THE RELATIVE IMPORTANCE OF GENETIC AND ENVIRONMENTAL FACTORS ON THE BUTTERFAT PRODUCTION OF HOLSTEIN-FRIESIAN CATTLE

By

Chen Kang Chai

A THESIS

Submitted to the School of Graduate Studies of Michigan
State College of Agriculture and Applied Science
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Animal Husbandry

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An Abstract of the Thesis

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It is generally recognized that both heredity and environment are important in the life of an individual and in the expression of various characteristics by the individual, and that their relative importance varies a great deal. Butterfat production of dairy cattle is considered as a characteristic that is inherited on quantitative basis and is highly affected by environment. Investigators have obtained different values as estimates of heritability of this trait ranging from .17 to .86. Lush considered the intra-sire correlation and regression of daughter on dam method as the best estimate of heritability of butterfat production and he reported values between .17 and .28 for different sets of data.

Three Michigan State Institution Herds, the Traverse City herd, the Ionia Hospital herd, and the Ionia Reformatory herd, were established more than twenty years ago. The butterfat production of the cows in these herds has been measured and recorded. This data seemed to be quite worthy material for a study of the effects of various factors on butterfat production, in another sample of individuals under different environment than others. Therefore, this study was made which besides yielding a heritability estimate, separated various components of environment as far as this data permitted.

There were 473 daughter-dam pairs for the heritability analysis, 2299 records for the herd comparison and repeatability analysis, 1817 records for month and year effect on butterfat production, and 1071 records for the analysis of calving interval effect on butterfat production.

The pooled estimate of heritability of lifetime butterfat production for the three herds was .31 by intra-sire regression of daughter on dam method. Computed to a single record base, it is equal to a heritability value for single records of .17.

The herd differences accounted for about 26 percent of the total variance and the cow differences (intra-herd) accounted for 34 percent. These variances, of course, include both genetic differences and differences caused by environmental effects. The portion of variance accounted for by differences in records of the same cow (intra-herd) was about 66 percent.

The repeatability estimate was .34 on an intra-herd base.

Yearly differences accounted for about 5 percent of the variation in butterfat production. Though small, this value is statistically significant. No yearly trend was found.

Month of calving accounted for about 2 percent of the total variance. It was a significant effect. There was a rather definite pattern for the effect of different months of calving on butterfat production. The high peak was in March; this dropped gradually in the summer, increased in September, and fell again after that until January.

The relationship of calving interval and butterfat production was non-linear. The effect of calving interval on butterfat production accounted 1.5 percent of the variance for the same lactation, and 3 percent for the next lactation. Both were significant. 400 to 419 days seemed to be the most favorable interval as far as a single records were concerned.

Percentage of Total Observed Variance Accounted for by Various Genetic and Environmental Factors

Variance accounted for		Percentage
Herd differences		26
Genetic differences between herds	4	
Environmental differences between herds	22	
Differences within herds		74
Cow differences	25	
Record differences (within cow variance)	49	
		100
Environmental effects		66
Year of calving	4	
Month of calving	2	
Preceeding calving interval	3	
Present calving interval	15	
Others	42	
Genetic		34
Additively genetic	17	
Dominance and interaction	17	
		100

The portion of variance accounted for by dominance and interaction in the above table includes a small portion due to permanent environmental peculiarities and also interaction between heredity and environment. Therefore, the portion accounted for by genetic effect actually should be less than 34 percent and for the environmental effects should be a little more than 66 percent.

Since the records used for each kind of analysis are not exactly the same, and because an allowance must be made for sampling error, the figures listed in the above table can only by considered as approximate estimates.

Approved –
R. H. Nelson

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Introduction

Until recent years, little was known about the relative importance of heredity and environment in the development of an organism. There was considerable controversy as to whether heredity was more important than environment, or vice versa. With advancing knowledge in the field of genetics, it became more generally recognized that both heredity and environment are indispensable in the life of each individual, and that the relative importance of each varied a great deal depending on both the organism and character in question. Heredity is fundamental and may be thought of as furnishing the foundation, with environment completing the structure.

This is true even for a qualitative characteristic, since genes cannot express themselves unless they have the proper environment. A being cannot develop beyond the limits set by its inheritance even in the optimum environment. A quantitative characteristic tends to be modified by environment more than a qualitative one.

The greater the effects of environment on the expression of the genes the more difficult it is for livestock breeders to recognize the true quality of an animal.

Consequently, mistakes are often made by breeders in culling animals with better genes than some of those which are saved. For this reason a measure of the approximate degree of modification of a characteristic by environment would be of value to breeders in selecting their animals.

Butterfat production is a quantitative character. The number of pairs of genes involved, and their behavior, as to the degree of dominance, etc. still has not been determined. However, it is an economically important and physiologically complex character, and is modified considerably by environment. The relative importance of heredity and environment is usually expressed as the portion of variance due to either one of them, and varies with different populations.

The purpose of this study is to determine the portion of variance in butterfat production determined by genetic differences and the portion by environment in three Michigan State Institution herds; the Traverse City herd, the Reformatory herd and the Ionia herd. These herds may be considered as sub-populations of the Holstein-Freisian breed.

There are many environmental factors. They are generally divided into tangible and intangible factors. The latter have no way of being controlled. The tangible factors, such as light, temperature, feeds, handling, etc. may be partially controlled by well designed experiments. In this data the only information available about environmental factors was for such things as calving interval, date of calving and year of calving. The approximate portion of variance resulting from each of these causes was determined. The optimum season of freshening and length of calving interval were found. In addition, the hereditability of butterfat production was calculated for each herd and for the three herds combined. The portion of variation due to herd differences and cow differences and the repeatability of a cow's production from year to year were computed.

Literature Review

Most of the literature concerned with hereditability of milk yield, butterfat production, or test of dairy cattle before 1941 has been tabulated by Lush (1941). Hence, the table, with minor remarks, is reproduced here. In addition, some studies made since that time have been inserted in the same table.

Table 1a - Summary of Evidence on Hereditability of Milk Yield, Butterfat Production and Test

Author	Characteristic	Difference between high and low groups		Heredita-bility [a]	Notes
		Dams	Daughters		
Gifford	fat (lbs.)	278.7	32.2	.23	21 Holstein-Freisian bulls[b]
Gifford	fat (lbs.)	240.0	61.6	.51	18 Guernsey bulls[c]
Copeland	fat (lbs.)	244.0	52	.43	20 Jersey bulls[d]
Edwards	milk (lbs.)	2856	592	.41	23 bulls[e]
Rice	milk (lbs.)	6373	1815	(.57)	10 bulls dairy breeds[f]
Rice	test (%)	1.09	0.47	(.86)	10 bulls dairy breeds[f]
"Brain Truster"	milk (lbs.)	5025	945	.38	1 bull with 151 daughters
Lush (1941)	butterfat (lbs.)	102.1	14.1	.28	103 bulls 676 daughter-dam comparisons[g]
Lush (1941)	milk (lbs.)	2629	432	.33	103 bulls 676 daughter-dam comparisons[g]
Lush (1942)	fat (lbs.)			.174	283 bulls, 2154 daughter-dam comparisons

a. Twice the intra-sire regression of daughters on dams.

b. A. R. records. Each bull had at least 24 daughter-dam comparisons. The mates of each bull were divided into high, medium, and low, thirds (approximately). Those given here are averages computed from Gifford's Table 12, giving equal weight to each sire.

(Continued)

c. A. R. records. Each bull had at least 17 daughter-dam comparisons. Mates divided approximately in high, medium, and low thirds. The figures quoted are from the summary of Copeland's Table 3.

d. R of M records. Each bull had at least 19 daughter-dam comparisons. Mates were divided approximately into high, medium, and low thirds. The figures quoted are from the summary of Copeland's Table 3.

e. Data from British milk recording societies in East Anglia and Lancastershire and from Agricultural College herds at Reading, St. Albans, and St. Paul. Mates are divided into high and low halves. The figures quoted are averaged from columns 4 and 5 of Edward's Table 3, giving each cow equal weight. As Edwards used average records where available (up to three lactations per cow), the hereditability figure shown here pertains to differences between average records rather than single records. If the intra-herd repeatability of single records in Edwards' material was .4, the hereditability of differences in single records would be somewhere between the .41 shown here and the .24 which would be approached if every mate had three records.

f. The data are official records from several dairy breeds. Each bull had at least 17 daughter-dam comparisons. For each bull the five "highest producing" mates and the five "lowest producing" mates were selected. Division seems to have been primarily on total fat production and was for milk and test only in so far as they were dependent (statistically) on total fat production. This makes the records for the dams' milk and test come much nearer to representing the dam's real ability than if division into high and low groups had been primarily on the milk records and the test records, respectively. The figures for hereditability, therefore, are much too high to be fairly comparable with the others, and come nearer to indicating the fraction of the differences in real ability (not records) which are due to additive hereditary differences between the cows.

g. The data are from Iowa Dairy Herd Improvement Associations prior to January 1, 1937. All records were age-corrected. Where the bull's mates had only one record, the data for her and her daughter were discarded. The mates of each bull were then divided into a high half and a low half, solely on the basis of the first record of each cow. If a bull has an even number of mates with two or more records each, all were used. If he had an odd number of such mates, the one whose first record was

(Continued)

median in size was discarded and her daughter was discarded with her. If a mate had more than one daughter she was used again as many times as she had daughters.

h. The data are from Iowa Dairy Herd Improvement Association during the period January 1, 1936 to December 31, 1939. It included seven breeds. Only the 305 days of lactation were studied. All records were corrected for age and were on the basis of twice a day milking. The intra-sire daughter-dam regressions varied some what from breed to breed, but their differences were not statistically significant. The result listed in Table 1a was pooling all the seven breeds together and was corrected to a single record.

Besides the different hereditability values given by different investigators in Table 1a, Gowen (1934) studied the Jersey Register of Merit data on milk yield and fat percentage. He assumed that there was no correlation between the environment of daughter and dam. He came to the conclusion that about 50 to 70 per cent of the variance in milk production and about 75 to 85 per cent of variance in fat percentage came from differences in the genetic make-up of the individual cows. Plum's (1935) analysis of the records of cows in Iowa Cow Testing Association led him to the figures shown in Table 1b.

Table 1b - Relative Importance of Cause of Variation in Butterfat Production

Causes of variation	Percentage of total variance	
Breed		2
Herd		
feeding policy of herd	12	
other causes (genetic or environmental)	21	
		33
Cow (mostly genetic)		26
Residual (year to year variations)		
feeding variations within the herd	6	
other year to year differences	1	
length of dry period	1	
season of calving	3	
other factors	28	
		39
Total		100

Among all the heritability values above, probably the result worked out by Lush is more accurate than others, since he used a large number of sires; hence fewer numbers of daughter-dam pairs for each sire. Then there would be less environmental portion contributed to the daughter-dam correlation as the large number of daughter-dam pairs of a sire is more likely to separate to different herds. Also his sample size is quite large. The results computed by Gowen are higher than all the others. It is likely due to a large environmental contribution to the daughter-dam correlation.

The only report about repeatability of milk and butterfat production is given by Lush (1941). In fact, the terminology is originated from the same investigator. He estimated repeatability for milk production .33, and butterfat production .43 from same set of data as he used for heritability estimates Lush (1941). Gowen (1935) reported a correlation of .40 between butterfat records of the same cow in a population of cows belonging to the same herd, or to a correlation of .60 between records of the same cow in a population of cows kept in many herds.

The influence of the month of calving on milk yield has been studied by numerous investigators. It has been thoroughly reviewed by Morrow et al. (1945). The high lights of all those investigations will be brought here mostly from his review for the time before 1945.

McCandlish (1920) and Moore (1921) both found fall freshening cows to excel in milk and butterfat production.

McDowell (1922) reported on a group of animals in cow testing associations totaling 10870 cow years. Milk production decreased in the order of fall, winter, summer, and spring calving. In a study of 1410 lactations from cows in the English milk Recording Societies, Hammomd and Sanders (1923) found the highest milk yield was secured on October freshenings, 6077 lbs., with a low three-consecutive-month period for May, June, and July, all below 5400 lbs. Turner (1923) reported on 3615 lactations of Guernseys, Holstein, and Jerseys, that had completed Advanced Register or Register of Merit records. There was a slight difference between breeds in their relation to month of freshening and milk yields. With the Guernseys the variation was not great, although May, June, July, and August freshening were the lowest in milk yield, with November being the highest, followed by January, February, and December. For the Holsteins, November was the high month, followed closely by January, March, and December. April and July freshenings gave the lowest milk yields. The 305 Jersey records showed considerable variation. January calvings resulted in a lactation yield of 9213 pounds of milk, with August showing 9126 pounds, and July 8949 pounds. The two lowest months were September with 7416 pounds, and June 7584 pounds.

Sanders (1927) observed from his studies in England that the months of October, November, and December were most favorable for freshening, with June and July resulting in the poorest yields. These figures were obtained after making corrections for length of dry period and length of service period. The shape of the lactation curve showed considerable seasonal variation, a factor considered to be largely responsible for the differences in total yield.

Cannon (1933) studied the records of 6800 cows in Dairy Herd Improvement Associations in Iowa. Highest milk yield was secured on animals calving in November--7798 pounds--with a uniform and regular decrease until June, when there was a yield of 6705 lbs.

Plum (1935) also used data from Iowa herds in Cow Testing Associations to study the causes of differences in butterfat production. He concluded that although cows calving during November to January produced 13.6 per cent more butterfat than cows calving in May to July, the actual influence of season of calving, as a factor, accounted for only 3 per cent of the total variation in butterfat production. Using the records of 319 Jerseys in the Florida Experiment Station herd, Arnold and Becker (1938) found the seasonal influence on milk yield to be non-significant, although winter and autumn freshenings gave somewhat larger yields than summer and spring. They suggest that the narrow range of seasonal variations in Florida temperature probably accounted for the small differences observed.

It is logical to suppose that the effect of calving on milk yield is influenced by the variations in feeding and management that accompany the different seasons. On this point it is interesting to note that Wylie (1925), working with 2900 records of Register of Merit Jerseys where feeding levels were maintained rather uniformly throughout the year, found much less seasonal influence than other investigators. Although July freshenings resulted in the highest and August in the lowest yields, with these two months excepted, fall and winter calvings gave higher average lactation yields than spring and summer.

The findings of Gooch (1935) on 679 lactations of 99 Jersey cows in a single herd varied considerably from the majority of data reported. With a low for August freshenings, production increased gradually up to April calvings, with a decline again to August. Early spring was apparently the most favorable season.

Dickerson (1940) in studying the relative importance of various sources of environmental variation in production, found the data on 1574 lactations of Holsteins to show lowest production for cows calving from April to September, and highest for cows calving from October to March.

Morrow (1945) studied 4030 lactation records from D. H. I. A. herd record books of 33 New Hampshire dairy herds. The study included five breeds; Ayrshire, Guernsey, Holstein, Jersey and Milking Shorthorn. For each breed, with the exception of Jersey, milk yields following summer freshenings were lower than those for fall and winter freshenings. Jerseys showed no significant relation between month of freshening and milk yield.

The lactation records of 15,442 cows in Dairy Herd Improvement Association herds from 12 states were analyzed by Woodward (1945). He found the variation in total milk production between the groups calving in different months of the year is somewhat less than might be expected, ranging from 8886 pounds for the cows calving in July to 9108 pounds for the cows calving in November.

Frick (1947) reported there were highly significant differences among cows freshening in different months. Four breeds (Guernsey, Holstein, Ayrshire, Jersey) with 22212 Connecticut cows were studied. He showed that cows freshening in February have the highest average and lowest was for cows freshening in July. In general, however, average milk yields consistently increased from the least favorable to the most favorable month, and consistently decreased from the most favorable to the least favorable month. Cows freshening in February produced 13.7 per cent more milk than those freshening in July.

Under western Oregon conditions the butterfat records of 2690 first-calf heifers was studied by Olonfa (1948). The season of the year in which a cow freshens had no appreciable effect on her yearly butterfat production in that data.

The calving interval equals the days of dry period plus the days of lactation. Hence, in general, the longer the dry period the longer will be the calving interval. Of course, there are some variations about the length of lactation, and that may cause the calving interval to fluctuate without relationship to the dry period. However, by using large samples, this error can be materially reduced. Therefore, literature dealing with either calving interval or dry period are reviewed here.

Sanders (1927) claimed that cows should calve at intervals of not less than a year, and not more than thirteen months. This optimum will probably be subject to a slight variation in particular cases. The work of Dickerson and Chapman (1940), who compared production records of lactations following dry periods of different length with those of the first lactation, found that low producing cows showed a higher percentage increase through lengthening the dry period than did high producing cows.

Dix, Arnold and Becker (1936) studied 291 lactations of Jersey cows in the Florida Agricultural Experiment Station herd. The yield following the dry period, 31-60 days, was used as 100 per cent, the percentage of base yield for the various classes were: initial lactation, 91.87 per cent; 30 days or less, 92.38 per cent; 61-90 days, 94.68 per cent; 91 days or more, 88.77 per cent. Maximum daily yield was highest for the 31-60 day class. Klein and Woodward (1943) have reported only on the production records of the same cow following dry period of different lengths. It was found that cows dry 1-2 months gave 9.2 per cent more milk than when dry 0-1 month; cows dry 2-3 months gave 4.3 per cent more milk than when dry 1-2 months; and that cows dry 3-4 months gave 1.4 per cent more milk than when dry 2-3 months.

Seath and Neasham (1942) are of the opinion that an ideal reproduction record would be one in which 12.5 per cent of the cows were dry each month during the year. Translated into dry period this would mean 47 days of rest on the basis of calving at yearly intervals. Johansson (1940) has reported the optimum calving interval is 14 months for heifers and 13 months for subsequent lactations.

Morrow (1945), by using 2631 lactations being available with the length of the preceding dry period known, found the highest production was in the group of dry periods from 80 to 89 days. However, he concluded if a smoothed curve were prepared from the data, the high point would coincide with a period approximately 65 days, with very little difference occurring between 45 and 85 days. On either side of these limits, production values were considerably decreased.

In regard to the year effect on production trend, Plum (1935) has reported only 2.8 per cent of the total variance was due to changes in yearly averages based on 5860 records from 1922 to 1932. However it was statistically significant.

Source of Data

The data for this investigation were taken from three of the Michigan State Institution herds. They are the Traverse City herd, the Ionia Hospital herd, and the Ionia Reformatory herd. The former is located at Traverse City and the latter two are located at Ionia. The Traverse City herd is the oldest and largest herd of the three. It was established in 1888, and has 124 cows and four bulls in service at the present time. The Reformatory herd has 72 cows and three herd sires. The Ionia Hospital herd is the smallest, having 44 cows and one bull in service now. The better sires were exchanged among the various Michigan State Institution herds to extend their use with a minimum of inbreeding.

Most of the records are D. H. I. A. records with a small percentage of H. I. R. records. The records used here are from 1927 for Traverse City herd, 1929 for Reformatory herd, and 1924 for Ionia Hospital herd up to 1945. There were fewer records made during the earlier yea rs and also considerably more of them were incompletely recorded than in the later years. For this reason, only the records from 1930 on were used for studying the effect of month of calving and year on butterfat production. However, for the heritability, and repeatability estimates and the effect of calving interval, the records starting from the earlier dates were used. It would be better to use exactly the same set of data for the different analyses, but this would considerably reduce the numbers available for each, either because requirements were different for each kind of study or because of some incompleteness in the records. In order to bring the samples for the different analyses as close as possible, the following procedure was used:

1. Select the sires with the most mates;
2. List all the cows having the same sire in one group and use all the available records for each cow;
3. Find the daughter or daughters of each cow and copy the number of the daughter and all her available records following her dam;
4. All the available records were used for heritability estimates, herd comparisons, effects of calving interval, month of calving and year of calving.

Some more descriptions will be given at the beginning of each analysis.

Records were corrected for length of lactation, times milked daily and age. 305 days, three-time milking and six to nine years of age were used as the basis for the conversion. The Holstein-Friesian Association conversion factors were used. Records shorter than 270 days were discarded and those from 270 to 305 days were treated as 305 day records.

Table 2a - Conversion Factors for Age and Times of Milking

Age	4X	3X	2X
2	.83	1.00	1.25
2½	.79	.96	1.20
3	.76	.92	1.15
3½	.73	.88	1.10
4	.71	.86	1.07
4½	.69	.84	1.05
5	.67	.82	1.02
6-9	.66	.80	1.00
10	.68	.82	1.03
11 and over	.69	.84	1.05

Table 2b - Conversion Factors for Length of Lactation Period

Days	Factor
306 - 319	.99
320 - 329	.97
330 - 339	.96
340 - 349	.95
350 - 359	.94
360 - 364	.92
365 -	.90

For examrle, for a cow that had a record of 500 pounds of butterfat on 4 times a day milking, with a 320-day lactation at three years of age, the calculation would be as follows:

$$500 \times .97 \times 1.15 \times .83 = 462.93 \text{ pounds}$$

If it is 3 times or 2 times milking, the factor 100 or 1.25, respectively would be used instead of .83 for the above equation.

Comparison of Herds

A general survey of the three herds to determine their average production level, and the variability of their production caused by herd differences, cow differences and individual record differences, served as a basic step for the further studies. This analysis is based on at least 40% of the records of each herd. Therefore, these records are a very large sample of its own parent population.

Table 2c - Average Production of the Three Herds

Herds	No. of cows	No. of records	Ave. no. of records per cow	Ave. butterfat production lbs.	Standard deviation lbs.
Traverse City	477	1182	2.5	443	73
Reformatory	216	651	3.0	492	99
Ionia	108	466	4.3	550	124
Weighted Ave.	801	2299	2.9	478	

Table 2c shows that the Ionia herd has the highest average; the Reformatory herd, second; and the Traverse City herd, the lowest. The standard deviations are proportional to average production in each herd. That is, the higher the production, the greater the variation of butterfat production. If we assume that the genes which are responsible for butterfat production have only an additive effect, the above order of the observed standard deviations is an unexpected result. If the individuals of a population carry more or less than 50% "good" genes, it is expected that that population will be less variable than a population of individuals with about 50% "good" or "bad" genes. The more they tend toward the extreme, the less their variation should be.

The proof for the above statement is, according to Castle (1921), that the variance of a population is equal to $2q(1-q)\alpha^2$, where q is the gene frequency of the "good" genes and α is the value increased from "bad" gene to "good" gene. Therefore, when the value of $q = .5$, the variance is the largest, and when $q >$ or $< .5$, the variance is smaller; the more the decrease or increase of q, the smaller the variance will be. Of course, there have been some assumptions for the behavior of the genes*.

According to Table 3c, the Ionia herd had the highest butter fat production. The cows in that herd must have had more "good" genes than cows in the other two herds. Similarly, the Reformatory herd must have carried more "good" genes than the Traverse City herd. The Traverse City herd must have had more than 50% "good" genes because its average production was higher than the breed average. From this it was expected that the variation in production in each herd would have been in the reverse order, that is, the Traverse City herd, the largest; the Reformatory herd, second; and the Ionia herd, the smallest. These results

* Assumptions of the behavior of the genes:

1. genes have equal effects; 2. no dominance; 3. genes combine additively; 4. all genes combine freely.

indicate that the genes for butterfat production behave not only additively, but that they show some degree of dominance and interact in various ways with each other, and that environment also plays an important part. These factors confuse the additive gene effects and helped cause the large variation in the herds of high producing individuals.

Table 2d - Analysis of Variance of Each Herd

Herds	Sources of variance	Degree of freedom	Sum of squares	Mean squares	F
Traverse City	Total	1,181	6,263,547	5304	
	Between cows	475	3,342,152	7021	1.69**
	Within cows	705	2,921,425	4144	
Reformatory	Total	650	6,221,529	9572	
	Between cows	215	3,204,830	14906	2.20**
	Within cows	445	3,016,699	6779	
Ionia	Total	465	6,035,679	12980	
	Between cows	107	4,040,405	37761	6.78**
	Within cows	358	1,995,274	5573	

Table 2e - Portion of Variance Due to Cow Differences

Herds	σ^2_{record}	$\sigma^2_{record} + K_o\,\sigma^2_{cow}$	K_o (1)	σ^2_{cow}	$\frac{\sigma^2_{cow}}{\sigma^2_{record} + \sigma^2_{cow}}$
Traverse City	4144	7021	2.46	1160	.22
Reformatory	6779	14906	3.00	2709	.28
Ionia	5573	37761	4.30	7485	.57

(1)

$$K_o = \frac{1}{n-1}\left(SK - \frac{SK^2}{SK} \right)$$

K is the number of records of each cow

n is the number of cows

S is the sign for summation

It is obvious from Table 2d that the differences between cows were highly significant. This was expected. Table 2e gives the portions of variance due to cow differences in each herd. Since the results show that the Ionia herd had the highest cow variance, and the other two were quite similar, the variance between records of the same cow will be in the reverse order. Consequently, the greater variation of the Ionia herd than the Reformatory herd and of the Reformatory herd than the Traverse City herd shown in Table 2d was mainly due to the difference between cows.

The differences of cow variances among the three herds make one wonder whether there was any genetic background involved. For this reason, a few cows were chosen at random from each herd and their pedigrees were checked. It was found that most of the cows in the Traverse City herd were related to bull 412017, and bull 486080, and also some slight inbreeding was found. Animals in the Reformatory herd showed the same tendency, but to a lesser degree than the Traverse City herd. Relationship among animals in the Ionia herd were very seldom found, although some of the bulls were related to the bull in the Traverse City herd. This may have been due to the comparatively late establishment of this herd. Very possibly, this different intensity of relationship of the animals in each herd was the main cause for the different variation of animals among the three herds.

Variance Due to Herd Difference

The procedure used for this analysis in combining the three herds is that given by Blum (1935). Because quite a few analyses will follow the same procedure later, the detailed steps for the calculation are given here. They will be omitted in the later ones.

Table 2f - Analysis of Variance of Herd and Cow Differences

Sources	Degree of freedom	Sum of squares	Mean squares
Total	2298	22,538,822	9808
Between herds	2	4,018,037	2009018
Within herds	2296	18,520,785	8066
Between cows	800	10,587,387	13234
Within cows	1496	7,933,398	5303

Total sum of squares = sum of squares of record of each herd - grand correction term

$$= 147{,}040{,}282 + 163{,}893{,}765 + 237{,}982{,}767 - \frac{1{,}100{,}065}{2299}$$

$$= 22{,}538{,}822$$

Sum of squares for herds = sum of the correction term of each herd - grand correction term

$$= 141{,}004{,}603 + 157{,}672{,}236 + 231{,}719{,}190 - \frac{1{,}100{,}065}{2299}$$

$$= 4018{,}037$$

Sum of squares within herds = total sum of squares - sum of squares for herds

$$= 22{,}538{,}822 - 4{,}018{,}037 = 18{,}520{,}785$$

Sum of squares within cows within herds = sum of sum of squares of the within term of each of the three herds

$$= 2{,}921{,}385 + 3{,}016{,}699 + 1{,}995{,}274$$

$$= 7{,}933{,}398$$

Sum of squares between cows within herds = sum of squares within herd - sum of squares within cows within herds

$$= 1,852,078 - 7,933,398 = 10,587,387$$

According to formula (6),

K_o (for between herds) = 706.5 records

σ^2(within herd) + K_o σ^2(between herds) = 2,009,018

σ^2(between herds) = 2832

Portion of variance due to herd difference =

$$\frac{\sigma^2(\text{between herds})}{\sigma^2(\text{within herd}) + \sigma^2(\text{between herd})}$$

$$= \frac{2832}{10898} = 26\%$$

Portion of variance due to within herd difference

$$= 100\% - 26\% = 74\%$$

K_o (cow difference intra-herd) = 2.87

σ^2(cow difference intra-herd) = 2763

Portion of variance due to cow difference intra-herd = 34%

Portion of variance due to record difference intra-herd = 66%

Portion of variance due to cow difference inter-herds = .74 x .34 = 25%

Portion of variance due to record difference inter-herds = .74 x .66 = 49%

According to the above analyses, record differences caused the main part of the total variation, and it is mainly due to environmental effect. However, both the genetic composition of the individuals and the environmental effect on them were important causes of herd differences and cow differences.

Plum (1935) has treated the portion of variance of herd differences as the correlation coefficient between the individuals within the herd, and he reported a value of .34 as compared with .26 from this data. He used 119 herds and the average number of records of each herd was about fifty records. Compared with the data used here, his herd size was much smaller and so the individual cows tended to be more correlated. Therefore, the value of the correlation coefficient between the individual cows within herds found here is reasonable.

Repeatability

"Repeatability", speaking in general terms, is the consistency of the cow's life time production. Statistically, it means the correlation between the records a cow has made. A machine cannot have exactly the same amount of out-put year by year. So, a cow, with a much more complicated mechanism, can never be expected to have the same production every year, since both external environment, such as management, and the internal functioning of every organ within the body are closely related to the milk production. Nevertheless, because of the inherent ability of a cow, the variation of a cow's record has, in general, certain limits. Numerically, this is called the coefficient of repeatability. This coefficient serves as a predicting factor for succeeding records based on preceding records that have been made by that cow.

Table 2e shows 22% of the total variance accounted for by cow differences in the Traverse City herd, 28% in the Reformatory herd, and 57% in the Ionia herd. They are still the results expected, as the Ionia herd is the smallest one and the records of many of the cows in the herd are close as is seen by a rapid glance. This merely indicates that the Ionia herd has been under a quite constant management month to month and year to year. Most of the cows were kept in a healthy condition and disease and other kinds of temporary internal disturbances were probably controlled better than in the other two herds.

Table 2f, by combining the three herds together, gives the average repeatability coefficient. It amounts to .25 for the inter-herd base, and .34 for the intra-herd base. The latter one, .34, is really the average of the coefficient of repeatability of the three herds. It will serve as a conversion factor later on.

Heritability Analysis

Definition: "Heritability" is the fraction of the observed variance which is caused by differences in heredity. In other words, it is the extent to which observed differences between individuals are caused by differences in the genetic make-up.

Let σ_H^2 = the part of variance due to differences in the genetic make-up of different individuals in the population.

σ^2_E = the part of variance due to differences in the environment under which different individuals developed.

σ^2_O = the observed variance of the different individuals in the population.

Then $\sigma^2_H + \sigma^2_E = \sigma^2_O$, $\sigma^2_H = \sigma^2_O - \sigma^2_E$, and $\frac{\sigma^2_H}{\sigma^2_H + \sigma^2_E} = \frac{\sigma^2_H}{\sigma^2_O}$, the portion of variance for which differences in heredity are responsible.

The value of heritability can be altered by changing either the σ^2_H or σ^2_E. Increasing the control of environment reduces σ^2_E and therefore makes the heritability of that characteristic higher than in the general population. Also, if assortive mating or inbreeding of separate lines is followed, the σ^2_H is decreased. Hence, any given characteristic in any breed will have different heritability values from one herd or group to another. The degree of difference depends on the system of mating and the environmental variation.

Discussion of Method

All methods of estimating heritability rest on measuring how much more closely related animals resemble each other than the less related animals. All the different genetically related individuals, such as isogenic lines, parents-offspring, brother-sister, and grandparents and grandoffspring, can be used for heritability studies.

The relationship that is most suitable depends on (1) whether there is enough data available regarding that relationship, (2) the environmental effect, and (3) the mating system. If the mating system was other than random, it can be eliminated by other means.

Variation within sets of identical twins is wholly environmental. Comparing this with fraternal twins rather than with pairs of individuals unrelated to each other would be a very simple and accurate method. It is the only method likely to measure all of the epistatic and dominance variations as well as the additive ones. Because of the rarity of identical twins in farm animals and because it is difficult definitely to distinguish them from fraternal twins, resulting in some sampling error, this method has not received very wide use. However, if the time comes when we can accurately identify the kind of twins, this method will give the best results if there are numbers enough in that population. For heritability estimates, the use of grandparents and grandoffspring, half-brother and sister, or half-sisters, and some other less related pairs tends to enlarge an error of any kind because of the higher number of multiplication to the correlation coefficient obtained from the observed data. In addition, in sib relationships, some environmental effect enters in, and makes the heritability value appear larger than it should. Lush (1947) has commented on Gowen's (1934) heritability study of Jersey cattle for this reason.

There is a method for computing heritability based on identical twins. It is the intraclass correlation method given by Snedecor (1946):

$$\frac{\sigma_m^2}{\sigma^2 + \sigma_m^2}$$

Where $\sigma^2 m$ is the mean square of twin pairs and σ^2 is the mean square of individuals. The calculation for these two values is the root procedure of analysis of variance of two-way classification. Actually, σ^2 is a measurement of variation due to environment and $\sigma^2 m$ is one due to hereditary effect. If they are relating with the above formula as set by the definition,

$$\frac{\sigma_m^2}{\sigma^2 + \sigma_m^2} = \frac{\sigma_H^2}{\sigma_H^2 + \sigma_E^2}$$

Then, $\sigma^2 m = \sigma^2 H$, $\sigma^2 = \sigma^2 E$

and $\sigma^2 + \sigma_m^2 = \sigma_E^2 + \sigma_H^2 = \sigma_o^2$.

Since Lush (1940) worked out the intra-sire regression or correlation method, most of the environmental contributions to the variation can be eliminated automatically by this within sire method because (1) the daughters and mates of a sire are nearly always kept in the same herd; therefore the effects of heterogeneity of management from herd to herd are left in the differences between sires and

(2) the offspring of one sire are usually nearly contemporary. In addition, the parent-offspring correlation or regression computed on an intra-sire basis goes far towards discounting any peculiarities of the mating system. For these reasons, the daughter-dam pairs, and the half-sister pairs by the same sire were selected as the basic material for the heritability estimates of butterfat production in this study.

Lush (1940) has given a method which is an approximation to the least square regression or correlation method. That is, by dividing the mates of each sire into a high half and a low half the difference between the means of their offspring when doubled and divided by the difference between the means of the dams, yields an estimate of the additive genetic portion of variance and a part of epistatic variance. Since the least square method is more accurate than the approximate method, the technique of analysis in this paper will follow the least squares procedure.

The background of the above procedure for the estimation of heritability is the path coefficient analysis which was derived by Wright (1934). Its application to the animal breeding program has also been given by Wright (1921). For making the explanation more clear, a diagram and derivation has been made as follows:

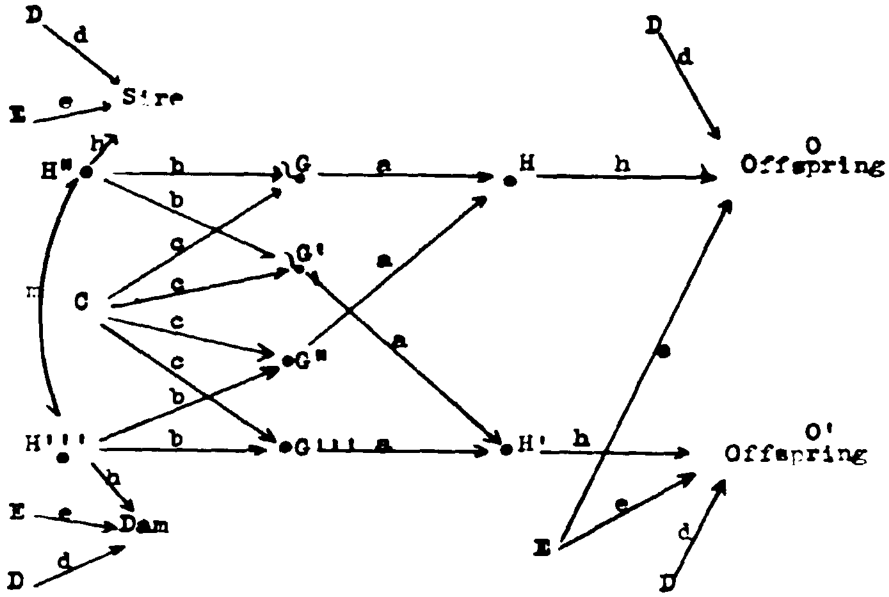


Figure 1. - A Diagram Illustrating the Relations Between Two Mated Individuals and Their Progeny.(Following Wright 1921)

O O' - The litter mates or full sibs
H, H', H", H''' - The genetic constitution of four individuals
G, G', G", G''' - Four germ cells
E - Environmental factors as are common to litter mates
C - Chance
D - Factors largely ontogenetic irregularity

The small letters stand for the various path coefficient.

$$h^2 + e^2 + d^2 = 1$$

$$r_{po} = hbah = abh^2$$

$$r_{oo'} = habbah + habbab + ee = 2a^2\, b^2\, h^2 + e^2$$

$$\because\ r^2{}_{GH} = a^2 = 1/2,\ b = \sqrt{\tfrac{1}{2}}\quad \text{(in random breeding population)}$$

$$\therefore\ a = b = \sqrt{1/2}$$

$$\therefore\ r_{po} = 1/2\ h^2$$

$$r_{oo'} = 1/2\ h^2 + e^2$$

$$\therefore\ h^2 = 2r_{po} \qquad (1)$$

$$h^2 = 2r_{oo'} - 2e^2$$

For the half brother-sister or half sister, or half brothers,

$$h^2 = 4r_{oo'} - 4e^2 \qquad (2)$$

From the equations (1) and (2), we can see the reason for multiplying parent-offspring correlation by 2, and multiplying the half-sib correlation by 4 in order to get the whole portion of variance due to heritability. In addition equation (2) shows that a certain environmental correlation is included in the estimation of heritability based on the half-sib correlation. However it is not included when there is no environmental correlation between the half-sibs. Actually, the latter case is impossible for the maternal half-sibs, because their prenatal environments are similar.

Lush (1940) illustrated very clearly the regression of daughter on dam as a method estimating heritability. The regression coefficient, mathematically speaking, is the slope of the line which is used to predict the dependent variable by the independent one. In other words, it is the measurement of how much, on the average, one unit change of the independent variable, for example the butterfat production of the dam, changes the dependent variable, in this case the daughter's production, above or below average. The higher the regression coefficient, the greater the variability due to inheritance, that is, the higher the heritability value, and vice versa. Under the intra-sire base, the regression of daughter on dam usually includes so little of the environmental effects that they can be ignored. To obtain the heritability value, this regression coefficient is doubled in accordance with Schmidt's principle of diallel crossing (Lush, 1940), and the equations derived from Wright's path coefficients above.

The statistics of correlation and regression are:

$$r = \frac{\Sigma XY - \frac{\Sigma X \, \Sigma Y}{N}}{\sqrt{\left(\Sigma X^2 - \frac{(\Sigma X)^2}{N}\right)\left(\Sigma Y^2 - \frac{(\Sigma Y)^2}{N}\right)}} \qquad (3)$$

$$b_{YX} = \frac{\Sigma XY - \frac{\Sigma X \Sigma Y}{N}}{\Sigma X^2 - \frac{(\Sigma X)^2}{N}} \qquad (4)$$

Since heritability is defined as $\frac{\sigma_H^2}{\sigma_O^2}$ or $\frac{\sigma_H^2}{\sigma_H^2 + \sigma_E^2}$, and usually the computed r and b doubled are used as the heritability value, we can set the following equalities:

Since:

$$H = \frac{\sigma_H^2}{\sigma_o^2} \quad , \; H = 2r_{xy}$$

Therefore, $$\frac{\sigma_H^2}{\sigma_o^2} = 2r_{xy}$$

and $$r = \frac{\text{cov. xy}}{\sigma_x \, \sigma_y}$$

Therefore, $$\frac{\sigma_H^2}{\sigma_o^2} \cong \frac{2 \text{ cov. xy}}{\sigma_x \, \sigma_y}$$

Since: $$H = 2b_{yx} = \frac{\sigma_H^2}{\sigma_o^2}$$

Therefore, $$\frac{\sigma_H^2}{\sigma_o^2} = \frac{2 \text{ cov.xy}}{\sigma_x^2}$$

From the above equations it is obvious that the covariance of parent and offspring is actually the genetic portion of the variance among the total observed variance. The product of the standard deviation of the parent and offspring, or the variance of the parent is an estimate of the total observed variances.

As

$$r = \frac{\text{cov xy}}{\sigma_x \, \sigma_y} \quad \text{and} \quad b = \frac{\text{cov xy}}{\sigma_x^2}$$

$$\frac{\text{cov xy}}{\sigma_x \, \sigma_y} \cdot \frac{\sigma_y}{\sigma_x} = \frac{\text{cov xy}}{\sigma_x^2} \qquad b = r\,\frac{\sigma_y}{\sigma_x} \qquad (5)$$

The correlation and regression are interchangeable. If there is no selection among the parents, the standard deviation of the parent should theoretically be equal to standard deviation of the offspring, that is $\sigma x = \sigma y$, and then $r = b$. Therefore, the use of the correlation or regression coefficient should be interchangeable. There should be not too much discrepancy between them in case there is no selection among the parents at all. If there is selection of the parents, according to Lush (1940),

"Selection of the dams will tend to lower the correlation coefficient, but will not bias systematically the regression of offspring on dam, although the dependability (fiducial limits) of that regression will be decreased."

Procedure for Heritability Analysis

The first step for the analysis of heritability was the analyzing of each herd. After that was done, the three herds were combined and the weighted average was computed. For each herd, a preliminary analysis, an intra-sire regressionand correlation and a half-sib correlation analysis were carried out. The method of analysis closely followed the method outlined by Snedecor (1946) or some other route statistical procedure. An interpretation will be given following the result of each analysis.

Heritability Analysis of Butterfat Production for the Ionia Reformatory Herd

1. Preliminary Analysis

There were 120 dam-daughter pairs under nine sires available for the heritability analysis in the Reformatory herd. The average production and the variance in production of the dam and daughter groups are given in the following tables:

Table 3a - Average Production of Dam and Daughter Groups

Sire	Number of dam-daughter pairs	Average butterfat-production of dams	Average butterfat-production of daughters
480572	11	499	463
808309	8	516	547
629478	22	517	472
576509	8	479	471
575183	29	490	472
744578	19	512	495
694844	10	506	495
401108	8	460	531
545551	5	507	489
522685	2	465	528
Total	120	500	487

Standard deviation of the dams' production = 74 lbs.

Standard deviation of the daughters' production = 64 lbs.

Coefficient of variation of the dams' production = 15%

Coefficient of variation of daughters' production = 13%

According to the results of Table 3a, the average of the dam's production was higher than the average of the daughter's production. This was logical because the dams were usually selected. However, the fact that the variability of the dams' production was higher than that of the daughters' production was due to the tendency of the daughter's production toward the herd average as a result of their dam's being selected.

Table 3b - Analysis of Variance of the Dams' Production

Sources	Degree of freedom	Sum of squares	Mean squares	F
Total	119	638051	5362	
Between mate groups	9	33160	3684	Non-significant
Within mate groups	110	60489	5499	

According to the results shown in Table 3b, there was no difference between the dams mated to different bulls. That means that the dams mated to different bulls were distributed at random as far as butterfat production was concerned.

Table 3c - Analysis of Variance of Daughters Between Different Sire groups

Source	Degree of Freedom	Sum of squares	Mean squares	F
Total	119	524727	4558	
Between sires	9	68572	7619	Non-significant
Within sires	110	456155	4147	

Table 3d - Analysis of Covariance and Test of Adjusted Means Between Daughter Groups

		Sum of squares and products			Errors of estimate		
Source	Degree of Freedom	Sx^2	Sxy	Sy^2	(1) Sum of squares	Degree of freedom	Mean square
Total	119	638051	121846	524727	501495	118	
Between sires	9	633160	-5875	68572			
Within sires	110	604891	127721	456155	429187	109	3937
For test of significance of adjusted means					72272		8030

(1) $Sy^2 = \frac{(Sxy)^2}{Sx^2}$ $F = \frac{8083}{3937} = 2.04*$

There was no statistically significant difference between daughters by different sires even at the 5% level, according to Table 3c.

The analysis of variance of Table 3c and 3d are a preliminary analysis of the daughters' butterfat production. Table 3c gives the result before adjusting. In other words, it gives the results in which the effects of the dams' production were blanded. It turns out non-significant, but the F value is close to the 5% level of significance. After the effect of the dams' production is deducted by the covariance method, the F value shows significance at the 5% level. That means the dams' production ability did have some effect on the variation of the daughters' production, although there has been no significant difference between the different dam groups as was shown in Table 3b. The interpretation for this may be (1) due to the difference of the intrinsic factor, e. g., the genetic make-up, of the dams being different among the different groups; (2) due to the different genetic composition of the sires for milk or butterfat production. We cannot expect all the sires to have the same transmitting ability for butterfat production unless they all come from the same highly inbred line. Consequently, the F value in Table 3d is reasonable and expected.

2. Intra-sire Correlation and Regression of Daughter on Dam Method

The results of the calculations of intra-sire correlation coefficient and regression of daughter on dam are entered in Table 3e.

Table 3e - Observed Intra-sire Correlation and Regression Coefficients

Sires	Number of dam-daughter pairs	Regression coefficient	Correlation coefficient
480572	11	.37	
808309	8	.17	
629478	22	-.57	
576509	8	.01	
675183	29	-.01	
744578	17	-.10	
694844	10	.37	
545551	5	8.92	
401108	8	.84	
522685	2	1.54	
Total	120	.21	.24

Table 3f - A Comparison of Daughters' Average, Equal Parent and Regression Indexes

Sire	Mean production of dam	Deviation from herd average	Mean production of daughter	Equal parent index	Regression index
480572	499	7	463 (10)	427 (9.5)	426 (10)
629478	517	25	472 (7.5)	427 (9.5)	467 (9)
576509	479	-13	471 (9)	463 (7)	474 (7)
675183	490	- 2	472 (7.5)	454 (8)	472 (8)
744578	512	20	495 (4.5)	478 (5)	491 (5)
694844	506	- 6	495 (4.5)	484 (4)	494 (4)
401108	460	-32	531 (2)	602 (1)	538 (2)
545551	507	5	489 (6)	471 (6)	488 (6)
522685	465	27	528 (3)	591 (2)	522 (3)
808309	516	24	547 (1)	578 (3)	542 (1)

Herd average = 492 b = .21

Regression index = herd average + daughters' average - expected daughters' average

Expected daughters' average = herd average - b (deviation of dams' average from herd average)

Table 3g - Analysis of Error Variance

Source	Degree of Freedom	Sum of squares	Mean squares	F
Within sire unadjusted Sy^2	110	456155	4149	
Due to regression	1	26968	26968	6.85*
Error for adjusted production	109	42918	3937	

The intra-sire correlation and regression of each sire group was carried out by straight forward correlation and regression methods using formulae (1) and (2). The intra-sire correlation and regression of the whole herd was calculated according to the covariance method. For the total regression and correlation, the covariance method is a determinative method by which almost the total effect due to sires is left out. Therefore, we consider those coefficients as being due to the dam's effect on the daughter, and hence are called intra-sire correlations and regressions of daughter on dam. In order to get the heritability value, based on formula (1) and the explanation in the discussion of regression, both the coefficients need to be multiplied by two.

In regard to the regression value for each sire group shown in Table 3e, some values are quite high, such as for sire 545551, b = 8.9166, while some other values are low, such as, in the 576509 group, b = .0074. The latter one shows almost no regression. In addition, there are also negative values. The cause of this heterogeneity among the regression values was (1) the effect of environment and (2) the small numbers included in each sire group. These values give us a clue to the importance of environmental effects, and the unreliability of small sample numbers for the butterfat production analysis. The effect of either one of them could bias the result an unbelievable amount.

Table 3f gives a comparison of three kinds of sire indexes. As we compare these computed values for regression index and equal parent index, the former gives lower values for bulls with high record daughters and higher values for bulls with low record daughters than the later one. As far as the rank is concerned, there are some minor changes among the three different indexs. In general, they agree fairly well. Nevertheless, on the genetic base, the latter two indexes seem more logical than the index based only on daughters' average.

Since environmental effects contribute a large portion of the variation in production of either milk or butterfat, any sire index is an approximation. Graves and Fohrman (1936) take a very sane view of the problem and state,

> "Environment plays a prominent part in the making of production records, and the use of correction factors often makes the effect of environment even more confusing....It is presumptuous to state a sire's ability in exact pounds of milk or fat when the estimate is based on a number of his daughters' records made under such varying conditions.

> If hairsplitting exactitude is set up merely as a means for deciding competitions between bull owners, then it is apt to prove detrimental to breed betterment because this competition offers a temptation to the overzealous."

Since a sample was theoretically taken from a random bred population, there should be no correlation or regression among the individuals themselves. That is, the expected value of correlation or regression should be equal to zero. In this data, an assumption was made that there was no correlation or regression between the dam and offspring, a test is given in order to determine whether this hypothesis is correct. For testing the significance of the correlation coefficient with the size of sample like this, the formula, $\frac{(r - o)}{\frac{1}{\sqrt{n}}}$, was applied. The result $\frac{.2432}{.0913} = 2.66$ is significant for 1% level.

Table 3g indicated that the variation in production due to regression is highly significant. It also shows that on the average the higher the dam's production, the higher the daughter's production. In other words, the daughters' records tend to follow their dams' production. This shows that, to some extent, butterfat production is inherited. The relationship between the r and b values and the question of which should be used as the better measurement for heritability will be discussed later.

The standard error of the correlation coefficient was calculated as follows:

$$S_r = (1 - r^2)/\sqrt{n - 2} = \left\{1-(.2431)^2\right\}/\sqrt{117} = .087$$

Since the heritability estimate is obtained by multiplying the correlation coefficient by two, the standard error of heritability is likewise obtained by multiplying the standard error of the correlation coefficient by two, which is, 2 x .087 = .174. Thus the heritability of butterfat production in the Reformatory herd by the intra-sire correlation method is 0.486 ± .174.

The standard error of the regression coefficient was calculated as follows:

$$S_b^2 = \frac{\dfrac{\text{sum of squares of standard error of estimate of error term}}{n-2}}{\text{Sum of squares of x of error term}}$$

$$= \frac{\dfrac{Sy^2 \;\; \dfrac{(Sxy)^2}{Sx^2}}{n-2}}{Sx^2} = \frac{\dfrac{456155 \;\; \dfrac{(127721)^2}{64891}}{119 - 2}}{604891} = .0061$$

$$S_b = \sqrt{.0061} = .0779$$

The heritability estimate is obtained by multiplying this regression coefficient by two which is equal to, 2 x .211 = .422. Similarly, the standard error of heritability is calculated by multiplying the standard error of regression by two, which is equal to 2 x .0799 = .146. Thus the heritability of butterfat production of cows in the Reformatory herd by the intra-sire regression method is .422 ± .146.

The comparison of the variability of the correlation and regression coefficient may give some information about the reliability of those estimates. The formula for the coefficient of variation is $\frac{\sigma}{m}$. In this case, the mean of the correlation coefficients is .243 and the mean of regression coefficients is .211. Therefore, the coefficient of variation of the correlation coefficient is equal to $\frac{.087}{.243} = .358$, and of the regression coefficient is equal to $\frac{.0779}{.211} = .369$. The variability between those two coefficients is very close. Therefore, as far as variability only is concerned either value may be used for the estimation of the heritability.

3. Paternal Half-sib Correlation Method

The records used for this method of analysis were the same as for the daughter-dam correlation and regression methods. The distribution of daughters under each sire has already been listed in Table 3a.

Table 3h - Separation of Components of Variance of Butterfat Production of the Daughters

Source	Degree of freedom	Sum of squares	Mean squares	Components
Between sires	9	68572	7619	$B + K_o A$
Within sires	110	456155	4147	B

In the Table 3h, the variance was divided into variation between sires and between daughters by the same sire. The variance component B represents variation between daughters by the same sire, while component A is the additional variance which can be ascribed to differences between sires. K_o is the average number of daughters under each sire. It is calculated by the formula (6).

For Table 3h

$$K_o = 14.29$$

$$B = 4147$$

$$B + 14.29 \quad A = 7619$$

$$A = 248$$

The ratio $\frac{A}{A + B}$ is the average correlation between daughters by the same sire. The average correlation multiplied by four is the estimated heritability of butterfat production by the half-sib method, and for this set of data is equal to

$$\frac{4A}{A + B} = \frac{4(248)}{4147-248} = \frac{992}{4395} = .23$$

The standard deviation of the half-sib correlation is

$$\sigma_r = \frac{B(B - K_oA)}{(A + B)^2 \sqrt{\frac{1}{2}(K_o-1)K_on}} = \frac{4147\ (4147 - 14 \times 248)}{(4147 + 248)^2 \sqrt{\frac{1}{2}(13)14 \cdot 10}} = .054$$

Table 3i - Summary of the Observed Values of the Estimation of Heritability

Method	Correlation coefficient	Regression coefficient	Heritability
Intra-sire regression of daughter on dam		.21 ± .078	.42 ± .156
Intra-sire correlation of dam and daughter	.24 ± .087		.49 ± .174
Paternal half-sib correlation	.056 ± .054		.23 ± .217

Heritability Analysis for the Traverse City Herd: The calculations for the Traverse City herd, the largest of the three herds, were the same as for the Reformatory herd. 280 daughter-dam pairs by 15 sires were included.

1. Preliminary Analysis

Table 4a - Average Production of Daughter-Dam Groups

Registration numbers of sire	Number of dam-daughter pairs	Average production of dam	Average production of daughters
659862	21	434	470
553353	35	440	407
700278	35	426	435
729194	71	456	454
813094	10	434	399
769913	15	468	441
787611	9	480	458
522658	4	420	444
353211	7	468	439
609774	8	422	462
486040	30	457	429
412017	6	475	450
566744	18	453	415
650025	11	449	461
Total	280	448	439

Standard deviation of the dams' production = 53 lbs.

Standard deviation of the daughters' production = 64 lbs.

Coefficient of variation of the dams' production =12%

Coefficient of variation of the daughters' production =15%

Table 4b - Analysis of Variance of the Dams' Production

Source	Degree of freedom	Sum of squares	Mean squares	F
Total	279	774925		
Between mates	14	63953	4568	1.70 (non-significant)
Within mates	265	710972	2683	

Table 4c - Analysis of Variance of Daughters' Production

Source	Degree of freedom	Sum of squares	Mean squares	F
Total	279	1165935		
Between sires	14	116445	8351	2.10*
Within sires	265	1049470	3960	

Table 4d - Analysis of Covariance and Test of Adjusted Means Between Daughter Groups

Source	Degree of freedom	Sum of squares and products			Errors of estimate		
		Sx^2	Sxy	Sy^2	Sum of sqs.	Degree of freedom	Mean sqs.
Total	279	774925	77641	1165935	1158156		
Between sires	14	63953	16339	116445			
Within sires	265	710972	61302	1049490	1044204	264	3955
For test of significance of adjusted means					113952	14	8139

$$F = \frac{8139}{3955} = 2.058*$$

A comparison of the averages, the standard deviations, and the coefficients of variation of butterfat production of dams and daughters, leaves little doubt that the dams were selected, since the dams' records were higher than the daughters' records, but the dispersion of their distribution was smaller than that of the daughters.

The result of the analysis of variance of the butterfat production of dams mated to different bulls was non-significant, while it was significant between the daughter groups as the F values show in Tables 4b and 4 c. This indicates that the dams were mated at random among all the sires. If there was no differences between the genetic producing ability of the sires for butterfat production, the F value should be non-significant for the sire effect on daughters' production. However the results show significance at the 5% level. This means there evidently are some significant differences between these sires' transmitting abilities for butterfat production. However, this difference will not effect the correlation and regression coefficients for the estimation of heritability, since the effect will be excluded by the intra-sire method.

The F value of Table 4d is significant at the 5% level. From Tables 4b and 4c, in which there was found to be no difference between groups of dams, while the daughter groups by different sires were different for butterfat production, the result of Table 4d is expected, and gives further proof of the difference between sires.

2. Intra-sire Correlation or Regression of Daughter on Dam Method

Table 4e - Intra-sire Correlation and Regression Coefficients

Sire	Number of dam-daughter pairs	Regression coefficient	Correlation coefficient
659862	21	.2123	
553353	35	.0224	
700278	35	.0267	
729194	70	.0304	
813094	10	.0467	
769913	15	-.3555	
787611	9	.1710	
522658	4	.4727	
353211	7	.4307	
609774	8	.6122	
486040	30	.6340	
412017	6	.0776	
566744	18	-.1209	
650025	11	-.7376	
Total	280	.0862	.0710

Table 4f - Test of Significance of Regression Coefficient

Source	Degree of freedom	Sum of squares	Mean squares	F
Due to regression	1	5286	5286	1.34
Error for adjusted production	264	1044204	3955	
Within sire of unadjusted production	265	1049490	3960	

The method of calculation for the coefficients listed in Table 4e was the same as that for Table 3e of the Reformatory herd. The fluctuation of the regression coefficients may be interpreted the same as for Table 3e.

For testing the significance of the correlation coefficient, the same formula was used as for the Reformatory herd. The result of this testing gave the value, 1.19, which is non-significant.

According to the results of the analysis of the significance of the regression and correlation coefficients, the value for either was not significantly different from zero. Since there were quite a few negative regression coefficients as Table 4e shows, this was to be expected. This means that in this set of data there was no way to predict the daughters' production from the dam's records.

The reason for the low heritability may be (1) dominance effects, (2) the environmental conditions were not good enough and the animals with genes for high production could not show their true ability. The result is perhaps the production records did not represent their true ability. I have visited this herd. This herd is a part of the Traverse City Mental Hospital, and some of the people working in the herd are just recovered or partially cured persons. The management appears below the average of the other two herds studied. For this reason (2) is more likely to have existed or played the main effect. There may have been some sampling error, but as the sampling size of this herd was the largest among the three, it should not have played any important role.

For obtaining a dependable heritability estimate, these three samples from each herd are pooled later. The data from this herd is considered as part of the total sample. Therefore, both the regression and correlation coefficients calculated for this herd are taken at face value, even though they are non-significant. Furthermore, this regression coefficient is used to compute the regression indexes to compare them with the other sire indexes.

Table 4g - A Comparison of Daughters' Average, Equal Parent and Regression Indexes (lbs. Butterfat)

Sire	Mean production of dam	Deviation from herd average	Mean production of daughter	Equal parent index	Regression index
659863	434	-9	470 (1)	506 (1)	471 (1)
553353	440	-3	407 (13)	374 (13)	407 (13)
700278	426	-17	435 (10)	444 (6)	436 (10)
729194	456	13	454 (5)	452 (5)	453 (5)
813094	434	-9	399 (14)	364 (14)	399 (14)
769913	468	25	441 (8)	414 (9)	439 (8)
787611	480	37	458 (4)	436 (7)	455 (4)
522658	420	-23	444 (7)	468 (4)	446 (7)
353211	468	25	439 (9)	410 (10)	437 (9)
609774	422	-21	462 (2)	502 (2)	464 (2)
486040	457	14	429 (11)	401 (11)	428 (11)
412017	475	31	450 (6)	425 (8)	448 (6)
566744	453	10	415 (12)	377 (12)	414 (12)
650025	449	6	461 (3)	473 (3)	461 (3)

b = .086

Herd average = 443 lbs.

It appears in Table 4g that the regression indexes rank exactly the same as the daughters' averages, and the actual values are also very nearly the same. This results from the low regression coefficient which causes the expected daughter's production to be very close to the herd average, e. g., regression index = W + D - e, where W is the herd average, D is the actual daughters' average, and e is equal to w - bx. As b value is small and bx is very close to zero, e will approach W. The result is, W + D - e = W + D - W = D. It is statistically true also that when b value is zero, the mean is the predicted value. Since the equal parent index is based on the assumption that the regression of daughter on dam is unity, the values based on it depart considerably from the regression index in this case.

The calculation of the standard error of the regression and correlation is exactly same as the calculation for the Reformatory herd.

$$S_b^2 = \frac{\dfrac{Sy^2 - (Sxy)^2/Sx^2}{n-2}}{Sx^2} = \frac{\dfrac{1049490 - (61302)^2/710972}{277}}{710972} = .0053$$

$$S_b = \sqrt{.0053} = .073$$

$$S_r = (1 - r^2)/\sqrt{n-2} = 1 - (.07096)^2/\sqrt{280} = .0598$$

3. Paternal Half-sib Method

Table 4h - Separation of Components of Variance of the Butterfat Production of the Daughters

Source	Degree of freedom	Sum of squares	Mean squares	Components
Between sires	14	116445	8318	$B + K_o A$
Within sires	265	1049470	3960	B

$$K_o = \frac{(280) - 9848}{(280)\ (13)} = 19$$

$$\frac{4A}{A - B} = \frac{4(229)}{3960 - 229} = .22$$

The standard deviation of the half-sib correlation is,

$$\sigma_r = \frac{B(B + K_oA)}{(A + B)^2 \sqrt{\frac{1}{2}(K_o - 1)K_on}} = \frac{3960(3960 - 229 \times 19)}{(3960+229)^2\sqrt{\frac{1}{2}(18)(19)(14)}} =$$

.038

Table 4i - Summary of the values of Estimation of Heritability

Method	Correlation coefficient	Regression coefficient	Heritability
Intra-sire regression of daughter on dam		.086 ± .073	.17 ± .15
Intra-sire correlation of dam and daughter	.071 ±.060		.14 ± .12
Paternal half-sib correlation	.056 ±.038		.22 ± .15

According to Table 4i, the heritability estimated by the correlation between half-sibs is higher than either the regression of daughter on dam or correlation between dam and daughter. This is logical since, as it was pointed out before, the correlation between half-sibs usually includes some environmental correlation, if any exists. Moreover, correlation due to interaction contributes more in the half-sib correlation than to the dam and daughter correlation.

Heritability Analysis for the Ionia Hospital Herd:

There were 73 daughter-dam pairs by six sires in the Ionia herd for the heritability analysis. Their distribution and the averages of the butterfat production of the dams and daughters are listed in Table 5a.

1. Preliminary Analysis

Table 5a - Distribution and Average Butterfat Production of Dam and Daughter Groups

Sire	Number of dam-daughter pairs	Average production of dam	Average production of daughters
519074	4	576	496
671583	15	569	597
568009	11	517	561
504402	16	573	570
574194	25	587	503
507031	2	534	522
Total	73	568	546

Standard deviation of dams' production = 64 lbs.

Standard deviation of daughters' production = 83 lbs.

Coefficient of variation of dams' production = 11%

Coefficient of variation of daughters' production = 15%

Table 5a shows that the averages of daughters' production were more heterogeneous than the averages of the dams' production. The mean of all the dams' production was higher than the mean of the daughters' production, but their standard deviations were in the reverse order. This is also shown by the values of the coefficients of variation. The results of this table simply indicate that the dams were selected.

Table 5b - Analysis of Variance of the Dams' Production

Source	Degree of freedom	Sum of squares	Mean squares	F
Total	72	301164		
Between mates	5	40149	8030	2.06 (non-significant)
Within mates	67	261015	3898	

Table 5c - Analysis of Variance of Daughters' Production

Source	Degree of freedom	Sum of squares	Mean squares	F
Total	72	507539		
Between sires	5	107808	21563	3.61*
Within sires	67	399731	5966	

The interpretation of Tables 5b and 5c are approximately the same as for the Traverse City herd.

Table 5d - Analysis of Covariance and Test of Adjusted Means Between Daughter Groups

Source	Degree of freedom	Sum of squares and products Sx^2	Sxy	Sy^2	Errors of estimate Sum of sqs.	Degree of freedom	Mean sqs.
Total	72	301164	37145	507539	502958	71	
Between sires	5	40149	-25467	106808			
Within sires	67	261015	62572	399731	249731	66	3788
For test of significance of adjusted means					253227	5	50645

$$F = \frac{50645}{3784} = 13.38^{**}$$

The F value of Table 5d comes out highly significant. It means that these sires differed in the level of production they transmitted to their daughters. Since the adjusted means are the average of the daughter groups by the different sires after adjustment for the dams' producing ability, the residual variation is accounted for as the effect due to the sire differences. It also indicated there was a certain amount of heterogeneity among the sires, and that the selection of sires should be carefully done in order to increase the production level.

2. Intra-sire Daughter-Dam Correlation or Regression of Daughter on Dam Method

Table 5e - Intra-sire Regression and Correlation Coefficients

Sire	Number of dam-daughter pairs	Regression coefficient	Correlation coefficient
519074	3	-.6532	-.9986
671583	14	.2945	.2650
568009	10	.3183	.3651
504402	15	.1462	.1575
574194	24	.3855	.6366
507031	1	-.1793	-.9629
Total	67	.2397	.1937

The method of calculation for the coefficients listed in Table 5e was same as that for Table 3e of Reformatory herd.

Table 5f - Test of Significance of Regression Coefficient

Source	Degree of freedom	Sum of squares	Mean squares
Due to regression	1	15000	15000
Error for adjusted production	66	249731	3784
Within sires of unadjusted production	67	399731	5966

$$F = \frac{15000}{5825} = 3.96$$

The F value of Table 5f is non-significant at the 5% level. An F value of 3.99 for 1 and 66 degrees of freedom is needed in order to be significant. However, it closely approaches the level of significance.

For testing the significance of the correlation coefficient, the same formula was used as for the Reformatory herd. The calculated value for this test is 1.64, which is non-significant.

Table 5g - A Comparison of Daughters' Average, Equal Parent and Regression Indexes (Lbs. Butterfat)

Sire	Mean production of dam	Deviation from herd average	Mean production of daughter	Equal parent index	Regression index
519074	576	26	496 (6)	416 (6)	490 (6)
671583	569	19	597 (1)	625 (1)	592 (1)
568009	517	-33	561 (3)	605 (2)	568 (2)
504402	573	23	570 (2)	567 (3)	557 (3)
574194	587	37	503 (5)	419 (5)	494 (5)
507031	534	-16	522 (4)	510 (4)	526 (4)

$b = .24$

Herd average = 550 lbs.

Table 5f shows that the rank by the equal parent index and regression index were the same, but there was a shift between (3) and (2) in comparison with the daughters' average. As far as the calculated values were concerned the regression index was closer to the daughter average than to the equal parent index. The reason for this was the low regression as has been pointed out in the interpretation of the heritability analysis of the Traverse City herd.

The calculation of the standard error of regression and correlation was exactly the same as the calculation for the Reformatory herd.

$$S_b^2 = \frac{\frac{Sy^2 - (Sxy) / Sx^2}{N - 2}}{Sx^2} = \frac{\frac{399731 - (62572)^2/261050}{70}}{261050} = .021$$

$$S_b = \sqrt{.021} = .145$$

$$S_r = (1-r^2)/\sqrt{n-2} = 1 - (.1977)^2/\sqrt{72-2} = .115$$

3. Paternal Half-sib Method

Table 5b - Separation of Components of Variance of Butterfat Production of the Daughters

Source	Degree of freedom	Sum of squares	Mean squares	Components
Between sires	5	107808	215616	$E + K_oA$
Within sires	67	399731	5966	E

$$K_o = \frac{(73)^2 - 1247}{(73)(4)} = 13.97$$

$$\frac{4A}{A-E} = \frac{4(1114)}{5966 + 1114} = .63$$

The standard deviation of the half-sib correlation is

$$\frac{B(B + K_oA)}{(A + B)^2\sqrt{\frac{1}{2}(K_o - 1)Kn}} = \frac{5966(5966-14x1114)}{(1114 + 5966)^2\sqrt{\frac{1}{2}(13)(14)(6)}} = .11$$

Table 51 - Summary of the Values of Estimation of Heritability

Method	Correlation coefficient	Regression coefficient	Heritability
Intra-sire regression of daughter on dam		.24 ± .14	.48 ± .29
Intra-sire correlation of dam and daughter	.19 ± .11		.39 ± .23
Paternal half-sib correlation	.16 ± .11		.63 ± .44

<u>Average Estimate of Heritability of Butterfat Production for the Three Herds</u>:

Since the three herds are located in two different sections of Michigan, and since their management and breeding systems cannot be the same, to generalize on this situation and to make the estimate of heritability applicable to more than a single herd, a summation of the estimates from each herd and an average of the estimated value of heritability is quite necessary. In addition, the size of the sample will be enlarged and the estimated value will be more reliable. The number of daughter-dam pairs sampled from each herd is fairly proportional to their herd size. Therefore, the pool of the three samples can be assumed as a stratified sample.

The method of calculating a weighted average is very useful method for pooling samples together. It has been worked out by Hazel and Terrill (1945). Their averages were calculated by weighting each of the individual estimates by the reciprocal of its squared standard error. They pointed out that this method is not without disadvantages, but it does, in general, give greater weight to those estimates which are based on the greatest amount of data. The following are the formulae used and the fundamental set-up for calculations.

General formula for weighted average of the standard deviation is

$$\sqrt{\frac{1}{\sum_{i=1}^{n}\left(\frac{1}{s_i^2}\right)}}$$

Weighted average of standard deviation for intra-sire regression of daughter on dam is

$$\sqrt{\frac{1}{\frac{1}{.021}+\frac{1}{.0061}+\frac{1}{.0053}}} = .0499$$

Weighted average of standard deviation for intra-sire correlation of dam and daughter is

$$\sqrt{\frac{1}{\frac{1}{(.1150)^2}+\frac{1}{(.087)^2}+\frac{1}{(.0598)^2}}} = .0453$$

Weighted average of standard deviation for paternal half-sib correlation is

$$\sqrt{\frac{1}{\frac{1}{(.0383)^2}+\frac{1}{(.109)^2}+\frac{1}{(.0542)^2}}} = .0301$$

The general formula for the weighted average of regression and correlation is

$$\frac{\sum_{i=1}^{n}\left(\frac{b_i}{S_i^2}\right)}{\sum_{i=1}^{n}\left(\frac{1}{S_i^2}\right)} \quad \text{or} \quad \frac{\sum_{i=1}^{n}\left(\frac{r_i}{S_i^2}\right)}{\sum_{i=1}^{n}\left(\frac{1}{S_i^2}\right)}$$

Weighted average of intra-sire regression of daughter on dam is

$$\frac{\frac{.0862}{(.0728)^2}+\frac{.2111}{(.078)^2}+\frac{.2397}{(.1457)^2}}{\frac{1}{.0052}+\frac{1}{.0061}+\frac{1}{.021}} = .1551$$

Weighted average of intra-sire correlation of dam and daughter is

$$\frac{\frac{.2431}{(.087)^2}+\frac{.071}{(.0598)^2}+\frac{.1937}{(.115)^2}}{\frac{1}{(.087)^2}+\frac{1}{(.0598)^2}+\frac{1}{(.115)^2}} = .1367$$

Weighted average of Paternal half-sib correlation is

$$\frac{\frac{.0547}{(.0382)^2}+\frac{.1573}{(.0750)^2}+\frac{.0564}{(.0542)^2}}{\frac{1}{(.0383)^2}+\frac{1}{(.0750)^2}+\frac{1}{(.0542)^2}} = .0630$$

Table 6a - A Summary of the Regression and Correlation Coefficient of the Three Herds

Herd	Paternal half-sib correlation	Intra-sire regression of daughter on dam	Intra-sire correlation of dam and daughter
Traverse	.055 ± .038	.086 ± .073	.071 ± .060
Reformatory	.056 ± .054	.211 ± .078	.243 ± .087
Ionia	.157 ± .109	.240 ± .145	.194 ± .115
Average	.063 ± .030	.155 ± .050	.137 ± .045

Table 6b - A Summary of Estimation of Heritability

Herd	Paternal half-sib correlation	Intra-sire regression of daughter on dam	Intra-sire correlation of dam and daughter
Traverse	.22 ± .15	.17 ± .15	.14 ± .12
Reformatory	.23 ± .22	.42 ± .16	.49 ± .17
Ionia	.63 ± .30	.48 ± .29	.39 ± .23
Average	.25 ± .12	.31 ± .10	.27 ± .09

By looking at Table 6a and 6b, we find that among the averages of the three herds, the intra-sire regression of daughter on dam had the highest value and the intermediate variability, and that the intra-sire daughter-dam correlation had the intermediate value, and the lowest variability, while the half-sib method was lowest heritability with the highest variability. For this set of data, it is believed

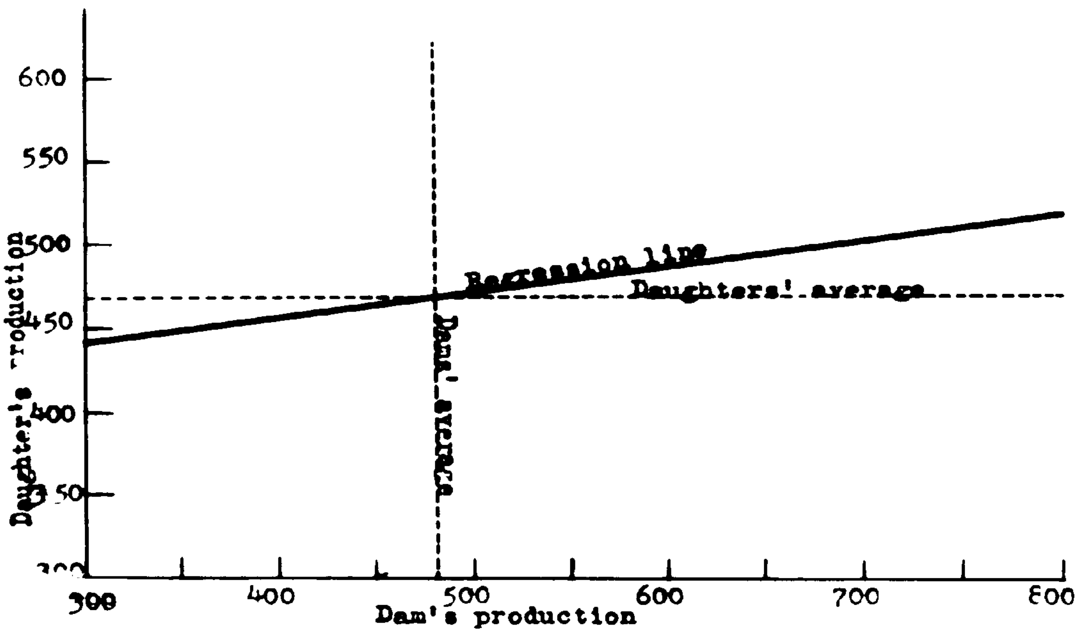


Figure 2 - Intra-sire Regression of Butterfat Production of Daughter on Dam

The above graph is made for the average of the daughters based on the daughters' production in the three herds, and for the average of the dams based on the dams' production of the three herds; the regression is based on the equation, $Y = 469 - b\ (X - 480)$

that the average of the intra-sire regression coefficients is the most reliable estimate of heritability. The reason for this will be given in the discussion.

Conversion of Regression Coefficient of the Average of the Records of a Cow into the Value for Single Records:

For the comparison of this heritability value, which was derived by using the life time average of butterfat production, with others, it is desirable to express the regression coefficient b of the total records of each cow in terms of what they would be if each cow had only one record. The calculation follows the formula which was given by Lush (1942).

$$b = b'\left(\frac{1 - (\bar{m}-1)r_{dd}}{\bar{m}} + \frac{\sigma_m^2 (1-r_{dd})}{\bar{m}^3}\right)$$

Where b equals the regression of daughter on dam when single lactation records of each are used, b' equals the regression when life time averages are used and $\bar{m}$ equals the average of the number of dam's records during life time. r_{dd} is the repeatability value. σ_m^2 is the variance of the number of records of each dam of the three herds

$$b = .1551 \left(\frac{1 - \overset{(1)}{(3.98-1)}\,\overset{(3)}{.34}}{3.98} - \frac{\overset{(2)}{4.56}\;(1.-.34)}{(3.98)^3} \right)$$

$$= .0853$$

$$h^2 = .0853 \times 2 = .17$$

(1)
$$m = \frac{n_1 \bar{x}_1 + n_2\bar{x}_2 + \dots n_k\bar{x}_k}{n_1 - n_2 + \dots n_k - k} = \frac{502 + 944 + 437}{120 + 280 + 73} = 3.98$$

$\bar{x}$ = the average number of records of each dam of a certain herd

n = the number of dam-daughter pairs of a certain herd

(2)
$$\hat{\sigma}^2 = \frac{n_1 s_1^2 + n_2 s_2^2 + \dots n_k s_k^2}{n_1 + n_2 + \dots n_k - k} = \frac{530.4 + 1080.8 + 430.7}{120 + 280 + 73 - 3} = 4.55$$

s^2 = the variance of the number of records of each dam for a certain herd

(3)
r_{dd} = .34, the repeatability

The Effect of Yearly Environmental Changes on Butterfat Production

The factors which account for this effect such as crops, economics, and climate, all have a direct or indirect effect on the butterfat production of dairy cattle. We were not interested in the factors, but rather in their results, and whether there was any significant difference between yearly averages, or whether any trends existed among the consecutive years, and what portion of the variation in the butterfat records was due to the differences between years. These were the main purposes of this analysis.

The method used for this study was the unequal subclass number analysis of variance given by Snedecor (1946). There were no records from 1934 to 1936 in the Traverse City herd, thus eleminating those three years from the analysis for that herd.

The average yearly butterfat production figures for each of the three herds are given in Table 7a. These figures in graphic form are shown in Figure 3.

Tables 7b and 7c indicate that there was a highly significant difference between different years for butterfat production either for a single herd or after combining the three herds. However, there was no indication that the averages of the late years were higher than the averages of the earlier years. The portion of the intra-herd variance which was accounted for by differences between years was close to five per cent.

For the trend analysis, there were several methods available, but some of them required tedious calculations. The method used here was a kind of test of randomness of sequences, the so called "runs" simplified by Hoel (1948). The average production for each year for each herd and the three herds together were assigned the letter a if they were less than the median and the letter b, if they were greater than the median. The four sets of averages gave rise to the following sets of arrangements.

Table 7a - A List of Year Averages of Butterfat Production

Year	Traverse City		Reformatory		Ionia		Total	
	Number of records	Averages	Number of records	Averages	Number of records	Averages	Number of records	Averages
1930	35	421.25	12	471.50	9	545.44	56	451.98
1931	45	429.13	19	504.52	10	563.70	74	466.67
1932	63	447.88	27	562.67	17	591.47	107	499.66
1933	32	445.18	27	539.30	18	565.72	77	506.36
1934	—	—	36	539.25	19	527.37	55	535.14
1935	—	—	25	465.36	18	573.83	43	510.77
1936	—	—	34	473.29	31	598.45	65	532.98
1937	50	420.76	40	473.27	29	553.58	119	470.78
1938	82	431.89	29	461.07	30	536.37	141	460.12
1939	83	439.01	38	492.26	35	580.51	146	516.86
1940	84	442.12	27	479.44	30	592.80	141	481.33
1941	79	462.75	26	538.62	29	600.21	134	507.22
1942	91	426.83	275	522.04	35	573.91	153	477.29
1943	75	442.36	29	492.76	36	516.22	140	471.79
1944	86	469.82	39	507.59	32	544.47	157	494.42
1945	93	434.43	34	449.09	26	543.35	153	467.30
1946	69	452.86	24	508.58	17	578.35	110	484.41
Av.	71.42	441.76	29	501.92	24.76	564.11	110.65	484.91

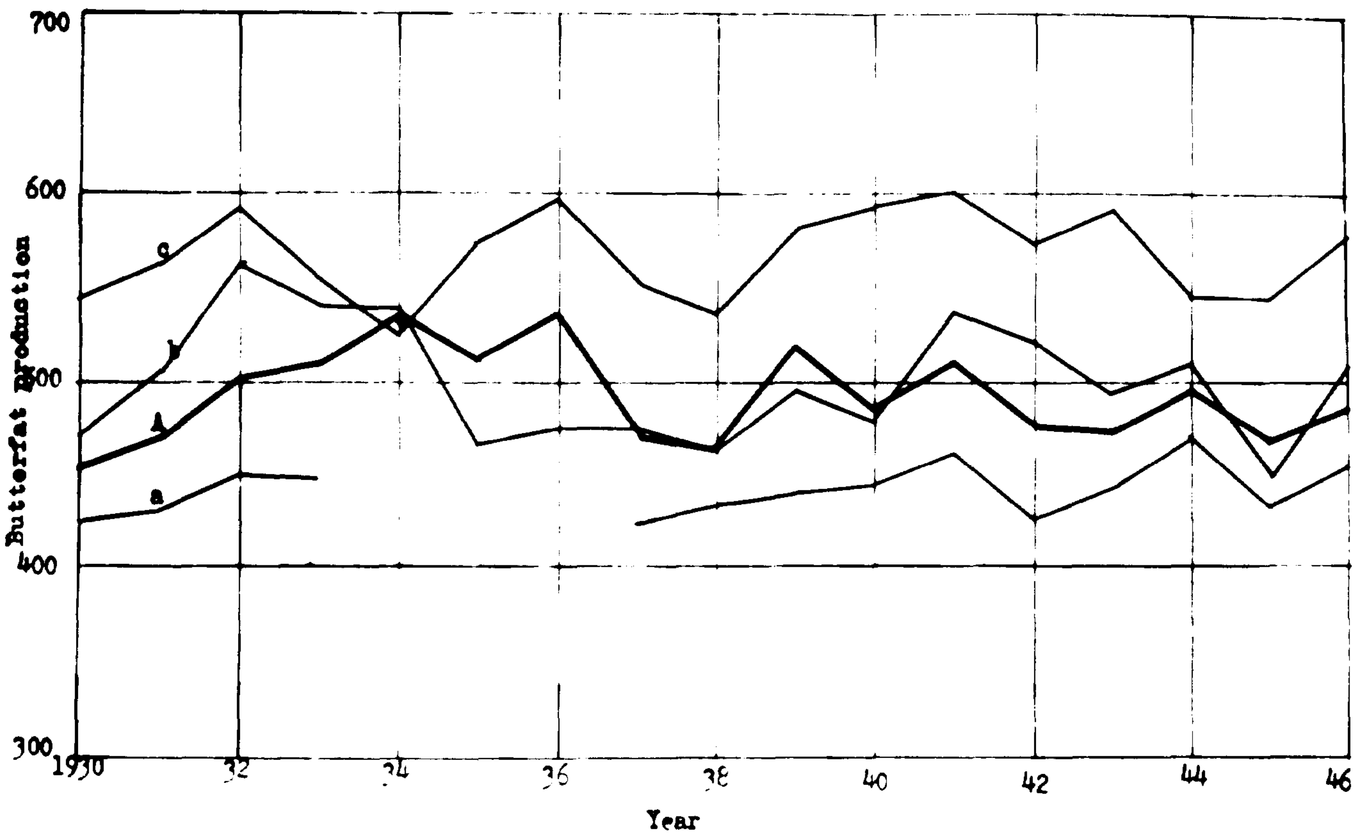


Figure 3 - Average Yearly Butterfat Production

a - Traverse City herd
b - Reformatory herd
c - Ionia herd
A - The three herds

Table 7b - Analysis of Variance of Year Effect on Butterfat Production of Each Herd

Herd	Source of variance	Degree of freedom	Sum of squares	Mean squares	F
Traverse	Total	966	4935052		
	Between years	13	191693	14746	2.96**
	Within years	953	4743359	4977	
Reformatory	Total	492	3673279		
	Between years	16	284122	25650	3.74**
	Within years	486	3262884	6855	
Ionia	Total	420	3690632		
	Between years	16	284122	17758	2.11**
	Within years	404	3406510	8432	

Table 7c - Analysis of Variance of Year Effect on Butterfat Production of Three Herds

Source	Degree of freedom	Sum of squares	Mean squares	F
Total	1880	16882308	8980	
Between herds	2	4583345	2291672	
Within herds	1878	12298923	6549	
Between years	45	886210	19694	3.16**
Within years	1833	11412713	6226	

Portion of intra-herd variance due to difference between years

$$= \frac{6549 - 6226}{6549} = 4.9\%$$

Portion of total variance due to difference between years

$$= \frac{8980 - 6226}{8980} = 3.7\%$$

Traverse City Herd,
Averages - 421, 449, 445,421, 432, 439, 442, 463, 427, 442, 469, 434, 453.

Median - 440.

Sequence of letters - aabbaaabbabbab.

Reformatory Herd,
Averages - 472, 505, 563, 539, 539, 465, 473, 473, 461, 492, 479, 539, 522, 493, 508, 509.

Median - 493

Sequence of letters - abbbbaaaaabbbbab.

Ionia Herd,
Averages - 545, 564, 591, 566, 527, 574, 598, 554, 536, 581, 593, 600, 574, 516, 544, 543, 578.

Median - 566

Sequence of letters - aabbabbaabbbbaaab.

Total averages - 452, 467, 500, 506, 535, 511, 533, 471, 460, 517, 481, 507, 477, 472, 494, 467, 484.

Median - 481.

Sequence of letters - aabbbbbaabbbaabaa.

Explanation of symbols,

n_a = the number of a's

n_b = the number of b's

r_a = the number of runs of a's

r_b = the number of runs of b's

$u = r_a + r_b$

For Traverse City Herd:

$n_a = 7$, $n_b = 7$, $r_a = 4$, $r_b = 4$,

$u = 8.$[1] non-significant

For Reformatory Herd:

$n_a = 8$, $n_b = 9$, $r_a = 3$, $r_b = 3$,

$u = 6.$ [1] non-significant

For Ionia Herd:

$n_a = 8$, $n_b = 9$, $r_a = 4$, $r_b = 4$,

$u = 8.$ [1] non-significant

For Total Averages:

$n_a = 8$, $n_b = 9$, $r_a = 4$, $r_b = 3$,

$u = 7.$ [1] non-significant

By inspecting the table [1], one sees the u values were all within the $p(u_{.05})$ and $p(u_{.95})$, although the Ionia herd was close to the significant value of $u_{.95}$. It was concluded, then, that the butterfat production had no year trend for either a single herd or the total of the three herds.

---

(1) The table for the test of runs is built up according to the formula:

$$P(r_a, r_b) = K \frac{(n_a-1)!\,(n_b-1)!\,n_a!\,n_b!}{(r_a-1)!\,(n_a-r_a)!\,(r_b-1)!\,(n_b-r_b)!\,n!}$$

$n_a = n_b$	5	10	15	20	25	30	40	50	60	70	80	90	100
$u_{.05}$	3	6	11	15	19	24	33	42	51	60	70	79	88
$u_{.95}$	8	15	20	26	32	37	48	59	70	81	91	102	113

In the foregoing table, $u_{.05}$ and $u_{.95}$ are the largest and smallest integers, respectively, such that $p[u \leq u_{.05}] \leq 0.05$ and $p[u \leq u_{.95}] \geq 0.95$. These values may therefore be used as 5% critical values for testing whether u is unusually small or large. Only the values of $u_{.05}$ and $u_{.95}$ for n_a ($=n_b$) from 5 to 100 are listed in the above table, according to Hoel (1948).

Effect of the Month of Calving on Butterfat Production

The influence of the month of calving on the total butterfat yield is a subject of considerable interest to herdsman and extension workers. Information on this subject would be helpful to a herdsman in deciding at what time of the year it is best to have his cows calve in order to take advantage of market needs and favorable prices of milk and feeds. In the meantime, the research man also is interested in finding out how large a portion of the total variation is that due to difference in month of freshening.

The same set of records used for the study of year effect was used for the study of the effect of month of calving on butterfat production. Thus, one group of lactation records represented all the cows that had calved in January, another group of records represented all the cows that had calved in February, and so on for each of the twelve calendar months.

Table 8a shows the number of cows that calved in each calendar month, and the average butterfat production for that month for each herd and for the total of the three herds. In this Table, the Traverse City herd and Reformatory herd show the highest butterfat production for the cows calving in March, and the lowest in August, while the Ionia herd shows the highest butterfat production in January and the lowest in October. The average of the three herds shows that cows freshening in June and August had the lowest butterfat production and those freshening in March had the highest production. The results of the three herds are similar to the results obtained by Frick et. al., (1947) and Woodward (1945).

As far as the average butterfat yield of the three herds for different months of calving is concerned, it is obvious that there were two peaks; the highest one in March, and the other in September. The sudden rise in July was mainly due to the high average of the Reformatory herd, and in this case, might be considered as a sampling error. As the curve is smoothed, it shows a gradual rise from January until early spring; then it drops in the summer and rises again until early fall, when it drops slowly until January.

Tables 8b and 8c show that the month effect on butterfat production was significant at the 5%, 1% level for the Traverse City herd, the Ionia herd and the sum of the three herds, respectively. The Reformatory herd showed a non-significant difference for month of calving. As this herd is located near the Ionia herd, the natural environment should

Table 8a - Average Butterfat Production of Cows Freshening in Different Months

Month	Traverse City		Reformatory		Ionia		Total	
	No. of records	Average	No. of records	Average	No. of records	Average	No. of records	Average
January	83	435	49	504	32	620	164	492
February	71	433	38	519	24	597	133	487
March	54	463	41	522	42	570	137	514
April	77	448	38	504	31	565	146	487
May	92	444	28	498	41	544	161	479
June	82	431	28	479	20	576	130	464
July	96	430	55	505	45	564	196	482
August	81	424	39	479	39	525	159	462
September	65	456	47	482	49	570	161	498
October	100	449	43	509	28	519	173	487
November	72	453	42	504	36	562	150	494
December	94	445	45	511	34	571	173	487
Average	80.58	442	41.16	502	35.08	564	156.75	485

Table 8b - Analysis of Variance of Butterfat Production of Month Difference for Each Herd

Herd	Source of variance	Degree of freedom	Sum of squares	Mean squares	F
Traverse	Total	966	4935052	5109	
	Between months	11	114473	10407	2.06*
	Within month	955	4820579	5048	
Reformatory	Total	493	3673279		
	Between months	11	92241	8386	1.13
	Within month	482	3581038	7430	
Ionia	Total	420	3690632		
	Between months	11	266199	34300	2.90**
	Within month	409	3424433	8373	

Table 8c - Analysis of Variance of Butterfat Production of Each Month for the Three Herds

Source	Degree of freedom	Sum of squares	Mean squares	F
Total	1880	16882308		
Between herds	2	4583345	2291672	
Within herds	1878	1298923	6549	
Between months	33	472913	14331	2.24**
Within month	1845	11826010	6410	

Portion of intra-herd variance due to month effect,

$$\frac{6549 - 6410}{6549} = 2.12\%$$

Portion of total variance due to month effect,

$$\frac{8980 - 6410}{8980} = 1.5\%$$

5% significant level for the difference of month average of the three herds is

$$t_{.05}\left(\sqrt{\frac{1}{n_1} - \frac{1}{n_2}}\right) = .033 \times 80.6 \times 1.9599 = 5.21$$

not be too different. Therefore, this smaller variation was likely the result of more constant management throughout the whole year, or sampling errors.

According to the level of difference needed for significance between averages of the three herds, the average for March was different from the averages of any month. Therefore, there is no doubt that March was the peak among all months of the year. The only peculiarity of the results is that the average of July was significantly higher than both June and August. However, this was true only for the Reformatory herd and the average of the three herds. The production of cows calving in July for the other two herds was in line with the the June and August calvings. Therefore, the higher average production for July calvers for the three herds resulted from the exceeding high production of the Reformatory cows calving in July. This high production for these cows may have been the result of certain management practices that compensated for the usual adverse conditions for cows calving in that month.

Effect of Calving Interval on Butterfat Production

The calving interval is the period between two suceeding calvings of the same cow. It is highly correlated with the length of the dry period. The dry period or calving interval has been known to have an effect on the milk yield or butterfat production of the same lactation. The shorter the interval of calving, the longer the cow carries the calf during the lactation. The longer the interval, the shorter the period of time the cow carries the calf during lactation, and it also usually results in a longer lactation. In addition, it is believed the interval of calving influences the next lactation. With a longer calving interval the cow has more time to recover, and build up her system for the next lactation and for the growth of the fetus during the later part of pregnancy. Therefore, the effect of the calving interval on butterfat production was broken into two parts; one was the effect on the butterfat production of the same lactation, and the other was on the following lactation.

The question often arises as to how frequently a cow should calve so that her milk or butterfat production over a long period may be at a maximum. It is common knowledge that too frequent calving, and too short periods of rest (which, in practice, are closely related), undermine the cow's constitution, and in some cases, reduce her yield to a much lower plane. After the optimum interval is determined, the second question one may ask is how important it is on the total variation of production. If it is not a very influential factor, we may choose to ignore it in order to simplify the herd management. The main purpose of study in this section is to attempt to answer these questions.

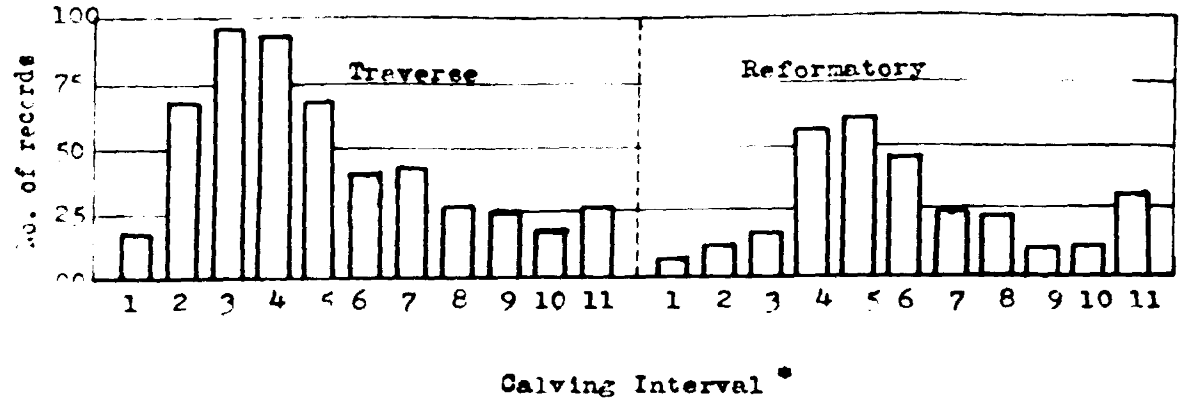
1. Analysis of Effect of Calving Interval on Butterfat Production

The records used for the analysis included all the available records up to 1946. Records without the date of freshening, and calving interval beyond 519 days were discarded. The days of each month were counted as 30.5 days except February, which was counted as 28 days. The range in length of intervals was from 300 days to 519 days. This range was divided into eleven classes. Each class had a 20-day interval. The distribution of the records and the average for each interval are listed in the following table:

Table 9a - Distribution of Records and the Average Butterfat Production for Different Calving Intervals of Same Lactation

	Traverse		Reformatory		Ionia		Total	
Interval	No. of records	Av.	No. of records	Av.	No. of records	Av.	No. of records	Av.
300-319	16	412	7	458	5	488	28	437
320-339	68	421	12	492	16	519	96	447
340-359	96	422	17	455	31	529	144	449
360-379	94	448	56	489	50	552	200	485
380-399	67	464	61	511	41	582	169	510
400-419	40	462	46	503	45	607	131	526
420-439	43	482	19	481	21	590	83	509
440-459	22	466	18	572	16	573	56	531
460-479	20	431	10	530	12	554	42	490
480-499	17	481	11	542	11	549	45	521
500-519	22	494	31	526	24	592	77	537

Figure 4 - Distribution of Records in Same Calving Interval



* Calving Interval (days)
1 — 300-319
2 — 320-339
3 — 340-359
4 — 360-379
5 — 380-399
6 — 400-419
7 — 420-439
8 — 440-459
9 — 460-479
10 — 480-499
11 — 500-519

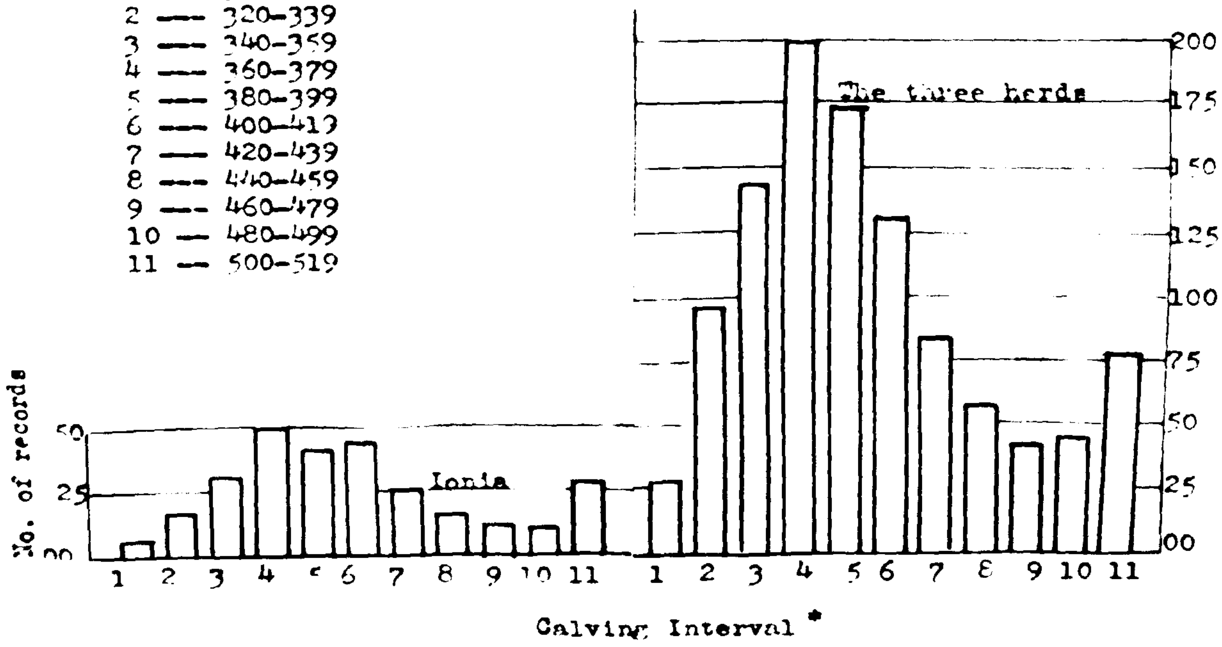
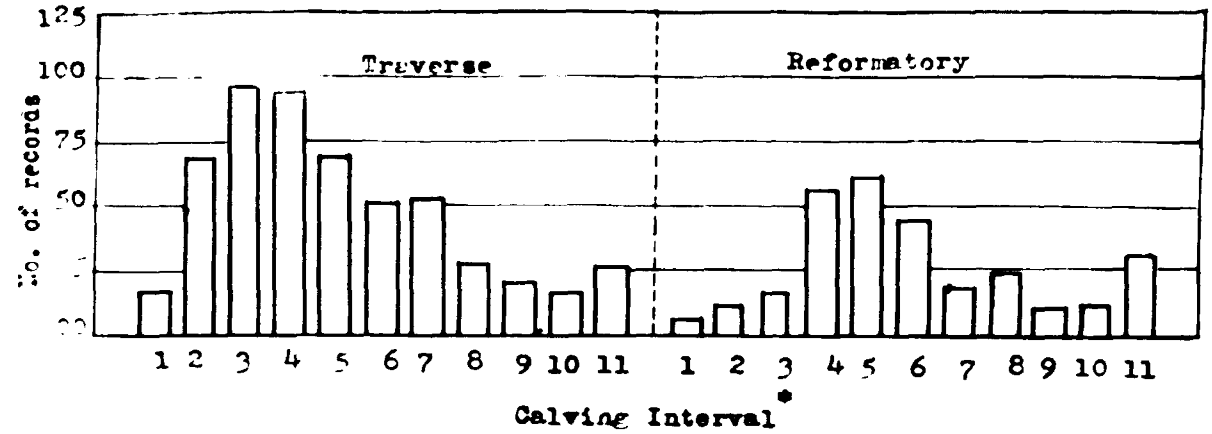


Figure 5 - Distribution of Records in Previous Calving Interval



* Calving Interval (days)
1 — 300-319
2 — 320-339
3 — 340-359
4 — 360-379
5 — 380-399
6 — 400-419
7 — 420-439
8 — 440-459
9 — 460-479
10 — 480-499
11 — 500-519

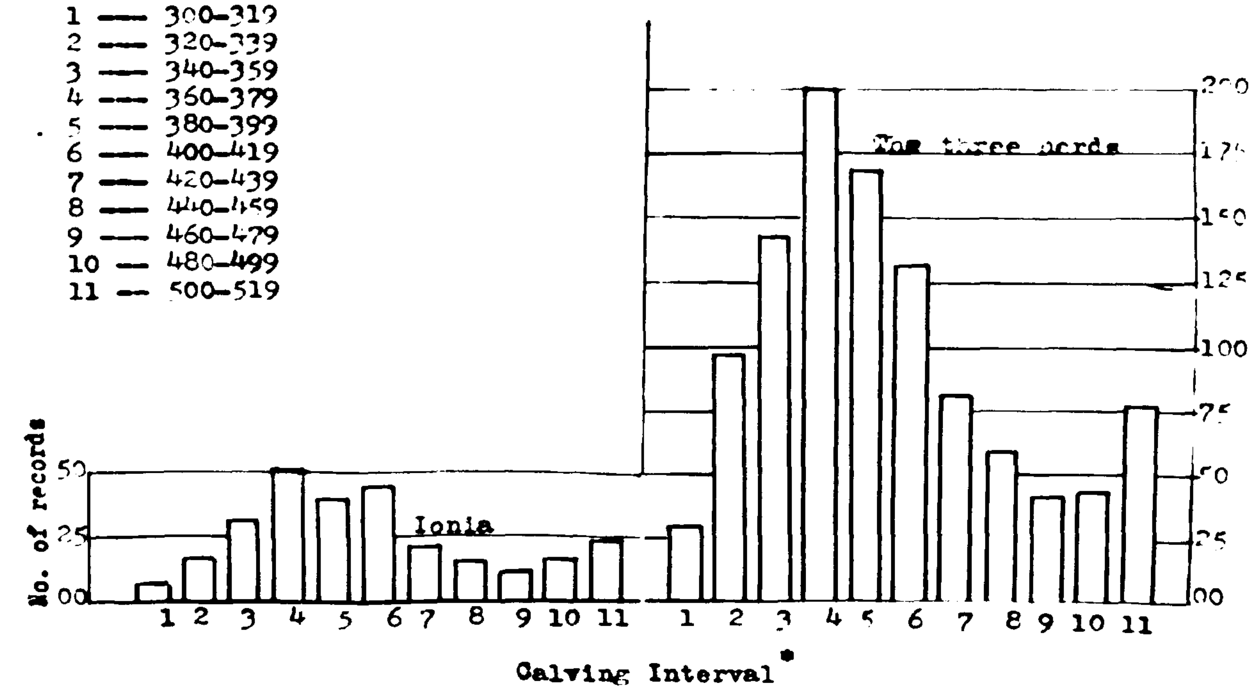


Table 9b.- Distribution of Records and the Average Butterfat Production for Different Calving Intervals of Next Lactation

Interval	Traverse No. of records	Traverse Av.	Reformatory No. of records	Reformatory Av.	Ionia No. of records	Ionia Av.	Total No. of records	Total Av.
300-319	16	415	7	470	6	507	29	447
320-339	68	415	12	484	16	523	96	440
340-359	95	438	17	478	31	553	143	468
360-379	93	434	56	503	51	540	200	480
380-399	68	454	61	494	40	564	169	494
400-419	41	444	45	480	45	606	131	512
420-439	42	455	19	503	21	580	82	498
440-459	23	441	20	523	15	553	58	498
460-479	20	397	10	513	12	567	42	473
480-499	16	462	11	457	17	572	44	503
500-519	22	466	31	520	24	591	77	527

As far as the distribution of the records was concerned, the highest frequency was in the interval of 360-379 days for both Tables 9a and 9b, except for the Traverse City herd which had the highest frequency in the interval of 340-359 days. Adding the three herds resulted in the highest concentration of records falling in the interval of 360-379 days, which is about one full year. By looking at the average butterfat production of each interval, we find a general trend for the longer the interval the higher the production, although there are some sudden drops in the different intervals of each herd. Both Tables 9a and 9b show a consistant increase in production from the 300-319 day interval to the 340-359 day interval for each herd and the total, but the Reformatory herd and the total of the three herds in Table 9b have some difference in order. This gives firm evidence that cows having calves with less than a year interval tend to produce less. The Traverse City herd had about 35% of its records falling in the interval from 300 to 359 days, while the Reformatory herd and Ionia herd have only 15% and 19% of their records falling in that interval. This may be one factor which pulled down the production of the Traverse City herd.

Table 9c - Analysis of Variance of Effect of Calving Interval on Butterfat Production of Same Lactation

Herd	Source of variance	Degree of freedom	Sum of squares	Mean squares	F
Traverse	Total	504	2452818	28819	
	Between interval	10	288188	28819	6.50**
	Within interval	494	2164630	4382	
Reformatory	Total	287	2099516		
	Between interval	10	202078	20208	2.95**
	Within interval	277	1897438	6850	
Ionia	Total	277	2157245		
	Between interval	10	976474	97647	22.08**
	Within interval	267	1180771	4411	

Table 9d - Analysis of Variance of Effect of Calving Interval on Butterfat Production of the Following Lactation

Herd	Source of variance	Degree of freedom	Sum of squares	Mean squares	F
Traverse	Total	503	2588881		
	Between Interval	10	152491	15249	3.08**
	Within Interval	493	2436390	4942	
Reformatory	Total	288	2479784		
	Between Interval	10	53174	5317	.61
	Within Interval	278	2426110	8727	
Ionia	Total	277	2699844		
	Between Interval	10	189344	18933	2.01*
	Within Interval	267	2510510	9402	

Table 9e - Analysis of Variance of Effect of Calving Interval on Butterfat Production for the Three Herds

Lactation	Source of variance	Degree of freedom	Sum of squares	Mean squares	F
In the same interval	Total	1070	9314749		
	Between herds	2	160517		
	Within herds	1068	9154232	8571	
	Between interval	30	1466740	48891	6.60**
	Within interval	1038	7687492	7406	
Following the last interval	Total	1070	10684297		
	Between herds	2	2915783		
	Within herds	1068	7768509	7273	
	Between interval	30	394999	13167	1.85**
	Within interval	1038	7373510	7103	

Calculations of portion of intra-herd variance due to calving interval effect on the butterfat production of the three herds,

For lactation following the last interval,

$$\sigma^2 + K_o\sigma^2(\text{interval}) = 13166.6, \text{ where } K_o = 31.93 \text{ according to formula (6)}$$

$$= 7103.6$$

$$\sigma^2(\text{interval}) = 189.88$$

$$\frac{\sigma^2(\text{interval})}{\sigma^2 + \sigma^2(\text{interval})} = \frac{189.88}{7293.48} = 2.6\%$$

For lactation in the same calving interval,

$$\sigma^2 + K_o\sigma^2(\text{interval}) = 48891, \quad \text{where } K_o = 31.92$$

$$\sigma^2 = 7406$$

$$\sigma^2(\text{interval}) = 1299.65$$

$$\frac{\sigma^2(\text{interval})}{\sigma^2 + \sigma^2(\text{interval})} = \frac{1299.65}{8705.65} = 14.93\%$$

One purpose of Tables 9d and 9e was to find whether the effect of the calving interval on butterfat fat production was statistically significant. The results shown in the three tables above are highly significant for both the calving interval effect on the same and next lactation of each of the three herds and their total, although the Reformatory herd for the effect of calving interval on the next lactation turns out non-significant. Since the results calculated from the three herds show the effect to be highly significant, the only explanation of the non-significance of the latter is the small sample size. As the size of the sample increases, the F value may be expected to be significant.

The other purpose of the analysis in the foregoing tables was to find what portion of the total variance was due to calving interval effect and to compare the calving interval effect on the same lactation and next lactation in an attempt to discover which was more important. The results indicate that the former is 14.9% and the latter is 2.6%. The calving interval apparently affected the same lactation five times more than it affected the next lactation. Incidentally, this will give support for the regulation of the Holstein-Friesian breed association which requires a certain calf-carrying period for the 10 month production record registration (Advanced Registry).

Table 9f gives the levels of significant differences between averages of production of each interval, except for the effect of the calving interval on the next lactation for the Reformatory herd which was left out because of the non-significant F value. These values can serve as a base for comparing the butterfat production of any two different calving intervals.

2. Regression of Butterfat Production on Calving Interval

Since most of the averages of butterfat production for different intervals are significantly different from one

Table 9f - 5% Significant Level of Difference for the Averages of Production of Different Calving Intervals

Herd	Effect of calving interval on the same lactation			Effect of calving interval on the next lactation		
	$t_{.05}$	σ	$(\sigma\sqrt{\frac{1}{n_1}+\frac{1}{n_2}})t_{.05}$	$t_{.05}$	σ	$(\sigma\sqrt{\frac{1}{n_1}+\frac{1}{n_2}})t_{.05}$
Traverse	1.966	66.19	8.22	1.966	7029	8.73
Ionia	1.973	66.49	11.28	1.973	96.96	13.89
Reformatory	1.973	82.76	13.72	1.973	93.40	____
Total	1.962	86.03	7.34	1.962	84.27	7.19

In the above table,

$\sigma = \sqrt{\text{mean square in within term}}$

$n_1 = n_2 =$ degree of freedom in within term of Tables 9c and 9e.

another and increases in length of interval were associated with increases in production according to Table 9a and Table 9b, a regression coefficient of production on length of calving interval was computed. For the Reformatory herd, even though the effect of calving interval on the next lactation was non-significant, there was a trend for longer intervals to result in higher production. Therefore there was no reason to omit the calculation of regression for this herd. Because this herd was needed for the calculation of the average regression of the three herds, the computation of regression of butterfat production on previous calving interval for this herd was still carried out. This computation can also serve as a double check of the non-significant result as in Table 9f.

Calculation of Linear Regression

The average production for each interval was plotted (Fig. 8 and 9). The plot shows some likelihood of linearity.

The formula used for calculating the regression coefficient for each herd is the route equation according to formula (4) on Page 32. By using the covariance method the combined regression coefficient for the three herds was obtained and herd difference effect was eliminated. X, the independent variable, represented the interval in days, Y, the dependent variable, represented the butterfat production. To save tedious calculations, the average of each class for the calving interval was used for all the X values of that class. The calculation of regression coefficient, b, of butterfat production on same calving interval of Traverse City herd is illustrated as follows, and omitted for the other herds.

$$\Sigma X = 195650$$

$$\Sigma X^2 = 1537600 + 7405200 + \ldots\ldots + 57222000 = 77113700$$

$$\frac{(\Sigma X)^2}{n} = \frac{38278922500}{505} = 75799846$$

$$\Sigma Y = 103690100$$

$$\Sigma XY = 880099120$$

$$\frac{\Sigma X \Sigma Y}{n} = 87600060$$

$$b = \frac{88099120 - 87600060}{77113700 - 75799846} = .38$$

Table 9g - Calculation of the Combined Regression Coefficient for the Three Herds

Source	Degree of freedom	Sum of squares x^2	Sum of squares xy	Sum of squares y^2
Total	1070	2979899	1463534	9314749
Between herds	2	109135	458461	2605570
Within herds	1068	2870764	1005073	6709179

Table 9h - Observed Regression Coefficient of Butterfat Production on Calving Interval

Herd	Regression of butterfat production on the same calving interval b_1	Regression of butterfat production on the previous calving interval b_2
Traverse	.38	.16
Reformatory	.36	.14
Ionia	.29	.31
Total	.35	.20

Table 9h indicates b_1 is larger than b_2 for each herd and their total, except in the Ionia herd where b_2 is little larger than b_1. The quantity b_1 has the largest value for the Traverse City herd, and b_2 has the lowest value in the Reformatory herd. For the total, b_1 is about 1.76 times larger than b_2. These results agree with the above analysis of variance. In these herds each additional day in length of calving interval resulted, on the average, in an increase of approximately one-third of a pound of butterfat for that lactation and one-fifth of a pound for the next lactation.

Table 9i indicates all the regressions were highly significant except for the regression of the succeeding lactation of the Reformatory herd, which is non-significant. The results also agree with the foregoing analysis.

Table 91 - Test of Significance of Regression of Butterfat Production on Calving Interval

	Herd	Source	Degree of freedom	Sum of squares	Mean squares	F
On same calving interval	Traverse	Total	504	2452818		
		Due to regression	1	189565	189565	42.13**
		Residual	503	2263253	4499	
	Reformatory	Total	287	2099516		
		Due to regression	1	98708	98708	14.11**
		Residual	286	2000808	6996	
	Ionia	Total	277	2157245		
		Due to regression	1	67586	67586	8.93**
		Residual	276	2089659	7571	
	Three herds	Total	1071	9314749		
		Due to regression	1	351882	351882	41.97**
		Residual	1069	2089659	8586	
On previous calving interval	Traverse	Total	503	2588881		
		Due to regression	1	35292	35292	6.94**
		Residual	502	2553589	5087	
	Reformatory	Total	288	2479784		
		Due to regression	1	15436	15436	1.60
		Residual	287	2464348	8586	
	Ionia	Total	277	2699844		
		Due to regression	1	77243	77243	8.13**
		Residual	276	2622601	9502	
	Three herds	Total	1070	10684297		
		Due to regression	1	113623	113623	11.49**
		Residual	1069	10570674	9888	

Test of Linearity

Quite a few investigators who studied the effect of the dry period or calving interval on milk or butterfat production concluded that the calving interval had no further effect when it exceeded a year in length. Moreover, some statistical analysis showed a slight decrease in production if the calving interval was too long. From the physiological point of view, there should not be too much effect from exceedingly long calving intervals. For these reasons, the writer was quite doubtful whether the relationship between the calving interval and butterfat production was linear. A test of linearity has been developed. It is based on the method illustrated by Lindquist (1940). The results were significant for the effect of calving interval on butterfat production both for the same or the succeeding lactation period.

Table 9j - Test of Linearity of Regression of Butterfat Production on Calving Interval of Same Lactation

	Degree of freedom	Sum of squares	Mean squares
Between intervals	10	1466740	
Within interval	1058	7687492	7266

Due to linear regression $= \frac{(\Sigma xy)^2}{\Sigma x^2} = \frac{(1005073)^2}{2870764} = 351882$

Table 9j - Continued

	Degree of freedom	Sum of squares	Mean squares
Between intervals	10	14466740	
Due to linear regression	1	351882	
Due to departure from linearity	9	114858	123873

$$F = \frac{123873}{7266} = 17.06^{*} \text{ for 9 and 1058 degree of freedom}$$

Table 9k - Test of Linearity of Regression of Butter-fat Production on Calving Interval of Previous Lactation

	Degree of freedom	Sum of squares	Mean squares
Between intervals	10	394999	
Within intervals	1058	7373510	7103

$$\text{Due to regression} = \frac{(\Sigma xy)^2}{\Sigma x^2} = \frac{(571404)^2}{2873551} = 113623$$

	Degree of freedom	Sum of squares	Mean squares
Between intervals	10	394999	
Due to Linear regression	1	113623	
Due to departure from linearity	9	281376	31264

$$F = \frac{31264}{7103} = 4.40^{**} \text{ for 9 and 1058 degree of freedom}$$

Calculation of Non-linear Regression

The results of testing of linearity in Tables 9j and 9k show that the regression of butterfat production on calving interval departed significantly from linearity in both cases. Therefore, the data were re-examined and different methods of plotting were tried. The plots made on semi-log paper were closer to a parabola than either non-logarithm plotting or double logarithm plotting. The plotting is shown on Fig. 6 and Fig. 7. Based on this plotting, a curvalinear equation was set up as follows:

$$y = ab^{cx} + dx^2 \qquad (I)$$

$$\log y = \log a + (cx - dx^2)\log b$$

$$\log y = \log a + c \log bx + d \log bx^2$$

$$\log y = A + Bx + Cx^2$$

$$y = 10^{A+Bx+Cx^2} \qquad (II)$$

The normal equations are formed as follows,

$$NA + B\Sigma x + C\Sigma x^2 = \log y$$

$$\Sigma xA + B\Sigma x^2 + C\Sigma x^3 = \Sigma x \log y$$

$$\Sigma x^2 A + B\Sigma x^3 + C\Sigma x^4 = \Sigma x^2 \log y$$

Based on the normal equations, the regression equations for butterfat production on the same calving interval were

(1)
$$y = 10^{2.52525} + .00121x + .0000027x^2 \qquad (III)$$

(2)
$$y = 10^{2.64121} + .00079x + .0000023x^2 \qquad (IV)$$

---

(1) The calculations are listed below:

$$1071A + 94320B + 1128640\ C = 2884.22748$$

$$94320A + 11286400B + 1618272000C = 255306.18$$

$$11286400A + 1618272000B + 259686400000C = 30629285.75$$

Simplify the above equations as follows,

$$A + 88.067226B + 10538.188609C = 2.693023 \qquad (1)$$

$$A + 119.686103B + 17157.251903C = 2.706809 \qquad (2)$$

$$A + 143.382478B + 23008.739331C = 2.713822 \qquad (3)$$

(2) - (1)

$$31.618882B + 6619.063299C = .013786 \qquad (4)$$

(3) - (2)

$$23.696370B + 5851.537423C = .007013 \quad (5)$$

Simplify equations (4) and (5),

$$B + 209.338942C = .000436 \quad (6)$$

$$B + 246.938135C = .000296 \quad (7)$$

(7) - (6)

$$37.599193C = -.000140$$

$$C = -.00000372$$

Substitute C in (6),

$$B - .00077874 = .000436$$

$$B = .0012147$$

Substitute C in (7)

$$B - .00091861 = .000296$$

$$B = .0012146$$

Substitute B and C in (1),

$$A + .1069752 - .0392021 = 2.693023$$

$$A = 2.62525$$

Substitute B and C in (2),

$$A + .1453927 - .0638825 = 2.706809$$

$$A = 2.62525$$

Substitute B and C in (3)

$$A + .1741667 - .0855927 = 2.713822$$

$$A = 2.62525$$

$$\therefore y = 10^{2.62525 - .00121x - .0000037x^2}$$

(2)

The calculations are listed below:

$$1071A + 94260B + 11277200C = 2877.22683$$

$$94260A + 11277200B + 1616136000C = 254156.41040$$

$$11277200A + 1616136000B + 259195040000C = 30466.70400$$

Simplify the above equations as follows,

$$A + 88.01120B + 10529.59850C = 2.68649 \quad (1)$$

$$A + 119.63930B + 17145.51241C = 2.69633 \quad (2)$$

$$A + 143.31004B + 22983.98893C = 2.70160 \quad (3)$$

(2) - (1)

$$31.62810B + 6615.91391C = .00984 \quad (4)$$

(3) - (2)

$$23.67074B + 5838.47652C = .00527 \quad (5)$$

Reduce equations (4) and (5),

$$B + 209.17835C = .000311 \quad (6)$$

$$B + 246.65374C = .000223 \quad (7)$$

(7) - (6)

$$37.47539C = -.000088$$

$$C = -.0000023$$

Substitute C in (6),

$$B - .00048111 = .000311$$

$$B = .00079211$$

Substitute C in (7),

$$B - .00056730 = .000223$$

$$B = .0007903$$

Substitute B and C in (1),

$$A + .0695[illegible]8480 - .02421807655 = 2.68649$$

$$A = 2.64121$$

Substitute B and C in (2),

$$A + .0945180470 - .0394346785 = 2.69633$$

$$A = 2.64121$$

Substitute B and C in (3),

$$A + .1132149316 - .0528317745 = 2.70160$$

$$A = 2.64121$$

$$\therefore y = 10^{2.64121 + .00079x + .0000023x^2}$$

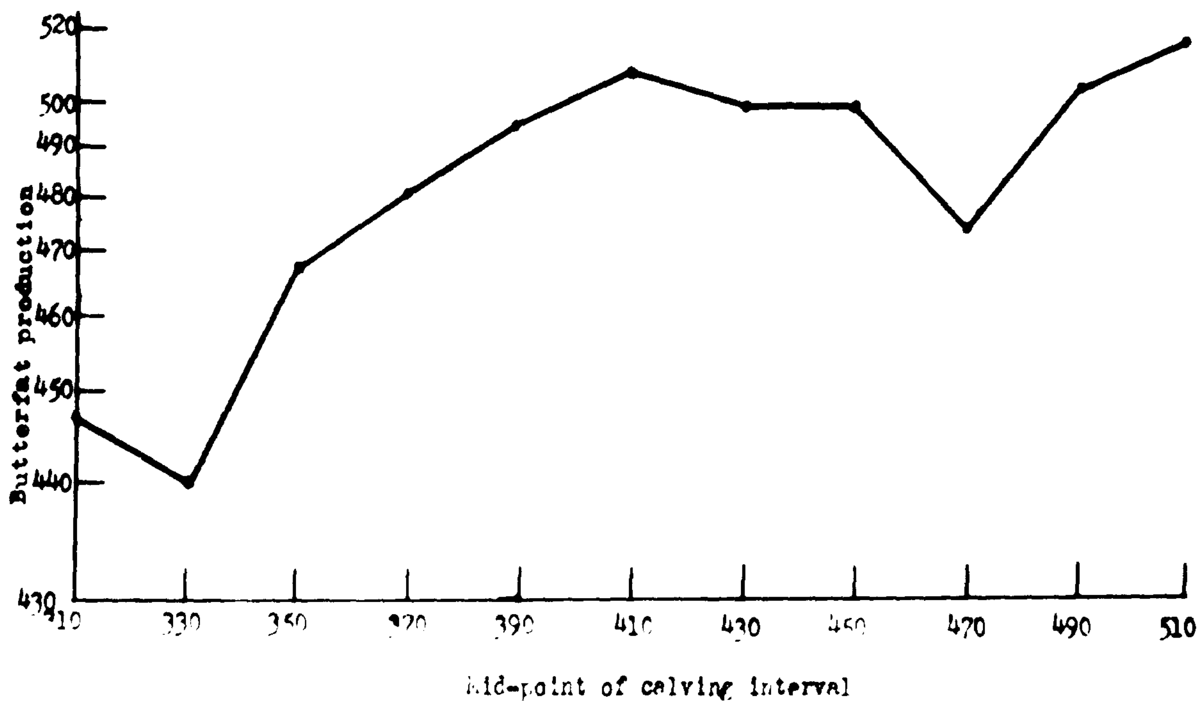


Figure 6 - Semi-logarithmic Plotting of Butterfat Production Against Same Calving Interval

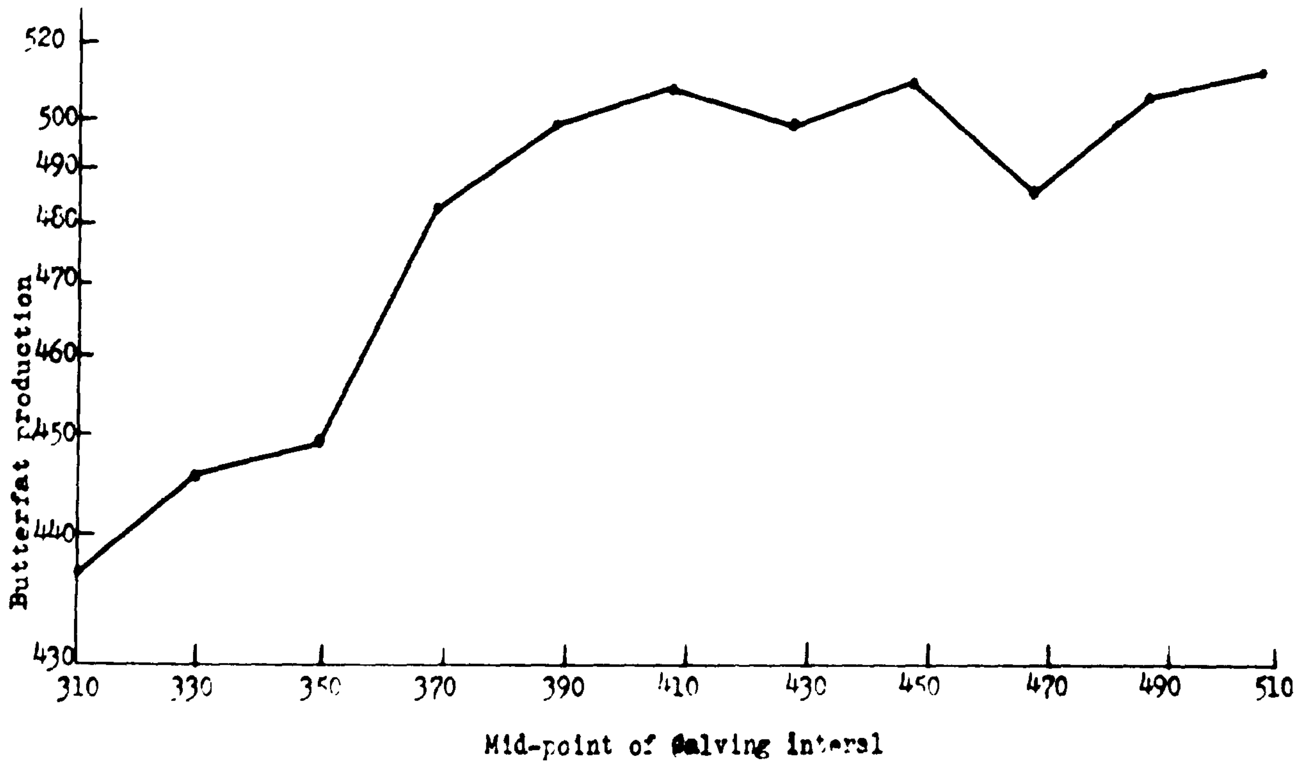


Figure 7 - Semi-logarithm Plotting of Butterfat Production Against Previous Calving Interval

According to equations (3) and (4), the predicted butterfat production y for different intervals was worked out and entered in Table 9L.

Table 9L - Calculated Values of Butterfat Production for Different Intervals

Interval	Butterfat Production of same lactation	of next lactation
300-319	422.0	437.7
320-339	444.0	453.0
340-359	465.0	466.8
360-379	483.6	479.0
380-399	499.3	489.4
400-419	512.0	497.9
420-439	521.4	504.5
440-459	527.3	509.0
460-479	529.8	511.4
480-499	528.6	511.6
500-519	523.9	509.6

Two graphs were constructed according to the values of the observed values and calculated values. For the purpose of comparison, the lines for linear regression were also added on the same graphs. It is clearly evident that the curvi-linear regression of butterfat production on the calving interval was much closer to the observed values than the linear regression. Therefore, the comparison of the error of estimate is unnecessary. We can safely conclude that the curvi-linear regression gave the best estimates.

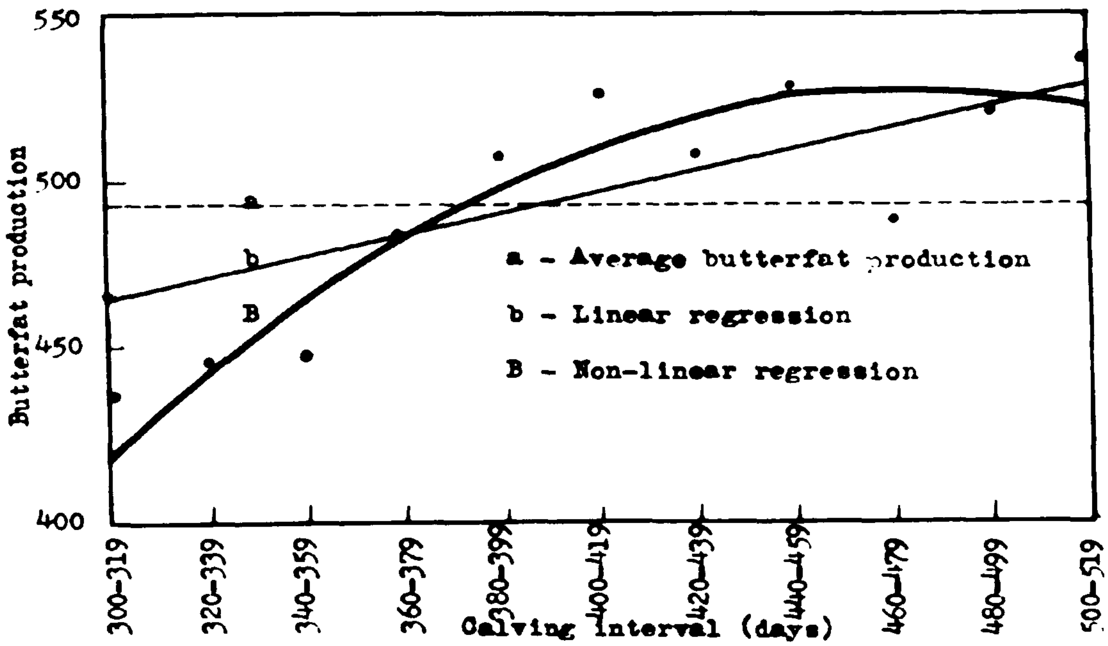


Figure 8 - Average Observed Butterfat Production Against Same Calving Interval and Their Linear and Non-linear Regression Lines

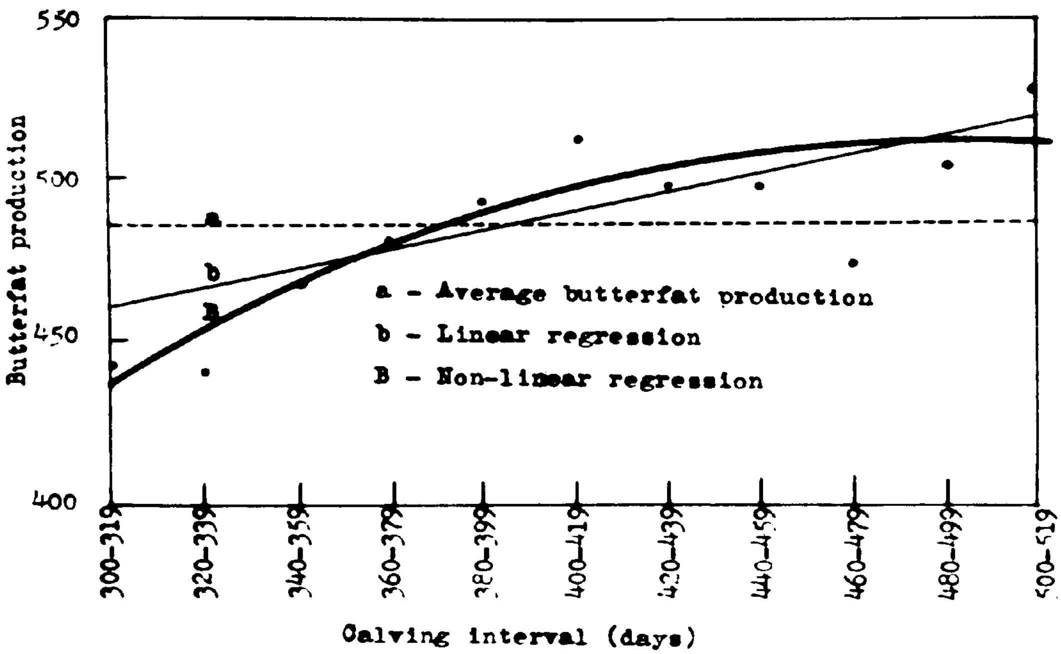


Figure 9 - Average Observed Butterfat Production Against Previous Calving Interval and Their Linear and Non-linear Regression Lines

Discussion

Herd Comparison

In this data herd differences and cow differences accounted for less of the variation in production than was reported by Plum (1935). This was expected since the herd differences and cow differences are due both to genetic differences of the cows and differences in environment between herds. Homogeneity of either the environment or the genetic constitution of the individuals can reduce the variation. Plum's data covered a total of 5860 records of which 56 per cent were records from grade cows and included 119 herds which probably were distributed over most of the state of Iowa. The average production of each of the three herds included in this study was above the breed average, and all animals were registered Holsteins. Moreover, quite a large portion of the animals were slightly related. Consequently, their genetic relationship was closer than the cows included in Plum's data. The second reason these results were expected was that more geographical differences and more herds were involved in his study which very likely made the environment of the cows in different herds more variable.

Since the heritability value obtained from this data was .17, genetic differences between the three herds acoounted for .26 x .17 = 4% of the variation and the remaining 22% was due to environmental differences. This assumes that the portion of inter-herd variance due to genetic differences between herds is the same as the portion of intra-herd variance due to genetic differences between cows.

Comparing the average butterfat production of the three herds, the Ionia herd was 8 pounds above the Reformatory herd, the Reformatory herd was 49 pounds above the Traverse City herd. The Ionia herd was 57 pounds above the Traverse City herd. Based on the assumption made above, and using .17 as the heritability value, the genetic difference would be 1.3 pounds for the Ionia herd over the Reformatory herd, 8.4 pounds for the Reformatory over the Traverse City herd, and 9.8 for the Ionia over the Traverse City herd. The other differences between the two herds were due to environment.

Since the averages for each herd are based on samples taken from the beginning of tests for that herd up to 1946, the above comparisons serve only as approximate differences for that period. The main purpose here is to point out that the herd differences were, for the most part, due to environment. For comparing the present situation of the three herds, it, of course, would be better to use the recent herd averages for a comparative basis.

Repeatability

The repeatability value obtained from these data was .34. Compared to .43 reported by Lush (1941) and a .40

by Flum (1935), it appears a little low. However, it does not differ a great deal from their values. This lower estimate is mainly due to the low values of the Traverse City and the Reformatory herds. This was likely due to the relatively more homogeneous population and environment found in those herds. Their lower values pull down the higher ones of the Ionia herd

Since repeatability is a measure of the consistency of a cow's production, it is not affected by the genetic constitution of the cow. In other words, whether cows have more homozygous or heterozygous pairs of genes, whether they are purebred, crossbred, grade or scrub cows has no effect on the value of repeatability. It is almost entirely determined by environmental effects on the cow during and shortly before the period during which she makes the record. Although herdsmen are always trying to improve the environment as much as possible, many natural factors are difficult or impossible to control and keep constant. Hence, repeatability will never be exceedingly high.

Other influences which might cause differences of repeatability besides uncontrollable natural conditions are: (1) the yearly improvement of management, (2) yearly change of management, and (3) yearly decrease in desirability of management. When one considers the economic conditions and the improvement of dairy husbandry in this country, the third possibility can be eliminated. Further study of the yearly herd averages leads one to believe that there were no very obvious trends to indicate a gradual increase or decrease in production for the Traverse City and Reformatory herds. Therefore, it was condluded that the higher repeatability value for the Ionia herd was that the individual cows composing this herd were kept under more constant environment from year to year than cows in the other two.

The repeatability value of the Ionia herd is also higher than the values computed by Lush and Plum, which are based on more herds and cows. If their computed values are assumed close to the average value for all herds, then the higher value for the Ionia herd indicates that the management of this herd was more constant than the average herd management, and that the cows are probably kept in a healthier, better condition than the individuals of most herds with less disease and undetectable disturbances which can increase the variation in records of the same cow.

The repeatability estimate of .34 is a measure of the real differences in ability of the cows in the three herds. Subtracting the heritability value, .17 from the repeatability value, 34, leaves a value of .17. This 17 per cent, according to Lush (1941), is due to three possible causes:

(1) Permanent differences between the dams caused by environmental peculiarities;

(2) Dominance exists;

(3) Genes have the effects of complementary, inhibitory or other epistatic interactions with other genes.

Heritability

The resemblance between parents and offspring is generally most useful in estimating heritability because it does not include dominance deviations and includes a smaller portion of interaction deviations present. Paternal half-sib resemblance is often useful, but the correlation is multiplied by four instead of by two. Therefore, the sampling errors are more serious in this resemblance than in the parent-offspring resemblance. Generally, the heritability computed by the paternal half-sib method should be higher than that computed by the correlation or regression of offspring on dam because the former includes more interactions and dominance effects. However, for this set of data, it is lower than the other two and has a higher standard error. For this reason it is less reliable as an estimate of heritability. The correlation between daughter and dam and regression of daughter on dam methods would be interchangeable for estimating heritability if the dams were an unselected group. Some selection usually has been practiced among the parents in most herds, although the question may well be raised whether or not that selection has often been as intense as is popularly supposed. Since the selection of the dams will tend to lower the correlation coefficient according to Lush (1940), but will not bias systematically the regression of offspring on dam, for this set of data the regression of offspring on dam was considered the best basis for estimating heritability.

The heritability value found in this study for single lactation records was .17. Incidentally, this value is the same as the .174 recently computed by Lush. This is a little less than has been found in previous studies which have more often given values of around .20 to .30. Lush (1942) reported the 5% fiducial limits for his value of .174 were .03 and .31. Therefore, it is very probable that most of the difference between the values reported in recent publications are the result of sampling variations.

Lush (1941) has pointed out that heritability estimates based on the intra-sire regression method, include only one-fourth of the two epistatic gene interactions, one-eighth of the three gene interactions, one-sixteenth of the four gene interactions, ad infinitum. Thus, the 17 per cent of variance accounted for by heritability includes not only the truly additive effects of genes, but includes also about one-half of the effects which depended on the interactions of different numbers of sets of genes. That such interactions exist cannot be denied in these data, since one-half of the two gene interactions, three-fourths of the three gene interactions, seven-eighths of the four gene interactions ad infinitum, are included with the dominance deviations and the permanent environmental effects, which all together constitute less than .34 - .17 = 17% of the variance for single records or .17/.34 = 50% of the variance in permanent abilities.

The rate at which the average production of a herd can be increased by culling low producing females and replacing them with the better daughters can be estimated from the expected regression of daughters toward the herd average. The regression coefficient is about .085 in these data - a little higher in some of the other studies. The annual turnover in dairy herds is around 25 to 30 per cent of the average number of cows in the herd during the year. Among the cows leaving the herd, at least one-third are due to old age, deaths, sterility, chronic disease, and sales which are not actually low producers. If one-eighth of the cows which have the lowest records will be discarded, the heifer calves sired by bulls with the same level of transmitting ability would average,

* for Traverse City herd, .24(73)(.17) = 3.0

* for Reformatory herd, .24(99)(.17) = 4.0

* for Ionia herd, .24(124)(.17) = 5.0

more pounds of butterfat per year when they come into production than the heifer calves from the preceding year would average. Selection of the sire can raise the selection differential. However, in culling the cows and young heifers it is very hard to reach the ideal, and culling only the cows or heifers that are lowest in production, or pro-

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* According to Lush (1947),
Butterfat increase = (selection differential)(standard deviation) (heritability)
For one-eighth portion culling, e. g. 87.5% of animals saved, selection differential equals to .24.

ducing ability will accomplish it. Because of this, the average increase per year will be even lower than the above computed figures.

Effect of Month of Calving on Butterfat Production

The results of the effect of month of calving on butterfat production in this study coincide roughly with most of the findings by other workers. Since there were geographical differences for different herds or subpopulations, we cannot expect all to have the same effects. However, a peculiarity of the results of this study was that, besides the high production peak in March, there was another peak in September which ranked next to March and was significantly higher than any other month. A comparison was made with the results of two recent investigations, and is shown in Fig. 10.

Since butterfat production is closely related to milk production, it would not be unreasonable to compare the month of calving effects on the butterfat production with its affect on milk yield, which was given by Woodward for 12 states and Frick for Connecticut.

Figure 10 shows production on per cent basis for each of the averages for different months of calving. The relatively small influence of month of calving on milk yield found by Woodward may have been due to his combining records of different states. If climatic differences should cause the association of month of calving with milk yields to vary among the different states, a combination of records from several states would tend to minimize fluctuation in yields.

Although this study is fairly close to the results of the Connecticut data except in July, both the Woodward study and the results from Connecticut data have shown that July is the least favorable month. This gives more evidence that the small jump in July in the present study must be due to particular environmental effects in the Reformatory herd which apparently compensated for the usual adverse conditions for cows calving in that month.

If this set of data is considered as a fairly random sample, then the next thing is to seek the factors involved in causing this effect. Obviously, the climate which affects the animal directly and indirectly through the crops are the most important, although other factors may be involved. First, for the indirect effect, it is known that there is a dry season usually during July and August in Michigan, and the pastures during this time are less prosperous than before and during the later growing months. Cows freshening from the middle of May to the middle of June have their high producing stage exactly in the hot, dry season. Most farmers know that this season decreases the cow's milk flow. Some herds may have some kind of temporary pasture during this period, but generally it cannot be managed well enough to completely make up the gap. Second, it has

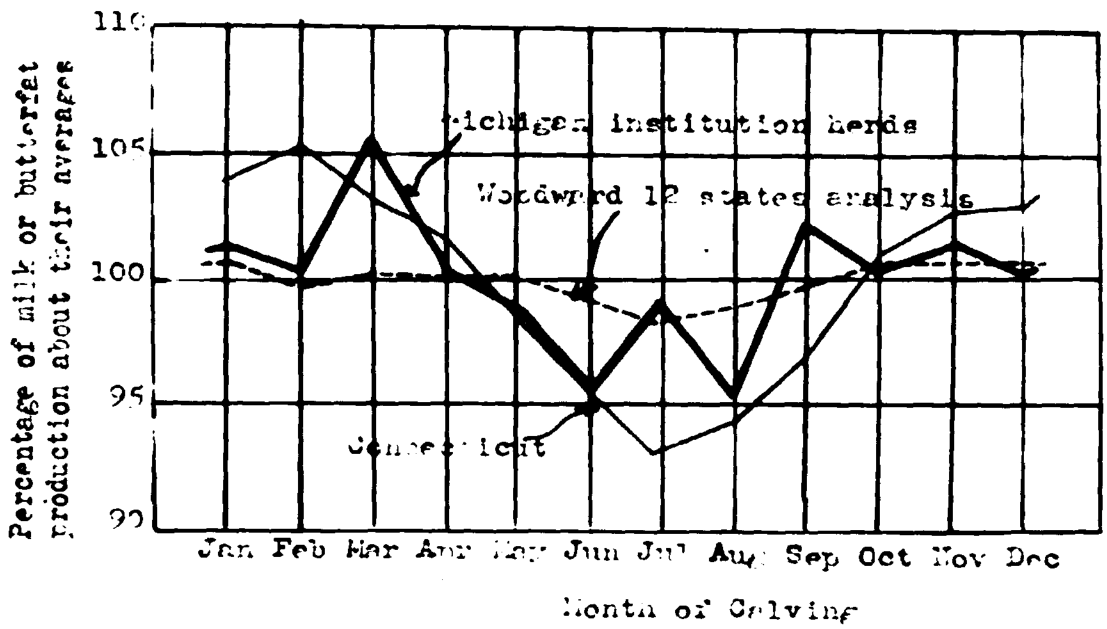

Figure 10 - A comparison of Month of Calving Affects on Butterfat Production or Milk Production for Three Different Studies

been established that the thyroid activity is related to the temperature. High temperature decreases the thyroid function, and hence reduces the metabolic rate. In addition, the fact that thyroxin or thyroprotein administration stimulates the milk secretion has been reported by Reineke and Turner (1944). Therefore, this drop in butterfat production during the summer could have been due to the functional decrease of the thyroid gland. The interpretation for the small drop during the winter time may be that the lack of pasture that caused the lower production could not be balanced by the increase of the thyroid activity due to low temperature. Whether there is a relationship between light and milk secretion or butterfat production has not yet been determined, although light does play a role in the reproduction cycle of quite a few species. To determine the relative importance of these factors, there must be a specially designed experiment.

A X^2 test has been made to test whether the distribution of freshening in each month for the three herds combined is about equal. The result was that X^2 equals 25.05. For 11 degrees of freedom, it was highly significant. When one inspects the records of each month, however, the distribution does not follow the pattern of the production level at all; that is, the number of cows freshening in the higher production months should be greater and the number freshening in the lower production months should be less.

The reason for this unreasonable distribution of freshening in each month may be, (1) farmers' ignorance of the effect and no control of the reproduction, (2) an increase in price per pound of butterfat can balance the decreased production due to freshening in the undesirable season.

The distribution of records in each calving interval shows the most records in the class from 360-379 days. Since the classification of records for each month is made by pooling all the records of cows in the month they are freshening, records of the same cow may appear in a certain month more times than other months. For this reason the month variation may include a portion of the cow's variation. In other words, this may cause a portion of variation due to month of freshening. However, its contribution should not be very great; hence can be considered unimportant.

Effect of Calving Interval on Butterfat Production

What is the optimum calving interval? In other words, how long should the calving interval be in order to obtain the maximum life time production? Different authors disagree. Some claim one year and others claim more than one year. Since different herds have different circumstances and different levels of management, a certain calving interval may be suitable for one herd, but too long or too short for another.

There has been no satisfactory design which can be used to determine optimum calving interval for the maximum life time production. As cows with short intervals will have more lactations within a certain period, their single records may be lower but their total production may be higher than the cows with longer calving intervals and with higher single records. However, these cows may have a shorter life period than the cows with longer intervals. On the other hand, even though cows with longer calving intervals may live a longer time they will have less lactations and their life time production may be less than that of the cows with shorter calving intervals. Probably either extreme is not correct for commercial herds.

In this paper, there is no way to determine the exactly right calving interval either, but it was found that the increase in production was more than 10 pounds for every 20 days increase of interval up to the 380-390 day interval for the same lactation and 400-419 day for the next lactation. From 419 days on the increase is less than 10 pounds and at a diminishing rate, and finally reaches the peak at 460-479 day interval for the same lactation and 480-499 days of interval for the next lactation. Then, production decreases very slowly with increasing length of interval. Therefore, 380-399 days was arbitrarily set as the optimum interval for this data, although, there is still good reason to take the 360-379 days or about one year as the optimum, depending on the type of management.

Since effects of calving interval occur up to 400 days with a gradual leveling off, the larger interval (400-419 day) was tentatively set as the standard. Using the calculated values of Table 9L, a set of correction factors for calving interval has been computed and listed in the following table:

Table 10a - Conversion Factors for Calving Interval

	Factors(1)	
Interval	For same lactation	For next lactation
300-319	1.21	1.14
320-339	1.15	1.10
340-359	1.10	1.07
360-379	1.05	1.03
380-399	1.02	1.02
400-419	1.00	1.00
420-439	.98	.98
440-459	.97	.98
460-479	.97	.97
480-499	.97	.97
500-529	.96	.96

(1) Factors = $\frac{\text{predicted butterfat production of 400-419 int.}}{\text{predicted butterfat production of x days int.}}$

Comparing this table with the conversion factors for age, times of milking and length of lactation period, as listed in Tables 2a and 2b, these factors appear of the same importance as the factors for age and times of milking, and more importance than the factors for length of lactation.

Summary and Conclusion

An analysis of variance of butterfat production records based on records converted to a 305 day lactation, twice a day milking and mature equivalent basis, of the Traverse City, the Ionia Reformatory and the Ionia Hospital herds of Michigan has been carried out. Due to the special requirements for certain kinds of analyses and the incompleteness of some records, the same set of records could not be used for each analysis. There were 473 daughter-dam pairs for the heritability analysis, 2299 records for the herd comparison and repeatability analysis, 1817 records for month and year effect on butterfat production, and 1071 records for the analysis of calving interval effect on butterfat production.

The pooled estimate of heritability of lifetime butterfat production for the three herds was .28 by half-sib correlation method, .27 by intra-sire correlation of dam and daughter method, and .31 by intra-sire regression of daughter on dam method. All are based on life time averages. The last one, .31, is taken as the most accurate value. Computed to a single record base, the latter is equal to a heritability value for single records of .17.

The herd differences accounted for about 26 per cent of the total variance and cow differences (intra-herd) accounted for 34 per cent. These variances, of course, include both genetic differences and differences caused by environmental effects. The portion of variance accounted for by intra-herd record differences was about 66 per cent. The repeatability estimate was .34 on an intra-herd base.

Yearly differences accounted for about 5 per cent of the variation in butterfat production. Though small, this value is statistically significant. No yearly trend was found.

Month of calving accounted for about 2 per cent of the total variance. It was a significant effect. There was a rather definite pattern for the effect of different months of calving on butterfat production. The high peak was in March; this dropped gradually in the summer, increased in September, and fell again after that until January.

The relationship of calving interval and butterfat production was non-linear. The effect of calving interval on butterfat production accounted for 15 per cent of the variance for the same lactation, and 3 per cent for the next lactation. Both were significant. 400 to 419 days seemed to be the most favorable interval as far as a single record was concerned.

Table 11a - Percentage of Total Observed Variance Accounted for Various Genetic and Environmental Factors

Variance accounted for		Percentage
Herd differences		26
Genetic differences between herds	4	
Environmental differences between herds	22	
Differences within herds		74
Cow differences	25	
Record differences (within cow variance)	49	
		100
Environmental effects		66
Year of calving	4	
Month of calving	2	
Preceding calving interval	3	
Present calving interval	15	
Others	42	
Genetic		34
Additively genetic	17	
Dominance and interactions	17	
		100

The portion of variance accounted for by dominance and interactions in the foregoing table includes a small portion due to permanent environmental peculiarities, and also interaction between heredity and environment. Therefore, the portion accounted for by genetic effect actually should be less than 34 per cent and for the environmental effects should be a little more than 66 per cent.

Since the records used for each kind of analysis are not exactly the same, and because an allowance must be made for sampling error, the figures listed in Table 11a can only be considered as approximate estimates.

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