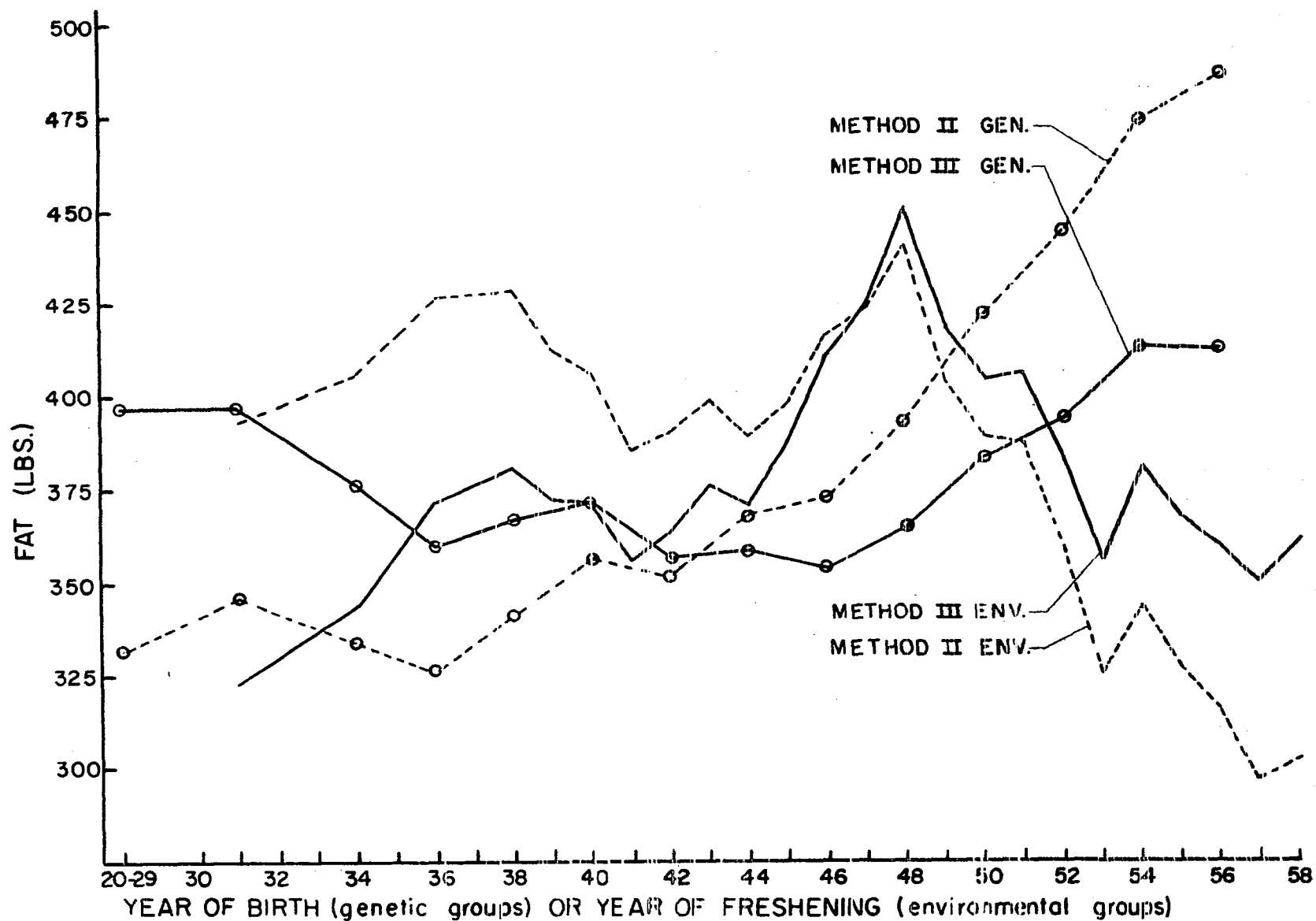


Figure 7. Environmental and genetic trends estimated from Method II milk data by the maximum likelihood method using repeatability values of $r = 0.30$ and $r = 0.50$ and including all records.

FIG. 7

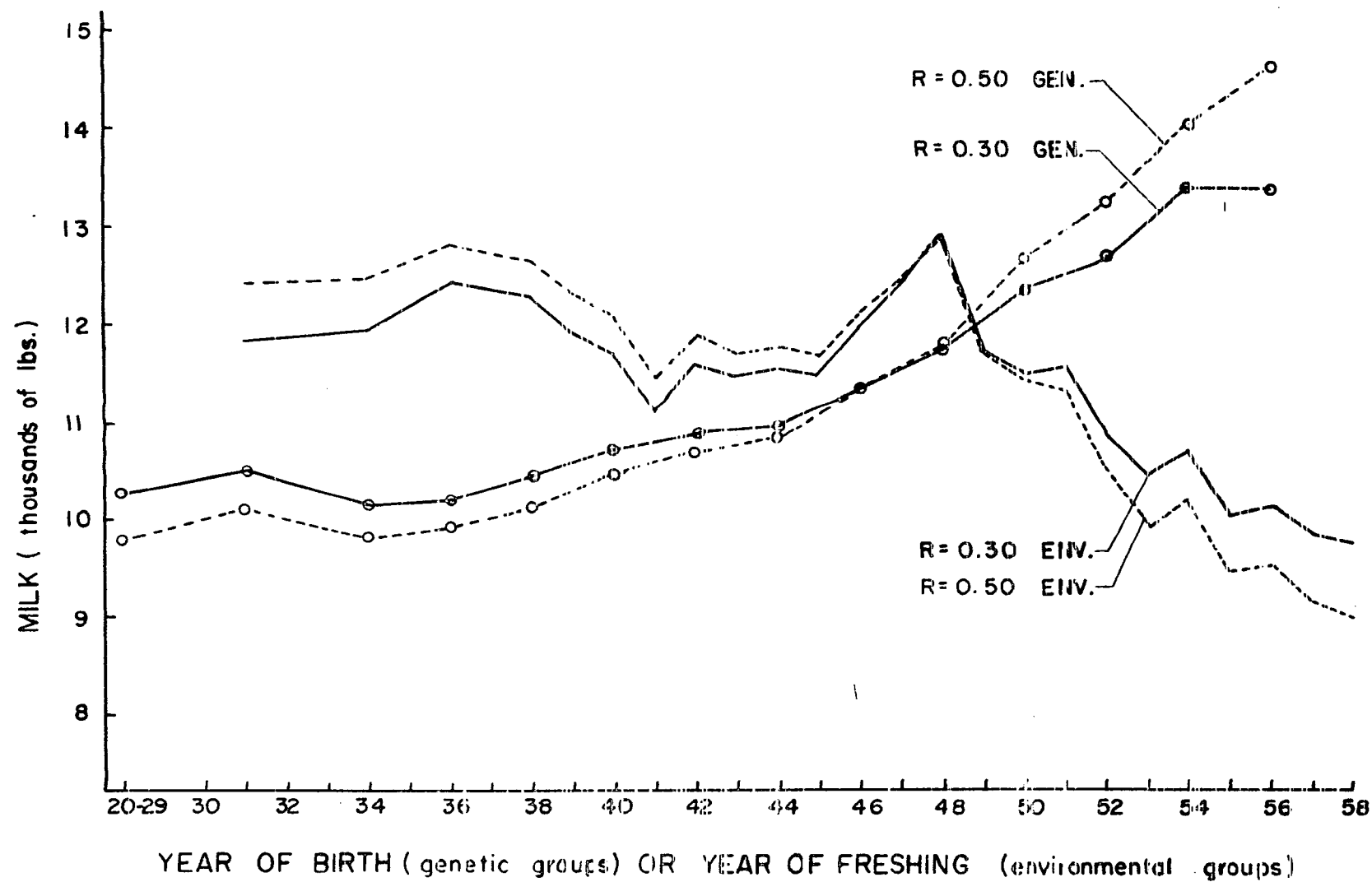


Figure 8. Environmental and genetic trends estimated from Method II fat data by the maximum likelihood method using repeatability values of $r = 0.30$ and $r = 0.50$ and including all records.

FIG. 8

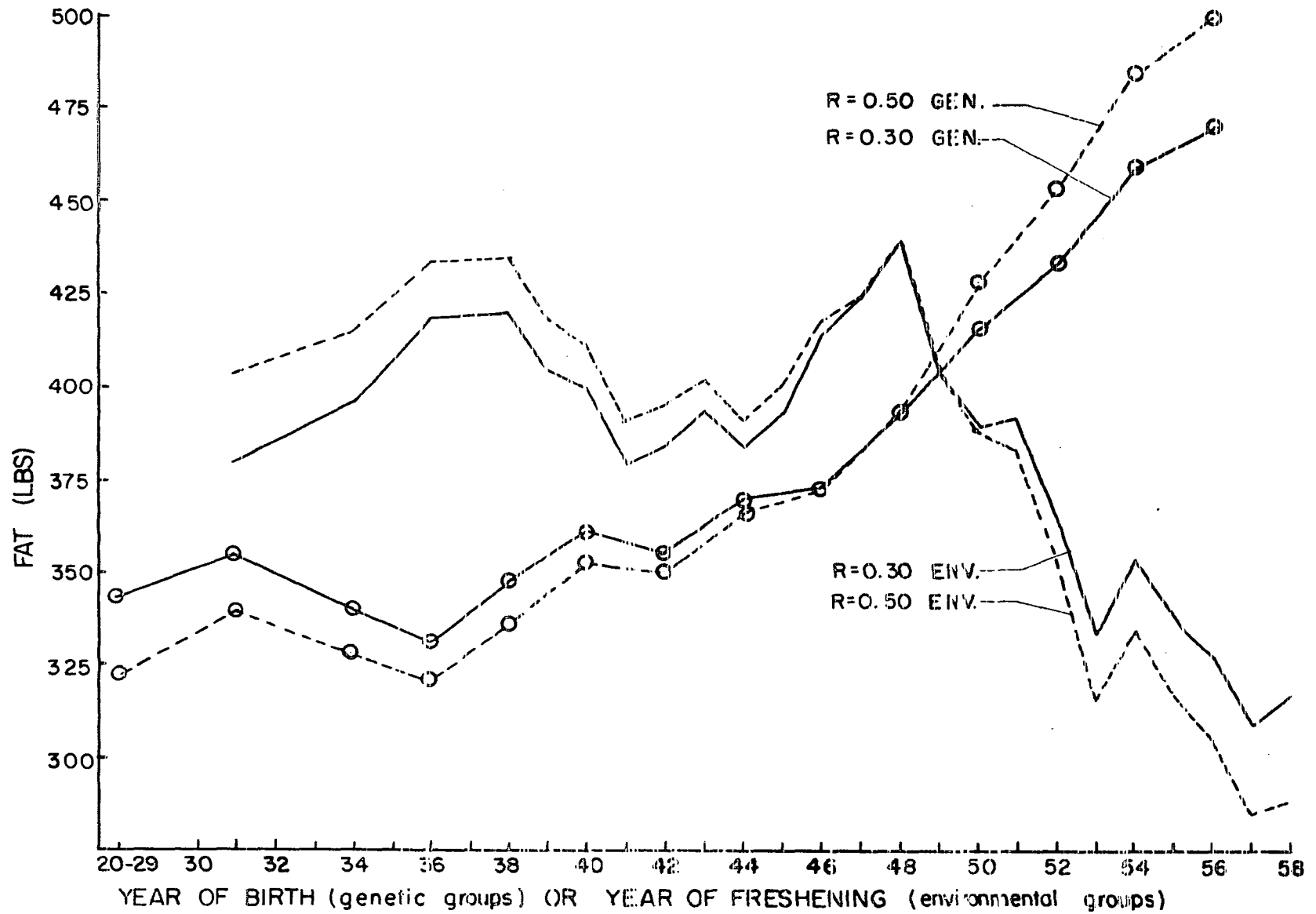


Figure 9. Environmental and genetic trends estimated from Method III milk data by the maximum likelihood method using repeatability values of $r = 0.30$ and $r = 0.50$ and including all records.

FIG. 9

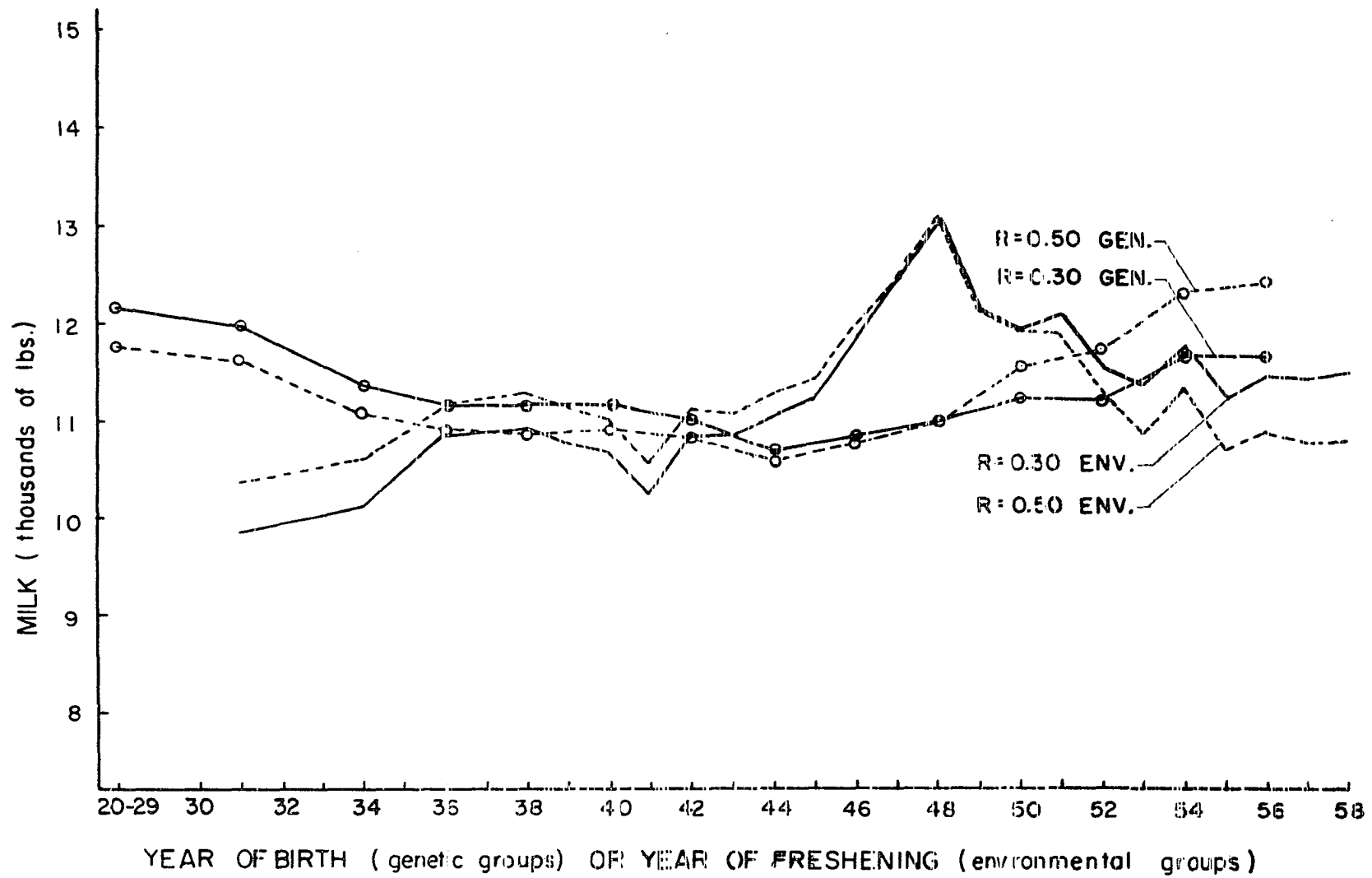
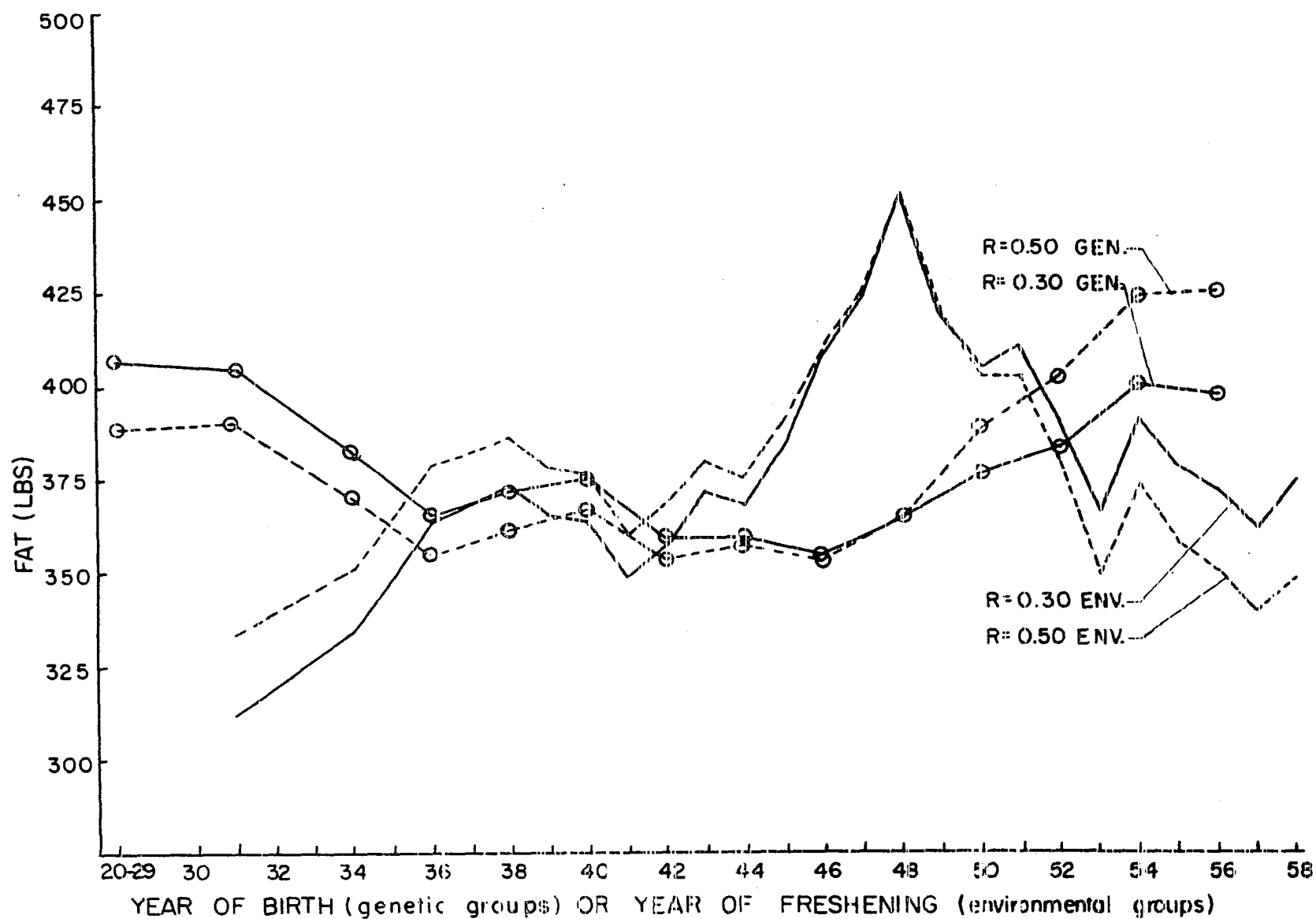


Figure 10. Environmental and genetic trends estimated from Method III fat data by the maximum likelihood method using repeatability values of $r = 0.30$ and $r = 0.50$ and including all data.

FIG. 10



in the genetic trend and a decrease in the environmental trend as time progressed. These results will be discussed in more detail in a later section.

4. Analyses considering selected data

a. Excluding low terminal lactations and lactations of cows born before 1928 As a check on the influence of the low terminal lactations by older cows whose preceding records were sufficiently high to warrant keeping them in the herd, low final records of 31 cows which had at least five previous lactations were removed from the data. In addition the 33 records by 15 cows which were born before 1928 were removed. The 64 deleted records averaged 10346 and 318 pounds for Method II and 10785 and 343 pounds for Method III for milk and fat, respectively.

The results of this analysis using a repeatability value of 0.40 are shown in Figures 11 and 12 for Method III milk and fat data, respectively. The removal of these records from Method III data decreased the final genetic estimate for fat 23.1 pounds and increased the final environmental estimate 27.3 pounds as compared with Method III estimates which were based on all records. A similar comparison of Method II estimates gave a decrease of 24.6 pounds of fat in the final genetic estimate and an increase of 28.2 pounds of fat in the final environmental estimate. Although this procedure of eliminating selected records is certainly open to question, it does indicate the influence a few abnormal records might have on the results.

b. Using first through sixth lactation of cows born in 1935 and later Several extraneous factors over which little control could

Figure 11. Environmental and genetic trends estimated from Method II and Method III milk data by the maximum likelihood method using a repeatability value of 0.40 and excluding low terminal lactations of 31 older cows.

FIG. II

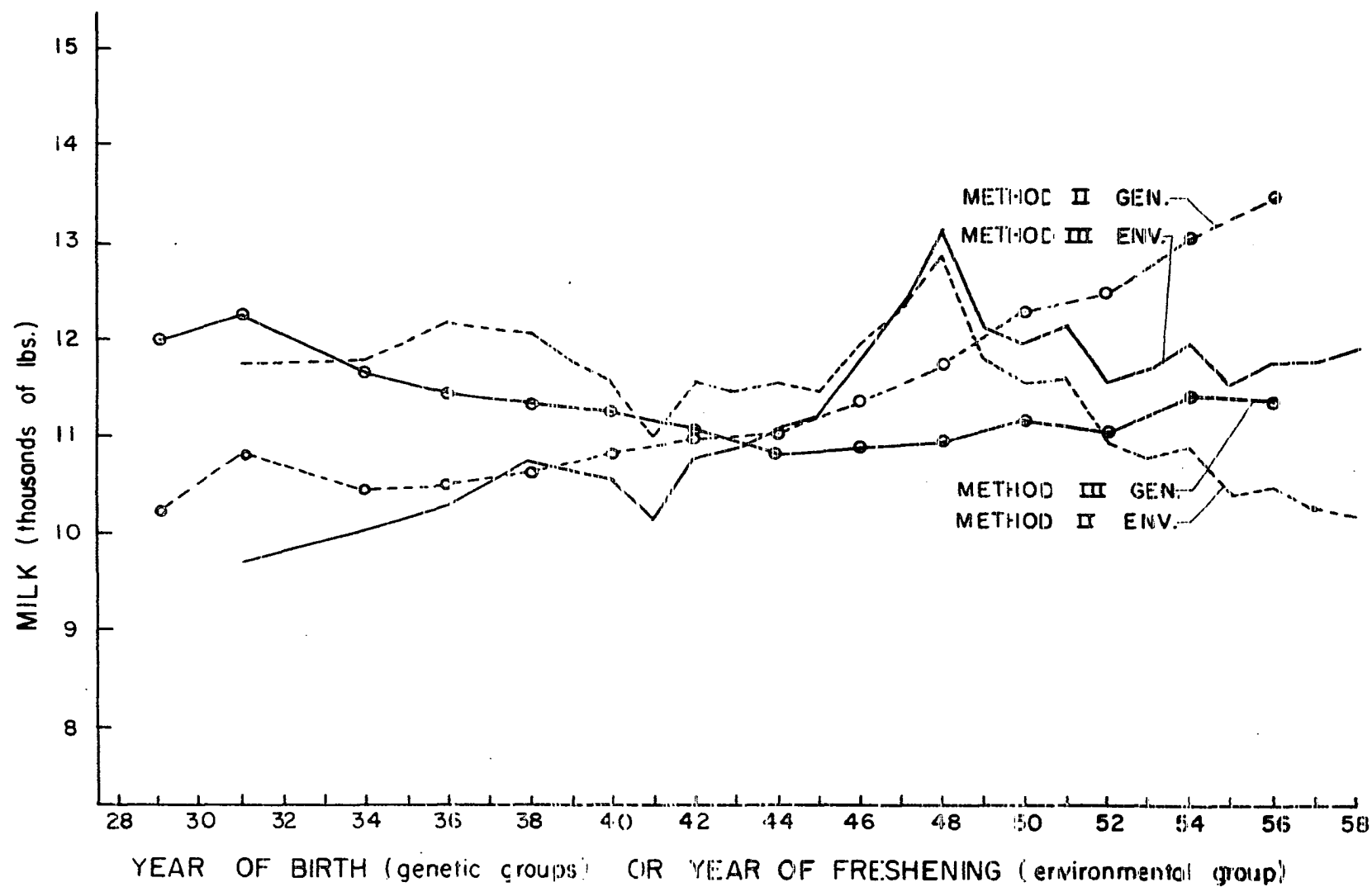


Figure 12. Environmental and genetic trends estimated from Method II and Method III fat data by the maximum likelihood method using a repeatability value of 0.40 and excluding low terminal lactations of 31 older cows.

FIG. 12

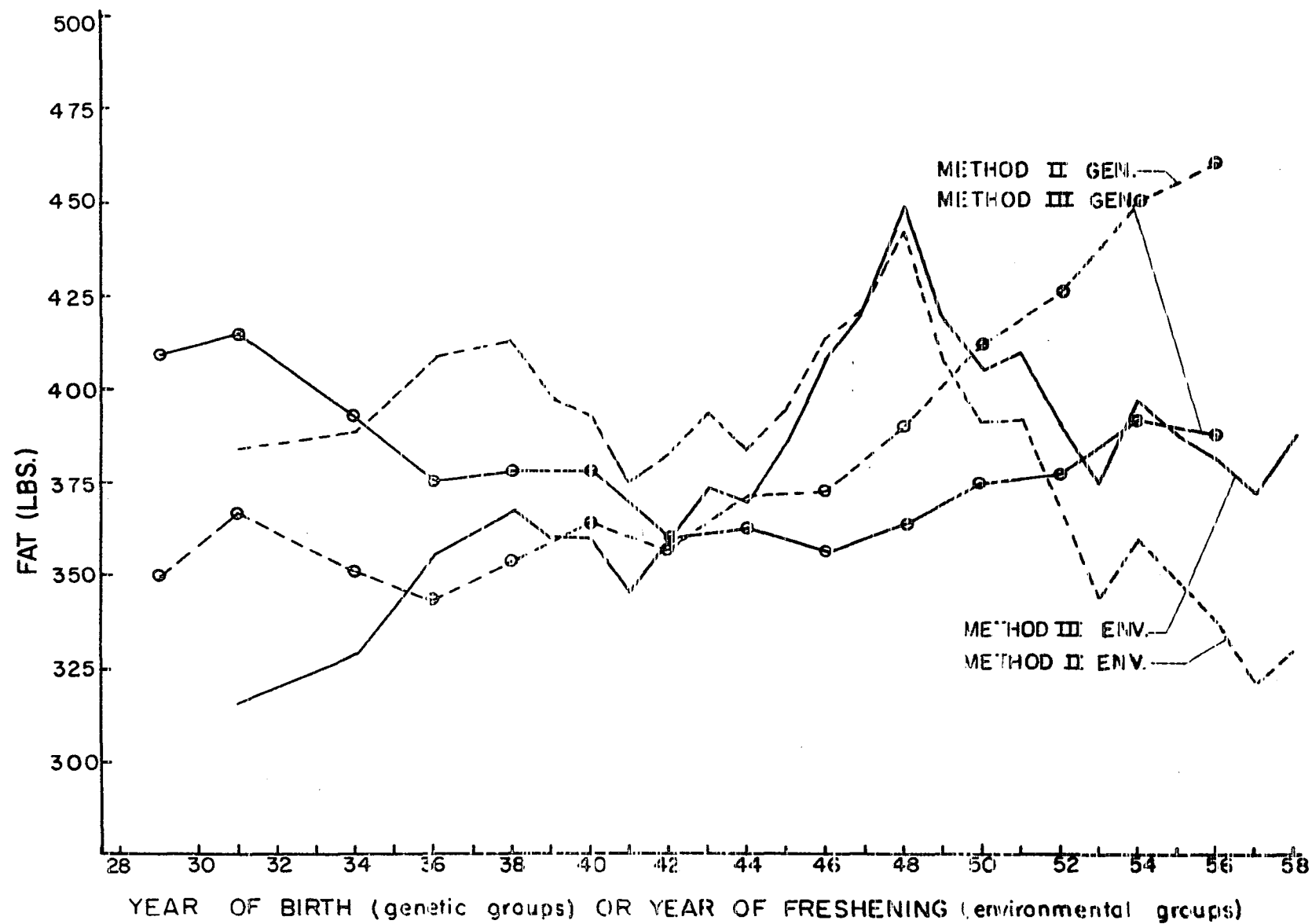
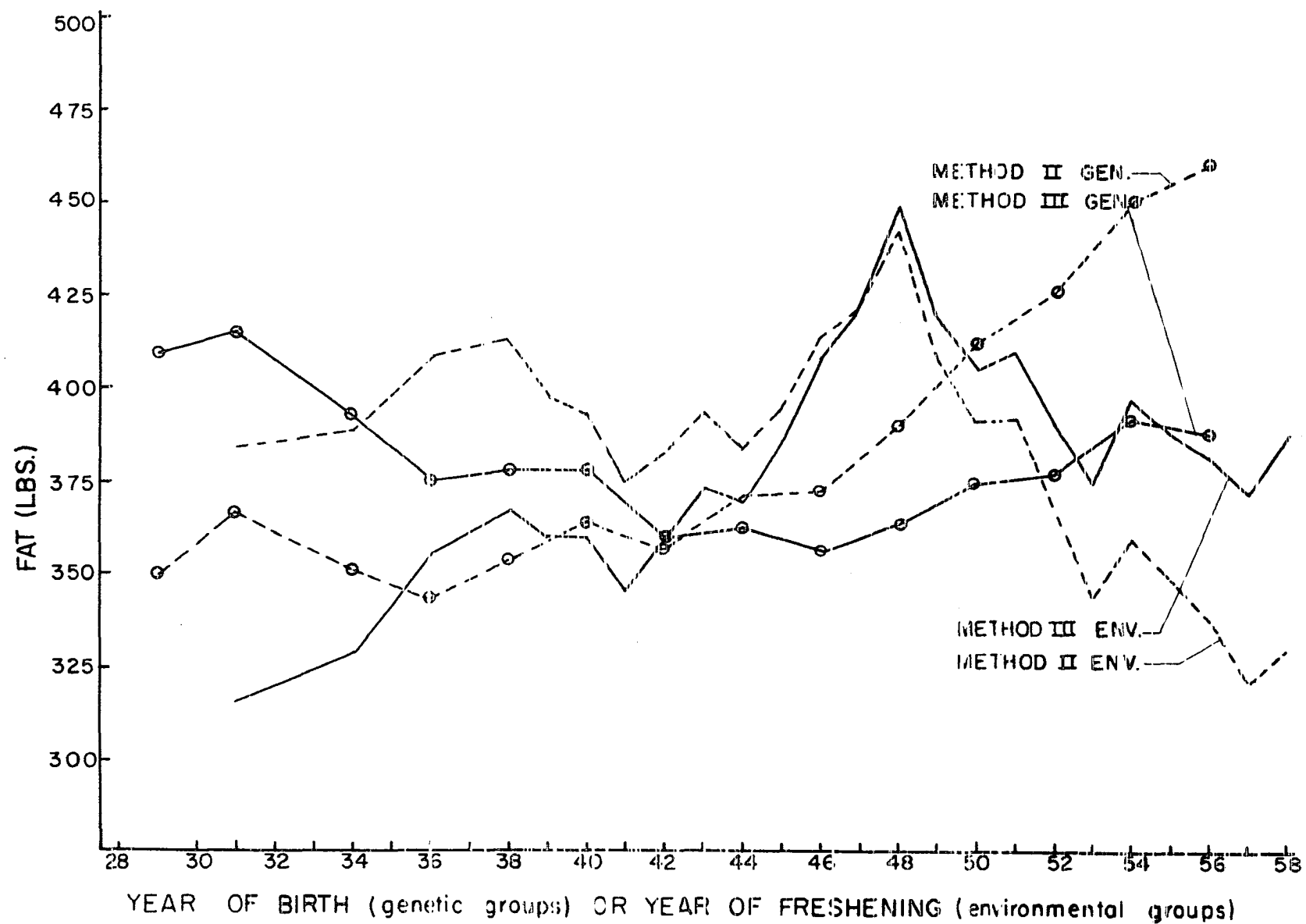


FIG. 12



be exercised may have influenced the data to an unknown degree in the early years of the experiment. Such factors were the introduction of animals after the herd was initially closed, the heavy losses to disease, and loss of the barn through fire in 1935. In addition the corrections for three- and four-time milking may not have adjusted accurately for individual variations in response to this management factor.

An attempt to avoid these influences was made by excluding all animals born before 1935 and consequently all records made before 1937. Based on the evidence presented in Section IV-C-4a of this thesis, a decision was made to exclude all lactations exceeding the sixth to remove most of the effects of low terminal records made by previously high producers. This decision to eliminate lactations exceeding the sixth was further supported on the basis that each additional record contributes less additional information than the preceding one did (17). Normally, much of the entire usefulness of additional records for indicating an individual's merit would be reached after two or three lactations. However, because of the age correction effects in these data, it seemed advisable to include the 1th, 5th and 6th lactations to provide sounder estimates of the genetic and environmental trends.

Data remaining, after the preceding conditions were met, included 582 cows with 1409 records which averaged 11501 pounds of milk and 386 pounds of fat on Method II data, and 11374 pounds of milk and 382 pounds of fat on Method III data. The analyses were made using a repeatability value of 0.40.

The estimates obtained are illustrated in Figures 13 and 14 for milk and fat, respectively. The estimates for Method III data agree

Figure 13. Environmental and genetic trends estimated from Method II and Method III milk data by the maximum likelihood method using a repeatability value of 0.40 and including only the first through sixth lactations of cows born in 1935 or later.

FIG. 13

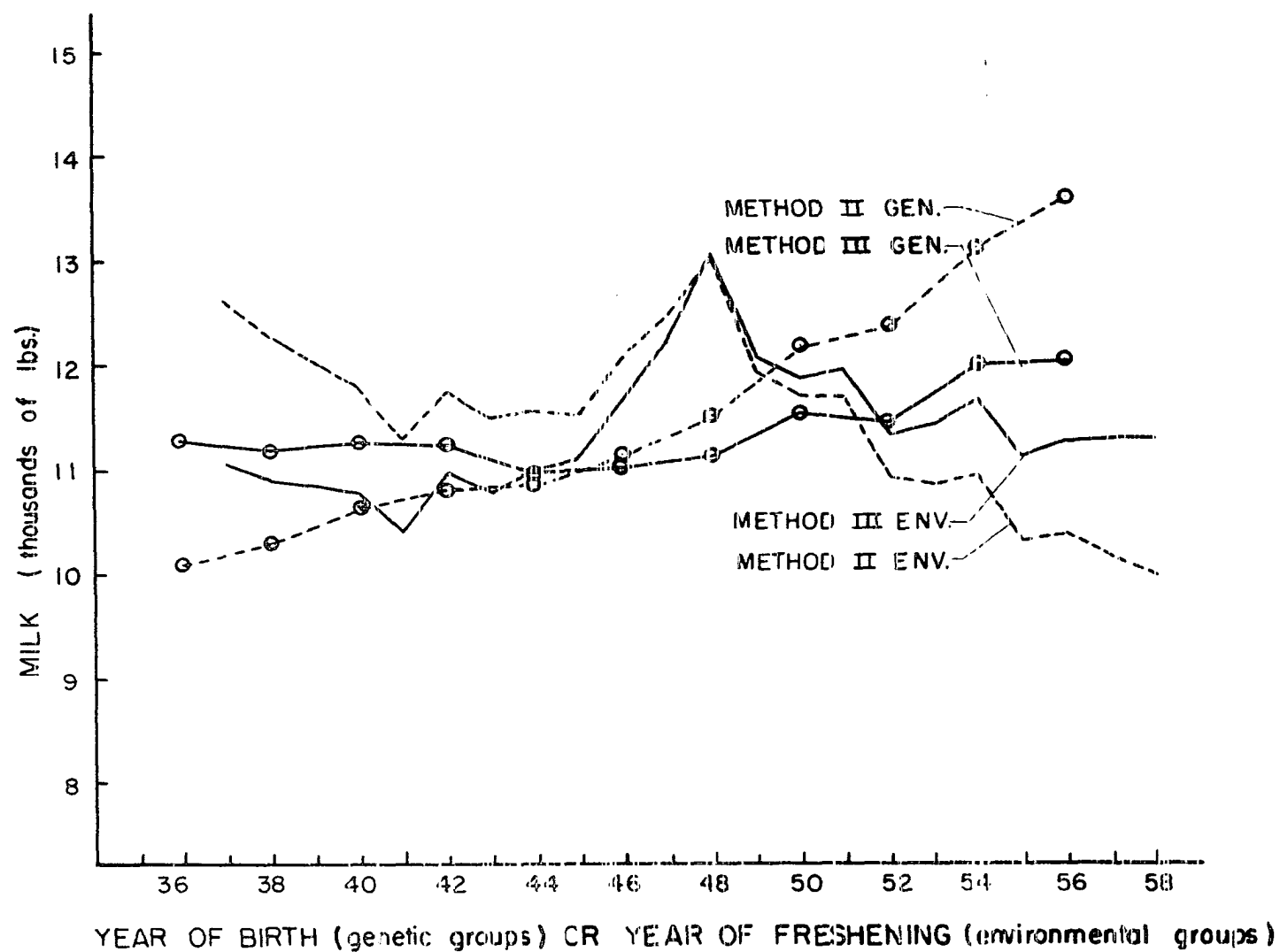
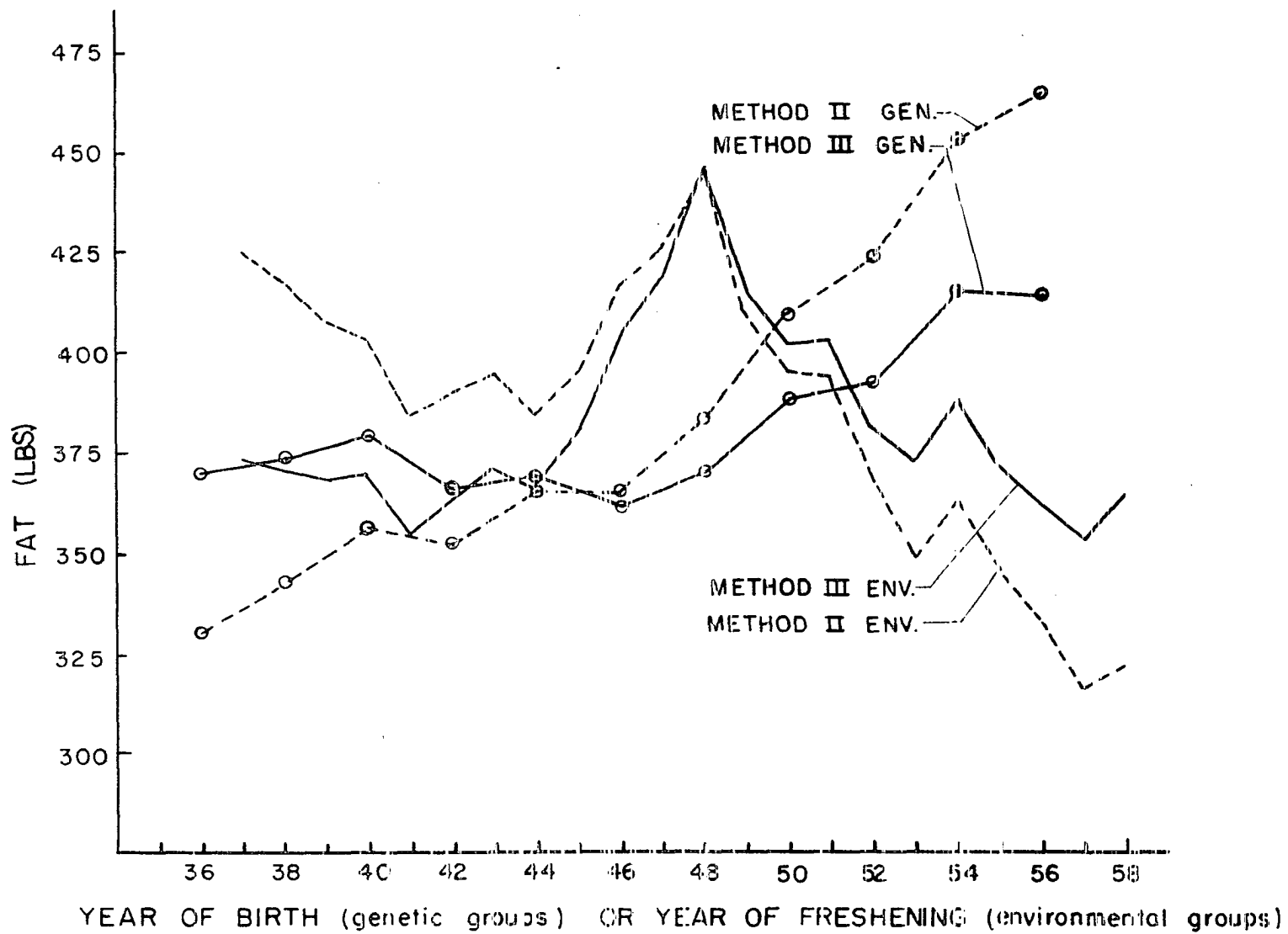


Figure 14. Environmental and genetic trends estimated from Method II and Method III fat data by the maximum likelihood method using a repeatability value of 0.40 and including only the first through the sixth lactations of cows born in 1935 or later.

FIG. 14



remarkably with those obtained in section IV-C-3-b using all Method III data. The differences between these two estimates using Method III data never exceed 11.1 pounds of fat or 330 pounds of milk for either genetic or environmental estimates in any given year.

The most important result from this analysis is seen in the estimates from Method II data. These estimates differ from the Method II estimates obtained in Section IV-C-3-b by as much as 22.9 pounds of fat and 660 pounds of milk. Even more significant is that these differences resulted from the Method II estimates in this section following more closely the pattern of the Method III estimates. This supports the hypothesis that one of the reasons the Method II genetic estimates obtained in Section IV-C-3-b were unrealistically high was the bias introduced by insufficient correction factors for the lactations made by cows past maturity.

c. Using second through sixth lactation of cows born in 1935 and later Since age correction factors play a large part in the difference between Method II and Method III estimates, it seemed that much of this influence could be eliminated by using only records for which age corrections were small or nil. Such an analysis was accomplished by removing all first lactations from the data used in the preceding analysis. The 827 records remaining averaged 11489 pounds of milk and 384 pounds of fat for Method II data and 11564 pounds of milk and 387 pounds of fat for Method III data. A repeatability value of 0.40 was used.

The estimates obtained are shown in Figures 15 and 16 for milk and fat estimates, respectively. Because of the reduction in the number of

Figure 15. Environmental and genetic trends estimated from Method II and Method III milk data by the maximum likelihood method using a repeatability value of 0.40 and including only second through the sixth lactations of cows born in 1935 or later.

FIG. 15

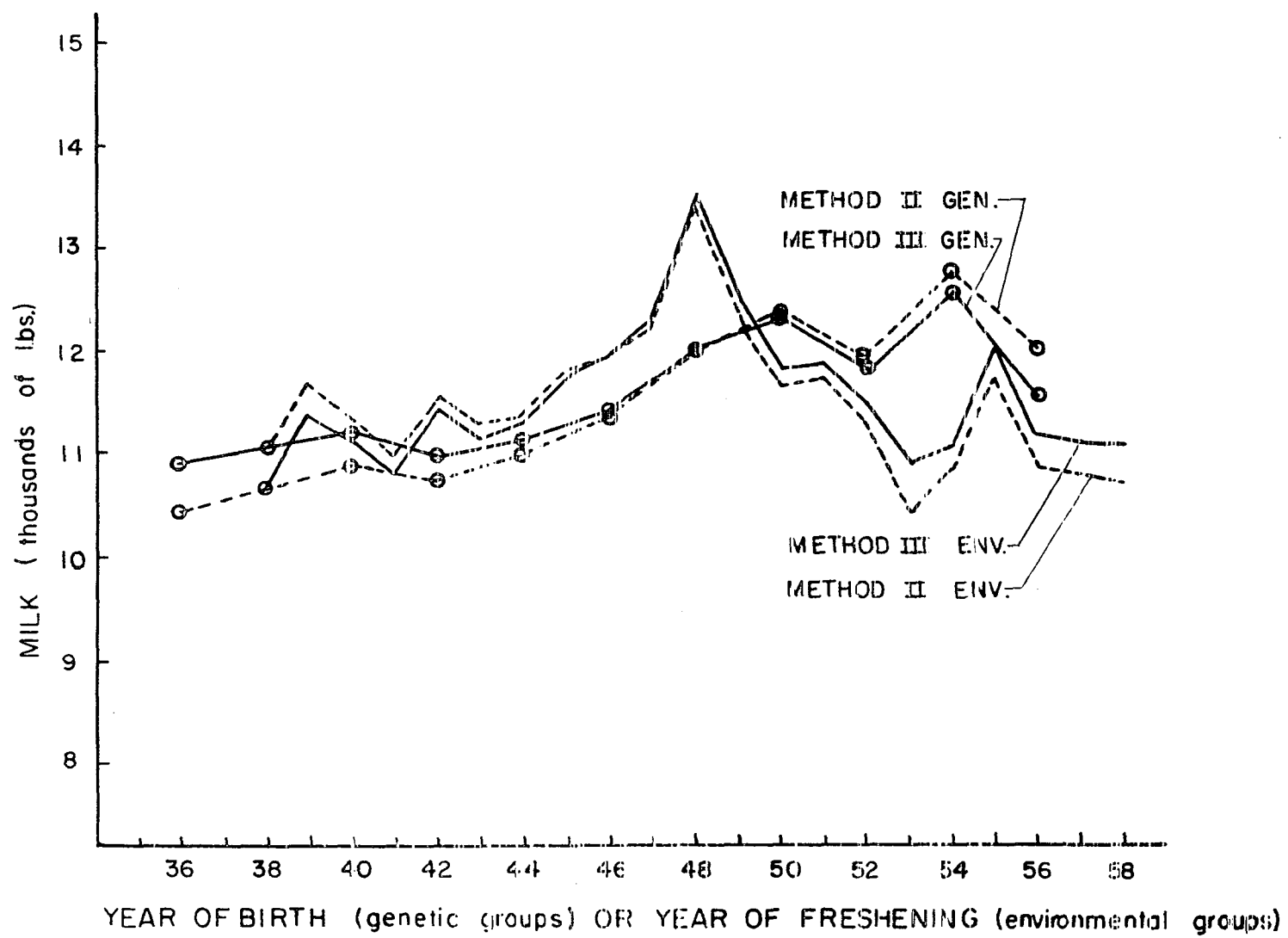
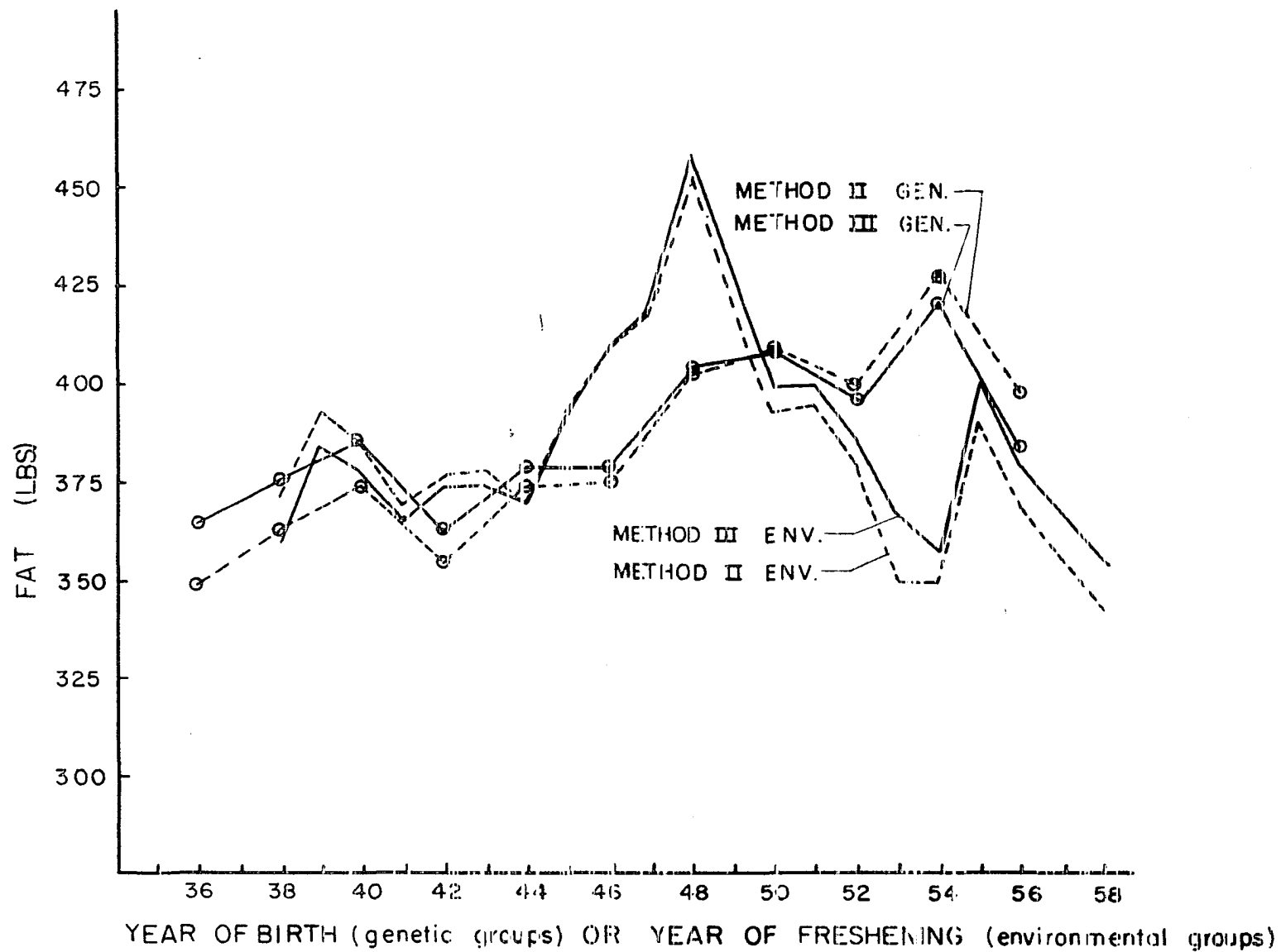


Figure 16. Environmental and genetic trends estimated from method II and Method III fat data by the maximum likelihood method using a repeatability value of 0.40 and including only second through the sixth lactations of cows born in 1935 or later.

FIG. 16



records used, these estimates are less reliable and undoubtedly have larger standard errors than estimates which were based on all available records. The records included in the later years are particularly reduced in number and this accounts for the lack of consistency in the trends after 1948.

However, the increased similarity between the estimates obtained using the Method II and Method III data give further weight to the hypothesis that incorrect age factors contributed to the inflated genetic estimates given in analyses which included all Method II records.

5. Analyses considering only Method III data

Presumably the analyses using repeatability values of 0.30, 0.40, and 0.50 bracket the true repeatability values that function in most milk and fat production data. It seemed logical to refine the estimates of genetic and environmental trends by using more precise values for repeatability in the Method III data.

The values chosen were 0.44 for milk and 0.35 for fat as obtained by intraclass correlation using Method III data (Table 10). Unpublished evidence by Wadell (38) later gave further support that those values were more nearly correct and unbiased than other repeatability estimates computed in section IV-B.

The genetic and environmental estimates obtained by the analysis are illustrated in Figure 17 for milk and Figure 18 for fat. Also shown on Figures 17 and 18 are the actual yearly averages for Method III data.

Figure 17. Environmental and genetic trends estimated from Method III milk data by the maximum likelihood method using a repeatability value of 0.44 compared with the trends in average production of the same environmental and genetic groups.

FIG. 17

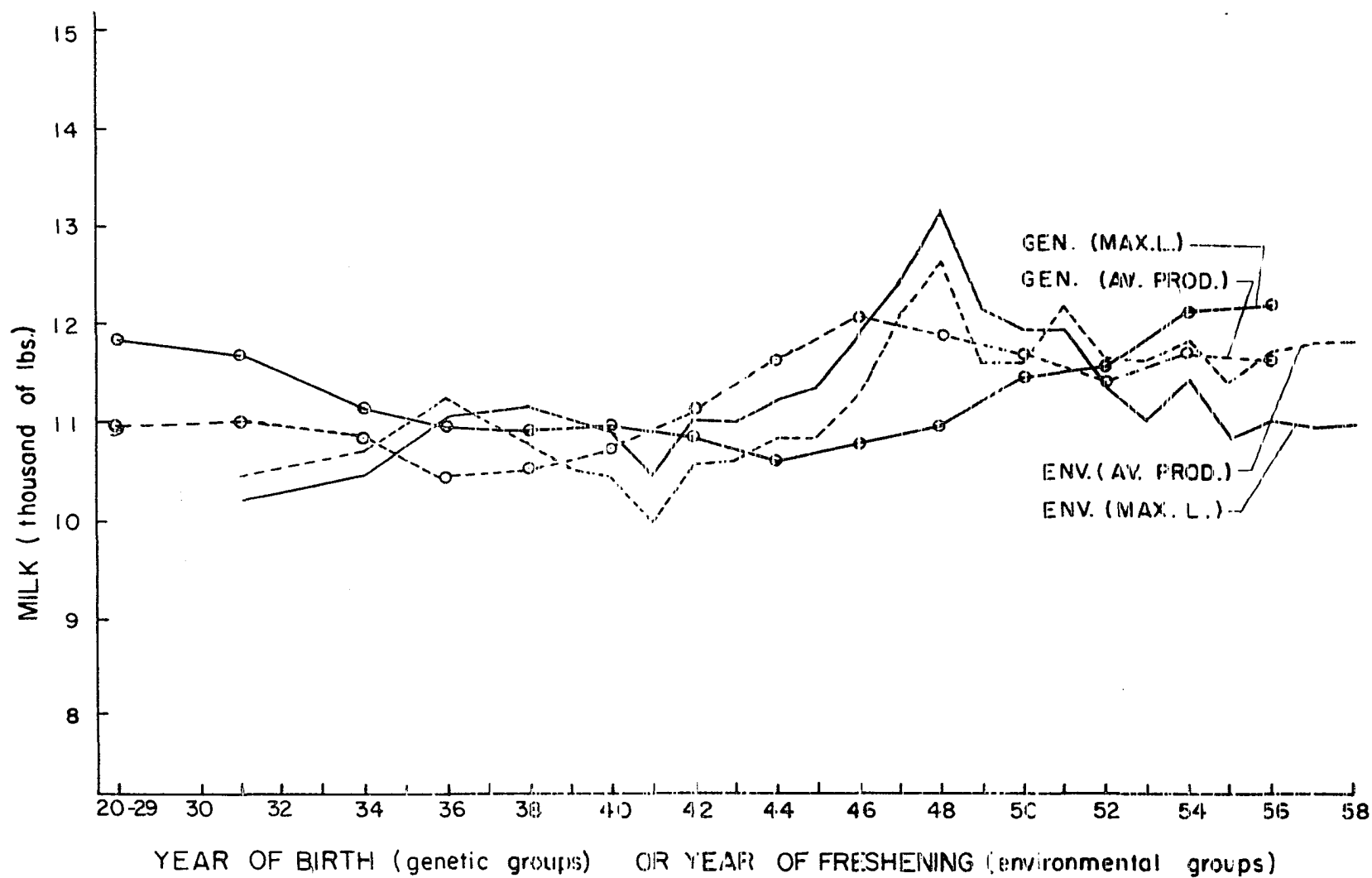
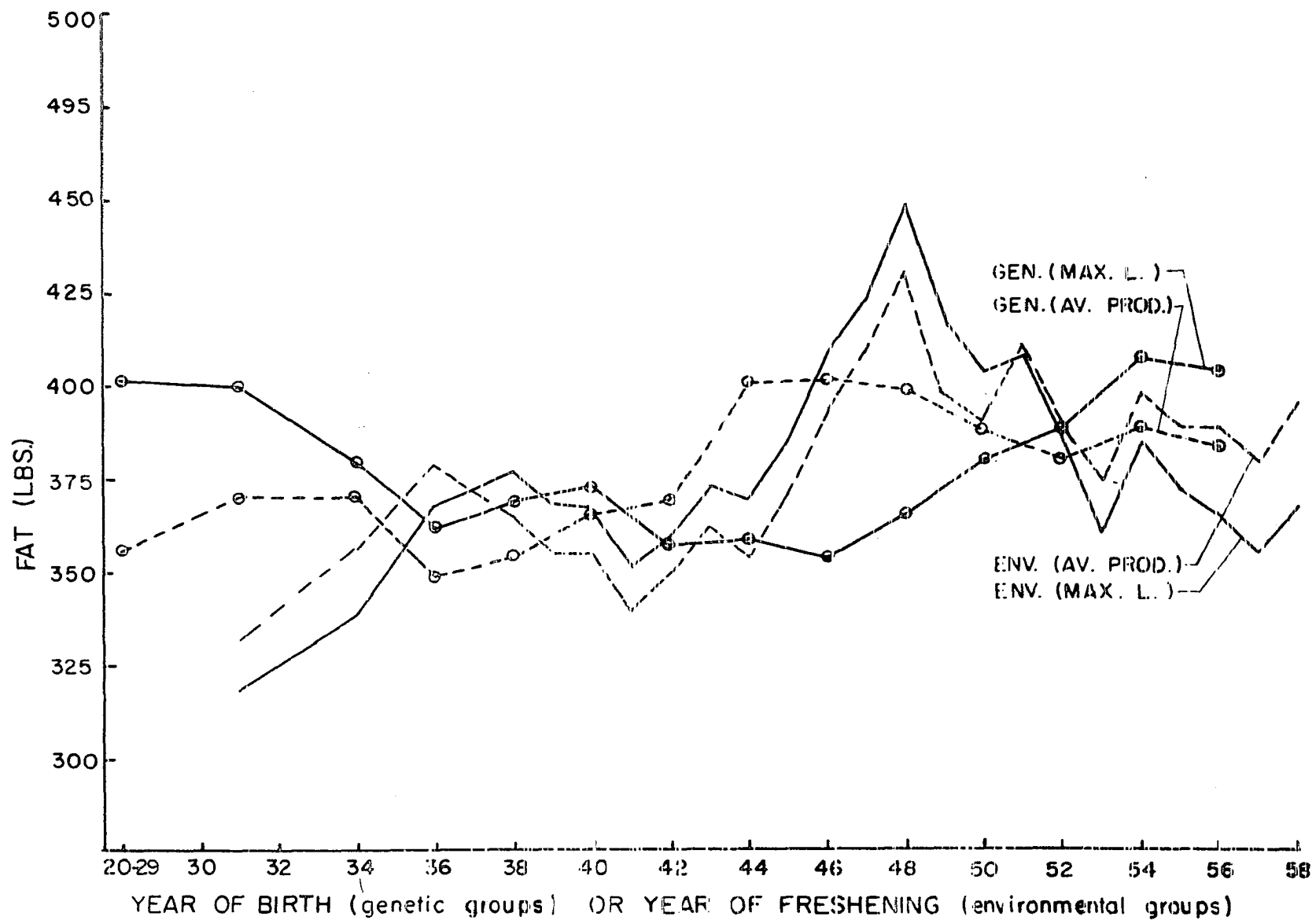


Figure 18. Environmental and genetic trends estimated from Method III fat data by the maximum likelihood method using a repeatability value of 0.35 compared with the trends in average production of the same environmental and genetic groups.

FIG. 18



D. Evaluation of Selection Practiced

An evaluation of the selection practiced was made utilizing the approach suggested by Rendel and Robertson (28). This approach considered the process of selection as composed of four parts; namely, the contribution of male and female parents to male offspring and of male and female parents to female offspring. In order to compare these results with those obtained from the maximum likelihood estimates, both Method II and Method III data are included in all calculations in this section.

1. Selection of dams of sires

Generation intervals do not divide conveniently in a population such as dairy animals and there is a continuous overlapping of one generation with previous or subsequent generations. The time interval was, therefore, arbitrarily divided into four-year periods (except for the first period which included five years) from 1930 through 1954. Sires born in the herd before 1930 were excluded from this section as well as the three proved sires introduced from other herds between 1932-1934, since an accurate evaluation of their ancestry would have been difficult and of doubtful value. The genetic superiority of each dam was estimated by the formula:

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

where

h^2 = heritability and was assumed to be 0.25,

r = repeatability and was assumed to be 0.40,

n = number of lactations.

Only the first five lactations of each dam were taken into account as

further lactations added very little to the estimate based on five lactations. The herd average used in each computation was a composite of the years in which the dam had lactations. The genetic superiority of each dam was expressed as a percent of the herd average.

Forty-three sires were born during this period and they were sons of 30 different dams. One dam left five sons who became herd sires, two dams left three sons each, five dams left two sons, and twenty-two dams left one son. Ten dams had their first offspring selected as herd sires and eleven dams' second offspring were chosen (one of these eleven dams was also in the previous group). The average age of the dams when their sons were born was 57.0 months (or roughly third lactation cows).

The dams were grouped in the four-year periods described above according to the birth dates of their sons. Each dam's record was weighted by the number of daughters her son sired. A summary of the genetic superiority of dams of sires is given in Table 17. Also included in Table 17 are the ages and inbreeding of the dams and the inbreeding of their sons.

The two sets of data gave similar results, with Method III data showing slightly larger values for genetic superiority than Method II data.

Selection for butterfat was stronger than for milk in the first period but thereafter selection was similar for both milk and butterfat in each set of data. The intensity of selection became stronger in the latter third of the interval. Inbreeding of dams increased slightly in later years while inbreeding of their sons increased at a faster rate, from

Table 17. Genetic superiority of dams of sires

Birth period of son	No. sons	Genetic superiority of dams as percent of mean				Av. age of dams	Av. inbr. of dams	Av. inbr. of sons
		Method II		Method III				
		Milk	Fat	Milk	Fat			
1930-34	6	3.48	5.29	3.55	5.44	43.2	1.5	0.3
1935-38	6	6.08	6.06	6.18	6.09	60.0	1.2	6.5
1939-42	7	4.34	4.83	4.42	4.88	49.0	1.3	6.4
1943-46	10	6.57	5.83	6.61	5.82	55.6	4.5	9.1
1947-50	7	9.16	9.05	9.49	9.43	51.1	5.7	11.6
1951-54	7	11.92	11.54	12.19	11.76	52.1	3.7	13.7
Average		6.92	7.10	7.07	7.24	57.0	3.2	7.9

0.3 in 1930-34 to 13.7 in 1951-54.

2. Selection of dams of cows

a. Year to year selection One measure of the selection practiced among cows was to compare the production level of cows retained for a succeeding year with the average of all cows in that year. The genetic superiority of selected cows was calculated for each year employing a formula similar to that in the preceding section:

i.e., genetic superiority

$$= \frac{\bar{n} h^2}{1 + (\bar{n}-1)r} \left[\text{selected cows' average} - \text{herd average} \right]$$

where \bar{n} = average number of records of herd members, and h^2 and r each had the same meaning and value as previously.

The genetic superiority of each year was expressed as a percent of the herd average. These values were pooled by the intervals shown in Table 18. These intervals were chosen to correspond with periods in the

Table 18. Genetic superiority of cows selected for retention for a succeeding year

Period	Average no. in herd	Average percent leaving	Genetic superiority of selected cows as a percent of herd average			
			Method II		Method III	
			Milk	Fat	Milk	Fat
1930-35	27.7	31.3	.43	.77	.32	.68
1936-39	47.8	30.4	.30	.56	.17	.38
1940-43	72.5	32.8	1.20	1.22	1.14	1.17
1944-47	67.2	39.8	1.64	1.65	1.72	1.82
1948-51	76.0	35.9	2.69	2.82	2.71	2.72
1952-55	74.8	42.5	2.01	2.06	2.06	2.06
1956-57	74.5	38.9	1.56	1.63	1.44	1.53

succeeding section.

The selection pressure was roughly twice as strong in each period after 1940 as in any period preceding 1940. The herd was increasing in numbers during the first two periods and this limited the amount of voluntary culling that could be done. After 1940 the herd was more stable in size and thus it became possible to increase the culling intensity. It was probably more than coincidence that the increased selection intensity began about the same time the selection index was put into practice. This may have had a powerful indirect effect by pointing out more vividly the ranking of the cows in the herd.

This method of evaluation does not cover a full generation and consequently may underestimate the intensity of selection.

b. Selection considering only cows with female descendants in the herd in 1958 Another means of evaluating the selection of dams in cows was to consider only those dams with female descendants in the herd

in 1958, i.e., the effective female breeding herd as seen in retrospect.

This method was employed using only dams born in 1952 or earlier. Many of the cows born after 1952 were still in the herd and had yet to have their fate determined. Thirteen cows born before 1952 were still in the herd in 1958 and perhaps could introduce a bias. However, since all but one of them had already left at least one female offspring each, it was decided to include all dams born in 1952 or before in order to make the study as current as possible.

An overall summary of the production of cows with and cows without descendants in the 1958 herd is given in Table 19.

Table 19. Average production of all cows born in 1952 or earlier, of those with and of those without descendants in the herd in 1958.

Classification	No. cows	No. records	Av. age at calv.	Average production			
				Method II Milk	Method II Fat	Method III Milk	Method III Fat
All cows	577	1564	48.0	11327	380	11263	378
Cows with descendants							
All records	199	741	54.9	11702	393	11721	394
Only 1st 5 records	198	646	46.9	11757	395	11693	393
Cows without descendants	378	823	42.2	10978	369	10851	364

The dams were divided into birth groups of four year intervals (except for the first group which included all cows born from 1922 through 1932) and the genetic superiority of each group computed using the formula given in the preceding section. Only the first five lactations of each

Table 20. Genetic superiority of dams of cows

Birth period of dams	No. dams	Genetic superiority of dams as percent of mean				Av. age of dams	Av. inbr. of dams
		Method II		Method III			
		Milk	Fat	Milk	Fat		
1922-32	24	.26	1.32	.14	1.20	58.7	3.5
1933-36	17	-.04	.30	-.24	.03	59.5	2.7
1937-40	30	1.93	1.52	2.06	1.66	51.2	3.9
1941-44	31	3.03	2.82	2.94	2.83	57.7	7.2
1945-48	41	1.42	1.98	1.32	1.87	57.7	9.6
1949-52	55	1.04	.76	1.24	.91	44.2	12.2
Average		1.27	1.45	1.24	1.42	55.8	6.5

cow were used. The results are listed in Table 20.

Although the overlapping of generations makes a precise comparison of Tables 18 and 20 impossible, the results can be compared roughly by allowing a time lag of three to four years for the birth periods of dams. For example, dams born during the period 1933-36 would be expected to exert most of their influence during the period 1936-1939. In this light, the two methods gave similar trends except that the highest genetic selection differential was reached about a generation earlier in Table 20 than in Table 18.

Although intentional selection might exert some influence, chance variation in the sex ratio and chance in whether a daughter lives to enter the herd play a large part in determining which cows contribute female offspring to a herd. Therefore it was not surprising that the planned selection, i.e., year to year culling, did not agree exactly with the selection attained, i.e., superiority of those cows who did

leave offspring. It was reassuring that the two sets of estimates followed the same trend.

c. Selection by lactation number Still another method of estimating the selection practiced was to consider the culling from lactation to lactation. The values obtained by this means are given in Table 21.

Table 21. Phenotypic selection for milk and fat due to lactation to lactation culling

Lactation	No. of cows	Percent culled	Phenotypic superiority as percent of mean			
			Method II		Method III	
			Milk	Fat	Milk	Fat
1	628	35.7	3.59	3.64	3.59	3.77
2	420	40.7	2.76	3.43	2.76	3.45
3	257	42.0	4.30	4.00	4.31	4.19
4	152	39.5	4.95	6.05	4.95	5.93
5	97	46.4	4.06	4.35	4.06	4.35
6	54	46.3	2.44	3.57	2.44	3.55
7	31	45.2	6.04	9.19	6.04	9.21
8	17	58.8	7.68	7.05	7.68	7.23
9	7	42.8	6.25	5.29	6.25	5.11
10	4	75.0	-16.28	-20.11	-16.27	-20.05
Mean selection differential			3.66	4.00	3.67	4.07

The proportion of cows culled each lactation generally increased as the cows became older, presumably because of the increased losses from infertility and disease among older cows. In addition, the policy of bringing every heifer into the herd for at least one lactation made it mandatory that a high percentage of the older cows leave each year to make room for the younger ones.

During the first six lactations, the culling differentials were highest in the third, fourth, and fifth lactations. The figures for seventh and later lactations were based on too few numbers to be relevant. The mean culling differentials were similar for the Method II and Method III data and averaged about 10 percent higher for fat than for milk.

It should be noted that the selection differentials listed in Table 20 are on a phenotypic basis.

3. Selection of sires of sires

Since most of the sires were used for only a short period of time, it would seem that progeny testing would have been of slight importance in the herd. However, it was possible to practice some selection among sires of sons by keeping sons from most of the sires until at least preliminary information was available on the sire's first daughters. The decision whether or not to use the son of a particular sire could thus be delayed, in some cases, until at least two years after the sire had left the herd (nine months gestation and fifteen months until service age for the bull calf).

Such a possibility prompted an investigation into the relative merits of sires which did leave sons and sires which did not leave sons in the breeding program. All lactations of each cow were averaged to give an estimate of her productive ability. These values were then averaged for all daughters of each sire and the resulting estimate used as an index of each sire's genetic value. Table 22 lists the indices for sires which left sons in the herd and Table 23 for sires which did not leave

Table 22. Average production of daughters of sires whose sons were used in the herd

Sire no.	Sire's inbr. %	Age of sire (mos.) ^a	No. sons	No. daus.	No. lact. of daus.	Daus. av. inbr.	Av. of daughters' lactations			
							Method II		Method III	
							Milk	Fat	Milk	Fat
456568	0	86	1	5	8	3.8	10583	394	10312	384
523140	7	51	1	5	11	1.0	13232	418	12948	409
656856	0	89	3	4	10	0	11220	404	11047	393
961	0	45	1	19	54	4.5	11004	359	10841	353
1195 ^b	1	55	3	24	72	5.5	10731	353	10595	349
1240	0	32	2	8	19	6.4	10843	352	10639	345
1250	0	45	2	11	40	3.2	10708	358	10632	355
1429	6	28	1	7	11	7.7	9709	325	9438	316
1463	2	29	1	10	23	7.3	9439	307	9267	302
1733	10	41	2	13	32	5.2	11329	358	11114	351
1821	4	35	3	12	31	4.2	11413	375	11223	369
1893	2	40	2	18	47	8.4	10538	368	10360	362
1957	3	38	1	22	85	5.8	10848	381	10760	373
2142	12	36	1	11	34	6.0	11912	383	11748	377
2211	10	30	1	1	1	5.0	8444	304	8140	293
2241	7	28	2	19	92	9.5	12469	407	12448	407
2285	7	36	1	12	28	6.7	12390	413	12175	406
2505	2	34	4	15	50	8.7	11330	380	11237	377
2551	10	39	1	13	17	9.2	9622	330	9317	319
2681	10	41	1	13	42	13.2	11980	414	11807	408

^aAge of sire computed from difference between sire's date of birth and modal date of his daughters' birth.

^bSire returned for further service after first group of daughters were tested.

Table 22. (Continued)

Sire no.	Sire's inbr. %	Age of sire (mos.)	No. sons	No. daus.	No. lact. of daus.	Daus. av. inbr.	Av. of daughters' lactations			
							Method II		Method III	
							Milk	Fat	Milk	Fat
2852	7	37	1	12	19	10.8	10987	368	10681	358
2881	17	38	1	18	27	13.8	10594	370	10267	359
2971	10	39	2	15	43	10.1	12182	390	11993	384
3185	17	33	2	17	31	13.4	11433	385	11153	376
3324	15	35	1	25	50	12.4	10851	375	10617	367
3507	21	34	1	13	28	15.7	13323	384	13063	377
3663	9	30	1	9	17	11.1	12348	415	12166	409
Average	7.0	40.9	1.6	12.9	34.1	7.7	11165	373.0	10963	366.2

Table 23. Average production of daughters of sires which did not leave sons in the herd

Sire no.	Sire's inbr. %	Age of sire (mos.) ^a	No. daus.	No. lact. of daus.	Daus. av. inbr.	Av. of daughters' lactations			
						Method II		Method III	
						Milk	Fat	Milk	Fat
544411 ^b	1	66	13	42	1.5	11992	386	11831	381
901	0	36	12	27	6.5	10475	338	10301	332
1116	1	27	4	20	7.0	11106	364	11102	364
1245	0	39	9	35	2.6	10887	356	10817	354
1571	13	28	6	23	3.8	10504	355	10383	351
1700	7	30	3	8	8.3	11950	405	11812	400
1716	1	33	19	48	6.2	11335	378	11123	371
2317	6	36	10	20	5.2	10193	345	9926	336
2434	2	36	10	22	11.2	11449	407	11221	399
2439	14	38	5	9	11.4	11121	387	10869	378
2543	21	34	6	7	8.2	10258	326	9910	315
2577	8	40	13	49	12.2	12179	396	11964	389
2712	11	43	9	28	7.8	11524	378	11343	371
2967	10	45	10	25	14.6	11648	377	11416	370
3023	4	45	9	17	10.6	11680	387	11382	377
3328	8	34	13	24	15.2	11730	388	11448	379
3537	9	36	7	17	11.2	11153	393	10923	385
Average	6.8	38.0	9.6	24.8	8.4	11246	374.5	11045	367.8

^aAge of sire computed from difference between sire's date of birth and modal date of his daughters' birth.

^bSire returned for further service after first group of daughters were tested.

sons in the herd. The average for sires which left sons was slightly less than the average for sires which did not leave sons. Although not encouraging, these results did not preclude there being differences within some periods of the twenty-nine year interval covered by this study.

To determine if differences within periods did exist, the sires were divided into groups based on the date of birth of their son or sons. These periods were the same as those chosen for the dams of sires in a previous section. Within each period, the average for all sires used, whether or not they left sons, was taken as the genetic mean of sires. The indices for sires that left sons were weighted by the number of sons and by the number of daughters of each son to give an estimate of the genetic mean of sires who contributed to the gene pool of the next generation through their sons.

The difference between the weighted mean of sires who left sons and the mean of all sires, expressed as a percent of the mean of all sires, was used as an estimate of the genetic superiority or inferiority of sires which left sons in the herd during that period. The results of these computations are given in Table 24. Perhaps the difference between the mean of selected sires and the mean of all sires should have been multiplied by a factor of two to give a sire due credit for his genetic merit. However, use of that factor would tend to double any errors of estimation and since the number of daughters per sire were small, it was decided to use the more conservative estimate.

The overall genetic superiority of sires with sons as shown in Table 24 was surprising in light of the comparison of Tables 22 and 23

Table 24. Genetic superiority or inferiority of sires of sires

Birth period of son	No. sons	Av. age of sires (mos.)	Average inbreeding of sires	Genetic superiority of selected sires as per- cent of mean of all sires			
				Method II		Method III	
				Milk	Fat	Milk	Fat
1930-34	6	48.3	1.2	2.23	3.20	2.02	2.98
1935-38	6	39.2	1.2	-.49	-.14	-.60	-.32
1939-42	7	51.3	4.6	-.83	-1.82	-.83	-1.61
1943-46	10	36.9	5.6	3.45	2.18	3.98	2.75
1947-50	7	36.6	7.1	.09	1.42	.46	1.86
1951-54	7	37.4	14.1	3.05	-.31	3.21	-.14
Average		41.6	5.6	1.25	.76	1.37	.92

in which the sires which left no sons had a slight superiority. The explanation of this paradox was found in that, by and large, the sons of the higher ranking sires were used more heavily than the sons of the lower ranking sires. That is to say that differential selection within the selected group took place. This was not without reason since more information would become available on a sire's half-sibs during his period of service. It would have been unwise not to reappraise a breeding program by using the sire more or less heavily depending upon whether the additional information increased or decreased the estimate of his genetic value.

This method of evaluating the sire contribution was, in a sense, a modified contemporary comparison. It circumvented the inherent errors in a daughter-dam comparison and since the sires were randomly mated to approximately 30 cows, there was no reason to suspect that the dams of heifers were a selected group. All the daughters born in the herd in

any given environmental period were included in the evaluation; consequently, for that group the totality of environmental effects would tend to equal zero. Sires which left sons and sires which did not leave sons were being evaluated in the same media during the same period. Herd differences, while a problem in conventional sire evaluation, were irrelevant because the sires were not being evaluated as to what they would do in another herd. This estimate desired was not of any one particular sire but rather of a composite of sires which did contribute to the next generation. Pooling the information for sires within birth-year groups would tend to reduce the sampling errors that exist when considering individual sires.

4. Selection of sires of cows

Progeny testing of sires of cows was negligible with only two sires (no. 1195 and 544411) returned for further service after their first group of daughters had come into production. As was seen in Tables 22 and 23, the average production of these sires' daughters was not noticeably different from most of the sires that were used for only one breeding season. It was apparent that selection among sires of cows was not of sufficient importance to be evaluated.

5. Summary of selection practiced

The selection practiced is listed in Table 25 by birth year groups for the four contributing components. In this table I_{CB} indicates the intensity of selection for dams of sires. This information was taken from Table 17. I_{CC} indicates the intensity of selection for dams of cows as computed in Table 20. Since the interval from dams to daughters

averaged one to two years longer than the interval from sires to daughters, the dams (with daughters) born in 1922-32 were paired with sires born in 1930-1934; dams (with daughters) born in 1933-36 paired with sires born in 1935-38, etc. The periods listed in Table 25 are in terms of the birth date of the sires for convenience but imply the above relationship with dams. I_{BB} indicates the intensity of selection for sires from which to breed sires and is taken from Table 24. I_{BC} indicates the intensity of selection for sires of cows, which in this herd was considered zero, but was included since a generation interval occurred even though there was no selection. The total generation interval in years and the total selection intensity are listed for each birth year group.

Table 25. Summary of sources contributing to the total selection intensity

Birth period of parents	Source of selection	Generation interval ($\frac{1}{2}L$) in years	Genetic superiority of parents			
			Method II		Method III	
			Milk	Fat	Milk	Fat
1930-34	I_{CB}	3.60	3.48	5.29	3.55	5.44
	I_{CC}	4.89	.26	1.32	.14	1.20
	I_{BB}	4.02	2.23	3.20	2.02	2.98
	I_{BC}	1.76	0	0	0	0
	$\sum L =$	17.27	$\sum I =$	5.97	9.81	5.71
1935-38	I_{CB}	5.00	6.08	6.06	6.18	6.09
	I_{CC}	4.96	-.04	.30	-.24	.03
	I_{BB}	3.27	-.49	-.14	-.60	-.32
	I_{BC}	2.90	0	0	0	0
	$\sum L =$	16.13	$\sum I =$	5.55	6.22	5.34
1939-42	I_{CB}	4.08	4.34	4.83	4.42	4.88
	I_{CC}	4.27	1.93	1.52	2.06	1.66
	I_{BB}	4.28	-.83	-1.82	-.83	-1.61
	I_{BC}	3.26	0	0	0	0
	$\sum L =$	15.89	$\sum I =$	5.44	4.53	5.65
1943-46	I_{CB}	4.63	6.57	5.83	6.61	5.82
	I_{CC}	4.81	3.03	2.82	2.94	2.83
	I_{BB}	3.08	3.45	2.18	3.28	2.75
	I_{BC}	2.91	0	0	0	0
	$\sum L =$	15.43	$\sum I =$	13.05	10.83	13.53
1947-50	I_{CB}	4.26	9.16	9.05	9.49	9.43
	I_{CC}	4.81	1.42	1.98	1.32	1.87
	I_{BB}	3.05	.09	1.42	.46	1.86
	I_{BC}	3.18	0	0	0	0
	$\sum L =$	15.30	$\sum I =$	10.67	12.45	11.27
1951-54	I_{CB}	6.84	11.92	11.54	12.19	11.76
	I_{CC}	3.74	1.04	.76	1.24	.91
	I_{BB}	3.12	3.05	-.31	3.21	-.14
	I_{BC}	3.07	0	0	0	0
	$\sum L =$	16.77	$\sum I =$	16.01	11.99	16.64

V. RESULTS AND DISCUSSION

A. Consideration of Selection Intensity

Since the estimated genetic superiority of selected animals was quite similar for milk and fat on both Method II and Method III data, discussion of the results of selection will be simplified by using only Method III milk data in this section of the thesis. Selection intensity will be expressed as a percent of the herd mean unless specifically stated otherwise.

1. Selection of dams of sires

In a closed herd of less than 120 breeding animals, the selection of dams of sires was, as expected, the largest source of genetic improvement. The genetic superiority of dams of sires ranged between 3.55 and 12.19 percent for the different birth year groups. The average genetic superiority of dams of sires for all periods was 7.07 percent. Rendel *et al.* (29) found a corresponding value of 6.2 percent for dams of sires which were used in the same herd in which they were bred and 3.9 percent for dams of sires sold to other herds.

The potential number of dams of sires was 584 (cows born after 1952 were excluded since their sons would not have had time to contribute to the gene pool during the period included in this study). The number of cows who actually became dams of sires was 30, i.e., 5.1 percent. The theoretical genetic superiority of the top 5 percent of cows in a herd was shown by Rendel and Robertson (28) to be roughly 10 percent of the herd mean. The average selection intensity attained was equivalent to nominating the top 20 percent of the cows as potential dams of sires

with perhaps 60-70 percent of their offspring being discarded at random (half of the offspring would be expected to be heifers and calfhood losses as well as factors other than dam's record would remove some of the bull calves from consideration). Since each sire was used about one year as compared to two or three years of service for sires in many herds, more dams had to be chosen to produce the required number of sires. This reduced the intensity of selection for dams of sires. The results found in the present study indicate that the selection of dams of sires since 1947 equaled the theoretical maximum.

One dam, No. 2386, produced five of the fourteen sires born during 1947-1954. Her estimated genetic superiority was 13.37 percent. Consequently, this one cow was primarily responsible for the increased estimates of genetic superiority of dams of sires during this period.

The average age of dams was 57 months when the son was born. Robertson and Asker (31) reported the average age of dams of registered males in the British Friesian breed to be 66 months. Since 10 of the 30 dams in the present study had their first offspring chosen as herd sires, and an additional 10 had their second offspring selected, it was expected that the average age of dams of sires in this herd would be younger than in the breed as a whole.

2. Selection of dams of cows

In Table 26 the genetic superiority of cows retained each year is compared with the genetic superiority of dams who had descendants in the herd in 1958.

Lack of closer correspondence between the two columns is a reflection

Table 26. Comparison of genetic superiority of dams having descendants with genetic superiority of cows selected each year

Birth period of dams	Genetic superiority of dams	Environmental period	Genetic superiority of selected cows
1922-32	.14	1930-35	.32
1933-36	-.24	1936-39	.17
1937-40	2.06	1940-43	1.14
1941-44	2.94	1944-47	1.72
1945-48	1.32	1948-51	2.71
1949-52	1.24	1952-55	2.06

of the degree to which parenthood was independent of culling. Animals culled after their first lactation frequently left daughters in the herd, whereas animals kept in the herd several lactations did not all have daughters.

Rendel and Robertson (28) have shown that with 0.35 mature heifers produced per cow in the herd per year and the mortality rates $1/6$ in each of the first three lactations and $1/3$ for the fourth and after, the expected genetic superiority of selected cows above their contemporaries would be 2.4 percent of the herd average. Assuming a total generation interval of 18 years, selection of dams of cows would contribute a 0.13 percent per year increase to the genetic mean of the herd.

Meek (22) reported a replacement percentage of 37.5 percent in the Iowa State University herd during 1940-1957. The replacement rate was 39.6 percent during 1930-39. On this basis the genetic superiority of dams of cows found in the present study was considerably smaller than expected. However, during the first decade the size of the herd increased

from a low of 16 cows in 1931 to 68 cows in 1940. Consequently the replacement rate of 39.6 percent, i.e., number of first calf heifers as a percent of herd size, for the 1930-1939 period was used more for increasing the size of the herd than for culling purposes. Considering the selection of dams of cows after the present herd size was attained, i.e., after 1940, the genetic superiority of dams of cows averaged 1.89 percent for dams with descendants and 1.21 percent for selected cows. Using a total generation interval of 16 years as found in this study, both methods of evaluating dams of cows gave an expected genetic gain of 0.12 percent per year from this source. This estimate is in good agreement with the value of 0.13 percent maximum calculated by Rendel and Robertson (28). Rendel et al. (29) in their study of 22 high yielding herds found that culling gave a probable annual genetic improvement of about 0.15 percent. Seath (33) reported an estimated genetic increase of 0.27 percent resulting from culling in D.H.I.A. herds. Rendel et al. (29) amended Seath's results by a factor of 2.25 to adjust for the generation interval, thus obtaining a value of 0.12 percent for the annual genetic increase attributable to culling. Both of these reports are in excellent agreement with the results found in the present study.

The phenotypic selection differential for cows from one lactation to the next as seen in Table 21 gave a mean of 3.67 percent. This is in general agreement with the corresponding value of 3.14 percent reported by Rendel et al. (29) and of 4.1 percent and 3.1 percent reported by Seath (33) from a study of Iowa and Kansas herds, respectively.

The average age of dams of cows was 55 months, or 6 months less than the estimate found by Robertson and Asker (31) in the British

Friesian breed. The policy in this herd of bringing all heifers into the herd for at least one lactation required removing enough older cows from the herd to make room for them and thus made the average generation interval less than in the general population.

3. Selection of sires of sires

The selection among sires of sires contributed nearly the same amount to the genetic progress as did selection of dams of cows. The selection among sires was severely limited by the nature of the breeding scheme whereby a sire would be used and out of the herd at an early age, usually before he was four years old. Only preliminary information at best was available when first decisions had to be made regarding which sires' sons were to be retained and only a little early indication of the production of their paternal sisters was available when the decision to start using them had to be made. This system maintained a short generation interval for sires and, as illustrated by Dickerson and Hazel (5), progeny testing is not advantageous in herds of less than 120 animals. Consequently any genetic superiority of sires was a bonus as long as the generation interval was not lengthened. The small negative values obtained for 1935-1942, as shown in Table 24, could easily be due to chance. The strong selection intensity for 1943-1954 reflects, no doubt, the intensified use of selection indices utilizing information on relatives, both direct and collateral, for predicting the probable breeding value of a sire.

4. Total selection practiced

The genetic superiority of selected parents was given in Table 25

for the four paths by which genes are passed from one generation to the next. These data were further summarized to determine the average generation interval and the genetic selection intensity per year. These results are listed in Table 27.

Table 27. Generation intervals and genetic superiority of selected parents by periods from 1930 to 1954

Birth period of parents	Generation interval ($\frac{1}{4}\Sigma L$)	Genetic superiority per year as percent of mean			
		Method II		Method III	
		Milk	Fat	Milk	Fat
1930-34	4.32 yrs.	.35	.57	.33	.56
1935-38	4.03 yrs.	.34	.39	.33	.36
1939-42	3.97 yrs.	.34	.28	.36	.31
1943-46	3.86 yrs.	.84	.70	.88	.74
1947-50	3.82 yrs.	.70	.81	.74	.86
1951-54	4.19 yrs.	.95	.71	.99	.75
Average	4.03 yrs.	.59	.58	.60	.60

Rendel et al. (29) have shown that in a closed herd in which there is no progeny testing the maximum rate of genetic improvement is about 1.0 percent per year.

In the present study, the intensity of genetic selection for milk yield (Method III) averaged 0.34 percent of the mean from 1930-1942. Several valid reasons were apparent for this selection intensity being so far below maximum. First would be the quadrupling of the herd size during this interval, as discussed previously. The small size of the herd in the early years limited slightly the selection differential that could be attained in selecting dams of sires. A high incidence of disease

removed many animals from the herd involuntarily, and this not only reduced the culling that could be practiced among younger animals, but also reduced the number of older animals whose genetic potential could be ascertained more accurately because of repeated records. As in any herd, the practice of a breeding program is dependent on management providing considerable freedom to cull beyond the unavoidable losses due to old age, injury, mastitis, tuberculosis, brucellosis, calf scours and other diseases. This is particularly limiting as regards selection of dams of cows, but it also decreases the intensity of selection of dams of sires.

A more realistic view of the genetic selection differential possible in well managed breeding herds can be seen by studying the results in this herd after 1942 when a more or less constant herd size was attained. Disease losses were reduced to reasonable expectations and no outside animals were being introduced into the herd. Complete information was available on all animals in the herd and there was some opportunity for voluntary culling. It is reasonable to assume that the management and environment of the herd had improved as a result of experience and of the addition of new barns. From 1943-1954 the overall selection intensity averaged 0.87 percent of the mean yield. This increase in intensity of selection over the 1930-1943 period was due to the average genetic selection differential being doubled among dams of sires, nearly tripled among dams of cows, and increased more than 12 fold among sires of sires in comparison with the earlier period. A reduced generation interval also increased the annual rate of improvement.

This rate of genetic progress compares favorably with the 0.7 percent

per year genetic improvement reported by Rendel and Robertson (28) from a study of a partially closed herd that had maintained records since 1903. Rendel et al. (29) found a probable genetic improvement of 0.3 - 0.4 percent per year due to selection of dams of cows and dams of bulls in 22 high yielding British herds of seven breeds. The estimated annual increase in genetic merit in the Idaho University Holstein herd of 8 lbs. butterfat per year as reported by Harvey (7) seems unreasonably high in comparison with the present study and with other studies discussed above.

The estimated genetic improvement of 0.87 percent per year (roughly 100 lbs. of milk or 4 lbs. of butterfat) is a good deal less than the breeder usually imagines he can achieve. Nevertheless, it is a realistic value and is certainly larger than the majority of our breeding establishments have attained as evidenced by the work of Rendel et al. (29).

This estimate of the rate of genetic improvement of the herd has several limitations. The first one is the application of heritability data derived from other herds. There is a fair amount of evidence, however, that within herds the heritability of milk yield is about 0.25 (16,35), and that value was used in this study. If the correct values of heritability for this particular herd should be nearer 0.20 or 0.30, the estimates of genetic selection would be lowered or raised by roughly one-fifth.

The use of different age correction factors seemed to affect the estimates of genetic superiority of selected parents very little as evidenced by the close similarity of the results for Method II and Method III data. Nevertheless, there would be some merit in adjusting the production of all cows to a 27 month old equivalent rather than mature

equivalent. All cows have first lactations, but few cows ever reach maturity. If the correction factors were in error for a given herd or area, a smaller bias would be introduced into the data by adjusting the part of the distribution curve that contained the lowest frequency of observations.

Another source of error is in the sampling error of the estimate, both statistical and Mendelian. However, the value of the estimates lies not so much in the absolute value of the advance calculated as in the comparison of them with the maximum reasonably possible.

Of practical importance also is the relative magnitude of the four components contributing to the genetic progress of the subsequent generation. Intense selection of dams of cows will increase the genetic value of a herd by 10 to 15 pounds of milk per year at most whereas careful selection of dams of sires can increase it by 50 to 60 pounds per year. The immediate increase in average production of the herd as a result of culling low producers is an extra benefit of real importance to the dairyman. This effect should not be confused with expected genetic gain of the subsequent generation as discussed above.

If the herd is not closed to outside breeding, there can also be considerable selection among sires of sires and among sires of cows. With artificial insemination and optimum use of progeny testing, in a population of 2,000 cows, Rendel and Robertson (28) illustrated that the maximum rate of genetic improvement per year would be of the order of 1.5 percent.

In the herd under study, progeny testing of sires was nil for sires of cows and limited for sires of sires. The possible gain from using

progeny tested sires from other herds would have to be weighed against the increased generation interval and against the decreased information available on half the breeding herd since in most cases the outside sire's ancestry would not be as familiar to the breeder as the ancestry of a sire from his own herd would be.

B. Consideration of Maximum Likelihood Estimates

1. Effect of different repeatability values

Since the maximum likelihood estimates required the use of age factors and the assumption of some value for repeatability, an important question arose as to what extent the estimated trends were biased by using values not appropriate to the herd under investigation. To give a more general picture of the trends the period was divided into four-year intervals (except for the first interval which included the extra years that didn't fit into a four-year group when counting back from 1958 for environmental intervals and from 1956 for genetic groups). The estimates that had been obtained using repeatability values of 0.30, 0.40, and 0.50 were averaged for the four-year intervals. The results are given in Table 28 for the environmental means and in Table 29 for for the genetic means.

In general, increasing the value used for repeatability caused the environmental trend to decrease and the genetic trend to increase. This effect was not perfectly linear. In Method II fat data, increasing the value of repeatability from 0.30 to 0.40 gave an increase in the estimated environmental trend of 0.92 pounds of fat per cow per year while increasing repeatability from 0.40 to 0.50 caused an increase of 0.81 pounds

Table 28. Environmental means estimated by the maximum likelihood method using repeatability values of 0.30, 0.40, and 0.50

Repeatability value	Age factors used	Environmental interval						
		1930-34	1935-38	1939-42	1943-46	1947-50	1951-54	1955-58
<u>Fat</u>								
r = 0.3	II	386	419	392	396	415	362	323
	III	321	369	359	383	424	390	372
r = 0.4	II	398	427	399	400	415	354	311
	III	331	376	365	387	424	383	360
r = 0.5	II	408	434	405	403	415	348	300
	III	341	363	371	390	425	377	350
<u>Milk^a</u>								
r = 0.3	II	1190	1236	1158	1162	1214	1090	997
	III	996	1088	1063	1124	1241	1172	1142
r = 0.4	II	1219	1155	1178	1173	1214	1070	962
	III	1022	1106	1080	1134	1242	1154	1109
r = 0.5	II	1244	1273	1195	1184	1214	1052	932
	III	1045	1122	1096	1145	1243	1136	1080

^aRounded to nearest 10 pounds.

Table 29. Genetic means estimated by the maximum likelihood method using repeatability values of 0.30, 0.40, and 0.50

Repeatability value	Age factors used	Birth group interval						
		1930-32	1933-36	1937-40	1941-44	1945-48	1949-52	1953-56
<u>Fat</u>								
r = 0.3	II	355	336	354	362	383	424	465
	III	404	374	374	360	360	380	399
r = 0.4	II	347	330	349	360	383	433	480
	III	397	368	369	358	360	389	413
r = 0.5	II	340	324	344	358	383	441	492
	III	391	363	365	356	359	396	425
<u>Milk</u> ^a								
r = 0.3	II	1048	1016	1058	1092	1157	1254	1360
	III	1195	1127	1116	1084	1092	1124	1168
r = 0.4	II	1028	1000	1042	1084	1157	1276	1400
	III	1177	1112	1102	1078	1090	1146	1204
r = 0.5	II	1010	985	1028	1078	1156	1296	1435
	III	1161	1100	1088	1071	1088	1164	1238

^aRounded to nearest 10 pounds.

of fat per cow per year. Corresponding values of 0.85 and 0.77 were found in Method III fat data. If the slight deviations from linearity are ignored within this range of repeatability values, the average change in the environmental trend for each increase of 0.01 in the value used for repeatability would be a decrease of 0.086 pounds of fat per cow per year for Method II data and 0.081 pounds of fat per year per cow for Method III data. Corresponding values for milk were found to be 2.3 and 2.01 pounds per cow per year. These results agreed closely with Henderson's (9a) estimates of biases from incorrect repeatability in several New York herds.

The effect of different repeatability values on the estimates of genetic trends, as shown in Table 29, were opposite to the effect on estimates of environmental trends.

These results were not surprising since the work of Henderson (8), Lush and Shrode (18) and Henderson et al. (10) had pointed out the fallacy of assuming perfect repeatability (i.e., $r = 1.00$) in estimating environmental trends or in determining age correction factors. The question to be answered in this study was to determine the magnitude of the error incurred by using incorrect values of repeatability within the range of values usually found for milk and fat yield in dairy cattle. Small biases, such as incorrect repeatability values, might not be apparent or effective when data covering short time intervals are studied but they accumulate and become more serious with longer time intervals.

The maximum likelihood method seems far less sensitive to incorrect values for repeatability than to incorrect values for age factors. However, using a repeatability value which is as much as 0.10 in error would introduce a serious bias into the estimates obtained from this method.

2. Effect of age correction factors

Tables 28 and 29 show clearly that the estimates obtained from Method II and Method III data differ markedly even when the same value is used for repeatability. The main difference between the two sets of age factors was that the factors for the first lactations averaged 0.046 lower for Method III than for Method II. The differences in age adjustments for other lactations were much smaller (see Table 5). An attempt to ascertain the source of the bias in the age factors and to determine which method was more nearly correct was made by using various segments of the data for computing maximum likelihood estimates. A repeatability value of 0.40 was used in this series of computations because such a value seemed to come closest to fitting both milk and fat yield for the different lactations. This factor could be slightly in error but the magnitude of any bias from this source appeared to be small in comparison to the age factor discrepancy.

The steps taken to determine why Method II and Method III data gave such different estimates were as follows:

1. The results obtained from the full volume of data were used as a standard with which to compare subsequent results.
2. Deleted were all lactations for 15 cows born before 1928 and the low terminal lactations of 31 other cows which had at least five previous lactations.
3. Next the lactations for all cows born before 1935 and all lactations exceeding the sixth on the remaining cows were deleted.
4. Same as Step 3 except that all first lactations were also deleted.

Maximum likelihood estimates of genetic and environmental trends were computed for these four portions of the data. The results of these computations are shown in Table 30 for environmental means and in Table 31 for genetic means. The estimates were grouped by years and averaged as described for Tables 28 and 29.

Step 2 demonstrated that low terminal lactations did have a depressing effect on the estimates of the environmental trend in later years. It was impossible to remove any terminal lactations before 1935 since a cow had to have at least five previous lactations before she could be excluded. Removal of these lactations raised the final environmental estimate 25 pounds of fat and 730 pounds of milk and decreased the final genetic estimate 24 and 690 pounds of fat and milk, respectively, for Method II data. Similar results can be seen for Method III data.

Step 3 removed that portion of the data which contained the possibly confusing effects of introducing unrelated animals from other herds and the managerial changes caused by the loss of a barn by fire. In addition, this step removed many of the lactations in which corrections had been made for milking three or four times per day.

In several cases, a cow was retained until she had a poor lactation and then she would be culled. This was certainly a logical management practice. It would not necessarily imply, however, that the general environment was declining because a previously high producing cow had a low lactation. Any number of events peculiar only to that one cow, such as a severe mastitis, ketosis or milk fever could cause that particular lactation, which then become terminal, to be low. Since step 2 had

Table 30. Environmental means estimated by the maximum likelihood method using repeatability of 0.40 with different segments of the data

Data used	Age factors used	Environmental interval						
		1930-34	1935-38	1939-42	1943-46	1947-50	1951-54	1955-58
<u>Fat</u>								
A ^a	II	398	427	399	400	415	354	311
	III	331	376	365	387	424	383	360
B ^b	II	386	411	388	397	417	367	336
	III	321	362	356	385	425	394	384
C ^c	II		421 ^d	396	398	420	369	329
	III		372 ^d	364	381	421	385	364
D ^e	II		372 ^f	381	388	422	368	365
	III		359 ^f	375	387	427	377	376
<u>Milk^g</u>								
A	II	1219	1155	1178	1173	1214	1070	962
	III	1022	1106	1080	1134	1242	1154	1109

^aUsing all lactations for all cows in the herd from 1930-58 inclusive.

^bSame as A^a except for deletion of all lactations of 15 cows born before 1928 and terminal lactations for 31 other cows which had at least five previous lactations.

^cIncluding the first up to and including the sixth lactation of all cows born in 1935 or later.

^dEstimate for 1937-38 only.

^eSame as c except for deletion of all first lactations from the data.

^fEstimate for 1938 only.

^gRounded to nearest 10 pounds.

Table 30. (Continued)

Data used	Age factors used	Environmental interval						
		1930-34	1935-38	1939-42	1943-46	1947-50	1951-54	
B	II	1176	1211	1147	1161	1215	1106	1035
	III	981	1050	1052	1123	1238	1184	1176
C	II		1245 ^d	1172	1167	1229	1111	1023
	III		1098 ^d	1075	1116	1230	1160	1123
D	II		1101 ^f	1138	1160	1244	1109	1106
	III		1062 ^f	1118	1154	1256	1136	1138

Table 31. Genetic means estimated by the maximum likelihood method using repeatability of 0.40 with different segments of the data

Data used	Age factors used	Birth group interval						
		1930-32	1933-36	1937-40	1941-44	1945-48	1949-52	1953-56
<u>Fat</u>								
A ^a	II	347	330	349	360	383	433	480
	III	397	368	369	358	360	389	413
B ^b	II	367	347	460	465	382	420	456
	III	415	384	379	363	361	377	392
C ^c	II		330 ^d	350	359	374	416	449
	III		370 ^d	376	368	367	390	414
D ^e	II		348 ^d	368	364	389	405	412
	III		364 ^d	381	370	391	402	402
<u>Milk^f</u>								
A	II	1028	1000	1042	1084	1157	1276	1400
	III	1177	1112	1102	1078	1090	1146	1204

^aUsing all lactations for all cows in the herd from 1930-58 inclusive.

^bSame as a except for deletion of all lactations of 15 cows born before 1928 and terminal lactations for 31 other cows which had at least five previous lactations.

^cIncluding the first up to and including the sixth lactation of all cows born in 1935 or later.

^dEstimate for 1935-36 only.

^eSame as c except for deletion of all first lactations from the data.

^fRounded to nearest 10 pounds.

Table 31. (Continued)

Data used	Age factors used	Birth group interval						
		1930-32	1933-36	1937-40	1941-44	1945-48	1949-52	1953-56
B	II	1082	1048	1074	1102	1156	1238	1331
	III	1223	1155	1129	1094	1093	1111	1138
C	II		1008 ^d	1045	1083	1132	1226	1336
	III		1127 ^d	1122	1109	1108	1150	1202
D	II		1043 ^d	1079	1089	1170	1218	1242
	III		1090 ^d	1114	1106	1174	1208	1211

shown the effect of low terminal lactations on the environmental and genetic estimates, this was circumvented to some extent by removing all lactations beyond the sixth. The estimates from Step 3 were, as expected, reasonably similar to those obtained using all data although the final environmental estimates were slightly increased with an opposite effect on the final genetic estimates.

Step 4 was the critical test for the age factors. It was to be expected that Method II and Method III data would give similar estimates when only the second through the sixth lactations were included since the age factors in the two methods were altered only slightly for these lactations. The question was whether the environmental estimates, based largely in this case on lactations of mature or nearly mature cows for which age factors were negligible, would more nearly approach the estimates derived from Method II or from Method III using all data. As was shown in Tables 30 and 31 these estimates did tend to follow more closely the pattern which Method III followed when all of the data were used.

Considering the Method III results as standard, each extra pound of fat by which Method II first lactations were built up biased the environmental trend downward by 0.29 pounds of fat per cow per year. Henderson (9a) reported similar estimates of the effect of a bias in age corrections.

The similarity of the Method II estimates of environmental trends when first lactations were excluded to the Method III estimates when all data were used can be seen more easily in Table 32, which is a condensation of Table 30. Table 33 gives a similar abbreviation of Table 31 for the genetic trends.

Table 32. Comparison of environmental means of data with and without first lactations included

Data used	Age factors used	Environmental interval					
		1937-38	1939-42	1943-46	1947-50	1951-54	1955-58
<u>Fat</u>							
A ^a	II	428	399	400	415	354	311
	III	381	364	387	424	383	360
D ^b	II	372	381	388	422	368	365
<u>Milk</u>							
A	II	1248	1178	1173	1214	1070	962
	III	1111	1080	1134	1242	1154	1109
D	II	1101	1138	1160	1244	1109	1106

^aUsing all lactations for all cows in the herd from 1937-58 inclusive.

^bUsing second through sixth lactations of all cows born in 1935 or later.

The genetic estimates from Step 4 included any gain that might have occurred as a consequence of culling on the basis of first lactation. If Method II age factors were unbiased, the final genetic estimates from Step 4 should have been higher than the final genetic estimates from Step 3. They actually were higher during the first two-thirds of the period but dropped below Step 3 in the final third of the period.

The lack of correspondence between the environmental estimates obtained from Method II data when the first through the sixth lactations were included and when the second through the sixth lactations were included supported the conclusion made in Section IV-A that the standard U.S.D.A. age factors overcorrected for 243-day records of first calf

Table 33. Comparison of genetic means of data with and without first lactations included

Data used	Age factors used	Birth group interval					
		1935-36	1937-40	1941-44	1945-48	1949-52	1953-56
<u>Fat</u>							
A ^a	II	326	349	360	383	433	480
	III	360	369	358	360	389	413
B ^b	II	348	368	364	389	405	412
<u>Milk</u>							
A	II	1004	1042	1084	1157	1276	1400
	III	1103	1102	1078	1090	1146	1204
D	II	1043	1079	1089	1170	1218	1242

^aUsing all lactations for all cows in the herd from 1937-58 inclusive.

^bUsing second through sixth lactations of all cows born in 1935 or later.

heifers in the Iowa State University herd.

It would seem from this empirical examination that overadjusting first lactations was the primary reason that Method II data gave an estimate of the environmental mean decreasing from 415 pounds to 311 pounds of fat during the 11-year interval from 1947 to 1958 while the genetic mean increased by 97 pounds of fat in the 11 years from 1945 to 1956. These trends were questioned originally for two reasons. The first was that it did not seem logical that during a period when feeding and management practices were being improved among the general population of dairy herds there would be a marked and consistent decrease in the

environment of the Iowa State University herd. Secondly, the increase in the genetic estimates was larger than 2 percent of the herd mean per year for a period of 11 years. This rate of increase was twice the theoretical maximum rate of increase expected for a closed herd of this size and was more than twice as large as the increase expected from the actual selection intensity.

It must be concluded that any biases arising from incorrect age factors for a given herd will drastically affect the estimates of genetic and environmental trends obtained by the maximum likelihood method. Criteria are lacking for measuring the suitability of age factors that are independent of either the genetic or the environmental trends. A major improvement in this direction might be to correct all lactations to a 27 month old basis. Although this would not resolve the possible bias in factors for converting, for example, from second to first lactation basis, it would reduce the fraction of the data which had to be adjusted by a large factor. This must be labelled conjecture without further evidence but it might be worth pursuing.

3. Genetic progress estimated by the maximum likelihood method

Biases in age factors or in repeatability values were shown in the preceding discussion to alter drastically the estimates of genetic and environmental trends by the maximum likelihood method. However, since the Method III data had been adjusted by age factors calculated from the herd under study and since an estimate of the repeatability of both milk and fat had been calculated by intraclass correlation on Method III data, it seemed logical to apply the maximum likelihood method using these

statistics.

A repeatability value of 0.35 was used for fat and 0.44 for milk as calculated in Table 10 for Method III data. The genetic and environmental means estimated by the maximum likelihood method are given in Table 34.

Table 34. Maximum likelihood estimates of environmental and genetic trends using repeatability values of 0.35 for fat and 0.44 for milk

Estimates of genetic means			Estimates of environmental means		
Birth interval	Fat	Milk	Environmental interval	Fat	Milk
1920-29	402	1185	1930-32	318	1022
1930-32	400	1170	1933-34	338	1047
1933-34	379	1116	1935-36	368	1108
1935-36	362	1098	1937-38	378	1117
1937-38	370	1095	1939	369	1104
1939-40	373	1098	1940	368	1092
1941-42	358	1088	1941	352	1048
1943-44	360	1062	1942	361	1105
1945-46	355	1080	1943	374	1102
1947-48	365	1099	1944	370	1124
1949-50	380	1147	1945	386	1137
1951-52	389	1160	1946	409	1193
1953-54	408	1215	1947	424	1245
1955-56	405	1222	1948	450	1315
			1949	418	1217
			1950	404	1195
			1951	409	1198
			1952	388	1137
			1953	362	1104
			1954	386	1147
			1955	373	1086
			1956	367	1105
			1957	356	1097
			1958	368	1100

Although the genetic means at the beginning and at the end of the period included in this study did not differ appreciably, there were some encouraging results between these two points. A decline was indicated for both milk and fat yield from the beginning of the experiment in 1930 until a low point was reached between 1941 and 1946. At this point a steady and consistent increase began in the estimated genetic merit of the herd. This culminated between 1953 and 1956 with the re-attainment of the peak that the original herd had in 1930. The herd had quadrupled in numbers during the period of the apparent decline in genetic merit. This had necessitated relaxing the selection pressure during that time. During this same period disease had been a major problem and further reduced the selection pressure for the dams of both bulls and cows, and indirectly of sires of bulls and cows. When it became possible to make culling effective and a selection index began to be used systematically, the response was indicated in the increased genetic estimates of the succeeding birth year groups. The genetic trends indicated by this and other maximum likelihood estimates are discussed and compared in greater detail in the next section.

C. Comparison of Genetic Progress Expected from Selection with Genetic Trends Estimated by the Maximum Likelihood Method

The estimates of genetic trends by the maximum likelihood method and the genetic progress predicted by the selection intensity provide two independent evaluations of the change in genetic merit of the herd during the period included in this study. Each method of evaluation was subject to sampling errors as well as to biases possibly introduced by assumptions that must be made in order to get a solution.

The maximum likelihood method, if the model chosen corresponded exactly to the biological facts, would provide unbiased estimates if the original data contained no biases. However, it was shown in Table 3 that biases existed in the U.S.D.A. (13) age correction factors as applied to 243-day records from this particular herd. The effects of these biases were demonstrated. In addition, different methods of estimating repeatability (Tables 7, 8, 9 and 10) gave values that ranged from 0.28 to 0.51. The consequence of this possible bias was evaluated. The intraclass correlation estimates of repeatability and the data adjusted to a Method III basis were used to compute the final estimates of genetic and environmental trends by the maximum likelihood method as listed in Table 34.

The estimates of selection intensity assumed values for repeatability and for heritability that were generally accepted as correct for the general population of dairy cows. However, it is possible that these estimates might be in error for this particular herd.

Nevertheless, some assumptions must be made in a study such as this or the problem becomes unmanageable. The magnitude and effect of the biases introduced by age correction factors and repeatability values were, if not fully pinpointed, at least bracketed in this analysis. The effect of assuming an incorrect value for heritability when estimating the selection intensity can be determined within reasonable limits.

The estimates of selection intensity agreed excellently as between Method II and Method III data. This implies that age correction factors (which were the only difference between Methods II and III) introduced a much smaller bias when comparing selected animals with the unselected

population from which they were chosen than when estimating environmental trends, and eventually genetic trends, by the maximum likelihood method. In estimating these trends any regular biases tend to accumulate instead of cancelling each other and, hence, even small biases can cause large errors in trends computed over long periods of time, although they might cause only tiny errors in comparisons among near contemporaries. Consequently, the genetic progress predicted from the intensity of selection was used as the standard by which the maximum likelihood estimates were evaluated.

The estimates of genetic trends by the maximum likelihood method as presented in the preceding section, i.e., grouped in four-year intervals, were used for comparison with the progress predicted by selection. The change in the estimated genetic mean of a four-year interval from the preceding four-year interval was expressed as a percent of the preceding interval, just as selection intensity was expressed as a percent of the mean of the unselected group.

A further assumption had to be made in order to compare these estimates. Generation intervals soon overlap in a manner that deny delineation. A few of the dams selected from one generation could conceivably produce offspring 12 or more years later, i.e., three or more average generation intervals. For purposes of comparisons, the assumption was made that parents born during 1930-34 contributed to the maximum likelihood birth group of 1933-36, parents born during 1935-38 contributed to the birth group of 1937-40, 1939-42 to 1941-55, etc. It must be granted that certain individuals, particularly those born in the last year of a parental interval, would contribute several offspring to the

birth group beyond the one assigned them but others, especially if born early in the parental interval and staying for only one or two lactations, would contribute offspring only in the first part of the birth group assigned to them. Likewise, the assumption was necessary that each four-year birth group interval (for the maximum likelihood estimates) provided the entire parentage for the succeeding four-year birth group interval. The discrepancies from these assumptions seemed unavoidable and in reality were probably minor, as they would cancel each others effects partially.

In Table 35 the estimates of the change in genetic merit are shown for Method II data.

For both milk and fat, the Method II maximum likelihood estimates were all strongly negative for the 1933-36 interval. During the remainder of the period the maximum likelihood estimates were much larger than the increase expected from the selection intensity. Considering Method II fat data with a repeatability of 0.30, the maximum likelihood estimates averaged 1.11 percent increase per year in the mean over the entire period as compared to an average increase of 0.58 percent per year predicted from the selection intensity. Method II milk data, using a repeatability of 0.40 for the maximum likelihood estimates, averaged 1.30 percent increase per year in comparison to a value of 0.59 percent per year as predicted from selection intensity for the entire period.

If the 1933-36 interval in which strong negative effects were estimated by the maximum likelihood method were excluded and the comparison made only on the results from 1937-1956, i.e., when the herd was totally closed to outside breeding and herd size was more or less stable, the

Table 35. Estimates of change in genetic merit of the herd using Method III data

Source of estimate	Birth group interval						Mean ^a	Mean ^b
	1933-36	1937-40	1941-44	1945-48	1949-52	1953-56		
<u>Fat</u>								
A ^c	0.57	0.39	0.28	0.70	0.81	0.71	0.58	0.58
B ^d	-1.78	1.34	0.56	1.45	2.68	2.42	1.11	1.69
C ^e	-1.63	1.44	0.79	1.60	3.26	2.71	1.36	1.96
D ^f	-1.57	1.54	1.02	1.74	3.78	2.89	1.57	2.19
E ^g		2.02	0.64	1.04	2.80	2.58	1.82	1.82
<u>Milk</u>								
A	0.35	0.34	0.34	0.84	0.70	0.95	0.59	0.63
B	-1.02	1.03	0.80	1.49	2.10	2.11	1.08	1.51
C	-0.91	1.05	1.01	1.68	2.57	2.43	1.30	1.75
D	-0.83	1.09	1.22	1.81	3.03	2.68	1.50	1.97
E		1.22	0.91	1.13	2.08	2.24	1.52	1.52

^aIncluding 1933-36.

^bExcluding 1933-36.

^cEstimated genetic superiority of parents contributing to each interval.

^dMaximum likelihood estimate using all data and a repeatability of 0.30.

^eMaximum likelihood estimate using all data and a repeatability of 0.40.

^fMaximum likelihood estimate using all data and a repeatability of 0.50.

^gMaximum likelihood estimate using first through sixth lactations of cows born in 1937 or later and a repeatability of 0.40.

correspondence between the two estimates was even less encouraging. For Method II fat data with a repeatability of 0.30 for the maximum likelihood estimate, the estimate of attained progress averaged 1.69 percent per year whereas the progress predicted from selection averaged 0.58 percent of the mean per year. A similar comparison for Method II milk data with a repeatability of 0.40 gave 1.75 percent and 0.63 percent per year for the two separate estimates.

A comparison of the estimates of attained progress using other values of repeatability can also be seen in Table 35.

The change in genetic merit of the herd for 1933-56, as estimated from Method III data, are given in Table 36. This table has one more line than Table 35, that addition being the maximum likelihood estimate computed using the repeatability values obtained for Method III data by intraclass correlation.

As in Method II data, a strong negative effect was shown for the 1933-36 interval in comparison with the preceding interval. Since the number of animals in the early years was few and, consequently, the computed standard errors of the maximum likelihood estimates were larger than for any other interval of this study, except the 1955-56 birth-year group, a comparison of the results excluding this interval appeared to be logical. The estimated decline in genetic merit during the early years of the study could indeed have been real. Certainly selection was not as intense during that interval as in the latter three intervals. The lesser intensity of selection, the increase in herd size, and the sampling errors inherent in small numbers could have produced a decline in spite of efforts to the contrary.

Table 36. Estimates of change in genetic merit of the herd using Method III data

Source of estimate	Birth group interval						Mean ^a	Mean ^b
	1933-36	1937-40	1941-44	1945-48	1949-52	1953-56		
<u>Fat</u>								
A ^c	0.56	0.36	0.31	0.74	0.86	0.75	0.60	0.60
B ^d	-2.48	0	-0.94	0	1.39	1.25	-0.13	0.34
C ^e	-2.43	0.07	-0.74	0.14	2.01	1.54	0.10	0.60
D ^f	-2.39	0.14	-0.62	0.21	2.58	1.83	0.29	0.83
E ^g		0.54	-0.53	-0.07	1.56	1.54	0.61	0.61
F ^h	-2.42	0.03	-0.87	0.07	1.67	1.43	-0.02	0.47
<u>Milk</u>								
A	0.33	0.33	0.36	0.88	0.74	0.99	0.60	0.66
B	-1.90	-0.24	-0.72	0.18	0.73	0.98	-0.16	0.19
C	-1.84	-0.23	-0.54	0.28	1.28	1.26	0.04	0.41
D	-1.75	-0.27	-0.39	0.40	1.75	1.59	0.22	0.62
E		-0.15	-0.29	-0.02	0.95	1.13	0.32	0.32
F ⁱ	-1.79	-0.25	-0.48	0.35	1.47	1.39	0.12	0.50

^aIncluding 1933-36.

^bExcluding 1933-36.

^cEstimated genetic superiority of parents contributing to each interval.

^dMaximum likelihood estimate using all data and a repeatability of 0.30.

^eMaximum likelihood estimate using all data and a repeatability of 0.40.

^fMaximum likelihood estimate using all data and a repeatability of 0.50.

^gMaximum likelihood estimate using first through sixth lactations of cows born in 1937 or later and a repeatability of 0.40.

^hMaximum likelihood estimate using all data and a repeatability of 0.35.

ⁱMaximum likelihood estimate using all data and a repeatability of 0.44.

Considering the average value for the birth year interval of 1937-56, Method III fat data gave estimates of 0.60, 0.34, 0.47, 0.60 and 0.83 percent of the mean for genetic superiority of parents, and maximum likelihood estimates using repeatability of 0.30, 0.35, 0.40 and 0.50, respectively. Corresponding values for Method III milk data were 0.66, 0.19, 0.41, 0.50, and 0.62 for genetic superiority of parents, and maximum likelihood estimates using repeatability of 0.30, 0.40, 0.44 and 0.50, respectively. This order of listing differs slightly from the order in Table 36 to give the progression in maximum likelihood estimates with increasing repeatability.

Considerable variation obviously existed between the selection intensity estimates and the maximum likelihood estimates within any given four-year interval. Using the overall average did tend to neglect these differences or to cancel them. However, this cancelling compensated somewhat for the artificial limits that had to be set in separating one birth group interval from the preceding or succeeding interval.

Method III estimates from selection intensity and Method III maximum likelihood estimates obtained using the intraclass correlation estimate of repeatability were in much closer agreement than the corresponding Method II estimates.

The necessity of assuming age correction factors and repeatability values in order to apply the maximum likelihood method of separating environmental and genetic trends poses serious limitations to its usefulness. Different age factors, whether or not they were biased, had no real effect on the estimation of selection intensity as evidenced by the excellent agreement of Method II and Method III estimates in Table 27.

However, the same data gave estimates of trends opposite in direction when subjected to the maximum likelihood computations. The Method II data, i.e., lactations corrected by the standard U.S.D.A. age factors (13), gave trends that implied a genetic improvement of 1.5 - 2.0 percent of the mean per year for the entire period. This was three to four times as large as the actual selection intensity should have produced and was one and one-half to two times as large as the maximum theoretical genetic progress predicted by Rendel and Robertson (28) for a closed herd of this size.

This was not intended as a criticism of the U.S.D.A. age factors. They probably are appropriate for 305-day records in average D.H.I.A. herds and for most types of studies they probably introduce little, if any, bias. But for a computation as cumulatively sensitive to bias as the maximum likelihood method, the standard U.S.D.A. age factors do not appear to be sufficiently accurate. Nor can any general set of corrections meet this test for any particular herd. Since the genetic progress in most herds will be less than one percent per year, the detection or determination of this progress can only be attained when the biases from various corrections or assumptions are reduced to much less than one percent. Since environmental trends affect the determination of age correction factors, and age correction factors affect the estimation of environmental trends, an iterative approach to this problem would appear to be the only means of solution.

Repeatability must also be unbiased if the maximum likelihood results are to be unbiased. The magnitude of the bias from incorrect repeatability is apt to be much less than the bias from errors in the age

correction. The approach suggested by Kempthorne and Von Krosigk (10) of incorporating repeatability in the model as one of the parameters to be estimated might resolve this bias.

VI. SUMMARY

The purpose of this study was to determine the genetic progress in milk and fat production of the Iowa State University Holstein herd from 1930 through 1958. The data included 1,747 lactations of 685 cows. All lactations were standardized to a 243 day, two-time milking, mature equivalent basis, using the U.S.D.A. (13) age correction factors. The records were subsequently adjusted to zero percent inbreeding to remove the effects of such inbreeding as had occurred in this closed herd.

In such studies of time trends any errors in age corrections tend to accumulate instead of cancelling, so that errors too small to be worth considering for ordinary purposes can introduce serious errors into the computed time trends.

Consequently the suitability of the U.S.D.A. age correction factors (developed for 305-day lactations in average D.H.I.A. herds) to 243-day records in this herd was investigated. The factors for first calf heifers overcorrected. Minor deviations were noted for other lactations. Age factors were therefore computed for the 243-day records used in this study and are listed in Table 5. In subsequent analyses, the computations were made in two ways. In Method II the data had been corrected by the U.S.D.A. factors and in Method III they had been corrected by age factors developed from these data themselves.

Repeatability values were computed both by intraclass correlation (Tables 8, 9 and 10) and by regression (Table 7). The former tended to underestimate repeatability. The latter tended to overestimate it, especially as between first and second lactations, and perhaps to

underestimate it for the later lactations. Intraclass correlation estimates ranged from 0.40 to 0.44 for milk and from 0.28 to 0.35 for fat. Weighted regression estimates were 0.514 and 0.513 for milk and fat, respectively.

Maximum likelihood estimates of genetic and environmental trends were obtained from data adjusted by each of the two sets of age correction factors. Method II data indicated, in general, a strong downward environmental trend and a strong upward genetic trend with the passage of time (Figures 5 and 6). Method III data, in general, indicated moderate upward trends in both environment and average genetic merit. Further analyses, in which first lactations and lactations beyond the sixth were removed from the data, indicated that the trends found by Method III were more nearly correct. Each pound which first lactations were built up by age correction factors decreased the computed environmental trend by 0.29 pounds of fat per cow per year.

Using different repeatability values had slight effect upon the maximum likelihood estimates of trends. This was ascertained by using $r = 0.30, 0.40,$ and 0.50 in separate computations. On the average, each increase of 0.01 in the figure used for repeatability decreased the environmental trend by 0.086 pounds of fat per cow per year.

Intensity of selection was evaluated for dams of sires, dams of cows and sires of sires (Tables 17, 20 and 24). Dams of sires were 7.07 percent and dams of cows 1.24 percent genetically superior to their herdmates (Method III milk data). Although the breeding system (use of young sires almost always) practically precluded progeny testing per se, information on dams and half sibs made possible some selection among

sires of sires, which were 1.37 percent genetically superior to all sires. Selection of sires of cows was discounted as negligible since only two sires were returned to the herd after their progeny test information was available. The average genetic superiority from these four paths was 0.34 percent of the mean per year from 1933 to 1944 and 0.87 percent of the mean per year from 1945 to 1956 for Method III milk data. The values were rather similar for Method III fat data and Method II milk and fat data, as shown in Tables 35 and 36. The increased selection intensity in the latter period presumably reflected the use of the selection index and the attainment of a more or less constant herd size as well as fewer involuntary losses from deaths and from discarding for disease control.

The genetic progress expected from selection during 1937-1956 averaged 0.66 percent of the mean per year, using Method III milk data while the genetic progress indicated by the maximum likelihood method, using a repeatability of 0.44 and the same data, averaged 0.50 percent of the mean per year (Table 36). Corresponding values for Method II milk data using a repeatability value of 0.40 were 0.63 and 1.75 percent of the mean per year, respectively. Fat data, as shown in Tables 35 and 36, gave values similar to milk data. The small age bias in Method II data did not cumulate enough to be serious when computing selection intensity among contemporaries, as is evidenced by the excellent agreement between Method II and Method III data. However, this small bias tended to accumulate and cause large errors in computing maximum likelihood trends over long periods of time, as is shown by the maximum like-

likelihood results from Method II diverging so much from those of the Method III data.

This study illustrates that the necessity of assuming or estimating age correction factors and repeatability values, in order to apply the maximum likelihood method of separating environmental and genetic trends, poses serious limitations to the usefulness of this method for detecting a genetic trend as small as an increase of one percent per year. Estimating genetic gain directly from the selection applied proved to be less subject to differences, or possibly biases, in age correction factors. It was, however, dependent on the correctness of the heritability values used.

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