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GENETIC FACTORS AFFECTING MILK PRODUCTION IN A SELECTED HOLSTEIN-FRIESIAN HERD

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ABSTRACT

Analyses were made of all normal lactation records (up to the ninth record of each cow) in the Missouri Station Holstein-Friesian herd from its foundation in 1902 to January 1, 1950. There were 314 cows with a total of 933 lactation records. The progeny of 34 herd sires were represented. Within the 34 sire progeny groups are 299 daughters with records and 270 daughter-dam pairs. All lactation records were standardized to a herd test, 305 day, 2x, mature equivalent basis by means of factors derived from the data.

A significant upward time trend in production was found. Differences between 5 year periods accounted for 5.5 per cent of the total variance in milk production, 20.4 per cent of the total variance in butterfat production and 38.8 per cent of the total variance in butterfat percentage. Estimates of the repeatability of contemporary production records were 0.41 for milk production, 0.36 for butterfat production and 0.61 for butterfat percentage.

Heritability estimates derived from the intra-sire regression of daughter on dam were found to be: 0.36 for milk production, 0.29 for butterfat production and 0.54 for butterfat percentage. Lifetime averages were used as the measure of each cow's producing ability but the heritability estimates were expressed on a single record basis. Variation of daughters and dams records was found to be essentially equal. When each cow's lifetime average was expressed as her "most probable producing ability" no increase was observed in the correlation between the records of daughter and dam.

The correlation between lifetime average milk and butterfat yield was found to be +0.89, between milk and butterfat per cent –0.10 and between butterfat yield and butterfat per cent +0.35. The corresponding genetic correlations were estimated by two methods: (a) by the ratios of appropriate regression coefficients and (b) by the ratios of genetic covariance to the geometric mean of genetic variance estimates. The estimated genetic correlations by method (a) were: +0.87 between milk and butterfat yield, –0.52 between milk yield and butterfat per cent, and –0.03 between butterfat yield and butterfat per cent. The three estimates by method (b) were: +0.99, –0.20 and –0.13 respectively. Both the gross and genetic correlations indicate that a slight but real relative decline in butterfat percentage may be expected to accompany increased milk production.

The effect of mild inbreeding was analyzed by the intra-sire regression of production on inbreeding. A significant decline of 66 pounds of milk and 2 pounds of butterfat per one per cent increase in inbreeding was observed. There was no significant effect on butterfat percentage.

The performance of herd sires as indicated by daughter-dam comparisons is presented for 20 sires having at least 5 daughter-dam pairs. Ten of these sires increased milk production, 15 increased butterfat production, and 13 increased butterfat percentage of their daughters over their corresponding dams. No evidence of nicking was found in a tabulation of sires' daughters according to their maternal grandsires.

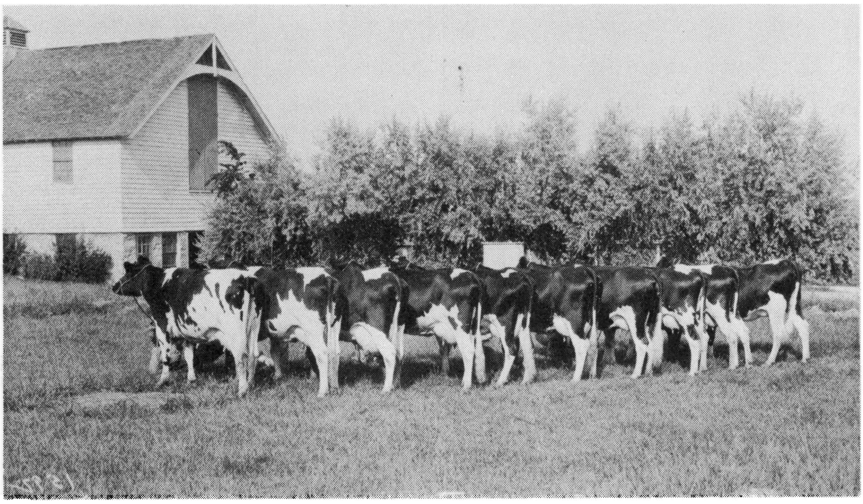


Plate 1. Ten of the daughters of King Fayne Ormsby 237602 a son of Sir Pietertje Ormsby Mercedes 44931. Photographed November 1924.

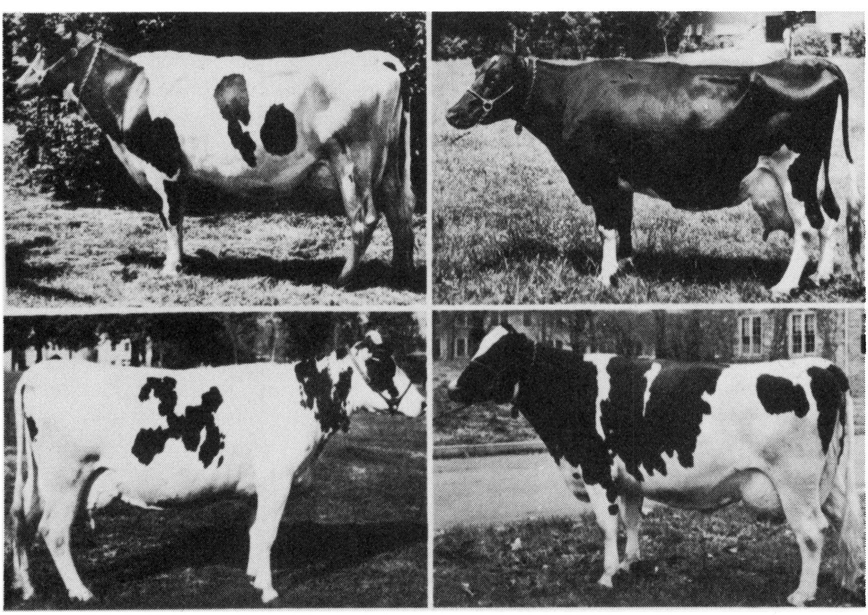


Plate 2. Some representative cows (1945-50) in the Missouri Station herd.

Upper left: U-Mo Vesper Man-O-War Ormsby Freda 1876318 (Herd No. 733) classified Very Good, a daughter of Man-O-War 69th.

Upper right: U-Mo Vesper Man-O-War Ormsby Louise 1880011 (Herd No. 739) classified Excellent, a daughter of Man-O-War 69th.

Lower left: U-Mo Aaggie Josephine Zora 1930407 (Herd No. 764) classified Good Plus, a daughter of Campus Aaggie Segis Sultan.

Lower right: U-Mo Vesper Man-O-War Zirc Ella 2064973 (Herd No. 793), an Excellent daughter of U-Mo Vesper Man-O-War Zirc.

A STUDY OF GENETIC FACTORS AFFECTING MILK PRODUCTION IN A SELECTED HOLSTEIN-FRIESIAN HERD

R. C. LABEN AND H. A. HERMAN*

INTRODUCTION

The modern dairy cow probably represents one of the greatest deviations from "wild" or "common" stock among our domestic breeds of livestock. Man has been in a large part responsible for this deviation, particularly in the last 2000 years, through various practices of selection and systems (accidental or designed) of breeding. An idea of the magnitude of this deviation from ancestral stock may be obtained by the comparison of a modern dairy cow, producing 8 to 10,000 pounds of milk on the average, with certain unimproved strains of cattle such as the British Park Cattle, producing enough milk to raise a calf, and others described by Sanders (1925). The time period involved in the development of dairy cattle has been many hundreds, perhaps thousands of years. Cattle are mentioned in the first chapter of the Bible and there are many references thereafter.

The translations of the agricultural writings of Cato and Varro (Harrison 1913) reveal that the early Romans gave some sound advice on methods of selecting breeding stock. Our modern methods of breeding and selection, however, were first diligently and successfully applied to animal husbandry by Robert Bakewell during the latter half of the eighteenth century. Bakewell and his immediate followers, Thomas Bates and Charles and Robert Colling, are credited with the practical demonstration of the principles of breeding and selection by which most of our present improved breeds of livestock have been developed.

All of the major dairy cattle breed associations in the United States were founded between 1870 and 1890 and systematic record keeping started on a small part of the dairy cattle population. The passage of the Morrill Act by Congress in 1862 laid the foundation for our Land Grant Colleges and state experiment stations. Many dairy cattle breeding experiments were started as these institutions became established during the period of agricultural expansion following the Civil War. It could not be denied that great progress had been made up to the turn of the century, but the amount and reasons would be difficult to estimate since very few accurate production records had been kept. Between 1890 and 1905 the Babcock test for butterfat was perfected, the Mendelian principles of heredity rediscovered,

*The authors are deeply indebted to Dr. Gordon E. Dickerson, Professor of Animal Husbandry, University of Missouri, for his assistance and counsel in the statistical analyses presented and for his critical reading of the manuscript.

and the first Cow Testing Association started. Thus, it has been only rather recently that we have started to develop the measures and methods necessary for the quantitative study of dairy cattle improvement. The first Cow Testing Association (now known as the Dairy Herd Improvement Association) in America was organized, in 1905, in Newaygo County, Michigan. Helmer Rabild, who was born in Denmark, where the first cow testing association was started in 1895, was the foster-father of this early development in Michigan. At that time. he was serving as an inspector for the Michigan Dairy and Food Department, but his leadership in improving dairying resulted in his joining the United States Department of Agriculture in 1908.

The first Cow Testing Association had 31 herds with a total of 239 cows on test. The average production per cow the first year was 5300 pounds of milk containing 215 pounds of butterfat. Gradually the record-keeping idea met favor with progressive dairy farmers and more and more leading dairy states began to form Cow Testing Associations. In 1949 there were 1,787 Associations with 33,851 herds containing 943,939 cows on test in operation in the United States. The average production per cow for 886,129 cows tested in 1948 is reported as 8 675 pounds of milk and 350 pounds of butterfat. On January 1, 1950 there were over 40,000 herds with 1,088,872 cows on test.

It is of interest to note that the D. H. I. A. tested cows have advanced from an average of 215 pounds of butterfat per cow in 1905 to 350 pounds in 1948; an increase of 135 pounds butterfat in 43 years. Meanwhile, the average milk cow has advanced from 146 pounds to about 200 pounds butterfat on the average. Improved breeding and selection, aided by accurate records, and better feeding and management account for the three times faster gain in the case of the D. H. I. A. tested cows. Prior to the Babcock test (1890) purebred cattle were tested for butter production. About 1900, short time records (1 day, 7 days, and 30 days) were much in vogue among many dairy cattle breeders. Few lactation records were made due to the expense of testing every milking for butterfat percentage. As the knowledge of scientific dairying increased it became apparent that a test for butterfat once a month was relatively accurate and the swing to monthly butterfat tests and the keeping of dairy milk weights began, thus paving the way for our present day Advanced Registry Testing programs. These programs are sponsored in some form by all dairy breed organizations. Short time records were of little value in breeding investigations because they gave no measure of persistency of production. The program of Selective Advanced Registry Testing, which included only a few chosen cows (usually the best producers), also failed to yield reliable data for proving sires and brood cows. Wisely, in 1928-29, the Herd Improvement Registry Test, which includes all cows in purebred herds, was inaugurated by the Ayrshire Breeder's Association and has now been adopted by all dairy breed organizations. This testing program promises to yield much more reliable data for use by the geneticist. One of the features of this program is the continuous testing of individuals, thereby providing several lactation records, rather than one record only.

Selective breeding has no doubt played an important role in improved production per cow in America, but no less important is the improvement in feeding and management practices made during the last 40 year period. Dairy cattle are evaluated primarily on the basis of the amount of milk and butterfat they produce. Accurate records are an absolute necessity for the intelligent evaluation of individuals. However, the importance of records has not been fully realized by the rank and file of dairymen because scarcely 5 per cent of our milk cow population is tested for production today.

Part of the present study deals with inherent accuracy of records. While only production of milk and butterfat is dealt with in the present study, the evaluation of individuals is often further complicated in practical breeding operations by consideration of body conformation or type. Both production and desirable type are essential, as well as longevity, efficient reproduction and other factors in our breeding cattle. From the standpoint of selection, however, the breeder faces a more difficult task as the number of goals he selects for increases.

The problem of improvment through breeding basically resolves itself into the problem of increasing in our dairy cattle population the frequency of those genes which exert a favorable effect on desired characteristics. It is important then to determine the extent to which observed variation in productivity is the result of variation in genetic constitution. Not only the amount, but also the manner in which the inheritance of productivity exerts itself will determine the kind of a breeding system that should be most useful in improvement.

Hereditary differences by no means completely determine the production record of a cow. Many managerial and physiological factors which are non-hereditary influence record size. These factors must be dealt with before estimates of genetic influences on production can be attempted.

OBJECTIVES AND METHODS

This study is based on analyses of milk and butterfat records made from 1902 to 1950 by purebred Holstein-Friesian cows in the Missouri Station herd. This herd has been maintained under a fairly uniform system of feeding and management and production records have been kept continuously the past 50 years.

The objectives of this investigation are:

1. To study and adjust the milk and butterfat records for variation due to major environmental factors peculiar to this particular herd.

2. To study the degree to which a single production record reflects the inherent productive ability of a cow in the Missouri Station herd.

3. To study the degree to which observed variations in milk and butterfat production and butterfat percentage are due to genetic differences between cows.

4. To estimate the gross and genetic inter-relationships between these three measures of productivity.

5. To determine the effect of mild inbreeding as practiced in this herd on the yield of milk and butterfat and on butterfat percentage.

6. To study the progeny performance of the sires used in the Missouri Station Holstein herd.

In the determination of these objectives interesting facts about the herd will be presented. Among them: the trend in productive level that has taken place during the period studied; the type of breeding program that has been used and the contributions of the various herd sires based on daughter-dam comparisons.

It is beyond the scope of this study to present a complete review of the literature pertaining to all factors influencing the production of milk and butterfat. Specific references pertinent to each of the subjects studied will be reviewed in the section concerned. Among the published reviews on the subject are those of Gowen (1927), Smith and Robinson (1933) and Shrode and Lush (1947); these deal primarily with inheritance in dairy cattle. Smith (1941 and 1946) presents two excellent reviews dealing primarily with work on the physiology of lactation and reproduction. References are cited to over 500 recent published works on the subject both here and abroad.

Methods used in this investigation include the analysis of variance and covariance as described by Fisher (1944). These statistical procedures are used to separate observed variation into several component parts. The method of intra-class correlation, suggested by Fisher, has been used to estimate the average association between records of the same cow within, and between time period groups. From the analysis of covariance simple regression and correlation coefficients have been calculated. The equation used to describe the association between age and production was derived as described by Ezekiel (1941). The use of the three recorded productive characteristics, milk, fat and fat percentage proved to be a valuable additional method of checking for errors in calculation as any deviation from reasonable association between the three factors would indicate an error. Inbreeding coefficients for all animals studied were calculated by the method described by Wright (1922). These calculations were accomplished in an orderly manner through the construction of a genetic covariance chart similar to that described by Emik and Terrill (1949). To facilitate handling, the records of milk production were expressed to the nearest 100 pounds, butterfat production to the nearest pound and butterfat percentage to the nearest one tenth of one per cent. The computation of sums of squares, cross products and of totals for the many sub-groups were greatly facilitated by the use of the International Business Machine card methods. These methods are described in detail by the various authors in parts 1, 8, 9, and 10 of the work edited by Baehne (1935).

BRIEF HISTORY OF THE MISSOURI STATION HOLSTEIN-FRIESIAN HERD

The Missouri Station Holstein-Friesian herd was started in 1902 by the purchase of four bred heifers for a total price of $600. The present herd descends from three of these cows. No females were added to the herd until 1931 when Mr. F. W. A. Vesper of Fredmar Farms, Jefferson Barracks, Missouri, gave the University 48 females and two bulls. Seventeen of these cows made records in the Station herd. These constitute the foundation generation of a second female line in the herd. Herd sires have been purchased from time to time. Of the 34 sires concerned in the present study 19 have been brought into the herd from outside sources.

Production records have been kept on all cows in the herd since 1900. They consist of daily milk weights for the entire period and monthly five-day composite samples tested for butterfat for the period up to about 1915. Monthly or bi-monthly butterfat tests are the basis of the estimation of butterfat production in more recent years. The Babcock test has been used exclusively. Practices of feeding and management, disease control, sire selection, and culling have been the basis of a program designed to demonstrate practical Missouri dairy husbandry procedures.

The herd has been tuberculin tested since 1905. In 1918, however, serious losses were incurred due to the failure of a single infected cow to react to the test. Tuberculosis losses for the herd are almost all due to this single outbreak. The herd has been Federally Accredited as tuberculous-free since 1922. No serious outbreaks of Brucellosis have occurred. A few sporadic losses of reactors have accounted for a small percentage of disposals. All cows in this study which have left the herd up to January 1950 are classified in Table 1:

TABLE 1.—REASONS FOR THE DISPOSAL OF COWS

Reason	Number	Per cent	Ave. No. Records
Sold for production	98	35.9	1.96
Sold for slaughter	43	15.7	3.65
Sterility	31	11.3	4.19
Died of infection or accident	22	8.0	2.50
Died from ingested hardware	16	5.9	2.75
Mastitis	21	7.8	2.81
Sold because of old age	18	6.6	7.06
Tuberculin reactor	13	4.8	3.08
Brucellosis reactor	11	4.0	1.82
Total or Average	273	100.0	3.01

The reasons for disposal were taken from the notation made on the herd record at the time of disposal. Considerable overlap of some of the categories is to be found. Those sold for slaughter are primarily the ones culled for low production or poor type or both, though sickness or other reasons are sometimes involved. Sterility accounts for a rather large percentage of the disposals. This group contains many older cows and the figure does not reflect chronic difficult breeding as the average calving interval for all herd test records of the sterile group was found to be 13.6 $\pm$ .30 months. This calving interval is only slightly longer than that for all herd test records (Table 6). The figure of 11.3 per cent is about the same as that found by Haden and Herman (1941) in a study of all three (Jersey, Guernsey and Holstein) herds at the University of Missouri. The losses due to disease have been low, those due to infection total 13.5 per cent and seem somewhat higher than might be expected. The actual age at disposal was not tabulated in this study. However cows completed an average of about three records and were approximately 5.8 years of age on completion of the third record. Production records for each of the disposal classes were tabulated to be presented in a future study.

An Agricultural Experiment Station herd is maintained for purposes of research demonstration and teaching. Thus in some instances an animal might be kept or disposed of for reasons differing from those in a practical farm herd. The history of this herd shows that it has been used for a considerable amount of research work. Eckles (1912) and Eckles and Palmer (1916 a and b) report the results of experiments on the plane of nutrition of dairy cattle which involved cows whose records are included in this study. Some of the more recent experiments include further studies on nutrition, endocrinology, temperature effects, milk secretion, etc. which have had some effect on production. In considering corrections to be applied to records for the present study, however, it was concluded that from the standpoint of all records involved those containing bias due to experimental treatment were relatively few. The herd as a whole was never subjected to experimental treatment that caused extreme variation in production. It was considered that a special study to endeavor to correct individual records for possible influences of various experiments was not warranted. No major changes in the feeding or management policies have been made over the entire period. There has been a gradual shift in the past 20 years favoring the 10 month rather than the 12 month herd test record. Cows on "official" test have been managed over the entire period for a 12 month record with extra feed and care, a longer calving interval and more frequent milking than cows on herd test. The herd has been under the supervision of only two men. Professor C. H. Eckles who founded the herd, and his successor Professor A. C. Ragsdale, the present Department Chairman.

While there is good reason to believe that the environment of this herd has been reasonably constant over the entire period a brief examination of the records reveals that two distinct types of environment have been maintained within the herd. The environment of Advanced Registry or "official" testing, and an environment comparable to good practical dairy farm conditions; that of Herd Improvement Registry or "herd" testing. It has been the general policy to place the first ten daughters of a bull on "official" test for their first lactation. These records deviate so far from the "herd" test records of the same cow, that a study of the effect of official testing was made.

STANDARDIZATION OF RECORDS FOR MAJOR NON-HEREDITARY SOURCES OF VARIATION

The data utilized here are the production records of milk, butterfat and butterfat percentage; the pedigree; ages and dates that concerned each record. All cows that had made a normal and complete lactation record in this herd up to January 1, 1950 were included. These data were taken from the Missouri Station herd books. All records of a cow up to and including her eighth lactation were used. By this plan only 18 suitable records were discarded. The amount of information derived regarding a cow's productive ability rises at a decreasing rate with additional records, particularly after the third record (Berry, 1945). Records at very advanced ages also usually contain a considerable amount of error due to permanent environmental changes such as damage to mammary tissue. In examining the records it was apparent that some abnormally low records were due to sickness or accident and many of the higher records were the result of the better than average environment of "official" testing. Berry and Lush (1939) and Lush *et al.* (1941) discuss the question of the omission of records from a cow's average. They point out that the omission of a record known to be made under abnormal circumstances, for which adequate correction cannot be made, might increase the value of the average. The criteria for omission must be simple and impersonal. The size of the record alone must not influence its use. In this study all records were used except those following early abortion or where the record carried the notation of serious illness or accident during the lactation. Imcomplete lactations were not extended. They were included unless the cow left the herd prior to the completion of 305 days on test. Under these criteria 314 cows had completed one or more lactations in the herd. A total of 933 records were used. Excluding the foundation cows, the progeny of 34 sires are represented in this group.

The average of all records, except as previously mentioned, has been used as the measure of a cow's productive ability. Several methods other than the use of lifetime averages might be used. Woodward and Graves (1946) utilize first records made under "official" testing conditions. Several other workers have employed this measure with the theory that the first record; made under optimum environment conditions, and during which udder infections and accidents are apt to have least influence, is the best measure of inherent productivity. Copeland (1938) advocates the selection of a cow's highest record as the best measure of her producing ability, particularly in daughter-dam comparisons for sire proof. Berry and Lush (1939) indicate why the selection of the highest or lowest record as an index of the cow's ability to produce is unsound.

Records are not perfectly repeatable. If so a single record would be of as much value in predictions as any or all other records of a given cow. Where cows have unequal numbers of records. as will always be the case in unselected data, the chances of having made the best or the poorest record will not be equal. For example, in this study, if the highest record were to be selected the probability of a cow with one record having made her highest is 1/8. If eight records have been completed this probability rises to 1. If a single record is to be used, the first record offers the most unbiased estimate of future and inherent productivity.

The most important causes of imperfect repeatability of lactation records are such incidents as the effects of difficult calving, indigestion, better or lower levels of nutrition, extreme weather conditions, and changes in milking or feeding practices. Since these sources of error tend to be random from one lactation to another of the same cow they will be cancelled in the process of averaging. Lush *et al.* (1941) point out that lifetime averages are effective in sharply reducing errors due to random, unrecorded, environmental variation. The reduction is 1/2 where two records are concerned, 1/3 where three are concerned etc. Where unequal numbers of records are used for the average production of a cow the method of correcting for incomplete repeatability as proposed by Lush (1945) is designed to place such averages on a comparable basis. This method gives greater weight to deviations from the herd average where the deviation is based on larger numbers of records. It will be used in the heritability and inbreeding study to be presented.

It was desired to express the records on a basis comparable to records made in a well-managed practical farm herd. This would indicate the use of a "herd test" record of 10 months duration made on twice-a-day milking. The value of a production record depends upon the accuracy with which it reflects the inherent producing capacity of a cow. Previous studies, particularly that of Dickerson (1941), indicate that this type of record, standardized for age, is very suitable for breeding analysis.

Methods for correcting lactation records for almost every conceivable source of non-genetic variability may be found in the literature. However it seems only reasonable that beyond a certain point the application of correction factors might add error and confusion rather than increase accuracy. Turner (1927) emphasizes that the use of great refinement of conversion may tend to give a false appearance of accuracy to individual records. Conversion or correction factors must be determined from average changes and can be used justifiably only in the statistical analysis of large numbers of records. Lush *et al.* (1941) state that objective correction factors for important environmental variations will add accuracy if the variation can be quantitatively measured but that "there are important practical reasons against correcting records too much lest they get too far from reality."

Correction for Length of Lactation

The amount of milk or butterfat produced during any lactation is governed by three major physiological elements of lactation; the height and persistency of the maximum yield and the length of the lactation period (Gaines 1927). Persistency, or the ability of a cow to maintain her maximum production, was not studied in the present data. Studies of this characteristic found in the literature include those of Turner (1927), Gaines (1927), Pontecorvo (1940), Johansson and Hansson (1940), Ludwin (1942), and Ludwick and Petersen (1943). Gaines and Davidson (1926) studied the problem of correction for length of lactation. They determined the correlation between length of record and total yield was of the order of 0.94. Depending upon persistency, they found the 305 day record to be from 87 to 90 per cent of the 365 day record. Johansson (1947) reports that from 20 to 30 per cent of the observed variance in persistency is due to genetic differences. Thus accurate adjustment for length of lactation by a percentage factor would depend upon a knowledge of persistency in the population concerned.

Many of the records entered in the Missouri Station herd books are of 365 day length. A preliminary study was conducted to determine the result of reducing them to 305 days by the factors 0.85 suggested by the Bureau of Dairy Industry (Rice, 1942 p. 566), and 0.90 used by the Holstein-Friesian Association (Norton, 1949 p. 187). The results of the application of these factors, and a derived factor 0.87 were tested against the actual 305 day partial record. In this herd the factor 0.85 underestimated and 0.90 overestimated the actual record. The derived factor 0.87 resulted in estimates not significantly different from the actual records, but considerable deviation in individual records was evident. The standard error of the mean difference between the actual and corrected records was 76 pounds of milk. Since some of the sub-groups in the present study contained only a few records it was deemed advisable to use the actual record wherever possible. The actual daily milk weights and pounds of butterfat as estimated by periodic tests were summed for the first 305 days of each lactation record.

Standardization for Age of Cow

It is well recognized that cows tend to produce more with advancing age and each succeeding lactation period. No quantitative study of such observations, however, could be made until large numbers of milk and butterfat production records were available. The influence of age was one of the first and most extensively studied variables of production. Haas (1898) and Wing and Anderson (1899) are among the first to report the observation that the yield of milk and fat increased with age up to about 7 years. Rietz (1909) appears to have been one of the first investigators to apply age correction to butterfat records. Eckles (1911) concluded from a tabulation of official testing records up to 1909 that "A dairy cow on the average as a two-year-old may be expected to produce about 70 per cent; as a three-year-old around 80 per cent; and as a four-year-old about 90 per cent of the milk and butterfat she will produce under the same treatment when mature." This 70-80-90 per cent rule was used as recently as 1934 in the study by Harris, Lush and Schultz. Lush and Shrode (1950) in a study of over 43,000 Holstein-Friesian records concluded that this rule removed some 52 per cent of the age variance. Gowen (1919) suggested the use of the "multiplication factors" that we use at present for age correction. Workers at the Missouri Station (Turner and Ragsdale

1923, and 1924, Turner 1925, and Gifford and Turner 1928) first published such factors in readily usable form. Where the averages of all records in each age group are expressed as the percentage of the mature average a bias due to culling is introduced. The mature group represents a more highly selected population than do the younger age groups. The lowest producers are usually allowed to produce only one or two records. This would tend to overcorrect early records. This complicating factor of selection has been recognized and Sanders (1928) appears to be the first to offer a method of treating it in age studies. Schmidt (1933), Gaines and Palfrey (1931) and Plum (1935) are among the others who have dealt with this problem by studying age changes within individual animals. Kendrick (1941) indicates that the D. H. I. A. age conversion factors now in use are based on the method of paired consecutive records as suggested by Sanders. Lush and Shrode (1950) have utilized a modification of this approach. These authors found that in the Holstein records they studied the D. H. I. A. factors removed 91 per cent and the Holstein H. I. R. factors (Norton 1949 p. 187) about 97 per cent of the variance due to age. They derived factors from the data that removed all but 1 per cent of the age variance.

In previous studies of records which involved age standardization, investigators have either used the published breed factors which seem to apply most logically to the population being studied, or they have derived factors from the records studied. Dickerson (1941) utilized the simple regression of yield on age. In his study all cows had five records and the regression of yield on age was found to be essentially linear up to about 5 years of age. This regression is usually not linear, but is a logarithmic function of the same type describing growth and age. Brody (1927) shows that age changes in milk yield and body weight may both be expressed by the same curvilinear equation.

The published age conversion factors which should most nearly fit the data studied here are the H. I. R. factors of the Holstein-Friesian Association (Norton, 1949, p. 187). These were applied and the results compared with those of factors computed from the data as will be described.

Factors for age conversion to maturity were calculated from the present data by the method described by Sanders (1928). Lactation number rather than chronological age was used as the basis for grouping. Only "herd test" records were used. Cows having first and second records, second and third, and so on were grouped. If the first records were set at 100, the comparison of the first with the second record of the same cows gave the percentage increase from first to second record of 106.5 (Table 2). Then with the second lactation value as a base, second and third records were compared, thus building up a composite curve—the change between each group being based on production of the same animals. The data used are recorded in Table 2. The cubic parabola $y = a + bX + cX^2 + dX^3$ was fitted to the estimates of comparative production. The solution of three simultaneous equations for the constants a, b, c and d yielded the estimating equation: $y = 82.8537 + 17.5984X - 2.0202X^2 + .0253X^3$.

TABLE 2.—THE DERIVATION OF AGE CONVERSION FACTORS FROM PAIRED CONSECUTIVE HERD TEST RECORDS

Lactation Number	No. Paired Records	Mean	Standard Error	Difference Between Means	Comparative Production	Estimated Comparative Production	Mature Equivalent Conversion Factors
1	108	7894	±175		100	98.8	1.268
2	108	8410	±164	516	106.5	111.0	1.129
2	93	8705	±203		106.5		
3	93	10028	±218	1323	122.7	119.2	1.051
3	57	10014	±274		122.7		
4	57	10096	±303	82	123.7	124.0	1.011
4	50	10218	±313		123.7		
5	50	10234	±285	16	123.9	125.3	1.000
5	37	10411	±365		123.9		
6	37	10370	±442	41	123.5	123.3	1.016
6	27	10967	±519		123.5		
7	27	10552	±524	415	118.8	118.3	1.060
7	18	10944	±613		118.8		
8	18	10089	±553	855	109.5	110.2	1.137

TABLE 3.—AVERAGE AGE AT EACH LACTATION

Lactation No.	No. Cows	Average Age Yrs.	Average Age Mo.
1	298	2	6
2	197	3	8
3	130	4	9
4	94	5	11
5	72	7	0
6	49	8	3
7	34	9	7
8	18	10	9
Over 8 rec.	8	12	4
1st. record made elsewhere	16		
	314		

The values of comparative production and the fitted curve for the description of the effect of age as measured by lactation number is plotted in Figure 1. The average ages at the start of each lactation in this herd are shown in Table 3. The numbers of records available for pairing, especially at the more advanced ages, were limited and the standard errors were very large. It was therefore deemed desirable to check their effect with age corrections accomplished with published factors.

The results of the analysis of variance of 383 milk records of 171 cows which had only "herd test" records are shown in Table 4. The standard deviation between records of the same cow is much smaller for the calculated factors. Since both the mean and the standard deviation change, the

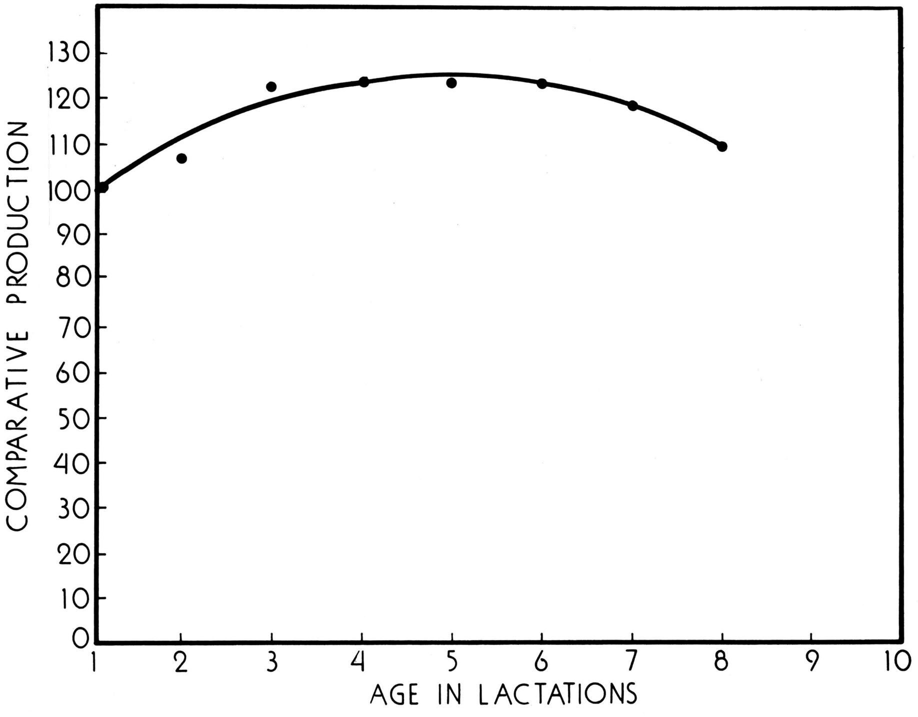


Figure 1. The composite curve of comparative milk production on age.

TABLE 4.—EFFECT OF AGE CORRECTION ON MILK PRODUCTION RECORDS (Calculated and Holstein H. I. R. Factors Compared)

Factor Used	No. Cows	No. Records	Mean	Total Std. Deviation	Intra-Cow Std. Dev.	Repeatability
Calculated	171	383	9917	2247	1699	.43
Holstein H. I. R.	171	383	9715	2265	1836	.35

coefficient of variation is a more valuable indicator. The values are 0.17 for the calculated factors and 0.19 for the H. I. R. factors, a small but significant difference.

The repeatability estimates are derived by the method of intra-class correlation. In this analysis they indicate that 43 per cent of the variance is associated with differences between cows and 57 per cent with differences between records of the same cow for the calculated factors. These percentages are 35 and 65 respectively for the H. I. R. corrected data. There appears to be a small advantage in favor of the calculated factors as they appear to reduce differences between records of the same cow more appropriately than the published H. I. R. factors.

Correction for Number of Daily Milkings and Environment Conditions Associated with Official Testing

Cows in the Missouri Station Holstein herd on Advanced Registry or "Official" test were provided an environment differing from that of "herd" or Herd Improvement Registry test in the following major respects:

(a) They were fed on a 10-15 per cent higher plane.
(b) They were milked three-times-a-day as compared to twice-a-day (in most cases).
(c) They were bred later in the lactation period.
(d) They were kept in box or tie stalls rather than in stanchions.
(e) They were milked and cared for by the most capable milkers.

Many experiments have been conducted to demonstrate the effect of feeding level on milk and butterfat production. Wing and Foord (1904) showed that liberal feeding of a highly digestible, high protein, ration to a poorly fed herd would increase milk and fat production up to 50 per cent.

Eckles and Palmer (1916 a and b) studied the influence of overfeeding and underfeeding on production in the Missouri Station herd. They found that underfeeding resulted in a weight loss but no reduction in yield immediately following calving. As lacation progressed, however, even a moderate reduction in feed caused a marked drop in production. The result of overfeeding was found to be primarily a gain in body weight rather than an increased milk flow. The effect of four levels of feeding on milk and fat yield was studied by Graves *et al.* (1940). Cows on alfalfa hay and pasture only; alfalfa, pasture and a supplement of 1 pound of ground barley per 6 pounds of milk produced about 68 and 83 per cent of their yield when on a full grain ration (1 pound grain to 4.3 pounds of milk). Jensen *et al.* (1942) thoroughly analyzed input-output relationships in milk production from data gathered at 10 agricultural experiment stations over a 3 year period. They found that from 15 to 20 per cent more milk was obtained from levels above the commonly accepted standard. Increased level of feeding raised the entire lactation curve and had no effect on butterfat per cent. Other recent experiments on this subject are those of Autrey. Cannon and Espe (1942), Yates, Boyd and Pettit (1942), Headley (1944), and Baker and Tomhave (1944). All are in substantial agreement with the findings of Jensen and coworkers.

The frequency of milking is another major reason for superior production of cows on official test. Table 5 summarizes the findings of several investigatations where frequency of milking was the major variable.

TABLE 5.—PERCENTAGE INCREASE OVER TWICE-A-DAY MILKING ATTRIBUTED TO 3 AND 4 TIMES-A-DAY MILKING.

Investigator	3X	4X
Woodward (1931)	20	—
Norton (1932)	20	31
Copeland (1934)	21	—
Ludwin (1942)	26	38

The factors most commonly used at present to reduce 3X records to 2X records are 0.80 or 0.833. The factor 0.80, representing a 25 per cent increase, is used by the Holstein-Friesian Association. The Bureau of Dairy Industry uses the factor .833, which represents a 20 per cent increase from 2X to 3X. Lush and Shrode (1950) present the most recent examination on the effect of frequency of milking. They found a distinctly wider 2X:3X ratio at ages under three years. They point out that if the extra milking has its primary effect through relieving udder pressure, a greater response might be expected in heifers whose udders are relatively less developed than older cows. The factor 0.80 for first lactations and .833 for later lactations fitted their data quite well.

The effect of breeding cows later in the lactation period (150-180 days) results in an increase in production for that particular record. The longer service period is reflected in calving intervals well over 12 months. Detailed studies on the effect of calving interval length and its components, the dry period, service period, and lactation period, have been made by Sanders (1927 *a* and *b*, 1928 *b*), Plum (1935), Lörtscher (1937), Dickerson and Chapman (1939), Johansson and Hansson (1940), Johansson (1947), and many others.

The depressing effect of pregnancy on lactation does not begin to operate until about the fifth or sixth month of gestation. Delayed breeding as compared to breeding for a 12 month calving interval may give an advantage of about 19 per cent in a current 12 month record as shown by Eckles (Eckles, Anthony and Palmer 1939). Using only the first 305 days of a lactation record would eliminate most of this advantage. It is primarily for this reason that the studies cited have found the 10 month partial record reasonably free of variation due to calving-interval differences.

The objective of the present study of official records was simply to find a reasonable means of converting them to a level comparable with the majority of records which were herd test records. Of the 933 records available 196 or 21 per cent were official records. They were the only records available on 37 cows. Most of these records were on 3X milking. Seven records on 4X were reduced to 3X by the factor 0.880. The majority of the herd test records were 2X records. One hundred forty eight were reduced to a 2X basis by the factor 0.833. Therefore the differences between the two testing systems in this study will contain the effect of one extra milking per day except where otherwise stated. Of the 196 A. R. records 115 were first, 16 second, 28 third, 15 fourth, 13 fifth, 7 sixth and 2 were seventh lactation records.

The official and herd test records for milk and butterfat yield were plotted against age in Figure 2. In this figure both official and herd test records are expressed on a 2X basis. The 2 and 2.5 year groups on official test are averages of 64 and 45 records respectively. The rise at 3 years and depression at 3.5 are averages of only 12 and 3 records respectively. Sufficient data were not available for conclusive evidence but no distinct advantage in the effect of A. R. testing in this herd was shown for any

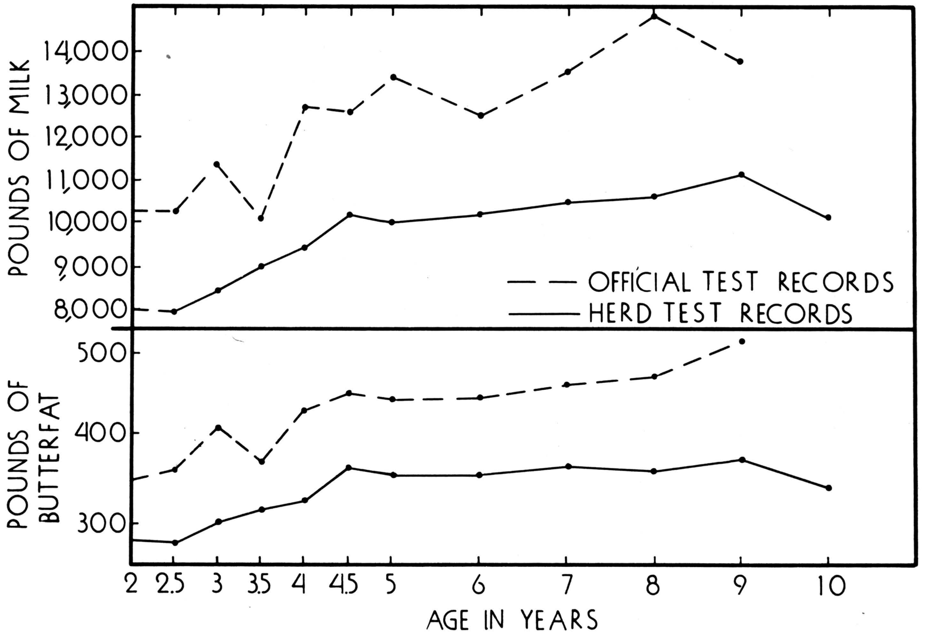


Figure 2. Comparison of Advanced Registry records with Herd Improvement Registry records. (All records on a 2X basis)

particular age group. However, the A. R. heifers must be relatively unselected as compared to older cows which are not placed on official test unless they show evidence of superior productivity. As all ages were reduced to 2X milking by the same factor age differences in a 2X:3X ratio would remain in Figure 2. If the effect of extra feeding and care remained fairly constant at all ages then the greater increase due to 3X milking of heifers could balance the effect of selection for higher production in later cows. Thus the total effect might be about equal at different ages but due to different factors. In Figure 2, where the official records are reduced to 2X milking, the weighted mean superiority of the official record is 2674 pounds of milk and 86 pounds of fat. The weighted ration A. R. : H. I. R. was 0.77 and 0.78 for milk and butterfat yield respectively. It was concluded that a reasonable reduction of the official records could be made by a single factor at all ages, and that the effect of the different number of daily milkings should not be reduced separately.

In order to determine the average superiority due to the better environmental conditions of A. R. testing, records of the same cow were compared. For this purpose all records were standardized for age, the A. R. records considered as 3X milking, and H. I. R. records as 2X milking records. There were 103 cows which had at least one A. R. and one H. I. R. record. The mean weighted intra-cow ratio of H. I. R./A. R. was calculated by the method indicated in formula (1).

(1)

$$\frac{\text{H. I. R.}}{\text{A. R.}} = \text{antilog} \frac{\Sigma_{nc} \left[(\log x_1 - \log x_2) \dfrac{n_1 n_2}{n_1 + n_2} \right]}{\Sigma_{nc} \left(\dfrac{n_1 n_2}{n_1 + n_2} \right)}$$

Here Σnc represents the sum of the fractions for each of n cows. The symbols X_1 and X_2 represent the means and n_1 and n_2 the numbers of H. I. R. and A. R. records respectively for each cow. The ratio so calculated was found to equal 0.68. This indicates that the official records averaged 47 per cent above the herd test records of the same cow.

If one extra milking per day accounts for a 20 to 25 per cent increase in production then the remaining 22 to 27 per cent of the superiority would be due to the higher feeding plane and other details of care. This is assuming that the length of calving interval has been effectively corrected for by standardizing length of lactation. Table 6 gives the average

TABLE 6.—AVERAGE CALVING INTERVALS ASSOCIATED WITH A. R. AND H. I. R. TESTING

Type of Record		No. of Records	Ave. Mo.
Cows with both A. R.	A. R.	139	$15.7 \pm .24$
and H. I. R. records	H. I. R.	269	$13.6 \pm .17$
Cows with H. I. R. records only		210	$13.4 \pm .18$
All H. I. R. records		479	$13.5 \pm .12$

length of calving intervals associated with the two methods of testing. It should be noted that the calving intervals associated with all H. I. R. records reflect good practical management and satisfactory reproductive efficiency. The practice of delayed breeding is reflected in the longer interval between calvings associated with official testing.

A study was made to determine whether any important time trends are shown in the differences between the two types of records made by the same cow. The results are presented in Table 7. There is an indication that the cows on official test in the past few years have not been pushed for high records to quite the extent they had prior to 1940.

It was concluded that factors of feeding and management associated with official testing as practiced in this particular herd increased a cow's production about 47 per cent over her herd test yield. The factor 0.68 was applied to reduce the 196 A. R. records to a herd testing basis.

TABLE 7.—INFLUENCE OF OFFICIAL TESTING BY TIME PERIODS (Average Pounds of Milk)

Period	No. Cows	A. R. Records (305 day 3X) No.	Ave.	H. I. R. Records (305 day 2X) No.	Ave.	Diff. A. R.—H. I. R.	% Inc. In A. R.
To 1920	10	17	16,412	45	11,109	5,030	47.7
To 1930	27	49	15,135	102	10,107	5,028	49.7
To 1940	44	54	16,969	148	11,318	5,651	49.9
To 1950	22	32	15,838	60	11,043	4,795	43.4
Total or Ave.	103	152	16,077	355	10,897	5,180	47.5

Eckles in 1924 (Eckles, Anthony and Palmer, 1939, pp. 360-361) from a study of 41 cows of 4 breeds in 4 herds concluded a cow might be expected to yield about 58 per cent of her official record when kept under ordinary conditions, 10 per cent less than was estimated in the present study. Woodward (1927) from a study of 22 cows which had completed lactations under both conditions concluded that cows on herd test averaged about 66 per cent of their official test milk record and about 67 per cent of their official test butterfat record. Ragsdale and Gifford (1929) graphically compare Advanced Registry and Cow Testing Association records and present conversion factors for the influence of official testing at advancing ages. The older cows showed greater response to official testing than the young cows. The A. R. to Cow Testing Association factor is 0.70 for two year olds and 0.61 for six year olds. Eckles has demonstrated that high producing cows respond more to better care than do low producing cows. Then the effect of more intense selection of A. R. cows (event as forced by minimum entrance requirements) might account for this change in response to the official testing regime with advancing age where the study is not on an intra-cow basis.

The effect of A. R. testing on subsequent herd test records was investigated but was not corrected for. Plum (1935) found evidence of a small after-effect of the previous year's feeding. This would be reflected through improved condition at the time of calving. Brody (1927) points out that the average cow on test reaches her maximum production at an earlier age than the average cow not on test. Graves and Fohrman (1925) from a study of original and re-entry records concluded that the re-entry records were larger not only due to advancing age but to a developmental influence of official testing in the first lactation. Davidson (1928) concluded the assumptions of Graves and Fohrman were not entirely warranted as only the better cows would tend to be re-entered on official test.

It would be interesting to determine whether official testing has a greater developmental effect on the mammary gland than the development due to average care during the first lactation. The present study does not include enough data to draw definite conclusions as to the carry-over effect of official testing versus herd testing. The data were tabulated, however, to show any trends that might be indicated.

The ratios of later herd test records of cows first tested on H. I. R. are presented in Table 8. It is apparent that the herd test records following A. R. testing are larger than those following H. I. R. testing in the first lactation. As the age of first lactation increases the superiority of following records declines sharply. A graphic comparison of later herd test records according to the type of first test is presented in Figure 3.

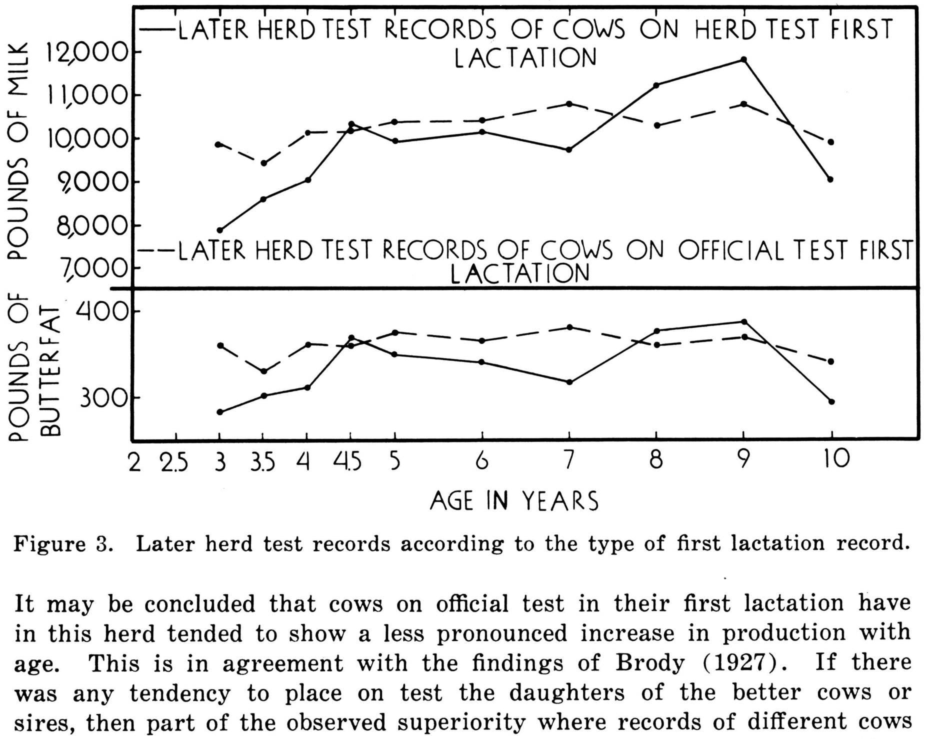


Figure 3. Later herd test records according to the type of first lactation record.

It may be concluded that cows on official test in their first lactation have in this herd tended to show a less pronounced increase in production with age. This is in agreement with the findings of Brody (1927). If there was any tendency to place on test the daughters of the better cows or sires, then part of the observed superiority where records of different cows are compared would be genetic. The number of records was too small to give any indication regarding the genetic differences that might have been involved.

The effect of season of freshening was not studied. This variable has been extensively studied by McDowell (1922), Johansson and Hansson (1940), Cannon and Hansen (1943), Woodward (1945), Frick *et al.* (1947) and many others. The effect of season varies widely from one location to another depending upon climatic conditions, and varies widely between herds in any particular locality depending upon feeding and man-

TABLE 8.—RATIO OF SUBSEQUENT H. I. R. RECORDS OF COWS TESTED ON A. R. TO COWS FIRST TESTED ON H. I. R.

	Ages of Later H. I. R. Records					
Milk Production	3	3½	4	4½	5	6
1st AR at 2 years / 1st HIR at 2 Years	1.27	1.05	1.19	1.02	1.01	1.08
1st AR at 2½ years / 1st HIR at 2½ years	—	1.10	1.12	.98	1.10	1.02
1st AR at 3 years / 1st HIR at 3 years	—	—	1.05	1.09	1.10	.88
Butterfat Production						
1st AR at 2 years / 1st HIR at 2 Years	1.28	1.07	1.16	1.03	1.06	1.10
1st AR at 2½ years / 1st HIR at 2½ years	—	1.12	1.30	.95	1.14	1.08
1st AR at 3 years / 1st HIR at 3 years	—	—	1.02	1.23	1.01	1.00

agement practices. Pasture conditions are one of the greatest causes of seasonal fluctuation in production.

The amount of pasture available for the Missouri Station milking herd has always been limited and supplemental feeding has been the rule. Season of freshening was considered to be a minor factor causing differences in production in this particular herd.

The slight downward trend of butterfat percentage with advancing age has not been considered in this analysis. Gowen (1923) showed that butterfat percentage declined slightly but significantly with age. He found the total amount to average 0.3 per cent over the period from two to twelve years of age. Turner (1936) presents a summary of several studies showing this decline but does not consider it to be of practical importance. Putnam *et al.* (1944) believed the decline in fat percentage is important and should be considered in age conversion factors. Lush and Shrode (1950) however, indicate that this decline is so slight that separate age conversion factors for milk and fat do not seem worth while.

The records used in the following analyses have been standardized to a 305 day, mature equivalent, twice-a-day milking, herd test basis. Further tests of the computed correction factors will be made in the repeatability analysis to follow.

THE EFFECT OF STANDARDIZATION AND ANALYSES TO DETERMINE THE REPEATABILITY OF MILK AND BUTTERFAT PRODUCTION AND BUTTERFAT PERCENTAGE

The amount of milk and butterfat that a cow produces in one lactation usually differs from the amount produced in other lactations. This difference in the yield of the same cow may be due to temporary environmental circumstances such as variation in the amount and quality of feed and changes in management practices. Animals also vary in their rate of growth and physiological development. Size is a factor in milk production. These variations tend to be cancelled when the average of all records of a cow is used. Permanent changes of an environmental nature may also occur. The growth of the cow with increasing age and development of the udder by recurrent periods of pregnancy and lactation, damage to the body by serious illness or the loss of a quarter represent changes of a more permanent nature. The degree to which a cow tends to produce the same amount of milk with the same percentage of fat from lactation to lactation is defined as the repeatability of these characteristics. Repeatability is measured by the average coefficient of correlation between records of the same cow.

Linfield (1900), in a study of production records at the Utah Station, recognized the large variation in production between the records of the same cow. He concluded that the average of several years' production was the most reliable index of a cow's productive capacity. Gavin (1913) estimated that the correlation coefficient between successive lactations did not rise above 0.60. Therefore he concluded that the estimation of one lactation yield from another cannot be made with great accuracy. Gowen (1920 *a* and *b*) calculated the correlations between pairs of records at different ages. All correlations were positive and of the order of +0.54 for milk yield and +0.52 for fat percentage. Gowen and Gowen (1922), in a study of Holstein-Friesian official records, estimated the average correlation of a 365 day lactation record with a subsequent lactation to be of the order of +0.67 for milk and +0.72 for percentage. Dickerson (1941) points out that these estimates are high due to the inclusion of considerable between herd variation and when expressed on an intra-herd basis the figure for milk production becomes about +0.50. Harris, Lush and Shultz (1934) found the correlation between butterfat records of the same cow to be +0.547 when all herds were considered as a single population. The correlation became +0.325 when calculated on an intra-herd basis. Where several herds are considered as a single population; the degree of likeness between records of any particular cow is due, not only to her own inherent productivity, but also to the fact that her records were made in the same herd and under similar conditions of feeding and environment. The intra-herd correlation more nearly expresses the degree of likeness due to inherent producing ability if testing environment within the herd is reasonably constant. An intra-herd repeatability of +0.40 was calculated by Plum (1935) from Iowa Cow Testing Association records.

Later studies have confirmed this figure as being typical of age-corrected 8 or 10 month lactation records made under practical farm conditions. Johansson and Hansson (1940) report an intra-herd repeatability of +0.36 for the corrected records of some 300 cows each of which had at least 5 records. Dickerson and Chapman (1940) utilized the intra-herd repeatability as a measure of the genetic value of five different kinds of production records. He reports an intra-herd correlation between age-corrected 305 day 2X butterfat records of +0.34. Verna (1945), in a study of the Iowa State College Holstein herd, found the repeatability of 8 month A. R. records to be of the order of +0.50 for milk, +0.43 for butterfat yield and +0.66 for butterfat percentage.

In the present study the increase in repeatability of records and the decrease in the standard deviation of records of the same cow were used to measure the effects of standardization for age and A. R. testing. This analysis was conducted on the 305 day milk records only. Through the analysis of variance estimates were made of the variance due to differences between cows (C), and due to differences between records of the same cow (R). The results are presented in Table 9.

TABLE 9.—ANALYSIS OF VARIANCE OF MILK PRODUCTION RECORDS OF 314 COWS AND 933 RECORDS TO DETERMINE EFFECTS OF STANDARDIZATION FOR AGE AND A. R. TESTING

Type of Record	Average Pounds	Total Std. Dev. Pounds	Total Std. Error Pounds	Within Cow Std. Dev. Pounds	Within Cow Coef. of Var.	Repeatability
1. 305 day, otherwise uncorrected	10,300	3050	±100	2565	0.24	0.29
2. 305 day, herd test, 2X, basis	9,344	2293	± 75	1862	0.20	0.34
3. 305 day, herd test, 2X, ME by H. F. Assoc. Factors	10,217	2201	± 72	1711	0.17	0.40
4. 305 day, herd test, 2X, ME by calculated factors	10,455	2204	± 72	1649	0.16	0.44

The correction for times-a-day milked and other factors associated with official testing in this herd reduced the within cow standard deviation 27 per cent. Age correction resulted in an additional decrease of 6 per cent on application of the Holstein-Friesian Association factors or 9 per cent on the application of the calculated age conversion factors. As the mean changes with the standard deviation the coefficient of variation is a better measure of these effects. It is reduced by 4 per cent by the first correction and an additional 3 or 4 per cent by age correction. The repeatability or degree of association between records of the same cow is increased 5 per cent by standardizing the official records to herd testing conditions and an additional 6 and 10 per cent respectively through age correction by the two different sets of factors. Another approach in analyzing these effects is presented in Table 10. The ratio C/C+R, in this simple analysis, is an estimate of the intra-class correlation, or average association between records of the same cow. It also may be considered as the percentage of the variance associated with differences between cows in this case. The remainder R/C+R is the percentage of the variance associated with differences between records of the same cow. In the

TABLE 10.—MAGNITUDE AND PERCENTAGE OF VARIANCE DUE TO DIFFERENCES BETWEEN COWS (C) AND DIFFERENCES BETWEEN RECORDS OF THE SAME COW (R) FOR RECORD TYPES 1, 2, 3 AND 4 TABLE 9.

Type of Record	Magnitude of Variance C	Magnitude of Variance R	Percent of Total Variance $\frac{C}{C+R}$	Percent of Total Variance $\frac{R}{C+R}$
1	273.02	658.09	29	71
2	179.76	346.52	34	66
3	192.11	292.96	40	60
4	214.30	272.13	44	56

records corrected only for length of lactation, 71 per cent of the variance was due to differences between records of the same cow. The percentage decreases to 66 when all records are standardized to a herd test basis. Further standardization to a mature equivalent basis by Holstein-Friesian Association factors reduces this figure to 60 per cent. A decrease to 56 per cent is obtained when the calculated age correction factors are substituted. The additional 4 per cent increase in repeatability obtained by the calculated factors seemed to justify their use in this study. It would appear, however, that the use of published age correction factors (Breed Association or DHIA) obtained from data similar to that being analyzed would probably be sufficiently accurate for all practical purposes.

An examination of the data revealed that milk production had gradually increased over the period studied and that fat production and especially fat percentage had increased even more. Thus estimates of repeatability based on the simple analysis above would be too high. If time trend was important then records of a cow would be similar due not only to her inherent producing ability, but due also to the fact that she produced during a definite time period in the herd. For the purpose of investigating the time trend the 314 cows were parted into 9 five year periods based on the year each entered the herd. All cows entering up to 1910 were placed in the first period. The details of this analysis of variance are given in

Table 11. The derivation of the general formulae for the coefficients of C and P, which represent the number of times each of these components of variance are represented in the mean square, has been worked out by Dickerson (Hetzer, Dickerson and Zeller 1944).

The averages of the nine periods are plotted in Figure 4. The scales of all charts in this study were chosen so that a standard deviation unit of each characteristic occupies approximately the same distance on the Y axis. The slopes of the lines thus gains a comparable illustration of the regression of production with respect to time periods. The sharp downward trend in production for the period from 1910 to 1915 is due to the entrance of the daughters of the second herd sire, Leland Sarcastic.

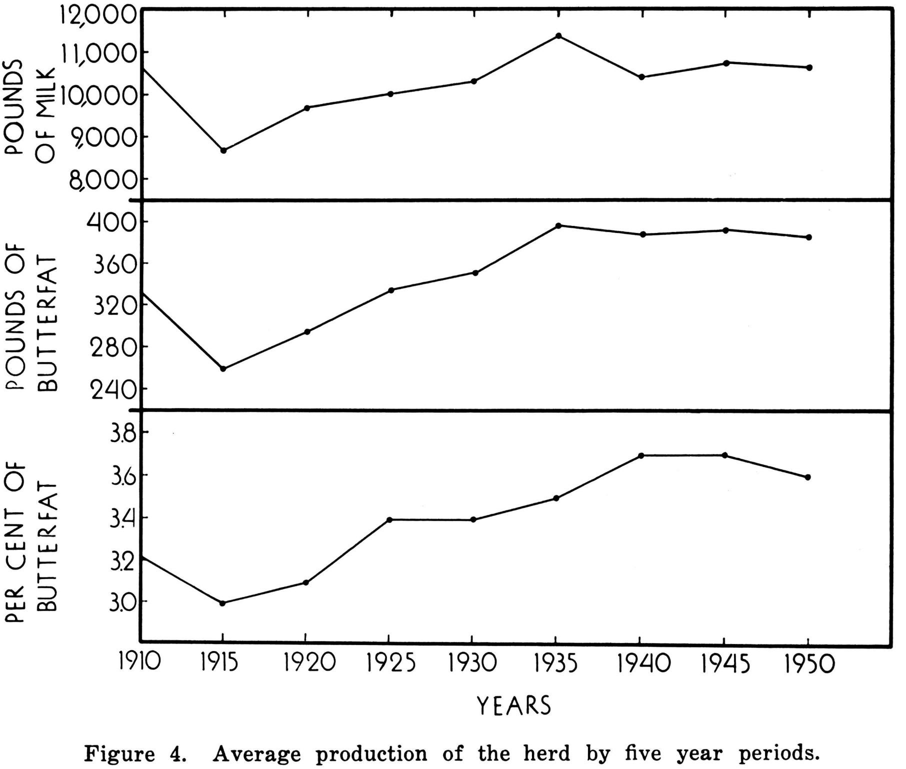


Figure 4. Average production of the herd by five year periods.

Writing in 1927 Professor Ragsdale says of this bull: "He was by Sarcastic Lad, the Grand Champion bull of the World's Fair at St. Louis in 1904. Twelve daughters resulted. They averaged 10,278 pounds of milk and 304 pounds of fat. This was 221.5 pounds fat less than their dams. This bull was used in 1907-08 and it required 20 years to build this herd back to almost the exact level of production it had at the time he was first used in it.

"Such is the all too often result of using an unproven bull (however good the pedigree) extensively in a high producing herd. The knowledge of

TABLE 11--ANALYSIS OF VARIANCE TO DETERMINE REPEATABILITY OF PRODUCTION RECORDS

Source	d/f	Sums of Squares	Interpretation of Mean Squares
Total	N-1	$\Sigma X^2 - \frac{(\Sigma X)^2}{n}$	
Periods	Np-1	$\Sigma\left\{\frac{(\Sigma X)_p^2}{np}\right\} - \frac{(\Sigma X)^2}{n}$	$R + \bar{k}_c^p C + \bar{k}_p^p P$
Cows Within Records	Nc-Np	$\Sigma\left\{\frac{(\Sigma X)_c^2}{nc}\right\} - \Sigma\left\{\frac{(\Sigma X)_p^2}{np}\right\}$	$R + \bar{k}_c^c C$
Records of same Cow	N-Nc	$\Sigma X^2 - \Sigma\left\{\frac{(\Sigma X)_c^2}{nc}\right\}$	R

Coefficients of C and P are derived from the general formula $\bar{k} = \frac{\Sigma\left(\frac{\Sigma k^2}{\Sigma k}\right)_c \Sigma\left(\frac{\Sigma k^2}{\Sigma k}\right)_g}{Nc - Ng}$

$$\bar{k}_c^c = N - \frac{\Sigma\left(\frac{\Sigma k^2}{\Sigma k}\right)_p}{Nc - Np} = 2.9247$$

$$\bar{k}_c^p = \frac{\Sigma\left(\frac{\Sigma k^2}{\Sigma k}\right)_p - \frac{\Sigma k^2}{N}}{Np - 1} = 4.5516$$

$$\bar{k}_p^p = \frac{N - \frac{\Sigma k^2}{N}}{Np - 1} = 116.0544$$

Repeatability Estimates:

for contemporary cows $r = \frac{C'}{C' + R'}$

for non-contemporary cows $r = \frac{C' + P'}{C' + P' + R'}$

such facts as these has led the Missouri Station and many leading breeders to adopt the general policy of using only proved sires and of proving out the young bulls before using the best of them extensively in the herd."

It is noted in Figure 4 that there was an upward trend in all production characters from 1915 until 1935 or 1940 where production has tended to level off. The percentage of butterfat shows the most marked upward trend. The Station Holstein herd, in its early days, was noted for high milk production, but also low butterfat test, particularly through the famous Missouri Chief Josephine, daughter of one of the foundation cows. She produced 26,861.5 pounds of milk and was second cow in the world in 1910 as a milk producer. The herd was, however, noticeably below the breed average in butterfat test. A very definite effort was made to breed for increased test. Figure 4 indicates that test has been successfully raised. As total milk production has also been increased, pounds of butterfat, which is the product of the two, shows a pronounced rise. The mean production over the entire period is given in Table 12 with measures of the total and within cow variation. The repeatability estimates are also given in Table 12. Differences between time periods would act in much the same manner as differences between herds in raising the estimated correlation between records of the same cow. Thus the estimate for contemporary cows is the better estimate of the inherent tendency of a cow to repeat her production record lactation after lactation.

TABLE 12.—AVERAGE PRODUCTION AND REPEATABILITY OF MILK, BUTTERFAT AND BUTTERFAT PERCENTAGE

Record	Mean	Standard Error	Within Cow Std. Dev.	Within Cow Coef. of Var.	Non-Contem. $\frac{C + P}{C + P + R}$	Contemporary $\frac{C}{C + R}$
Milk Prod.	10,455	± 72	1649	.16	.44	.41
Fat Prod.	364	± 3	57	.16	.49	.36
Fat %	3.49	±.01	.16	.05	.76	.61

TABLE 13.—PERCENTAGE OF THE TOTAL VARIANCE ATTRIBUTED TO PERIODS, COWS, AND RECORDS FOR MILK AND BUTTERFAT PRODUCTION AND BUTTERFAT PER CENT

Source of Variation			Variance Estimates		% of Total Variance		
Between Time Periods (P)	8	27	1300	4.19	5.5	20.4	38.8
Between Cows Within Periods (C)	305	188	1815	4.03	38.6	28.5	37.4
Between Records Within Cows (R)	619	272	3259	2.57	55.9	51.1	23.8

The relative importance of the time trend in the three characteristics studied is illustrated in Table 13 where the percentages of the total variance associated with P, C, and R are given. The mean squares from the analysis of variance are given in Table 14. Period differences are highly significant for all three characteristics. Although period differences were highly significant for milk production they account for only one twentieth of the total variance in that characteristic. About one fifth of the variance in fat production and over one third of that in fat percentage was associated with differences between periods.

TABLE 14.—THE MEAN SQUARES OF TABLE 11 FOR MILK AND BUTTERFAT PRODUCTION AND BUTTERFAT PERCENTAGE

Source	d/f	Milk	Fat	%
Total	932	486	6362	10.76
Periods	8	4213**	162365**	507.26**
Cows	305	821**	8568**	14.36**
Records	619	272	3259	2.57

** = P<.01

Results of Standardization of Records and of Repeatability Analyses

The increase in production with increasing age is by no means a function of age alone. It is due to the complex interaction of many factors, among them: growth as measured by gain in weight and size, the development of the mammary system through recurrent pregnancy, and lactation. In part the growth of an animal is influenced by inherent factors and in part by the feeding and management practices peculiar to the herd it is raised in. The effect of age and body growth alone is reflected in the studies of age at first calving. Eckles (1915) concluded that calving at extremely early age is detrimental to the best development of milking function while nothing is gained by too great a delay of first calving. The depressing effect on growth due to very early first calving is not a result of the energy requirement of pregnancy as shown by the experiments of Eckles (1916), but to the high energy demands of lactation. Chapman and Dickerson (1936) found that calving as early as 26 months was not detrimental to the animal and resulted in a slightly increased lifetime productive efficiency. The early bred heifers were slightly smaller at the first and second lactations but not at maturity. Other workers, Reed *et al.* (1924), Turner (1932), Dickerson and Chapman (1940), and Hansson (1941) have shown that there is an optimum age for first calving from the standpoint of lifetime production and production in the first period. Production ceases to rise appreciably beyond a first calving age of 36 months in most studies. Efficiency from a lifetime productive basis falls sharply after an age of 30 months at first calving. If reproductive efficiency is poor, the number of lactations will lag behind the chronological age of a cow. Neither tell the complete story. However where cows calve at nearly one year intervals lactation number from a physiological standpoint might be a better measure of mammary gland development. In the present study maximum production was reached in the fifth lactation, which corresponded to a mean age of seven years. Eckles (1911) found maximum production was reached in the fourth lactation in a study of Jersey and Holstein cows. Maynard and Meyers (1918) found maximum milk production was reached in the eighth lactation. Hammond and Sanders (1923) found maximum production reached in the fifth lactation. Glen and McCandlish (1930) concluded that for practical purposes milk and butterfat production increase from the first to the fifth lactation. They compared classification by age and lactation number and found the results quite similar. Bartlett (1934) reported maximum yield in the sixth lactation with a decline following. The age correction factors derived in this study based on lactation number have increased the association between records of the same cow slightly more than the Holstein-Friesian H. I. R. factors.

Tabulation of these corrected records by age groups revealed that the calculated factors brought immature records closer to the mature level than did the Holstein H. I. R. factors. The D. H. I. A. factors would have over corrected the present data. At ages above eight years, however, the calculated factors far overcorrected records. Since there were few older records, this did not introduce much error. The method of building up a composite curve has exaggerated the decline in production after maturity.

The analysis for repeatability has revealed that all three measures,—milk, butterfat production, and per cent of fat,—have varied significantly between time periods. It would seem reasonable that a good portion of the time differences are due to genetic changes. The progeny of the second herd sire are largely responsible for the sharp decline in production in the early years of the herd. While relatively minor changes in feeding plane or management could result in a marked change in total milk and butterfat production, rather drastic changes in environment are necessary to change butterfat percentage. Butterfat percentage has shown almost a steady increase with over $\frac{1}{3}$ of the total variance in this character due to time period differences. These differences are due to changes in the genetic level of the herd plus feeding, care and management trends.

The C component of variance (Table 12) contains differences between cows that entered the herd during specified five year periods. It indicates the real genetic differences between cows plus permanent environmental differences such as injuries or better or less than average care throughout the cow's life. The error term or R component of the analysis contains variance between records of the same cows caused by uncorrected environmental changes. Averaging the records of a cow will further reduce any random errors in this component. The amount of C variance in relation to R is about $\frac{2}{3}$ for milk production, $\frac{9}{16}$ for butterfat production, and slightly over $1\frac{1}{2}$ for butterfat percentage. The relative magnitude of the period changes (P) as compared with cow differences (C) within periods are $\frac{1}{8}$ for milk production, $\frac{3}{4}$ for fat production and of equal size for fat percentage. Thus while period and cow differences have a very low probability of being due to change alone for any of the three characteristics (Table 13), they are of greatest magnitude for fat percentage, least for milk production, and intermediate for butterfat production which is the product of the other two.

The period differences are also reflected in the differences between repeatability estimates for contemporary and non-contemporary cows (Table 12). Removing period differences reduces the correlation between records of the same cow to the extent that these records are alike due merely to the fact that they were made within a certain period during which genetic and environmental levels were different from other periods.

The repeatability estimates of records of contemporary cows are an indication of likeness between records due to the inherent ability of a cow to produce. They are likewise an indication of the reliability of a single record as an index from which to predict future records of a cow. The estimates are in general agreement with those found in the literature. The analysis of the correlations between the three measures of production may shed light on the reason or reasons why in this particular study the repeatability for butterfat production falls slightly below that of milk production while the value for fat percentage is very high. Previous studies have reported both higher and lower values for butterfat production than for milk production. For all practical purposes they appear to be equal and of a magnitude not greatly different from 0.40.

THE HERITABILITY OF PRODUCTION OF MILK, BUTTERFAT, AND BUTTERFAT PERCENTAGE

The heritability of a characteristic refers to the degree to which observed variation in that characteristic is due to the average effects of the genes carried by each individual. Heritability may be thought of also as that fraction of their productive superiority which selected parents transmit to their offspring. In the production of milk, for instance, it has been shown that although a great many environmental factors cause differences in production, only the differences due to genetic factors are passed on to succeeding generations. Methods of estimating the degree of heritability are based on the resemblance between groups of animals of known genetic relationship. Whatley (1942) has estimated the genetic variance in growth rate of pigs by five different methods. Methods of estimating heritability are discussed by Lush (1940 and 1945).

The correlation between daughters' and dams' records of production was one of the first methods of approaching the problem of hereditary influence in dairy cattle. It is still the most common basis of estimating the degree of hereditary variation in dairy cattle data. Rietz (1909) reports on the inheritance of butterfat production. He found the correlation between daughter and dam records to be of the order of 0.30. The data used were 7 day "Official tests" published in volumes 11-18 of the Holstein-Friesian Advanced Register. Turner (1927), Gifford and Turner (1928), and Gifford (1930) found daughter-dam correlations for butterfat yield to be of the order of 0.26 to 0.35. Smith and Robison (1933) present an extensive list of correlations between milk, fat and percentage of various pairs of relatives computed by many different investigators. Daughter-dams correlations ranged between 0.36 to 0.50 for milk production, 0.23 to 0.40 for fat production, and 0.30 to 0.42 for fat percentage.

Gowen (1934) concluded the general size of the daughter-dam correlation for milk and fat percentage tended to be 0.40. It was later concluded that these estimates would be reduced somewhat if expressed on an intra-herd basis.

When these correlations or the corresponding regressions are computed between animals whose probable genetic likeness may be estimated from the laws of inheritance, the heritability of productive characteristics may be measured. The parent-offspring relationship is one of the most valuable for this purpose. In milk production sires do not themselves express the characteristics measured, and it is agreed that each parent contributes equally to the inheritance of milk and butterfat yield, except for sex-linked genetic factors. The most valuable estimate of heritability may be obtained, then, by doubling the intra-sire daughter-dam regression. The figure will contain all of the additive genetic effects. None of the effects of dominance will be included since dominance is due to combinations of two allelic genes and only one gene of the pair is transmitted in the gamete. A portion of the epistatic effects (those due to the interaction of non-allelic genes popularly termed "nicking" effects) will be included. This portion would be one-fourth of the 2-gene epistatic interactions, one-eighth of the 3-gene, and so on (Lush *et al.* 1941). Another but less efficient method of estimating heritability is that of dividing mates of a sire into low and high groups and observing the regression of their daughters toward the mean of the parental generation (Lush and Arnold 1937). Four times the correlation between half sibs will also yield an estimate of hereditary variance. This method, and the intra-sire daughter-dam regression method have been utilized in this study.

Gowen (1934) estimated one-half of the variation in milk yield, and four-fifths of the variation in fat percentage was due to hereditary differences. Shrode and Lush (1947) conclude that these estimates if reduced to an intra-herd basis would be of the lower order usually found. Lush and Shultz (1936) estimated the heritability of butterfat production to be 0.25 and of butterfat percentage to be 0.50. Johansson and Hansson (1940) estimated the genetic portion of the intra-bred variance in single records to be 0.30 to 0.40 for fat yield and 0.70 to 0.80 for fat per cent. Lush *et al.* (1941) using the intra-sire regression of daughters on dams estimated heritability to be 0.33 for milk yield and 0.28 for fat yield. Lush and Strauss (1942) estimated the heritability of single butterfat records to be 0.17. Johansson (1947) further substantiates the heritability estimates of Johansson and Hansson mentioned above. Most of the studies reported in the literature have found the intra-herd heritability of differences in single milk and butterfat production records to be of the order of 0.2 to 0.3. Estimates of butterfat percentage appear to be from 0.5 to 0.8.

In the present analysis the standardized lifetime averages were used as the measure of each cow's producing ability. Thirty-four sires were represented in the 270 daughter-dam comparisons. The intra-sire comparison tends to place the data on a reasonably contemporary basis and should minimize the likeness between daughters and dams due to the time trend in this herd. The average intra-sire correlation and regression

TABLE 15.—THE INTRA-SIRE CORRELATIONS AND REGRESSION COEFFICIENTS BASED ON LIFETIME AVERAGES OF 270 DAUGHTER-DAM COMPARISONS WITHIN 34 SIRE GROUPS

Record	Correlation	Regression of Dtr. on Dam
Milk Production	.32 $\pm$ .05	.33 $\pm$ .06
Butterfat Production	.27 $\pm$ .06	.29 $\pm$ .07
Butterfat Percentage	.43 $\pm$ .05	.39 $\pm$ .05

estimates based on lifetime averages are presented in Table 15. The five per cent fiducial limits of the regression coefficients are for milk 0.21 and 0.45; for butterfat 0.16 and 0.42; and for butterfat per cent 0.28 and 0.50. These coefficients indicate that by chance one time out of twenty the respective regressions might be as low or as high as the limits stated. The average number of daughter-dam comparisons is nearly eight per sire; the range, however, is from 1 to 40. These regression estimates are based on lifetime averages. In order to express heritability on the basis of single records it is necessary to take into account the reduction in variability of the independent variable caused by the averaging process. The variance of the mean of n records, $V\bar{x}_n$ contains the additively genetic variance (G), plus the variance due to dominance, epistasis and permanent environmental deviations (C), plus 1/n of the error variance, as expressed in (2) below.

$$(2) \quad V_{\bar{x}_n} = G + C + E/n$$

The fraction of the variance of the lifetime averages due to additively genetic differences between mates of a sire is:

$$(3) \quad H_{\bar{x}_n} = \frac{G}{G + C + E/n}$$

The quantity G + C is equal to the repeatability (r) of records as calculated in the previous section, and E is then equal to $(1 - r)V_x$. When the number of records per dam varies, let n = d. From the previous formula (Table 11) then:

$$(4) \quad \bar{d} = \frac{N - \Sigma\left(\frac{\Sigma d^2}{\Sigma d}\right)S}{N_D - N_S} = 4.48$$

a value which is slightly below the actual mean number of records in the dam's lifetime average. The heritability of lifetime averages is estimated by doubling the intra-sire daughter-dam regressions of Table 14. The heritability of single records, H, may then be calculated thus:

$$(5) \quad H_{\overline{x}_n} = \frac{H}{r + \frac{1-r}{\overline{d}}}$$

$$(6) \quad H = (H_{\overline{x}_n})\left[r + \left(\frac{1-r}{\overline{d}}\right)\right]$$

Applying this method to the present data the estimates of the heritability of single records of the three characteristics studied are presented in Table 16 with the corresponding repeatability estimates. Lush and

TABLE 16.—ESTIMATES OF THE REPEATABILITY AND HERITABILITY OF SINGLE RECORDS

Record	Repeatability	Heritability
Milk Production	0.41	0.36
Butterfat Production	0.36	0.29
Butterfat Percentage	0.61	0.54

Strauss (1942) estimated the regression coefficients of single records, b_{yx}, as shown in formula 7.

$$(7) \quad b_{yx} = b_{\overline{yx}}\left[\frac{1 + (m-1)r}{\overline{m}} + \frac{\sigma^2_m (1-r)}{\overline{m}^3}\right]$$

Here M refers to the number of dams records. When applied to this study, essentially the same heritability estimates are derived. The mean number of dam's records is 4.57 and the variance 5.90. By doubling the intra-sire regressions obtained by applying (7) above the heritability estimates of milk yield, butterfat yield, and butterfat percentage are 0.38, 0.31 and 0.56, respectively.

The heritability estimates indicate that in the Missouri Station herd, approximately 1/3 of the observed variance is milk and butterfat yield, and ½ of the observed variance in butterfat percentage of the dams may be attributed to the additive effects of genes. Two factors which may be operating to make these estimates slightly higher than some found in the literature, particularly those of Lush and Strauss (1942) and Ward and Campbell (1940), might be more accurate correction of the records for non-genetic environmental influences, or failure of the intra-sire grouping to remove entirely the effects of the time trend. However they are in substantial agreement with the majority of previously reported estimates.

Other methods of estimating heritability were applied to the present data to further indicate the behavior of the variation of production records in this herd. The analysis of variance indicated in Table 17 was calculated using the records of 299 cows who were daughters of the 34 sires

TABLE 17.—THE ANALYSIS OF VARIANCE FOR ESTIMATED HALF SISTER AND FULL SISTER CORRELATIONS

Symbol	Source of Variation	d/f	Composition of M. S.
S	Between Sires	$N_S - 1$	$1/n_S E + F + \bar{d}_S D + \bar{s}_S S$
D	Between Dams within Sires	$N_D - N_S$	$1/n_D E + F + \bar{d}_D D$
F	Within Sire and Dam	$N - N_D$	$1/n_F E + F$
E	Between Records within Cows	$N_R - N_C$	E

tabulated for this study. The error term mean square for this analysis, the variance between records within cows, was taken from the repeatability study of the previous section. Since the S, D and F components of variance of Table 17 were calculated on the basis of lifetime averages the amount of this error variance contained in their mean squares will be *1/n* of what it would have been had single records been used. Here *n* is the number of records averaged per cow. This error variance is derived from the general formula of Table 11, by using *1/n* in place of *n*,

TABLE 18.—VARIANCE ESTIMATES FOR THE DETERMINATION OF HALF SISTER AND FULL SISTER CORRELATIONS

Source	d/f	Variance Estimates Milk	Butterfat	Per Cent
S	33	65.19	1790.84	4.9296
D	231	62.14	724.45	.2796
F	34	78.40	631.62	3.5039
E	305	272.13	3259.45	2.5703

The values of $1/n_S$, $1/n_D$ and $1/n_F$ are 0.6277, 0.5663. and 0.4093, respectively. The values d_S, s_S and d_D are computed in the same manner as the corresponding coefficients in the repeatability analysis, except that each daughter's average was used as the unit of observation. The variance estimates thus computed are presented in Table 18. The intra-class correlations between paternal half sisters, maternal half sisters, and full sisters may then be estimated as indicated by formulas 8, 9, and 10.

		Milk	Fat	%
(8) Paternal 1/2 Sib r	$= \dfrac{S}{S + D + F + E} =$	0.14	0.30	0.45
(9) Maternal 1/2 Sib r	$= \dfrac{D}{2D + F + E} =$	0.13	0.14	0.04
(10) Full Sib r	$= \dfrac{S + D}{S + D + F + E} =$	0.27	0.39	0.46

These are expressed as heritability estimates in Table 19. (Those estimates beyond the limits of reason due to excessive experimental error are not listed.) The sire component of variance, (S), contains in it most of the time trend effects. Time trend effects were quite pronounced for percentage and for pounds of butterfat and somewhat less pronounced for milk production. This may be observed more clearly by comparing S and D in Table 18. The paternal half sister correlation will be quite free of dominance, epistatic and permanent environmental deviation. Due to the low number of sires it will contain a large amount of error, and this error will be multiplied by 4 in determining heritability on this basis.

TABLE 19.—HERITABILITY ESTIMATES FOR SINGLE RECORDS BASED ON SISTER CORRELATIONS

Method	Heritability Estimate		
	Milk	Fat	%
4X Paternal ½ Sister r	0.56	-----	-----
4X Maternal ½ Sister r	0.52	0.56	0.16
2X Full Sister r	0.54	0.78	0.92

For these reasons estimates above the value of 1, which are meaningless, are obtained for fat and percentage and a very high estimate is obtained for milk production. The variance between dams within sires will be relatively free of time-trend bias, thus formula (9) is proposed, where 2D is used in the denominator rather than S + D since it would be expected that sires and dams should contribute about equally. This of course yields an estimate of H for milk production of about the same size as the paternal half sister correlation method. The estimate for butterfat yield remains very high. The behavior of the variance components for percentage is extremely erratic. The F component is too large. The data were carefully checked and it appears that the small sample of full sisters available contained extreme variation within full sister sets. This component when removed from the D mean square largely accounts for the very low variance estimate for D. This intra-class correlation then becomes unreasonably low for maternal half sisters.

It is concluded that suitable heritability estimates by these methods cannot be obtained from the present data. This is due primarily to the pronounced time trend which is reflected in the variation between sires, and to the low number of full sisters.

The number of records on which each cow's average is based varies from one to eight in this study. A deviation from the herd average of a cow's lifetime average when based on one or two records would not seem to deserve the confidence of a deviation based on a larger number of records. The estimate of repeatability of records gives an indication of the amount of confidence a single record deserves as an indication of the cow's real ability. Where repeatability and the herd average is known, the most probable real producing ability may be predicted as proposed by Lush (1945). This procedure may be indicated as:

$$(11)\ \text{Most probable ability} = \frac{nr}{1 - r + nr} C + \frac{1 - r}{1 - r + nr} H$$

where C is the cows' average record, H is the herd average, r the repeatability and n the number of records in C.

Berry and Lush (1939) refer to three groups of workers who accomplish the mathematical derivation of this formula independently and from slightly different viewpoints. Berry (1945) derives a slight modification of this formula in which heritability rather than the repeatability value is used in the numerator. For any value of r, the amount of emphasis placed on the cow's own average increases as n becomes larger. If anything is to be gained by this procedure, it would seem to be that records so "regressed" to the herd average for cows with n varying from 1 to 8 should contain less error and more of the variation in "regressed" yields should be due to real genetic differences between cows.

For the purpose of predicting most probable producing ability it would appear that a contemporary herd average should be used for each cow. For this purpose a moving three year herd average over the period studied was computed. This is plotted in Figure 5. Cows with from one to three records were regressed to the three year average nearest the mid-point of their productive period. All cows with over three records were regressed toward the average for the whole period during which they produced in the herd. The intra-sire, daughter-dam regression and correlation coefficients were then computed using the lifetime averages so corrected. The repeatability estimates used were those calculated from the data presented. The results appear in Table 20. The correlations

TABLE 20.—INTRA-SIRE CORRELATIONS AND REGRESSIONS OF DAUGHTER ON DAM BASED ON MOST PROBABLE PRODUCING ABILITY

Record	Correlation	Regression
Milk yield	.30 ± .06	.27 ± .02
Butterfat yield	.24 ± .06	.22 ± .06
Butterfat percentage	.45 ± .05	.35 ± .05

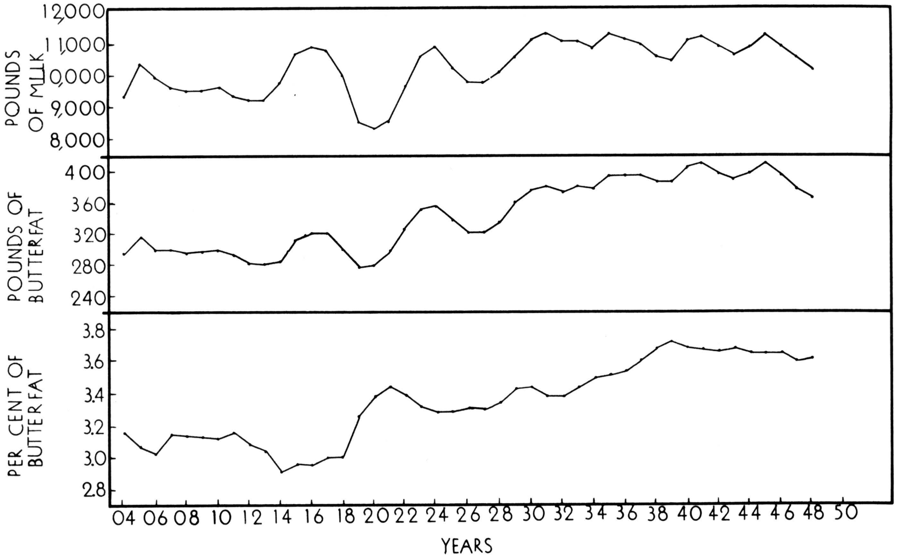


Figure 5. Moving three year herd average for milk and butterfat production and butterfat per cent.

between daughters' and dams' average records, when corrected for unequal numbers according to the repeatability of the records, has not been improved. In order to determine the effect of the use of this moving average, all milk records were "regressed" to the general mean, 10,455 pounds of milk. It was recognized that this procedure would tend to raise early records toward a level above that which actually existed in the early years. It would also move later records toward a level slightly below their contemporary average.

No improvement resulted in the correlation between daughters' and dams' records within sire groups for milk yield. The correlation was 0.29 and the corresponding regression 0.26. When the dams average only was regressed toward the general mean the correlation remained essentially the same, 0.31. The regression coefficient increased to 0.46. By

TABLE 21.—INTRA-SIRE STANDARD DEVIATIONS OF PRODUCTION RECORDS

		Standard Deviation		
Source	d/f	lbs of Milk	lbs of Fat	% of Fat
Dams	236	1618	51	0.24
All Daughters	236	1717	57	0.23
Paternal ½ Sisters	202	1768	59	0.23
Full Sisters	34	1378	44	0.21

this procedure it would be expected that the regression would be distinctly larger since $b = r_{xy} \frac{\sigma y}{\sigma x}$ where σy is the standard deviation of the daughter's records and σx the standard deviation of the dam's records. The correction for most probable producing ability distinctly reduces variability, thus when x only is reduced b would become larger than r.

Heritability Estimates

Regression and correlation are related statistics. Their computation may be expressed as:

$$(12) \quad r_{xy} = \frac{\Sigma xy}{\sqrt{(\Sigma x^2)(\Sigma y^2)}}$$

$$(13) \quad b_{yx} = \frac{\Sigma xy}{\Sigma x^2}$$

By multiplying numerator and denominator of the formula for b by $\sqrt{\Sigma y^2}$ and dividing both by degrees of freedom, it can be seen that $b = r \frac{\sigma y}{\sigma x}$. In the comparison of daughter and dam records, it would be expected that the standard deviation for dam's records, σx, would be lower than that statistic for daughter's records, because the dams are, to some extent, a selected group. Moreover, in these data, the dams' averages were based on a mean of 4.5 records while the daughters averaged only 3.1 records each. However, the fact that daughters in the same sire progeny are half sisters whereas the dams may be from several different sires, tends to reduce σy relative to σx. The intra-sire variance between dams remains as great as that between daughters and the correlation and regression coefficients are nearly equal. Only in the instance where dam variability was deliberately reduced by the regression of those records toward the herd average did the two measures of association separate markedly. This same observation was made by Lush and Strauss (1942). The standard deviations concerned are listed in Table 21. The small group of full sisters when removed from the total group of daughters increases the variation slightly but not enough to account for the correlation and regression coefficient being so close together. The dams had a slightly higher standard deviation of butterfat percentage, which caused the regression to be slightly smaller than the correlation for this characteristic (Table 15).

When each average is expressed as the most probable producing ability (Table 20) the intra-sire correlations are somewhat higher than the regression estimates. This might be expected where the variation in the original records showed so little difference. The application of formula (11) moves those averages based on fewer records closer to the herd average. The daughters on the average had 3.1 records as compared with

4.5 records for the dams. Thus the daughter records were "smoothed" further toward the herd average and had a lower standard deviation than did the dams. It is not clear why in the original records the dams' averages were nearly as variable as their daughters within sire groups.

It is not entirely clear why the correction of lifetime averages for imperfect repeatability (expressing them as most probable producing ability according to the number and repeatability of the records involved) has not increased the correlation between daughters and dams. If this process further reduced environmental error, more of the remaining variation should be hereditary. Evidentally the process has raised some records and lowered others and the net effect has been no real improvement in record value. Lush, Norton and Arnold (1941) and Bonnier (1946) suggest such a cancelling effect. The present observations suggest that nothing is to be gained, therefore, from the standpoint of genetic progress, by this procedure as compared to the use of the "unregressed" lifetime averages, regardless of the numbers of records concerned.

An interesting relationship exists between the repeatability estimates and heritability estimates. The first, a measure of the inherent producing ability of a cow, contains the effects of additive inheritance, dominance, epistasis and permanent environmental effects. The second, a measure of the transmitted differences, contains the additive genetic effects and only a fraction of the epistatic effects. Thus it would be expected that heritability estimates would be somewhat lower than repeatability estimates. This is generally observed to be true. In this analysis the two measures are listed together in Table 16. These estimates are quite typical of those reported in previous studies. The fact that the two estimates are not greatly different would tend to indicate that simple additive inheritance is of most importance in these productive characteristics.

INTERRELATIONS BETWEEN MILK PRODUCTION, TOTAL BUTTERFAT AND BUTTERFAT PERCENTAGE

Dairymen have long recognized that within a breed the high milk producing cows often tend to have a slightly lower butterfat test. Analyses of production records has usually revealed a low negative correlation between these two variables. This has often been interpreted as an indication that milk yield and fat percentage are independent.

Gaines and Davidson (1923) point out that from the standpoint of energy metabolism the two factors are not independent. They argue that to secure simultaneous high test and high total milk production would require an extraordinary output of energy. They found the correlation between milk yield and fat percentage to be - 0.198 for a sample of Holstein yearly records and – 0.212 for similar Jersey records. Gaines (1940) states that the low correlation observed between these two characteristics is biologically significant and is in agreement with the constant energy theory. This theory states that milk yield, as affected by butterfat percentage, is inversely proportional to milk energy per unit of milk where all other factors are constant.

Krizenecky (1934) compiled the results of all studies on these interrelationships to that date. His summary is shown in Table 22.

TABLE 22.—CORRELATIONS BETWEEN MILK AND BUTTERFAT YIELD AND BUTTERFAT PER CENT (KRIZENECKY 1934)

	No. of Studies	Range	Average
Milk and Fat Yield	19	+0.50 to +0.99	+0.84
Milk and Fat Per Cent	58	-0.02 to -0.51	-0.20
Fat Yield and Fat Per Cent	1	—	+0.16

From a study of ten European breeds he found the average to be:

$$r_{mf} = +0.91, \quad r_{m\%} = -0.18, \quad r_{f\%} = +0.11.$$

In a later study Krizenecky (1943) found essentially the same values. Gaines (1940) from the constant energy theory referred to above, develops the expected correlation $r_{m\%}$ of -0.241.

These interrelationships have been studied in the present analysis. An attempt has also been made to determine the genetic as well as the over-all-correlations between the three productive measures. In Table 23 the over-all-correlations between the three productive characteristics are presented for this study. These correlations are based on lifetime averages. This fact might make them differ from other studies since record to record variation is partly cancelled by the averaging process. Additional information on these records is summarized in Table 24. Butterfat percentage, which is the ratio of butterfat to milk yield, shows much less variation

TABLE 23.—CORRELATIONS BETWEEN MILK AND BUTTERFAT YIELD AND BUTTERFAT PER CENT

	Number	Correlation
Milk and Fat Yield	299	+0.89
Milk and Fat Per Cent	299	-0.10
Fat Yield and Per Cent	299	+0.35

TABLE 24.—THE AVERAGE SIZE AND VARIABILITY OF RECORDS IN CORRELATION STUDY

	Mean	Std. Dev.	Coef. of Var.
Milk Yield	10,395 lbs.	1879 lbs.	18.08
Butterfat Yield	363 lbs.	70 lbs.	19.28
Butterfat %	350 %	0.31 %	8.86

than either of the other characteristics. The ratio between milk and fat yield is more highly inherited and not changed readily by feeding or management practices which influence rate of secretion. Milk production however, as previously discussed, is easily changed by environmental factors. Thus, as pointed out by Gaines (1943), conditions which tend to raise or lower milk yield also raise or lower butterfat yield. A high positive correlation is always observed between the two.

The correlation coefficients of Table 23 may be expressed as regressions by using standard deviation ratios derived from Table 24. These regressions indicate a 3.3 pound increase in butterfat yield for each 100 pound increase in milk yield. This value is slightly less than would be predicted from the mean butterfat percentage of 3.5. The negative correlation of Table 23, when transformed to regression, indicates that a one per cent increase in butterfat test was associated with about a 600 pound decrease in milk production. A one per cent increase in fat percentage also was associated with a 79 pound increase in fat yield.

Gaines (1943) concluded that milk energy yield as measured by 4 per cent fat-corrected-milk is unaffected by changes in fat percentage. For this to be true in the present data, the negative correlation between milk yield and per cent would need to be slightly over twice as large as was found.

This discrepancy does not indicate that the constant energy theory is invalid, but rather that in this sample total energy output was not near its physiological limit. In this herd both test and milk production have risen, milk production slightly and test markedly. Total energy output then has not remained stationary but has increased in this herd. When cows approach the physiological limit of energy output, then selection to increase one characteristic would result in readjustment of the others so that total energy yield would remain essentially unchanged. It would be very difficult to state where such a limit might be. It would vary with feeding level, and with such management practices as times a day milked. We apparently have a long way to go in the breeding and care of most of our dairy cattle before physiological limits are reached.

Bonnier and Hansson (1946) and Hansson and Bonnier (1949) have analyzed the variation in fat lactose and protein percentages between and within cow groups of various degrees of relationship to study the influence of heredity on milk composition. Their objective was to determine whether there is genetically controlled qualitative variation in the activity of mammary gland secretory cells. They concluded that protein and lactose percentages at fixed fat levels are determined mainly by genetic factors.

The genetic correlation between two productive traits would estimate the degree to which the genetic factors affecting one trait may also affect the other. Procedures for estimating the genetic correlation between two productive traits have been proposed by Hazel (1943) and Hazel *et al.* (1943). The authors apply these methods to swine data. Two methods are described. In the first one trait in one animal is correlated with the other trait in a relative. The following ratio of regression coefficients then will yield an estimate of the genetic correlation between the two traits. The genetic correlation between milk and fat yield is illustrated by formula (14).

$$(14) \qquad r_{G_M G_F} = \sqrt{\frac{(b_{O_M D_F})(b_{O_F D_M})}{(b_{O_M D_M})(b_{O_F D_F})}}$$

Here O refers to daughters' records and D to dams'. The regression estimates necessary in addition to those of Table 15 are listed in Table 25. From these figures the following genetic correlations are derived: between milk and butterfat yield +0.87, and between milk yield and butterfat percentage -0.52.

TABLE 25.—ADDITIONAL INTRA-SIRE REGRESSION COEFFICIENTS FOR ESTIMATING GENETIC CORRELATIONS

Traits Correlated	Regression
Daughters' Milk on Dams' Fat	+8.1558
Daughters' Fat on Dams' Milk	+0.0088
Daughters' Milk on Dams' %	-1392.2911
Daughters' % on Dams' Milk	-0.000025
Daughters' Fat on Dams' %	-8.0105
Daughters' % on Dams' Fat	+0.000571

No rational estimate of the correlation between total fat yield and per cent can be obtained from the ratio of regression coefficients as they are of opposite sign. In this case an arithmetic rather than a geometric average might be used. In order to do this it is necessary to express the two coefficients in the numerator on a comparable basis. This may be done by changing them to units of standard measure by multiplying them by the appropriate standard deviation ratio. By this procedure little error is introduced as it has already been shown that the standard deviations of daughters' and dams' records is not greatly different. This may be expressed:

$$(15) \qquad b_{O_F D_{\%}} \cdot \frac{\sigma\,\%}{\sigma\,F} = r_{O_{\%} D_F}$$

$$(16) \qquad b_{O_{\%} D_F} \cdot \frac{\sigma\,F}{\sigma\,\%} = r_{O_F D_{\%}}$$

then:

$$(17) \qquad r_{G_F G_{\%}} = \frac{\dfrac{(r_{O_{\%} D_F})\,(r_{O_F D_{\%}})}{2}}{\sqrt{(b_{O_{\%} D_{\%}})\,(b_{O_F D_F})}}$$

In order to average the two regressions they are transformed to Fisher's z values, the average z obtained, then transformed back to r. By this method the genetic correlation between butterfat yield and test is estimated to be -0.03, or essentially zero.

The above estimates would indicate that a large per cent of the genes influencing milk secretion also favorably influence butterfat secretion. There is a lower but marked tendency for the opposite to be true of genes affecting milk yield and butterfat test. The very low genetic correlation between fat yield and test would here seem to indicate that test is nearly completely determined by total milk yield.

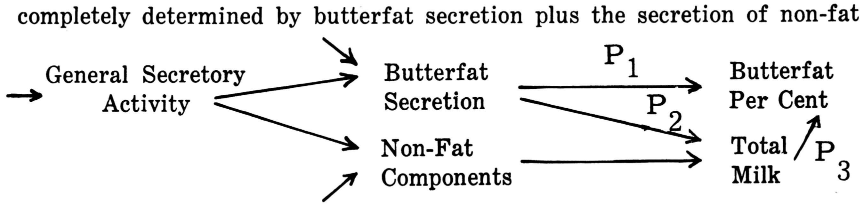
A second method of estimating genetic correlations can be applied if valid estimates of genetic variance and covariance can be obtained (Hadel *et al.* 1943). This correlation between two traits will then be their genetic covariance divided by the geometric mean of the two genetic variance estimates.

The present analysis was not specifically designed for this particular purpose as cross products between individual single records of milk, fat and test were not derived. Therefore, the within sire and dam term, which contains error plus full sister differences, was used as the error term to derive the estimates of variance and covariance of Table 26. Here the between sires term, which ordinarily would be the best estimate of genetic variance and covariance. contains all of the variation due to the time trend and is far too large. The use of the components for dams within sires as an alternative yields the following estimates of genetic correlation: between milk and butterfat yield +0.99; between milk yield and butterfat percentage, -0.20; and between butterfat yield and percentage, -0.13.

TABLE 26.—VARIANCE AND COVARIANCE ESTIMATES FOR DETERMINING GENETIC CORRELATIONS

		Variance			Covariance		
	d/f	Milk	Fat	%	M-F	M-%	F-%
Between Sires	33	67.22	1,813.79	4.9477	+ 302.94	+ 8.54	+80.04
Dams within Sires	231	100.07	1,178.72	0.6379	+ 302.94	+ 1.58	— 3.51
Within Sire & Dam	34	189.78	1,965.71	4.5559	+ 535.87	—12.24	+ 5.18

The relationship between these three productive characteristics might be considered as illustrated below. In this scheme total milk production is completely determined by butterfat secretion plus the secretion of non-fat



components. These two elements may be determined by a host of factors which influence both, here labeled general secretory activity, and by a large number of factors which may influence each separately. Butterfat percentage is completely determined by the amount of butterfat in relation to the total amount of milk. For the determination of the paths of influence P_1, P_2 and P_3, which would give a better idea of the genetic cause and effect relationships, the genetic correlation between butterfat yield and non-fat components would be necessary. This was not computed in the present study. However, if the correlation between milk and fat production is taken to represent the total effect of all direct and indirect factors on fat secretion and total milk secretion, then the path coefficients P_1 and P_3 (Wright 1934) may be solved from the three genetic correlations that have been obtained. These values would in this case be the standard partial regressions:

$$(18) \qquad B\%\, F \cdot M = \frac{r_{F\%} - (r_{M\%})(r_{MF})}{1 - r^2_{FM}}$$

$$(19) \qquad B\%\, M \cdot F = \frac{r_{M\%} - (r_{F\%})(r_{FM})}{1 - r^2_{FM}}$$

The values obtained are presented in Table 27 together with a summary of the genetic correlations. These partial regressions indicate that for one standard deviation increase in milk production, test is decreased by 2.03 or 3.58 standard deviations. However, as fat secretion is positively correlated with total milk, for every standard deviation increase in

TABLE 27.—VALUES OF GENETIC CORRELATIONS AND THE STANDARD PARTIAL REGRESSIONS DERIVED FROM THEM

Genetic Correlations and Standard Partial Regressions	Method of Estimating Genetic Correlation	
	Ratio of b's	$\frac{Cov_{12}}{\sqrt{V_1 V_2}}$
r_{MF}	+ 0.87	+ 0.99
$r_{M\%}$	- 0.52	- 0.20
$r_{F\%}$	- 0.03	- 0.13
$B_{\%F \cdot M}$	+ 1.74	+ 3.42
$B_{\%M \cdot F}$	- 2.03	- 3.58

fat, test tends to increase 1.74 or 3.02 standard deviations, thus partly cancelling the depression first mentioned. The net result is a slight downward trend of test as milk yield increases.

By multiplying the path coefficients by the appropriate standard deviation ratios obtained from Table 24, the results may be expressed in terms of pounds and per cent as partial regressions. Thus:

$$(20) \qquad B_{\%F \cdot M} \frac{\sigma\%}{\sigma F} = +0.0077 \text{ or } +0.0151$$

$$(21) \qquad B_{\%M \cdot F} \frac{\sigma\%}{\sigma M} = -0.000335 \text{ or } -0.000591$$

which indicates that, if fat production is held constant, a 1000 pound increase in milk would be accompanied by a decrease in fat percentage of 0.335 or 0.591 per cent. An increase of 10 pounds in butterfat yield, at constant milk production, would tend to increase fat percentage by 0.077 or 0.151 per cent. For example, a 1000 pound increase in milk yield, accompanied by a 35 pound increase in butterfat yield might be expected to show a net decrease of 0.05 or 0.06 per cent of butterfat.

The path of influence between fat and milk is not bi-directional as assumed in these calculations. The missing relationship of the diagram, the correlation between fat yield and non-fat components would give a better picture of the cause and effect relationships involved. The only conclusions that might be warranted from the present data are that the observed tendency of total milk and total fat to vary together indicates that general factors, affecting secretory activity, are more important than factors specifically and independently affecting fat secretion alone, or non-fat components alone. The genetic as well as the gross observed correlations bear out the observation that a slight but real decline in test may be expected with an increase in milk production. Both production and test can be raised by selection, but the rate of increase in total milk will be slightly greater than the rate of increase in fat secretion and fat percentage in turn will rise but at a slower rate than if the variables were independent.

The genetic correlations between productive characteristics are of importance in the formulation of selection indices. In simple terms, the amount of progress that can be made by selection for any one characteristic is determined by its heritability and the amount of selection that can be practiced. In practical breeding we seldom select for one characteristic alone, but for several. Genetic inter-relationships between productive characteristics then become important in deciding how improvement might be most efficiently accomplished.

The correlations derived here will be the basis of a future study on selection and selection indices for dairy cattle breeding, and of a more complete investigation of genetic causes and effects in milk production.

THE EFFECT OF MILD INBREEDING ON PRODUCTION

Inbreeding has played an important role in the development of many of our breeds of livestock. Bakewell successfully used the method as a tool in his breeding operations with sheep and Shorthorn cattle. Generally, inbreeding has found little favor in practical breeding programs. Its deleterious effects have been long known and well recognized. It it quite generally agreed that only superior stock can be successfully inbred. The occurence of abnormalities from matings of closely related animals all of which are more or less heterozygous, has been the principle reason for its disfavor among many breeders. The object of inbreeding experiments with dairy cattle has been to increase uniformity of type, production and transmitting ability and maintain or increase over-all performance and appearance. Attempts to produce superior homozygous lines in dairy cattle have not been very successful because of the many genes involved and the heterozygosity of our dairy cattle population in general.

Inbreeding experiments with dairy cattle have been conducted by the Bureau of Dairy Industry at its Beltsville station and by the New Jersey and California Experiment Stations. With few exceptions a decline in many characteristics has been noted as the degree of inbreeding progressed.

Results of the Beltsville inbreeding experiment are reported by Woodward and Graves (1946) and Swett *et al.* (1949). A marked decline in milk yield was noted when inbreeding reached 25 per cent and above. In this work breed differences are confused with inbreeding observations. Butterfat test decreased rapidly but this was probably due to the use of Holstein sires on foundation stock of Guernsey breeding. The above workers found that measures of producing ability were more definitely influenced by intensive inbreeding than were measures of body, organ and gland sizes.

Bartlett and coworkers (1939, 1942, 1944) report the New Jersey Station inbreeding experiment results. Only one of four foundation sires of this experiment produced progeny with production that withstood the effects of inbreeding. Inbred descendants of this sire showed little difference from outbred controls for coefficients of inbreeding up to 20 per cent. The average milk and butterfat production of inbred daughters was generally somewhat lower than that of outbred controls. Five animals, inbred over 20 per cent showed a marked reduction in production. Little difference was noted between inbred and outbred groups as to butterfat percentage.

Preliminary results of the effect of inbreeding on production in Holsteins at the California Station are reported by Ralston *et al.* (1948). With each successive generation of sire-daughter matings birth weight and rate of growth declined. Butterfat production declined 5.1 pounds per one per cent increase in inbreeding.

Nelson and Lush (1950) report the results of an experiment to determine the effect of mild inbreeding accompanied by selection for high production. They found a decrease of 4.5 pounds of butterfat for each one per cent increase in inbreeding within sire progeny groups.

Tyler *et al.* (1949) analyzed the milk and butterfat production records of 47 outbred and 42 inbred daughters of 5 sires. The intra-sire decrease in production per one per cent increase in inbreeding was found to average 74 pounds of milk and 2.3 pounds of butterfat. They observed no apparent effect of inbreeding on butterfat percentage.

In the above mentioned studies inbreeding has been measured by the coefficient proposed by Wright (1922).

The data used in the present analysis of Holstein cattle in the Missouri Station herd are the inbreeding coefficients, determined by the application of Wright's formula. The 305, 2X mature equivalent, herd test records were used. The lifetime average of each cow was used as the measure of her productivity. Lifetime averages, regressed to the herd mean as previously discussed were also used. Production records of milk, butterfat, and test, and inbreeding coefficients, of 299 cows representing the progeny of 34 sires were available. Correlation and regression analysis was conducted on an intra-sire basis. The amount of inbreeding in this herd is low and it has been the result of a general line-breeding program to the Ormsby family. Only 20 cows have coefficients of inbreeding about 20 per cent, none of the cows with records had coefficients above 29 per cent. Due to the frequent introduction of unrelated sires the amount of inbreeding has not risen steadily over the 48 year period involved. The average inbreeding of heifers entering the herd by five year periods is shown in Table 28. The increase in inbreeding during the last ten years has been

TABLE 28.—AMOUNT OF INBREEDING BY FIVE YEAR PERIODS

Period	No. Cows	Ave. Coefficient of Inbreeding
1903 to 1910	13	0.022
1910 to 1915	15	0.010
1915 to 1920	19	0.053
1920 to 1925	34	0.075
1925 to 1930	18	0.012
1930 to 1935	52	0.014
1935 to 1940	46	0.015
1940 to 1945	49	0.069
1945 to 1950	68	0.086
Total and Average	314	0.047 ± 0.004

due to a line-breeding program directed toward the Ormsby-bred herd sire Man-O-War 69th through the use of six of his sons.

The findings of the intra-sire correlation and regression of production on inbreeding are presented in Table 29.

TABLE 29.—THE INTRA-SIRE CORRELATION AND REGRESSIONS OF PRODUCTION ON INBREEDING

Record	Correlation	Regression
Milk Production	$-0.22 \pm 0.06^{**}$	-66.08^{**}lbs.
Butterfat Production	$-0.21 \pm 0.06^{**}$	-2.07^{**}lbs.
Butterfat Percentage	$+0.07 \pm 0.06$	+0.003 %

$^{**}P < 0.01$

These coefficients for milk and butterfat are significant at the one per cent level of probability for this amount of data, but are not significant for butterfat percentage. The regression estimates indicate that milk production decreased about 66 pounds and fat production about 2 pounds for each increase of one per cent in inbreeding. The percentage of butterfat is evidently unaffected by this amount of inbreeding so far as can be determined from data available.

These findings are in agreement with those of Tyler *et al.* (1949), and Nelson and Lush (1950) which were based on similar material and methods of analysis.

The records were sorted into inbreeding groups and the averages of these groups are shown in Table 30. The effect of inbreeding on the average records is not noticeable up to about 15 per cent. From this

TABLE 30.—THE EFFECT OF MILD INBREEDING
(Lifetime Averages of 299 Cows from Intra-Sire Groups)

Inbreeding Group	No. Cows	No. Sires	Milk	Average Fat	%	Records Per Cow
00	103	21	10,410	355	3.41	3.3
.01 - .05	113	20	10,668	380	3.56	3.2
06. - .10	32	12	10,388	361	3.48	2.8
.11 - .15	21	9	10,524	367	3.49	2.4
.16 - .20	10	5	10,010	357	3.57	2.6
.20	20	8	8,840	318	3.60	1.9
Average			10,395	363	3.50	

grouping it would appear that the percentage of butterfat increased with inbreeding. The regression is positive (Table 29) but not significant for the volume of data available. The effect here may be due to the inverse relationship between milk yield and test rather than to any effect of inbreeding itself. The intra-sire effect of inbreeding is shown more clearly in tabular form by Table 31. The number of daughters in the various categories of inbreeding are very small, particularly where there was no design in the early program of the herd to obtain inbred and outbred daughters from each sire. It is evident that while the general trend

TABLE 31.—DAUGHTER'S PRODUCTION BY SIRES HAVING THREE OR MORE DAUGHTERS IN TWO OR MORE INBREEDING GROUPS

Sire No.	No. Dtrs.	Inbreed Group	Ave. Milk	Ave. Fat	Ave. Per Cent
3	4	.00	10,650	337	3.17
	4	.01-.05	8,425	270	3.27
5	6	.06-.10	8,967	268	2.97
	3	.11-.15	9,033	280	3.13
7	13	.01-.05	9,092	299	3.30
	4	.06-.10	8,800	310	3.55
15	5	.00	10,340	374	3.66
	9	.01-.05	11,755	430	3.67
	3	.06-.10	11,467	405	3.50
21	6	00	10,317	374	3.65
	30	.01-.05	10,814	398	3.69
	3	.20-.30	8,633	321	3.77
26	6	.01-.05	11,367	409	3.66
	6	.10-.15	11,483	408	3.55
28	4	.01-.05	11,600	417	3.60
	3	.10-.15	9,933	362	3.63
30	4	.01-.05	10.575	382	3.62
	6	.06-.10	11,083	416	3.78

in production is downward, considerable variation between sires as to the effects of inbreeding exist. This was found to be true by Tyler and co-workers in their study.

The lifetime averages of the more highly inbred cows (10 per cent and over) tended to be based on fewer records. Thus we might have less confidence in them as measures of the cows' real ability to produce. When all averages were "regressed" to a contemporary herd average as previously described, the regression of production on inbreeding was found to be as indicated in Table 32.

TABLE 32.—THE INTRA-SIRE CORRELATION AND REGRESSIONS OF PRODUCTION ON INBREEDING BASED ON MOST PROBABLE PRODUCING ABILITY

Record	Correlation	Regression
Milk Production	–0.16*	–30.74**lbs.
Butterfat Production	–0.15*	– 0.88* lbs.
Butterfat Percentage	+0.09	+0.002 %

**P <0.01
*P <0.05

On this basis the direction of the effect of inbreeding remains downward but the amount of the effect per unit increase in inbreeding is approximately halved for milk and fat yield but unchanged for test. The level of significance of the regression of butterfat yield on inbreeding tends to decrease. It indicated that in one time out of twenty, for a sample this large, a coefficient of - .88 might occur by chance alone. In the study of the heritability of the "regressed" records their exact value is not clear. The reduction in the regression would be expected from the mere statistical effect of applying the formula for most probable producing ability. The variation in the dependent variable is distinctly reduced. However, if the variation in "regressed" records were more largely genetic, the correlation with inbreeding should have been increased, not reduced, in size. This may mean that the "regressed" values are a poorer measure of inherent producing ability due to the introduction of yearly fluctuations. The total standard deviation of milk records was reduced 35 per cent and that of fat records 31 per cent by "regressing" the records to the herd average. The independent variable, inbreeding, of course remained unchanged.

The results of this study of the effect of inbreeding in the Missouri Station Holstein herd indicate a significant decline in milk and butterfat production. No change in butterfat percentage may be attributed to the mild inbreeding practiced in this herd.

SIRE PERFORMANCE

The transmitting ability of the 34 sires included in this study, as measured by the production of their progeny, is of much practical interest. The sires are listed in sequence of their use in the Missouri Station herd in Table 33. Twenty of the sires had at least five daughter-dam comparisons. The amount of inbreeding and the average production of the progeny are given in Tables 34 and 35. Figure 6 shows a graphic comparison of the milk production of the daughters and dams.

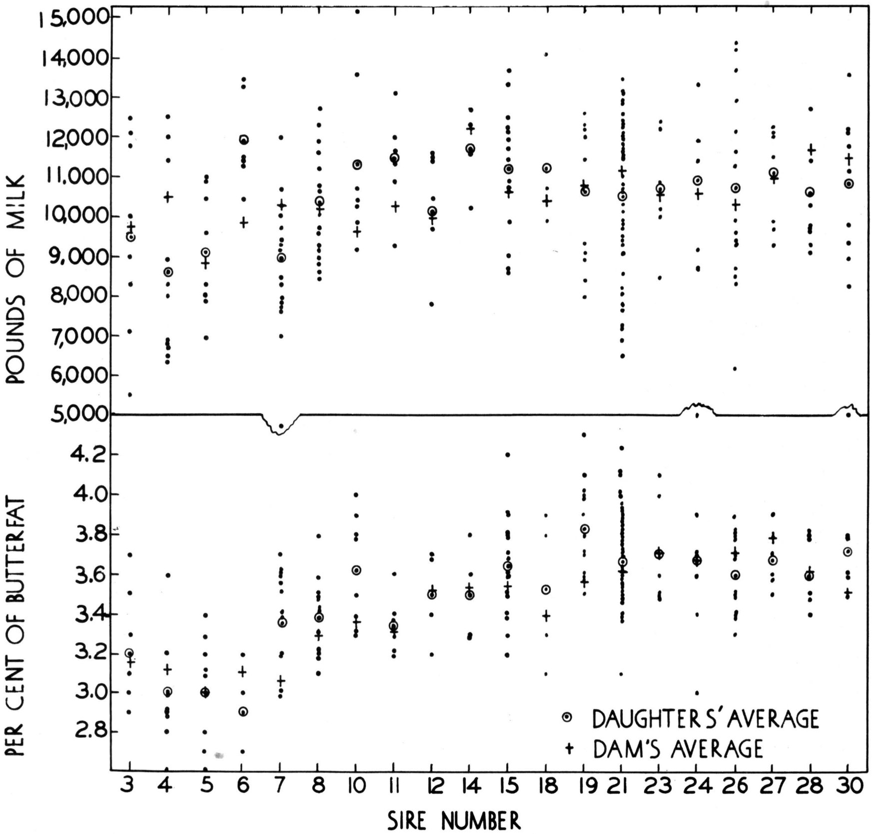


Figure 6. Daughter-Dam comparisons of the most extensively used herd sires.

The progeny of only eight of the sires had an average coefficient of inbreeding over five per cent. Sire 5 is a son of sire 3 out of one of the foundation cows. Several half sister and cousin matings resulted in an average inbreeding coefficient of 0.07 per cent for his daughters. Sire 7 is a paternal half brother of sire 3 and his progeny contain two sire-daughter matings, so that the average inbreeding of the group is about seven per cent. Sire 21, Man-O-War 69th, was used more extensively than any other sire in the group. He was in active service at the age of eighteen years. The inbreeding of his progeny is due to two sire-daughter matings and six sire-granddaughter matings. He also carried a slight relationship to the herd through his grandsire Sir Pietertje Ormsby Mercedes 37th who was the grandsire of bull 10 as well

TABLE 33.—LIST OF HERD SIRES STUDIED

Sire Code No.	Name	Reg. No.	No. of Tested Dtrs.	Year Born
1	Gerben Hengerveld Sir De Kol	26780	2	1899
2	Missouri Chief Bassano	26553	1	1897
3	Pontiac Cronus	28835	8	1900
4	Leland Sarcastic	42451	12	1906
5	Sir Carlotta Pontiac	38652	11	1905
6	Missouri Chief Josephine Lad	70875	7	1910
7	Sir Korndyke Hengerveld De Kol	41266	24	1905
8	King Fayne Ormsby	237602	22	1917
9	Campus Sir Korndyke Zeus	273498	3	1919
10	Sir Fonda Hengerveld Ormsby	365514	8	1921
11	Grahamholm Colantha Sir Aaggie	457192	6	1924
12	Grahamholm Colantha Duke	455570	5	1924
13	Commander Ormsby	335433	3	1920
14	King Lothian Sweet	554188	6	1927
15	Campus Aaggie Segis Sultan	586515	20	1928
16	U-Neb. Count Ormsby Caesar	415211	5	1923
17	Fredmar Korndyke Lad	445805	4	1923
18	Triune Supreme	543327	11	1927
19	Abbekerk Sylvius Lad 24th	587730	13	1928
20	Man-O-War 56th	608782	3	1929
21	Man-O-War 69th	639850	46	1930
22	U-Mo Vesper Triune Supreme Von	714072	2	1934
23	Campus Fonda Ormsby Master	541169	7	1927
24	U-Mo Vesper Man-O-War Nero	733630	7	1935
25	U-Mo Vesper Man-O-War Vim	733631	1	1936
26	U-Mo Vesper Man-O-War Zirc	733633	18	1936
27	U-Mo Vesper Man-O-War Zev	733632	9	1936
28	U-Mo Aaggie Sultan Tom	763391	10	1937
29	U-Mo Man-O-War Leader	806024	2	1939
30	Kanowa Minerva Posch Ormsby	816269	10	1940
31	U-Mo Man-O-War Ace	837287	4	1941
32	U-Mo Posch Ormsby Forward	875292	1	1942
33	U-Neb Pan Achievement	895685	5	1943
34	Hamer Ormsby Chieftain Posch	947834	3	1944

Sires listed 24, 26, and 27 are sons of Man-O-War 69th and their progeny contain several full and half-sib matings which represent the most highly inbred groups in the herd.

TABLE 34.—THE PERIOD OF USE AND AVERAGE INBREEDING OF DAUGHTERS OF SIRES WITH FIVE OR MORE DAUGHTER—DAM COMPARISONS

Sire No.	No. of Dtr.-Dam Prs.	Period Dtrs. Enter Herd	Ave. Inbreeding of Dtrs.
3	8	'07 - '10	0.010
4	11	'11 - '13	0.000
5	11	'14 - '17	0.070
6	7	'15 - '19	0.034
7	19	'18 - '23	0.065
8	22	'22 - '27	0.000
10	8	'28 - '30	0.024
11	6	'29 - '31	0.000
12	5	'30 - '32	0.034
14	5	'33 - '34	0.000
15	18	'34 - '40	0.031
18	6	'32 - '38	0.012
19	13	'36 - '38	0.000
21	44	'38 - '49	0.050
23	7	'39 - '40	0.034
24	7	'41 - '43	0.127
26	16	'41 - '49	0.118
27	7	'42 - '49	0.113
28	9	'42 - '44	0.078
30	10	'45 - '49	0.055

Nearly half of the sires listed in Table 32 were bred in the University of Missouri herd. These are numbers 5, 6, 7, 9, 15, 22, 23, 24, 25, 26, 27, 28, 29, 31 and 32. Eleven sires represent outcrosses; that is, they were almost totally unrelated to any members of the herd. This group consists of sires numbered 2, 4, 8, 11, 12, 14, 16, 17, 18, 19 and 33.

Three of the early herd sires, numbers 1, 3 and 7, were collateral relatives of Sir Pietertje Ormsby Mercedes through De Kol 2nd by a line of descent representing nine generations. King Fayne Ormsby, sire number 8, a son of "Old Sir Piet", was the first of the "Ormsby" sires used in the herd. The remaining sires purchased have largely been members of the Ormsby family. The relationship to Sir Pietertje Ormsby Mercedes is carried largely through his son Sir Pietertje Ormsby Mercedes 37th. These are sires numbered 10, 13, 20, 21, 30 and 34. This line up of sires has resulted in a mild linebreeding program within the Ormsby cattle maintained at the Missouri Station.

TABLE 35.—DAUGHTER-DAM COMPARISONS OF SIRES HAVING AT LEAST FIVE TESTED DAUGHTERS FROM TESTED DAMS IN THIS HERD

Sire Code No.	Average Milk Yield Dtrs.	Dams	Difference	Average Test Dtrs.	Dams	Difference
3	9,538	9,688	- 150	3.22	3.16	+.06
4	8,563	10,545	- 1,982	2.90	3.10	- .20
5	9,127	8,863	+ 264	3.04	2.98	+.06
6	11,914	9,814	+2,146	2.90	3.10	- .20
7	8,937	10,321	- 1,384	3.37	3.06	+.31
8	10,309	10,204	+ 105	3.38	3.29	+.09
10	11,312	9,650	+1,662	3.62	3.36	+.26
11	11,367	10,250	+1,117	3.35	3.30	+.05
12	10,220	9,980	+ 240	3.50	3.52	- .02
14	11,700	12,120	- 420	3.50	3.54	- .04
15	11,161	10,589	+ 572	3.63	3.54	+.09
18	11,250	10,433	+ 817	3.53	3.40	+.13
19	10,562	10,692	- 130	3.83	3.57	+.26
21	10,534	11,130	- 593	3.68	3.63	+.05
23	10,714	10,586	+ 128	3.70	3.70	+.00
24	10,971	10,586	+ 385	3.67	3.77	- .10
26	10,694	10,344	+ 350	3.60	3.71	- .11
27	11,143	10,986	+ 157	3.68	3.78	- .10
28	10,578	11,722	- 1,144	3.61	3.60	+.01
30	10,880	11,370	- 490	3.72	3.50	+.22

In recent years a more intense secondary line breeding program has been directed toward Man-O-War 69th through the use of his sons in the herd. This bull and two of his sons are shown in Plate 3.

The performance of sires having five or more daughter-dam comparisons is presented in Table 34. On the basis of daughter-dam comparisons ten sires increased the milk production of their daughters above the levels of the dams. Fifteen increased butterfat production and thirteen increased the butterfat percentage of daughters over their dams. The distribution of the daughters' milk production and butterfat percentage is shown in Figure 6. A glance at the daughter-dam comparison Table 34 calls attention to the damaging influence of Leland Sarcastic, sire 4. All of his daughters except two of those below the group average produced offspring who entered the herd. It is of interest to note that sire 6, Table 34, a son of Leland Saracastic, and the cow Missouri Chief Josephine sired daughters with the greatest increase in milk yield and one of the greatest decreases in fat percentage of any of the sires studied.

In the case of sires 1 to 4. each was used largely on the daughters of the preceding sire. In the case of sires numbered 5 and above the mates of each sire represent several previous sires. As cows made more than

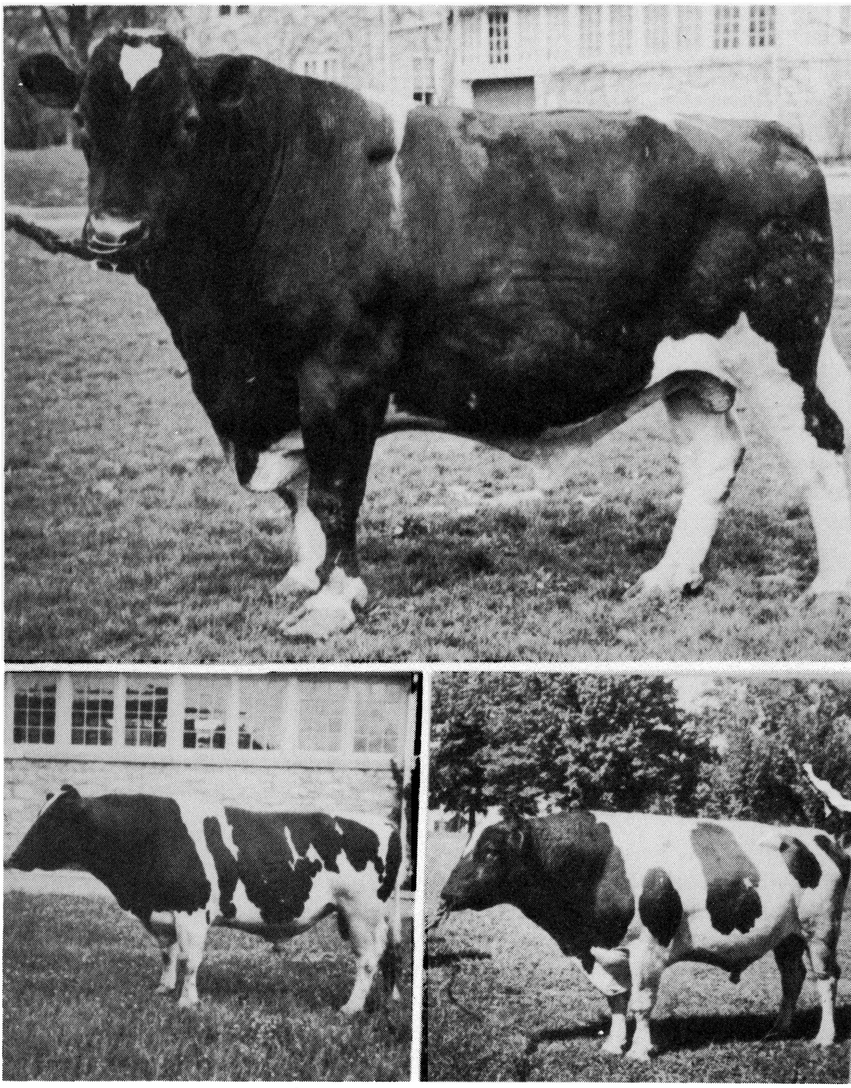


Plate 3. Three of the Missouri Station herd sires.

Top: Man-O-War 69th 639850 at the age of eighteen years. This bull was a grandson of Sir Pieterje Ormsby Mercedes 37th 110160.

Lower Left: U-Mo. Vesper Man-O-War Zirc 733633 and

Lower right: U-Mo Vesper Man-O-War Zev 733632, twin sons of Man-O-War 69th pictured above.

a single record and were kept in the herd longer they were often mated to two or more sires. There is a great deal of generation overlapping shown in Figure 6. The sires are plotted in the order of their use so that the general trend in production from 1902 to 1950 is shown.

The daughter-dam comparisons for all 34 sires indicate the 17 sires had progeny whose average milk production was above the level of their dams. Twenty-one sires brought about an increase in butterfat production and 20 in butterfat per cent. The over all daughter-dam difference for all sires was - 88 pounds milk, - 0.5 pounds fat and+ 0.05 per cent of fat.

Pictures of several of the outstanding females representing the middle and late periods of the herd are shown in Plates 1 and 2 on page 3 of this publication. From the early period, Missouri Chief Josephine is shown in Plate 4. Her first record was completed in 1905. Her lifetime average of five records was 13,000 pounds of milk testing 2.7 per cent. She left two daughters and a son, Missouri Chief Josephine Lad 70875, in the herd. Carlotta Pontiac, another daughter of a foundation cow, is also shown in Plate 4. Her lifetime average of eight records was 12,500 pounds of milk testing 3.0 per cent. Plate 1 shows ten of the daughters of King Fayne Ormsby. The averages of eight of these daughters are compared with those of their dams in Table 35 and in Figure 6. Four of the recent outstanding females are shown in Plate 2. Freda, herd number 733, is in the herd at this date, but the others have left the herd. Freda in her first eight records averaged 13,500 pounds of milk testing 3.6 per cent of butterfat. Louise, herd number 739, produced an average of 12,300 pounds of 3.8 per cent milk in six lactations. Zora, herd number 764, averaged 10,800 pounds of 3.9 per cent milk in four lactations. Ella, herd number 793, averaged 12,900 pounds of 3.8 per cent milk in seven lactations. All of these averages are expressed in terms of herd test, 305 day, 2X, mature equivalent records.

Dairy cattle breeders have long attempted to explain favorable results of breeding on the basis of "nicking" or epistasis. With this thought in mind the daughter-dam comparisons for each sire were grouped according to maternal grandsires as a preliminary step in an investigation of "nicking". The data give no evidence that "nicking" or epistatic interaction has been a factor of importance in sire performance in this study. Evidence that epistatic interaction may be important in the performance of certain sires has been reported by Heizer *et al.* (1938) and Johnson *et al.* (1940). Seath and Lush (1940), however, compared the variation between maternal grandsire groups with that within the groups for several sires and concluded that "nicking" was of little consequence if it occurred at all. Epistasis did not appear to warrant consideration in the proving of sires in the present study.

Due to the fact that both cows and sires are kept in a herd for varying lengths of time, and that cows may produce several offspring by as many different sires, it is not possible to show progress per generation in the simple manner that applies to a one sire herd. Female generations may be readily separated if the foundation cows are designated as generation O,

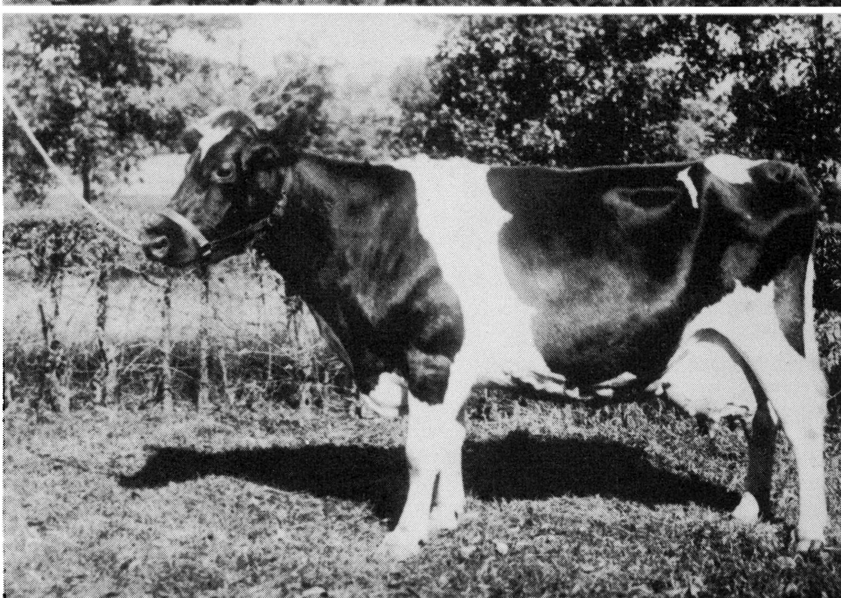


Plate 4. Two of the early females from the Missouri Station herd, daughters of two of the foundation cows.

Top: Missouri Chief Josephine 64867 (Herd No. 207) a daughter of Missouri Chief Bassano 26553.

Bottom: Carlotta Pontiac 84294 (Herd No. 209) a daughter of Pontiac Cronus 28835.

their offspring generation 1, and so on. These generations for cows in this study are listed in Table 36. Those cows designated as "selected" are cows which had at least one daughter in the herd. Slightly over 50 per cent of the cows completing at least one record left daughters in the herd who in turn made at least one production record. The members of each generation are the daughters of from 2 to 14 different sires thus progress per generation is difficult to assign. For both lines "selected" dams averaged about 200 pounds of milk more than all dams per generation. This differential, however, ranged from - 293 pounds to + 534 pounds of milk. The differential for butterfat percentage ranged from + 0.21 to - 0.19 and averaged about + 0.02 per cent per female generation. Plotting the production per generation gave a picture very similar to that shown in Figure 4.

TABLE 36.—FEMALE GENERATIONS REPRESENTED IN THE HERD

Female Generation	Period Members Entered Herd	Total Number	Number Selected	Per Cent Selected	Number of Different Sires
University Line					
0	'03	4	3	75	
1	'05 - '12	7	7	100	4
2	'08 - '21	18	13	72	5
3	'11 - '33	25	15	60	6
4	'14 - '37	31	19	61	9
5	'20 - '39	27	15	56	9
6	'23 - '47	33	15	45	14
7	'28 - '48	30	13	43	13
8	'32 - '49	25	12	48	18
9	'34 - '49	19	5	26	9
10	'38 - '49	10	2	20	6
11	'42 - '48	4	3	75	2
12	'46 - '49	3	1	33	3
Total		236	123	52	—
"Vesper" Line					
0	'32 - '33	17	8	47	4
1	'32 - '45	15	10	67	6
2	'37 - '44	17	11	65	8
3	'43 - '49	14	6	43	7
4	'42 - '49	9	2	22	5
Total		72	37	51	—

The dams studied averaged approximately 4 lactation records each. Table 3 shows the average age at the start of the fourth lactation to be nearly 6 years. This would indicate a genertion interval of about 6 years in this herd. Lush (1945) states the average generation interval for dairy cattle (D. H. I. A.) is from 4 to 4.5 years.

In the rising segment of the curve as shown in Figure 4, an increase of approximately 1500 pounds of milk, 100 pounds of butterfat, and 0.5 per cent in butterfat test per cow is noted. This would reflect a progress per generation from 1915 to the present date of about 259 pounds of milk, 17 pounds of butterfat and .09 per cent of butterfat.

The standard deviation between cows is of the order of 2,000 pounds of milk, 70 pounds of butterfat, and 0.31 per cent of butterfat. The maximum selection differential obtainable (Lush 1945 p. 148), where fifty per cent of the population is saved, is 0.80 of a standard deviation. If heritability is about 0.33 then the progress per generation would be about 0.80 x 0.33 or 0.26 standard deviations. If heritability were 0.50 then the fraction would be 0.40. Maximum progress per generation then (where the number saved is the only limiting factor) would be 520 pounds of milk, 18 pounds of butterfat, and 0.12 per cent butterfat. From this reasoning the progress in milk production over the past 35 years has been about one-half the estimated maximum according to Lush, while progress per generation in butterfat yield and butterfat per cent has approached the estimated maximum rate as observed in similar studies.

DISCUSSION

The objective of this study has been to standardize the records of the Missouri Station Holstein-Friesian herd for the major recorded non-hereditary sources of variation, then to investigate some of the genetic factors involved in milk and butterfat production.

A time period of nearly half a century is covered. When production is plotted against time as in Figures 4 and 5 it is observed that the general trend in production over most of the period has been upward. When the records are analyzed for differences between periods these prove to be unquestionably real (Table 14). The three factors studied—milk yield, butterfat yield, and butterfat percentage—each show distinct changes in amount with respect to time trend.

When the herd's history was subdivided into five year periods (Table 13), the percentage of the total variance associated with differences between periods has been about 5 per cent for milk production and 20 per cent for butterfat production and nearly 40 per cent for butterfat percentage. Total production has been improved, but butterfat test which is the ratio between total milk and butterfat yield has been moved upward most markedly.

The environment of the herd has always been good. No marked changes in feeding, management or breeding policies have been recorded. Studies of the reasons for disposal (Table 1) and of the average calving intervals (Table 6) indicate good practical herd management.

The records studied were readily standardized for length of lactation by merely totaling the actual production for the first 305 days. It has been previously demonstrated that this procedure quite effectively removes variation due to length of calving interval as well.

Standardization of records for age presented a more difficult problem since many factors are involved in the observed curve of production on increasing age. Age-conversion factors as commonly used possess many faults as age only generally reflects increasing body size and weight, mammary gland development and finally senescence. Methods of expressing milk yield independent of age and liveweight difference have been proposed by Gaines and co-workers at Illinois (Gaines *et al.* 1940, Gaines 1940 *a, b,* and Gaines *et al.* 1947). These workers present evidence to support their theory that milk energy yield (FCM) per unit of body weight at the initation of lactation is a measure of lactational ability more free of age effect than is age-corrected milk yield. Kleiber and Mead (1941 and 1945) are in disagreement with the above theory in that they believe the use of the three-quarters power of body weight rather than the first power more accurately portrays lactational capacity. This second theory is supported by Brody and co-workers at Missouri (Brody 1945, ch. 22).

The use of these methods of standardization necessitate the use of a constant-energy milk yield, best expressed as 4 per cent fat corrected milk (Gaines and Davidson 1923). It would then be impossible to study separately the inheritance of milk and butterfat production and butterfat percentage. Body weight is also seldom available at a definite period in each lactation.

The applicability of published age conversion factors to this particular herd was questioned. In order to satisfy this doubt, factors were derived from the present data. These were found to be only slightly superior to the published Holstein-Friesian Association H. I. R. factors. The number of records available in any single herd for an age class is usually small. Time trends would further tend to increase variability within age classes, although it should not greatly change the relation between production and age where herd management is uniform.

The great influence of environment on milk yield is demonstrated by the difference between age-corrected "Official Test" and "Herd Test" records. In the Missouri Station herd, cows on official test averaged 47 per cent more milk than the same cows on herd test. Essentially no change occurred in butterfat percentage. Differences between the two systems of testing in this herd included a slightly longer calving interval, higher feeding plane, box or tie stalls rather than stanchions and three times a day as compared to twice a day milking. A slight "carry over" effect of the official testing regime was noted in the subsequent lactation. If there was any tendency to select the better cows or heifers for official testing a genetic factor would be included in this observation. Linfield (1900) was probably first to express the idea that good feeding tends to develop the latent capacity of a good dairy cow and may enable her to do better in succeeding lactations. How this applies to the adequate feeding of herd testing conditions versus the more-than-adequate (for practical farm conditions) feeding of official test conditions is not completely agreed upon. The definition of an adequate feeding level will be controlled by many factors, of which the milking capacity of the cows and feed-cost factors probably are most important. Production tends to increase at a decreasing rate with additional feeding and times a day milking. Cost factors will largely determine the feeding and management level most practical under farm conditions.

If environmental variation could be completely removed from records, and they could be perfectly standardized for age and developmental differences, then any single record would probably accurately measure a cow's inherent producing ability. It is, however, impractical to correct for a large number of factors and impossible to eliminate completely differences due to environmental influences as these cannot all be accurately recorded and measured. The degree to which a single record indicates inherent productivity may be estimated by the average correlation between records of the same cow. This is referred to as the repeatability of records, r. Then (1 - r) is an estimate of the influence of temporary environmental differences between records. The repeatability findings for the standardized records of the present study are given in Table 12. The values of 0.41 for milk, 0.36 for butterfat, and 0.61 for butterfat per cent are in general agreement with findings reported in the literature. It would be concluded then that the corrections for major environmental influences have been no better nor worse than in previously reported studies.

Repeatability was studied for several purposes: to give one estimate of the effects of record standardization; to find, for this herd, the r value that should be used to predict the most probable producing ability of a cow; to compare repeatability with heritability estimates from the same data; and to add further information as to the actual probable magnitude of this value in a selected herd.

While repeatability indicates the inherent producing ability of a cow, only a portion of this will be due to genetic factors which may be transmitted to offspring. The simple additive genetic effects will, but dominance effects will not be transmitted. Only a fraction of the genetic effects due to epistatic interaction will be transmitted to the offspring in the gamete. The repeatability estimate also includes permanent environmental effects. These, of course, cannot be transmitted. Thus heritability estimates will be expected to be lower than repeatability estimates (Plum 1935).

These two estimates from the present study are listed together in Table 16. The proximity of these figures may indicate that additive inheritance is of primary importance in differences between productive ability of individuals. If so, the simple and widely used principle of mass selection, as discussed by Wright (1939), should result in efficient genetic progress.

However, if dominance and epistatic deviations are of little importance, then it becomes more difficult to explain the important and consistently observed depressing effects of inbreeding.[1] Inbreeding reduces heterozygosity; this must bring about a reduction in dominance deviations as well. In

[1]Dr. G. E. Dickerson. Private communication with the author.

almost all cases of productive characteristics of farm livestock a lowering of production is noted as inbreeding progresses. This reduction has been observed to take place even when fairly intensive selection is directed toward maintaining production. This situation may indicate heterozygosity has some advantage in selection practices. It is thus somewhat puzzling that evidences of dominance and epistatic deviations are not greater than usually observed.

The most perplexing finding of this study is the failure of the estimated most probable producing ability of cows to show an increase in the correlation between daughter and dam records. This evidently means that while we have less confidence in a lifetime average based on a single record as an indication of real ability, the chances that this single record is above or below the actual ability are equal and regressing it toward the herd average will not improve its value. The diagram below where L represents probable limits of actual producing ability illustrates this idea. If Cow A has a lifetime average of only one record, on the basis of repeatability studies we have less confidence in this value as an indication of real ability, than in the average of Cow B who has five records. However, the actual ability for Cow A might vary with equal probability from L_1 to L_2. The true ability of Cow B will vary within a more narrow range, L_3 to L_4, but with equal probability of approaching either limit.

L_1 L_3

Ave. of Five Records

Ave. of One Record

L_4

Herd Average

L_2

Cow A Cow B

This is contrary to the hypothesis of Berry and Lush (1939), Lush (1945), and Berry (1945). Their basic idea is that where no record is available, the population average is the best estimate of a cow's ability. Therefore where only one or two records are available, as compared with larger numbers, the deviations from the population mean may be brought back toward this mean for a better estimate in accordance with the repeatability and number of records concerned. In the population studied the results observed might be due to the effects of cow selection. Selection could cause the lifetime average to be biased upward, and the amount of bias increases the longer a cow remains in the herd. The present interpretation of the findings has broad implications to our systems of weighting information for selection purposes. It must be further investigated.

The study of the interrelationships between the three productive measures indicates that the secretion of total milk and butterfat are largely determined by the same genetic factors. The correlations between milk and fat support the validity of the general practice of applying the same age-conversion factors to both. Since milk and butterfat are not independent a study of the genetic relationships between fat and non-fat components is proposed. This should give a better understanding of the genetic cause and effect relationships existing in milk secretion.

The present findings on the effects of mild inbreeding add additional evidence to the accumulating literature indicating a slight but significant downward trend in milk and fat yield but no change in butterfat test. In terms of the probable effects of intense inbreeding (50 to 100 per cent) the downward trend may be very pronounced.

The percentage of butterfat is sometimes thought of as a separate characteristic, and when treated as such it shows a high degree of repeatability and heritability. Real genetic change should thus be quite readily accomplished. The time trend of butterfat percentage in this herd has been definitely upward due to a deliberate attempt to improve butterfat test. The position of the herd in relation to the breed average has been a factor in the upward trend which is followed by the tendency to level off over the past few years as the breed average was approached. (Figures 4 and 5.) Were it not for the reduction in milk yield due to a single early herd sire, the improvement in milk production to the present level would probably be of doubtful significance. The present findings are interpreted to indicate genetic improvement in all three characteristics studied, particularly in butterfat percentage.

SUMMARY

1. An analysis has been made of all normal lactation records (up to the ninth record of each cow) in the Missouri Station Holstein-Friesian herd from its foundation in 1902 to January first 1950. There were 314 cows with a total of 933 lactation records. The progeny of 34 herd sires are represented with a total of 299 tested daughters. A total of 270 daughter-dam pairs were available for comparison.

2. All lactation records were standardized to a herd test, 305 day, twice-a-day milking, mature equivalent basis. The factors used for the standardizations for major non-hereditary sources of variation were derived from the data.

3. The derived age conversion factors for this herd differed only slightly from the published Holstein-Friesian Association H. I. R. factors. Advanced Registry testing, which included three times-a-day milking, accounted for an average increase in milk and butterfat production of 47 per cent over the production of the same cow under herd test conditions. Compared to the otherwise uncorrected 305 day records, the correction for Advanced Registry testing reduced the coefficient of variation between records of the same cow by 4 per cent and increased the correlation between these records by 5 per cent. Age conversion by the Holstein-Friesian Association factors and by the presently derived factors reduced the above coefficient of variation by 7 and 8 per cent respectively and increased the correlation by 11 and 15 per cent respectively.

4. A significant upward time trend in milk and butterfat production and in butterfat percentage was found for the Missouri Station herd. Differences between 5 year time periods accounted for 5.5 per cent, 20.4 per cent, and 38.8 per cent of the toal variance in milk production, butterfat production and butterfat percentage respectively. On the basis of contemporary records estimates of how nearly a cow tends to repeat her performance record after record (repeatability) were 0.41 for milk production, 0.36 for butterfat production and 0.61 for butterfat percentage.

5. The lifetime average was used as the measure of each cow's producing ability. Heritability estimates were derived from lifetime averages but are expressed on the basis of single records for comparison with previous studies. Heritability estimates derived from the intra-sire regression of daughter on dam were: for milk production 0.36, for butterfat production 0.29, and for butterfat percentage 0.54. The variation of daughters' and dams' records was found to be essentially equal, thus intra-sire daughter-dam correlation and regression estimates of daughter on dam were of equal magnitude. When each cow's lifetime record was expressed as her most probable producing ability no increase was observed in the correlation between the records of daughter and dam. An attempt to estimate heritability by half sister and full sister correlations was not entirely successful.

6. The correlation between lifetime average milk and butterfat yield was found to be +0.89; between milk yield and butterfat per cent, -0.10; and between butterfat yield and butterfat per cent, +0.35. The corresponding genetic correlations were estimated by two methods: (a) by the ratios of appropriate regression coefficients and (b) by the ratios of genetic covariance to the geometric mean of genetic variance estimates. The estimated genetic correlations by method (a) were: +0.87 between milk and butterfat yield, -0.52 between milk yield and butterfat per cent, and -0.03 between butterfat yield and butterfat per cent. The three estimates by method (b) were: + 0.99, -0.20 and -0.13 respectively. Both the gross and genetic correlations indicate a slight but real relative decline in butterfat percentage may be expected to accompany increased milk production.

7. The effect of mild inbreeding was analyzed by the intra-sire regression of production on inbreeding. A significant decline of 66 pounds of milk and 2 pounds of butterfat per one per cent increase in inbreeding was observed. There was no significant effect on butterfat percentage.

8. The performance of herd sires as indicated by daughter-dam comparisons is presented for 20 sires having at least 5 daughter-dam pairs. Ten of these sires increased milk production, 15 increased butterfat production, and 13 increased butterfat percentage of the daughters over their corresponding dams. No evidence of nicking was found in a tabulation of sires' daughters according to their maternal grandsires.

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