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To the Committee on Graduate Study:

I submit herewith a thesis written by Mr. Paul C. Swanson and entitled "Inheritance of Milk and Butterfat Production in Dairy Cattle," and recommend that it be accepted for nine quarter hours credit in partial fulfillment of the requirements for the degree of Master of Science, with a major in Dairy Husbandry.

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At the request of the
Committee on Graduate Study,
we have read this thesis,
and recommend its acceptance.

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**THE INHERITANCE OF MILK AND
BUTTERFAT PRODUCTION IN DAIRY CATTLE**

A THESIS

**Submitted to the Graduate Committee
of
The University of Tennessee
in
Partial Fulfillment of the Requirements
for the degree of
Master of Science**

Paul C. Swanson

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P R E F A C E

One of the problems constantly facing the dairy breeders of today is how to breed dairy cattle for high milk production as successfully as they are now breeding for other characteristics. To accomplish this it is necessary that every breeder have a knowledge of scientific breeding as related to milk and fat secretion and to be able to apply it to their own herd. The object of this paper is twofold: First, to make a thorough study and review of literature of inheritance of milk production, and, second, to carry on an original investigation for the purpose of making a further investigation of inheritance and how it might be applied to the practical breeder.

Special acknowledgment is due to Professor C. E. Wylie, of the Dairy Department, and C. A. Willson, Dean of the College of Agriculture, both of the University of Tennessee, for their aid and helpful suggestions in writing this thesis. Credit should also be given Mr. H. W. Norton, of the Holstein-Friesian Association of America, for cooperating in supplying records for this study.

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INTRODUCTION

Cattle have been known to produce milk since the earliest record of their existence. However, the scientific breeding of dairy cattle for high milk production did not begin until the latter part of the nineteenth century. Originally the cow produced milk only for the purpose of nourishing her young. For this reason the cow gave only small quantities of milk and secreted milk only for a short period of time. In other words, if the cow secreted enough milk to properly nourish her young she had performed her duty.

When it was discovered that cows milk was an excellent food for humans, as well as for nourishing young calves, man began to select cows that gave the most milk. It is true that cows have been selected, to some extent, for several hundred years but selecting for milk production on the basis of genetic principles and heredity is still in its infancy.

Numerous studies of inheritance of milk and fat secretion have been carried on rather extensively in the past fifteen years. However, at the present time very little is actually known about how milk and butterfat are inherited and how to distinguish between inheritance and environment. Most authorities realize that in taking the dairy breeds as a whole there has not been any great improvement in milk production which might be attributed to the proper selection of hereditary factors that make for high production. * It is true that some outstanding breeders have increased production of their herds by proper selection and mating.

* The greatest general improvement in production, however, has been the result of better feeding and management rather than the selection of animals of good transmitting ability. The results that have brought about the improved care and management of the cow have partly blinded

us to the need of improvement within the animal itself.

The study of inheritance of milk production is much more complex than is the inheritance of type and other external characteristics. The external characteristics of a dairy animal are very poor indications of the transmitting ability of the milk yield of that animal. Milk records first aided scientific cattle breeding by providing records of production for the females of the herd. Later it was found that the transmitting ability of sires was even more important because (1) the greater influence which the bull exerts by reason of his more numerous progeny, and (2) because by studying the records of these progeny a more accurate assessment might be made of his hereditary factors for transmitting milk production than can be obtained by the individual cow.

The inheritance problem has been tackled from many angles and conclusions have been published in almost every conceivable manner. Paper after paper has been written on inheritance of milk secretion but very few of the reported results are conclusive because the assumptions made cannot be proved due to the lack of sufficient data and the complex nature of the problem.

The importance of this problem cannot be over emphasized. When we realize that the average production of all milk cows in the United States is only about 160 pounds of fat, one can see the progress has been slow. While Dairy Herd Improvement Associations records average about double the above amount the greater amount of this increase has been due to better feeding and continual culling rather than through heredity. Of the 25,000,000 milk cows in the United States only about

5% are purebreds, and less than 10% of the purebreds have production records. Since most improvement through heredity will be made with purebreds, one can readily see that scientific breeding is still in its infancy.

The content of this thesis will deal with two things: (1) A general survey of the literature presented up to the present time, and (2) an original investigation of the problem of genetics and inheritance of milk and fat production that might give some new information to the breeder of purebred dairy cattle.

PART I

REVIEW OF LITERATURE

PART I

METHODS OF STUDYING INHERITANCE

There are two methods by which one might make a study of inheritance in dairy cattle. One method is to establish a breeding herd and by the actual breeding of animals determine, if possible, what factors are responsible for milk production and butterfat percentage. This is accomplished by making a large number of crossings and matings of animals of different breeds, of different levels of production, etc. The second method is a process of studying a large number of production records of a large number of animals and by this method try to draw some conclusions as to the mode of inheritance of milk and fat production.

While the first method would perhaps be the ideal method of making inheritance studies, it has not been used very extensively for several reasons. (1) The time of reproduction in dairy animals is very long, (2) only a limited number of animals can be used, (3) the cost is very excessive, (4) it would require twenty to thirty years to get definite and conclusive information, and (5) environmental factors will vary considerably from year to year. Many other reasons might also be stated. The second method is most commonly used because a larger number of animals can be taken into consideration and information can be gathered in much less time. In the past most all inheritance studies have been based on "Advanced Registry" records or "Register of Merit" records, depending on the breed involved.

The study of "Advanced Registry" or "Register of Merit" records have many objections. Turner (39) says, "It was recognized at the outset of the work (referring to his studies) that there are a number of serious objections to the use of Advanced Registry data in the study of

the inheritance and mode of transmission of the factors which combine to produce in the mature animal the potential possibilities for a certain production of milk and fat during a lactation period."

The objections of these records just mentioned may be divided into two classes. The first class of objections is due to the rules and regulations of the "Advanced Registry" and "Register of Merit" tests. (48) The second objection is the difficulty of determining the full inheritance of the animals from the quantitative characters being considered.

The minimum entrance requirements of the Register of Merit and Advanced Registry rules automatically eliminates the lower grades of producers. When only official records are considered it will not be possible to get a true cross section of the records of all cows. This may in some cases prevent one from getting a random sample of the population, because of the fact that the cows which failed to meet the breed association requirements for official records, would not be included in the study. However, in many cases, records which, because of the high average merit, will not be affected by the entrance requirements.

The second objection which is one of the expression of quantitative character is greatly influenced by environment. The production of milk and butterfat during a lactation period is influenced by feed and management, not only while the animal is in milk, but also during the period of growth and development. Pregnancy, seasonal variations, seasons of freshening and number of milkings also influence the production of milk and percent of fat as pointed out by Gaines and Davidson, (12) Turner, (42) Sanders, (35) and others. Graves and Fohrman (20) have presented data which show that initial records made by cows at various

ages are, on the average, poorer than those made by cows of the same age but which had been previously tested. They concluded that official testing tends to develop the productive ability of dairy cows, and that the extra feeding and care given these cows have an appreciable and positive effect on her production during subsequent lactations. Turner says, in referring to the above statement, "The data might equally as well be taken to indicate that the breeders owning the better cows make a practice of testing cows as two-year-olds and that the cows which make their initial records at more advanced stages are either cows of poorer quality or are owned by breeders who are taking up testing for the first time and are inexperienced in feeding and managing of test cows and are unable to bring out fully their potential producing capacity."

STANDARDIZATION OF RECORDS

The first thing one must do in studying records to determine the mode of inheritance is to make records comparable with each other. It is generally known that milk and fat production, on the average, gradually increases as the dairy cow becomes more mature and that at a certain age her production will begin to gradually decline. Many conversion factors have been worked out for the different breeds of dairy cattle so that the mature equivalent production of milk or butterfat might be determined. Most all of these conversion factors have been determined by tabulating a large number of records according to age and length of record. Turner (39) reports the results of a study of some 13,000 Jersey records and a total of 46,000 records for all breeds studied. The data reported by Turner shows that fat production increases gradually up until between seven and eight years and then gradually decreases with the onset of old age. The conversion factors are determined by the ratio of the average production at maturity to the average production at various age intervals. To convert a record to its mature equivalent it is only necessary to multiply the fat production by the age conversion factor for the age at which the record was made. It has been pointed out by Turner (39) and others that it is doubtful if one can justify the use of conversion factors to a single record but when applied to groups of records it is a fairly accurate method of determining mature equivalents.

A large number of conversion factors have been worked out by various men for each breed of dairy cattle for D. H. I. A. records, Advanced Registry records, Herd Test records, and many others. Many people as well as breeders have looked upon conversion factors as an

unfair method of making comparisons. It is also the contention of many that the conversion factors are too high and will on the average make a converted record higher than it should be. Rice (31) states, "In other words, when we use the ordinary conversion factors, we are well on the safe side, because actually cows on the average will make more in the mature classes than the use of the commonly accepted conversion factors would indicate." This statement is based on a number of tabulations and comparisons made on entries and reentries of Guernsey cows. To simplify the work Rice recommends the following age conversion factors for milk for all breeds.

<u>Age</u>	<u>Factor</u>
2 - 0	1.35
2 - 6	1.25
3 - 0	1.20
3 - 6	1.15
4 - 0	1.10
4 - 6	1.10
5 - 6	1.05
over 6	1.00

Even if the factor is only approximately correct, the fact that the same factors are used on both the dam and the daughters, would make the comparison a fair one. It is also necessary to make the number of days that the milk record represents equal in order to make a fair comparison. Rice (31) and Turner (39) found that to convert a 305 day record to a 365 day basis it should be multiplied by 1.15. Gifford (15) gives a conversion factor for correcting the length of lactation period based on the average rate of decline of 3000 lactation records in Table I.

31. Rice, V. A., Breeding and Improvement of Farm Animals, p. 322.

TABLE I. CONVERSION FACTOR FOR COWS MILKED LESS THAN 365 DAYS--
BUTTERFAT BASIS.

Lactation Month	Days on Test	Conversion Factor
7	212	1.56
8	243	1.39
9	274	1.26
10	305	1.15
11	336	1.07
12	365	1.00

Because of the fact that cows are milked either two, three, or four times a day some factor must be used to standardize the number of milkings, and also to compare D. H. I. A. records with Advanced Registry records. Rice (31) found that to convert a record based on two time milking, it should be multiplied by a factor of 1.20, to convert a three times a day milking record to four times a day milking, multiply by 1.15, and to convert a two time milking to a four time basis multiply by 1.37.

Wylie (44) has formulated a score card that standardizes all records on the basis of (1) Mature animals, (2) For one year, (3) Milked three or more times daily, and (4) Producing a living calf. The Wylie score card for standardization of milk records is given in Table II. The figures are based on the results of Gowen, of Maine, the Missouri station, Graves, Fohrman, Hinton, the Illinois station, Copeland and others. The percentages represent the amount of butterfat which is to be added to the actual record. The amount of butterfat to be added is determined by taking a certain percentage of the actual record according to conditions under which the record was made. These amounts are then added to the original record.

TABLE II. SCORE CARD FOR STANDARDIZING MILK RECORDS.

I. Butterfat - Fill in actual pounds of butterfat.				
II. Age - Beginning of record:				
2 yrs. 6 mos. or under	Add	30%	of actual record	
2 yrs. 7 mos.		29%	"	"
2 yrs. 8 mos.		28%	"	"
(Decrease 1% per month)				
3 yrs.		24%	"	"
4 yrs.		12%	"	"
5 to 9 yrs. inclusive		0%	"	"
10 yrs.		1%	"	"
11 yrs.		2%	"	"
12 yrs.		3%	"	"
13 yrs.		4%	"	"
14 yrs. or over		5%	"	"
III. Length of Test:				
(1) 305 days or less		14%	"	"
(2) 306 to 335 days, inclusive		10%	"	"
(3) Over 335 days		0%	"	"
IV. Number of Milkings:				
(1) 2 milkings per day		20%	"	"
Not more than 610 milkings in 305 days				
Not more than 730 milkings in 365 days				
(2) 2 and 3 milkings per day		10%	"	"
Not more than 670 milkings in 305 days				
Not more than 790 milkings in 365 days				
(3) 3 or more milkings per day		0%	"	"
More than 670 milkings in 305 days				
More than 790 milkings in 365 days				
V. Calving Record:				
(1) Living calf carried less than 200 days		2%	"	"
(2) Living calf carried 200 days or more		3%	"	"
(3) No record, or calf dead		0%	"	"

Graves and Fohrman (20) found that the increase in production with increase in age is not all due to age but partly to development, due to better care and management during the initial record. Quoting directly, "There is sufficient evidence to prove that official testing develops the productive ability of dairy cows, and that the feeding and

care combined with prolonged milking period during which the cow is encouraged to yield her utmost, have an appreciable and positive effect on her production during subsequent lactation periods." In Jerseys they found that development was responsible for 11% of the increase in records and that in Guernseys development was responsible for 12.2% of the increase.

The factor of feed and management perhaps causes the greatest amount of variation in records and is a factor that cannot be standardized by any definite conversion factor.

Edwards ⁽¹⁰⁾ says, "In dairy cattle breeding investigations, the student has to decide upon the extent to which correction factors will aid him in eliminating other than hereditary factors influencing milk yield. He is aware that the major influence--feeding, must go uncorrected."

Gowen ⁽¹⁹⁾ has attempted to separate roughly the variations of environment and the variations of inheritance as they have influenced milk secretion of Jersey Register of Merit cows. He concluded that variations in care and management of cows, insofar as they are common to such close relatives as sisters, are much less important than those of heredity. Inheritance was found to control 50-70 percent of the variations for milk yield, environment common to sisters 5-10 percent, and factors (some hereditary and some environmental) common only to the cow herself 20-45 percent. For butterfat percentage inheritance controlled 75-85 percent of the variations, environment common to sisters none, and influence common only to the cow herself control 15.25 percent of the variations.

RECORDS USED IN INHERITANCE INVESTIGATIONS

Gifford (15) states, "The correct analysis of data representing a measured character of any group of individuals can be made only when it is possible to get a random sample of the variates studied." In practically all cases in which inheritance studies have been made, either Register of Merit or Advanced Registry records have been used. While semi-official or official records are the best records on which to make inheritance studies they are not without fault as has been pointed out by many investigators. Graves and Fehrman (20) point out three objections to the use of Advanced Registry records as follows:

(1) Records may be from a selected group of individual animals as certain requirements must be met before the records will be accepted by the breed associations.

(2) Cows on official test are usually those which the breeder thinks, in advance, will qualify.

(3) Cows receive better care when on official test.

It has been found that there are a few individual sires whose averages for their daughters are materially greater than they would have been had there been no elimination of the poor producers due to entrance requirements of the breed associations.

The work of Ragsdale and Gifford (30) points out the results of entrance requirements as illustrated in Figure 1. Figure 1 illustrates the results of minimum entrance requirements as is indicated by the two curves on the chart which show the production of all the tested daughters of King of the Pontiacs, and King Pontiac Dione. The curved line of the bull, 'King Pontiac Dione', shows that 45 percent of his daughters averaged less than 500 pounds of fat, 42 percent produced

about 550 pounds of fat and only 15 percent of the test daughters produced 650 pounds of fat. If all daughters were tested the curve would be complete there being a few low producing daughters and a few high producing daughters with the greatest number of the daughters falling in the intermediate group. The broken line indicates what the rest of the daughters might have produced, had they all been tested or if there were no entrance requirements. In other words about 50 percent of the daughters of King Pontiac Dione failed to meet entrance requirements of Advanced Registry or were not tested because the owner did not think they would qualify. Thus, the average actual production of King Pontiac Dione's daughters should probably be about 450 pounds of fat rather than 516 pounds of fat. The same would probably be true of most all cases in which there are a large number of daughters grouped in the lower classes and in which there is a distinct cutting off of the frequency distribution curve, indicating the average to be higher than it should be.

In case of the bull 'King of the Pontiac' there is almost a complete frequency distribution curve which indicates that in this case the minimum entrance requirements had little if any effect on the true average production of his daughters. All of the 55 tested daughters of this bull produced above 500 pounds except one.

The changes of average production with time due to improve methods of care and management will have some effect in comparing records. Since the care and management of animals on Advanced Registry records is more nearly alike than it would be under cow testing association conditions, Advanced Registry records are to be preferred in genetic studies of milk secretion.

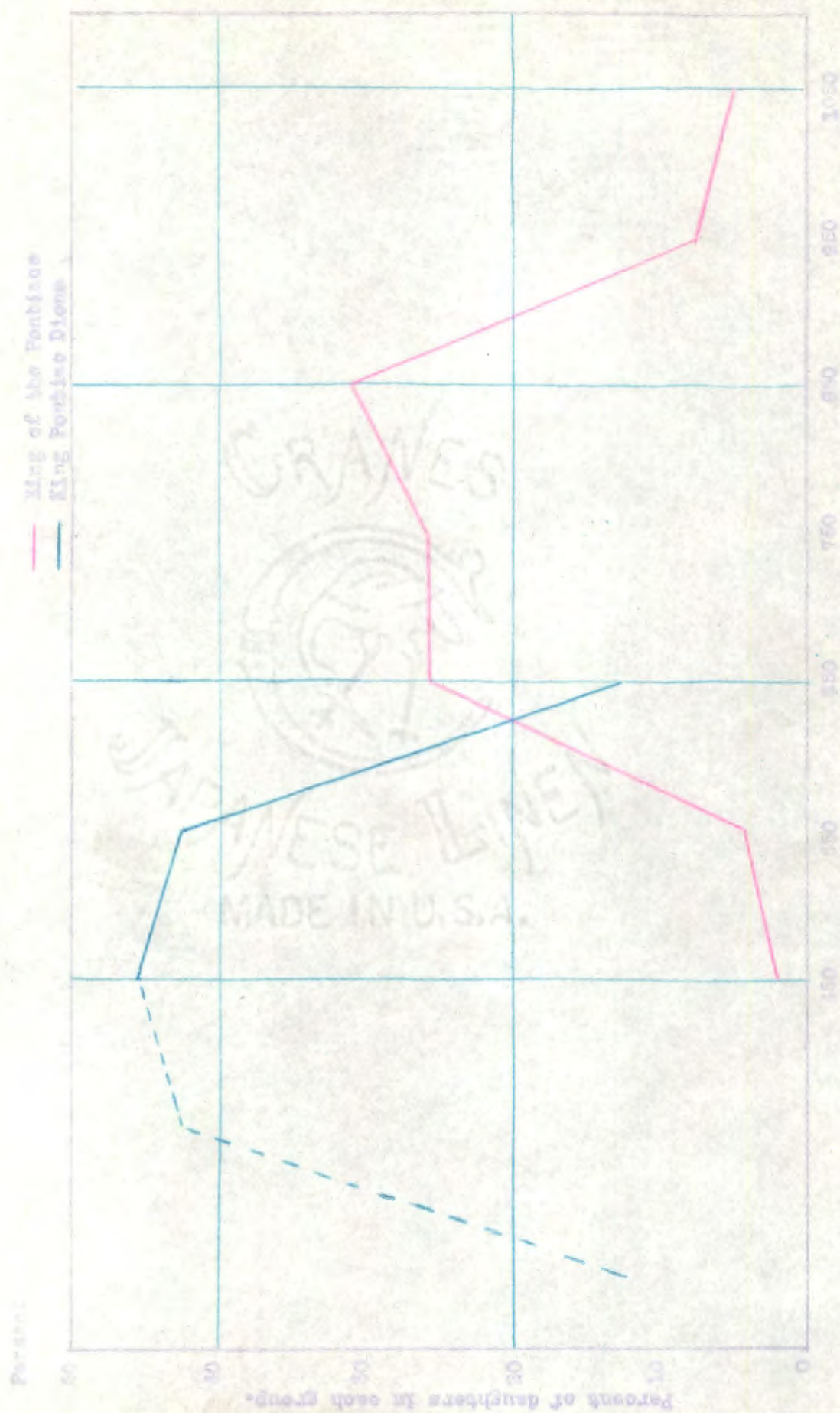


Fig. 1.--Butterfat Production. The effect of the minimum entrance requirements on the distribution and average production of daughters of King Pontian Dione in contrast to the daughters of King of the Pontians.

INFLUENCE OF THE NUMBER OF DAUGHTERS ON THE SIRE'S AVERAGE OR IN DAM-DAUGHTER COMPARISONS

Davidson (8) presented a study based on Register of Merit records in which he concluded that "On the average, the first six tested daughters of a Jersey sire is the smallest number of tested daughters, the average of whose production closely approximates the average production of the first fifteen tested daughters of the sire." There was considerable variability, however, when only six daughters were used in the average. Copeland (6) has made a study trying to determine the least number of tested daughters, the average of which would closely approximate the average of all the daughters of any bull. Copeland found that the degree of correlation increases very rapidly until the number of daughters reaches eight or ten and thereafter the gain in correlation is slight. The pounds variation is still rather high when ten daughters were compared. He also found that in the majority of the cases the average of the first few daughters was less than the average of all tested daughters. Figure 2, worked out by Copeland, (6) gives the coefficient of correlation of the records of various numbers of daughters as compared to average fat yield of all daughters. The numbers on the bottom of the Figure represent the correlation when 1, 2, 3, 4, etc., number of daughters are compared to the average of all daughters. The Chart shows that, when 10 daughters are used in a comparison, the coefficient of correlation is nearly 9, indicating that the production of the first ten daughters is relatively good indication of the production of the remaining daughters.

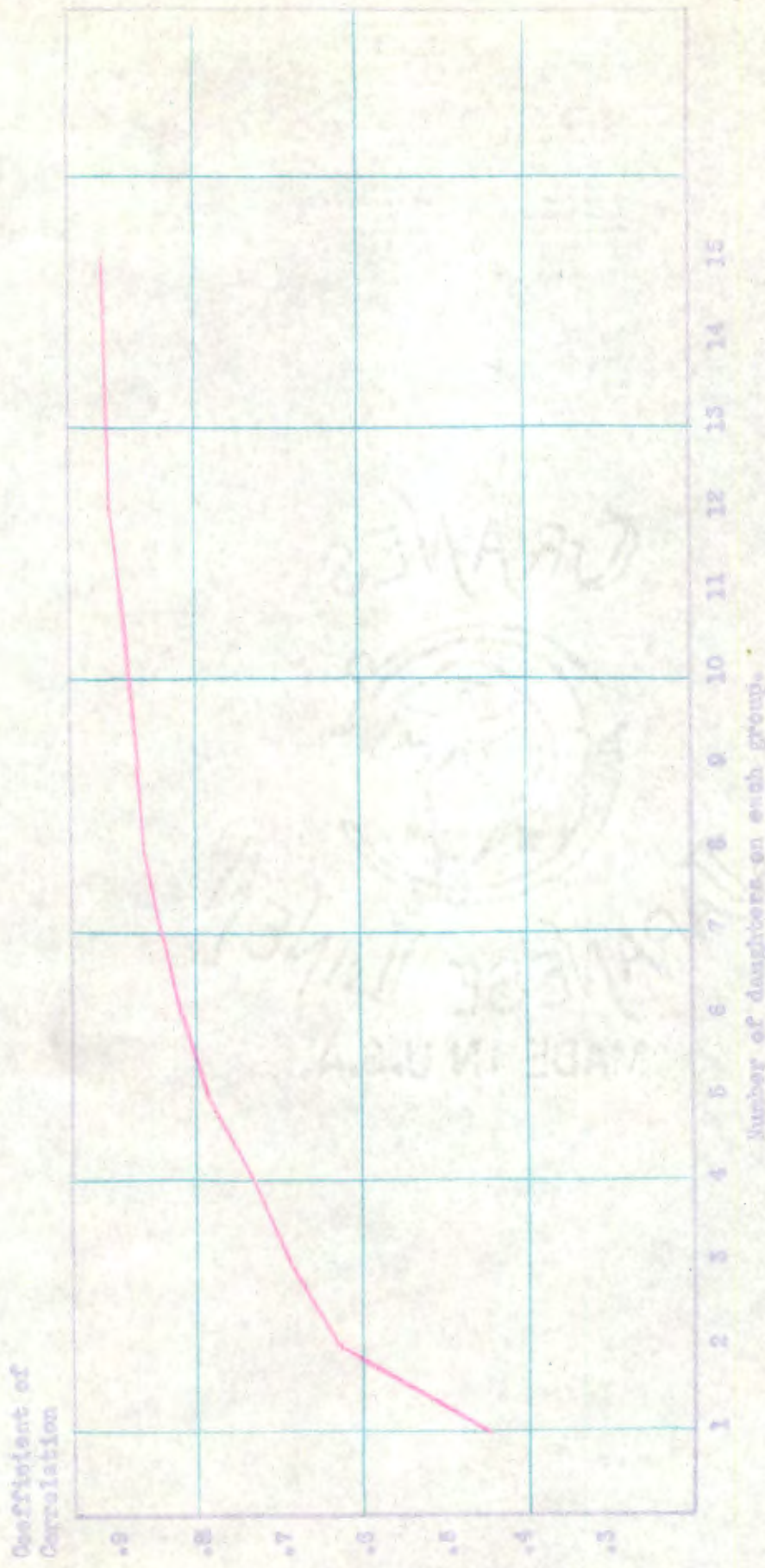


Fig. 2.--Coefficient of correlation between the average fat yields of each group of daughters and the average fat yields of all tested daughters of each of 100 sires.

CORRELATION OF TYPE AND PRODUCTION IN STUDYING INHERITANCE

There has been much discussion over the problem of type and production. There is no doubt but that the ideal cow should be both a good producer and of excellent type. Although the physical characteristics of a dairy animal give some indication of the possibilities of their production, it is generally conceded by authorities that the correlation of type to production may be very low. It has been definitely proven that many winners in the show ring have been poor producers themselves or were poor transmitters of production. There is no doubt but that good type and high production may often be found in the same animal but they are not closely correlated. In other words, an animal may have type and high production, or type and low production, or vice versa.

It is undoubtedly true that shape and size of an individual cow bear some relation to her producing ability. Gowen, (16) in defining the ideal as quantity production of milk or butterfat, found the following points of confirmation to be important.

- (1) The cow should be better than the average weight for her breed.
- (2) She should be of good wedge shaped form, particularly in the region of the shoulders.
- (3) Her milk veins should be of good size.
- (4) Her udder should be of good size and quality.

Gowen also says, "A few words of caution: if the measure of worth is to be the relation of energy intake of the food the animal consumes to the energy value found in milk, then the effect of weight on quantity of milk produced seems to be offset by the extra energy

necessary to maintain body weight. It is also shown that the cow's confirmation is on the whole a rather inferior means of predicting future milk producing capacity. It has one advantage over the other method: it shows the present status of the cow's physical health and whether the mammary gland is physiologically normal."

As to whether the shape and size of parents are related to the producing ability of their daughters is a different question. Gowen⁽¹⁶⁾ found no correlation of significance between body type of the sire or dam and the productive ability of the daughter in milk, butterfat, or butterfat percentage. Turner, of Missouri, and Graves, of the U. S. D.A., have made similar statements that type is not a good test of a good sire. Prentice⁽²⁷⁾ states that the present score card is merely a survival of the unscientific methods of the past, when the general opinion was that form and function were so closely associated that you could distinguish between good and bad animals.

THEORIES OF THE MODE OF INHERITANCE OF MILK, BUTTERFAT AND BUTTERFAT PERCENTAGE

It might be proper at this time to discuss some of various theories that have been presented in regards to how milk production and butterfat percentage are inherited.

It has been definitely proved that the determiners of heredity are borne on the chromosomes.* The presence of these genes on the chromosomes determines the presence of the character of the adult animal. Turner (39) says, "The 'character' which is visible in a physical sense is the resultant of the presence and activity of a gene or genes in the cells of the developing organism and is not the gene or factor itself. Thus a 'character' may be the resultant of one gene or of many genes acting together. On the other hand, a single gene may influence many characters."

The character with which we are concerned is that of lactation milk and fat secretion of the dairy cow. The character of milk production is probably the result of many genes, as to how many no one knows. In addition to characters which are directly related to milk secretion there are apparently other characters that indirectly influence milk and fat secretion. ^{and} Turner, Ragsdale, & Brody (41) point out that body size appears to influence maximum production. Turner (39) suggests also that the character of persistence of milk production and fat secretion may depend on something in the nature of a hormone. In speaking of milk production as a character, it is believed to be a re-

* Morgan, T. H., The Theory of the Gene, p. 45. Yale Uni. Press.

sult of many characters, each of which may be dependent on one or more genes for its expression.

It is generally agreed that cattle have 18 pairs of autosomes plus the sex chromosomes, giving the female a total of 38 chromosomes and the male 37, the male being heterozygous and carrying one sex chromosome while the female has two sex chromosomes. This being true, any gene carried on the sex chromosome can be transmitted by the males to their daughters only, and not to their sons. This would be called sex-linked genes or sex linkage. *Duckham * 3*

It is definitely known that the sire and dam contribute the same number of chromosomes to the female offspring and also to the male with the exception of sex chromosomes. Each chromosome, whether from the male or female, contains the same number of genes.

The simplest factor manifestation is where apparently one factor conditions the development of a certain characteristic as polledness in cattle. In contrast to this, as pointed out by Rice, (31) it is considered that milk production is no doubt dependent on a great many factors, since milk production is a complex physiological phenomenon dependent, among all other things, on the capacity, temperament, and vitality of the cow. ^{states} Rice emphasizes that determiners are not characteristics. ^{+ but} An animal does not inherit characteristics from its ancestors, but rather it does inherit potentialities. As to whether this potentiality develops to its fullest extent or not depends upon environment. In other words, environment may inhibit the full expression of the genes. Thus, even if a cow inherits high milk production, it may not show up to the full extent due to influence of environment. As pointed out earlier in this paper, the influence of environment greatly complicates the inheritance of milk production. *and*

Genes which occupy corresponding positions on the chromosome pair and influence the character are called allelomorphs one of which comes from the male and one from the female. If the genes on both the allelomorphs are the same, it will be pure for that factor. However, the genes may be different in which case there may be a complete suppression of the activity of one character, or both may be active, causing a production of a character intermediate between the two characters. Thus, the character expressed will depend on whether the character is dominant, recessive, or intermediate. When one character is expressed and the other allelomorph is suppressed the former is dominant and the other is a recessive character. When an intermediate character is produced, in addition to lack of dominance, the results may be due to a blending inheritance caused by several genes all of which may affect the same characteristic. As to whether or not blending inheritance is the result of equal contribution from each gene, or that the genes of allelomorphic pairs may contribute unequally, has been a question that has not been definitely proved.

As has already been stated, it is believed that milk and fat secretion in dairy cows is influenced by many genes. While many estimates have been made as to the number of factors responsible for milk and fat production, they are all speculative.

Turner (39) points out that extreme variations in fat production in dairy cattle, anywhere from 100 pounds of fat up to 1300 pounds of fat, are exceptionally wide and indicates that probably many genes, representing different amounts of milk, are concerned. Von Patow, Wilson, Castle, and others, have made attempts to determine the number of factors responsible for milk and fat production, but no definite number can be stated.

Smith and Robison (37) state the following theories as those that have been advanced by various workers.

1. Two pairs of factors responsible for milk yield.
2. Four pairs producing 16 grades of milk--four dominants producing individually 20, 15, 10, and 5 pounds and four recessives producing 4, 3, 2, and 1 pound of milk.
3. Fat transmission based on one factor and perhaps one other modifying one.
4. Segregation of two factors in a 7:1 ratio, one factor being dominant and the other sex-linked.
5. Butterfat and milk yield dependent upon three homomeric factors, but independent of each other.
6. Three homomeric factors plus another factor which influences butterfat content--milk and butterfat being in some way connected.
7. Several factors with greater importance of the female than of the male.
8. Ten factors affecting milk yield and butterfat percentage.
9. Many genes of varying effect but those influencing high production being dominant.
10. Multiple factors with or without connection between milk yield and butterfat.

The question of the amount of dominance in milk production is a much discussed factor and has much conflicting evidence. Warwick and Copeland (43) say, "While there is a difference of opinion as to whether there is dominance--and the evidence is conflicting--the occurrence of apparently high 'prepotent' bulls on rare occasions points toward some dominance." Smith and Robison (37) have presented evidence to point toward sex linkage of part of the dominant factors.

A number of cross-breeding experiments of cattle of high production with cattle of low production indicate a tendency toward partial dominance.

Gowen (17) found that milk production was intermediate between the dam and sire but approaching more closely the higher producing parent. The experiment consisted of controlled matings of three groups of cattle, namely, Holsteins, Jerseys, and Aberdeen Angus. The results may be summarized as follows: When the high milking group is crossed to a medium milking group, the milk yields of the resulting cross breeds were found to be intermediate between the two groups approaching most closely those of the high group. When the high milking group is crossed with the low milking group the resulting cross breeds have milk yields closely resembling those of the medium group. Cole says, "Similar results (referring to those of Gowen) have been obtained in our Angus-Jersey cross breeding experiments at Wisconsin, and have been reported also by Castle for Bowler Holstein-Friesian X Guernsey cross-bred herds, and by Ellinger in the cross of Red Danish with Jersey. It may be of interest to give the figures in the last two cases." (4)

INHERITANCE OF MILK YIELD

	Holstein- Friesian X Guernsey	Red Danish X Jersey (1st. 10 weeks)
	<u>Lbs.</u>	<u>Kg.</u>
Purebred high parent	9,475	895.7
Purebred low parent	5,593	711.5
Cross breeds	8,663	832.4
Intermediate of parent breeds	7,534	803.6
Difference between parent breeds	3,882	184.2
Excess of cross-breeds over intermediate	1,129	28.8
Percentage increase of cross-breeds of inter breed difference	29	15

It was further found, that in regard to inheritance of butterfat percentage, that in the Holstein-Guernsey cross, the butterfat percentage was nearest the high testing breed while in the Red Danish X Jersey cross the butterfat percentage was nearest the low testing breed.

Dr. Yapp (47) found that in crossing Holsteins and Guernseys the F. generation showed a percent fat content intermediate between the parents with a slight inclination toward the higher testing parent. Turner (39) states that these figures mentioned cannot be considered as critical proof of partial dominance of milk and fat secretion of the high parent. Some of the objections to this test as pointed out by Turner are as follows:

- (1) The lack of a measure of the sire in the cross except through his daughters.
- (2) The increase in production of the crossbreds above the mid-parental production may be due to heterosis.
- (3) In a population the frequency distribution would be asymmetrical as is illustrated by a 3:1 ratio in simple dominance. On the contrary no such distribution is found.

In general the information stated does indicate that both parents transmit inheritance to their offspring and that the production of the offspring is some where between the two parents.

ANALYSIS OF PROGENY PERFORMANCE STUDIES

As has been previously pointed out the best method of increasing production is through proven sires and by studying the progeny of the sire or dam. Since the sire has no way of indicating its potential production directly it must be determined through the transmitting ability to the daughters. The number of female progeny from a dam is so small that it is difficult to determine her transmitting ability. For this reason the male or the sire's performance, as indicated by its daughters, is the best method of improving the production of a herd.

It has been definitely proven that the dam's own record merely represents her phenotype while the genotype is represented by her transmitting ability to her offspring. Thus, the dam's record does not indicate the production of her daughters unless she is homozygous.

Rice (31) says, "There are two possible interpretations of improved performance: (1) that selection in itself modifies the germinal elements and that by selecting in a specific direction the hereditary material itself is actually molded in a corresponding fashion, and (2) that the effectiveness of selection depends upon the isolation of hereditary material of the most excellent sort. It will be seen that the two views are diametrically opposed to each other and it is necessary to make a choice of one or the other interpretation. If the first explanation is accepted it will involve only mass selection of those individuals that are themselves better than average production. If performance brings about the development of more favorable material, or if selection in itself has a creative effect in a given direction, then it would seem that mass selection must result in increased production."

Mass selection was practiced at the Maine Experiment Station from 1899 to 1907. Only females were used as breeders, that produced 160 eggs in their first year, and only males whose mothers laid

at least 200 eggs their first year were used. Under this system their egg production decreased rapidly. Here mass selection failed to increase production in the hereditary material involved. After 1907 all females were selected from high producing mothers, the female progeny of which were all high producers and in case such a female failed to yield high-producing progeny she was not retained. Males were selected from high producing mothers whose female progeny were all high producers. With this system production increased steadily from 1908 to 1920.

Lush (23) states that only under rare conditions would a progeny test, based on as few as four daughters' averages in an unselected population, be as accurate an indicator of a dam's breeding value as the dam's own record of performance.

"If the trait is highly hereditary, in the narrow sense of the word, or if the progeny resembled each other very much for reasons of having been exposed to common environment many more than 4 daughters may be required, or it may even be quite impossible for the progeny test to average more accurate in a whole population than the dam's own performance no matter how many daughters there are."

He states that the superiority of the progeny test is greatest for traits which are least hereditary. He realizes, however, that the progeny test is necessary where one sex cannot express the trait as in milk and fat production.

Gifford (15) points out that the principal criticism of the progeny performance records, as a measure of the transmitting ability of sires and dams, has been the difficulty in equitably evaluating the dam's contribution and the sire's contribution to the daughters' production.

The study of progeny performance records has brought out many views and also many points of value as well as of interest in regard

to how milk and butterfat are transmitted from one animal to another.

Production of Dams and Daughters Compared. Turner, (39) and Gifford⁽¹⁵⁾ have made some studies of the production of dams and daughters compared with the Jersey and Holstein breeds respectively. The comparison of the dam's production record and the daughter's record furnishes a good indication as to the phenotype of the dams to which the sires are mated, as well as their genotype, as portrayed by the daughters' records of production. It has been pointed out by many that the difference of the daughter's production compared with that of the dam does not necessarily indicate the transmitting ability of the sire because in one case the dam's production may be low while in another instance it may be high. Gifford, (15) in order to make the sire's transmitting ability fairly constant, grouped the sires according to the average progeny performance and then calculated the coefficients of correlation for each sub group. The coefficient of correlation of the fat records of the dams and that of the daughters was found to be .197. In other words he found that, on the average, there was an increase of approximately 20 pounds of butterfat of the yearly production of the daughters for each increase of 100 pounds fat in the average yearly records of the dams, above the potential transmitting ability of the sire. The potential transmitting ability of a sire is considered to be the average production contribution to his daughters when the dams do not add any genetic contributions.

"As the dams increase in productive ability and increase the productive ability of their daughters by supplying the germ plasma factors for high production, the effect is shown only when the sires are recessive for the same factors. Therefore, the sire's progeny performance record would be greater than his potential transmitting ability only when the dams with which he

was mated supplement the factors for high production contributed by the sire.

"In other words, since it is relatively easy to determine the progeny performance of the sire and thereby obtain an approximated measure of his transmitting ability, the sire can be given credit for the average of his daughter's production ability to a very great extent which from strict genetic analyses may be considered to come jointly from the sire and dam because they contribute the same factors. The dam is given full credit only for that part of the daughter's production which she individually added to the germ plasma factors to increase the production above that of the sires potential transmitting ability." (15)

The following formulae worked out by Gifford gives the sire's potential transmitting ability when a large number of dam daughter comparisons are available:

$$\text{Spt} = d - .2 D$$

Spt is the sire's potential transmitting ability, d the average yearly butterfat records of the daughters, and D is the average yearly production of the dam of the daughters.

Turner made some tabulations of Jersey records that were similar to those of Gifford. Table III gives the relationship between the dam's average production and the sire's progeny performance when the sire's transmitting ability was fairly constant. (39)

TABLE III. RELATION BETWEEN DAM'S AVERAGE PRODUCTION AND THE SIRE'S PROGENY PERFORMANCE. (JERSEY DATA)

Sires grouped by dam, average fat production.	Daughter's Dams av. fat production.	No. of Dams
<u>Lbs.</u>	<u>Lbs.</u>	
700 and over	604	374
650 - 699	606	363
600 - 649	578	582
550 - 599	538	1117
500 - 549	508	700
450 - 499	468	442
400 - 449	453	129

Goodale's (14) data on the study of Guernsey sires show, "That those sires whose daughters average the largest yield of butterfat were mated to cows of superior average butterfat production, while the sires, whose daughters averaged the least, were mated to cows whose average was comparatively low." Apparently a similar relation holds true for Jersey data.

Turner found the average correlation coefficient to be .131 between the dams and daughters production. This is considered a coefficient of partial correlation in which the sire is constant. He points out that this low correlation indicates a presence of partial dominance in milk production. In assuming lack of dominance the parent offspring partial correlation should be 0.5. With the assumption of dominance the parent offspring correlation would vary from about .2 with complete dominance up to 0.5 with varying degrees of dominance. This data of Turner and Gifford indicate the probability of partial dominance of milk and fat secretion. This plan is followed by them because the dam's potential transmitting ability is difficult to determine and it is, therefore, almost impossible to determine directly what part of the joint contribution is due to the dam.

They conclude that, because the dam's contribution to the offspring is so low, some dominance must be present. If dominance was lacking, instead of the dam supplementing the sire's potential transmitting ability, the entire contribution of the dam would be effective. If dominance is present a dominant gene from the sire and a recessive gene from the dam would be the same as a dominant gene from both parents. If dominance is entirely absent Aa is of less

value than AA so that if the dam contributed "A" instead of "a" there would be a difference. Since the dam's contribution to the daughters appears to supplement the sire's potential transmitting ability rather than be additive it indicates partial dominance.

Gowen (18) in comparing the correlation coefficients for the milk yields of half sisters with the sire as a common parent and of half sisters with the dam as common parent found that the correlation coefficient was practically the same, 0.362 and 0.381 respectively. The correlation coefficient for the relation of milk yields of full sisters was found to be .548. This would indicate that the dam's record does influence the production of the progeny.

Warwick and Gopeland (43) state that proving sires on the basis of daughters alone is not adequate for critical testing, and to present on theoretical grounds, a genetically sound procedure for testing bulls they should be tried out by using poor producers as dams, in making progeny tests rather than a random sample of dams or high producing dams. To prove this they assumed that (for simplicity) a herd had been bred up until it was homozygous for all but five factors. An increment value of one was assumed for each of the five factors. This increment is to be added to a basic residual production level. Animals with a value of 0 - 4 was classed as "poor" to "medium" producers and those with a value of 5 as good producers.

A random sample would probably give a group heterozygous for all 5 pairs. With this in mind they examined the evidence as to what the results would be if good producers were used as test daughters as compared with the second group of poor producers. The good producers have a value of 5 and the poor producers a value of one.

It is evident that if it were possible to have all homozygous high producing cows, the extent of range of variation of the production of their daughters would be the same as for those of low producers and if dominance is absent they would be as good for testers as low producers which are homozygous. However, such a homozygous high group is impossible. The maximum variability of the daughters of poor test cows is no greater than the least number of possible variations of good test cows when used on six different types of bulls. This is based on the assumption that good test cows were heterozygous for 5 pairs. To get all variations in the theoretical example the minimum population would be 1024 for the heterozygous group and 32 for the low producing group.

With the above theory in mind Warwick and Copeland suggest the use of low producing dams based on (1) minimum, (2) average, and (3) maximum production of the daughters. A bull is considered excellent if the daughters included none below the average and whose average was close to the midpoint between the dam's average production and the maximum of the breed.

Graves (21) found a remarkable variation between records of daughters of any sire and their dams. He also states that the prepotency of a sire cannot be indicated by the coefficient of variability of his daughters. It was found in this study of Holstein sires that the coefficient of correlation for butterfat yield between the dams and daughters varied widely for different sires, regardless of whether the daughters of the sire are better or poorer than their dams. It was found that when a large number of daughters were compared with records of their dams that there was a limited correlation

or tendency for high record daughters to come from high record dams.

Graves concluded that both parents contribute equally to the inheritance governing milk and butterfat producing capacity of their daughters. However, if one parent is homozygous or pure for heredity factors determining high production and the other parent is heterozygous in its inheritance then the homozygous parent will have the greatest influence on the producing capacity of the daughters. Yet this daughter will transmit to part of her progeny the inheritance for low production that she may have received from her heterozygous parent. When two heterozygous parents are crossed the production may range from a very high to very low yield.

Influence of the Sire and Dam on the Average Production of the Son's Daughters. Turner (39) expressed the relationship between the son's daughters' production to that of the sire's daughters' production as follows:

Son's daughters' yearly fat production = $302.3 \div 0.491$ sire's daughters' fat production.

Thus, if a son of a proven sire having 20 daughters with an average yearly fat production of 675 pounds is used on average cows what would be expected of his daughters?

$$\begin{aligned} \text{Son's daughters' production} &= 302.3 \div 0.491 \times 675 = 302.3 \div \\ &324.7 = 627. \end{aligned}$$

In working out a similar expression for the contribution of the dam's record upon the son's daughter's record the following equation is used by Turner.

Son's daughter's fat production = $463.1 \div .176$ dam's fat production.

In other words, for each 100 pounds of fat, above 463 pounds,

on the part of the dam causes an increase of only 17.6 pounds of fat in the average production of the son's daughters.

The dam's sire's daughters or the dam's half sisters' records were almost three times as valuable as her own record for determining the transmitting ability of the son's daughters. It is expressed as follows:

Son's daughter's yearly fat production = $304.5 \div 0.485$
dam's sire's daughter's production.

Gifford (15) found somewhat similar results in studies made with Holsteins. They concluded that the dam's record was a poor index of her transmitting ability to her son's daughters.

SYSTEMS OF INDEXING BULLS

The subject of bull indexes has become more and more important, especially in late years. At the present time there are a large number of proposed formulae or indexes for the purpose of selecting good sires. The purpose of a good index is to get a genetic picture of a bull by studying his mates and daughters since the bull himself gives no milk. The following hypotheses have been suggested for indexing bulls.

Pearl, Gowen, and Miner Index. This index as given by Rice (31) consists of (1) plotting the curve of variability of Advanced Registry records and (2) to divide it into quartiles and classify the offspring of each sire in terms of percentage, on the basis of the relative standing of each dam with her daughter. The highest quarter was called A, the second B, the third C, and the fourth D. If a bull had four daughters, two of which were in the second quarter, while the respective dams were in the first quarter, one daughter in the second quarter, while her dam was in the third quarter, and one daughter was in the fourth quarter, while her dam was in the first quarter; the bull's index would be $50AB \div 25CB \div 25AD$. While this method does give a relative comparison of the daughters and dams it does not indicate the pounds of milk and the percent fat that the bull will transmit. Furthermore, this formula may become very complicated as is the case of the bull Springfield Owl which had the following formula:

$12AA \div 4AB \div 4AC \div 23BA \div 12BB \div 4BC \div 8CA \div 8CB \div 4CD \div 12DA \div 4DB \div 8DD$.

Pearl-Graves Index. Pearl and Graves later worked out an index based on the average production of milk and butterfat by mates

and daughters of a bull. The index of the bull is the difference (plus or minus) in milk, total fat, and fat percentage of the average of the dams and the daughters. While Graves and Pearl did not work together their index is essentially the same except that Graves stated the number of daughters that were equal to above or below the production of their dams. They are both often referred to as the same index.

Yapp Index. (31) This index is based on the theory of blending inheritance. The transmitting ability of the bull is expressed in terms of 4 percent milk by the formula $X = 2A - B$. X is the sire's potential transmitting ability, and A equals the daughters' average record converted to a 4 percent fat basis and B equals the dam's records converted to a 4 percent basis. In other words this formula states that the average production of the daughters is just halfway between the dam's production and the sire's transmitting ability. This index adopts the theory quite generally except that when two parents are crossed the progeny will be about midway between the parents when the character is determined by multiple factors. One objection to this method is that the potential amount of milk and the percentage of fat of a bull cannot be determined because the milk is converted to a four percent fat basis.

The Turner Index. Turner (40) first thought that the sire's transmitting ability could be determined by the following equation:

Sire's potential transmitting ability =

$$\frac{\text{Daughters' fat production} - .15 \text{ dam's fat production}}{0.85}$$

This formula was the result of studies made by Turner in which he found that for each increase of 100 pounds of fat on the part of the dams the daughters increased 15 pounds. Later Turner (39) suggested that the transmitting ability could be more closely computed

by multiplying the dam's average butterfat records by .15 and subtracting it from the average of the daughter's record. In other words, the sire's ability equals the daughter's average fat production $-.15$ of the dam's fat production.

It should be understood that the above formula does not necessarily mean that 85% of the hereditary factors for milk production are contributed by the sire. The fact that Turner's index is based on dominance of some factors indicates that the only time that the dam can influence the daughter's production is when they contribute one or more allelomorphic genes to the sire's recessive genes, or if reversed, the only time the sire can cause improvement over the dams is when he contributes one or more dominant genes to supplement the recessive of the dams. Because of the relative ease of determining the progeny performance of the sire, and thereby obtaining a rough measure of his transmitting ability, the sire is given credit for part of the daughters' production that should be considered to have come jointly from both the dam and sire.

Gifford-Copeland Index. Gifford ⁽¹⁵⁾ found about the same results as Turner and worked out the following formula: $S + d = .2D$, when S is the sire's transmitting ability, d the average yearly butterfat record of the daughters and D is the average yearly production of the dams of the daughters. Gifford and Copeland later agreed that the actual production of the daughters was the best index of the transmitting ability for the sire.

The Mount Hope Index. The precise form of the Mount Hope Index is presented by Prentice. ⁽²⁷⁾ This index was worked out by Dr. H. D. Goodale based on the fact that high milk production is

27. Prentice, E. P., Profitable Breeding of Dairy Cattle, p. 188.

partially dominant while butterfat percentage is slightly recessive. This index has been worked out for milk, percent of fat, and for total fat. All records are computed to their mature equivalent.

"If the daughter's average exceeds the dam's average add three-sevenths (or .4286) of the difference to the daughter's average to get the bull's milk index figure. If the daughter's average be less than the dam's average, subtract seven-thirds (or 2.333) of the difference from the daughter's average to get the bull's milk index."

"The index for percentage of butterfat is obtained likewise, but with different fractions. If the daughter's butterfat average percentage exceeds the dam's butterfat average percentage, add three halves (or 1.5) of the difference to the daughter's average to get the bull's butterfat percentage index. If the daughter's average be less than the dam's average, subtract two-thirds (or .6667) of the difference from the daughter's average to get the bull's index."

To get the total fat index, multiply the milk index by the index figure for percentage of butterfat.

Equal Parent Index. (27) To make calculations more simple, a modified form of the Mount Hope Index has been devised. In this index the sire and the dam both contributed equally to the production of the offspring. In other words, if the daughters are better than the dams the difference is added to the daughters to get the bull's index. If the daughters are lower producers than the dams the difference between the two is subtracted from the daughters to get the bull's index figure. This may be done for determining milk, total

fat and butterfat percentage of a sire.

The Mount Hope and the Equal Parent Index take butterfat percentage into account also.

Parental Pedigree Index. Savage and Crows (36) have worked out an index for forecasting the daughter's production from parental pedigrees. It is the purpose of this index to determine the potential transmitting ability of a young bull before he has any daughters of his own. In all other indexes mentioned, the index of that bull cannot be made until he has at least five tested daughters. Thus, the bull will be at least five or six years old before he can be indexed or proven.

The index of the bull by the Parental Index is measured by two criteria. These are the dam's record and the records of her paternal half-sisters. To measure the sire's influence, the mean of the paternal half-sisters' records was calculated. This mean was then averaged with his dam's record and this figure termed the pedigree index of the bull in question.

Geneticists will object to an index based on these factors in that the dam's record is not necessarily a measure of her genotype and a bull's paternal half sisters are not entirely a measure of his sire's transmitting ability in that the paternal half-sisters are also influenced by their dams. This is true, but if an index based on such factors will, in practice, reduce hazards in breeding, it would seem logical to utilize such an index. (36)

On the basis of equal inheritance from both parents, the daughters will receive half of her inheritance from each parent. By taking the means of the mate's production and confirming it in

an average with the Pedigree Index the production of the daughters can be determined.

Yapp has also worked out an index or formula for young bulls that do not have any daughters. The formula is as follows:

$$S = \frac{A}{H} \times \frac{M}{H+1} \times R$$

The sire's potential ability is represented by S, A equals the herd average or breed average, M the number of records of relatives tested. All records are adjusted to 4 percent fat corrected milk.

Rice Pedigree Index. (31) Since proven bulls are few and far between and because a bull cannot be proven until he is at least five or six years old Rice has worked out a pedigree index for unproved bulls which is somewhat different from that made by Savage and Crowe.

Figure 3 gives the results of a genetic study of two full brothers, Winterthur Bess Ormsby Boast and Winterthur Bess Ormsby Great. The first pedigree index on the first bull had an error of 2 percent and the pedigree index of the second bull had an error of 3 percent. The indexes of the sire and two grand sires could be determined. For example, King of the Ormsbys' index was determined and found to be 24,051 lbs. of milk and 5.71% fat. This is determined by the equal parent index. The fraction to the left of King of the Ormsbys indicates, by the numerator, the number of dam-daughter comparisons available and the denominator the number of registered daughters. The fraction to the right of King of the Ormsbys indicates by the numerator the percentage of daughters which exceeded their dams in milk and by the denominator the percentage of daughters that exceeded their dams in fat percentage. The grandsires of Fig. 3 are

figured in a similar manner.

To determine the cow's part in the transmitting ability, as in the case of Spring Brook Bess Burke 2nd., the sire's index, as well as the index of the daughters and sons, are used. The sire's index is included to get the records of the dam's half-sisters. The index of the 2 daughters of Spring Brook Bess Burke is determined. The index of the sons is also determined if it is possible to do so. Thus, her index, on the bases of the daughters, is determined and also her index on the bases of the sons. These two indexes, together with her own record and her sire's index, give what will probably be the transmitting index of the cow. The indexes of the other cows are determined in a similar manner.

The two parent indexes were added together to get the average index and in like manner the indexes of the grandsires and grandams were averaged. Since the first generation is of greater importance, 0.6 of their averaged index, and 0.4 of the 4 grandparents averaged indexes were added together to give the pedigree index of the two brothers which is 23647 pounds of milk and 3.32% fat.

Rice worked out the pedigree indexes of 24 bulls and found the average error to be about 5.3%. In case a bull calf is sired by a young bull without tested daughters, or out of a young cow without a record, the procedure adopted here is to figure the pedigree index of the calf's sire and also of the dam. After this was done the pedigree index of the young bull was determined.

Winterthur Bess Ormsby Boast: 25 daughters 22858 3.53 Cows bred to ave. 23647 3.82 Pedigree index <u>2146505</u> 2 <u>7.39</u> 23252 3.57 Daughters should have done. 22806 3.72 Daughters did. (error 2%)		Sir Pieterbje Ormsby Mercedes: $\frac{46}{96}$ 23,601 3.61 $\frac{49}{53}$ ✓ King of the Ormsbys: $\frac{84}{185}$ 24,051 3.71 $\frac{60}{76}$ Pedigree Index <u>23,647</u> 3.82 <u>1</u>		Spring Brook Bess Burke 2nd. Two daughters. Trans. Index 23,600 4.08.	
Winterthur Bess Ormsby Great: 6 daughters 20,551 3.51 Cows bred to ave. 22,099 3.66 Daughters should have done. 20,484 3.63 Daughters did. (error 8%)		Sir Pieterbje Ormsby Mercedes: $\frac{43}{96}$ 23,601 3.61 $\frac{49}{53}$ ✓ Bess Johanna Ormsby One daughter. Record 30,143 3.97 Her index 16,171 4.15 Sire index 23,601 3.61 Trans. index 23,305 3.91		Spring Brook Bess Burke 2nd. Two daughters. Trans. Index 23,600 4.08.	

Figure 3. A Genetic Study of Two Full Brothers.

COMPARISON OF THE PREDICTION VALUE OF BULL INDEXES

Since many of the indexes have been based on totally different genetic theories, many authorities have made comparisons of the various indexes to determine their prediction value. Since the Graves index and the Pearl, Gowen, and Miner index do not give actual milk and fat production for the sire's potential level of production they cannot be compared.

Rice (32) made a study of twenty bulls selected at random from the four major breeds of dairy cattle. Table IV gives his results of the study of the prediction value of bull indexes based on milk production. In making this comparison the index of the sire was determined by taking the records of the first ten dam and daughter comparisons. With the bull index of the sire determined on the basis of the first ten daughters the production of the remaining daughters was determined from the average of the dam's production and the sire's index. The difference between the calculated figure and the actual production of the remaining daughters represented the degree of error of the index. The average error of the three indexes was surprisingly close but favoring the intermediate index. The percent error for the intermediate (equal parent) index being 7.9%, for the Mount Hope 8.5%, and for the Gifford index 10.2% error.

In a similar table worked out by Rice for butterfat percentage the percent error was as follows:

Mount Hope index	0.13%.
Intermediate index	0.13%.
Gifford index	0.17%.

TABLE IV. PREDICTION VALUE OF BULL INDEXES BASED ON THE AMOUNT OF MILK PRODUCED.

No. of Sire	Intermediate		Mt. Hope		Gifford	
	:Dau. :Dam :Pairs	:Index on :First 10 :Daughters	:Error on :all later :Daughters	:Index on :First 10 :Daughters	:Error on :all later :Daughters	:Index on :First 10 :Daughters
1	51	11,175	0.8	9,995	1.4	10,092
2	45	10,481	2.8	9,757	3.3	10,276
3	17	13,777	15.0	12,352	11.2	12,957
4	35	14,219	7.5	13,694	7.2	12,852
5	58	14,064	6.2	13,629	7.4	13,303
6	72	8,613	11.2	5,291	12.0	10,449
7	109	12,875	2.2	11,916	5.3	10,376
8	17	12,529	4.6	11,616	7.8	11,682
9	31	10,740	1.3	10,340	.4	9,853
10	31	12,306	7.7	10,941	12.0	8,922
11	53	17,605	17.2	15,121	16.3	12,451
12	38	26,655	9.1	25,285	10.0	24,212
13	25	7,684	12.8	4,929	18.6	9,751
14	82	12,596	8.4	11,762	8.6	11,504
15	52	10,520	14.4	10,240	15.4	9,911
16	31	11,052	0.7	10,123	.6	9,663
17	23	17,032	11.1	16,371	11.9	14,606
18	31	15,292	9.7	14,122	8.0	14,255
19	23	15,437	8.3	15,248	9.7	15,133
20	36	14,822	8.0	13,344	3.0	11,873
Average error:		7.9		8.5		10.2

To further show that the production of the dam should be considered in the index Rice (32) made a study of the production levels in both amount of milk and the percentage of fat of the daughters of high producing cows and those of low producing cows, the daughters being from the same sire in both cases. The production of the 5 high producing dams and the production of the 5 low producing dams was determined as well as the production of the resulting daughters. Table V includes ten bulls and shows that the daughters of high producing cows averaged 924 pounds of milk more than the average of all daughters and the daughters of the low producing dams produced 891 pounds of milk less than the average of all daughters. Similar results were obtained for inheritance of butter-fat percentage.

TABLE V. INFLUENCE OF DAMS ON THE DAUGHTERS' PRODUCTION.

	Dams' Average	Daughters Average
High dams	16,403 $\frac{1}{2}$ lbs. milk 5.6% B. F.	14,449 lbs. milk 5.35% B. F.
Average of all Daughters		13,494 lbs. milk 5.14% B. F.
Low dams	10,030 lbs. milk 4.51% B. F.	12,603 lbs. milk 4.88% B. F.

Peterson's Comparison of Indexes. Petersen (29) took twenty Jersey bulls that had twenty or more daughters of tested dams. The index was calculated for each bull as follows:

1. All twenty daughters and their dams.
2. First ten daughters and their dams.
3. Second ten daughters and their dams.
4. Ten daughters from 10 high dams.
5. Ten daughters from 10 low dams.

He found fairly good agreement between indexes calculated from the first ten daughters and the second ten daughters. However, when the Mount Hope and the Intermediate index were calculated for the ten high and the ten low dams with their daughters, neither index showed good agreement. The Gifford index which was the average mean of the daughters showed excellent agreement between the production of the daughters of low and high dams. In six out of the twenty cases of the Gifford index, the daughters of the ten low dams exceeded the daughters of the ten high dams. In the majority of cases there was no appreciable difference.

Quoting directly, Peterson says, "It would appear from these studies that where good bulls are used the bull index is not reliable but that the daughters from such bulls out of the poorer dams have nearly as good a chance on the average as the daughters from the better dams. That a fair measure of a bull is the arithmetical average of his daughters, environment being taken into account."

Copeland's Comparative Study of Bull Indexes. Since Copeland⁽⁶⁾ found that the average records of the first ten tested daughters gave a close approximation of the record of all a bull's progeny, he proposed to find out if a dam-daughter comparison is really essential. To determine this, a study was made to compare the Mount Hope Index and the Yapp Index with the average of the bull's first ten daughters as a measure of determining the bull's index. In making this comparison the average of the first ten daughters was compared with the average of the second ten daughters and with the average of all tested daughters. The variations in pounds of fat were calculated in each instance. The Mount Hope Index was computed for the first ten daugh-

ters out of tested dams. This index was also computed for the second ten daughters, and also for all dam-daughter comparisons. Variations in the indexes were then determined. Similar calculations were made on the Yapp Index.

Copeland concluded that the average variation of the records of the first ten daughters compared with that of the second ten daughters, and also compared with the records of all daughters was much less for the Gifford Index than for the Mount Hope and the Yapp Index.

Gifford's Comparison of Breeding Indexes. ⁽¹⁵⁾ In order to determine the value of the sire indexes, Gifford made a study of daughters out of dams of various productions of 25 Holstein-Friesian sires. Indexes were determined from the same sires, using the same dam and daughter pairs in which the dams were classified as to low, medium, and high production groups. The average of the daughters in each of these groups was also compared. Gifford found the average deviation for the indexes, in most cases, was much higher than was obtained when the dams' records were not considered.

Figure 4 gives the variations in the different indexes calculated from the production of the dams and their respective daughters when the dams were classified as low, medium, and high producers. The Mount Hope, Yapp and Pearl Indexes had a much greater variation in the indexes. Theoretically the indexes would be the same for all groups if the index were perfect. Figure 4 indicates that the error of the Yapp Index is about two and one-half times greater than the one in which the daughter's production represents the bull index. The Mount Hope Index had over three times as great an error as did the index in which the daughter's production represented the bull's index.

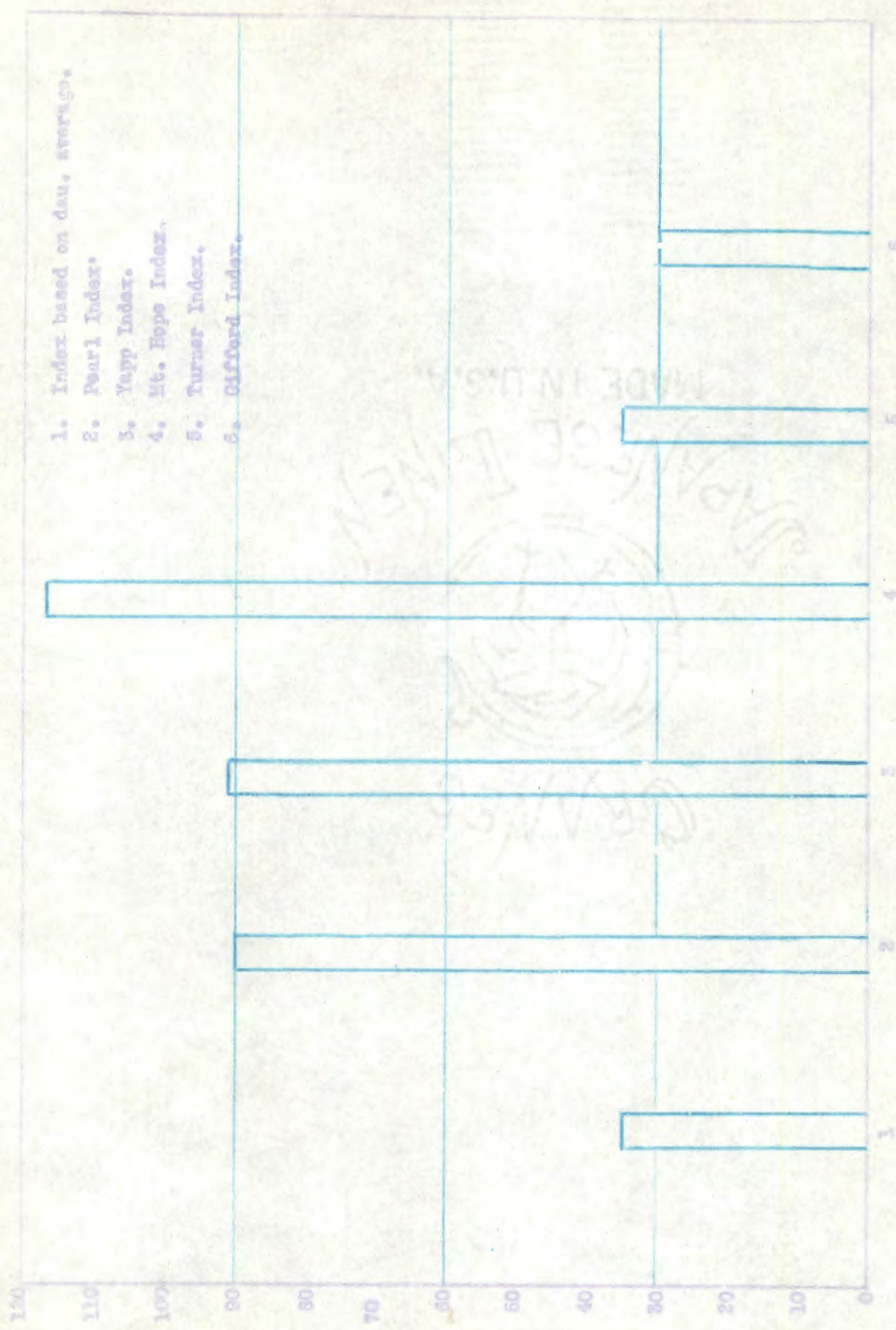


Fig. 4.--Degree of error of various indexes. Summary of results of a comparison of 25 sires.

Edwards Comparisons of the Bulls Transmitting Ability by the Various Indexes. Edwards (10) proved several bulls by five different indexes. His results were very similar to those of Gifford. Bulls with ten or more daughters were used. The dams were arranged into two groups, low production and high production. The daughters were classified in the same groups as their dams. The daughters of the three groups of dams were averaged. The bull was given three indexes as follows, (1) on the progeny of the high producing dams, (2) low producing dams, and (3) the index of the progeny of all dams. Results of the index were as follows.

TABLE VI. AVERAGE DEVIATION FROM INDEX OF ALL PROGENY. AVERAGE OF 23 SIREs.

	Low Dams Lbs. of Milk	High Dams Lbs. of Milk
Average of daughters index	450	450
Pearl Index	1160	1160
Yapp Index	1200	1200
Wright Index	940	970
Mt. Hope Index	1660	2670

The above table agrees with the results given by Gifford. The daughter's average as the index of a bull's transmitting ability proved to be the most accurate.

Criticism of the Average of the Daughters as an Index of a Bull's Transmitting Ability. Prentice (28) criticizes Gifford's method of comparing indexes. He states that in the Average Daughter index a comparison was made of the expected production with that of the actual production, which was alright. "In the case of the Mount Hope Index, however, both in his work with Holstein-Friesian cattle published in research bulletin 144 and in his work with Guernseys published in the Guernsey Breeders Journal, Professor Gifford unfortunately reversed the process and taking the actual production of the bull's daughters, assuming all variations were to be charged to the

sire and none to the dam, he computed the sire's theoretical index from the daughters' production.

Prentice states that bulls when mated to cows of very unequal productive ability, but whose daughters make the same average would be of equal rank according to Gifford's Index. He points out that, the fact that the daughters of dams of the low producing group were 20 pounds below the average of all daughters and that the daughters of the high group of dams were 30 pounds above the average of all daughters, indicates that the dams have an influence on the progeny. The above figures were taken from Gifford's studies of Guernsey sires.

Comparison of the Parental Pedigree Index with the Intermediate or Equal Parent Index. Savage and Crowe (36) compared the percent error of the Parental Pedigree Index in determining the daughters' production of a young bull with that of the Intermediate Index. They found that the Parental Index of a young unproven bull was just as accurate as the Intermediate bull index based on the daughters of a proven bull. After the Parental Pedigree Index was determined, the parental expectation was determined by the same method as that of determining the expectation for the Intermediate Index.

Table VII gives the comparison of the Parental and the Intermediate index expectation and shows how nearly each index forecasts the daughters' means and the deviations of the daughters' means from the expectations. According to this table the Intermediate index forecasted the daughters' means of 70 bulls within 50 pounds of the butterfat from their daughters actual means. This is 60% of the 117 bulls used in the comparison. Of the remaining 40% of the 117 bulls 21% fell more than 50 pounds below the expectation and 19% fell more than 50 pounds above the expectation. In the Parental Index method, 70% of the bulls that were forecasted came within 50 pounds of the

daughters' actual means; 19% of the remaining 30% fell more than 50 pounds below the expectation and 11% fell more than 50 pounds above the expectation. For all 117 bulls the Parental expectation deviated 39 pounds from the daughters' actual average while the equal parent expectation deviated on the average 46 pounds of fat from the actual average.

TABLE VII. COMPARISON OF PARENTAL AND MOUNT HOPE EXPECTATION.

Deviation of Daughters Average from Expectation:	Parental Expectation				Mount Hope Expectation			
	Number of Bulls		Pro-gressive Total	Expecta-tion	Number of Bulls		Pro-gressive Total	Expecta-tion
Pounds Fat	Above Expecta-tion	Below Expecta-tion			Above Expecta-tion	Below Expecta-tion		
0	0	0	0		0	0	0	
1-10	7	8	15		11	13	24	0
11-20	9	19	28		7	7	14	24
21-30	8	10	18		7	7	13	38
31-40	1	7	8		7	7	10	51
41-50	4	9	13		4	5	9	61
51-60	4	9	13		5	5	10	70
61-70	1	2	3		5	3	8	80
71-80	4	2	6		3	5	8	88
81-90	1	3	4		3	3	6	96
91-100	1	1	2		2	2	4	102
101-110	0	1	1		1	1	2	106
111-120	1	4	5		1	3	4	108
121-130	0	0	0		0	0	1	112
131-140	1	0	1		1	1	1	113
141-150		0			0	1	1	114
151-160					0	1	1	115
161-170					0	0	0	116
171-180					0	0	0	116
181-190					0	0	0	116
191-200					1	0	1	117
Total	42	75	117	117	53	64	117	117

STANDARDS FOR TESTING INDEXES

It will be noted that in the several indexes suggested for studying the transmitting ability of a bull, there are several different methods of approach in attempting to determine the transmitting ability. Some of these give indexes in pounds of milk, percent fat and total fat that the sire should transmit to its offspring, others indicate the difference between the production of the dams and daughters only, and others indicate the potential production of the sire, itself. Some are based on partial dominance, others on equal contribution and others disregard the dam's contribution entirely.

Rice has set up the following standards for testing the validity and usefulness of a bull index. (32)

1. An index must be simple and easily understood by the average dairyman. This is based on the fact that regardless of how accurate an index may be if it cannot be applied by the average dairyman it is of little use.
2. It must employ both dams' and daughters' records since it is a fair assumption that both parents contribute something to the offspring.
3. The index must be a numerical statement of the bull's potential milk and butterfat levels.
4. The index must be based on a sound genetic theory.
5. The index must have a high prediction value. The index must indicate the future breeding value of a young bull and indicate with some degree of certainty the production of its daughters.

Gifford (15) makes the following statement in regard to the value of a sire's transmitting ability:

"The value of any measure of a sire's transmitting ability is whether or not such a measure can be used to predict the production of future daughters more accurately than simply using the sire's average progeny performance record. In other words, if the variability of the daughters' records is less when predicted by the theoretical measure than it is when records are predicted from the average of the sire's progeny records, it is of practical value. If it is not, then such a measure is of little value. Too, such a measure should give the sire approximately the same index measure whether he is mated with a group of high producing dams or with a group of low producing animals if the number of dams and daughters pairs within the group is large enough to indicate the sire's transmitting ability."

APPLICATION OF BREEDING INDEXES

Norton (26) says, "All the practical breeder can do is to ask himself two questions about every index in which he is interested: (1) to what conditions does the index apply, that is, how were the daughters managed? And (2) were daughters and dams managed alike?"

If a bull index is based on only a few daughter-dam pairs it is not safe to place complete confidence in the index. If it is very high or very low one would expect the true breeding value of a bull to be nearer the breed average. This is termed "regression." The following regression percentages have been calculated by the Iowa Experiment Station. (26) If the index is based on six pairs, the best estimate of a bull's transmitting value lies about 45% of the way from the index to the breed average. If based on ten pairs the amount of regression that is allowed toward the breed average is 31%; if on 15 pairs, 23%; if on 25 pairs, 15%; etc.

"The index is an estimate based on the available information and subject to error from several sources. First, it applies only to conditions under which the daughters made their records, and these conditions might be different for any two bulls whose indexes might be compared. Second, it is important that daughters and dams receive equally good management. Third, indexes are usually based on a relatively small number of daughter-dam pairs, leaving opportunity for wide variation from the true value. Indexes with more pairs deserve more confidence. Fourth, very high indexes are apt to be higher than they should be, and very low indexes are apt to be too low. Fifth, the dams may have been selected for high records, so that their records may be higher than their breeding value." (26)

Lush says, "The equal parent index, based on all records of each daughter, fairly compared with all records of her dam, is a valuable measure for the herd owner for owners of closely related

animals. It means very little to those who know nothing of the feeding and herd management of the bull's daughters and their dams."⁽²⁵⁾

Rice (31) emphasizes that an index does not attempt to predict what the individual offspring of an indexed bull will produce. The index is based on averages of eight to ten records and is useful only in predicting what a group of daughters will do.

GERM PLASM STUDIES

During the past two years the United States Department of Agriculture has started a program of making a search for the best inheritance of plants and animals. (49) One of the purposes of the germ plasm studies is to judge the worth of a sire in a herd and to determine whether a dairyman is gradually increasing the production of his herd or if he is going backward. In other words, it is a herd analysis of the breeding program of that herd. The bases on which the worth of a sire was judged were (1) Improvement or lowering of production of the daughters over the dams, (2) the proportion of daughters equal to or better than their dams, and (3) the relation of the production of the dams to the herd average. These three bases are determined or judged by a system of plus and minus scoring. To arrive at the inheritance that a series of sires has left in a herd, consideration is given to the ratings of the sire for each character.

Method of Scoring Sires for Inheritance for Fat Percentage--

Level of Milk Production and Level of Fat Production.

Percentage increase or decrease of the daughters compared with the dams.

1. One plus point for each 0.2 percent increase over the dam.
2. One minus point for each 0.2 percent decrease below the

dams.

Percentage of daughters better than the dams.

1. One plus point for each 1 percent or fraction thereof above 50 percent.
2. One minus point for each one percent or fraction thereof below 50 percent.

Percentage by which the average of the dams is above or below the herd average (correction of level of production.)

1. One plus point for each 0.5 percent by which the average of the dams is above the herd average, or two points for each one percent above the herd average.

2. One minus point for each 0.5 percent by which the average of the dam is below the herd average.

Rating of sires on basis of total number of points scored under the above three headings.

	<u>Fat Percentage</u>	<u>Milk and Butterfat</u>
1. E (Excellent)	/70 points or more	/ 100 points or more
2. G (Good)	/35 to / 69 points	/ 50 to / 99 points
3. F (Fair)	0 to / 34 points	0 to / 49 points
4. U (Undetermined)	- 1 to - 14 points	- 1 to - 14 points
5. P (Poor)	-15 points or more	- 15 points or more
6. N. P. All sires with less than five daughter dam pairs		

were marked N. P., or not proven.

Table VIII gives the results of a germ plasma study of two successive bulls used in a dairy herd, one of which classified excellent, while the bull following the good bull classified as poor. It should be understood that this classification refers only to this herd and will not apply to another herd of a different production.

TABLE VIII. GERM PLASM SURVEY OF TWO SUCCESSIVE BULLS IN A HERD.

Name of Sire	North Star Hona Homestead 379355			Sir Colantha Ormsby Veeman 356098		
	2)			3)		
a. No. of tested pairs	7			9		
	% B'fat	lbs. Milk	lbs. B'fat	% B'fat	lbs. Milk	lbs. B'fat
b. Average of daughters	3.42	21165	721	3.59	15651	564
c. Average of their dams	3.38	15417	516	3.36	18535	626
d. Increase (b - c) or decrease (c - b)	+0.04	+5748	+205	+.23	-2904	-62
e. $\frac{d}{c} \times 100$ (percentage)	+1.2	+37.3	+39.7	+6.4	-15.7	-9.9
f. No. daughters equal to or better than dams	3	7	7	7	2	4
g. $\frac{f}{a} \times 100$ (percentage)	42.9	100.0	100.0	77.8	22.2	44.4
h. Cumulative herd average	3.39	14989	504	3.44	17387	595
i. $\frac{g}{h} \times 100$ (percentage)	99.7	102.9	102.4	97.7	106.6	105.2
j. Score of bull for e	+6	+188	+199	+32	-79	-50
k. Score of bull for g	-8	+50	+50	+28	-28	-6
l. Score of bull for i	-1	+6	+5	-5	+13	+10
m. Total of j, k, and l	-3	+244	+254	+55	-94	-46
n. Classification of bull	U	E	E	G	P	P
Notes on feeding and o. Management	9 cows 3 milkings 1 cow 2 milkings A. R. S. O.			3 milkings		
p. Total daughters sired that calved in this herd	11			10		
q. Total daughters tested	10			10		
r. $\frac{q}{p} \times 100$ (percentage)	90.9			100.0		
s. Qualifying statements	1 short record not included					

Ave. for all dcs. tested 3.49 19544 678 3.61 14862 537

INHERITANCE OF BUTTERFAT PERCENTAGE AND THE INFLUENCE OF ENVIRONMENT

Considerable work has been done in attempting to study the inheritance of butterfat percentage as well as milk production. As has been pointed out previously in this paper butterfat percentage as well as milk production and total fat are probably influenced by several factors.

Comparison of Butterfat Percentage of the Dam with that of the Daughter. Bartlett (1) made a study of Holstein cows with records of 600 pounds of fat or more to see what effect the percent test of the dam had on the butterfat percentage of the daughters. He found that, although the tendency is for all fat percentages to center toward the breed average, daughters of high testing dams tend to inherit the dam's test and that daughters of low testing cows tend to inherit their dam's test. The following formula will predict the relation of butterfat percent of the mother and the daughter:

Daughter's butterfat percentage = $2.118 \div 0.4049$ dam's butterfat percentage.

A significant correlation coefficient between dam and daughter was found to be 0.4169. "When mated to 4 percent cows the progeny of 118 sires varied widely in their butterfat tests; however, with an increase in the average test of the daughters of any particular sire the test of his daughters out of certain dams increased to a marked degree with the increase of the fat test of such dams." (1)

The fat test of the sires dam did not appear to have any significant correlation with the fat test of the sires daughters.

Copeland (7) concluded from a study of Jersey records that both the sire and the dam contribute to the inheritance of their daughters'

fat percentage. Graves,⁽²¹⁾ work indicated that the production records of the daughters of each sire and their dams seemed to show that the daughters percentage of butterfat follows that of the dams fairly closely. He suggests that this may be due to the following reasons: (1) There may be less variability in the percent of fat than in milk yield. (2) Inheritance of percent of fat may be better fixed than is the inheritance of milk yield.

Transmission of Butterfat Percentage by Holstein-Friesian Sires.

Baker⁽²⁾ concluded that certain blood-lines carry factors for high butterfat percentage to a greater degree than others, and also that some blood-lines carry factors for low butterfat percentage to a marked degree. He further states that it would be possible to bring a low testing herd up to or slightly above the average of the breed by the use of sires from high testing blood lines. However, the only possibility of maintaining a herd that would continually be above the breed average would be to always use sires whose potentialities are for high butterfat percentage. Baker emphasizes that both the dam and sire contribute to the offspring.

Burrington and White⁽³⁾ found that the butterfat percentage tended to remain constant in some families regardless of the bulls used. In studying the transmitting ability of the offspring of two distinct foundation cows at the Connecticut Station it was found that even though the same sire was used in both families the average tests of the two families are as far apart today as when the two foundation cows were bought. The percent test of one foundation cow was 3.45 and for the other 3.25 percent. Only one animal in the high test family tested less than 3.25 percent and only two in the low test family tested over 3.45 percent. The high test family reached as

high as 3.89% and the low test family as low as 2.67% for individuals.

Figure 5 gives the percent fat in both families for daughters of several bulls. It will be noticed that the lines do not cross at any time. The fact that the lines tended to be parallel a good part of the time indicates that the bulls did affect the test, but that it affected the test about the same degree in both families. This chart does not show much of a tendency for fat percentage to go toward the breed average.

Effect of Environment on Butterfat Tests. Wylie ⁽⁴⁵⁾ has pointed out that Tennessee Jerseys have a much higher butterfat test than Jerseys of other states. He has also shown evidence that indicates a large variation in butterfat percentages of Register of Merit records within different sections of the state. Table IX gives the relation of the richness of milk of Register of Merit cows in several counties of Tennessee in which cattle have been tested. Only counties with at least 20 tested cows are recorded.

TABLE IX. RELATION OF BUTTERFAT PERCENTAGE OF JERSEY CATTLE TO LOCATION BY COUNTIES IN TENNESSEE.

County	No. Cows	Average % Fat
Williamson	123	5.99
Gibson	24	5.78
Maury	188	5.69
Rutherford	190	5.68
Marshall	128	5.63
Davidson	321	5.55
Wilson	100	5.49
Sumner	43	5.48
Giles	23	5.46
Hamilton	27	5.38
Bedford	38	5.35
Shelby	145	5.30
Loudon	22	5.26
Hawkins	40	5.21
Knox	150	5.17

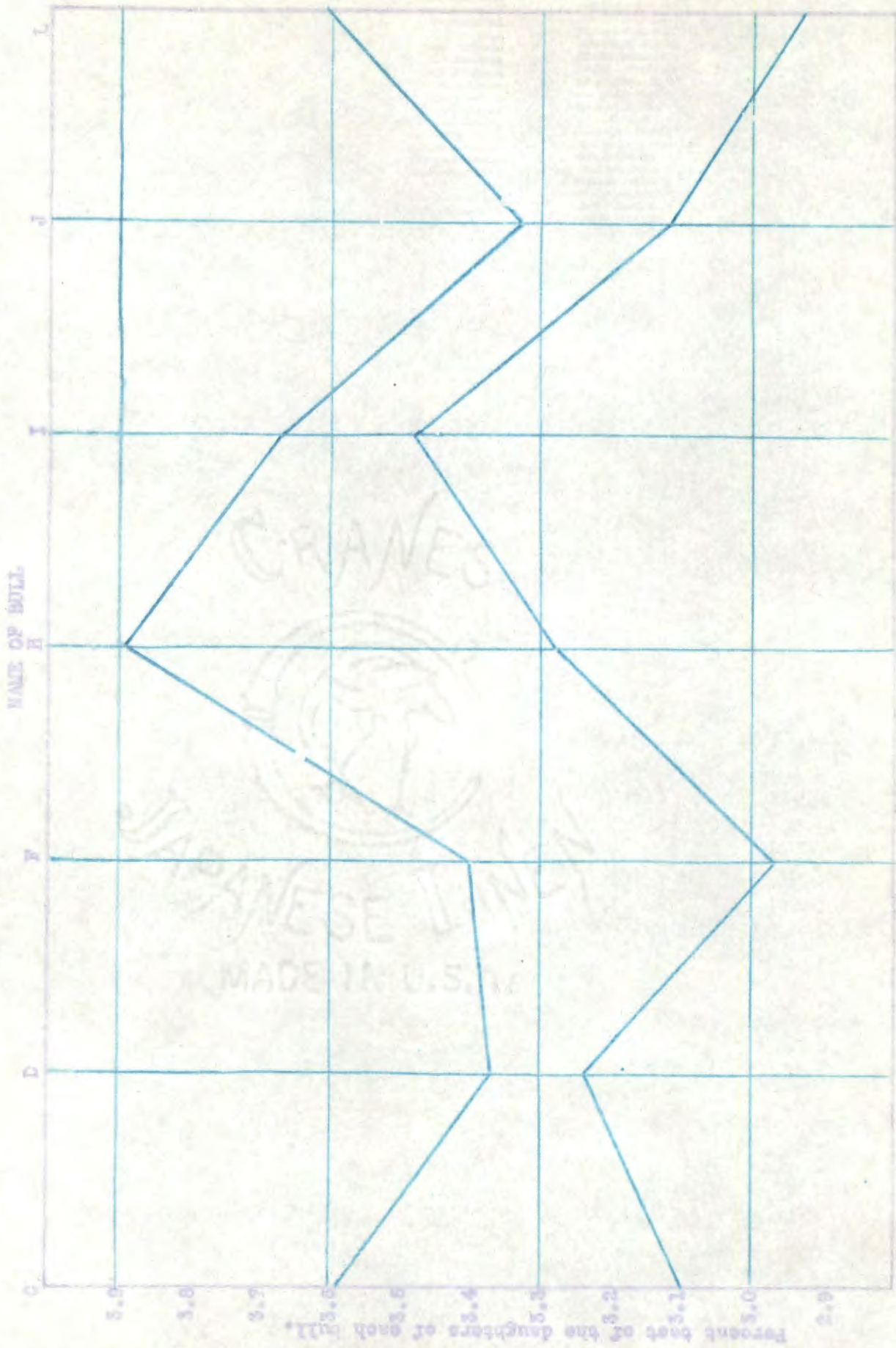


Fig. 6.—Percent of fat of offspring of two distinct families when bred to the same bulls.

Table II shows a difference of .8 of a percent fat between Register of Merit Records in Williamson and Knox Counties. The question that arises is: Is this difference due to breeding and inheritance or is it due to environment? Wylie (45) has suggested that this difference is due to phosphate since the sections of the state that were richest in phosphate also had the highest butterfat tests and the poor phosphate sections had the lowest butterfat tests. If it is due to inheritance, it would indicate that butterfat percentage can be influenced by heredity considerably. If the difference is due to environment it will make heredity studies more difficult than in the past and will make such records, if used in inheritance studies, incomparable unless some adjustment can be made for these variations.

CORRELATION OF MILK YIELD, BUTTERFAT TEST, AND TOTAL BUTTERFAT

There has been considerable discussion both pro and con as to whether milk and butterfat percentage are correlated or whether they are entirely independent of one another.

Copeland (7) and Graves (21) found that a parent may be prepotent in increasing the fat percentage of the offspring separately without affecting the milk yield or it may increase or decrease both butterfat percentage and milk yield. Copeland made his studies with Jerseys and Graves studied the inheritance of butterfat percentage on Holsteins. Copeland found that even though there was a negative correlation between fat percentage and milk yield there was a distinct positive correlation between total fat production and fat percentage. He found the correlation between milk and fat percentage to be -0.311 while the correlation of total fat to fat percentage was $+ .253$.

Table X indicates that there is a distinct relation between test and total fat yield. In this table the records were grouped according to the butterfat tests. The butterfat yield of cows testing 4.20% to 4.4% was 487 pounds while cows testing 6.6 or higher averaged 580 pounds of fat. This is an increase of about 20 percent in total fat yield while the milk yield decreased about 25 percent for the two groups respectively.

Yapp (46) found a definite correlation between milk and test and concluded that the total pounds of fat was about constant regardless of test when the milk was corrected to four percent fat corrected milk. Gains and Davidson (18) state, "The milk yield of cows

4% basis:

$$F. C. M. = .4M / 15 F.$$

In this formula, F. C. M. equals 4% fat corrected milk, M equals milk yield, and F equals fat yield.

Roberts (34) also found a significant relation between milk production and percent fat varying from -0.559 to -0.437 when calculated according to age on Jerseys, and from - .251 to -0.337 on Guernseys. The correlation for Holsteins was found to be much less, having a correlation coefficient of only -0.088 to -0.16. In Ayrshires no significant correlation was found.

Graves (21) found the coefficient of correlation varied widely and found that no sire showed complete prepotency for raising and lowering both milk yield and percentage of butterfat for all his daughters. The breeding of individual sires indicates that a sire may be prepotent in increasing the milk yield and decreasing the percentage of the daughters as compared with the dams or he may be prepotent in lowering the yield of milk and increasing the percent of butterfat or he may either raise or lower both the milk yield and fat percentage.

Graves concluded that milk yield and fat percentage were inherited independently in Holsteins. He found a negative correlation in some cases and a positive correlation in other instances.

Copeland (7) concluded that total butterfat production can be increased by selection for high test as well as selection for high milk yield. A study of Register of Merit records of all animals with over 700 pounds of fat reveals the average test to be 5.56 percent while the breed average for Register of Merit Jerseys is 5.26 percent.

Graves (21) found that many of the sires that made the greatest increase in milk yield also increased the average percentage of fat very materially, whereas only a few sires that increased the milk yield of daughters decreased the percentage of butterfat.

CONCLUSIONS

1. The study of the inheritance of milk and butterfat production of dairy cows is a relatively new subject, and one in which there has been very little accurate and conclusive data assembled.
2. There are two methods of studying inheritance of milk production; (1) to establish a breeding herd under controlled conditions so that environmental factors can be separated from those of inheritance, and (2) an analysis of statistical and genetical data.
3. All records of production and conditions should be standardized as much as possible in order to make records comparable. Care and management, which is the largest environmental factor causing variations in production, cannot at the present time be satisfactorily adjusted to an equal basis for all animals in a comparison.
4. Nearly all statistical studies of inheritance of milk and fat secretion have been based upon Advanced Registry records. However, Advanced Registry records may often be misleading because they may not represent a true cross section of the production of a group of animals due to selection of only the best animals in some cases.
5. Type is a very poor indicator of the transmitting ability of the production of a dam or sire. Type, however, is apparently transmitted by the parents more uniformly than is milk production.
6. Most authorities agree that each parent contributes some inheritance for milk and fat production to the offspring. The amount that each parent contributes to the offspring cannot be definitely stated, although many theories and assumptions have been proposed.

7. It is the general consensus of opinion that the inheritance of milk and fat secretion is affected not by one gene but by several genes or factors.
8. The majority of authorities believe that milk yield and butterfat percentage are inherited independently of each other even though there is a partial negative correlation between milk and butterfat percentage.
9. Butterfat percentage is probably subject to less variation than is milk production. This is true for both environmental and hereditary factors.
10. It is definitely known that the production record of a dam does not necessarily indicate her transmitting ability as to production. In other words the dam's record is only an indication of her phenotype for milk production and not necessarily her genotype.
11. A bull index is a measuring stick for determining the breeding value of a sire, but it must be remembered that an index is only an estimate and is subject to error from many sources.
12. The production of the same animal may vary considerably from one year to the next. The more records of production one can secure on an animal or a group of animals the more accurately one can determine the breeding value of the animal, provided they are properly analyzed.
13. At the present time little is actually known about how milk and butterfat production are inherited. Although many theories have been presented most of them lack sufficient evidence and proof to make them valid. It is true, however, that great progress has been made by some breeders while many others have been going backward.

14. There appears to be a tendency for the production of dairy cattle to move toward the breed average regardless of its inheritance.

PART II

ORIGINAL INVESTIGATION

PART II

ORIGINAL INVESTIGATION

In order for a breeder to make continuous progress in breeding dairy cattle for production he must know something of the principles of heredity and genetics. In the past fifty years great advancement has been made in the field of nutrition and in care and management of dairy cattle. While proper feeding and management are very necessary for cattle to produce large quantities of milk, nothing in the world can make a cow produce milk unless she has inherited some characteristics for producing milk, whether it be in large or small quantities. It has been pointed out before hand that there has been considerable work done in an attempt to study the inheritance of milk and fat production in dairy cattle.

The purpose of this investigation is to further investigate the problem of inheritance of milk and butterfat production in dairy cattle and to apply the principles of genetics to the practical breeding of dairy cattle. One cannot hope to continually increase the production of a herd unless he understands animal breeding. It is not difficult to breed a herd of dairy cattle capable of averaging 300 pounds of fat a year, however, to make an improvement on a herd that averages 400-500 pounds of fat yearly, is, indeed, a difficult problem.

Plan of Investigation. The plan of this investigation is to make a statistical analysis of a large number of milk and butterfat records in an attempt to further determine the mode of inheritance of milk and butterfat and how it is transmitted from the parents to the offspring. To study inheritance, it is necessary to eliminate, as far

possible, other factors other than the one that is being dealt with. If the environmental factors cannot be eliminated they should at least be as identical as possible in all comparisons. This investigation is divided up into the following parts:

1. A study of a number of records for the purpose of determining a more accurate conversion factor for adjusting records to a mature equivalent basis.
2. A comparative analysis of the Mt. Hope, Intermediate, and Gifford Indexes, their application and value in determining the transmitting ability of the bull or dam to their offspring.
3. A study of the relationship of milk yield, total fat production, and butterfat percentage to each other, if any.
4. Discussion of results of this investigation and how they might be applied to the dairy breeder.

It is also the aim of this investigation to give some added information to the following questions: (1) Are present conversion factors for adjusting milk and fat records to a mature equivalent basis, too high? (2) Can a bull index be used as a method for determining the breeding value of a herd sire? (3) Can a genetically sound index be given for determining the production of the offspring based on the records of the ancestry? (4) Is there any indication of dominance in milk and butterfat production in dairy cattle? (5) Are milk and butterfat percentages inherited independently of one another or are they related to each other? (6) Can statistical data, based on production records, be used in making inheritance studies of milk and butterfat production?

STATISTICAL DATA USED IN THE INVESTIGATION

In the past, practically all inheritance studies based on statistical data have been made from tabulations of Advanced Registry or Register of Merit records. The main reason that Advanced Registry records have been used is because of the fact that they were easily accessible to most every one and because they more nearly represented the inheritable capacity of a dairy animal than did any other type of production records available in the years past. It has been pointed out in the review of literature, however, that those records are objectionable for several reasons when used as data for inheritance studies. The biggest objection to the use of Advanced Registry records is that they represent only a selected group of animals and thus do not indicate a true cross section of the average production of all the offspring from a dam or sire. The owner usually does not put an animal on test unless he thinks she has the ability to make a high record and he may even take an animal off test if he sees that she is not going to make a good record. The average of all the tested daughters of a sire may be 600 pounds of fat but if all his registered daughters were tested, the average might be only 400 pounds. It is impossible to determine much about the transmitting ability of this bull if only the daughters with Advanced Registry records are considered.

In an attempt to remedy the objections stated above most of the records used in this investigation will consist of Herd Test records. In using herd test records there is little chance for selection of only good individuals from which to make high records. In the herd test it is necessary that every registered animal in a herd be tested regardless of how good a producer she is. The writer realizes that even

in the herd test it is not possible to get all daughters tested, but a larger percent will be tested than in the case of Advanced Registry testing. As to care and management, it is questionable as to whether Advanced Registry or herd test records are the most desirable for studying inheritance. Another advantage of herd test records is that each animal will have a larger number of records, in most cases, thus getting a more definite picture as to a cow's actual producing ability.

In this investigation, all tabulations are based upon Holstein-Friesian Advanced Registry or Herd Test records. All records used in comparing the accuracy of bull indexes and those used in determining the relation of the daughters' records to those of the parents are based upon herd test records. Some of the records used in studying the inheritance of butterfat percentage are Advanced Registry records because in some instances there was not sufficient information available from the herd test records.

STANDARDIZATION OF MILK RECORDS

A great many factors or formulae have been proposed for the purpose of adjusting all production records for milk and butterfat to a mature equivalent basis. In most instances these factors have been the result of a tabulation of a large number of production records which were classified according to age only. In many instances and perhaps in most cases the records tabulated for the two-year-old group were from entirely different cows than those in the three or four-year-old group. In other words, since the cows in the five-year-old group may be an entirely different group than those in the two-year-old group, we do not know whether the cows that made the five-year-old records would have made the same records as two-year-olds, as did the group from which the average production for two-year-olds was determined. For this reason the factor for adjusting records might be either too high or too low. Furthermore, the number of milkings per day was usually not considered as a factor that might cause variations. It is thought, however, that when several thousand records are tabulated the objections mentioned would be more or less neutralized.

It has been the opinion of many people that conversion factors for standardizing records to maturity are too high. Because of this fact, it was thought advisable to take animals that had at least four yearly records of production and by this method draw up a new set of factors in which the average of the records of the five-year-old class would be, in most cases, made by the same animals as those in the two-year-old class. In this tabulation all records were made on class C milking and are taken from Volume 6 of the Holstein-Herd Test Record

Book. The purpose of this tabulation is two-fold: (1) To determine whether most present factors for standardizing records are too high and (2) to determine whether standardization factors can be applied to averages of several animals only, or if it is at all practical to use them when dealing with individual animals also.

Results of Study for Determining a Conversion Factor for Standardizing Milk Records. A tabulation was made of 113 different cows in which 105 had at least four records of production and the other eight had three records of production making a total of 470 records in the whole tabulation. It should be stated here that it was not possible to get the records for every cow for the same years in all cases. All records used were at least 260 days in length. Since the average number of days of the records for the various years of age varied a few days, an adjustment was made to make the number of days equal in all cases.

Table XI gives the relationship of age to yield of milk, total butterfat, and percent butterfat. Milk yield reached its peak at seven years of age and then began to gradually decline while total butterfat reached its peak at six years, and butterfat percentage reached its peak at five years of age. It will be noticed that, in general, the factor for milk yield and butterfat yield is very nearly the same but being slightly lower for fat in every case up to seven years of age. This table indicates that the percentage of butterfat is not affected by age to any significant extent. Figure 6 illustrates graphically the comparison of the factors for correcting milk yield, butterfat percentage, and total butterfat. Figure 7 compares the conversion factors as given by the American Jersey Cattle Club, Rice,

TABLE 11. RELATIONSHIP OF MILK AND BUTTERFAT YIELD TO AGE.

Age in Years	2	3	4	5	6	7	8	9
Length of Records	330	350	330	330	330	330	330	330
Average Pounds Milk	9,230	10,500	11,300	11,650	12,440	12,630	11,820	10,770
Average % Butterfat	3.39	3.43	3.44	3.46	3.59	3.54	3.35	3.26
Pounds of Fat	313	360	389	403	422	423	393	351
Factor for Milk	1.37	1.21	1.12	1.09	1.02	1.00	1.07	1.17
Factor for Total Fat	1.35	1.18	1.11	1.06	1.00	1.00	1.09	1.20
Factor for % Fat	1.02	1.01	1.01	1.00	1.02	1.03	1.03	1.06
Number of Records	51	68	86	96	72	51	51	15

All animals used in the above tabulation had at least four records of production, although they do not represent the same years in every case.

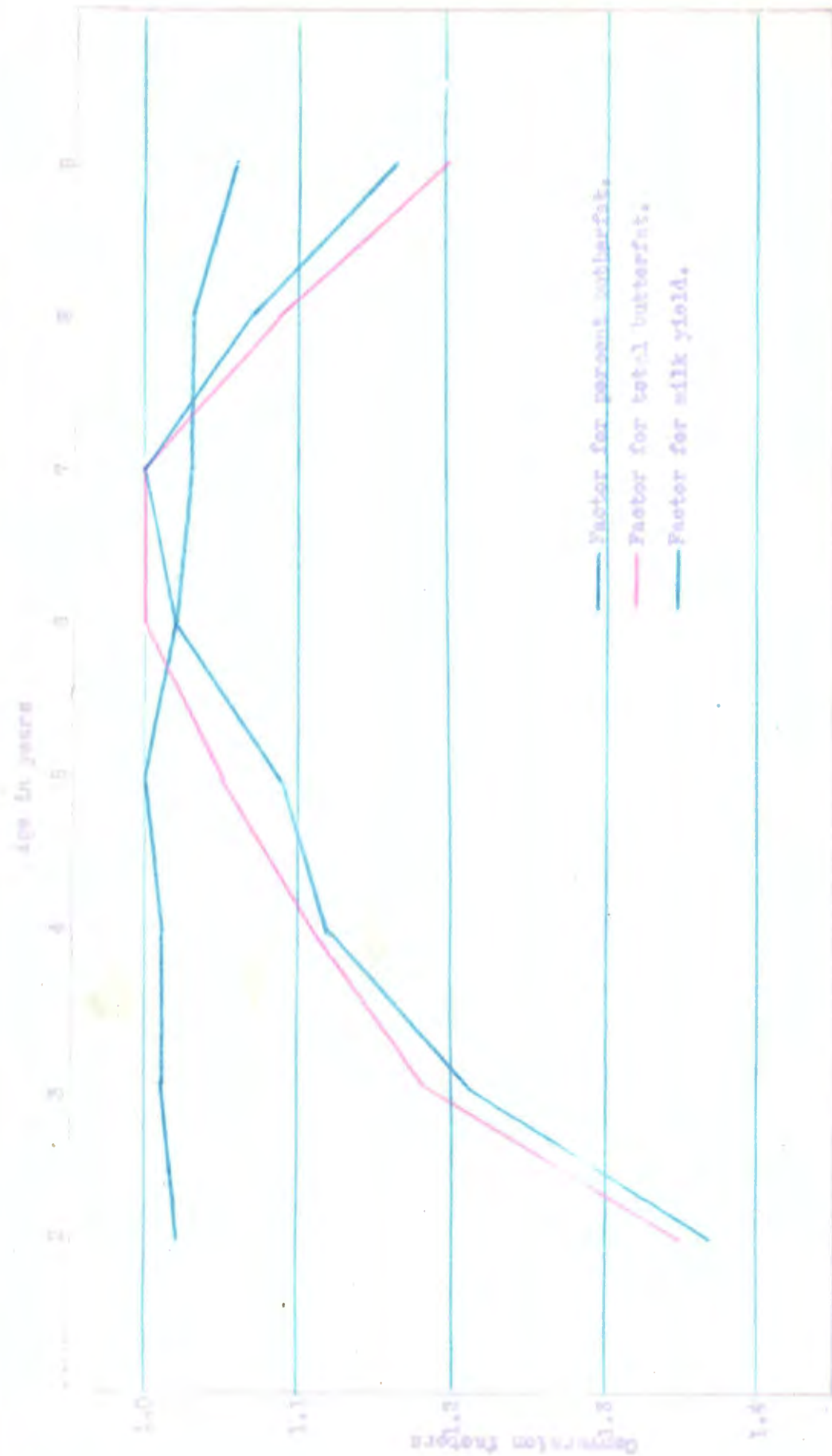


Fig. 8.— Conversion factors for standardizing milk, butterfat and butterfat percentages to a mature basis.



Fig. 7.--Comparison of authors conversion factors with those of other authorities.

the Dairy Herd Improvement Association, and the conversion factor worked out by the writer. It will be noticed that all factors are very close together. The conversion factor worked out by the American Jersey Cattle Club and by Rice are based on Advanced Registry and Register of Merit records. The writer's conversion factor is based on Holstein Herd Test records.

Of the 113 cows with records which were summarized in Table XI there were 38 cows that made four consecutive records from two to five years inclusive. The conversion factor based on these 38 cows was found to be practically identical to the factor based on the records of all 113 cows. While these results are based on only a small number of records, they agree very well with conversion factors as worked out by many other authorities, indicating that the most commonly accepted factors are not too high for converting records to a mature basis when they are applied to the average of several records.

Application of Conversion Factors to Individual Cows. Even though conversion factors may prove to be fairly accurate when dealing with averages of records of several animals, it does not necessarily indicate that they are just as accurate when applied to records of individual animals. For this reason, some tabulations were made for the purpose of determining whether conversion factors are applicable when applied to individual records. The records of 38 cows which had four consecutive records made between the ages of two and five inclusive were used.

The four records of each animal were ranked according to their production. The length of lactation period was also considered in ranking the records according to production. If one cow made her best

record as a three-year-old, that record was ranked first; if her second best record was made as a four-year-old, it was placed second; if the two-year-old record was third best, it was placed third; and if the five-year-old record was the lowest, it was placed last. This classification was made for each of the 38 cows. By this method one is able to determine two things: (1) What percent of the animals made their best records as two-year-olds, what percent made their best records as three-year-olds, what percent made their best record as four-year-olds, and the percent of the animals that made their best record as five-year-olds; and (2) one is able to determine what percent of the records were highest, second highest, third highest and fourth highest for the two, three, four, and five year-old groups.

Table XII gives a summary of results. The figures in the vertical column represent the percentage of the total records for each year that were the highest, second highest, third highest, and fourth highest for each of the four years. The figures going horizontally represent the percent of the best records that were made as two-year-olds, three-year-olds, four-year-olds, or as five-year-olds; the percent of the second best records that were made for each of the respective years, etc. The table shows that only 52.8% of the best records were made at five years of age and that 31.6% were made at four years of age, 10.4% at three years of age, and 5.2% at two years of age. In reversing the process, 63.5% of the lowest records were made at two years of age and 5.2% of the lowest records were made at five years of age. In only eight instances out of 38 or approximately 21% of the time was there a gradual increase in production of an animal with records from from two to five years of age.

TABLE XII. VARIATIONS FROM THE NORMAL RELATIONSHIP BETWEEN PRODUCTION AND AGE.

Rank of	Percentage in Each Age Classification				
Record	2 Yr.	3 Yr.	4 Yr.	5 Yr.	Total
1	5.2	10.4	31.6	52.8	100
2	7.8	28.4	44.8	21.0	100
3	23.7	42.1	15.2	21.0	100
4	63.3	21.1	10.4	5.2	100
Total	100.0	100.0	100.0	100.0	

The grouping of records of 38 cows with four records each from 2 to 5 years inclusive, according to the year that they made their best, 2nd. best, 3rd. best, and 4th. best record. All figures are in percents.

Figure 8 illustrates in graphic form the contents of Table XII. Each group of lines represents a horizontal column of the table. The first group on the left of the figure represents the percentage of the best records that were made at each of the respective ages listed. The second group of lines on the graph represents the second highest records made for each of the respective ages, etc. for all ages. An analysis of Table XII and the graph would indicate that standardization factors are not very accurate when applied to individual animals. For example: There is only about a 52% chance that the best record of a cow will be made at five years of age. However, Table XI shows that conversion facts used on the averages of records of several animals are practical and fairly accurate.

Rank of children according to percent of correct answers

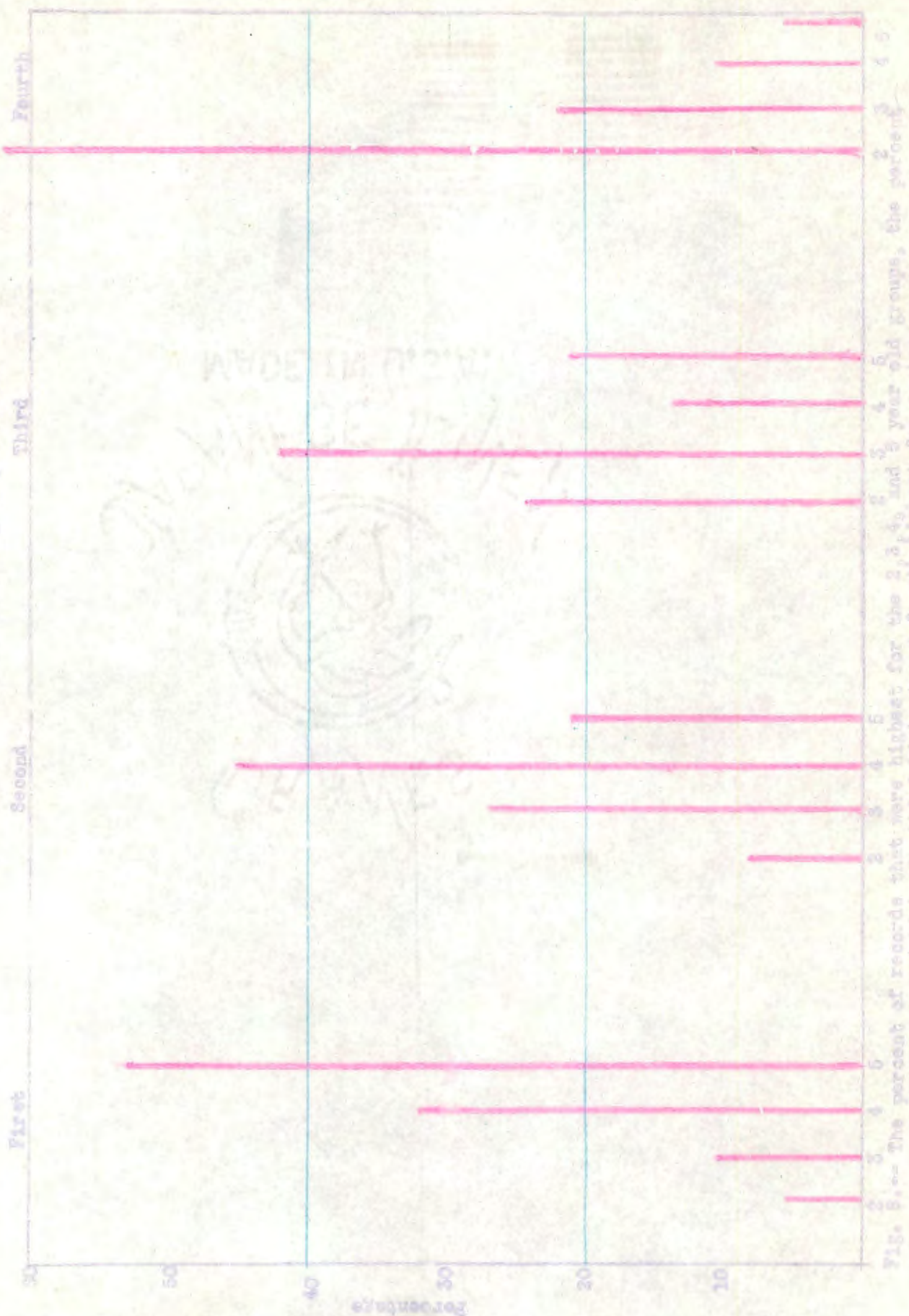


Fig. 5. -- The percent of correct answers for the 2nd, 3rd, 4th, and 5th old groups, the percent of correct answers for each age.

AN ANALYSIS OF BULL INDEXES

As sires do not have the ability to produce milk there have been many attempts made at working out some formula or factor for determining the potential level of production of the sire. The only way to determine this is through the production records of his daughters. Because of the fact that the dams probably also influence the daughters' production it is difficult to determine the sire's potential level of production. It is generally conceded that the dam does not necessarily transmit to her offspring the same factors for high or low milk production that she possesses herself. In other words, the dam's record does not indicate her transmitting ability for milk production. It is, therefore, logical to believe that the same would hold true for the sire; however, since the sire has a greater number of progeny than does the dam, the average of all daughters of a sire will more likely give a more accurate estimate of the transmitting ability of the bull than the few daughters of a dam would indicate as to her transmitting ability. Because of these complex factors it is difficult to attempt to determine what the potential level of production of a sire is.

Various indexes have been proposed for determining the sire's production level, in which the bull is given a numerical figure for his potential producing ability in terms of pounds of milk or pounds of butterfat. The three most common sire indexes that are being used at the present time are the Mount Hope Index, the Intermediate (Equal Parent) Index, and the Gifford (sometimes called Gifford-Copeland) Index. Each of these indexes is based on different genetic principles

as to how milk and butterfat are transmitted, but they are all aimed at the same end, that of indicating the potential level of production of the sire. The Mt. Hope Index is based on partial dominance in which high milk yield is partially dominant to low milk yield and high butterfat percentage is recessive to low butterfat percentage. The Intermediate Index is based on no dominance in which both parents contribute equally to the progeny. The Gifford Index is based on the theory that the dam's record has no influence on the daughters' production and therefore the average production of the daughters represents the bull index regardless of what dams they may be out of. The Mt. Hope and Intermediate Indexes give a figure which represents the potential level of the bull, and the calculated production of the daughters will be somewhere in between the two parents. The Gifford Index is based on the principle that the average production of the first ten tested daughters represents the bull's potential level of production and also the future daughter expectation. In other words, the bull's potential level of production and his daughters' production are represented by the same index figure.

With these facts in mind, it was thought advisable to make a comparison of the three indexes mentioned above to determine which index would have the least error in predicting the production of the future daughters or in indicating the potential level of production of the sire.

In making this comparison 15 sires, which had 20 or more dam-daughter comparisons, were selected at random from the Holstein Herd Test records. The records used were furnished by the Holstein-Friesian Association of America. The records were all adjusted to a mature "3" basis and in case the animal had more than one record the average of all records was taken. These records were adjusted to mature "3"

basis by the Holstein-Friesian Association of America using the conversion factors given in Table XIII. Only the milk records were con-

TABLE XIII. CONVERSION FACTORS FOR CONVERTING MILK RECORDS TO MATURE "B" BASIS DEVELOPED FROM APPROXIMATELY 10,000 HERD TEST LACTATION RECORDS. *

Age	A	B	C	Age	A	B	C
2	1.04	1.25	1.53	4 1/2	0.87	1.05	1.31
2 1/2	1.00	1.20	1.50	5	0.85	1.02	1.28
3	0.96	1.15	1.44	6 - 9 mo.	0.83	1.00	1.25
3 1/2	0.92	1.10	1.38	10	0.85	1.03	1.29
4	0.89	1.07	1.34	11 and over	0.87	1.05	1.31

A = 4 times a day milking, B = 3 time milking, and C = 2 time milking.

verted to mature equivalent by use of the conversion factor. The mature "B" basis for total fat was determined by taking the average percentage of butterfat for all records of each animal times the average mature "B" base equivalent for milk yield. Since the length of lactation was not taken into consideration the records were adjusted by the writer to a 365 day basis by using the factor given in Table I of this paper.

In making the comparison of the Mt. Hope, Intermediate, and Gifford Indexes, the average of the first ten daughters listed and their respective dams (if the dams were used in the comparison) was determined. They may not necessarily be the first ten tested daughters. From the above information the index of the sire was calculated, by the method used in each of the three indexes, based on

* Holstein-Friesian Herd Improvement Registry Year Book, p. 660 Vol. 6.

the first ten listed daughters. With the bull index determined on the basis of the first ten listed daughters, the average production of the second ten listed daughters could be determined. The calculated production of the second ten daughters is then compared with the actual production of those same daughters and the percent error determined for each of the three indexes.

Table XIV gives the degree of error of each index for 15 different sires. This table does not indicate the degree of error of the actual index of the bull but gives the percent error of the daughter expectation which can be calculated when the bull index is known. The average percent error for each of the indexes was surprisingly close. The percent error for the Mount Hope Index was 7.6%, for the Intermediate 7.9%, and for the Gifford Index 7.3%. In all three indexes the calculated production was too high about 50% of the time and too low about 50% of the time. In the Mount Hope Index the percent error for each sire varied from as low as .6% to as much as 14.9% either plus or minus. The variation of error for the Intermediate Index was from $\pm .6\%$ to $\pm 17.7\%$. The variation in the Gifford Index was from $\pm .2\%$ to $\pm 17.3\%$.

Figure 9 illustrates graphically the percent error of the calculated production of daughters for the three indexes, compared with their actual production. It should be noted that in the case of individual sires the degree of error was practically the same for all three indexes. Results of the above comparison indicates that any one of the three indexes would be as accurate as the other for predicting the production of future daughters.

TABLE XIV. COMPARISON OF THE DEGREE OF ERROR OF THE MOUNT HOPE, INTERMEDIATE, AND THE GIFFORD INDEXES BASED UPON 15 Sires WITH AT LEAST 20 DAM-DAUGHTER COMPARISONS.

No. of Sire	No. of Dam- Daughter Pairs	Ave. of all Dams, M. H.	Ave. of all Daughters, M. H.	Ave. First ten Dams	Ave. First ten Daughters	Ave. Second ten Dams	Average Second ten Daughters	Mount Hope Index Based on First ten Daughters	Calculated Prod. of Second ten Daughters	% Error of Cal- culated Pro- duction	Intermediate In- dex Based on First 10 Dams	Calculated Prod. of Second ten Daughters	% Error of Cal- culated Pro- duction	Gifford Index on First ten Daughters	% Error of Calculated Production
1	34	394	498	374	476	417	531	520	488	- 8.1	578	498	- 6.0	476	-10.4
2	20	525	514	529	535	518	502	538	532	+ 6.0	541	530	+ 5.6	535	+ 6.5
3	25	462	555	499	528	419	569	541	504	-11.4	557	488	-14.2	528	- 7.2
4	30	519	492	497	448	516	542	334	461	-14.9	399	457	-17.7	448	-17.3
5	31	489	474	473	486	503	435	492	500	+14.9	499	501	+15.2	486	+11.7
6	31	516	560	490	572	500	557	607	577	+ 3.6	654	577	+ 3.6	572	+ 2.7
7	22	464	449	459	446	474	457	416	484	- .7	433	453	- .9	446	+ 2.4
8	25	464	494	504	529	433	455	540	508	+11.6	554	494	+ 8.6	529	+16.3
9	30	499	512	506	466	510	543	373	469	-13.6	426	468	-13.3	466	-14.2
10	29	494	523	477	535	541	514	559	553	+ 7.6	593	567	-10.3	535	+ 4.1
11	45	524	474	505	470	540	471	388	494	+ 4.9	445	492	+ 4.4	470	+ .2
12	24	458	488	455	494	453	496	511	493	- .6	533	493	- .6	494	- .4
13	36	481	481	488	456	473	487	381	445	- 8.6	434	454	- 6.8	456	- 6.4
14	24	622	592	643	618	614	577	560	598	+ 3.6	593	603	+ 4.4	618	+ 7.1
15	28	462	598	459	552	478	539	593	558	+ 3.5	647	562	+ 6.1	552	+ 2.4
Total	434								Average	+7.6			+7.9		+7.3
									Minus Error	-8.3			-8.6		-8.3
									Plus Error	+6.9			+7.3		+6.4

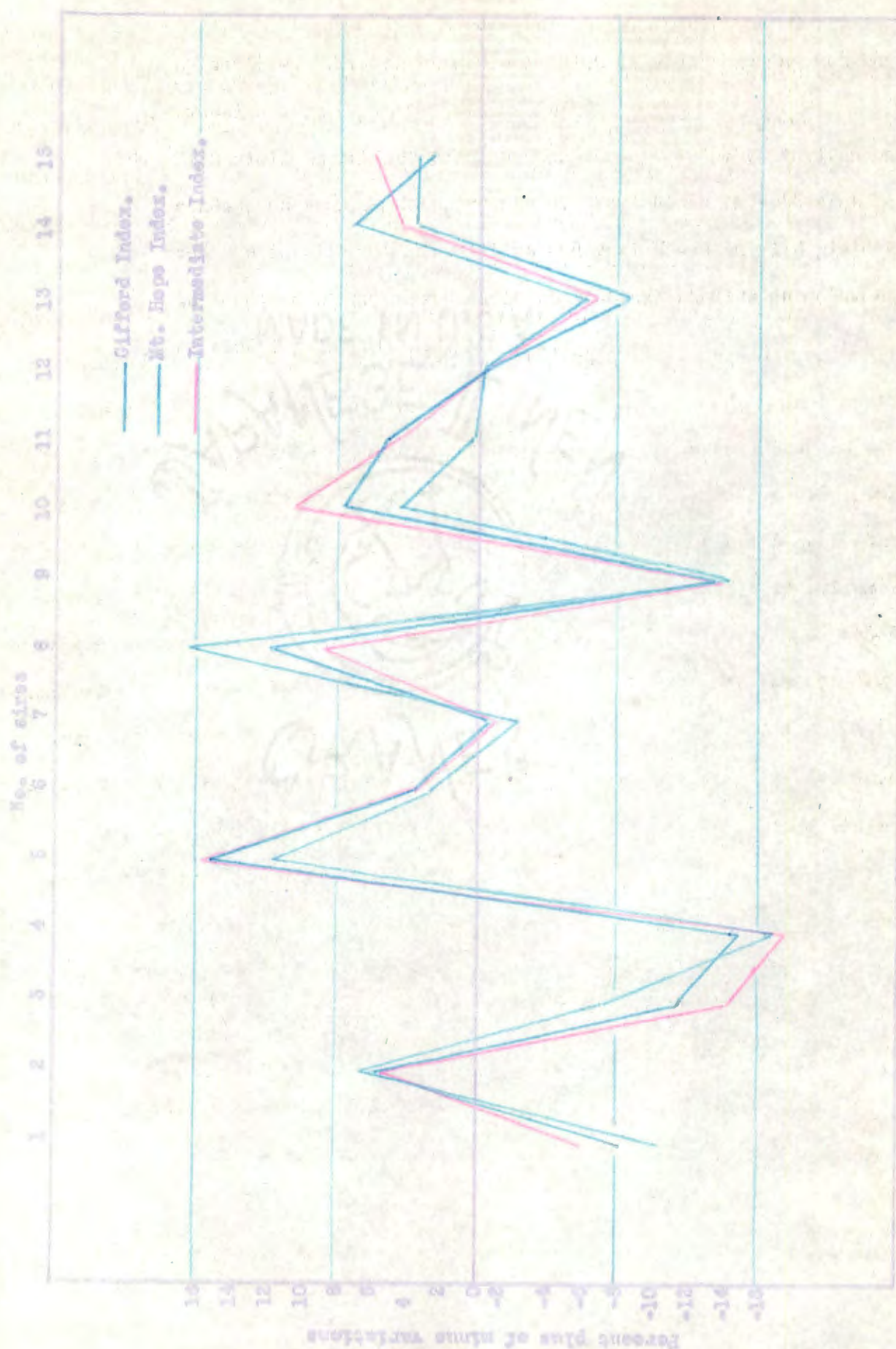


Fig. 9.--Comparison of the degree of error of the Cliford, Mt. Hope, and Intermediate indexes on a percentage basis. Comparison of 15 sires with 20 dam-daughter comparisons.

Next a comparison was made of the Mount Hope, Intermediate, and Gifford Indexes by comparing the variation of the bull index, when based on the average of all daughters, the first ten listed daughters and the second ten listed daughters. In this comparison the percent error was determined on the bull index itself and not on the calculated daughters expectation figure as was the case of the comparison made in Table XIV. In this analysis three indexes were made for each bull; that is, one index was made, based on the average of all dam-daughter pairs, the same index was calculated on the first ten daughters and on the second ten daughters. If the indexes used in the comparison were reasonably accurate the bull index based on all daughters should be practically identical to the index based on the first or second group of ten daughters. The indexed calculated on the average of all dam-daughter pairs was used as a standard and the difference between the index calculated on the first and second ten daughters as compared with the indexed based on all daughters was recorded as the percent error.

The results of this comparison are summarized in Table XV. The percent error for the average of all 15 bulls was $\pm 9.45\%$ for the first ten daughters and $\pm 9.5\%$ for the second ten daughters, when the Mount Hope Index was used. When the same comparison was made for the Intermediate Index the percent error for the two groups was some less; being $\pm 7.5\%$ for the first 10 daughters and a $\pm 8\%$ error for the second ten daughters. The percent error for the Gifford Index was only about one-half as great as it was for the other two indexes, it being $\pm 3.9\%$

TABLE XV. DEGREE OF ERROR IN BULL INDEXES WHEN THE INDEX OF THE FIRST AND SECOND TEN DAUGHTERS ARE COMPARED WITH THE INDEX OF ALL DAUGHTERS.

	Groups	Mt. Hope		Inter- mediate		Gifford	
		Bull Index	% Error	Index	% Error	Index	% Error
1.	All Dau.	543	--	602	--	498	--
	1st. ten	520	-4.2	578	-4.0	478	-4.4
	2nd. ten	580	+6.8	645	+7.1	531	+6.6
2.	All Dau.	438		503		514	
	1st. ten	538	+10.2	541	+7.5	535	+4.1
	2nd. ten	465	-4.7	485	-3.4	502	-2.3
3.	All Dau.	595		648		555	
	1st. ten	540	-9.2	557	-14.1	528	-4.9
	2nd. ten	633	+6.4	719	+10.9	569	+2.5
4.	All Dau.	429		465		492	
	1st. ten	334	-22.1	399	-14.2	448	-8.9
	2nd. ten	553	+23.9	588	+22.1	542	+10.1
5.	All Dau.	439		459		474	
	1st. ten	492	+12.1	499	+8.7	486	+2.5
	2nd. ten	276	-37.1	367	-20.0	435	-8.2
6.	All Dau.	579		604		560	
	1st. ten	607	+4.8	654	+8.3	572	+2.1
	2nd. ten	581	+ .3	614	+1.6	557	-.6
7.	All Dau.	414		434		449	
	1st. ten	416	+ .5	433	-.2	443	-.7
	2nd. ten	417	+ .7	440	+1.4	457	+1.8
8.	All Dau.	507		524		494	
	1st. ten	540	+6.5	554	+5.7	529	+7.1
	2nd. ten	464	-9.5	477	-9.0	455	-7.9
9.	All Dau.	518		525		512	
	1st. ten	373	-28.0	426	-18.8	486	-9.0
	2nd. ten	557	+7.5	576	+9.7	543	+5.0
10.	All Dau.	535		552		523	
	1st. ten	559	+4.5	593	+7.4	535	+2.3
	2nd. ten	451	-15.7	487	-11.7	514	-1.7
11.	All Dau.	357		424		474	
	1st. ten	388	+8.7	445	+4.9	470	-.8
	2nd. ten	310	-13.2	402	-5.2	471	-.6

TABLE IV Continued

Groups	Mt. Hope		% Error	Inter- mediate		% Error	Gifford	
	Bull	Index		Index			Index	% Error
12.	All Dau.	501		518			488	
	1st. ten	511	+1.9	533	+2.9		494	+1.2
	2nd. ten	514	+ .6	539	+4.0		496	+1.6
13.	All Dau.	481		481			481	
	1st. ten	381	-20.7	434	-7.7		453	-5.2
	2nd. ten	495	+2.5	501	+4.1		487	+1.2
14.	All Dau.	522		562			592	
	1st. ten	560	+7.3	593	+5.5		613	+4.4
	2nd. ten	491	-5.9	540	-3.9		577	-2.5
15.	All Dau.	537		534			543	
	1st. ten	593	+1.0	647	+2.1		552	+ .7
	2nd. ten	565	-3.7	602	-5.4		539	-1.6
Average								
1st. ten			±9.45		±7.5			±3.9
2nd. ten			±9.5		±8.0			±3.7

error for the first ten daughters and $\pm 3.7\%$ for the second ten daughters. The degree or percent of error for the Mount Hope Indexes varied from $\pm .3\%$ to as high as $\pm 37\%$ for each of the individual sires. In case of the Intermediate Index the variation of error for the various sires was from ± 0.2 to $\pm 22.0\%$ and for the Gifford Index the variation was much lower, ranging from $\pm 0.5\%$ to $\pm 10\%$.

Figures 10, 11, 12 show diagrammatically the variations in pounds of fat, that occurred when three indexes were worked out for each of the Mount Hope, Intermediate and Gifford Indexes respectively. These graphs show that the three indexes, worked out by each of the three different methods, showed considerable variation. If the index was 100 percent accurate each of the three lines would follow the same course, however the lines would not be straight because the indexes will vary with different bulls as is indicated. Figure 12, which compares the three indexes worked out by the Gifford method, agree much better than they do in the case of the other two indexing methods.

Table XVI includes the summary of Table XV. Table XVI gives the average error of the first and second groups of ten daughters each when worked out by the Mount Hope, Intermediate, and the Gifford method of indexing. The table also divides the average error for each group for each of the three indexes into the plus or minus percent of error.

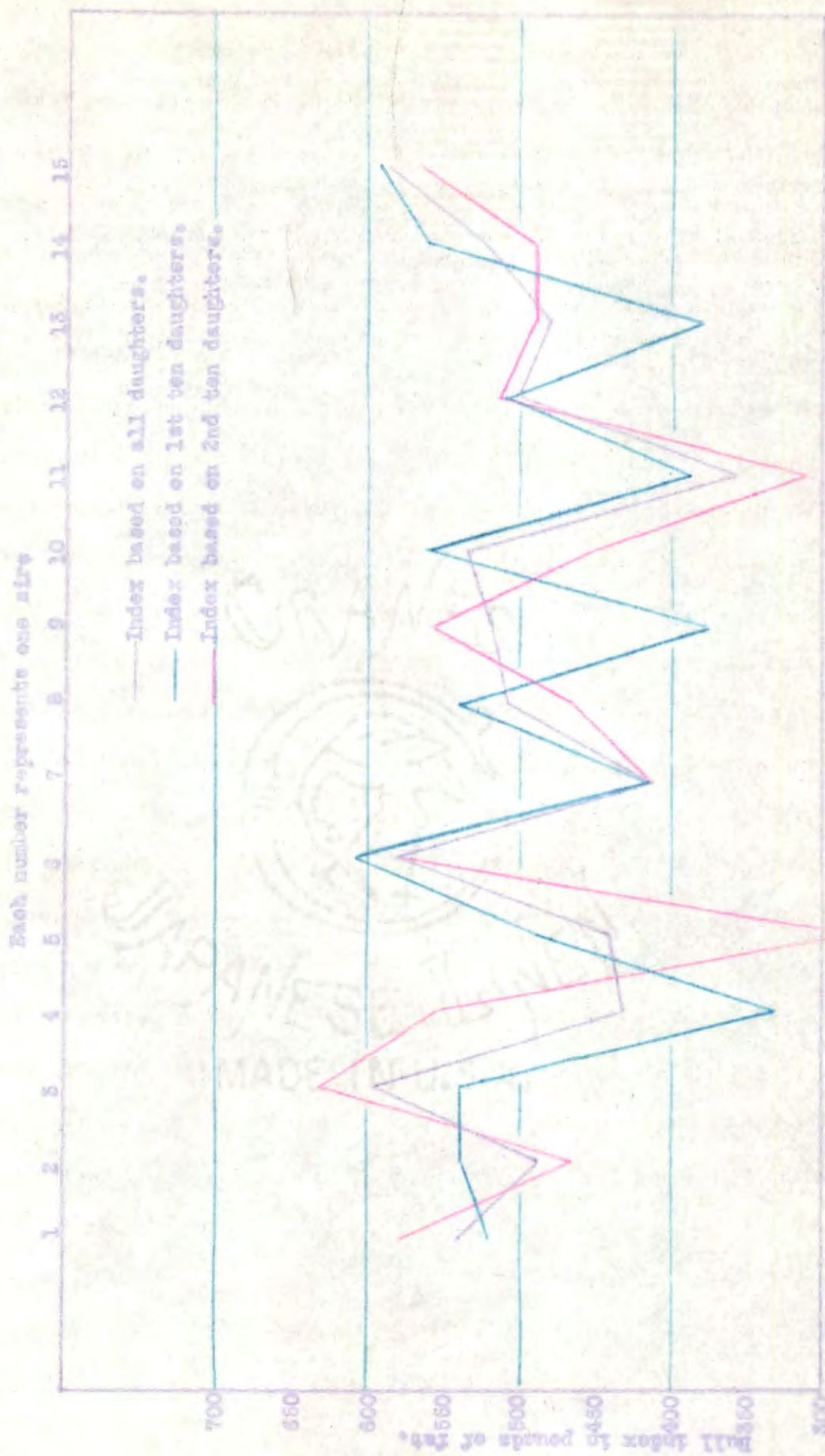


Fig. 10.--Comparison of the variation of the Mt. Hope index when determined on all dam-daughters, 1st ten dam-daughters, and 2nd ten dam-daughters for 15 Holstein sires.

Each number represents a different sire

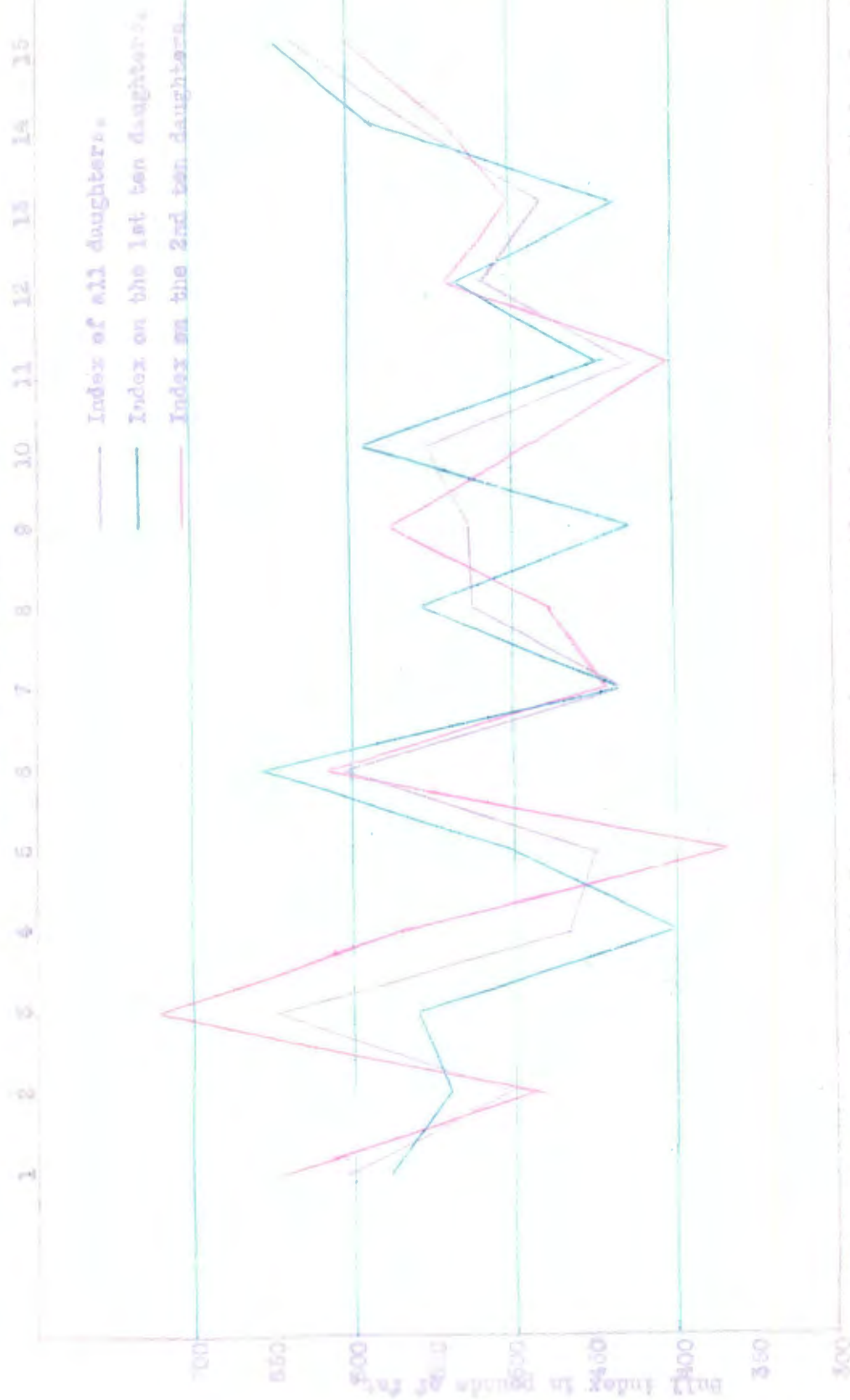


Fig. 11.—Comparison of the Intermediate (equal-parent) index when determined on all dam-daughters, 1st ten dam-daughters, and 2nd ten dam-daughters for 15 different sires.

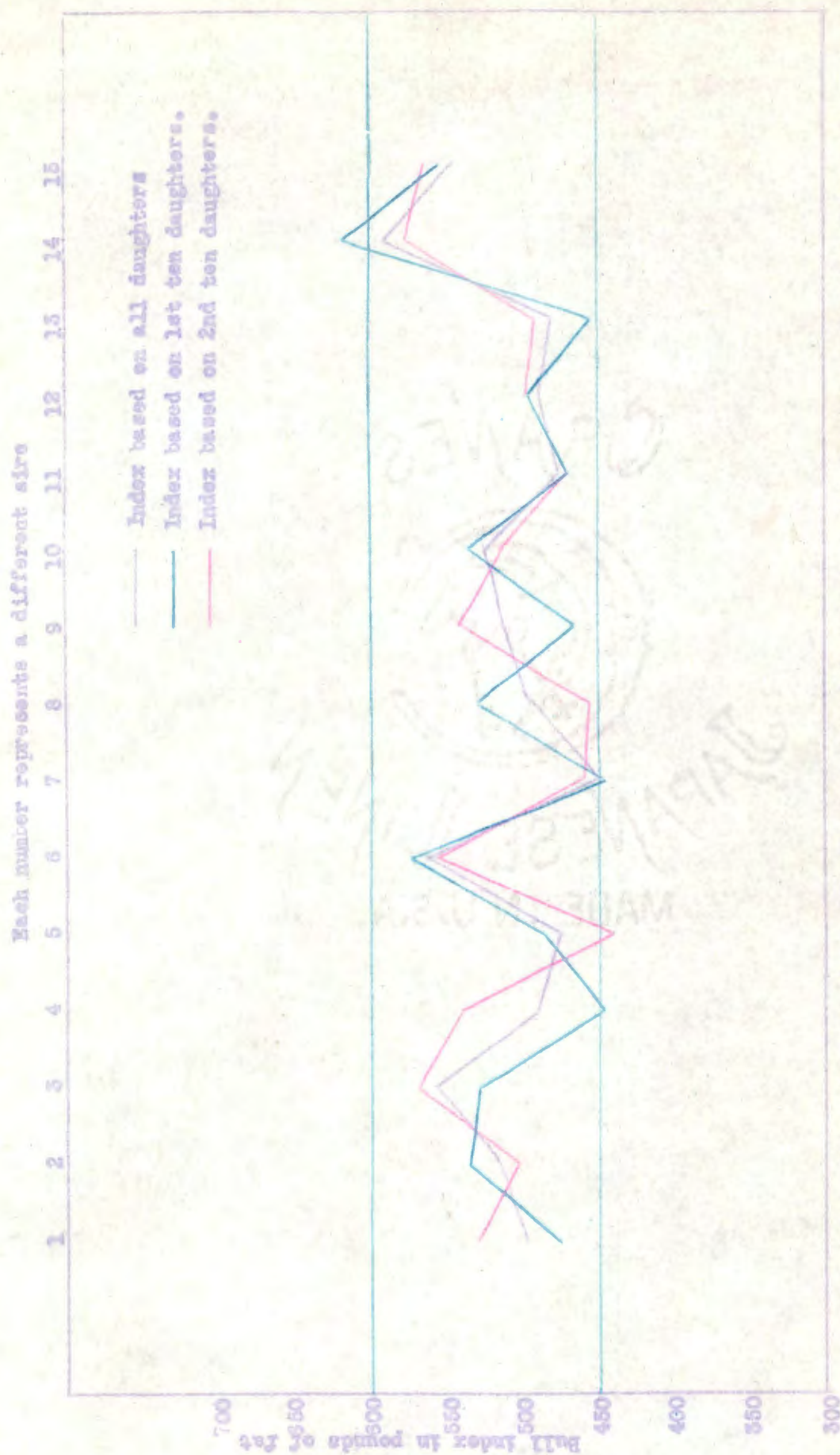


FIG. 12.— Comparison of the Gifford index when determined on all daughters, 1st ten daughters, and 2nd ten daughters for 15 different sires.

TABLE XVI. COMPARISON OF THE AVERAGE ERROR FOR EACH OF THE THREE INDEXES WHEN DIVIDED INTO PLUS OR MINUS ERROR.

Group	Mount Hope		Intermediate		Gifford	
	%	%	%	%	%	%
1st. ten	± 9.5	-16.8	± 7.5	-3.2	± 3.9	-4.8
Daughters		+5.7		+5.9		+3.0
2nd. ten	± 9.5	-12.7	± 8.0	-3.4	± 3.7	-3.2
Daughters		+6.7		+7.6		+4.4

For example: The Mount Hope Index had an average error of 9.50% for the first ten daughters, however, when the percent error for each of the sires was grouped as those that were too low and those that were too high it was found that the average percent minus error was -16.8% while the average percent plus error was only +5.7%. The same applies to the Intermediate and Gifford Indexes. In the Intermediate and Gifford Indexes the minus error is about the same as the plus error. While the Intermediate and Gifford indexes show considerable error, the fact that they vary as much one way as the other, indicates that it is a normal variation. In case of the Mount Hope Index, however, the minus error is much greater than is the positive error which might indicate that the principle on which that index is based did not hold true in this comparison. The Mount Hope Index is based on the fact that high milk yield is dominant to low milk yield. When the daughters produce less than the dams the sire index is very low when worked out by the Mount Hope Index. The greatest errors in the Mount Hope Index occurred on sires in which the daughters produced less than the dams giving the sire a lower index than it should be thus making a high percent negative error. Thus, results of this table tend to disprove the theory of dominance of high milk yield judging from the sires used in this comparison.

Results of the comparison of the Mount Hope, the Intermediate, and the Gifford Indexes as given in Table XIV show that the error for all three indexes was practically the same. In this index a comparison was made of the error of the calculated daughter expectation with the actual expectation. In the second comparison, the comparison was based on the error of the actual indexes when the index was worked out on the average of all daughters, or daughters and dams as the case may be, and also on the first and second daughters groups. In the second comparison the error for the Gifford method was much smaller than in the first comparison, the error of the Intermediate Index was about the same, and the error for the Mount Hope Index was larger.

Influence of the Dam's Record on the Production of the Daughters.

Using the same material as in the other index comparisons the dams to which the 15 sires were mated were grouped as the average of all dams, the low producing dams, the medium producing dams, and the high producing dams. The average of the daughters of each of these groups was also considered. These figures are all based on milk yield. Table XVII compares the daughters production with that of the dams out of the same sires, but in which the dams were grouped as low, medium, and high producers. It is surprising how closely the production of the daughters of each of these dam groupings correspond to each other. The average milk yield of the low producing dams for all 15 sires was 12,600 pounds, for the medium producing dams 14,800 pounds, and for the high producing dams 17,400 pounds of milk. The striking thing is that the daughters of the low producing dams averaged 15,434 pounds of milk, the daughters of the medium producing dams averaged 15,600 pounds of milk, and the daughters of the high producing dams

TABLE XVII. THE DEGREE OF ERROR OF THE GIFFORD INDEX, INTERMEDIATE BULL INDEX, AND THE INTERMEDIATE INDEX DAUGHTER EXPECTATION WHEN THE DAMS ARE CLASSIFIED AS LOW, MEDIUM, AND HIGH PRODUCERS.

	Classification	No. of Dam-Daughter Pairs	Dams Production	Daughters Production	Gifford Index % Error	Intermediate Index of the Bull	% Error	Intermediate Index Expectation	% Error
1.	All	34	11,930	14,252		16,572			
	Low	11	9,565	14,061	-1.3	18,567	+12.0	13,065	- 7.1
	Med.	11	11,902	14,706	+3.2	17,510	+ 5.6	14,236	- 3.2
	High	12	14,116	14,094	-1.1	14,072	-15.1	15,334	+ 8.6
2.	All	20	15,684	16,230		16,776			
	Low	7	14,021	16,886	+3.9	19,751	+17.8	15,398	- 2.9
	Med.	7	15,579	16,133	-1.2	16,687	- .5	16,177	+ .3
	High	6	17,750	15,581	-4.0	13,312	-20.6	17,263	+10.8
3.	All	25	13,758	19,447		25,136			
	Low	8	9,708	18,876	-3.0	28,044	+11.6	17,422	- 7.7
	Med.	8	14,214	19,958	+2.6	25,702	+ 2.2	19,675	- 1.5
	High	9	16,952	19,501	+ .3	22,050	-12.3	21,044	+ 7.9
4.	All	30	15,417	15,580		15,743			
	Low	10	13,576	16,547	+5.8	19,518	+30.3	14,659	-11.4
	Med.	10	15,393	14,185	-9.8	12,977	-17.5	15,688	+10.4
	High	10	17,250	16,008	+2.7	17,250	+18.4	16,496	+ 3.0
5.	All	31	14,660	13,413		12,166			
	Low	10	12,630	13,560	- .4	14,090	+15.8	12,398	- 7.0
	Med.	11	14,225	13,112	-2.3	11,999	- 1.3	13,195	+ .6
	High	10	17,168	13,796	+2.8	10,424	-14.3	14,667	+ 6.3
6.	All	31	15,786	15,890		15,994			
	Low	10	13,795	17,448	+9.5	21,101	+31.3	14,894	-14.6
	Med.	10	15,496	15,646	-1.5	15,796	- 1.2	15,745	+ .6
	High	11	17,870	14,695	-8.1	11,510	-28.0	16,932	+15.2
7.	All	22	14,848	13,815		12,782			
	Low	7	13,414	13,362	-3.4	13,510	+ 4.1	13,098	- 2.0
	Med.	7	14,575	13,842	+ .2	13,112	+ 2.6	13,679	- 1.2
	High	8	16,468	14,189	+2.6	11,910	- 6.8	14,625	+ 3.1
8.	All	25	14,529	15,638		16,747			
	Low	8	12,238	15,226	-2.7	18,214	+ 8.8	14,497	- 4.8
	Med.	8	14,505	16,182	+3.4	17,859	+ 6.6	15,626	- 3.4
	High	9	16,476	15,521	- .7	14,566	-13.0	16,611	+ 7.0

TABLE XVII (Continued).

Classification	No. of Dam-Daughter Pairs	Dams Production	Daughters Production	Gifford Index % Error	Intermediate Index of the Bull	% Error	Intermediate Index Expectation	% Error
9. All	30	15,027	14,256		13,485			
Low	10	12,853	13,478	-5.8	14,119	+ 5.4	13,159	- 2.3
Med.	10	14,863	14,022	-1.7	13,181	- 2.2	14,174	+ 1.1
High	10	17,394	15,279	+6.7	13,174	- 2.3	15,435	+ 1.0
10. All	29	16,090	17,095		13,100			
Low	10	11,872	17,296	+1.2	23,720	+31.0	14,986	-13.3
Med.	10	15,874	17,389	+1.7	18,904	+ 4.4	16,987	- 2.3
High	9	21,011	16,544	-3.3	12,077	-33.2	19,550	+13.1
11. All	45	15,982	14,511		13,040			
Low	15	13,914	14,334	-1.2	14,750	+13.1	13,477	- 6.0
Med.	15	15,608	14,305	-1.4	13,002	- .3	14,524	+ .1
High	5	16,425	14,893	+2.6	11,361	- 2.9	15,732	+5.6
12. All	24	14,356	15,155		15,954			
Low	8	12,500	14,784	-2.5	17,068	+ 7.9	14,226	- 5.6
Med.	8	14,341	15,164	+ .1	15,987	+ .2	15,147	- .1
High	8	16,228	15,517	+2.3	14,806	- 7.2	16,091	+3.7
13. All	36	14,387	14,532		14,667			
Low	12	12,179	13,446	-3.1	14,713	- .3	13,423	- .2
Med.	12	14,254	14,436	- .3	14,718	- .3	14,461	- .2
High	12	16,729	15,681	+6.7	14,893	+ 1.5	15,198	+3.6
14. All	24	18,495	17,346		16,197			
Low	8	16,225	17,006	-2.0	17,777	+ 9.7	16,211	- 4.7
Med.	8	18,050	18,543	+6.5	19,046	+17.5	17,124	- 7.7
High	8	21,209	16,481	-5.2	11,733	-27.4	18,703	+13.5
15. All	28	13,964	16,141		18,318			
Low	9	11,516	15,401	-4.8	19,286	+5.3	14,917	- 3.1
Med.	9	13,770	16,592	+2.7	19,414	+6.0	16,044	- 3.3
& High	10	16,343	16,430	+1.7	16,517	-3.8	17,331	+ 5.5
All	434	14,994	15,553					
Low		12,665	15,434	±3.7		±13.5		±6.2
Med.		14,843	15,618	±2.57		± 4.5		±2.4
High		17,425	15,614	±3.4		±14.8		±7.5

averaged only 15,600 pounds of milk. The difference in production between the low and the high producing dams was nearly 5,000 pounds while the difference between the respective daughter groups was only approximately 200 pounds.

In five of the fifteen sires used in the tabulation the daughters of the high dam group produced less than did the daughters of the low dam group. There were only two sires that had daughters out of the high dam group that averaged more than the dams, and there was only one sire that had daughters out of the low dam group that averaged lower than the dams. In other words, the dam's production apparently had no definite effect on the production of the daughters but that there was a tendency for the daughters to approach the breed average. Table XVII indicates that the daughters of each of the dam groups more or less approached the production of the average of all the daughters of each sire. Figure 13 gives the comparison of the average of all daughters, and the daughters of the dams when the dams are grouped into low, medium, and high producers.

With the dams classed as low, medium, and high producers as well as being all grouped into one group it is possible to make four indexes on each sire. Theoretically, if the index is reliable, the index should be approximately the same when based on each group of dams and their daughters. Table XVII gives the results of the Gifford and Intermediate indexes when applied to the different dam daughter groupings. The percent error for the Gifford index was calculated by determining the difference in the production of the daughters from each of the low, medium, and high dam groups with the average of all daughters. The Intermediate Index was calculated in two ways. In the

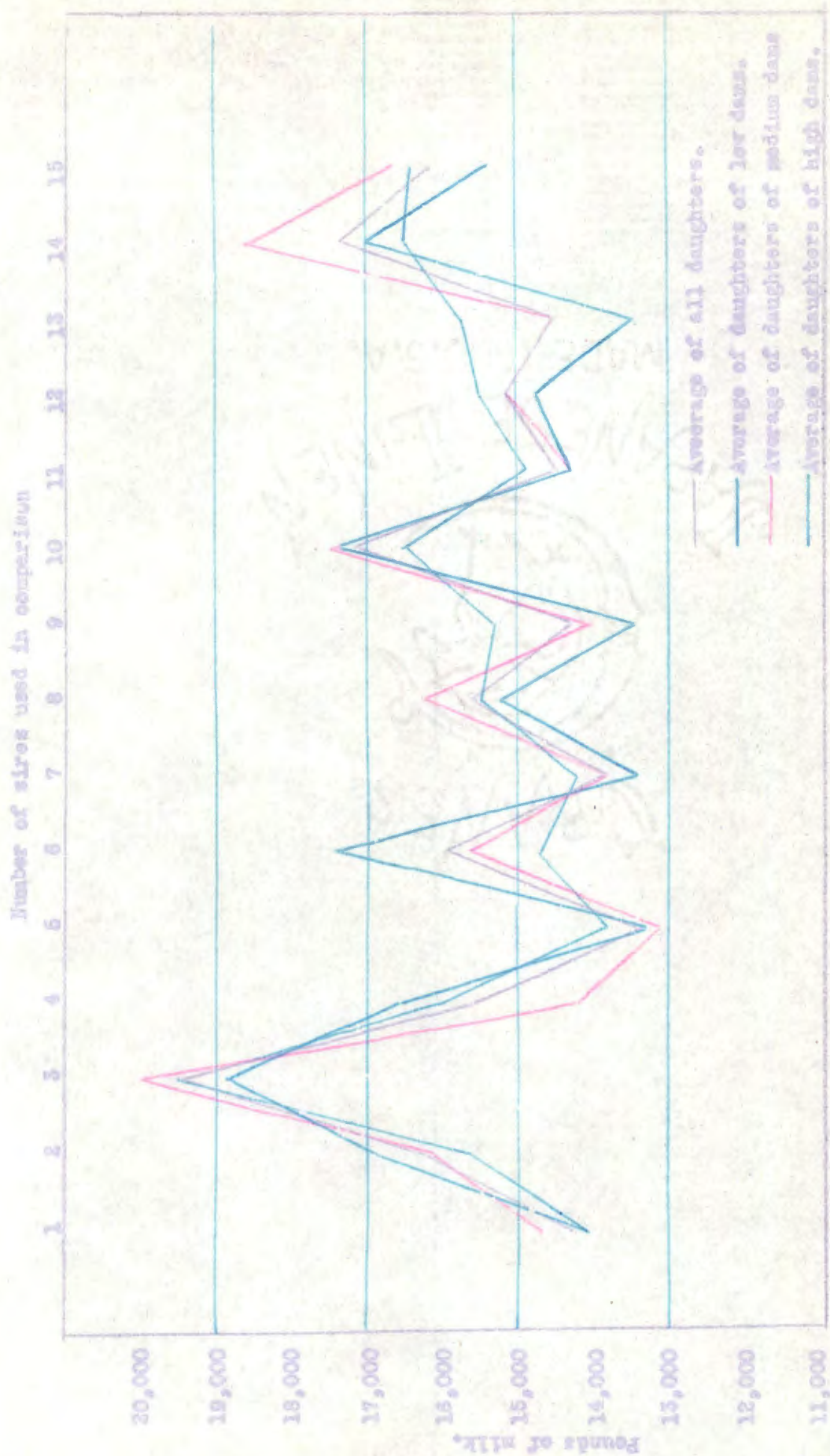


Fig. 13.—The average production of all daughters and of the daughters when their dams were all grouped as low, medium and high producers.

first calculation the actual bull index was determined for each of the four groups, thus giving four indexes. The indexes of the low, medium, and high dam-daughter groups were compared with the index based on all dam daughters and the percent error determined. In the second method of calculating the Intermediate Index, the calculated daughter expectation was determined for the low, medium, and high producing groups. The calculated production was compared with the actual production of each of the three groups and the degree of error determined.

The percent error for the Gifford Index was considerable less than for the Intermediate Index. The average percent error of all 15 sires for the Gifford Index was $\pm 3.7\%$ for the low group, $\pm 2.6\%$ for the medium group and $\pm 3.4\%$ for the high group. In most instances the index based on the low dam-daughter group was too low. The Gifford Index of the medium or high daughter groups varied both ways, being about as much too high in some cases as they were too low in other cases. The Intermediate Index for the sire's potential level of production showed considerable error when based on the low and high groups. For the low group it was practically always too high and for the high group it was almost always too low, while for the medium group the percent error was quite low. The percent error for the Intermediate Index, in which the error of the daughters expectation was determined, was only about one-half as great as in the other Intermediate Index comparison. In the last comparison the index of the low dam-daughter group was, in every case, too low, and in the high dam-daughter group the index was too high in every case. This is the reverse of the re-

sults found in the first Intermediate Index in which the bull's potential level of production was compared. Results of Table XVII would indicate that the average production of the daughters of a sire are subject to less error than is the Intermediate Index, which would lead one to the conclusion that an index based on equal inheritance from both parents and with no dominance, is not an accurate index for determining the transmitting ability of a sire.

The fact that the dam's production does not indicate the production capacity of the daughter does not necessarily mean that the dam does not contribute equally with the sire to the offspring. It does indicate, however, that the dam, in many cases, does not transmit the same qualities for production that she possesses herself.

Figure 14 is a comparison of the percent error of the Gifford Index and the Intermediate Index expectation. This graph clearly shows that the index proposed by Gifford, in which the average production of the daughters represents the bull's index, is in some cases too high and in other instances too low but the percent error being low in all cases. The variation of the Intermediate index expectation is too low in every case for the daughters of low producing dams and too high in every instance for daughters of high producing dams.

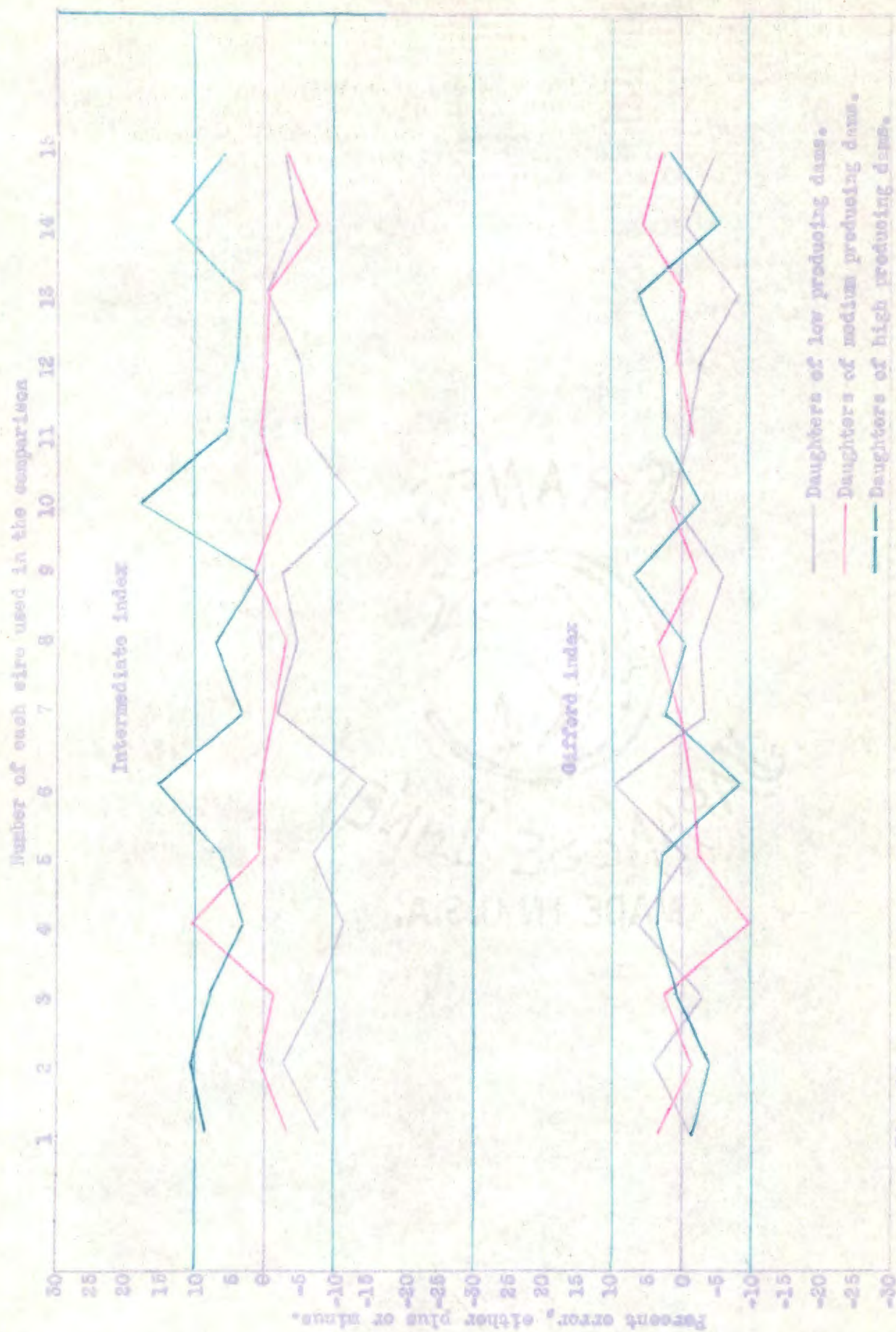


FIG. 14.—A comparison of the error of the Gifford and Intermediate index expectation when made on a percentage basis. The degree of error is plus or minus.

RELATIONSHIP BETWEEN BUTTERFAT PERCENTAGE, MILK YIELD, AND BUTTERFAT PRODUCTION

There has been no definite agreement among authorities as to whether or not milk and butterfat percentage are inherited independently of each other or if they are linked together. It is indicated in the survey of literature that the general assumption among men who have studied the problem is, that in general an increase in milk yield causes a decrease in butterfat percentage and that a decrease in milk yield causes an increase in butterfat percentage of the milk. Some authorities believe that butterfat percentage has no significant effect on the total fat production while others indicate that it does. There is no doubting of the fact that the high butterfat percentage breeds, such as the Jerseys and Guernseys, produce considerably less milk than does the Holstein breed, and they do have a much higher butterfat test than do the Holsteins. It is also quite definite that as the length of the lactation of a producing cow increases the milk decreases in yield and butterfat percentage increases. Many have assumed that similar conditions exist for milk yield and butterfat percentage for different cows within the same breed and give data to back up their assumption.

The writer has made a study of the relation or correlation between milk yield and butterfat percentage from several different angles. First, a group of 246 sires, which had at least six tested daughters, were arranged in the order of the average butterfat test of their daughters, making a total of 4,608 daughters used in the study. These figures were taken from the Holstein-Friesian Herd Improvement Registry Book Volume 6. The average milk and butterfat yield had already been adjusted to a mature equivalent $\bar{M}$ basis. Since the percent butterfat has

been shown to vary very little in regard to age it was not adjusted.

Table XVIII gives some very interesting results of the relationship between butterfat percentage, milk yield, and total butterfat production. The sires were grouped, according to the average test of their daughters, into three groups as is indicated by the table. The average figures given in the table are the mean average of the three

TABLE XVIII. THE RELATION OF BUTTERFAT PERCENTAGE TO MILK YIELD AND TOTAL BUTTERFAT PRODUCTION WHEN SIRES ARE GROUPED ACCORDING TO THE AVERAGE TEST OF THEIR DAUGHTERS.

Group	No. of Sires	No. of Records Included	Average % Fat	Average Lbs. Milk	Average Lbs. Fat
1	58	1546	3.0-3.3	13,560	436
2	146	2727	3.3-3.6	13,709	482
3	42	535	3.6-4.0	13,550	504
Average	246	4508		13,637	475

groups. The table indicates that, regardless of the average test of the daughters of each sire, the average milk yield was the same. The average milk yield of the daughters of the sires in the group that had an average test of 3.0-3.3% was 13,560 pounds of milk. The milk yield for the group of sires, with daughters testing 3.6-4.0% was 13,550 pounds, or practically the same as that of the first group. There is a very significant difference, however, in the average total butterfat production for each of the three groups. The group of sires whose daughters tested 3.0-3.3% average only 436 pounds of fat while the group of sires, whose daughters tested 3.6-4.0%, average 504 pounds of fat. This was an increase of 15.6% in the total fat yield in the high testing group over that of the low testing group. Figure 15 shows

in graph form the correlation of fat yield and milk yield to butterfat percent.

The same sires as used in the above study were arranged according to the average butterfat production of the daughters and the average test determined for each group. Table XIX indicates the same results as found in Table XVIII; that is, as the butterfat production increases the test increases.

TABLE XIX. RELATION OF BUTTERFAT TOTAL PRODUCTION TO PERCENTAGE TEST.

Group	Classification of Sires	No. Sires In Each Group	Average Butterfat Percentage
1	400 or less	37	3.35
2	400 - 450	67	3.36
3	450 - 500	69	3.42
4	500 - 550	44	3.45
5	550 - 600	20	3.53
6	600 - Over	9	3.64

When the sires were grouped according to the average milk production of their daughters and the average test determined for each group there was no definite relationship found between the milk yield and butterfat percentage. Table XX indicates that the average test for the sires, whose daughters averaged above 17,000 pounds of milk, was about the same as for the sires whose daughters averaged less than 10,000 pounds of milk. None of the tabulations show milk and butterfat percentage to be negatively correlated, but they do indicate a positive correlation between total fat and butterfat percentage. It should be noted, however, that the above comparisons are not made on individual records of cows but are based on the average of all records of the daughters of a sire when they are adjusted to a mature B basis. In

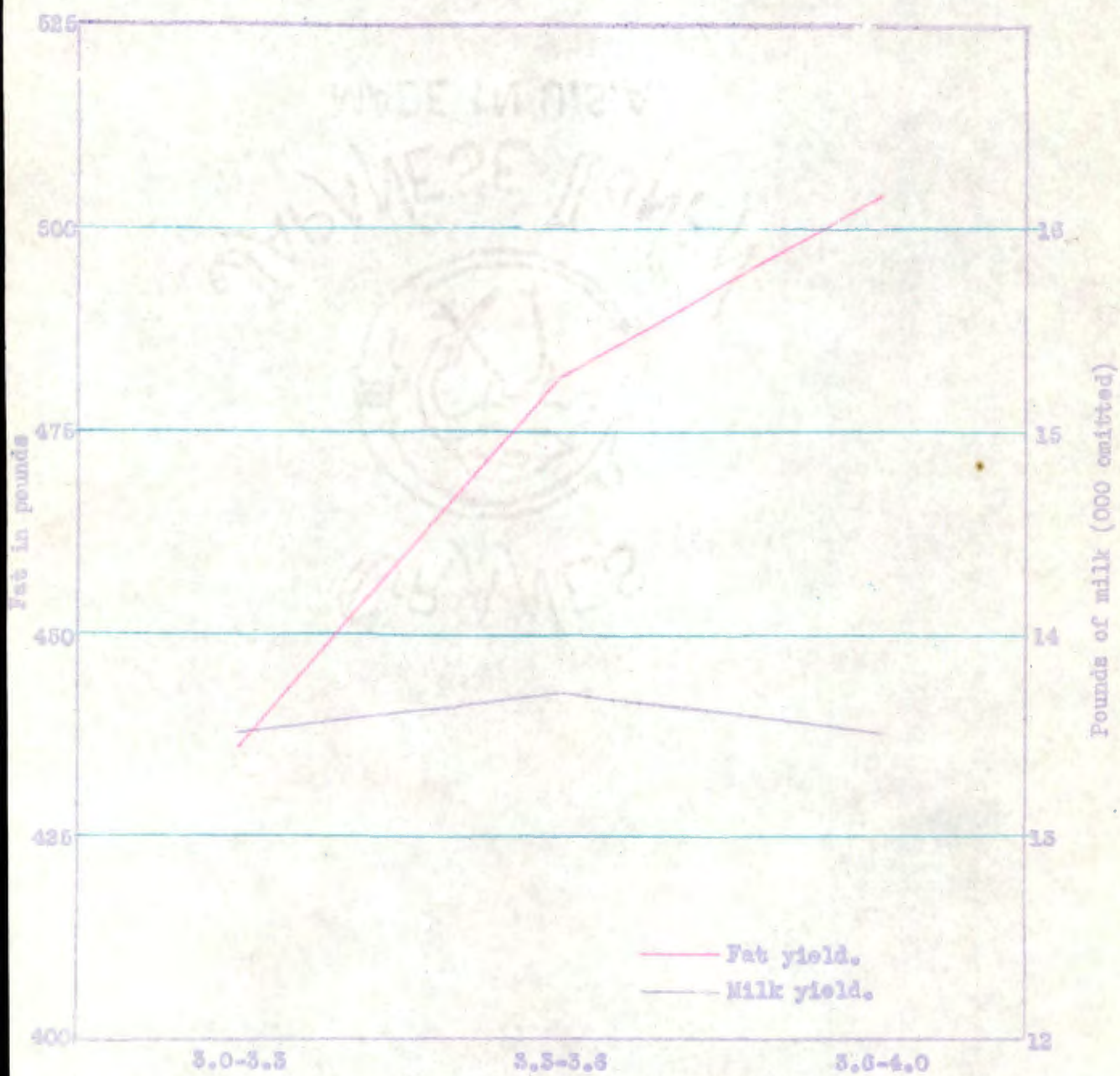


Fig. 15.--Milk yield and total butterfat yield when records are grouped according to butterfat percentage.

TABLE XI. RELATION OF MILK YIELD TO BUTTERFAT TEST WHEN THE SIRES ARE GROUPED ACCORDING TO THE AVERAGE MILK YIELD OF THEIR DAUGHTERS.

Classification of Sires	No. Sires In Each Group	Average Butterfat Percentage
<u>Lbs. B. F.</u>	<u>No.</u>	<u>%</u>
Less than 10,000	4	3.49
10,000 - 11,000	13	3.43
11,000 - 12,000	29	3.48
12,000 - 13,000	42	3.42
13,000 - 14,000	53	3.36
14,000 - 15,000	45	3.39
15,000 - 16,000	36	3.50
16,000 - 17,000	17	3.36
17,000 - 18,000	6	3.48
18,000 - and over	2	3.60
Average test		3.42

other words, it appears that the bull transmits butterfat percentage independently of the milk yield when based on average records of the sire's daughters. Figure 16 gives the relationship of variation in percentage butterfat when records are grouped according to milk yield and butterfat yield.

When individual records are used in comparing the relationship of milk yield, butterfat percentage, and total butterfat, some rather marked differences occurred. A tabulation was made of 1722 individual records taken from Volume 46 of the Holstein Advanced Registry year-book. These records were classified according to their butterfat percentage. Results of this study are summarized in Table XXI.

It will be noted that when individual records were grouped according to butterfat percentage there is about the same percent increase in total fat as was found in Table XVIII. The average total fat for cows with records testing between 2.8 and 3.0 was 559 pounds



Fig. 10.— Average test of records when grouped according to milk yield and butterfat yield.

TABLE XXI. RELATION OF MILK YIELD, BUTTERFAT PERCENTAGE AND TOTAL BUTTERFAT TO EACH OTHER WHEN INDIVIDUAL RECORDS ARE COMPILED ACCORDING TO BUTTERFAT PERCENTAGE.

Range of % Fat	No. of Records	Fat Average for each Group	Average Milk Yield of each Group
2.8 - 3.0	81	559	18,921
3.1 - 3.3	465	563	17,767
3.4 - 3.6	673	593	17,052
3.7 - 3.9	380	615	16,212
4.0 - over	123	645	15,643
Mean Average		593	16,984

while the cows that tested over 4.0% average 645 pounds of fat yearly or an increase of 15.0% over that of the lowest testing group. There was also a marked decrease in milk yield when the fat percentage increased. Those animals that had records that averaged over 4.0% produced 17% less milk than did the low testing group. Figure 17 explains, on a graph, the relation of milk and butterfat to the percentage of butterfat when records were grouped according to their average percent test. The two lines of the graph cannot be directly compared in this graph because the line representing the milk production is not on the same scale as the line representing the total fat yield, however, it does show that relationship of each one individually to the butterfat percentage.

The same records as used in the above comparison were arranged according to their total fat yield and total milk yield and the average percent test was determined for each group. This comparison is summarized in Table XXII.

TABLE XXII. RELATION OF BUTTERFAT PERCENTAGE TO MILK AND FAT PRODUCTION WHEN RECORDS ARE GROUPED ACCORDING TO THEIR MILK YIELD AND TOTAL FAT.

Grouped as to Fat Yield	Ave. Test for Each Group	Grouped as to Milk Yield	Average Test of Each Group
Lbs.	%	Lbs.	%
300 - 400	3.38	Less - 10,000	3.65
400 - 500	3.47	10,000 - 12,000	3.54
500 - 600	3.49	12,000 - 15,000	3.54
600 - 700	3.52	15,000 - 18,000	3.50
700 - 800	3.52	18,000 - 21,000	3.48
800 - 900	3.55	21,000 - 24,000	3.44
900 - over	3.63	24,000 - 27,000	3.40
		27,000 - over	3.41

Figure 13 compares directly the relation of butterfat percentage to fat production and milk yield when grouped as such.

Relation of Milk to Fat Percentage in Comparing Dam and Daughter Records. To treat the subject of milk yield and its relation to butterfat percentage from a somewhat different angle the records of the daughters of 15 sires were compared with those of their dams to see if the daughters increased or decreased in both milk and test, or if they increased in milk and decreased in test, etc. This information was taken from the same records as those used in the study of bull indexes earlier in this paper. The daughter of each sire was grouped into one of the following groups: (1) daughters increased or decreased in both milk yield and fat percentage; (2) the daughters either increased in milk and decreased in fat percent or decreased in milk and increased in fat percent; (3) the daughters either increased or decreased in milk while the fat percentage remained the same; or (4) the milk yield of daughters remained the same as that of the dams and the fat percent increased or decreased.

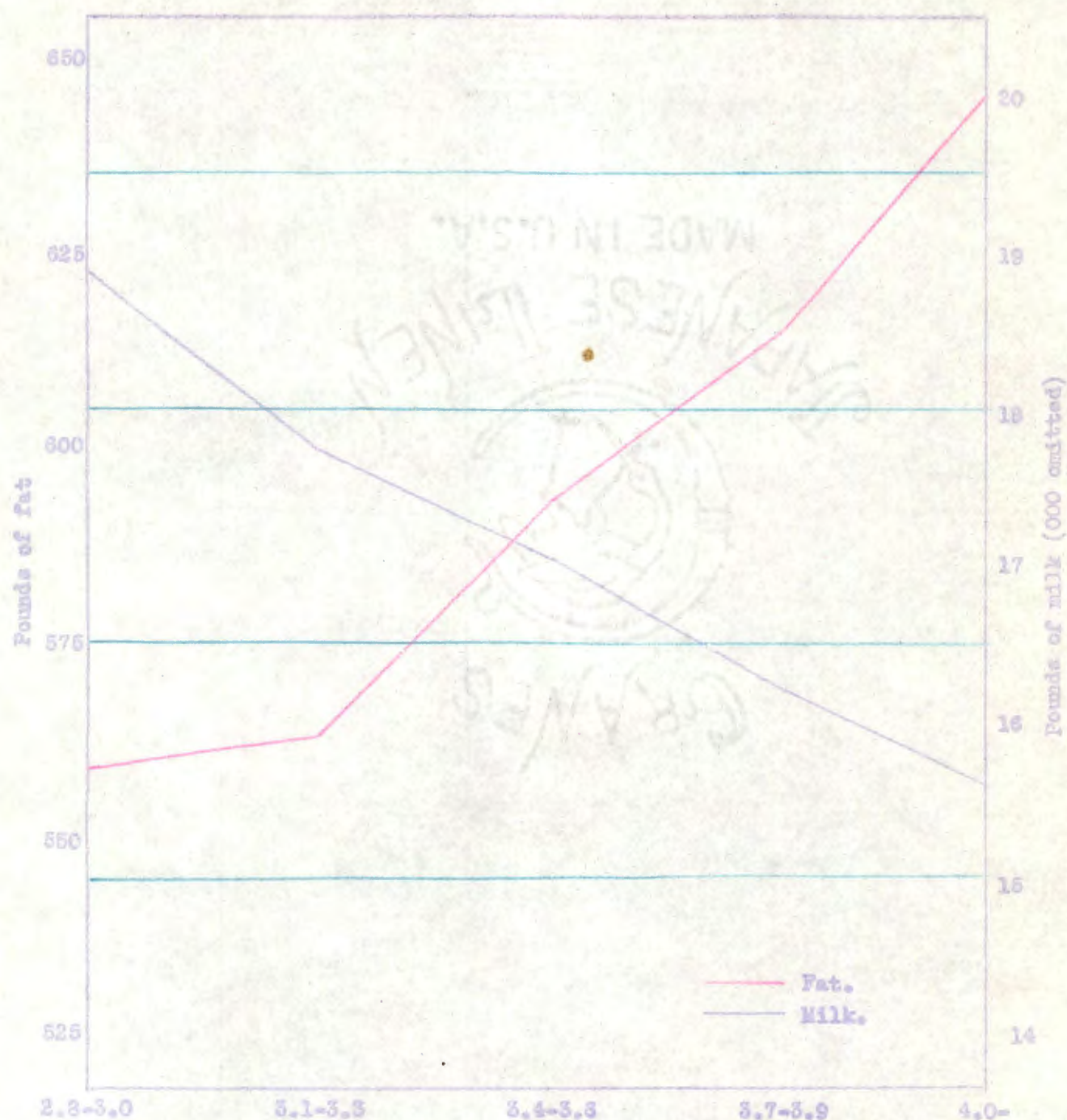


Fig. 17.--average fat and milk yield when grouped according to butterfat percentage.



Fig. 18.—Average test of records when grouped according to milk yield and to butterfat yield.

Table XXIII indicates the relation of butterfat percentage and milk yield of daughters as compared to the dams. In other words, does the same relationship hold true between fat percentage and milk yield here as in the other comparisons made? Sire number 1 had 34 dam-daughter comparisons; 17 of the daughters increased or decreased in both milk yield and in butterfat percentage as compared to their dams, indicating that milk and butterfat percentage were positively correlated. Twelve of the daughters increased in milk yield and decreased in fat percentage or decreased in milk yield and increased in fat percentage, indicating a negative correlation between milk yield and percent of butterfat. Two of the daughters inherited the same fat percentage as that of the dams but the milk yield went either up or

TABLE XXIII. RELATION OF MILK YIELD AND BUTTERFAT PERCENTAGE OF DAUGHTERS AS COMPARED TO THEIR DAMS.

No. of Sire	No. of Comparison	Increase or Decrease in Both Milk and B. F. %.	Increase in Milk and Decrease in B. F. % or Decrease in Milk and Increase in B. F. %.	Increase or Decrease in Milk with B. F. % the same.	Increase or Decrease in B. F. % with Milk the same.
1	34	17	12	2	3
2	20	7	7	5	1
3	25	8	16	4	2
4	30	16	12	2	1
5	31	8	17	4	2
6	31	11	15	3	2
7	22	7	12	2	1
8	25	7	16	1	1
9	30	8	16	1	5
10	29	12	15	2	0
11	45	12	25	6	2
12	24	7	15	1	1
13	36	6	24	5	1
14	24	9	10	4	1
15	26	17	8	3	0
Total	434	146	220	45	23

down. Three daughters inherited practically the same milk yield as their dams but the butterfat percent was higher or lower. The last two instances indicate no definite relationship between milk and butterfat percentage. When the total for all sires is considered for each of the four groups, 220 records or 50.7% indicated a negative correlation, 146 or 33.7% indicated a positive correlation, while 68 or 15.6% indicated no definite correlation either way.

Results of Table XXIII would indicate that milk yield and butterfat percentage are inherited independently of each other from the parents to the offspring. Of course, it must be remembered that the sire as well as the dam will affect the milk yield and butterfat percentage but these records studied indicate that if low milk yield is transmitted from parents to the daughter they may inherit low percentage butterfat or a high percentage butterfat regardless of milk yield.

Influence of Environment and Locality on Butterfat Percentage Inheritance Studies. In the survey of literature mention was made of the fact that butterfat percentage may vary considerably in different localities or in different states. The question that arises is, is the difference in butterfat percentage in different localities due to environment or inheritance or both? With this in mind a tabulation was made of all Register of Merit records made in Tennessee in the past six years, with a few from 1927—1929 being included. The records were grouped according to counties and the average butterfat percent determined of all Register of Merit records in each county. The counties were classified into three groups, namely, East Tennessee, Middle Tennessee, and West Tennessee. Table XIV gives a comparison

of the counties and of the three sections of Tennessee in regard to the average butterfat percentage. The average test for all counties in West Tennessee was 5.46%, for Middle Tennessee 5.55%, and for East Tennessee 5.34%, with an average of 5.5 for the state.

TABLE XIV. AVERAGE BUTTERFAT TESTS OF COUNTIES AND SECTIONS OF TENNESSEE WITH REGISTER OF MERIT RECORDS.

County	No. of Records	Average Test
West Tennessee		
Obion	5	5.51
Weakley	35	5.86
Madison	4	5.24
Shelby	227	5.36
Gibson	51	5.77
Mean Average		5.46
Middle Tennessee		
Davidson	256	5.50
Wilson	120	5.48
Williamson	66	5.59
Rutherford	50	5.52
Marshall	125	5.54
Giles	24	5.48
Hedford	28	5.43
Maury	167	5.7
Robertson	28	5.63
Putnam	20	5.29
Mean Average		5.55
East Tennessee		
Anderson	12	5.60
Knox	90	5.38
Hamilton	9	5.31
Monroe	11	5.11
Sullivan	77	5.30
Mean Average		5.34
State Average		5.50

It has been suggested by Wylie (45) that the difference in percentage of butterfat in these three sections was due to phosphate. The Middle and West Tennessee sections are very rich in phosphate, especially Middle Tennessee, while East Tennessee is a poor phosphate

area. The average butterfat percentages for Middle and West Tennessee are very similar to those determined by Wylie. For East Tennessee Wylie found the average test to be 5.1%. Records tabulated by the writer indicated that the average for East Tennessee was 5.34% or an increase of 0.24 of one percent. Practically all records, tabulated by the writer, were made after the time of Wylie's tabulation. If the variations are due to environment, which they probably are, it makes it difficult to determine much about the inherited characteristics of butterfat percentage, especially in regard to its correlation to milk yield. It might be possible that part of the correlation between milk yield and percent fat is caused by environmental conditions rather than inheritance. The fact that in some cases there was a definite correlation between milk and butterfat percentage while in other instances there was no correlation might indicate that environment may play a part in the relationship.

DISCUSSION AND APPLICATION OF INHERITANCE IN DAIRY CATTLE

In studying inheritance of milk and butterfat production of dairy cattle it is very difficult to make any definite conclusions or definite applications that might be of value to a breeder of purebred or grade cattle. Mention has already been made of the difficulties that one must encounter when studying genetics of milk and butterfat yield. Even though very little is definitely known about the complex study of inheritance of milk secretion, the subject has been attacked from almost every conceivable angle by numerous workers. Almost all authorities who have studied the subject have contributed something; at least they have suggested possibilities and given new light on the subject.

In this investigation it is impossible to study in detail all of the phases of inheritance of milk and fat secretion, however, an attempt has been made to study and analyze some of the factors responsible for milk yield, how they are transmitted to the offspring, how they are affected by environmental conditions and how they can be applied to breeding of cattle. An attempt will be made to answer the questions indicated in the plan of the present investigation in the light of the results of this investigation.

We know that environment is the greatest obstacle that must be overcome in order to study inheritance. The inherited capacity of a dairy animal is subject to environmental influences which limit the genetic capacity of the milk yield of the animal. It is reasonable to expect that many factors are responsible for milk and butterfat

production. The fact that variations in milk yield are so great, even under common environment, indicates that more than one factor is responsible for milk production.

To make records comparable some method of adjusting records must be adopted. This investigation, as well as tabulations made by others, indicates that standardized records are practical and necessary in determining the breeding value of a bull or dam. When averages of groups of records are used, standardization factors are very applicable and fairly accurate. It must be remembered, however, that when individual records are adjusted, the percent error is often great because of the fact that in many instances there is not a steady increase in milk yield with increase in age. Table XII illustrates the variations that occur when standardization factors are applied to records of individual animals. No definite conversion factors can be applied to the part that care and management play in making high records. For the breeder to satisfactorily use conversion factors he must also consider the conditions under which records are made in order to compare records.

To make progress in breeding dairy cattle for production it is necessary to use bulls that are capable of transmitting high production to all their offspring. An analysis made of three of the most common bull indexes have brought out some interesting points in regard to their value and application. Indexes at their best are only an approximate guide for determining the value of a bull. A bull index alone without some knowledge of the animals themselves and the conditions under which their records are made, are subject to great error. Indexes based on only a few daughters may often be too high, partly because a few daughters will not give a true random sample and also because of the fact that many of

the poor daughters may not be tested and will not be included in the index. A bull index based on Herd Test records will probably be more accurate than will an index based on Advanced Registry records, because in the Herd Test all registered daughters in the herd must be tested while this is not required in the case of Advanced Registry testing.

It is difficult to point out any certain criteria that should be considered in selecting an index. The three indexes studied in this investigation are each based on different principles of inheritance in regard to transmitting production to the offspring. In the first place a bull index should be simple enough so that it can be worked by the average purebred dairy breeder. Each of the three indexes, namely, Mount Hope, Intermediate (Equal Parent Index), and the Gifford Index would qualify under this criteria with the possible exception of the Mount Hope Index which may become confusing to some people. A bull index should give the sire's potential production in actual pounds of milk and butterfat. All three indexes will qualify for this statement. A third criterion of a bull index is that it should be genetically sound. This is really the important factor that determines the value of an index. Each of the three indexes are based on different principles. Are each of the indexes genetically sound or does any one of them have a sound scientific basis? This question is difficult to answer because the principle involved in any one of the three indexes has not been definitely proven to hold true in regard to the transmitting ability of the sire as well as to the sire's potential level of production. The first comparison of the three indexes showed

that one index was about as good as the other in estimating the production of future daughters if the bull had at least ten daughters previously tested. All three indexes were apparently as much too high in some cases as they were too low in other instances. In this comparison the production of the first ten daughters was compared to the production of the second ten daughters. The extreme errors of the indexes on individual sires was about equal for each index. This would indicate one index to be as good as the other.

When the second comparison was made of the three indexes there was considerable variation in error. This comparison showed the variation in the bulls indexes when determined on the basis of all daughters (or dam-daughters pairs as the case may be), the first ten and the second ten daughter comparisons. In this comparison the Mount Hope Index gave the greatest variation. The fact that the Mount Hope Index is based on dominance of high production over low milk yield appears to be the reason for so great an error in the Mount Hope Index. Since high milk yield is dominant to low yield, daughters that averaged lower than their dams gave the sire a very low index indicating a large error. The theory of the Mount Hope Index does not seem logical because if high milk yield is always partially dominant then there would be a gradual improvement in the herd with every generation. If the Mount Hope Index is determined on a group of cows in which the daughters produced considerably less than their dams the bull will receive a very low index and in some cases it may even be a negative number. This is impossible as every dairy bull should be able to transmit some production to the offspring. For example: Bonheur Wayne 18th. No.

591426 had six daughters which averaged 321 pounds of fat and the dams averaged 551 pounds. According to the Mount Hope Index the bull would have an index of -216 pounds of fat which is, of course, ridiculous. The bull S H S Pontiac Matador Lyons No. 481033, which had seven dam-daughter comparisons, would have an index of -29 pounds of fat according to the Mount Hope Index. P O H Della Ollie Combination No. 560630, with nine dam-daughter pairs, would have an index of 39 pounds. King Ona Pietertje Champion, with nine comparisons, has an index of 44 pounds of fat. The above figures indicate that even when nine dam-daughter comparisons are available the Mount Hope Index is apparently not based on the right genetic principal. In other words, the theory that high production is dominant to low production, does not hold true in many instances. It is very doubtful that the bulls mentioned could have as low a potential level of production as indicated.

It is no doubt true that both parents contribute to the inheritance of milk yield of the daughters. Just how it is transmitted no one knows. Since the mode of inheritance of milk yield is not definitely determined, it is almost impossible to say if an index is sound or not. The Intermediate Index based on equal inheritance from both parents with a blending inheritance seems logical, however, since the dam's record does not always represent the daughter's production, and one might assume the same result in regard to the sire, this index may be unsound in practice. The sire, however, usually has a sufficient number of offspring so that the average of all daughters should indicate the ability of the sire to transmit production. The Gifford Index does not take the dam's record into consideration in determining the sire's index, but it lets the average of the daughters represent

the bull's index. In practical application the Gifford system is apparently as accurate in predicting the daughter's production as the other indexes studied and in some instances more accurate. Yet one cannot truthfully say that the dams do not affect the production of the daughters. In the Gifford Index they recognize the daughters' records as indicating the transmitting ability of the sire but they do not recognize the dams' records as indicating any relation to the production of the daughters, which indicates that in one instance the cow's record represents the transmitting ability while in another instance it does not.

From the results of this investigation, as well as the results of other investigators, one cannot definitely say which index is genetically sound or if any one of the three is sound. The fact that the production of all animals tend to work toward the breed average may be one reason why the Gifford Index has the smallest error under all conditions. The Gifford or Intermediate Indexes are perhaps the best measures that we have at the present time for determining the sire's index or his transmitting ability. This brings up the question: are bull indexes accurate enough to be of value to a dairy breeder? If a breeder is in the market for a bull, and he finds a bull with a high index, should he buy that bull? Indexes may easily be misleading if not interpreted correctly. Indexes based on less than ten daughters or dam-daughter comparisons are questionable. Furthermore, unless something is known about the care and management of the animals when the records are made, indexes may have considerable error. It is also possible that indexes may be based on only the best tested daughters and thus not be a fair indication of a bull's value, or it may be that only the best daughters had records which would give a bull a higher

index than he should have.

There has been considerable discussion about whether or not dominance is present in inheritance of milk and fat production or whether it is a blending inheritance. From the results of Table XIV one cannot determine if dominance is a factor in inheritance or not. Table XV and XVI, however, would indicate that the type of dominance on which the Mount Hope Index is based is questionable because of the great error in the index when the daughters average less than their dams. It may be possible that dominance is responsible to some extent for milk yield even though high milk yield may not be dominant to low milk yield as in the Mount Hope theory. The fact that the daughters' average for various groups was almost identical with each other regardless of the production of the dam would lead one to believe that dominance or at least partial dominance is responsible for milk yield to some extent.

If some factors responsible for milk yield are partially dominant to other factors, one cannot determine which parent contributes which. For instance; if the sire contributes a factor AA and the dam aa both would contribute jointly to the offspring but the dam's contribution would have little or no effect if 'A' is dominant to 'a'; or if both parents contributed Aa the daughter's production would be the same as if only one parent contributed that factor. If the above assumption is true then it would appear that the sire would be responsible for the daughter's inheritance except when the dam contributed a dominant factor of which the sire's allelomorph was recessive or vice versa. Since it is easier to determine the transmitting ability

of a sire than that of the dam it is given credit for the production of the daughter even though both parents may contribute jointly. The amount of dominance that is present, if any, would be difficult to determine and no estimation could be made from the limited investigation that has been carried on in connection with this paper. The above explanation seems to be a logical explanation of why the daughters production of a sire was practically constant when the dams were grouped as low, medium, and high producers. If this explanation is true then the Gifford Index could be considered justifiable even if the dams were not considered. There is no indication of complete dominance because there seems to be no definite segregation as is found in independent inheritance.

Before any definite conclusions can be made in regard to the method of milk inheritance, a more thorough and detailed investigation would have to be carried out.

Inheritance of Milk Yield, Butterfat Percentage and Total Butterfat. Apparently milk yield and butterfat percentage are inherited independently of each other even though there may be a significant negative correlation between milk yield and butterfat percentage in many instances. When sires were grouped according to the average butterfat percentage of their daughters, the average milk yield remained constant regardless of whether the sire transmitted a high test or a low test to their daughters. It was also found that as the percentage of fat increased the total butterfat increased also. The sires that had a high potential butterfat percentage increased the total fat yield of their daughters 15 percent above the average of the daughters of the low testing group.

When individual records of cows were grouped according to their butterfat percentage there was a significant negative correlation between milk yield and butterfat percentage. Holsteins with Advanced Registry records that average 5.0% fat produced 17% more milk than did the animals testing 4.0%. The percent increase in total fat yield of the high testing group was 15% above the yield of the 3% group even though the milk yield decreased 17% in the high testing group.

The third comparison was made in which the correlation of milk and percent fat was determined by comparing the daughters' records with those of their dams. The fact that in only 50% of the instances was there a lower milk yield for the daughter's record as compared to the dam when the daughter's percent fat increased, or vice versa, indicates that the milk yield is transmitted separately from the butterfat percentage. In the other 50% of the time there was either a positive or no correlation between milk yield and butterfat percentage. In other words, the milk yield and percent fat of the daughters both increased over the dams or one was constant while the other increased or decreased.

Both the first two comparisons indicate that selecting animals with high test will also increase total yield of butterfat. It might not prove economical, however, to go to extremes to have a high testing herd because of the high cost of producing rich milk. Environment apparently also has considerable influence on milk yield and fat percentage. Results of tabulations of Tennessee Register of Merit Jerseys reveal that the average test of the animals in Middle Tennessee are about .2 of one percent higher than those of East Tennessee.

The average test of Tennessee Jerseys is about 5.5% as compared with 5.26% for all states. We know that butterfat percentage of milk is lower in the summer than in the winter due to environmental conditions. It is also known that milk yield of the same animal may vary 100 percent while the butterfat percentage may or may not change. Conversion factors reveal that on the average butterfat tests are rather stable as compared to variations in milk yield. All these facts show that it is extremely difficult to draw conclusions based on statistical data of which nothing is known as to the environmental influences under which the animals made their records. The fact that milk yield varies so much while butterfat percentage is fairly stable makes correlation coefficients between milk and butterfat percentage rather questionable when based on statistical data.

CONCLUSIONS

1. Inheritance of milk yield and butterfat production is a very complex study because, (1) it is difficult to distinguish between inheritance and environment, and (2) because of the complex nature of the gene. Environment may greatly limit the inherited capacity of an animal.
2. Conversion factors are necessary to make records comparable and are justifiable when applied to groups of records. Conversion factors applied to individual records are questionable.
3. Conversion factors that have been worked out by various investigators are not too high when one is interested in group averages for milk and butterfat records.
4. Conversion factors are not necessary for butterfat percentage.
5. In this investigation the Gifford Index (considering all comparisons) had the lowest percent error in predicting the bull's potential level of production or the daughters expectation.
6. When the calculated production of the second ten daughters was compared to the actual production of the second ten daughters, neither of the three indexes, namely, the Mount Hope, Intermediate, or Gifford Indexes appeared to be superior to the other two. All three indexes showed an error of between 7-8%.
7. When the actual bull indexes were compared by working out the index based on all comparisons, first ten daughters, or dam-daughter comparisons as the case may be, and the second ten comparisons, there was considerable variation in the error for each of the three indexes. In this comparison the Mount Hope had the greatest error and the Gifford Index the smallest error.

8. In comparing the Intermediate Index with the Gifford Index when the dams were grouped according to low, medium, and high producers, the Intermediate Index had twice as great an error as did the Gifford Index, although both were reasonably low. In this comparison the calculated daughters production was compared to the actual production.
9. When the dams were grouped as all, low, medium, and high producers the daughters production was about the same for each group regardless of the dams production.
10. The principle of the Mount Hope Index is questionable as a measure of determining a sire's index, especially if the daughters are poorer producers than their dams.
11. Partial dominance may be responsible for the daughters production being rather constant regardless of the dams production.
12. The value of a bull index is weakened considerably unless something is known about the environmental conditions under which the records were made.
13. Milk yield and butterfat percentage are apparently inherited independently of each other even though individual records of cows within the same breed may indicate a small negative correlation between milk yield and butterfat percentage.
14. There is a significant positive correlation between fat percentage and total butterfat yield in Holsteins. Cows that test 4.0% will average about 15% more total butterfat than will cows testing 3.0%.
15. This study indicates that total fat production in Holsteins can be increased by selecting breed animals that transmit high fat

percentage. From an economical point of view this may not be practical.

16. Milk yield is subject to a greater variation due to environmental conditions than is fat percentage. Variations in butterfat percentage in different localities and variations in milk yield due to feed and other causes limit statistical studies as methods of studying inheritance.

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