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# GENETIC AND ENVIRONMENTAL CONTRIBUTIONS TO THE ECONOMIC CHARACTERISTICS OF THE MICHIGAN STATE COLLEGE DAIRY

HERD

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# BEERAPPA CHANDRASHAKER

### A THESIS

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

DOCTOR OF PHILOSOPHY

Department of Animal Husbandry

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#### INTRODUCTION

#### BASIS DEFINED

Fundamentally, genetical investigations, whether through biometrics or through Mendelian experimentation depend primarily on variation. There could be no selection if the population were homozygous and it continued to remain so, because of no mutations. By variation is meant the differences between individuals in any given related population. While dealing with quantitative characteristics, such as milk, butterfat or wool production, one is actually thinking of a continuous variation, whose visible "average effect" could be changed by the substitution of a "good" or a "bad" gene by selection. Whereas in case of qualitative characteristics such as color, polled and horned conditions, would constitute a discontinuous variation, based on the effect of the "unit" or discrete nature of a gene. And any problem of genetics that attempts to unravel the complex mechanism of inheritance must proceed to do so either on the basic assumption of one or the other form of variation. While Galtonian approach provides a basis to solve continuous variations, the solution for discontinuous variation should be sought from Mendelian concept of hereditary transmission. No matter whatever approach one takes, a knowledge of the

historidal development of these variations, whose differences at present have largely disappeared, would be essential to visualise them in their proper perspective-the rich and ever unfolding science of Genetics.

### VARIATIONS: HISTORICAL BACKGROUND AND THEIR SYNTHESIS

The first formulation of the fundamental theory of evolution by Darwin in 1859 based on the one hand to enormous facts from which he induced evolutionary process and on the other hand starting from few principles he deduced further the principle of natural selection. By logical thinking based on these facts he presented three observations, from which he drew two deductions: the facts are 1) the tendency of all organisms to increase in a geometrical ratio, due to the fact that in the early stages offspring are always more numerous than parents, 2) that in spite of the tendency to progressive increase, the numbers of a given species remain more or less approximately constant, and 3) variation; that all organisms vary appreciably. From the first two facts he deduced the struggle for existence or survival, since a larger number of younger ones are competing always against their older ones for survival. And from the first and the third fact he deduced the theory of natural selection of favourable variations against unfavourable variations. He believed that favourable variations which are minute and continuous are transmitted by heredity and the

unfavourable variations die and fail to reproduce. This phenomenon came to be known as the differential transmission of inherited variation. While he was willing to subscribe to some extent to the earlier Lamarckian theory of inheritance of acquired characters through use and disuse of them, he on the other hand went to the length of dismissing as "unimportant" any variation which was not inherited.

Amplifying on his theory of natural selection and domestication, namely, the accumulative selection and correlated variation, Darwin further proposed, among others, two outstanding conceptions, which even today not only stood the test of time but also have contributed in no small measure to our knowledge and thinking of genetics. He pointed out in his treatise on "Variations of Animals and Plants," (1868, p. 14) the principle of accumulative selection thus:

Man may select and preserve each successive variation, with the distinct intention of improving and altering a breed, in accordance with a preconceived idea; and by thus adding up variation, often so slight as to be imperceptible by an uneducated eye, he has effected wonderful changes and improvements. It can, also, be clearly shown that man . . . by preserving in each successive generation the individuals which he prizes most, . . . slowly, though surely, induce great changes.

Continuing his inquiry further, he observed the importance of correlated variation in precise terms in "Origin of Species" (1875, p. 14) as:

Hence, if man goes on selecting, and thus augmenting, any peculiarity, he will almost certainly modify unintentionally other parts of the structure, owing to the mysterious laws of correlation.

These concepts provide ample thought for multifactorial inheritance, which was not fully understood at that time, besides, it strengthened the theory of continuous variation in the population.

Following Darwin's formulation of evolution, a tremendous force of scientific exploration ensued, with Weisman seeking to clarify variation with his somatic and germplasm theory, wherein which the variations in the germ plasm were alone transmitted. This theory is generally known as the Continuity of Germ Plasm Theory, which later on formed the basis of two fundamentally distinct categories, viz., modification in the soma and mutation in the germ plasm.

Another highly significant contribution which drew its inspiration from the fountain head of Darwinian conception, was the application and development of statistical mathematics to the problems of biology--called biometrics, by Galton and later by Karl Pearson and his school. They conceived their method on the basis of a continuous variation but shortly after it suffered a set back in its avowed purpose because of the material Galton chose to express the mode of hereditary transmission. The material selected for his study was the stature of the man, which is a quantitative character. These characters show continuous variation as they are governed by several genes. Since he attempted to explain a continuous variation on the basis of particulate or discontinuous

nature of hereditary transmission, he did not at first succeed though he and later Pearson were able to show the variation to be at least partially heritable. Thus biometrics had to go for a time into recluse and its full acceptance as a mode of genetical study had to be delayed until a later date.

In the wake of these developments, Bateson in 1894, threw a challenge and attacked the whole foundation of the Darwinian edifice, which was threatened to be rased and replaced by a new theory. He contended that the whole basis of evolution was due to discontinuous variation and sought to substitute it in place of Darwin's. Without going into the merits or the demerits of the theory advanced by Bateson, it would suffice to note that it marked a new era of mutation theory, which postulated that large mutations and not the small "continuous variations" were the cause of evolution. The theory was later formulated by de Vries in 1901 and 1905 and was adopted by several other workers notably Morgan, T.H. in 1926.

In 1900, shortly after Bateson's work, the rediscovery of Mendel's breeding experiment with peas carried on from 1857 to 1865, revealed some of the basic principles of hereditary transmission. Mendel, the father of systematic experimental genetics, was successful

to a large extent because he reduced his problem to its simplest form consisting of two contrasting characters. From his work it was shown that recombination of existing genetic units will produce and modify new heritable variations, which lead to the establishment of the two basic laws of inheritance, viz., segregation and independent assortment. In essence Mendelian heredity is based on the inheritance of particulate or discrete units. The units are the Mendelian factors or genes, and their different forms are called alleles or allelomorphs. These genes are located on chromosomes as seen under the microscope, and due to the particulate nature of inheritance, the type and the proportion of these units could be calculated in the offspring after a cross. In the study of Mendelian factors, which implies unit inheritance, one would thus, be dealing with a discontinuous or discrete variation, generally known as the inheritance of qualitative characters. Post-Mendelian additions, such as linkage, corrosing over, etc., added further proof on the discontinuity of the variation, thereby drawing sharper differences between the two types of variations.

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Thus, these two conflicting theories of variations;, one, that of Darwin's continuous variation which formed the basis of biometrics of Galton and his school and the other the discontinuous theory of Mendel based on his

unique experimentation with unit characters, clearer in their own approaches to genetical laws, came therefore, face to face. Since, the workers on each side of these theories refused to acknowledge the others merit, a compromise and blending of these theories had to be brought about before biometrics could be accepted as an important method in genetical research. The biometricians thought that the continuity in phenotypic expression should correspond to the continuity in genotype, while the Mendelians considered that any phenotypic continuation was incompatible with the discontinuous genetic material.

Gradually the one gene-one character theory of Mendel became enlarged into the phenomenon of pleotropism. At the same time the existence of multiple factors as casual agents of a single character, advanced by Nilsson-Ehle in 1909, came more and more into the favour. Additional light thrown by these helped a good deal to narrow down the differences between the two theories. But it was not until the work of Johannsen, W. (1926) who, while experimenting with beans in 1909, formulated the pure line theory and showed that a character is the product of nonheritable environment and the heritable genotype, and that both contribute to the phenotypic variation. He expressed in his book "Elemente Der Exakten Erblichkeitslehre" (1926, 3rd. Edn. p. 202) thus:

Und innerhalb der reinen Linie sind die oft so grossen individuellen phanotypischen Variationen auch Ausdrucke der modifizierenden Einflusse ausserer Verhaltnisse.

\*The unique resultant contributory effect of these findings and theories in the post-Mendelian period was the smoothing of discontinuous theory, which finally came to be regarded basically same as the continuous theory: the discontinuity observed in the genotype due to Mendelian factors (genes), was rendered continuous in phenotype due to the effects of environment. And as Huxley (1943) expressed it more clearly that it is possible theoretically for a gene to alter its character by "mutating step by small step" from one member of allelomorph series to another and that discontinuous germinal changes are perfectly capable of producing continuous changes in somatic characters.

Thus, the synthesis of the biometrical and Mendelian approaches to genetical problems marked a great step in the advancement of this particular branch of science: the former provided a method to handle continuous variations and the latter showed the principles on which the analysis of genetical problems must be based. The only fundamental difference between the two as pointed out by Pearl (1915) is that biometrics deals

<sup>\*</sup>Since then one refers to a character as a product of <u>both</u> heredity <u>and</u> environment and not as a case of whether heredity <u>or</u> environment.

primarily with the ancestry, while Mendelism deals primarily with the progeny or the filial generations, hence, both are essentially statistical and also essentially biological.

In any animal genetical investigation, therefore, biometrics occupies a very important place and its application depends fundamentally on continuous variation in the attributes of a population. One should not consider it, however, as being superior to the methods of actual experimentation.

#### BIOMETRICS

In biometrical studies one attempts to accomplish two things, namely, on the one hand to furnish a description of a group of objects or events in terms of the group's attributes rather than in terms of the individuals composing the group, and on the other hand the prediction of the individual case on the basis of mathematical theory of probability, from a precise knowledge of the group or mass. --Pearl (1915)

In essence one will be measuring quantitative characteristics or the continuous variations observed in the phenotype of a group, and then establish a genetical relationship; both in type and degree, by discounting or attempting to discount the influences of environment and that of nonaddative hereditary variations; such as dominance and interaction.

Following the methods of Galton and his school (correlation), notable contributions to biometrics for

correlating quantitative characteristics have been the development of analysis of variance and its extension; covariance and correlation by Fisher (1925) and the method of path coefficient by Wright (1921, 1934). These methods, as discussed before, primarily aim at establishing the type and the degree of genetical relationship.

While the approaches advanced by Fisher have been profusely used in the present study, which will be explained under the respective methods for estimating heritability etc., it was thought pertinent and important to include in the present discussion a brief description of the basic concepts on which the path coefficient method has been developed. A working knowledge of the methods supplied by these outstanding workers have become powerful tools in the study of any mathematical genetics.

The principle of path coefficient has been employed to determine the relative importance of heredity and environment, both of which constitute the "observable" characteristic of an animal. Here again the hereditary variance is further made up of the variance due to additive genetic fraction and the variance resulting from dominace and interaction, which act in a nonadditive or nonlinear pattern. The additively genetic variance resembles more closely the transmitting ability of an individual; meaning closer resemblance to its "expected" value. In most of the genetical studies one is interested in separating this effect from a complex nature of a characteristic to determine genetical correlation. The variances due to dominace and interaction in an animal, though they contribute to the variability in a population, are not transmitted due to the Mendelian laws of segregation and recombination. Similarly, the environmental influences are non-transmissable. While the "observed" value of a characteristic is the result of the combined effect of all of these variances, the "expected" value is mostly the result of the additive genetic variance only.

The figure (1) will illustrate the relationship of various factors that enter in the making of an "observable" characteristic based on path coefficient method.



KEY P - Phenotype or Character H - Heredity E - Environment G - Genetic or the breeding value of an individual in a population D - Dominance I - Interaction or **Epistasis** rEH- Correlation between environment and heredity

FIGURE (1)

#### PATH COEFFICIENT:

The method has been developed on the main basis of cause and effect between variables; the cause being the independent variable and the effect being the dependent variable. The relationship that might exist between these variables has been attempted to be measured by this method. One proceeds, however, on the assumption that there exists a linear relationship between the variables and that the influence of the causes combine approximately by addition.

The path coefficient has been defined as:

The ratio of the standard deviation of the effect when all causes are constant except the one in question, the variability of which is kept unchanged, to the total standard deviation. (Wright, 1921).

Seeking further clarification of the method, he has stated a few of the most important principles involved thus:

- 1) The path coefficient differs from a coefficient of correlation in having a direction or path, which is represented by straight line. The straight lines have arrows at one end indicating the direction from an independent variable to a dependent variable. In case of residual correlation between variables, it is represented by double-headed arrow.
- 2) Variability between cause and effect measured by standard deviation.
- 3) The path coefficient squared measures the degree of determination by each cause and is called the coefficient of determination. It is

convenient to represent path coefficient by single small letters.

- 4) If the causes are independent of each other, the sum of the squared path coefficient is unity. If the causes are correlated, terms representing joint determination must be recognized.
- 5) The squared path coefficient and the expression for joint determination measure the portion of the squared standard deviation (variance) of the effect due to the causes singly and jointly, respectively.
- 6) The correlation between two variables can be shown to equal the sum of the products of the chains of path coefficients along all of the paths by which the variables are connected.

From these statements, two equations have been developed, namely, 1) expressing the complete determination of each variable by others, and 2) expressing the correlation in terms of path coefficients.

The following figure (2) and the equations will illustrate the basic concept of the path coefficient:



The X and Y represent the effects (dependent variables) and A, B, C, D, represent the causes (independent variables). a, b, c, d, and a', b', c', d' are the respective paths leading to X and Y. The correlation between causes B and C are represented by  $r_{BC}$ . Since variable X is dependent on A, B, C, it could be equated as:

$$X = A + B + C \qquad (1)$$

By simple algebra, if X is squared, the <u>whole</u> term on the right hand side must be squared which reduces it to a trinomial expansion. Thus the variance of X, which is the sum of squared deviations divided by "n" can be shown to be equal to the sum of the variances plus any joint terms resulting from the existence of correlation between the variables. The formula (1), expressed in terms of variances reduces itself thus:

If no relationship exists between A and B or A and C, the formula simplifies into (3):

$$\sigma_{\rm X}^2 = \sigma_{\rm A}^2 + \sigma_{\rm B}^2 + \sigma_{\rm C}^2 + \sigma_{\rm B}^2 \sigma_{\rm C}$$
(3)

Dividing throughout by  $\frac{2}{6X}$  (3) becomes,

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By definition of path coefficient  $a = \frac{\sigma_A}{\sigma_X}$ ,  $b = \frac{\sigma_B}{\sigma_X}$ ,  $c = \frac{\sigma_C}{\sigma_X}$ , therefore, the complete measure of determination of X in terms of the other variables becomes:

$$1.0 = a^{2} + b^{2} + c^{2} + 2r_{BC}bc \qquad (5)$$

In other words the variance of the X, the effect, is completely determined and is equal to the squared path coefficients leading to it plus any terms resulting from the effects of joint causes. Similarly, a relation could be established for X or for any other effects.

The correlation between two variables (X and Y) can be shown to be equal to the sum of the products of all the path coefficients connecting the two variables, thus:

$$\mathbf{r}_{\mathbf{X}\mathbf{Y}} = \mathbf{b}\mathbf{b}^{\dagger} + \mathbf{c}\mathbf{c}^{\dagger} + \mathbf{b} \mathbf{r}_{BC}\mathbf{c}^{\dagger} + \mathbf{c}\mathbf{r}_{BC}\mathbf{b}^{\dagger}$$
(6)

Path coefficients can be measured by use of the least square method--linear. Nelson (1943) has pointed out that the least square method, to determine the path coefficients from each of the causes to a single effect would result in a more complete estimate of the correlation coefficients. •

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By path coefficients the following formula could be derived from the figure (1) on page 9.

$$\sigma^{2}_{P} = \sigma^{2}_{H} + \sigma^{2}_{E} + 2r_{HE}\sigma_{H}\sigma_{E}$$
(7)  
But:

$$\mathcal{C}^{2}_{H} = \mathcal{C}^{2}_{G} \qquad \mathcal{C}^{2}_{D} \qquad \mathcal{O}^{2}_{I} \qquad (8)$$

The formula (7) can thus be written as:

$$\mathcal{C}_{P}^{2} = \mathcal{C}_{G}^{2} + \mathcal{C}_{D}^{2} + \mathcal{C}_{I}^{2} + \mathcal{C}_{E}^{2} 2r_{HE}^{HE}$$
 (9)

By dividing throughout by  $\mathcal{J}_{P}$ :

$$\frac{\partial^2 P}{\partial P} = \frac{\partial^2 G}{\partial P} \frac{\partial^2 P}{\partial P} \frac{\partial^2 P}{\partial P} \frac{\partial^2 F}{\partial P$$

By definition of path coefficient  $\underbrace{\mathcal{G}}_{\mathcal{P}}$  hg from figure (1): Thus formula 10 becomes:

1.0 
$$= h^2 g^2 h^2 d^2 h^2 i^2 e^2 2r_{HE} eh * (11)$$

If no correlation exists between H and E,  $2r_{HE}$  eh becomes equal to zero.

Thus it could be seen that an observable characteristic or phenotype is the product of several factors, and

 $2r_{\text{HE}}$  eh is also written as 2 cov. or  $\frac{2}{0}$ .

the greater the accuracy one develops in eliminating the non-transmissable variances from the total, the more precise will be the prediction of the genetic merit or correlation.

This useful knowledge of path coefficient has been utilised in the present study for the ensuing discussion on heritability, which is an important tool in the hands of a breeder. Thus, any heritability estimate of characteristics would be fundamentally an extension of the path coefficient principle.

# ANALYSIS OF VARIANCE, ITS DERIVATIVES, THEIR USE IN BIOMETRICS:

Since the time it was first presented by Fisher in 1925, it has become one of the most useful tools in the field of biometrics. It has provided the workers with a very powerful and effective means of breaking down the "causation complex" into its elements. The analysis of covariance and intraclass correlation are all extensions of this fundamental concept.

Under path coefficient it was considered that the variance of <u>a</u> sample with "n" variates could be used to estimate the variance of the population. But when one is dealing with "N" variates in a large sample, whose constituent parts are made up of "k" sub-samples with "n" variates in each (N<sub>-</sub> nk) of them, the estimate of the population variance would then consist of two independent variances, namely, the variance of the subsamples drawn at random and the variance of the means of these sub-samples (the variance of all the sub-samples put together is better estimate than the variance of one sample).

Either of these variances could be used to estimate the population variance. The variance of the sub-samples is termed as the variance <u>within</u> group or <u>random</u> variance or error term, and the variance <u>between</u> the sub-sample means as the between the group variance or the systematic variance. While the variance within the group is the best estimate of the variance of the population, which is always true under any condition, the variance between the groups depends upon whether or not the sub-samples are under any systematic influence. For example daughters of different sire groups or as a result of different treatment of sub-samples, in other words, whether or not the sub-samples came from the same parent population or from different populations.

The differences between these two variances are then tested by means of "F"-test, which is a ratio between the variance over that of the within the variance. If F-test proves to be insignificant, one would conclude that no significant difference exists between the two

variances and that any one of them would be a good estimate of the population. If F-test turns out to be significant, it indicates that the differences between the sub-samples are real and not due to any chance in random sampling. It cannot, therefore, be used as an estimate of the population variance. And where one is interested in obtaining a measure of population variance, as in the different methods of heritability estimates, this systematic difference, if significant by F-test, must be removed from the total variance. If not significant either of these two variances might be used to estimate the population variance.

The following is the fundamental indentity of analysis of variance:

nk-1	k-1	k(n-1)
S(X-X)	S(X <sub>8</sub> -X <sub>m</sub> )	S(X-X <sub>B</sub> )
- 2	2	- 2

where  $nk_{\pm} N$ ,  $X_{m}$  grand mean of the whole sample, and  $\overline{X}_{8}$  = the mean of the sub-sample. The factors in the denominators represent the degrees of freedom. The first term on the right hand side is the variance between the means of the sub-samples and the second term is the variance within the group (error term).

The analysis of covariance is an expension of this principle used for two or more sets of variables. The

error term in this is corrected not only by the analysis of variance method but also by multiplying it with the coefficient of regression of the dependent variable on the independent variable. The regression coefficient is given by the ratio of the covariance to the variance of the independent variate, which tells in actual units the nature of relationship existing between two things. In the ratio, the unit of the independent variable is one and is understood when expressed in terms of the regression coefficient.

The regression coefficient which results from the use of two or more sets of variables in the analysis of covariance, has been used in the present study to obtain correlation coefficients and heritability estimates.

Thus, it could be seen that the concept of analysis of variance is an important addition in solving genetical problems.

# DIFFERENCE BETWEEN REGRESSION COEFFICIENT AND CORRELATION COEFFICIENT:

Since these two terms are used so often in biometrical studies, one is often asked to express the differences between them:

Correlation is an attempt to summarise in one number the degree of relationship existing between two

things. The method used to obtain it is essentially an averaging process by which an average relationship is established. The primary use of it is to show in one number the relationship existing between two variables.

Regression coefficient summarises in one number the <u>nature</u> of relationship existing between two variables.

The relationship between these two statistics expressed mathematically would thus be:

 $r_{xy} = \sqrt{byx \cdot bxy} = Geometric average of the two regression coefficients.$ where r = correlation coefficient, b = regression coefficient and x and y are the independent and dependent variables.

Also:

$$b_{x,y} = r \frac{\delta_x}{\delta_y}$$

The value of correlation coefficient can range from -1.0 to + 1.0. When the correlation coefficient is +1 or - 1, there is perfect positive or negative relationship between the two variables. The primary disadvantage of correlation is that it always assumes linear relationship, whether that assumption is correct or not.

The square of the correlation coefficient  $r^2$ , as pointed out in path coefficient, is the coefficient of determination, which gives a measure of the percentage of the variance of dependent variable (Y) that has been accounted for by the relationship with the independent variable (X). The regression coefficient does not assume any linear relationship. Since the main purpose of the regression coefficient is to describe the nature of relationship and to show the rate of change in one factor in terms of another, it is found both in linear and non-linear functions. In a linear function, as the increment is constant the "b" becomes constant, while in a non-linear function since the increment is variable, the "b" also becomes variable with (X). As "r" approaches 1, the value of "b" is a more accurate estimate of the genetic variance of daughters on dams, but as "r" becomes zero, the value of "b" loses much of its significance.

Lush (1940) pointing out the differences between these two statistical terms as applied in genetics, reported that while selection of dams would reduce the parentoffspring correlation coefficient, it would not bias, the regression coefficient of these related animals.

In a population where no selection has been practiced, either of these statistics i.e. "b" or "r", could be used with advantage to determine genetical relationship. But where selection has been done the regression coefficient is a better measure than correlation coefficient particularly in heritability estimates. However, while selection of dams would reduce the "r", the selection of offspring would

impair both the statistics.

One of the chief differences between the intrabreed daughter-dam correlation and regression. and the intra-herd intra-sire correlation and regression of daughter on dam, is that in the case of the former the environmental component is not removed. while it is discounted in the latter. Thus a genetic correlation which to some extent also includes a fraction of envir-onmental influences is obtained by the latter method, which is the basis in the present heritability estimates. As Lush (1942) pointed out, the intra-breed daughter-dam correlations are usually 2 to 3 times larger than the intra-sire daughter-dam correlation. This difference is due to the fact that breed is not an homogeneous population and that a certain amount of leterogeneity exists from animal to animal, herd to herd, and the progenies of one sire with the other.

### PART I

#### HERITABILITY

### Lush (1949) has defined heritability as:

that fraction of the observed or phenotypic variance which is caused by differences between genes or the genotypes of the individuals in a particular population. It is used both in broad and narrow sense. In a broad sense it refers to the functioning of the whole genotype as a unit in contrast to the environment. According to the laws of Mendelian heredity of segregation and recombination of genes, it is impossible that the genotype as a unit would be transmitted. Instead some of the genes may interact with others in such a way as to produce a non-additive effect, which in certain combinations have effects quite different from their average effects in a given population. The differences between the actual effects in each combination and their average effects in the whole population are called dominace deviations and epistatic deviations, which are seldom, if at all, transmitted. Since, they would not materially add to ones estimate of heritability of characteristics, these nonadditive influences are generally discounted. The heritability in its narrow sense would then include only the average effects of the genes i.e. the additive genic differences.

The breeder is mainly interested in heritability in its narrow sense, since it expresses the fraction of the phenotype that one could recover in the offsprings. Theoretically, heritability could range from 0 to 1, though these extremes rarely occur. High or low heritability would indicate high or low heredity of a characteristic.

In deriving the mathematics of heritability by path coefficient, the following terms have been used,

#### which signify thus:

2 - Phenotypic variance, also called observed, to-6P tal, or actual variance.

••

- 2 Hereditary variance (in the broad sense).
  6 Also called the genetic or the genotypic variance.
- 2 = Environmental variance, which includes both 6 E temporary and permanent effects of environment.
- 2 = Variance due to the interaction between *O*HE heredity and environment.
- 2 Genic variance. Also called genetic, addiof tively genetic, or hereditary variance in the narrow sense.
- ? Variance due to dominance.
- 2 Variance due to epistasis. Also called non-1 linear interaction.

<u>Note</u>: In biometrics, particularly in heritability estimates, since one is interested in the study of the differences between individuals rather than actual values i.e. variations, it would be best to express these differences in terms of their squares or variances. While working with actual data, these differences are expressed in terms of regression and correlation.

## MATHEMATICAL DERIVATIONS OF HERITABILITY:

As has been already pointed out an observed characteristic or phenotype is the product of the combined effects of environment and hemefity in their broadest sense. By heredity in the present context is meant the whole combination of the genes in an individual. Some characteristics may be affected more by the one than the other. Mathematically a phenotype could be a function of heredity and environment, thus:

$$P = f(H,E)$$
(12)

To determine P the best way would be to combine the differences in heredity and environment, which could be expressed as figure (1):

$$\mathbf{P} = \mathbf{H} + \mathbf{E} \tag{13}$$

According to path coefficient, H and E are the causes and P is the effect. The effect and the causes stated in terms of variances could thus be expressed as in formula (7) on page 16. Since the 2 could be subdivided into 3 variances, 1) due to additively genetic, 2) due to dominance, and 3) due to interaction, formula (7) could be expanded as referred to in formula (9) on page 16. Due to the linear a nature of the relationship between the variables G, D, T, no correlation exists, except in the case of two related individuals, which may show some correlation in any one or all of these variances. Further. if heredity and environment are uncorrelated, the covariance term  $2r_{HE} \stackrel{\sigma}{\to} \stackrel{\sigma}{\to} E$  would be equal to zero, which would then reduce the formula (9) to its simplest form showing more clearly the relationship that exists between phenotype,

heredity and environment, thus

$$\boldsymbol{\sigma}_{\mathrm{P}}^{2} = \boldsymbol{\delta}_{\mathrm{G}}^{2} + \boldsymbol{\delta}_{\mathrm{D}}^{2} + \boldsymbol{\delta}_{\mathrm{I}}^{2} + \boldsymbol{\sigma}_{\mathrm{E}}^{2} \qquad (14)$$

By using the formula (9), one could then express heritability in terms of mathematics, thus:

1) In the broad sense:

Heritability =	$\frac{\sigma_{\rm H}^2}{\sigma_{\rm P}^2}$ =	$\frac{\sigma_{\rm G}^2 + \sigma_{\rm D}^2 + \sigma_{\rm I}^2}{\sigma_{\rm G}^2 + \sigma_{\rm D}^2 + \sigma_{\rm I}^2 + \sigma_{\rm H}^2}$
By path coefficient h $=$ in the broad sense = h <sup>2</sup> .	or <sub>H</sub> −op	Therefore heritability

2) In the narrow sense:

Heritability 
$$\frac{\sigma_{G}^{2}}{\sigma_{p}}$$
 =  $\frac{\partial_{G}}{\partial_{g}}$   
By path coefficient hg =  $\frac{\sigma_{G}}{\sigma_{p}}$ . Therefore heritability  
in the narrow sense =  $h^{2}g^{2^{2}}$ .

Thus, expressed mathematically, heritability represents a ratio, which could be altered by change in values in the nuemrator or denominator. Since the denominator includes the numerator, any change in values in the


numerator automatically affect the denominator. Further, since these values refer to a particular characteristic in a given population, heritability estimates would also therefore apply only to the characteristic in the population under study.

### IMPORTANCE OF HERITABILITY:

In any planned breeding program through selection a breeder is most interested in knowing what fraction of the total variation observed in a population for a given characteristic could be recovered in the progeny. Thus, an estimate of heritability in that particular characterp istic would be important and useful to him, since it would indicate the improvement he can effect per generation, on an average, through selected parents. Any improvement in the genetic material credited to his herd by the breeder would be permanent.

As Briquet, Jr. and Lush (1947) have concluded that when heritability is high, there is less room to influence a characteristic by the dominance, epistasis, and environmental effects to any appreciable extent. In such instances, mass selection (phenotypic selection) without any attention to progeny, pedigree, etc. is most effective in producing the desired effect. If heritability in its narrow sense is low the breeder must lay less

emphasis on mass selection and more attention to progeny selection, pedigree estimates, sib relations etc., since there is considerable room for the non-additive variations including the effects of environment on the genotypic expression of the individuals. In other words, the various aids in mass selection have been advanced, to solve selection problems where heritability is low.

If epistasis forms a large fraction of the total variance, the selection should be practiced between families and the linebreeding type of inbreeding followed in order to create new lines distinct from each other.

If overdominance is important, Lush (1949) points to the development of inbred lines, then testing these in crosses with each other, and then multiplying the ones which cross most favourably so as to develop them on a commercial scale.

If variance due to the interaction between heredity and environment is large, Lush (1949) suggests producing a separate variety for each ecological niche, if it is large enough to justify the cost.

Estimates of heritability could be used profitably as genetic constants in setting up selection indexes.

Finally, heritability estimates provide an important source of information in measuring the relative importance of characteristics for developing culling programs and

selection of breeding animals

One of the principal purposes of the study is to determine the estimates of heritability of some economic characteristics, such as milk production, butterfat production, and butterfat test, in the Michigan State College dairy herd, which consists of all the five common breeds.

### SOURCES OF ERROR IN HERITABILITY ESTIMATES:

Errors due to sampling may bias heritability estimates. To overcome such errors one should increase the volume of the data. Certain kinds of relatives, such as sibs developed in the same uterus, or animals raised under similar conditions may show environmental correlations, which would result in poor estimates. Errors may be introduced into the estimates as a result of mating systems practised in the herd which might be different from random. In such instances corrections should be made for the particular system of breeding, Hazel et al (1945). If the genotype as a whole function in a way different from the additive effects of all the genes, it may result in producing small or large deviations between genotype and phenotype of the individuals.

#### **REVIEW OF LITERATURE**

### A. METHODS OF ESTIMATING HERITABILITY:

Lush (1940, 1945, and 1949) has proposed several methods of estimating heritability, and one or several of these methods have since been used in large numbers of investigations to estimate heritability. Fundamentally these methods depend upon the similarity of related individuals. The closer the relationship the more accurate one could predict the genetic relationship and thereby the more reliable will be the heritability estimate. In other words, with the help of these methods one tries to find to what extent phenotypic likeness parallels the genotypic likeness. Or in terms of statistics it is the regression of the genotypic differences on phenotypic differences. Estimating heritability among unrelated animals would be most unprofitable because of the existence of very little genetic correlation.

Generally the methods for estimating heritability include: the study of isogenic lines, parent-offspring correlation, and regression, developing high and low lines by selecting in the opposite directions from the same initial population, full sib and half sib resemlances (correlation).

Since these methods have been dealt with in detail

by Lush (1940, 1945, and 1949) it was thought to summarise very briefly the various methods separately.

# Isogenic Line Method: Use of Identical Twins and Homozygous Lines.

In view of the very rare occurrence of the isogenic lines, particularly in dairy cattle it has not much practical importance. The only examples of isogenic lines are identical twins (homozygous). In a later study on twins it will be shown that these very seldom occur.

Any variation within an isogenic line is wholly environmental The relationship between two individuals of same genotype or between identical twins is 1.00 or 100 per cent, hence the ratio of the variance or the correlation coefficient is the estimate of heritability. This method is the only method which will measure in animals both the additively genetic variance as well as the non-additive variance due to dominance and epistasis.

The heritability estimate could be obtained in two ways, 1) the method of intraclass correlation as outlined by Snedecor (1946), where the variance between the isogenic lines is compared with the variance within the population under study, and thus, obtain directly an estimate of heritability. The variance within the isogenic line is wholly environmental; 2) the method of

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single classification of analysis of variance method. If (T) is equal to total observed variance, (H) the variance between the members of same isogenic line which is environmental and (E) the variance within the randomly chosen population under study, which is genetic, one can write the relationship as:

T = H + E or E = T - H

Then heritability could be expressed and obtained directly thus:

Heritability =  $\frac{E}{T} = \frac{T - H}{T}$ 

Some of the disadvantages of this method besides being rarely applicable to farm animals, are 1) that environment under which the individuals of an isogenic line are raised may be entirely different from those in the general population. Consequently it might result in an overestimate of heritability of a given characteristic; 2) the variance between the lines might include some interaction between environment and heredity, which might also increase the heritability estimates; 3) identical twins in farm animals are so rare and even if they do occur it is immensely difficult to identify them. However, if one could develop by intense inbreeding, homogenous lines with q = 1.0, one might probably overcome this problem, since any variance within a homozygous line is entirely environmental. But the expense and the time involved for such an undertaking in farm animals does not warrant such a costly venture. Besides, mutation pressure might upset the homozygosity by changing the frequency of "q".

#### Selection Experiment Method:

Several workers have used this method in their inveatigations. One of the classical examples of this method was presented by "Student" (1934) on his analysis of Illinois selection experiment for high and low oil content in corn. By using the contrasting lines and their progenies of the succeeding generations, he was able to determine the genetic variance from the differences between these lines.

The method depends on seeking to develop a high and a low line by mass selection in the opposite directions, from an initial population so that a regression (slope) of offspring on parents might be obtained. Since any phenotypic characteristic is the product of joint effects of both environment and heredity, the heredity alone being transmitted, the offspring therefore show a tendency to regress to the herd average in a random population.

The principle involved in the method is that differences produced between two lines are divided by the total amount by which phenotypes of the parent in all the generations exceeded the mean of the generation in which they were born, Lush (1949). By path coefficient, as the correlation between parent and offspring, is 0.50 of the hereditary variance;  $(r_{OP} = 1/2 h^2)$ , it should be multiplied by 2 to obtain an estimate of heritability. Since correlation is the geometric average of two regressions  $b_{OP}$  and  $b_{PO}$ , the same factor 2 is used to multiply the regression coefficient to get an estimate of heritability.

Besides genetic, some of the epistatic variance might be included in the estimate, but the effect of dominance would be excluded from it. After the lst. and 2nd. generation of selection the epistatic effect becomes so diluted that it would not effect the heritability estimates in its narrow sense. Thus to obtain a more reliable estimate of heritability, one would do well to discard the first two generations. The differences between the first two generations and the later generations could be used to estimate the variance due to epistasis.

The method has its greatest advantage where selection has been practiced for only one characteristic. But where more than one characteristic is involved, which would be the case generally, one might obtain an erroneous estimate of heritability. Further, it is rarely to be

expected that a breeder could afford to practice selection in the opposite direction, besides selection for more than one generation poses problems of replacements which must be made within each line itself. And finally, for an adequate control of environment for both the lines it becomes necessary for selection in the opposite direction to be practiced in a contemporary control line.

# Intra-Sire Daughter-Dam Regression or Correlation Methods

It is one of the most frequently used methods. The principle is fundamentally based on path coefficient and coefficient of relationship between the parent and offspring. It could be shown by path coefficients that the correlation between parent and offspring is half the heritability estimate  $(r_{OP} = 1/2 h^2)$ , hence the correlation or regression is multiplied by 2 to give an estimate of heritability. In other words, since each parent contributes, on the average, only half of the inheritance to its offspring the "r" or "b" must be doubled in estimating heritability.

The correlation between parent and offspring includes half of genic variance and somewhat less than one fourth of epistatic variance but does not include the variance due to dominance. Further, the correlation

might include some of the environmental variance, which could be reduced to zero by proper experimental design. Hence, the main object of setting up the analysis of parent-offspring data on an intra-sire basis is to eliminate this environmental variance and also to discount for any non-randomness in breeding system. In the case of environmental correlation it is offset by this method because, 1) the daughters and the mates of a sire are kept nearly always in the same herd. And therefore the differences in the management from herd to herd would be removed along with the differences between sires instead of contributing to the daughter-dam correlation; 2) the offspring of a sire are nearly contemporary, which eliminates any deviations in management contributing to daughter-dam comparison.

Since heritability by this method expresses the fraction of the variance which existed among the females mated to the same sire, any deviations from random mating are eliminated.

The main procedure in the method involves estimating how much difference could be expected between their offspring per unit of phenotypic differences between those dams. In term of statistics, it seeks to determine the regression of genic differences among those dams on the phenotypic differences among them. The use of offspring

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in the method is, thus, merely to indicate genic values of their dams.

Broadly the steps in the calculation, which also apply to other methods involving parent-offspring and sib comparisons, are: 1) discount the environmental variance, 2) multiply the resultant correlation by the appropriate factor to change it to heritability estimate, and 3) correct for any non-randomness in mating system. If the population is breeding at random no correction is needed, otherwise, divide by 1+m if the population was inbred, or by  $1+r_{SD}$ , if it was phenotypic assortive mating. Here "m" is the relationship between mates and "r"<sub>SD</sub> is the phenotypic correlation between mates. Intra-dam regression of effspring on sire could also be done similarly, but is rarely done due to meager data because of fewer offspring produced by dams as contrasted to sires.

## Full-Sib Correlation Method:

It is very similar to parent-offspring correlation method. The coefficient of genetic relationship between full sibs in a randomly bred population is 0.50, i.e. they inherited half of the genic variance from their parents. Therefore, as in the gase of parent-offspring correlation, the regression or correlation is multiplied by 2. But the phenotypic resemblance, besides containing half of the genic variance, also contains about one fourth of epistatic variance, a little less than one fourth of dominance variance, and the variance due to common environment between full sibs. Since the estimate contains the fraction of the dominance as stated above and some amount of environmental variance, it would be somewhat higher than the estimate by the parent offspring method.

It is important in this method, therefore, to discount for environmental variances, otherwise the estimate would be biased. Any error of sampling would automatically be multiplied by 2. The best way to overcome this shortcoming is to analyse the data on a intra-herd basis.

The procedure in calculating is similar to the one enumerated in parent-offspring method.

### Half-Sib Correlation Method:

Unless very large amounts of data are available, which would substantially reduce the errors of sampling, this method is not as accurate as other methods described so far.

The coefficient of genetic relationship between half sibs, if randomly bred, being 0.25, the correlation should be multiplied by 4 to get an estimate of heritability.

Generally, the method is worked out on the basis

of parental half sib and the data analysed by intra-class correlation by analysis of variance method as outlined by Snedecor (1946).

The estimate includes genic variance, a small fraction of epistatic variance but does not include any dominance. As regards the environmental variance, if the data were analyzed on paternal half sib basis, it would not include any of the maternal environment. But if they were analysed on a maternal basis, the estimate would include 4 times the maternal environment and nothing from the paternal if the differences in half sibs are as large as those of the non-sibs. Further, it exaggerates sampling error when multiplied by 4, which is a distinct disadvantage inherent in the method.

To discount these environmental influences would be to run the analysis on intra-herd and intra-seasonal basis. Intra-seasonal analysis would correct for any differences between seasons which are apt to occur in old herds.

Since the method primarily concerns the comparison of sibs and does not take into account parental phenotypes it could be used with advantage in those animals whose traits are measured by destroying them, such as the carcass of meat animals.

The procedures in calculating are similar to those

noted in parent-offspring method.

## Mid-Parent-Offspring Correlation or Regression Method:

The method is similar to the parent-offspring method, except that in the place of one parent, the average of both the parents are included in the study.

The estimate under this method includes genetic variance and somewhat less than half of the epistatic variance as was the case in the parent offspring method. Dominance is excluded and if the population has been properly randomized environmental variance also would be eliminated.

By the theory of path coefficient as shown in Figure (3) the correlation between parental averages (mid-parent) must be multiplied by 1.41 to obtain an estimate of heritability.

This method cannot be applied for characteristics if expressed in one sex only. Also it cannot be used for estimating such traits which one could only measure by destroying the animals as in the case of meat stock.

The procedure is similar to intra-sire offspringdam method. Derivation of the factor 1.41 by path



X and X' = Observed characters in sire and dam.

FIGURE (3)

The degree of determination for Figure (1,b) is:  $1 = s^2 + s^2$  or  $1 = 2 s^2$  $s = \sqrt{\frac{1}{2}}$ 

The correlation between mid-parent and offspring from Figure (1,a) would be:

> $r_{OM} = 2 \times hgabhgs$ = 2 h<sup>2</sup>g<sup>2</sup>ab $\frac{1}{2}$

Since ab by path coefficient is equal to  $\frac{1}{2}$ , the formula becomes:

$$r_{OM} = 2 \times \frac{1}{2} \times \sqrt{\frac{1}{2}} h^2 g^2$$

 $r_{OM} = \sqrt{\frac{1}{2}} h^2 g^2$  $h^2 g^2 = r_{OM} / \sqrt{\frac{1}{2}}$  or 1.41 x  $r_{OM}$ 

Heritability = 1.41 x  $r_{OM}$  .

## Diallel Crossing Method:

This method consists of breeding two sires to the same females at two different times and then analysing the differences in full sibs, maternal or paternal half sibs. The resultant regression or correlation is then multiplied by the appropriate factor to get an eestimate of heritability.

If the data used were from full sibs, the estimate would contain some fraction of dominance, epistatic and environmental variance as pointed out in the discussion under full sibs. But, if the estimate was determined from the half sibs, the dominance would be excluded.

The method was originally used to measure the breeding merit of the sires and it could be used with advantage in meat animals or in those where the traits could be measured in both the male and female progeny. It, therefore, has no practical value as a method for heritability estimates in dairy cattle.

A. METHODS USED IN THE PRESENT STUDY:

For a best estimate of heritability of all the

three economic characteristics: milk production,

butterfat production, and percentage of butterfat in the M.S.C. dairy herd, the following three methods were chosen for the present study:

- 1) Intra-sire regression of daughters on dam method,
- 2) Intra-sire daughter-dam correlation method, and
- 3) Paternal half-sib correlation method

Finally, to obtain a best aggregate estimate, the weighted average of these methods, the weighted average of five breeds and the weighted average of three methods and five breeds have been calculated. The methods, procedures, calculations and discussions are presented on the following pages.

The data was further made use of, in addition to the heritability estimates, to a study of the following factors which have important bearing in dairy cattle breeding enterprises:

- 1. Repeatability of milk yield
- 2. Repeatability of butterfat production
- 3. The effect of the month of calving on the following lactation
- 4. Sex ratio
- 5 Twin ratio

# C. HERITABILITY AND REPEATABILITY ESTIMATES FOR TRAITS IN DAIRY CATTLE

The heritability estimates for the economic characteristics in dairy cattle, investigated in the present study are the milk production, butterfat production, and butterfat test. The repeatability estimates are confined only to the milk and butterfat. Due to the very slight variation in butterfat test that exists between one lactation and another of the same cow, it could be considered for all practical purposes to be close to 100 per cent. Hence, the calculation of the repeatability of the test was thought to be unnecessary.

Only the literature pertaining to milk production, butterfat production, and butterfat test have been reviewed here. A general review of the heritability of these traits previous to 1941 was presented by Lush (1941), while the review on repeatability previous to 1940 was made by Dickerson (1940). To these have been added those estimates not included in the above reviews as well as those investigations published subsequent to them.

The reviews on these topics have been set out for the sake of brevity in a tabular form, Table I below:

## TABLE I

## ESTIMATES OF HERITABILITY AND REPEATABILITY FOR VARIOUS

## CHARACTERISTICS IN DAIRY CATTLE

## I. HERITABILITY: A. MILK

Herita- bility (percent)	Method used determine heritability	to		Reference	
41	Regression	of	Daughter	Edwards 1932	
57	Regression	of	Daughter	Rice 1933	
53 or 56	5 Full sib	on Dam Full sib	Gowen 1934		
38	Regression on Dam	of	Daughter	"Brain Truster" 1936	
33	Regression on Dam	of	Daughter	Lush and Arnold 1937	
38	Regression on Dam (dan record with	of 1s' 1 da	Daughter lst. aughters)	Lush et al 1942 (Iowa D.H.I.A. records)	
68	Regression of Daughter on Dam (dams' later records with daughters)		Daughter later daughters)	11 11 11 -	
I. HERITABII	LITY: B. BUTT	ERI	FAT		
23	Regression on Dam	of	Daughter	Gifford 1930	
51	11 II	11	π	Gifford 1930	
43	π	Ħ	11	Copeland 1932	
12	12 Intra-herd daughter- dam correlation		ughter- on	Plum 1935	
25 (abou	it) Intra-sire dam correla	da itic	aughter- on	Lush and Shultz 1936	

TABLE I I. HERITABILITY: B. BUTTERFAT (Continued)

<b>\$</b> 2	on dam Full sibs	Gowan	זר
<u>HERITAI</u> 86	BILITY: C. BUTTERFAT TEST Regression of Daughter	Rice	19
17.0	#Intra-sire regression	Chai	19
31.0	*Intra-sire regression	Chai	19
27.4	Intra-sire linear regression	Beardsley et a	1 19
17.4	#Intra-sire regression	Lush and Strau	s 19
26.8	*Intra-sire correlation	Lush and Strau	s 19
26.8	*Intra-sire regression	Lush and Strau	s 19
75	Regression of Daughter on Dam (dams' other records-except lst and 2nd-with daughters)	<b>τι τι τι</b>	
30	Regression of Daughter on Dam (dams' 2nd. record with daughters)	11 11 11	
62	Regression of Daughter on Dam (dams' later records with daughters)	<del>17</del> 17 17	
25	Regression of Daughter on Dam (dams' 1st record with daughters)	Lush et al 194 (Holstein HIR records)	2
28	Intra-sire regression	Lush 1940 "	
27.5	Regre <b>ssion of</b> Daughter on Dam (dams' 1st record with daughters)	Lush 1940 (Iow DHIA records	()
28	Regression of Daughter on Dam	Lush and Arnol 1937	d

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 TABLE I
 I.
 HERITABILITY:
 C.
 BUTTERFAT
 TEST
 (Continued)

50(about)	Intra-sire correlation	Lush	1936

# II. REPEATABILITY: A. MILK

65	Intra-breed correlation	(Jerseys-all herds) Gowen 1920
66	Intra-breed correlation	(Holsteins-all herds) Gowen 1924
73	Within-herd correlation	Sanders 1930
37	All sires correlation (uncorrected records)	Gain <b>es 1935</b>
32	All sires correlation (corrected)	Gaines 1935
48	First record over later records of dams	Lush et al 1942

# II. REPEATABILITY: B. BUTTERFAT

69	Intra-breed correlation	(Jer <b>seys-all</b> herds) Gowen 1920
71	Intra-breed correlation	(Holsteins-all herds) Gowen 1924
54.7	Intra-herd analysis of variance (Lactation records)	Harrish et al 1934
54	Intra-herd analysis of variance (C.T.A. records	Harrish et al 1934
60	Intra-breed correlation (All herds)	Plum 1935
40	Intra-herd analysis of variance	Plum 1935

TABLE I II. REPEATABILITY: B. BUTTERVAT (continued)

43	First record over later records of dams	Lush and	Arnold 1937
75	Intra-breed correlation (Jersey R. of M. Cows)	Copeland	1938
88	Intra-breed correlation (Jersey Herd Test cows)	Copeland	1938
68	Intra-breed correlation (Holstein HIR records)	Berry and	i Lush 1939
43	First record over later records of dams	Lush	1940
43	First record over later records of dams (Iowa DHIA records)	Lush et a	<b>19</b> 42
40	First record over later records of dams(Holstein HIR records)	Lush et a	al 1942
34	Analysis of variance	Chai	195 <b>1</b>

Note: The repeatability estimates on Intra-breed correlations based on all kerds in the above review show markedly high values. This is due to not discounting the effects of temporary enviornment or to differences in herd enviornment.

- \* Expressed in terms of the average of all records.
- # Expressed in terms of what it would be if each cow had only one record. The formula used to transform the heritability estimate based on the average of all the records to one record is as follows, Lush (1942):

$$\mathbf{b} = \mathbf{b}^{\frac{1}{2}} \left[ \frac{1 + (m - 1)\mathbf{r}_{dd}}{m} \right], \text{ if all the dams had the same number of records (m).}$$

$$\mathbf{b} = \mathbf{b}^{\frac{1}{2}} \left[ \frac{1 + (\overline{m} - 1)\mathbf{r}_{dd}}{\overline{m}} + \frac{\frac{2}{m}(1 - \mathbf{r}_{dd})}{\overline{m}^{3}} \right]$$

The estimate on single record is generally lower than that on average records.

where m is the average of lactation records of all dams when they are variable, b is the regression of daughter on dam when single records of each are used, b' is the regression when lifetime averages are used,  $r_{dd}$  is the repeatability within herds; i.e. the average correlation between successive lactations of the same dam, and  $\mathcal{J}_m$ is the variance of the (m) lactation records of dams.

## SOURCE OF DATA

The data used in the present study are the pro- ~ duction records of the dairy herd of Michigan State College at East Lansing, accumulated over a period of several years. The earliest production records date as far back as 1919. The college, a part of the State Agricultural Experiment Station, intended mainly for teaching and demonstrational purposes to the farmers of the state of Michigan, is comprised of all the five common dairy breeds viz. Holsteins, Jerseys, Ayrshires, Guernseys, and Brown Swiss. All of these animals have been registered in the respective Pure Breed Associations. Records of cows transferred from time to time for experimental purposes such as nutrition etc. have been excluded from the study so as to keep down the influence of environment as low as possible.

A total of 473 cows from all five breeds were

available for a preliminary study. Cows that were sold or disposed of otherwise or such of those with lactation periods less than 275 days were not included in the study. It was thought that any cow with less than 275 days of lactation period might have been under a dominating influence of environment such as, state of health, age, etc. Generally under normal conditions of heredity the occurrence of such low periods of lactation are rare, if not completely absent. In the present analysis, inclusion and study of such extreme values of production would not serve any useful purpose. Further by adjusting these incomplete records to mature equivalent one would be only giving far considerable weightage which might not exist, thus introducing inaccuracies.

### NEED FOR STANDARDIZATION OF RECORDS:

To provide a basis of comparison between cows and also to predict the relative breeding efficiency of sires, it would be necessary to adjust or standardise the records for environmental variations. The interplay of physiological factors, the effect of age, the climatic influences within and between years, management, number of times milked per day, and length of lactation period are some of the environmental factors which have a definite bearing on the expression of an animal's productive

characteristic-phenotype. To correct for all factors, however, would be impossible as good deal of effort and time is involved but by adjusting at least for two or three most important environmental conditions a comparative reliability could be attained on the average to a whole or part of the population. Finally, it is of utmost importance that correction factors should not be subjective.

1. Cows born as identical twins which have the ability to react alike to changes in environment would produce differently under different management conditions, Lush, (1937).

2. Cows with larger body size have greater feed capacity and thus production of more milk. Turner (1929) reported that when age was held constant there was on the average an increase of 20 pounds of butter fat for an increase of 100 pounds of body weight. He further stated that about 25 per cent of the total increase in fat is due to live weight of animal and 75 per cent of increase is due to the development of udder.

3. Breed differences also influence production; breeds which produce a milk of high fat content give less milk than those which are lower testers, for example, Holsteins and Jerseys, Gaines (1931). He also pointed out that efficiency of production in dairy cattle decreases with increasing body weight of the cow.

Within the breeds, heifers are more persistent than cows, because a heifer is increasing in size and in the amount of secretory tissue in the udder. But as regards the efficiency, Edwards (1936) reported that cows are more efficient producers than heifers. He also reported that stage of lactation in dairy cattle generally effects the gross efficiency, i.e. steady decline in efficiency from 38.75 to 29.25 per cent with the advancement of lactation.

4. Kendrick (1941), has concluded that a cow milked 4 times a day increases her production by 35 per cent and when milked 3 times a day the increase is about 20 per cent over what it would have been on a 2 times a day milking basis. Likewise more milk is produced in a 365-day period than in 305-day period. Edwards (1936) also found that 3-X milking is better than 2-X milking.

5. On the effects of management on production, a classical study was made by Eckles (1939), who compared the milk and fat production of the same cows under different conditions. Forty one cows under farm conditions produced an average of 8395 pounds of milk and 343 pounds of butterfat but under official test conditions this was raised to 14331 pounds of milk and 564 pounds of butterfat, an increase of 70.7 per cent in milk and 64.9 per cent in butterfat respectively.

6. As regards the relationship between age and production, several notable contributions have been made, all of which agree as to the non-linear relationship between these two factors. The classical work in this field was reported by Pearl (1914), who derived the nonlinear formula between age and production as follows:

 $Y = A + BX + CX + D \log X$ , where Y is the production and X is age.

He brought this relationship in more precise terms and stated:

The amount of milk produced by a cow in a given unit of time (7 days, 1 year etc.) is a logarithmic function of the age of the cow. . . Milk flow increases with increasing age but at a constantly diminishing rate (the increase in any given time being inversely proportional to the total amount of flow already attained) until a maximum flow is reached. After the age of maximum flow is passed the flow diminishes with advancing age and at an increasing rate. The rate of decrease after a maximum, on the whole, is much slower than the rate of increase preceding the maximum.

The above law applies both to the absolute amount of fat produced as well as to milk. Drop in the rate of secretion is not as pronounced because the size of the cow does not change greatly after maturity. Later, Pearl and Patterson (1917) working with 5821 Jersey 7-day records and Pearl, Gowen, and Miner (1919) working with 2153 yearly-records in the Register of Merit of Jersey Breed, also showed the logarithmic form of the curves, which most closely fitted a non-linear second degrees equation as that of the above. They also reported that the maximum yield was attained about the age of 8 years and 7 months.

Gowen (1920) in his studies with Jersey breed, whose records extended as far back as 1897, independently reached similar conclusions.

Brody et al (1923) studying nearly 50,000 records of different breeds not only agreed with the findings of the early workers, but also concluded further, that milk and fat production gradually increase as the dairy cow becomes mature and then gradually decrease with the onset of old age; thus under similar conditions of feeding and management a heifer is expected to increase her yearly production at each succeeding lactation period until she reaches maturity. Thus, production gradually increases up until between seven and eight years of age and then gradually decreases with the onset of old age. This is in essence similar to the conclusions of Pearl (1914).

The Figure (4) on page 56 illustrates the relationship of age with the various traits in dairy cattle.

From the foregoing discussions, it can be seen that an animal's characteristic is a complex combination of both genetic and environmental factors, both of which have varying effects on the phenotypic expression. To obtain a better evaluation of the genetic merit, it is





of primary importance in any study involving genetic relationship of individuals in a population, to correct for these environmental influences so as to keep them as uniform as possible. However, it should be understood that a standard record will seldom be exactly the same as the one actually made under standard environmental conditions, but it provides a practical approach for comparison of individual merit, as long as the corrections are not subjective.

Since breed differences exist, all of the records were adjusted separately by use of the conversion or correction factors. To avoid any possible source of error while correcting for too many factors at one time, it was thought to standardize three of the most important environmental influences:

1. Age

- 2. Length of lactation period
- 3. Times of milking per day

#### 1. AGE CONVERSION FACTORS:

The correction factors used in the present study were those published by Kendrick (1941) separately for different breeds. While developing these factors it was recognized that different breeds mature and decline at different rates and at different ages. For example, the Holsteins,

Jerseys, Ayrshires, and Guernseys mature at about six years of age, while Brown Swiss reaches maturity at around seven years of age. Since these factors were compiled from various D.H.I.A. records made all over the country, they are considered as being fairly free from bias. Age at the time of calving was rounded off to the nearest month and the records made during that lactation period following each calving were adjusted to the production at the age of maturity.

### 2. LENGTH OF LACTATION PERIOD:

Length of lactation periods of all those records exceeding 305-day period were adjusted back to 305-day period. Such of those records with less than 305-day but not less than 275 days of lactation were considered to be the expressed merit of a cow and hence not adjusted. The use of 305-day lactation period reduces materially the variation in the length of lactation, thus giving a basis of comparison. Since fewer records are met with requiring the use of factors, it increases the accuracy and gives a better evaluation of the cow's actual merit.

## 3. NUMBER OF MILKINGS PER DAY:

The State College Herd was on the basis of 3X milking per day almost throughout the period covering the present study. But from July 1, 1949 the milkings per day were
changed to a 2x basis. In view of the fact that almost all of the records were made on a 3X milkings per day program, no attempt was made to convert these to a 2X basis so as to reduce a source of error. But, such of those few lactation records made on 2X were adjusted to 3X per day, after they were transformed to mature equivalent-305-day period.

As the present study is primarily concerned in determining the extent of genetic correlation between the dams and their daughters, only those cows which had their dams' records were used in the final analysis of the data. This obviously resulted in the elimination of a considerable number of cows from the study.

Table II shows the number of cows that were available in the preliminary and in the final study, number of Sires and the number of Daughter-Dam comparisons.

**TABLE II**NUMBER OF COWS IN THE PRELIMINARY AND FINAL<br/>STUDY AND NUMBER OF SIRES IN EACH BREED

Breed	Number o Sires	of Number of Cows at the Beginning of Study	Number of cows avail- able for final Analysis	Average Number of Records of Cow	% de- crea- se -1	No. of baught- dr-Dam Compar- sons
Holsteins	21	170	146	2.4	14	91
Jerseys	20	101	85	2.7	16	60
Guernseys	16	90	66	2.7	27	48

(continued next page)

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TABLE II (Continued)

			Average	2.6		
Total	72	473	396	13.0	16	271
Ayrshires	8	58	55	2.3	5	38
Brown Swiss	7	54	44	2.9	18	34

The reduction in the size of the samples, as can be seen in the above table calls for consideration of the often-raised question as to the reliability of the statistics of such samples. In Animal Breeding Research projects one commonly encounters such small samples, because of the time involved in the accumulation of data. It was thought pertinent to the study to state the methods developed for adjusting small samples.

"Student" (1908) in his classical work was the first to develop a method to adjust for small samples. He stated that while in the case of larger samples one could predict more precisely the parameter of a normally distributed parent population, but in the case of smaller samples one meets with two sources of uncertainty: (1) owing to sampling errors the mean deviates more or less from the population, and (2) the sample not being large enough to determine the normality of the distribution. How could one, therefore, adjust for these sources of uncertainty so as to obtain a fair estimate of the population variance; an important source of information in the present study? By dividing the sum of squares by the number of degrees of freedom, (n-1), instead of by the sample size "n", smaller samples are corrected. This is precisely what one does in any Analysis of Variance and Covariance.

The theory and the mathematics concerning the use of (n-1) as detailed by Lindquist (1940) has been described here in the following few steps:

The general formula for the variance of a sample with "n" number of variates is:

S<sup>2</sup> = <u>Sd<sup>2</sup></u> N S<sup>2</sup> = Variance d = Deviation of an individual variate in the sample from

Let us take "k" random samples of "n" cases from a

the mean of its sample.

population whose true mean is "m".

Let the mean of the lst sample be  $X_1$  and the deviation of its variates from the mean be  $d_1$ .

Let d<sup>1</sup> represent the deviation of X variates from the true mean (m) of the population.

Then:

$$d_{1} = (X - X_{1}) \text{ and } d_{1}^{1} = (X - m)$$

$$d_{1} - d_{1}^{2} = (X - \overline{X}_{1}) - (X - m)$$

$$= (m - \overline{X}_{1})$$

$$d_{1}^{1} = d_{1} - (m - \overline{X}_{1})$$

Squaring both sides:

$$d_1^2 = d_1^2 - 2d_1(m - \bar{x}_1) + (m - x_1)^2$$

For "n" number of variates in sample 1:  $Sd_1^2 = Sd_1^2 - 2Sd_1(m - \bar{x}_1) + n(m - x_1)^2$ 

Since  $Sd_{1} =$  ), the above formula could be reduced by transposition:

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population mean for all the "n" number of variates in all the "k" samples, thus the grand total N = nk. The above formula could then be expressed in a general form as:

 $S(Sd^2) = Sd^{1^2} - nS(m - X_p)^2$ , where p is equal to the mean of any sample for 1 to k.

By expressing the above equation in terms of a variance for one sample would be:

$$\frac{(\mathrm{Sd}^2)}{\mathrm{n}} = \frac{\mathrm{Sd}^{1^2}}{\mathrm{n}} - \frac{\mathrm{n}\mathrm{S}(\mathrm{m}-\mathrm{\bar{x}})^2}{\mathrm{n}}$$

For "k" number of samples:

$$S(Sd^2) = Sd^{1^2} - nS(m - \bar{X}_p)^2$$
, where N = nk

or:  

$$\frac{1}{N} \frac{S(d^2)}{dt} = \frac{Sd^{1^2}}{N} - \frac{S(m - \bar{X}_p)^2}{k}$$

If "k" becomes infinitely large, then the  $(\underline{Sd}^2)$  would still be the variance of the sample but  $\underline{Sd}^2$  would also come closer to population variance and  $\underline{S(m - \bar{X}_p)^2}$  would be the variance of the sample means from the population mean or  $\sigma_m^2$ . But  $\sigma_m^2$  is equal to  $\frac{2}{\rho_{pop}} / n$ , or  $\sigma_m = \frac{\rho_{pop}}{\sqrt{n}}$ .

Then the formula for the variance of a sample distribution could be written as:

$$\frac{(\mathrm{Sd}^2)}{n} = \frac{2}{pop} - \frac{1}{n} \frac{2}{pop}$$

$$\frac{(\mathrm{Sd}^2)}{n} = \operatorname{2pop} \left(1 - 1\right) \quad \operatorname{or} n - 1 \quad \operatorname{2pop} n$$

By multiplying both sides by n = 1, the equation becomes:

$$\frac{(\mathrm{Sd}^2)}{\mathrm{n}-1} = 2^{2} \mathrm{pop}$$

Therefore, the <u>best</u> estimate of a population variance is:

$$\mathcal{Z}_{pop} = \frac{(Sd^2)}{n-1}$$

This relationship has been made use of for finding the standard deviation of the differences of the means (standard error of the differences of means), thus:

Standard error of a mean 
$$(\sigma_{\overline{x}}) = \sqrt{\frac{(Sd^2)}{n-1}} = \sqrt{\frac{(Sd^2)}{n(n-1)}}$$

"Student" (1908), who first derived this fundamental principle, made use of it in "t" test for <u>testing</u> <u>smaller samples</u>: "t" =  $(\bar{x}_1 - \bar{x}_2) - 0$ 

$$\frac{(\mathrm{Sd}^2)}{\sqrt{n(n-1)}}$$

Another important application of this method of obtaining a best estimate of the population variance from a randomly drawn sample by use of (n - 1) instead of "n", could be seen in the method of analysis of variance and covariance developed by Fisher (1938)

The purpose of this discussion was to point out at length that smaller samples could be used to estimate the parameters of a normally distributed population provided valid corrections are made to reduce the possible sources of error.

# ANALYSIS OF DATA

Heritability estimates in dairy herds have been generally confined to butterfat production for several reasons: First, on account of the wide spread routine program of testing of the percentage of butterfat, the records of D.H.I.A. and Purebred Associations are made and published on the basis of butterfat production, which have provided the necessary source of data in several studies. Second, since a breeder is paid and his income based on the amount of butterfat he produces rather then on the amount of milk, any study which purposes to serve him as guidance must be in that direction. And third, the amount of milk produced and the amount of butterfat are directly and significantly correlated. As reported by Gowen (1924) the correlation coefficient between milk yield and butterfat by correlation coefficient was 0.8927 ± .0075 and by partial correlation coefficient

method with age held constant it was  $0.863 \pm .009$ . Further the amount of butterfat is a multiple of butterfat test and milk yield in a given time. Hence the milk production records are of value in calculating the amount of butterfat.

The amount of butterfat in a given lactation is less variable and more constant than milk, as it is less subjected to environmental conditions such as temperature, amount of water intake and the nature of feed. Woodward (1923) has reported that mineral and water do not affect the test. While feeding of 7 - 11 pounds daily of cotton seed and linseed oil meal caused an increase of the fat content of milk, the usual quantities fed to dairy cattle failed to show any increase. Six -  $7\frac{1}{2}$  pounds daily of gluten feed had no effect on test. Hot weather, however, lewer the test. He thus concluded that feeds rich in fat have no appreciable effect on butterfat.

M'Candlish and Struthers (1921, 1935) working in England, on the feeding of butterfat and cream have similarly shown that there is no significant difference in the production of butterfat and thus it is less variable. While it is generally agreed that the level of fat intake has no influence on the fat in the milk, Maynard et al (1934) have recommended in order to meet the normal body requirements, a minimum level of 4 per cent of fat in grain mixtures, which should be fed at the rate of 1 pound of grain mixture to every  $3 - 3\frac{1}{2}$  pounds of milk, along with adequate amount of hay and corn. Feeding of fat above this level is not only not economical but also not justified.

From the foregoing discussion it could be seen that the butterfat test is less subject to change than milk yield.

In countries like India and some other Eastern countries, where very little routine testing for butterfat is made, the breeder is generally at loss in his selection on the basis of butterfat and has to depend mostly on milk production records.

The records used in the present study contained adequate quantitative information on the three characteristics, milk yield, butterfat production, and butterfat test. An attempt, therefore, has been made to present comparative estimates of heritability for all these three characteristics.

The mean and the standard deviation for milk, butterfat and butterfat test in all the five breeds were computed and shown in Table III as a preliminary routine study. These values were obtained from the adjusted production records of individual cows.

TABL	E III:	SHOWIN FAT TH	NG THE ME IST FOR A	AN AND LL THE	STAND, FIVE	ARD DE BREEDS	TATV	TON OF	MILK, BU	TTERFAT A	ND BUTTER-
No.	Breed		Number		lbs. Milk			<u>Г</u> б	lbs. itterfat	Butt	erfat Test
			of Cows	Mean - E		Std. + E	Dev.	Mean + E	Std. Dev <u>-</u> E	• Mean - E	Std. DeV. <u>+</u> E
-	Holstei	l n s	182	14612	± 24	324 <u>+</u>	17	6+464	115±6	3.4±.25	0.35±.18
8	Jersey	ß	120	7987	± 14	158+	10	425±5	<u>50</u> <u>+</u> 3	5.3+57	0*62+440
ŝ	<b>Åyrs</b> hiı	8 0 L	76	10153	<del>-</del>	202+	16	6-104	75±6	4.0 <u>+</u> 80	0.704.57
4-	Guerns	ey e	96	8695	н +	108+	100	421-10	101-7	97-6-1	0.45±33
5	Brown	Swiss	68	13195	+ 25	202+	18	543 <u>-</u> 10	84±7	4.1+57	0.47 <u>-</u> 41
	Total		542	54642				2290		21.7	
· · · <b>*</b>	Weight Average	eđ	•	11294		232		t60	92	4.3	0.50
Note	ю. *	Weight. Weight	ed averag ed averag	e of H	eans = tandar	₹(n z d5Devi	atio	ns, se	e conclus	ion for f	ormula.
	E = St.	andard	lo rorra	mean	or sta	ndard	devi	ation (	calculate	d from th	e formulae:
	Standaı	rd Erre	or of mea	n = S/	<ul> <li>- u</li> </ul>	1-4					

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Standard Error of Standard Deviation =  $S/\sqrt{2n-1}$ 

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• •  The Standard Error of Differences between the means of the dams and the daughters for each breed and the corresponding "t" values were calculated in order to test the significance between these averages, as shown in Table IV.

TABLE IVSHOWING THE STANDARD ERROR OF DIFFERENCES<br/>(STANDARD DEVIATION OF THE DIFFERENCES OF THE<br/>MEAN) AND "t" TEST BETWEEN DAMS AND DAUGHTERS<br/>FOR THE THREE CHARACTERISTICS IN ALL THE FIVE<br/>BREEDS

Breed	Number Pairs o Daughte Dams	of Dam of er-	s Daughters	Std. Error of Differences $S_{e} = \frac{1}{n_1 - 1} \frac{1}{n_2}$	or "t" test "-
Holsteins	91	Milk ( 14566	Pounds) 14657	48	1.895
Jerseys	60	8323	7650	29	23.3 **
Ayrshires	<b>≁ 3</b> 8	10427	987 <b>8</b>	47	11.7 **
Guernseys	48	8726	8664	23	2.7 *
Brown Swiss	34	13271	13119	51	3.0 **
		Butter	fat (Pounds)	)	
Holsteins	91	494	493	17	0.06
Jerseys	60	432	417	14	1.10
Ayrshires	38	<b>4</b> 0 <b>9</b>	405	18	0.22
Guernseys	48	421	420	13	0.08
Brown Swiss	34	552	533	21	0.90

TABLE IV	(Continued)	
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Holsteins	91	Percenta 3.5	age Butte 3.4	rfat (B.F. 0.17	Test) 0.60
Jerseys	<b>6</b> 0	5.2	5.4	0.26	0.80
Ayrshires	38	3.9	4.1	0.28	0.70
Guernseys	48	5.0	4.9	0.28	0.40
Brown Swiss	34	4.2	4.1	0.20	0.50

\* Significant at 5% level \*\* Highly significant at 1% level

The above table shows that, except in the case of milk yield in the Holsteins, the average of the daughters, both for milk and butterfat production in all the five breeds do not indicate any consistent increase over their dams. The "t" test in the case of Holstein daughters was found to be insignificant, indicating that the difference between the dams and the daughters is only due to random errors of sampling and not to any superiority of merit of daughters.

The milk yields in the other four breeds show a reverse situation; the dams averages are much higher than that of the daughters. The "t" test on these differences proved to be significant, pointing that the average production of the dams was superior to that of the daughters. These significant differences could be explained on the ground that these average yields being somewhat higher than the general breed averages, there is always a tendency on the part of the daughters to regress towards the breed averages. Unless intensive breeding for higher yields has been practiced in a herd, it would be difficult to maintain or increase over the productions of the dams.

The non-significance of "t" test in case of the percentage of butterfat would also indicate that the variation within a breed may not be significant.

#### CALCULATION OF HERITABILITY OF MILK PRODUCTION

Estimates of heritability of milk production were computed separately for each breed and a weighted average was obtained as one statistic.

From the various values in the tables of analysis of covariance, the calculations were developed for the

half-sib method, and for the intra-sire regression and correlation methods.

The corrected average milk production of dams was treated as an independent variable, X and that of the daughters as dependent variable Y. In other words Y was considered as function of X; Y = f(X). The data were then grouped on an intra-sire basis and the usual analysis of covariance was carried out for these two variables, X and Y, as outlined by Snedecor (1946).

For a detailed explanation of the procedures, one breed namely, Ayrshire, was chosen at random. The completed analysis of covariance for Ayrshires is given in Table VI.

Preliminary to the analysis of covariance, the sums, sum of squares and cross products of X and Y variates, under each sire have been shown in Table V. To facilitate handling of large figures of milk production while squaring etc., each record of dam and daughter was divided by a constant, (C) = 10, and then the records corrected to the nearest round figure. It should be noted, however, that by dividing with a constant, 10 the variance of the distribution is not altered. Because if the variates in a normal distribution are increased or decreased by a constant "C", then the measure of variability is not affected.

Sire	Number of Pairs of Dam- Offspring	Sum of X	Sum of Squares of X	Sum of Y	Sum of Squares of Y	Sum of products of X and Y
I	6	5351	4840535	5582	5329056	4931974
II	6	7146	9019020	5413	4996291	6479026
IIII	2	2003	2019617	1785	1619793	1806735
IV	6	6967	8145713	5757	5610221	66400 <b>55</b>
V	2	1968	1936512	1600	1281800	1574400
, VI	8	7243	6651697	8473	9177705	7644537
VII	7	7381	8222025	7616	8371856	8099305
VIII	1	1568	2458624	1317	1734489	206 <b>505</b> 6
Total	38	39627	43283743	37543	38121211	39241088

TABLE VPRELIMINARY DATA FOR THE STATISTICS OF MILK<br/>PRODUCTION OF AYRSHIRE HERD

CALCULATION PROCEDURES FROM TABLE V

<u>A. Correction Term</u>: For  $X = \frac{(SX)^2}{N} = (39627)^2/38 = 41323661$ For  $Y = (SY)^2/N = (37091496)^2/38 = 37091496$ For XY = (SX) (SY)/N = (39627) (37543)/38 = 39150433

# B. Total Sum of Squares:

For  $X = SX^2 - C.T_{x} = 43283743 - 41323661 = 1960082$ 

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For  $Y = SY^2 - C.T._y = 38119411 - 37091496 = 1027915$ For  $XY = SXY - C.T_{xy} = 39241088 - 39150433 = -90655$ 

C. Between Sires Sum of Squares:

For 
$$X = S(SX)^2/N - C.T_x = (5351)^2 /6+(7146)^2/6+$$
  
 $\cdot \cdot \cdot (1568)^2/1 - C.T_x = 790782$   
For  $Y = S(SY)^2/N - C.T_y = (5582)^2/6+(5413)^2/6+$   
 $\cdot \cdot \cdot (1317)^2/1 - C.T_y = 376671$   
For  $XY = S(SX) (SY)/N - C.T_{xy} = (5351) (5582) /6+$   
 $\cdot \cdot \cdot (1568) (1317)/1 - C.T_{xy} = 88405$ 

TABLE VI ANALYSIS OF COVARIANCE OF MILK PRODUCTION OF DAMS AND THEIR DAUGHTERS FOR AYRSHIRE HERD ON INTRA-SIRE BASIS

Source of	Degrees of	Sums	of Squares	and Products
Variation	rreedom	Sx <sup>2</sup>	Sxy	Sy <sup>2</sup>
Total	37	1960082	90655	1027915
Between Sire	s 7	790782	88405	376671
Within Sires (or ERROR)	30	1169300	2250	651244

The object of carrying out an analysis of covariance is to separate the controlled i.e. correlated variations of X and Y from that of uncontrolled i.e. independent variation. The mean square of this uncontrolled variation will be the best estimate of the variance of the population. Since the within-the-sires or error line is the uncontrollable variation, it could be used to determine the unbiased estimate of the population regression and correlation coefficients between X and Y variates; dam and daughters.

TABLE VIIANALYSIS OF VARIANCE OF MILK PRODUCTION OF<br/>DAMS (X) IN AYRSHIRE HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	37	<b>196</b> 0082		
Between Sires	7	<b>79</b> 0782	1129689	2.90 *
Within Sires (or ERROR)	30	1169300	389767	

\* Significant at 5% level.

TABLE VIIIANALYSIS OF VARIANCE OF MILK PRODUCTION OF<br/>DAUGHTERS (Y) IN AYRSHIRE HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	37	1027915		
Between Sires	s 7	376671	538101	2.48 *
Within Sires (or ERROR)	30	651244	217081	

\*Significant at 5% level.

In order to test for any variation in the production of milk of dams and that of daughters between the various sire groups, analysis of variance was developed separately from the Table VI of analysis of covariance as shown in Table VII for dams and Table VIII for daughters. The data in both the tables were then subjected to "F" test. In both instances the F-values between sires were significant at 5% level indicating that a value (statistic), as large or larger than these values would be expected to occur by chance alone less than 5% of the time. In other words, in the case of dams, the mean milk production of one group of dams was significantly different from that of the other group of dams mated to different sires and similarly, in the case of daughters, the average milk yield between groups of different sires was significantly different. One is therefore, justified in the use of analysis of covariance method to remove these variances due to different groups of dams and daughters before one proceeds to estimate any genetic relationship--correlation and regression coefficients.

## A. INTRA-SIRE CORRELATION AND REGRESSION METHOD:

The calculation procedures for determining coefficients of correlation and regression and the respective standard errors are presented in the following steps:

a) Correlation Coefficient =  $r_{y.x} = S_{xy}/\sqrt{S_x^2 \cdot S_y^2} =$ 

$$\sqrt{(1169300)(651244)} = 0.003$$

b) Standard error of the correlation coefficient was calculated by using the formula:  $S_{error} =$  $1 - r^2/\sqrt{n-2} = 1 - (0.003)^2/\sqrt{38-2} =$  $0.999991/\sqrt{36} = 0.1667$ 

The heritability estimate was obtained by multiplying above correlation coefficient by 2, which is equal to  $2 \ge 0.006$ .

The standard error of heritability was like obtained by multiplying the standard error by 2, which is equal to  $2 \times 0.1667 = 0.333$ .

Thus the heritability estimate of milk production for Ayrshire herd of the Michigan State College by intrasire correlation method is  $0.003 \pm 0.333$ .

- c) Regression coefficient of  $\pm b_{y.x} = Sxy/Sxy^2 = \frac{2250}{1169300} = 0.002$  daughters on dams
- d) Standard error of the regression coefficient was calculated as follows:

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S^2 error = Standard error of estimate of the error term/
n-2
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Sum of squares of "x" of the error term

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$$= \frac{Sy^{2} - (Sxy)^{2}/Sx^{2}}{\frac{n-2}{Sx^{2}}} \qquad \text{OR}$$

$$= \frac{[Sy^2 - b(Sxy)]}{Sx^2} / n-2$$

$$= \frac{651244 - 4.2750}{36} = 0.015376$$
1169300

$$S_{error} = \sqrt{0.015376} = 0.124$$

The regression coefficient was then multiplied by 2 to get an estimate of heritability, which is equal to  $2 \times 0.002 = 0.004$ .

Similarly, the standard error of the regression was multiplied by 2 to obtain the standard error of heritability, which is  $2 \ge 0.124 \ge 0.248$ .

Thus the heritability of milk production of Ayrshire herd of the Michigan State College by intra-sire regression method is 0.004+0.248.

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**TABLE IXCORRELATION AND REGRESSION DATA FOR THE EIGHT**<br/>AYRSHIRE SIRES IN RESPECT TO DAUGHTERS AND<br/>DAMS PRODUCTION OF MILK

Sire	Degrees of Freedom	Sum Squares	s of and Produ	icts	Correlation Coefficient	Regres- sion Coef-
		Sx <sup>2</sup>	Sxy	Sy <sup>2</sup>	r	ficient
I	5	68335	-462440	135935	48	-0.68
II	5	508134	32143	112863	0.13	0.06
III	1	13612	19057	26680	1.00	1.40
IV	5	55865	-44782	86379	-0.65	-0.80
v	1	0	0	0	0	0
VI	7	84066	-26705	203739	-0.20	-0.32
VII	6	439288	68777	85648	0.36	0.16
VIII	0	0	0	0	0	0
Total	. 30	1169300	2250	651244	0.003	0.002 *
Note:	x = X -	$\overline{\mathbf{X}}, \mathbf{y} = \mathbf{Y}$	- Y and x	y = (X-)	x) (Y-Y).	

Table IX, above shows the calculation of  $Sx^2$ , Sxyand  $Sy^2$  for individual sires in the herd. The totals of these three columns are equal to the values found in the respective columns of within-the-sire (or error) line in the table of analysis of covariance; Table VI. From the above table the correlation and regression for each sire was also calculated.

To break down the within-sire values into their \* "r" and "b" calculated from the totals. individual components would be valuable as a measure of verfication and check. But, of more importance is the fact that it provides a clue to the composition and character of the sums of squares and products within the error term (line). It would be further evident that they are pooled values from all the groups, each deviation involved being measured from its own group mean. Hence, the within-sire regression of Table VI is an average of the eight sire group regressions of Table IX. The withinsire values or the total values in either tables could be used in the following calculation of the required statistics.

#### B. HALF-SIB CORRELATION METHOD:

The intra-class correlation, which is the basis of this method was calculated from the data in Table VIII; Analysis of Variance of milk production of daughters (Y). They are paternal half-sibs in relation within each sire group. The procedure as detailed by Snedecor (1946) was used for calculation in this method.

The general formula for intraclass correlation is:

$$r_{I} = s_{m}^{2} / (s^{2} + s_{m}^{2})$$

Where:

S<sup>2</sup>

- the random or the estimated variance of the error term i.e. of the population, assumed to be equal for all sub-samples.

S<sub>m</sub><sup>2</sup> - the unbiased estimated variance related to the difference among population means arising from genetic and environmental conditions peculiar to the sub-samples as a whole. This can be expressed as equal to:

E Mean square between sires - Mean square of error term

Average number in each sire group (K<sub>0</sub>)

 $S^2 + S_m^2$  = the sum of these two is the variance of individuals picked at random from the entire universe made up of the sampled populations.

The formula of intraclass correlation thus could be expanded to suit the calculation directly from analysis of variance table:

$$r_{I} = \frac{(S^{2} \text{ between sires } - S^{2} \text{ within sires})/K_{o}}{S^{2} \text{ between sires } - S^{2} \text{ within sires})/K_{o} + S^{2} \text{ within}}$$

$$= \frac{S_{m}^{2}}{(S_{m}^{2} + S^{2})}$$

First, calculate the average number as follows:  $K_0 = (1/n-1) \cdot (Sk-Sk^2/Sk)$  where "n" = number of sire groups, and k = number in each sire group.  $K_0 = (1/8-1) \cdot (38 - (6^2+6^2-2^2+6^2+2^2+8^2+7^2+1^2)/38 = 4.6)$ Now, substituting in the formula, where:  $S^2$  between sires = 538101  $S^2$  within sires = 217081  $K_0 = 4.6$  $S_m^2 = (538101 - 217081) / 4.6 = 321020/4.6 = 69787$ 

Therefore:

 $r_I$  = intraclass correlation = 69787/(69787 + 217081)= 0.243 Standard error of this correlation was calculated by using the same formula as was in the case of intra-sire correlation coefficient:

$$S_{I}(error) = (1-r_{I}^{2})/\sqrt{n-2} = (1-0.243^{2})/\sqrt{38-2} = 0.94095/6 = 0.157$$

The paternal half-sib correlation of 0.243 was multiplied by 4 to get the estimate of heritability, which is equal to 4 x 0.243 = 0.972.

Likewise, by multiplying the standard error of intraclass correlation, the standard error of heritability was obtained, which is equal to  $4 \ge 0.157 = 0.394$ .

Thus, the heritability of milk production of Ayrshire herd of the Michigan State College by paternal half-sib correlation method is 0.972<u>+</u> 0.94.

Heritability calculation procedures by all the three methods for the remaining four breeds; Holsteins, Jerseys, Guernseys, and Brown Swiss were exactly similar to the ones described above. Hence, the following pages contain the various tables, which present for each breed the successive steps in the calculation of estimates of heritability of milk production.

Breed	Tal	bles		Pages
Holstein	XXII,	XXIII,	XXIV	98
Jersey	XXV,	XXVI,	XXVII	99
Guernsey	XXVIII,	XXIX,	XXX	100
Brown Swiss	XXXI,	XXXII,	XXXIII	101

From the foregoing tables, the coefficients of correlation and regression, and the paternal half-sib intraclass correlations for the remaining breeds were calculated in an identical manner and summarized in Table X. The values of this table were multiplied by the respective factors and estimates of heritability obtained for all the five breeds by the three methods, as shown in Table XI.

**TABLE XI**CORRELATIONS, REGRESSION AND STANDARD ERRORSOFTHE ADJUSTED MILK PRODUCTION OF COWS

Breed	No. Sires	No. Pairs Daughter- Dams	Paternal Half-Sib Correlation		Intra-Sire Regression		Intra-Sire Correlation	
			rI	S <sub>I</sub> (err	or) b	Sb	r	<sup>S</sup> r
Hols.	21	91	0.140	0.104	-0.135	0.129	-0.110	0.10
Jers.	<b>2</b> 0	60	0.260	0.122	0.128	0.158	0.106	0.130
Guern	. 16	48	0.045	0.147	-0,051	0.149	-0.050	0.147
Ayrs.	ප්	38	0.243	0.157	0.002	0.124	0.003	0.167
Br.Sw.	7	34 -	0.134	0.174	-0.108	0.140	-0.135	0.174
TOTAL	72	271						

The factors used to transform the above values to estimates of heritability are as follows:

- 1. Paternal half-sib correlation x 4 = Heritability, since the relationship between half-sibs if 25%.
- 2. Correlation coefficient x 2 = Heritability
- 3. Regression coefficient x 2 = Heritability The relationship in the case of daughter and dam (2 & 3) is 50%.
- TABLE XIESTIMATES OF HERITABILITY AND STANDARD ERRORSFOR THE ADJUSTED MILK PRODUCTION OF COWS

Breed Pa Ha Me		aternal alf-Sib ethod	Intra-Sire Regression Method		Intra-Sire Correlation Method	
	Herit- ability	Standard error	Herit- ability	Standard error	Herit- ability	Standard error
Hols.	0.560	0.416	-0.269	0.258	-0.220	0.210
Jers.	1.040	0.488	0.255	0.316	0.211	0.260
Guern	-0.180	0.588	-0.101	0.298	-0.100	0.294
Ayrs.	0.972	0.628	0.004	0.248	0.005	0.333
Br. Sv	•0.536	0.696	-0.215	0.281	-0.269	0.348

From the above table, it can be seen that there is a considerable variation among the three different methods in the heritability estimates, which could be attributed, first, to the large sampling errors and sample sizes, and second, to the obvious differences in the calculation procedures for "r" and "b". While "r", correlation coefficient, summarises in one number the degree of relationship existing between two variates, the "b", the regression coefficient establishes the nature of relationship between them, hence, slightly different values are used in their calculation. It was, therefore, thought to combine all the different values in the Table XI and obtain an average as one estimate of the heritability of milk production.

Hazel and Terrill (1945) worked out a method of combining the sets of heritability values and their standard errors into a single figure. The best estimate of heritability was, thus, arrived at by averaging the values of three methods and five breeds. These averages were taken by weighting each of the individual estimates by the reciprocal of its squared standard error. Likewise, the weighted average of the standard error of heritability was calculated by taking the square root of the reciprocal of the sum of the reciprocals of the squared standard errors. While the method has some disadvantages, its usefulness lies in the fact that it gives greater weights to estimates based on greatest amount of data.

The weighted average of heritability was obtained by the use of the following formula:

Weighted Average = 
$$(\frac{h_1/S_{h_1}^2}{(1/S_{h_1}^2) + (1/S_{h_2}^2) + \dots + (h_n/S_{h_n}^2)}$$
  
(1/S<sub>h1</sub>) + (1/S<sub>h2</sub>) + ... + (1/S<sub>hn</sub>)

where  $h_1 \dots h_n =$  heritability estimates, and  $S_{h_1} \dots S_{h_n}$ .

The weighted average of the standard errors of heritability was obtained by use of the following formula: Weighted Average Error of Heritability =  $\sqrt{\frac{1}{(1/S_{h_1}^2) + (1/S_{h_2}^2) + ... + (1/S_{h_n}^2)}}$ 

where  $S_{h_1} \dots S_{h_n}$  are the individual standard errors of heritability.

The various statistics involved in the above two formulae were calculated for all five breeds and three methods and tabulated in Table XII. As the heritability estimates were already given in Table XI, they are not repeated in Table XII.

TABLE XIISQUARED STANDARD ERRORS AND THEIR RECIPROCALS<br/>OF THE HERITABILITY OF MILK PRODUCTION

Breed	H <b>alf-sib</b> Method		Intra-Sire Regression Method		Intra-Sire Correlation Method		Reciprocal Sum of 2 Methods	
	$s_{h1}^2$	1/S <sub>h1</sub>	s <sup>2</sup> h <sub>2</sub>	$1/s_{h_2}^2$	s <sub>h3</sub>	1/S <sup>2</sup> h3	$S(1/S_{h_n}^2)$	
Hols.	0.173	5.78	0.069	15.02	0.044	22.68	43.48	
Jers.	0.238	4.20	0.100	10.01	0.068	14.79	29.00	
Guern.	0.346	2.89	0.089	<b>1</b> 1.26	0.086	11.57	75.72	
Ayrs.	0.394	2.54	0.062	16.26	0.111	9.02	27.82	
Br.Sw.	0.484	2.06	0.079	12.66	0.121	8.26	22.98	
Recipro sum of breeds	ocal 5	17.47		65.21		66.32	149.00	

Ş

Breed	Heritability	Standard error
Holsteins	-0.133	0.152
Jersey <b>s</b>	0.346	0.186
Guernseys	-0.120	0.111
<b>Ayrs</b> hire <b>s</b>	0.093	0.189
Brown Swiss	-0.263	0.208

TABLE XIII WEIGHTED AVERAGE OF THREE METHODS (MILK PRODUCTION)

TABLE XIVWEIGHTED AVERAGE OF FIVE BREEDS (MILK<br/>PRODUCTION)

Method		Heritability	Standard error		
Paternal correlat	half-sib ion	0.484	0.238		
Intra-sir regressi	e on	-0.081	0.124		
Intra-sire correlation		-0.079	0.123		
TABLE XV	WEIGHTED BREEDS	AVERAGE OF THREE	METHODS AND FIVE		
Trait		Heritability	Standard error		
Milk Prod	uction	-0.014	0.08		

i

Thus, the final estimate of heritability of milk production of the Michigan State College dairy herd, which is the weighted average of all five breeds and three methods is  $-0.01\pm0.08$ .

By definition heritability estimate for any hereditary characteristic could only vary from 0 to 100 per cent, though the extreme instances are rare. In view of the negative estimate for milk yield, it was uncided to observe the results by further analysing the data on an intra-breed regression of daughter on dam basis in an attempt to find out any possible sources of error.

### Procedures and Calculations:

The principle on which the method is based is to divide the production (phenotype) of the dams with their daughters into high and low lines over that of the herd average. The ratio of the differences of the daughters over the differences of the dams would be the regression coefficient (b) of offspring on dams. This when multiplied by 2 gives the estimate of the heritability for the given characteristic.

In the present study, the dams with their daughters were divided into high and low groups on phenotypic basis. This would eliminate any system of mating and thus reduce the herd to a level of random breeding method. The Holstein herd was chosen at random for showing procedures and calculations for estimating heritability by this method. The corrected daughter-dam records used in the regression coefficient method were used <u>in toto</u> in this method Table XVI below gives the mean production for the high and the low lines of dams and their daughters.
TABLE XVIAVERAGE MILK PRODUCTION OF HIGH AND LOW LINEDAMSANDTHEIRDAUGHTERSFORTHEHERD

Herd averag (Pounds)	e	Number*	Average Production of dams (Pounds)	Number	Average Production of Daughters (Pounds)
14566	High	Line 49	16832	49	15072
	Low	Line 42	11921	42	14172
Difference			4811		900

(Total number of dams and daughters 182)

Calculation of Regression, (b):

 $b_{\rm PO} = \frac{900}{4811} = 0.187$ 

Heritability =  $b \ge 2 = 0.187 \ge 2 = 0.374$ 

Thus, the heritability estimate of milk production by regression of daughter on dam method in the Holstein herd of the Michigan State College dairy herd, was found to be 0.374.

In the case of the other four breeds -- Jerseys, Ayrshires, Guernseys, and Brown Swiss -- the procedure was exactly the same, only the tables are shown here. a

<sup>\*</sup> Division of the herd into high line and low line is generally such that the number of animals in both lines are about equal. As the division in the present study for all breeds was made on the basis of herd averages, there is slight difference in the number of animals in each line.

TABLE XVIIAVERAGE MILK PRODUCTION OF HIGH AND LOW LINEDAMS AND THEIR DAUGHTERS FOR THE JERSEY HERD<br/>(Total number of dams and daughters 120)

Herd Averag (Pounds)	: <b>e</b> _	Number	Average Production of Dams (Pounds)	Number 1	Average Production of Daughters (Pounds)
8323	High Line	33	9465	33	7886
	Low Line	27	6927	27	736 <b>5</b>
Difference			2538		521

TABLE XVIIIAVERAGE MILK PRODUCTION OF HIGH AND LOW LINE<br/>DAMS AND THEIR DAUGHTERS FOR THE AYRSHIRE HERD<br/>(Total number of dams and daughters 76)

Herd Averag (Pounds)	e	Number	Average Production of Dams (Pounds)	Number	Average Production of Daughters (Pounds)
10427	High Line	17	12344	17	9966
	Low Line	21	8875	21	9807
Difference			3469		159

TABLE XIX AVERAGE MILK PRODUCTION OF HIGH AND LOW LINE DAMS AND THEIR DAUGHTERS FOR THE GUERNSEY HERD (Total number of dams and daughters 96)

Herd Aver (Pounds)	ag <b>e</b>	Number	Average Production of Dams (Pounds)	Number	Average Production of Daughters (Pounds)
8726	High Line	22	9611	22	8370
	Low Line	26	7976	26	8913
Differenc	e		1635		-543

TABLE XXAVERAGE MILK PRODUCTION OF HIGH AND LOW LINE<br/>DAMS AND THEIR DAUGHTERS FOR THE BROWN SWISS<br/>HERD

(Total number of dams and daughters 68)

Herd Averag (Pounds)	e		Number	Average Production of Dams (Pounds)	Number	Average Production of Daughters (Pounds)
13272	High	Line	15	15479	15	13030
	Low	Line	19	11528	19	13191
Difference				3951		-161

From these tables, the regression coefficients for each breed and the corresponding heritability estimates were calculated in exactly the same manner as that of Holstein herd. The various statistics for all the five breeds have been shown in the table XXI below:

TABLE XXITHE REGRESSION COEFFICIENTS AND THE HERITABILITY<br/>ESTIMATES BY THE REGRESSION OF DAUGHTERS ON DAMS<br/>METHOD FOR ALL FIVE BREEDS

Breed	Total of Daughters and Dams	Regression Coefficient (b)	Heritability (b x 2)
Holstein	182	0.187	0.374
Jerseys	120	0.205	0.410
Ayrshires	76	0.046	0.092
Guernseys	96	-0.332	-0.664
Brown Swiss	68	-0.041	-0.082
Total	542		

92

i

To obtain one regression coefficient for the whole Michigan State College herd, the differences of the daughters and the differences of their dams for all the five breeds were added. The ratio of these two statistics was equal to the coefficient of regression, which when multiplied by 2 gave the heritability estimate for the whole herd:

> The total differences in the means of the daughters from all five breeds 876 pounds The total differences in the means of the dams from all the five breeds 16494 pounds The coefficient of regression  $(b_{OP}) = 876/16404 =$ 0.053. The heritability estimate for all the five breeds = b x 2 = 0.53 x 2 = 0.106 or 0.11.

Thus the heritability estimate for milk production for the Michigan State College dairy herd by the Regression of Daughters on Dams Method, which is an average of all breeds is equal to 0.11 or 11 per cent.

Since estimates of heritability in the present study were based on all the records of the dams put together instead of being based only on the later records of the dams and the average performance of the later daughters, it is probable that a small fraction of the epistatic variance might be included in the estimate. But, as a very small fraction of the total variance could be shown to be due to epistasis, if any, no attempt was therefore made to separate it. Further, in view of the comparatively smaller size of samples in the present study it was considered unimportant to subdivide the dams' records into first and later records

The results of several other investigators in heritability estimates by this method, notably among them are Gifford (1930), Edwards (1932), Copeland (1932) and Lush (1941) have been reviewed in an earlier section.

A short discussion bearing on the differences between the heritability estimates by the present method and the earlier methods seems to be appropriate and important at this stage. The weighted average of heritability by the earlier methods was -0.01 for milk yield. As already pointed out that any heritability estimate should be in the range of 0 to 100 per cent, though it is not likely to have the extreme values of 0 or 100. But a negative heritability for a characteristic, which is both hereditary and environmental is impossible and meaningless. However, the occurrence of such negative estimates should not be looked on with any disfavour. On the other hand they point out certain drawbacks in data in genetical problems, which should be eliminated by reducing residual errors, by removing environmental influence and by use of fewer correction factors for a trait on an objective basis. One best way to achieve this

objective would be to increase the size of the samples by many times over the original sample from which a negative result was obtained.

The negative heritability estimates by regression of daughter on dam method in the case of Guernsev and Brown Swiss herds, might be due to peculiarities in selection of breeding stock and other management practices. such as: 1) Disposal of potentially good producing calves and heifers before they come into full production. Thus by Mendelian segregation it might be possible that poor producers though born to high producing parents are left behind while the good producers might be removed unknowingly from the herd. 2) Use of good bulls on poor producers and vice versa. This would result perhaps in offspring which migh show regression far beyond the herd average. Besides, as pointed out by Lush (1941) a bull with a false index might be responsible for giving a false regression far beyond the herd average. A falsely high bull index could be obtained by using dams with single records which are low and compare them with the records of the daughters subsequent to their freshening. 3) Culling dairy stock, particularly the females on the basis of type. Type and production in dairy cattle show, if any, very poor correlation, which according to Lush (1945) varies anywhere between -0.07 to +0.19 and any culling based on type, therefore, would eliminate some potentially good producers and retain in the herd some cows with good conformation but poor in production and vice versa.

Lush (1941) further reported that by selecting dams which have breeding values above the average of population from which they were selected but lower than the average of the records for which they were selected, would bias and also most severely affect the differences between daughters and dams. Formula for determining breeding values are discussed in a later section.

Finally, since milk yield is subjected to larger variations than butterfat or percentage of butterfat, it could be offered as one of the explanations to the peculiarities in the above estimates.

**A** schematic representation of the Regression of Daughters on Dams Method from Lush (1940, 1941) as an example is shown in Figure 5 below:

INTRA-SIRE REGRESSION OF OFFSPRING ON DAM METHOD

(After Lush 1940 and 1941)



- X = 102
- Y = 44
- Z 14
- W = 28

REPEATABILITY AND

HERITABILITY IN FAT PRODUCTION (Based on pounds of BF)

Figure 5. Intra-sire regression from first record (X) of mates to the later records of the same cows (Y) and to the records of their daughters (Z).

Y/X = Repeatability of differences in single records = 44/102 • 0.43

 $\begin{array}{c} \underbrace{ \begin{array}{c} \mathbb{W} \\ \mathbb{X} \end{array}} & \text{ or } \underbrace{ 2 \ \mathbb{X} \ \mathbb{Z} } = \\ & \underbrace{ \begin{array}{c} ( \text{additive plus a little} \\ \text{of the epistasic} \end{array}) \\ \underbrace{ 2 \ \mathbb{X} \ \mathbb{Z} } \\ \underbrace{ 2 \ \mathbb{X} \ \mathbb{Z} } = \\ & \underbrace{ \begin{array}{c} ( \text{additive plus a little} \\ \text{of the epistasic} \end{array}) \\ \underbrace{ 2 \ \mathbb{X} \ \mathbb{Z} } \\ \underbrace{ 2 \ \mathbb{X} \ \mathbb{Z} } \\ \underbrace{ \begin{array}{c} \mathbb{Z} \ \mathbb{X} \ \mathbb{Z} \\ \text{of the epistasic} \end{array}) \\ \underbrace{ \begin{array}{c} \mathbb{Z} \ \mathbb{X} \ \mathbb{Z} \\ \mathbb{Z} \end{array}} \\ \underbrace{ \begin{array}{c} \mathbb{Z} \ \mathbb{X} \ \mathbb{Z} \\ \mathbb{Z} \end{array}} \\ \underbrace{ \begin{array}{c} \mathbb{Z} \ \mathbb{X} \ \mathbb{Z} \\ \mathbb{Z} \end{array}} \\ \underbrace{ \begin{array}{c} \mathbb{Z} \ \mathbb{X} \ \mathbb{Z} \\ \mathbb{Z} \end{array}} \\ \underbrace{ \begin{array}{c} \mathbb{Z} \ \mathbb{X} \ \mathbb{Z} \\ \mathbb{Z} \end{array}} \\ \underbrace{ \begin{array}{c} \mathbb{Z} \ \mathbb{X} \ \mathbb{Z} \\ \mathbb{Z} \end{array}} \\ \underbrace{ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \end{array}} \\ \underbrace{ \begin{array}{c} \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \end{array}} \\ \underbrace{ \begin{array}{c} \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \end{array}} \\ \underbrace{ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \end{array}} \\ \underbrace{ \begin{array}{c} \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \end{array}} \\ \underbrace{ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \end{array}} \\ \underbrace{ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \ \mathbb{Z} \end{array}} \\ \underbrace{ \mathbb{Z} \ \mathbb{Z} \end{array}} \\ \underbrace{ \mathbb{Z} \ \mathbb{$ 

and later lactations of the same cow.

# HOLSTEIN HERD

TABLE 22: ANALYSIS OF COVARIANCE OF MILK PRODUCTION OF DAMS AND THEIR DAUGHTERS FOR HOLSTEIN HERD ON INTRA-SIRE BASIS

Source of Variation	Degrees of Freedom	Sums of Squares and Products			
		Sx <sup>2</sup>	Sxy	Sy <sup>2</sup>	
Total	90	8582186	1101979	10417624	
Between Sires	20	3322784	1810191	2565389	
Within Sires (or ERROR)	70	5259402	-708212	7852235	

TABLE 23: ANALYSIS OF VARIANCE OF MILK PRODUCTION OF DAMS(X) IN HOLSTEIN HERD

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Square	F-value
Total	90	8582186		
Between Sires	20	3322784	166139	2.2*
Within Sires (or ERROR)	70	5259402	75134	
F-test sign:	ificant at 59	6 level.		

# TABLE 24: ANALYSIS OF VARIANCE OF MILK PRODUCTION OF<br/>DAUGHTERS (Y) IN HOLSTEIN HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	90	10417624		
Between Sires	20	<b>2565</b> 389	128270	1.4
Within Sires (or ERROR)	70	7852235	112175	

#### JERSEY HERD

TABLE 25: ANALYSIS OF COVARIANCE OF MILK PRODUCTION OF DAMS AND THEIR DAUGHTERS FOR JERSEY HERD ON INTRA-SIRE BASIS

Source of Variation	Degrees of Freedom	Sums of Sx <sup>2</sup>	f Squares Sxy	and Products Sy2
Total	59	1283807	323997	1608158
Between Sires	19	722195	252300	785738
Within Sires (or ERROR)	40	561612	71697	822420

TABLE 26: ANALYSIS OF VARIANCE OF MILK PRODUCTION OF DAMS(X) IN JERSEY HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean S	quare F-value
Total	59	1283807		
Between Sires	19	722195	38010	2.71**
Within Sires (or ERROR)	40	561612	14040	
** Highly sign	nificant at 19	6 level.		

TABLE 27: ANALYSIS OF VARIANCE OF MILK PRODUCTION OF<br/>DAUGHTERS (Y) IN JERSEY HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	59	1608158		
Between Sires	19	785738	413546	2.01*
Within Sires (or ERROR)	40	822420	205605	
* Significant	at 5% level.			

#### GUERNSEY HERD

TABLE XXVIIIANALYSIS OF COVARIANCE OF MILK PRODUCTION<br/>OF DAMS AND THEIR DAUGHTERS FOR GUERNSEY<br/>HERD ON INTRA-SIRE BASIS

Source of	Degrees of	Sums of Squares and Products		
Variation	rreedom	Sx <sup>2</sup>	Sxy	Sy <sup>2</sup>
Total	47	539092	-63063	663336
Between Sires	15	84214	-40021	1 <b>9</b> 2990
Within Sires (or ERROR	32	454878	-23042	470346

TABLE XXIXANALYSIS OF VARIANCE OF MILK PRODUCTION OF<br/>DAMS (X) IN GUERNSEY HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squa <b>re</b>	F-value
Total	47	539092		
B <b>etwee</b> n Sires	15	84214	56143	Not sig.
Within Sires (or ERROR)	32	454878	142149	

F-value not significant.

# TABLE XXXANALYSIS OF VARIANCE OF MILK PRODUCTION OF<br/>DAUGHTERS (Y) IN GUERNSEY HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	47	663336		
Between Sires Within Sires (or ERROR)	15 32	192990 470346	128660 146983	

F-value not significant

# BROWN SWISS HERD

TABLE XXXIANALYSIS OF COVARIANCE OF MILK PRODUCTION OF<br/>DAMS AND THEIR DAUGHTERS FOR BROWN SWISS<br/>HERD ON INTRA-SIRE BASIS

Source of	Degrees of	Sums of Squares and Products		
	rreedom	Sx <sup>2</sup>	Sxy	Sy <sup>2</sup>
Total	33	1818202	-135765	1037460
Between Sires	s 6	360676	21250	102446
Within Sires	27	1457526	-157015	935014

TABLE XXXIIANALYSIS OF VARIANCE OF MILK PRODUCTION OF<br/>DAMS (X) IN BROWN SWISS HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Sq <b>uare</b>	F <b>-v</b> alue
Total	33	1818202		
Between Sire	<b>s</b> 6	360676	60113	
Within Sires (Or ERROR)	27	1457526	53982	

TABLE XXXIIIANALYSIS OF VARIANCE OF MILK PRODUCTION OF<br/>DAUGHTERS (Y) IN BROWN SWISS HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F <b>-v</b> alue
Total	33	1037460		
Between Sire	<b>8</b> 6	102446	17074	
Within Sires (Or ERROR)	27	935014	34630	

#### CALCULATION OF HERITABILITY OF BUTTERFAT PRODUCTION

In America and in European countries, where butterfat testing among the dairy herds has been generally practiced, an effective way of expressing an animal's productive capacity and transmitting ability is based on the amount of butterfat produced by it.

Gowen (1924) showed that after the age of maximum productivity, the milk yield of a cow declines at an ever increasing rate as age increases, whereas the amount of butterfat is relatively less affected by its age. The correlation coefficient for mean milk production with age was shown to be  $+0.4332 \pm 0.0108$ , while in the case of butterfat it was +0.376. Copeland (1927) analysing 365-day Jersey records has shown the correlation between butterfat and butterfat test to be  $+0.23 \pm 0.03$ .

These results indicate that butterfat shows less relationship to age than milk. Besides, milk yield is more subject to environmental conditions, such as temperature, management conditions etc., than the production of butterfat. Hence, it provides a better source of information as to the merit of a dairy cow than milk production.

As was in the case of milk, the methods used in estimating the heritability of butterfat production are:

1. Intra-sire correlation coefficient method.

2. Intra-sire regression coefficient method

3. Intra-class paternal half-sib correlation method.

Methods 1 and 2 are based on the intra-sire analysis of covariance, while the 3rd. method is on the analysis of variance of intra-sire paternal half-sibs.

As a primary step in the use of these methods, the butterfat production records of each cow were corrected and the life-time averages were obtained. Age, length of lactation - 305 days and the times of milking per day, were the three main sources of environmental variations for which all of the daughter-dam records were adjusted. Correction factors of Kendrick (1941) were used separately for each breed.

For purposes of analysis, the dams and daughters were grouped on an intra-sire basis for each breed, the former being the independent variable, X, and the latter being the dependent variable, Y, in a given population.

The Guernsey breed was chosen for showing the detailed description of the calculation. Table XXXIV summarizes the preliminary statistics; the sums, sums of squares, and products of these two variables. The methods used in the analysis of these data, were those outlined by Snedecor (1946).

Sire	Number of Pairs of Dam Daughters	Sum o X	ofSum of Squares X	Sum of Y	Sum of Squares Y	Sum of Products of X and Y
I	5	1874	722796	2366	1126308	886660
II	1	336	112896	392	153664	131712
IIII	4	1794	814508	1599	667209	707025
IV	5	21 <b>71</b>	971367	2291	1057681	1004050
v	4	1644	708738	1632	673874	672838
. VI	3	1436	689706	1238	523050	597647
VII	1	<b>5</b> 06	256036	416	173056	210496
VIII	2	680	231200	1003	503029	341020
IX	1	340	115600	443	19624 <b>9</b>	150620
X	1	516	266256	389	151321	200724
XI	6	2533	1081575	2324	902888	978480
XII	4	1657	696567	1695	744941	714337
XIII	7	3096	1393010	2599	<b>9</b> 80 <b>565</b>	1145685
XIV	1	470	220900	475	225625	223250
XV	1	340	115600	458	209764	155720
IVI	2	800	<b>32</b> 0882	859	368941	343621
Total	48	20213	8717637	20179	8658165	8463885

.TABLE XXXIV PRELIMINARY DATA FOR THE STATISTICS OF BUTTERFAT PRODUCTION OF GUERNSEY HERD

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#### CALCULATION PROCEDURE FROM TABLE XXXIV:

The procedure for obtaining analysis of covariance and variance on an intra-sire basis was exactly similar to those followed for the Ayrshire herd in the previous section while estimating the heritability of milk production.

A. Correction Term:

For 
$$X = (SX)^2/N = (20213)^2/48 = 8511779$$
  
For  $Y = (SY)^2/N = (20179)^2/48 = 8483168$   
For  $XY_{=}(SX)(SY)/N = (20213) (20179)/48 = 8497461$ 

B. Total Sum of Squares:

For 
$$X = SX^2 - C.T_x = 8717637 - 8511779 = 205858$$
  
For  $Y = SY^2 - C.T_y = 9268165 - 8483168 = 174997$   
For  $XY = SXY - C.T_{xy} = 8463885 - 8497461 = -33576$ 

C. Between Sires Sum of Squares:  
For X = 
$$S(SX)^2/N - C.T_x = (1874)^2/5^+ \dots + (800)^2/2 - C.T_x = 59947$$
  
For Y =  $S(SY)^2/N - C.T_y = (2366)^2/5^+ \dots + (859)^2/2 - C.T_y = 67110$   
For XY\_=  $S(SX) (SY)/N - C.T_{xy} = (1874) (2366)/5^+ \dots + (800)^* (859)/2 - C.T_{xy} = 37364$ 

These data were summarized in the analysis covariance Table XXXV, and the values within sire line (Error line) were used for further calculation of correlation and regression coefficients.

#### GUERNSEY HERD

TABLE XXXVANALYSIS OF COVARIANCE OF BUTTERFAT PRODUCTION<br/>OF DAMS AND DAUGHTERS FOR GUERNSEY HERD ON<br/>INTRA-SIRE BASIS

Source of D	egrees of	Sum of S	Sum of Squares and Products		
Variation F	reedom	Sx <sup>2</sup>	Sxy	Sy2	
Total	47	205858	-33576	174997	
Between Sire	s 15	59947	-37364	67110	
Within Sires (or ERROR)	32	145911	3788	107887	

TABLE XXXVIANALYSIS OF VARIANCE OF BUTTERFAT PRODUCTIONOF DAMS (X) IN GUERNSEY HERD

Source of Dea Variation Fre	grees of eedom	Sum of Squares	Mean Square	F- <b>v</b> alue
Total	47	205858		
Between Sires	15	59947	3997	0.88
Within Sires (or ERROR)	32	145911	4560	

F-value not significant.

TABLE XXXVIIANALYSIS OF VARIANCE OF BUTTERFAT PRODUCTION<br/>OF DAUGHTERS (Y) IN GUERNSEY HERD

Source of D Variation F	egrees of reedom	Sum of Squares	Mean Squa	re F <b>-v</b> alue
Total	47	174997		
Between Sire	<b>s</b> 15	67110	4474	1.33
Within Sires (or ERROR)	32	107887	3372	

F-value not significant

The appropriate "F"-test to determine whether or not any significant variation in the yield of butterfat exists between the dams of the various sire groups, showed the "F"-value to be insignificant, indicating that the variance between the sires was nearly equal to the variance within the sires and that these two independent estimates of the variance of the population differ only by chance. Similarly, the "F"-test for the butterfat production of the daughters of various sire groups also gave the insignificant "F"-value.

#### A. INTRA-SIRE CORRELATION AND REGRESSION METHOD:

The calculation procedures for finding "r" and "b" and their respective standard errors come from analysis of covariance Table XXXV. The within sire value (error line) which gives the most probable estimate of the population parameters were used in the calculation.

These statistics++"r" and "b" can be arrived by two different methods, namely, 1) Breaking down the values in the within sire line to individual sire basis and calculating for each sires the "r" and "b" and then finally averaging these coefficients. Since this method was shown in detail while estimating the heritability of milk production of Ayrshire herd in the previous section,

it will not be repeated here. 2) Direct calculation of "r" and "b" from the error line, which corresponds to the average values for "r" and "b" in (1) above.

> Calculation of "r" and "b" and their standard errors by method (2):

- a) Correlation coefficient =  $r_{y \cdot x} = \frac{Sxy}{\sqrt{Sx^2 \cdot Sy^2}} = (daughters on dams) 3788/\sqrt{(145911) (107887)} = 0.030$
- b) Standard error of the correlation coefficient:  $S_{error} = 1 - r^2 / \sqrt{n-2} = 1 - (0.030)^2 / \sqrt{48-2} = 0.146$

Multiplying "r" by 2, the estimate of heritability for butterfat production was obtained, which is found to be equal to 0.030 x 2 = 0.060.

Standard error of heritability was also likewise obtained by multiplying the standard error by 2, which is found to be equal to  $0.146 \ge 0.292$ .

Thus, the heritability estimates of butterfat production in Guernsey herd of the Michigan State College by the intra-sire correlation coefficient method is 0.060 0.292.

c) Regression coefficient of  $b_{y,x} = Sxy/Sx^2$  .

3788/145911 - 0.026

d) Standard error of the regression coefficient:

S <sup>2</sup> erro	r <sup>=</sup> Standard error of estimate of the error term/n-2
	Sum of squares of "X" of the error term
	$\frac{-\frac{Sy^2 - (Sxy)^2 / Sx^2}{n-2}}{0R}$
	$Sx^{2} = Sy^{2} - b(Sxy) /n-2$
	Sx <sup>2</sup>
Serror	= 0.0161 = $\sqrt{0.0161}$ = 0.127

To get an estimate of heritability the regression coefficient was multiplied by 2, which is equal to  $2 \ge 0.026$ 0.052.

Likewise, the standard error of heritability was obtained by multiplying the standard error or regression by 2, which is equal to  $2 \ge 0.127 = 0.254$ .

Thus, the heritability estimate of butterfat production in Guernsey herd of the Michigan State College by intra-sire regression coefficient method is  $0.052 \pm 0.254$ .

#### B. HALF-SIB CORRELATION METHOD:

The procedure elaborated by Snedecor (1946) for intra-class correlation was utilized for determining heritability by the paternal half-sib method. The

tabulated data in Table XXXVII, Analysis of Variance of Butterfat production of Daughters (Y) were used in the calculation.

Substituting the following values in the intraclass correlation formula referred to on page the intra-class half-sib correlation turned out to be:

> $S^2$  within sire = 3372  $S^2$  between sires = 4474  $K_0 = 2.9$

 $S_{m}^{2} = (4474 - 3372) / 2.9 = 380$   $r_{I} = 380 / (380 + 3372) = 0.1013$ Standard error for intra-class correlation is:  $S_{I(error)} = (1-r_{I}^{2})\sqrt{n-2} = (1 - (0.101)^{2}\sqrt{48-2} = 0.146)$ 

The paternal half-sib correlation of 0.1013 was multiplied by 4 to obtain an estimate of heritability which is equal to 4 x 0.1013 = 0.405.

Similarly, the standard error of heritability was obtained by multiplying by the standard error of correlation which is  $4 \ge 0.146 = 0.584$ .

Hence, the heritability estimate of butterfat production of Guernsey herd of the Michigan State College by paternal half-sib method using the intra-class correlation is 0.405 ± 0.584.

Since the calculation procedures for an estimate

of heritability of butterfat production in the other four breeds, Holsteins, Jerseys, Ayrshires and Brown Swiss is exactly the same, only the pertinent tables and data are presented in the following pages.

Breed	Tables	Pages
Holsteins	XLI, XLII, XLIII	116
Jers <b>eys</b>	XLIV, XLV, XLVI	117
Ayrshires	XLVII, XLVIII, XIL	118
Brown Swiss	L, LI, LII	119

From these tables, the required statistics--the coefficients of correlation and regression, and the paternal half-sib intra-class correlation coefficient were calculated for each of the remaining four breeds and thus the resulting values for the whole herd were tabulated in Table XXXVIII. These coefficients were then multiplied by the respective factors to obtain heritability estimate for all five breeds and three methods, as shown in Table XXXIX.

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CORRELATIONS, REGRESSION AND STANDARD ERRORS OF THE ADJUSTED BUTTERFAT PRODUCTION OF COWS TABLE XXXVIII

Breed	No. of Sires	No. of Pairs of Daughter-	Paternal half- Sib Correlatio	Intra-S n Regress	Sire sion	Intra- Correl	Sire ation
			rI <sup>S</sup> I (err	or) b ł	0 0	ഗ് പ	و
Holsteins	21	16	0.1659 0.1030	0.0838	0.124	0.072	0.106
Jerseye	20	60	0.3183 0.1179	0.187	0.164	0.148	0.128
Guernseys	16	84	0.1013 0.1460	0.026	0.127	0.030	0*146
Ayrshires	tO	38	0.1364 0.16 <b>3</b> 6	0.105	0.144	0.121	0.164
Brown Swiss	7	34	0.4182 0.1459	-0.131	0.139	<b>-0.</b> 164	0.172
Total	72	271					

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The above correlations and regression were then multiplied by the appropriate factors, as indicated on page 84.

TABLE XXXIXESTIMATES OF HERITABILITY AND STANDARD ERRORSFOR THE ADJUSTED BUTTERFAT PRODUCTION OF COWS

Breed	Pat hal met	cernal Lf-sib Chod	Int: regi met)	ra-sire ression nod	Intr corr meth	ra <b>-sire</b> relation n <b>od</b>
	Herit- ability r <sub>I</sub> x A	Standard y error <sub>+</sub> S <sub>I</sub> x 4	Herit- ability 6 x 2	Standard error S <sub>c</sub> x 2	Herit- ability r x 2	Standard error S <sub>c</sub> x 2
Holsteins	0.664	0.412	0.168	0.247	0.143	0.211
Jerseys	1.273	0.472	0.374	0.327	0.297	0.257
Guernseys	0.405	0.584	0.052	0.254	0.060	0.292
Ayrshires	0.546	0.654	0.209	0.287	0.241	0.328
Brown Swiss	1.673	0.583	-0.262	0.278	-0.329	0.344

Just as in the case of milk production, the weighted average of heritability and that of the standard error of butterfat production for all five breeds and three different methods was obtained by use of the formula suggested by Hazel and Terrill (1945).

The desired statistics, such as the squares of the standard errors and their reciprocals required in the use of the above formulae were calculated and shown separately in Table XL. These values were then used along with the heritability estimates in the formulae and the weighted average was thus obtained for five breeds and three methods, which in turn were pooled and a final weighted average for the Michigan State College herd was presented.

TABLE XLSQUARED STANDARD ERRORS AND THEIR RECIPROCALSOF THE HERITABILITY OF BUTTERFAT PRODUCTION

Breed	Half- method	sib 1	Intra- regres method	-sire ssion l	Intra- correl method	sire ation	Recipro sum of methods	ca] 3
•	s <sup>2</sup> h1	1/S <sup>2</sup> h1	s <sup>2</sup> h <sub>2</sub>	1/S <sup>2</sup> h2	s <sup>3</sup> h <sub>3</sub>	1/S <sup>2</sup> 3	s(1/s <sup>2</sup> <sub>h</sub>	)
Ho <b>lsteins</b>	0.170	5.88	0.061		7 0.045	22.47	44.72	
Jerseys	0.223	4.49	0.107	9.34	0.066	15.15	5 28.98	
Guernseys	0.341	2.93	0.064	15.53	0.086	11.70	30.16	
Ayrshires	0.428	2.34	0.082	2 12.14	+ 0.108	9.27	23.75	
Brown Swiss	<b>0.3</b> 40	2.94	0.077	12.94	, 0.118	8.45	5 24.33	
Reciprocal Sum of 5 Breeds	:	18.58		66.32	2	67.01	, 151.94	-

Breed	Heritabilit	y Sta	andard error
Holsteins	0.212		0.149
J <b>er</b> sey <b>s</b>	0.473		0.186
Guernseys	0.090		0.182
Ayrshires	0.255		0.205
Brown Swiss	-0.052		0.203
TABLE XLII	WEIGHTED AVERAGE OF PRODUCTION)	F FIVE BREEDS	(BUTTERFAT
M <b>et</b> ho <b>d</b>	]	Heritability	Standard erro

TABLE XLI WEIGHTED AVERAGE OF THREE METHODS (BUTTERFAT PRODUCTION)

	neiiuduiiiuy	
Paternal half-sib correlation	0.846	0.081
Intra-sire regression	0.093	0.123
Intra-sire correlation	0.117	0.122
TABLE XLIII WEIGHTED AVERAGE BREEDS	OF THREE METH	ODS AND FIVE
Trait	Heritability	Standard error
Butterfat Production	0.20	0.081

Thus, the final estimate of heritability of butterfat production of the Michigan State College dairy herd, which is the weighted average of all the five breeds and three methods is  $0.20 \pm 0.081$ . İ

#### HOLSTEIN HERD

TABLE XLIV ANALYSIS OF COVARIANCE OF BUTTERFAT PRO-DUCTION OF DAMS AND THEIR DAUGHTERS FOR HOL-STEIN HERD ON INTRA-SIRE BASIS

Source of	Degrees of	Sums of Squares and Products				
	rreedom	Sx <sup>2</sup>	Sxy	Sy <sup>2</sup>		
Total	90	1112470	262644	1145677		
Between Sires	20	561534	216503	393243		
Within Sires (or ERROR)	70	550936	46141	752434		

TABLE XLVANALYSIS OF VARIANCE OF BUTTERFAT PRODUCTION OF<br/>DAMS (X) IN HOLSTEIN HERD

Source of Variation	Degrees	of	Freedom	Sum of Squares	Mean Square	F-value
Total	90			1112470		
Between Sires	20			561534	28077	3.57**
Within Sires (or ERROR)	70			550936	7871	

**\*\*** F-test highly significant at 1% level

TABLE XLVI ANALYSIS OF VARIANCE OF BUTTERFAT PRODUCTION OF DAUGHTERS (Y) IN HOLSTEIN HERD

Source of Variation	Degrees of	Freedom	Sum of Squares	Mean Squar	e F-value
Total	90		1145677		
Between Sire	<b>s 2</b> 0		393243	19662	1.83*
Within Sires (or ERROR) 6666	70		752434	10749	

\* F-test significant at 5% level

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#### JERSEY HERD

TABLE XLVIIANALYSIS OF COVARIANCE OF BUTTERFAT PRO-<br/>DUCTION OF DAMS AND THEIR DAUGHTERS FOR<br/>JERSEY HERD ON INTRA-SIRE BASIS

Source of	Degrees of	Sums of Squares and Products			
	-	Sx <sup>2</sup>	Sxy	Sy <sup>2</sup>	
Total	59	269496	86679	373 817	
Between Sire	s 19	157827	65828	196973	
Within Sires (or ERROR)	<b>4</b> 0	111669	20851	176844	

TABLE XLVIIIANALYSIS OF VARIANCE OF BUTTERFAT PRODUCTION<br/>OF DAMS (X) IN JERSEY HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Sq <b>uares</b>	F-value
Total	59	269496		
Between Sire	es 19	157827	8307	2.98**
Within Sires (or ERROR)	<b>3</b> 40	111669	2791	

\*\* F-test highly significant at 1% level TABLE XIL ANALYSIS OF VARIANCE OF BUTTERFAT PRODUCTION OF DAUGHTERS (Y) IN JERSEY HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	59	373817		
Between Sire	<b>s</b> 19	196973	10367	2.34*
Within Sires (or ERROR)	<b>4</b> 0	176844	4421	

\* F-test significant at 5% level.

# AYRSHIRE HERD

TABLE LANALYSIS OF COVARIANCE OF BUTTERFAT PRODUCTION<br/>OF DAMS AND THEIR DAUGHTERS FOR AYRSHIRE HERD<br/>ON INTRA-SIRE BASIS

Source of	Degrees of	Sums of	Sums of Squares and Products				
Variation	Freedom	Sx <sup>2</sup>	Sxy	Sy <sup>2</sup>			
Total	37	273154	50338	151100			
Between Sir	•e <b>s</b> 7	130001	35360	43395			
Within Sire (or ERROR)	e <b>s</b> 30	143153	14978	107705			

TABLE LIANALYSIS OF VARIANCE OF BUTTERFAT PRODUCTION<br/>OF DAMS (X) IN AYRSHIRE HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F <b>-v</b> alue
Total	37	273154		
Between Sire	e <b>s</b> 7	130001	18572	3.89**
Within Sires (or ERROR)	<b>3</b> 0	143153	47 <b>7</b> 2	

\*\* F-test was highly significant at 1% level.

TABLE LIIANALYSIS OF VARIANCE OF BUTTERFAT PRODUCTIONOF DAUGHTERS (Y)INAYRSHIREHERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	37	151100		
Between Sire	8 7	43395	6199	1.73
Within Sires (or ERROR)	30	107705	3590	

F-test was found to be not significant.

# BROWN SWISS HERD

TABLE LIIIANALYSIS OF COVARIANCE OF BUTTERFAT PRO-<br/>DUCTION OF DAMS AND THEIR DAUGHTERS FOR<br/>BROWN SWISS HERD ON INTRA-SIRE BASIS

Source of Variation	D <b>egr</b> ees of Freedom	Sums	of Squares	and Products
		Sx <sup>2</sup>	Sxy	Sy <sup>2</sup>
Total	33	298524	-31306	197778
Between Sires	6	70556	-1424	52836
Within Sires (or ERROR)	27	227968	-29882	144942

TABLE LIVANALYSIS OF VARIANCE OF BUTTERFAT PRODUCTION<br/>OF DAMS (X) IN BROWN SWISS HERD

Source of Variation	Degrees of Freedom	Sum <b>of</b> Squares	Mean Square	F-value
Total	33	298524		
Between Sires	6	70556	11759	1.39
Within Sires	27	227968	8443	
(or ERROR)				

F-test was found to be not significant TABLE LV ANALYSIS OF VARIANCE OF BUTTERFAT PRODUCTION OF DAUGHTERS (Y) IN BROWN SWISS HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	33	197778		
Between Sire	<b>s</b> 6	52836	8806	1.64
Within Sires (or ERROR)	27	14494	5368	

F-test was found to be not significant.

HERITABILITY OF BUTTERFAT PERCENTAGE

One could express the percentage butterfat in milk as merely the ratio of fat to milk from which the amount of butterfat that a cow yields is calculated. In other words butterfat can be expressed as the multiple of milk production and butterfat percentage. While considering the inheritance of milk and fat production it is nearly impossible to separate the two factors, since one who aims at increasing the yield of milk also increases the fat. But certain definite relationships do exist butween milk and fat percentage, between fat percentage and age of the cow, fat percentage and the effect of environment such as nutrition and the seasons, that it deserves to be studied from the point of heritability estimates as a definite and distinct characteristic of a dairy cow.

While it is generally agreed that the milk yield has a logarithmic curve in relation to age, Pearl (1914), Gowen (1920) and Turner (1927), it was shown by Gowen (1924) in a study of the associationship of age to percentage of fat of a large number of Holstein-Friesian cows, that a clearly linear relationship exists between the two. He found a correlation coefficient between butterfat and age to be one of negative;  $-0.075 \pm 0.0133$ , indicating that butterfat percentage has but a slight

relation to the age of the cow. During the whole life of a cow, from two years to fifteen years of age the difference in test was, on the average, 0.13 per cent. Eckles (1939), while working with Official Test records of all the five breeds and also the ordinary records of Jersey and Holstein cows made under ordinary conditions, also reached similar conclusions and pointed out that there is no variation in the butterfat percentage of any consequence due to age. A cow of a high-testing breed averaging 5 per cent of fat as a young aminal will decline to about 4.5 per cent if she continues to produce to 14 years of age, Figure (4).

The percentage of fat in milk is generally higher in colder months than in the hot months of the year.

During the lactation period the percentage of fat in milk varies inversely with the amount of milk secreted, although not in direct proportion. The decline in butterfat percentage usually occurs during the first month, although in some breeds it is in the second month of lactation. From the second and third month there is a gradual but consistent increase in the per cent fat. These increases, however, are not significant enough to justify the use of correction factors, Figure (4).

As regards the relationship between milk and the

percentage of fat several workers have reported that the relationship generally is one of negative correlation. Gaines (1927), while analysing the Holstein records reported an inverse correlation of -0.229 ±.012. At the same time work carried out on the continent by Bonnier (1927) with 79 cows of Swedish Ayrshire breed also showed a negative correlation between milk and the butterfat test. His correlation figures varied between 0.0169 and -0.8337. A similar analysis by Copeland (1927) of the Jerseys in the Jersey Consolidated Volume resulted in a negative correlation of -0.33 + 0.03. It was also shown by Gaines (1927) that the relationship between these two variable factors was not linear. However, it should be noted that although there exists a negative correlation between milk yield and the percentage of fat, the milk yields do not decrease in the same ratio as the fat percentage increases, otherwise there would be no justification for breeding of higher testing cows.

As to the nature of inheritance, Copeland (1927) further pointed out that the high testing sires and dams produce offspring which generally continue to test higher than the breed average, while the offspring from low testing sires and dams show performances below the herd average. These results could be explained on the basis of Galton's Law of equal inheritance from sire and

dam.

The methods used in estimating the heritability of butterfat test where similar to those used for milk and butterfat production, namely:

1. Intra-sire correlation coefficient method.

- 2. Intra-sire regression coefficient method.
- 3. Intraclass paternal half-sib correlation method.

In the method 1 and 2 the "r" and "b" were derived from the intra-sire analysis of covariance Tables, and in the method 3, the " $r_I$ " was obtained from the Tables of the analysis of variance of intra-sire paternal halfsibs in each breed.

While use of correction factors for adjusting the environmental differences in the case of milk and butter fat production were made for each lactation record, the percentages of butterfat performance of the daughters and dams were not corrected. The reason was that environmental factors, such as age, nutrition and managemental practices etc., have little or no significant effects on the test, which thus, do not justify the use of correction factors.

For calculation purposes the butterfat test of each record of daughter and dam were pooled together and a lifetime average was obtained.

The lifetime averages of butterfat test for dams
and daughters were classified for each breed on an intra-sire group basis for the purpose of carrying out the usual analysis of covariance and variance, as outlined by Snedecor (1946). The dams were treated as the independent variable, X, and the daughters as the dependent variable, Y, in a given population. The calculation procedures were very similar to those followed in the previous sections for milk and butterfat production. However, for completeness of presentation of the methods, the Brown Swiss breed was selected for calculation details.

Table LVI summarizes the preliminary statistics; the sums, sums of squares and products of these two variables.

TABLE LVIPRELIMINARY DATA FOR THE STATISTICS OF BUTTER-<br/>FAT TEST OF BROWN SWISS HERD

Sire	NumberPair of Dam- Daughters	s Sum of X	Sum of Squares of X	Sum of Y	Sum of Squares of Y	Sum of Products of X and Y
I	8	33.6	141.34	30.3	115.07	127.29
II	10	42.9	184.59	41.6	173.46	178.79
III	10	41.2	170.06	42.3	179.37	174.24
IV	1	4.4	19.36	3.8	14.44	16.73
V	1	3.7	13.69	4.2	17.64	15.54
VI	2	8.5	36.13	8.1	32.85	34.41
VII	2	7•4	27.38	8.1	32.31	29.97
Tota	1 34	141.7	592.55	138.4	565.64	576.97

# CALCULATION PROCEDURE FROM TABLE LIII

A. Correction Term:

- For  $X = (SX)^2/N = (141.7)^2/34 = 590.56$ For  $Y = (SY)^2/N = (138.4)^2/34 = 563.37$ For  $XY_{\pm}(SX)(SY)/N = (141.7) (138.4)/34 = 576.80$
- B. Total Sum of Squares: For X =  $SX^2 - C.T_x = 592.55 - 590.56 = 1.99$ For Y =  $SY^2 - C.T_y = 565.64 - 563.37 = 2.27$ For XY=  $SXY - C.T_{xy} = 576.96 - 576.80 = 0.16$
- <u>C. Between Sires Sum of Squares</u>: For  $X = S(SX)^2/N - C \cdot T_x = (33.6)^2/8 + (42.9)^2/10 + \dots + (7.4)^2/2 - C \cdot T_x = 591.46 - C \cdot T_x$  = 0.90For  $Y = S(SY)^2/N - C \cdot T_y = (30.3)^2/8 + (41.6)^2/10 + \dots + (8.1)^2/2 - C \cdot T_y = 564.45 - C \cdot T_y$  = 1.08For  $XY = S(SX) (SY)/N - C \cdot T_{xy} = (33.6) (30.3)/8 + \dots + (7.4) (8.1)/2 - C \cdot T_{xy} = 576,66$  $- C \cdot T_{xy} = -0.14$

These data are set forth in the Table LIV, of analysis of covariance and by using the within sire line values the desired statistics, namely, correlation and regression coefficients, were calculated. Further, these data were grouped and tabulated separately in Tables LV and LVI or analysis of variance to test for the significance of the "F"-value.

TABLE LVII ANALYSIS OF COVARIANCE OF PERCENTAGE OF BUTTERFAT PRODUCTION OF DAMS AND DAUGHTERS FOR BROWN SWISS HERD ON INTRA-SIRE BASIS

Source of	Degrees of	Sum of Squares and Products				
Variation	rreedom	Sx <sup>2</sup>	Sxy	Sy <sup>2</sup>		
Total	33	1.99	0.16	2.27		
Between Sire	es 6	0.90	-0.14	1.08		
Within Sires (or ERROR)	s 27	1.09	0.30	1.19		

TABLE LVIII ANALYSIS OF VARIANCE OF PERCENTAGE OF BUTTER-FAT PRODUCTION OF DAMS (X) IN BROWN SWISS HERD

Source of D Variation F	egree <b>v</b> of reedom	Sum of Sq	uares Mean Squa	re Fevalue
Total	33	1.99		
Between Sires	6	0.90	0.150	3.75**
Within Sires (or ERROR)	27	1.09	0.040	

\*\*F-value highly significant at 1% level.

TABLE LIX ANALYSIS OF VARIANCE OF PERCENTAGE OF BUTTER-FAT PRODUCTION OF DAUGHTERS (Y) IN BROWN SWISS HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	33	2.27		
Between Sire	<b>s</b> 6	1.08	0.188	4.09**
Within Sires (or ERROR)	27	1.19	0.044	

\*\* F-value highly significant at 1% level.

The "F" tests in both dams and daughters showed a high degree of significance at 1% level, which could be interpreted as indicating that the variance between the sire groups i.e. systemic or group variance, was significantly different from one another in respect of percentage of butterfat production. In a study involving genetic relationship one must remove this group variance as it would constitute one of the sources of errors.

# A. INTRA-SIRE CORRELATION AND REGRESSION METHOD:

The within sires values in the analysis of covariance Table XXXV, which is the best estimate of the population parameters, were used to calculate the "b" and "r". In order to avoid repetition, direct calculation of "b" and "r" from individual sires by breaking down the values in the error line, the average of which gives identical results, was not employed.

- a) Correlation coefficient=  $r_{y.x} = \frac{Sxy}{\sqrt{Sx^2}} \sqrt{\frac{Sy^2}{Sy^2}} = 0.30/\sqrt{1.09}\sqrt{1.19} = 0.2636$
- b) Standard error of the correlation coefficient:  $S_{error} = (1-r^2) \sqrt{n-2} = 1-(0.264)^2/\sqrt{34-2} = 0.1645$

Multiplying the correlation coefficient by 2, the estimate of heritability for the percentage of butterfat production was obtained, which is found to be equal to,  $0.264 \ge 2 \ge 0.5272$ .

Likewise, the standard error of heritability was obtained by multiplying the standard error by 2, which is equal to,  $0.1645 \ge 0.329$ .

Thus, the heritability estimate of the percentage ofbutterfat production of the Brown Swiss herd of the Michigan State College by intra-sire correlation method is  $-0.527 \pm 0.329$ .

> c) Regression coefficient of =  $b_{y.x} = \frac{S_{xy}/S_x^2}{aughters on dams}$ = 0.30/1.09 = 0.2752

d) Standard error of the regression coefficient:  $S^2_{error} = Standard error of estimate of the error term/n-2$ 

Sum of squares of "x" of the error term

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$$= \frac{Sy^{2} - (Sxy)^{2}/Sx^{2}}{\frac{n-2}{Sx^{2}}}$$
 OR  
$$= \frac{Sy^{2} - b(Sxy)/n-2}{Sx^{2}}$$

= .03175Serror=  $\sqrt{.03175}$  = 0.178

The regression coefficient and the standard error were multiplied by 2 to get an estimate of heritability and its standard error, which are equal to,  $0.2752 \times 2$ = 0.5504 and 0.5640 x 2 = 1.1280, respectively.

Thus, another estimate of heritability of the percentage of butterfat production in Brown Swiss herd of the Michigan State College, by intra-sire regression coefficient method is 0.5504+1.1280.

# B. HALF-SIB CORRELATION METHOD:

The intra-class correlation as the basis for this method was worked out from Table LIX in exactly similar manner as in milk and butterfat productions.

As the method was explained in detail in previous sections, only the direct calculations have been presented here.

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Formula for intra-class correlation coefficient:

$$\mathbf{r}_{I} = \frac{s_{m}^{2}/(s^{2}+s_{m}^{2})}{k_{o}}$$

$$K_{o} = \frac{1}{(n-1)} \cdot (\frac{s_{k}^{2}/s_{k}}{s_{m}}) = \frac{1}{(6-1)} \cdot (\frac{34}{(8^{2}+10$$

$$S^2$$
 between sires = 0.180  
 $S^2$  within sires = 0.044  
 $S_m^2 = (S^2$  between sires -  $S^2$  within sires)/4.3 = 0.03163  
 $r_1 = 0.03163/(0.03163 + 0.044) = 0.4182$ 

Standard error for intra-class correlation is:  

$$S_{I(error)} = (1 - r_{I}^{2})\sqrt{n-2} = (1 - 0.4182)^{2}/\sqrt{34-2}$$
  
 $= 0.1459$   
Heritability =  $r_{I} \ge 4 = 0.4182 \ge 4 = 1.6728$   
Standard error of heritability =  $S_{I(ERROR)} \ge 4 = 0.1459$   
 $\ge 4 - 0.5836$ 

Hence, the heritability estimate of percentage of butterfat production of Brown Swiss herd of the Michigan State College, by paternal half-sib method using the intraclass correlation is found to be 1.6728 <u>+</u> 0.5836.

For the remaining four breeds, Holsteins, Jerseys, Guernseys, and Ayrshires, tables have been presented separately in the following pages, which explain the procedural sequance in heritability estimates.

Breed	Tables	Pages
Holsteins	LXVII, LXVIII, LXIX	136
Jerseys	LXX, LXXI, LXXII	137
Guernseys	LXXIII, LXXIV, LXXV	138
Ayrshires	LXXVI, LXXVII, LXXVIII	139

TABLE LX CORRELATION, REGRESSION AND STANDARD ERRORS OF THE ADJUSTED PERCENTAGE OF BUTTERFAT PRODUCTION OF COWS

Breed	No. Sires	No. 5 Pairs D- Dams 1	Paternal half- Intra-Sire Intra-Sire Sib correlation Regression Correlation					e on
			r <sub>I</sub>	S <sub>I</sub> (error)	b	S, s	r S <sub>r</sub>	
Hols.	21	91	0.3808	0.0906	0.2625	0.193	7 0.2591	0.0989
Jers.	20	60	0.2575	0.1226	0.0638	0.167	2 0.0501	0.1307
Guern.	16	48	-0.0207	0.1475	0.2393	0.030	7 0.3414	0.0630
Ayrs.	8	38	0.4816	0.1445	0.2540	0.192	4 0.2153	0.1589
Br. Sw.	6	34	0.4182	0.1459	0.2752	0 <b>.1</b> 78	0 0.2636	0.1645
Total	72	271						

By multiplying the above correlation and regression coefficients by the appropriate factors, the desired heritability estimates were obtained and set forth in Table LXI.

TABLE LXI ESTIMATES OF HERITABILITY AND STANDARD ERRORS FOR THE ADJUSTED PERCENTAGE OF BUTTERFAT PRODUCTION OF COWS

Breed	Paternal half-sib method		Intra regre metho	-sire ssion d	Intra-sire correlation method		
	h <sub>l</sub> Herit- ability r <sub>I</sub> ¥ 4	Standard error S <sub>I</sub> x 4	h <sub>2</sub> Herit- ability b x 2	Standard error S <sub>e</sub> x 2	h3 Herit- ability r x 2	Standard error S <sub>e</sub> x 2	
Hols.	1.5232	0.3624	0.5250	0.2074	0.5182	0.1978	
Jers.	1.0292	0.4904	0.1276	0.3344	0.1002	0.2618	
Guern.	-0.0828	0.5900	0.4786	0.0614	0.6828	0.1260	
Ayrs.	1.9264	0.5780	0.5080	0.3848	0.4306	0.3178	
Br. Sw.	1.6728	0.5836	0.5504	0.3560	0.5272	0.3290	

These estimates were pooled together and a final weighted average of heritability and its standard error was calculated in the same manner as was done in the case of milk and butterfat productions.

The desired statistics, such as the squares of the standard errors and their reciprocals, which are an integral part in the application of the two formulae, were calculated and summarized in Table LXII.

TABLE LXII SQUARED STANDARD ERRORS AND THEIR RECIP-ROCALS OF THE HERITABILITY OF PERCENTAGE OF BUTTERFAT PRODUCTION

Breed	H <b>alf-sib</b> method		Intra- regrea metho	Intra-sire regression method		<b>sire</b> ation	Reciprocal sum of 3 methods	
	S <sup>2</sup> h1	1/S <sup>2</sup> h]	S <sup>2</sup> h <sub>2</sub>	1/S <sup>2</sup> n <sub>2</sub>	Sh3	1/S <sup>2</sup> h3	S(1S <sup>2</sup> <sub>h<sub>n</sub></sub> )	
Hols.	0.1313	7.62	0.0430	23.26	0.0391	25.57	56.45	
Jers.	0.2405	4.16	0.1118	8.94	0.0685	14.60	27.70	
Guern.	0.3481	2.87	<b>0.003</b> 8	253.17	0.0159	62.89	328.93	
Ayrs.	0.3341	2.99	0.1481	6.75	0.1010	9.90	19.64	
Br. Sw.	0.3406	2 <b>.9</b> 4	0.1267	7.80	0.1082	9.24	19.98	
Recipro sum of breeds	cal 5	20.58	0.1267	309.92	2	122.20	452.70	

# TABLE LXIIIWEIGHTED AVERAGE OF THREE METHODS (PERCENT-<br/>AGE OF BUTTERFAT PRODUCTION)

Breed	Heritability	Standard Error
Holsteins	0.657	0.133
Jerseys	0.248	0.190
Guernseys	0.512	0.055
Ayrshires	0.685	0.226
Brown Swiss	0.706	0.224

TABLE LIV	WEIGHTED	AVERAGE	OF	FIVE	BREEDS	(PERCENTAGE	OF
	BUTTERFAT	PRODUCT	rior	1)			

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Method	Heritability	Standard error		
Paternal half-sib correlation	n 1.27	0.220		
Intra-sire regression	0.474	0.057		
Intra-sire correlation	0.654	0.090		

TABLE LVWEIGHTED AVERAGE OF THREE METHODS AND FIVE<br/>BREEDS

Trait	Heritability	Standard error	
Percentage of butterfat production (Butterfat test)	0.56	0.047	

Thus, the final heritability estimate of the percentage of butterfat production (butterfat test), which is the weighted average of all five breeds and three methods, of the Michigan State College herd is,  $0.56 \pm 0.047$ .

TABLE LVIHERITABILITY ESTIMATES OF THE THREE MAIN<br/>ECONOMIC CHARACTERISTICS OF THE MICHIGAN<br/>STATE COLLEGE DAIRY HERD, WHICH CONSISTS OF<br/>THE FIVE MAIN BREEDS--HOLSTEINS, JERSEYS<br/>GUERNSEYS, AYRSHIRES, AND BROWN SWISS

Traits	Heritability	Standard error
Milk production	-0.01	80.0
Butterfat production	0.20	80.0
Percentage of butterfat production (butterfat test	0.56	0.05

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## HOLSTEIN HERD

TABLE LXVIIANALYSIS OF COVARIANCE OF PERCENTAGE OF<br/>BUTTERFAT PRODUCTION OF DAMS AND THEIR<br/>DAUGHTERS FOR HOLSTEIN BREED ON INTRA-<br/>SIRE BASIS

Source of	Degrees of	Sums of Squares and Product		
Variation	freedom	Sx <sup>2</sup>	£xy	Sy <sup>2</sup>
Total	90	9.16	2.73	11.60
Between Sire	e <b>s</b> 20	3.56	1.26	5.85
Within Sires (or ERROR)	в 70	5.60	1.47	5.75

TABLE LXVIIIANALYSIS OF VARIANCE OF PERCENTAGE OF<br/>BUTTERFAT PRODUCTION OF DAMS (X) IN HOL-<br/>STEIN HERD

Source of Variation	Degrees (	of F	reedom	Sum of Squares	Mean Squar <b>e</b>	F-value
Total	90			9.16		
Between Sires	20			3.56	0.168	2.1*
Within Sires (or ERROR)	70			5.60	80.08	

\*F-test significant at 5% level.

TABLE LXIXANALYSIS OF VARIANCE OF PERCENTAGE OF BUTTERFAT PRODUCTION OF DAUGHTERS (Y)IN HOLSTEINHERDHERD

Source of Variation	Degrees	of	Freedom	Sum of Squares	Mean Square	F- <b>v</b> alue
Total	90			11.60		
Between Sire	s 20			5.85	0.293	3.56**
Within Sires (or ERROR)	70			5.75	0.082	

\*\* F-test highly significant at 1% level.

#### JERSEY HERD

TABLE LXXANALYSIS OF COVARIANCE OF PERCENTAGE OF BUTTER-<br/>FAT PRODUCTION OF DAMS AND THEIR DAUGHTERS FOR<br/>JERSEY BREED ON INTRA-SIRE BASIS

Source of Variation	Degrees of Freedom	Sums of <sub>Sx</sub> 2	Squares and Sxy	d Products Sy <sup>2</sup>
Total	59	8.60	1.43	16.90
Between Sire	s 19	3.27	1.09	8.23
Within Sires (or ERROR)	40	5.33	0.34	8.67

**TABLE LXXI**ANALYSIS OF VARIANCE OF PERCENTAGE OF BUTTER-<br/>FAT PRODUCTION OF DAMS (X) IN JERSEY HERD

Source of 'I Variation I	Degrees of Freedom	Sum of Squares	Mean Sq <b>uare</b>	F <b>-v</b> alue
Total	59	8.60		
Between Sires	<b>s</b> 19	3.27	0.172	1.29
Within Sires (orERROR)	40	5.33	0.133	

F-test not significant.

TABLE LXXIIANALYSIS OF VARIANCE OF PERCENTAGE OF BUTTER-<br/>FAT PRODUCTION OF DAUGHTERS (Y) IN JERSEY HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Sq <b>uare</b>	F-value
TOTAL	59	16.90		
Between Sire	s 19	8.23	0.433	2.00*
Within Sires (or ERROR)	40	8.67	0.217	

\* F-test significant at 5% level.

# GUERNSEY HERD

TABLE LXXIIIANALYSIS OF COVARIANCE OF PERCENTAGE OF<br/>BUTTERFAT PRODUCTION OF DAMS AND THEIR<br/>DAUGHTERS FOR GUERNSEY BREED ON INTRA-<br/>SIRE BASIS

Source of	Degrees of	Sums of Squares and Products			
Variation F:	Freedom	Sx <sup>2</sup>	Sxy	Sy <sup>2</sup>	
Total	47	11.00	6.65	6.28	
Between Sire	s 15	2.14	4.50	1.92	
Within Sires (or ERROR)	32	8.86	2.12	4.36	

TABLE LXXIVANALYSIS OF VARIANCE OF PERCENTAGE OF BUTTER-<br/>FAT PRODUCTION OF DAMS (X) IN GUERNSEY HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	47	11.00		
Between Sir	res 15	2.14	0.143	0.52
Within Sire (or ERROR)	<b>s</b> 32	8.86	0.277	
F-test not TABLE LXXV	significant. ANALYSIS OF FAT PRODUCT: HERD	VARIANCE ( ION OF DAU(	OF PERCENTAGE HTERS (Y) IN	OF BUTTER- GUERNSEY
Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	47	6.28		
Between Sir	es 15	1.92	0.128	0.94
Within Sire (orERROR)	s 32	4.36	0.136	

F-test not significant.

#### AYRSHIRE HERD

TABLE LXXVIANALYSIS OF COVARIANCE OF PERCENTAGE OF<br/>BUTTERFAT PRODUCTION OF DAMS AND THEIR<br/>DAUGHTERS FOR AYRSHIRE BREED ON INTRA-<br/>SIRE BASIS

Source of	Degrees of	Sums of	Squares a	nd Products
Variation	Freedom	Sx <sup>2</sup>	Sxy	Sy2
Total	37	5.71	3.50	5.87
Between Sire	s 7	3.82	3.02	3.23
Within Sires (or ERROR)	30	1.89	0.48	2.64

TABLE LXXVIIANALYSIS OF VARIANCE OF PERCENTAGE OF<br/>BUTTERFAT PRODUCTION OF DAMS (X) IN<br/>AYRSHIRE HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	37	5.71		
Between Sir	e <b>s</b> 7	3.82	0.546	8.67**
Within Sire (or ERROR)	<b>s</b> 30	1.89	0.063	

\*\* F-test highly significant at 1% level.

TABLE LXXVIIIANALYSIS OF VARIANCE OF PERCENTAGE OF<br/>BUTTERFAT PRODUCTION OF DAUGHTERS (Y) IN<br/>AYRSHIRE HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	37	5.87		
Between Sire	<b>s</b> 7	3.23	0.464	5.27**
Within Sires (or ERROR)	20	2.64	0.088	

\*\* F-test highly significant at 1% level.

#### PART II

# REPEATABILITY OF PRODUCTION CHARACTERISTICS: MILK AND BUTTERFAT

1. INTRODUCTION:

A knowledge of repeatability of economic characteristics in modern animal breeding and selection techniques, has become a tool of considerable value:

l. To predict the probable future producing
ability or performance of an animal, such as, a) production
in cows, b) prolificacy in sows, c) fleece weight in sheep
and d) sire performance in beef cattle.

2. To obtain an estimate of the upper limit of heritability.

3. Where subjective estimates are made of characters, such as coat color, which change but little from year to year repeatability tests the accuracy of such estimates, Briquet and Lush (1947).

4. To estimate progress made per generation in selection on the basis of an average of "n" records.

5. To study repeatability of type ratings in dairy cows, Johnson and Lush (1942). While very little correlation exists between type and production in dairy cows, purebred associations do insist on excellent types and conformation as one of the means in the improvement of purebreds.

#### 2. WHAT IS REPEATABILITY:

Repeatability is the coefficient of correlation (r) between recurrent expressions of a characteristic by the same animal within its herd. Since all of the genetic variance is contributed to repeatability estimates, one could consider it as an expression of its genetic merit repeated from one lactation to the other in the same animal. This relationship that exists among the production records of the same cow has been popularly termed as "repeatability." As indicated by Lush (1945), it is, therefore, not a basic biological constant but a description of a given population.

#### 3. <u>REPEATABILITY AND ITS PLACE IN AIDS TO SELECTION:</u>

To the breeder, while the estimates of heritability of economic characteristics serve as a definite guide in planning a breeding program, not infrequently he is confronted with another problem. That is, the problem of culling and selection of individual animals, particularly the breeding females in order that he might ultimately increase the frequency of the "good" genes in his herd.

Depending on the genetic composition of a certain

characteristic to which the breeder looks forward in his selection, he could be aided by three different methods, namely, 1) phenotypic selection, 2) pedigree estimates, 3) progeny test. However, it would profit one to be aware of some of the inherent limitations in selection. First, as pointed out by Stewart (1945), that selection for one or several characters basically depends on not only the genetic variability of the population from which selections are made but also on the proportion of available animals that are required for breeding purposes, and that progress through selection is equal to that of the selection differential, that is due to heritable differences in the genotypes of females. Second, that though selection alters the type, it does not greatly reduce the variability in the population, Lush (1945).

Culling or selection among several cows on the average of the adjusted records for each cow would be generally misleading, since the cow with the least number of records will have the greatest error and would be far from providing a true picture of its merit. Whereas if one could obtain a measure which would express the correlation among the records of individual cows, then they could be easily reduced to a comparable basis. Where the repeatability of a characteristic, which is "r" is very high, that is, nearer to 1.0, the most probable future producing ability of the could be estimated from its first record alone just as well as from her any or all of the records. For characteristics where "r" is small the first record is not reliable and for reliability an average of several records, at least four, should be taken in order to reduce the environmental variations. In cases where a cow has not made any records, the herd average should be used for estimating the producing ability, because of the tendency of the cows to regress towards herd average.

The formula often employed for predicting the probable future producing ability of a cow is:

Y = Herd Average + <u>nr</u> x (Her average-Herd average) 1 - r+nr

where n = the number of records made, r = repeatability, which is the fraction of the total variance among the corrected records which is due to permanent differences between cows, and 1 - r is the fraction of the variance caused by temporary environmental conditions which vary from one record to another of the same cow. As shown by Lush et al (1941) that the fraction  $\frac{nr}{1-r}$  would test the real ability of the cow for "n" number of completed records in comparison to the average of the population. As "n" increases the percentage of the real ability of the cow also increases and where "n" is equal to 5 and "r" is equal to 0.4, the real ability would be equal to 77 per cent, of the cows actual average.

Again if one desires to estimate a cow's breeding value instead of the real producing ability, the "r" in the numerator must be replaced by the heritability fraction (h), which would be somewhat less.

The measure of repeatability could also be used for correlating for purposes of comparison a non-consecutive record with the average of the consecutive records or another non-consecutive record or vice versa. As for example one could correlate the first record with the average of the next four records. The formula generally used for such correlation and comparison is, Berry and Lush (1939):

$$R = r \sqrt{\frac{n}{1-r+nr}}$$

Although the phenotypic selection based on production records of an animal is the most effective method for selection for breeding purposes or for culling in a herd, it is sharply limited by conditions which vary from lactation to lactation for the same cow. An attempt has been made in the foregoing to present the methods to overcome these sources of error, i.e. the fraction of the total variance due to environmental conditions; 1) by use of larger number of "n" records, and 2) by obtaining an estimate of "repeatability" of the same cow.

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Therefore, a measure of repeatability has a definite and important place in phenotypic selection or culling. It is also inexpensive except what it costs to postpone culling until two or more observations are made, Lush (1945).

#### 4. RELATIONSHIP OF HERITABILITY TO REPEATABILITY:

1. Heritability is the study of a genotype in a given population, whereas the repeatability concerns with the study of a characteristic (phenotype), which is variable in a particular population and is expressed in an individual severally at different times during its life.

2. Heritability is the fraction of the total variance in a given trait which is due to the additive effects of genes, Hazel (1942), whereas, repeatability is the fraction of total variance among the corrected records of the same cow, which is due to permanent non-transmissable differences between the cows. The permanent differences include the differences due to dominance, epistasis, and also such effects of environment which are permanent, such as poor management of calves at birth which might result in stunted growth, etc. While these are not heritable, they differ from one animal to the other. 3. Since repeatability includes both the effects of permanent non-transmissable differences and genetic variance, the estimate could be used generally as an upper limit of heritability at least in the broad sense, Stewart (1945). It could be larger than heritability but it could hardly be less.

# 5. METHODS OF ANALYSIS OF DATA FOR REPEATABILITY:

The method employed in estimating repeatability is that of single way classification of analysis of variance, where k = the number of observations (records) corrected for temporary environmental conditions, and n = the number of cows.

Different methods are employed for estimate of repeatability. Lush (1940) has shown that repeatability can be determined by regression of daughter on dam, while Dickerson (1940) and Briquet (1947) have reported the use of analysis of variance method. Stewart (1945) has also recommended the use of partial correlation method for estimating repeatability.

In the present study the estimates of repeatability were obtained from analysis of variance by using the following formula:

The formula --

Repeatability = 
$$\frac{S^2 \text{ within cows}}{S^2 \text{ within cows}} + S^2 \text{ between cows}$$

In order to arrive at the above statistics for use in the formula, the mean square or the variance in the table of analysis of variance should be split into their respective component parts for the sub-samples. Table LXXIX shows the mean squares and their component parts that make up the total variance.

TABLE LXXIXBREAK UP OF MEAN SQUARES IN ANALYSIS OF<br/>VARIANCE TO THEIR COMPONENT PARTS

Source of Variation	Degrees of Freedom	Mean Square <b>s</b>	Components of Mean Squares	
Total	nk - 1	T		
Between Cows	n - 1	C	$S^2 + S^2$ between co	ws
Within Cows (or ERROR)	n(k - 1)	E	<sub>S</sub> 2	, -

Each record of a cow was corrected for three main environmental conditions: 1) age, 2) length of lactation period - 305 days, 3) times of milking per day -3X. Unlike the daughter-dam comparison on intra-sire basis in heritability estimates, all animals of a breed with more than one record were pooled together. Since the use of correction factors in repeatability estimates has been a subject of much controversy, it is not within the scope of the present study to go into the merit or demerit on this subject. It has been however, agreed by Sanders (1930) and later on by Dickerson (1940) that age-corrected 305-day records are most satisfactory for selection purposes, since they are easily available and easier to compute.

Table LXXX shows the number of cows in each breed, the average number of records per cow etc., as a preliminary step in the analysis of the data.

TABLE\_LXXXPRELIMINARY DATA SHOWING THE NUMBER OF COWS<br/>AND AVERAGE NUMBER OF RECORDS FOR EACH BREED

Breed	Number of <b>Rees</b>	Average number sof Records per Cow	Average Pounds of Milk per Cow	Average Pounds of Butterfat per Cow
Holstein	279	3.4	15,096	509
Jersey	186	3.6	8,229	432
Guernsey	155	4.3	9,415	455
Ayrshire	52	2.7	11,071	435
Brown Swiss	117	3.6	12,923	530

## A. CALCULATION OF REPEATABILITY OF MILK AND BUTTERFAT PRODUCTION

Repeatability estimates were made for two characteristics, namely, milk and butterfat separately for each breed. And in case of the percentage of butterfat--BF test-- since the variations from one record to the other in the same animal are generally so small, if any, the repeatability estimates were not calculated.

Since the methods for both milk and butterfat production are identical, only one of them was chosen for a detailed explanation of the procedures.

#### B. ESTIMATES OF REPEATABILITY OF BUTTERFAT PRODUCTION:

Separate estimates for each breed were made and the Holstein herd was selected for illustrating the method in detail. The statistics necessary for setting up an analysis of variance table were obtained as follows:

#### CALCULATION PROCEDURE:

I. Correction Term =  $(SX)^2/N = (142123)^2/279 = 72397660$ II. Total Sum of Squares =  $SX^2 - C.T. = 75702823 - C.T. = 3304163$ 

III. Between Cows Sum of Squares =  $S(SX)^2/N - C.T. =$ (3902)<sup>2</sup>/7 + (6122)<sup>2</sup>/10+...+(2560)<sup>2</sup>/N - C.T. = 74451354 - C.T. = 2053694

These data were set forth in Table LXXXI below and further statistics desired for calculating repeatability were obtained therefrom.

TABLE LXXXIANALYSIS OF VARIANCE OF BUTTERFAT PRO-<br/>DUCTION OF COWS OF HOLSTEIN HERD BASED ON<br/>THE NUMBER OF RECORDS

Source of Variation	Degrees of Freedom	Sum of Mean Components F-value Squares Square of Mean Square
Total	278	3304163
Between Cow	s 81	2053694 25354 S <sup>2</sup> +KS <sup>2</sup> between 3.99**
Within Cows (or ERROR)	197	1250467 6348 S <sup>2</sup> cows
** F-test h:	ighly signi:	ficant at 1% level.
$K_{o} = 1/1$	n-1 (Sk - SI	$k^2/Sk$ ) = 1/82-1(279 - 1191/279)
		= 1/81(279 - 4.27) = 3.4
S <sup>2</sup>	between con	ws = 23334 = 6348 = 19007
8	between con between con	ws = $19007/K$ = $19007/3.4$ = 5590
Substituting	g the value	s in the formula:
Rep <b>eat</b> al ( r	pility = $S^2$	/(S <sup>2</sup> +S <sup>2</sup> between cows)
	<b>=</b> 631	48/ (6348+5590) <u>=</u> 0.53
Standar	d error of 1	repeatability:
	1 - 1	$r^2/n-2 = 1-53^2/279-2 = 0.7191/16$
		0.43

Thus, the repeatability of the records of the butterfat production in Holstein herd of the Michigan State College was found to be equal to  $0.53 \pm 0.43$ .

Since the methods for estimating repeatability of butterfat production for the other four breeds, namely, Jerseys, Guernseys, Ayrshires, and Brown Swiss, were exactly similar, only the analysis of variance tables for each of these breeds have been given below.

TABLE LXXXIIANALYSIS OF VARIANCE OF BUTTERFAT PRODUCTION<br/>OF COWS OF JERSEY HERD BASED ON THE NUMBER<br/>OF RECORDS

Source of Variation	Degrees Freedom	of	Sum of Squares	Mean Square	Components of Mean Square	F-value
Total	185		1317174			
Between Cows	51		763913	14979	S <sup>2</sup> +K S <sup>2</sup> bet	3.63*
Within Cows (or ERROR)	134		553261	4129	s <sup>2</sup> cov	Ϋ́S

\* F-test highly significant at 1% level.

Source of Variation	Degrees Freedom	of	Sum of Squares	Mean Squar <b>e</b>	Components F-value of Mean Square
Total	154		879002		
Between Cows	35		422051	12059	S <sup>2</sup> +K S <sup>2</sup> bet. 3.14*
Within Cows (or ERROR)	119		456951	3840	S <sup>2</sup> Cows
TABLE LXXXIV	ANALYS OF COV OF REC	SIS VS ( CORI	OF VARIA OF AYRSHI DS	ANCE OF IRE HERI	BUTTERFAT PRODUCTI D BASED ON THE NUME
Source of Variation	Degrees Freedom	of	Sum of Squares	Mean Square	Components F-value of Mean Square
Total	51		574350		
Between Cows	18		431233	23957	S <sup>2</sup> +K S <sup>2</sup> <sub>bet</sub> 5.52*
Within Cows (or ERROR)	33		143117	4337	S <sup>2</sup> Cows
* F-test hig	hly sign	nif	icant at	1% leve	el.
TABLE LXXXV	ANALYSI OF COWS NUMBER	[S ( 5 0] OF	OF VARIAN F BROWN S RECORDS	NCE OF I SWISS HI	BUTTERFAT PRODUCTIC ERD BASED ON THE
Total	116		1182623		
Between Cows	31		77991 <b>9</b>	25159	S <sup>2</sup> +K S <sup>2</sup> bet. 5.31*

TABLE LXXXIII ANALYSIS OF VARIANCE OF BUTTERFAT PRO-

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\* F-test highly significant at 1% level.

In all the five breeds the F-test was found to be highly significant indicating that the permanent environmental differences and probably the genotypes between the cows were different and significant, and that values as large as or larger than the F-values would be expected to occur by chance alone less than one per cent of the time. These permanent environmental differences are not transmissable and may be due to dominance, epistasis, or management practices when the animals were young which resulted in permanent effect on them, for example, stunted growth, differences in nourishment while young, etc.

From these tables the desired statistic, such as the components of mean square-within cows and between cows variances were calculated for the remaining four breeds in exactly the same manner as that of Holstein breed. The final repeatability estimates of butterfat production in the different breeds of Michigan State College dairy herd have been summarized in the Table LXXXVI below.

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<sub>S</sub>2 S<sup>2</sup>between Breed Number Repeatability -Std. of Records  $S^2/(S^2+S^2_{bet. cows})$ COWS Error Hols. 6348 279 5590 0.53 0.43 Jers. 186 0.48 4129 0.59 3014 0.67 Guern. 155 3840 1911 0.44 0.37 0.12 Ayrs. 52 4337 7267 Br. Sw. 0.46 117 4738 5626 0.74 TOTAL 789 23392 23408

TABLE LXXXVI ESTIMATES OF REPEATABILITY OF BUTTERFAT PRODUCTION IN JERSEYS, GUERNSEYS, AYR-SHIRES, HOLSTEINS AND BROWN SWISS

In order to obtain one statistic as an estimate of all the five breeds, the respective calculated variances of each breed was combined by the following formula:

- a) Repeatability Estimate =  $\frac{\sum S}{\text{within cows}}$ (R) - All five breeds =  $\frac{\sum S}{\sum (S_{\text{within cows}+S^2 \text{ between cows})}}$ =  $\frac{23392}{46800}$  = 0.499 or 0.50
- b) Standard error for the combined repeatability =  $1 r^2 / \sqrt{n 2k}$  where n is equal to the total number of animals from all the five breeds and k is the total number of breeds included in estimating combined repeatability.

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$$= 1 - (0.50)^2 \sqrt{789 - 10}$$
$$= 0.750/27.9 = 0.269$$

Thus, the combined repeatability estimate for butterfat production in all the five breeds of the Michigan State College dairy herd was found to be  $0.50 \pm 0.269$ .

# E. CALCULATION OF REPEATABILITY OF MILK PRODUCTION:

Gowen (1924) has shown very high degree of positive correlation between milk yield and butterfat production, both by direct correlation and by partial correlation coefficient methods. By direct correlation he found that "r" was  $0.8927 \pm 0.0075$  and by partial correlation method where age was held constant the "r" was 0.363 $\pm 0.009$ . It does show, therefore, that environmental conditions including the permanent differences that affect the production of butterfat also influence the milk yield. Gaines (1936) while working with 10,307 365-day records of Jersey Registry of Merit also concluded that <u>size</u> and <u>age</u> have substantial influences on milk yield and butterfat production:

With regards to size Edwards (1936) in England, studying 2400 records accumulated over a period of 12 years between 1922 and 1934, has reported that hereditary environmental conditions being equal, larger cows produce
more milk than smaller cows.

Earlier work by Turner et al (1924), in their attempt to analyse the records of all the breeds, had also reached similar conclusions as regards size. It was pointed out by them with particular reference to Jersey cows that after the animal reaches 470 pounds of body weight, there is an increase of 20 pounds of fat for each 100 pounds of body weight with age held constant. The increase in body weight contributes about 20 per cent to the total increased fat yield with age, while the other 80 per cent increased fat yield with age is due to other factors accompanying increased maturity.

Swett et al (1937) in a comparative study of conformation, anatomy and udder characteristics between the beef and dairy breeds, i.e. the Herefords and Holsteins respectively, observed that specialized beef breeds, which have more compact body conformation do not inherit mammary development sufficient to become liberal milkers.

With regards to age in relation to milk production, Pearl and Patterson (1917) investigating the change in milk flow with age on 5821 seven-day records of Jersey cattle showed the correlation coefficient between age and milk production to be  $+ 0.1925 \pm .0085$ . In a study of the variations and correlations in milk secretion with age by Gowen (1920) on 1741, 8-month milk yield records of Jersey cows concluded that the correlation coefficient between age and milk yield to be +0.2596 + .0151.

Since several other factors influencing production have already been dealt with in detail in earlier sections, their repetition here has been avoided.

In spite of the high correlation that exists between milk yield and butterfat production, the main object of determining the repeatability of milk yield has been to provide a source of guidance to the breeder for culling or for selection in places where no system of butterfat testing is practiced and has to depend upon milk yields.

To save the repetition of the methods and procedures used in developing the repeatability of milk yield, which is identically the same as in butterfat, it was considered to be enough to present tables of analysis of variance separately for each breed in the following pages. These tables however, provide the basis for estimating repeatability of milk yield.

TABLE LXXXVII ANALYSIS OF VARIANCE OF MILK YIELD OF COWS OF HOLSTEIN HERD BASED ON THE NUMBER OF RECORDS

Source of Variation	Degrees of Freedom	of	Sum of Squares	Mean Square	Compo of N Squar	onents Mean re	F-value
Total	278		30298259				
Between Cows	81		19563824	241529	s <sup>2</sup> +k	S <sup>2</sup> bet.	4.43*
Within Cows (or ERROR)	197		10734435	54490	) s <sup>2</sup>	COV	VS
* F-test hig	hly sign:	ifi	icant at	1% leve	1.		

TABLE LXXXVIIIANALYSIS OF VARIANCE OF MILK YIELD OF<br/>COWS OF JERSEY HERD BASED ON THE NUMBER<br/>OF RECORDS

Source of Variation	Degrees Freedom	of Sum of Squares	Mean Squa <b>re</b>	Components of Mean Square	F-value
Total	185	5655630			
Between Cows	51	3639070	71354	S <sup>2</sup> +K S <sup>2</sup> bet.	4•74*
Within Cows (or ERROR)	134	2016560	15049	S <sup>2</sup> Cows	5
* F-test hig	hly sign	ificant at	1% lev	el.	
TABLE LXXXIX	ANALYS OF GUE RECORD	IS OF VARI RNSEY HERD S	ANCE OF BASED (	MILK <b>YI</b> ELD ON THE NUMBE	OF COWS Ir of
Source of Variation	Degrees Freedom	of Sum of Squares	Mean Square	Components of Mean Square	F-value
Total	154	3842221		· ·	
Between Cows	35	1949390	55697	$S^{2}+K$ $S^{2}_{bot}$	3.50 *

Within Cows 119 1892831 15906 S<sup>2</sup> Cows (or ERROR)

\* F-test highly significant at 1% level.

TABLE XC ANALYSIS OF VARIANCE OF MILK YIELD OF COWS OF AYRSHIRE HERD BASED ON THE NUMBER OF RECORDS

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Source of Dea Variation Fra	grees of eedom	Sum o <b>f</b> Squares	Mean Square	Components F of Mean Square	-value
Total	51	2770847	18 - 29 - 19 - 29 - 29 - 29 - 29 - 29 - 29		
Between Cows	18	2057170	114287	$S^{2}+K S^{2}_{bet}$	5.28*
Within Cows or ERROR	33	713677	21627	COWS	
F-test highly	y signif	icant at	1% leve	el.	
TABLE XCI AN O Ri	NALYSIS F BROWN ECORDS	OF VARIAN SWISS HEI	NCE OF M RD BASEI	AILK YIELD OF D ON THE NUME	F COWS Ber of
Source of Variation	Degrees Freedom	of Sum of Squar	of Mear res Squa	n Component are of Mean Square	s F-value
Total	116	61883	39		
Between Cows	31	387071	42 12486	$53 S^2 + K S^2_{bet}$	4.58*
Within Cows (or ERROR)	85	231759	9 <b>7 27</b> 26	56 S <sup>2</sup> Con	IS

\* F-test highly significant at 1% level.

NOTE: The milk yield of individual records in all five breeds were reduced by a constant 0.10 i.e. 10 %, to facilitate calculation of analysis of variance in the above tables, which does not alter the variances. The desired statistics from these tables, such as, the components of mean square and the respective repeatability estimates were calculated as similar to butterfat and summarized in Table XCII that follows.

TABLE XCIIESTIMATES OF REPEATABILITY OF MILK YIELD IN<br/>ALL THE FIVE BREEDS OF DAIRY HERD

Breed	Numbe of <b>Ree</b>	r S <sup>2</sup> :ord	S <sup>2</sup> between cows	Repeatability = S <sup>2</sup> /(S <sup>2</sup> +S <sup>2</sup> <sub>bet.</sub> cow	Std. Error s)
Hols.	279	54490	55012	0.50	0.45
Jers.	186	15049	15640	0.49	0.56
Guern.	155~	15906	9254	0.63	0.49
Ayrs.	52	21627	34319	0.39	0.12
Br. Sw.	117	27266	26886	0.50	0.70
TOTAL	789	134338	141111		

A single estimate of repeatability for all the five breeds was then obtained and the standard error calculated in a manner similar to that of butterfat. Thus:

- a) Repeatability Estimate (R) - All five breeds - 134338/275449 - 0.49
- b) Standard error of the combined repeatability =  $1 r^2/\sqrt{n 2k} = \frac{0.7599}{27.9} = 0.272$

Where n is the total number of animals from all the five breeds and k is the total number of breeds included in estimating combined repeatability.

Thus, the combined repeatability estimate for milk yield in all the five breeds of the Michigan State College dairy herd was found to be 0.49±0.272.

From these studies, it could be concluded that repeatability estimates,  $0.50 \pm 0.269$  for butterfat and  $0.49 \pm 0.272$  for milk show what fraction of the total variance among the records of the cows was due to the permanent differences between the cows which made those records. The rest of the variance was caused by the temporary environmental influences, which have so much effect on the size of the records.

In view of the high correlation between milk and butterfat, the repeatability estimate for both these characteristics from the present study seems to show very little difference between them. Therefore, it could be said that either of these estimates might be used with certain advantage depending upon the circumstances and the nature of the records available (milk or BF) for culling or for selection.

## PART III

# INFLUENCE OF THE MONTH OF CALVING ON BUTTERFAT PRODUCTION

Of value to the breeder for efficient planning and production, it was thought pertinent to include in the scope of the present study the effects of the month of freshening (calving) on the yearly production of butterfat. In view of the high significant correlation of  $+0.863 \pm 0.009$  reported by Gowen (1924), between milk and butterfat yields, only the effects on butterfat production were studied. Turner (1927) has shown that a rapid increase in butterfat production occurs immediately following freshening and remains at a peak level during the first three to four months of lactation. It would seem reasonable to assume that a breeder would be most interested to get the maximum benefit of the yield without being adversely affected by environmental influences.

It is thus a study of an aspect of environmental influences with particular reference to the degree of heat tolerance that an animal possesses. From management and economic considerations, there are reasons for having cows freshen in different seasons; particularly either in fall or spring, but the main object of the present study has been to test statistically whether or not there is any significant relation between the month of calving and the production in the lactation period following it.

In range herds and in animals subjected to extreme temperatures one would observe a good deal more fluctuation in their production than those kept under barn conditions where the temperature is cooler and in some places is controlled. The higher the heat tolerance among the dairy cattle the smaller the variation in the yield. Rhoad (1938) has reported that animals adapted to tropical climates have better heat tolerance than the European breeds of cattle. While genetic material is not generally affected by the environment, it does influence the expression of the phenotype.

Seath (1947) studying the rectal temperatures of Jerseys and Holsteins during the years 1944 and 1945, reported that heritability of heat tolerance to be about 15.1 to 30 per cent, which would thus explain the greater susceptibility of dairy cattle for large variations in temperature.

Experimenting under controlled conditions, Ragsdale and Brody (1922) on the effect of temperature on the percentage of fat in milk reported that the per cent of fat increased almost 0.2 per cent for every 10° F decrease in temperature between the limits of  $30^{\circ}$  F to  $70^{\circ}$  F. In a more exhaustive investigation Ragsdale et al (1948) have again shown that the critical temperature for Holsteins is about  $75^{\circ}$  F to  $80^{\circ}$  F and for Jerseys  $80^{\circ}$  F to  $85^{\circ}$  F. Any increase in temperature above these levels would depress feed consumption and milk production. At  $105^{\circ}$  F both virtually stopped. On reducing the temperature to a level of  $50^{\circ}$  F -  $60^{\circ}$  F feed consumption and milk yield returned to normal. The effects of temperature are more pronounced as is generally true in tropical countries such as some parts of India where the yield becomes reduced during the hot summer months and gradually returns to normal with the approaching cooler seasons.

Studies on the effect of month of freshening on milk production by Arnold and Becker (1935) using analysis of variance method on 319 lactation records of Jersey cows accumulated over a period between 1917 -1933 found no significant difference under the climatic conditions of Florida. A similar experiment by Morrow et al (1945) on 4030 lactation records of grades and all breeds of purebreds also concluded that there is not only no effect on the length of lactation but also there is no significant relationship between month of freshening and milk yield, under New Hampshire conditions. While studying under Western Oregon conditions, 2690 records of all breeds following calving, Oloufa and Jones (1948) also arrived at similar results.

But Sanders (1927) in England, in his studies on the variations in milk yield after freshening in relation to seasons of the year, pointed out that best months for calving would be October, November and December, which would result in highest yields. Cannon (1933) analysing 68,000 Cow Testing Association records for 1925-1930 belonging to all breeds reported that those freshened in November had highest milk yield and those in June had the least. Earlier work by Wylie (1925) on 2900 Jerseys Registry of Merit records completed in 1921, showed that freshenings occurring in July, October, November, December, January, February and March had highest milk yield. Those that freshened in August had the lowest milk yield. Since some of these works generally suffer from statistical analysis it would be difficult to conclude whether or not they were statistically significant. Even if they had proved to be significant by statistical tests, they would have only provided further proofs on the modifying effects of environmental (seasonal) conditions, which vary from one locality to another.

From these considerations, it seems therefore, that

any external factor or factors that would influence the first few months of production following calving, would to a great extent affect the total production of an animal during that year. Thus, it was thought desirable to study the relationship, if any, between the month of calving on yearly butterfat production on the Michigan State College dairy herd.

The total number of births from the five breeds with lactation records following freshening have been summarized in Table XCIII below on a monthly basis. The average monthly production of cows in each breed following freshening has also been shown in Table XCIV.

TABLE	XCIII	NUMBER	OF	CA	LVES	BORN	I TO	COWS	S WI	TH	RECO	RDS
		FOLLOW	ENG	FF	RESHEN	JING	DURI	NG 1	HE	VAF	RIOUS	
		MONTHS	OF	A	YEAR							

Breed	No. of Cows	f	Months							T	TotalNo.			
														of
		ู่ ไลทุบล <b>ท</b> ั้ง	February	March	April	N.ay	June	July	August	September	October	November	December	Records
Hols.	123	13	8	7	10	14	6	20	7	11	8	11	8	123
Jers.	75	9	4	7	6	9	5	4	3	7	5	11	5	75
Guern	• 55	4	5	7	5	2	2	4	2	4	4	8	8	55
åyrs.	42	2	3	3	3	7	5	2	2	3	2	5	5	42
Br. S	w• 37	4	3	3	3	4	3	2	3	2	0	6	4	37
Total		32	23	27	27	36	21	32	17	27	19	41	30	332

TABLE XCIVMONTHLY AVERAGE PRODUCTION OF COWS IN ALL FIVE<br/>BREEDS FRESHENING IN THE DIFFERENT METHODS

Breed		Months										
	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
Hols.	577	530	539	478	581	550	490	533	477	435	484	526
Jers.	401	385	422	436	458	450	397	443	423	394	444	481
Ayrs.	<b>3</b> 84	480	408	467	<b>3</b> 84	448	414	412	491.	497	425	426
Guern.	478	483	411	440	375	384	423	466	483	434	414	478
Br. Sw	•58 <b>8</b>	530	472	488	502	5 <b>1</b> 1	586	531	483	0	563	582
Weight Averag	ed e504	488	453	461	<b>49</b> 8	480	<b>4</b> 68	495	466	431	464	497

It could be observed from the above table that the births have been fairly well distributed in all the twelve months of a year, and that no definite system of calving seems to have been followed in the Michigan State College dairy herd.

As a helpful adjunct to the present study, the mean annual temperature and rainfall and the range at East Lansing, where the college herd is located, covering the period of study from 1919 to 1950 both inclusive, has been shown in the following Table XCV.

Nature of Environmental Condition	Mean (yearly)	Range (yearly)
Temperature	47.2° F	50.6 - 44.6° F *
Rainfall	31.0 inches	39.7 - 18.5 inches

TABLE XCV THE NEAN AND THE RANGE IN TEMPERATURE AND RAIN-FALL BETWEEN 1919 - 1950 AT EAST LANSING

\* Range of temperature within a year was 13.2 - 74.1° F on monthly average. ANALYSIS OF THE DATA:

To study the effects of month of freshening on the yields of butterfat, the usual method of analysis of variance as outlined by Snedecor (1946) was used. Each breed was considered separately. The main object of running analysis of variance has been to separate from the total variance, the variance due to the effects of month and that due to random variance and test the former by the latter by means of "F"-test.

Before subjecting the data for analysis of variance, the yearly butterfat records following each calving were classified and then adjusted for three main environmental influences, namely, 1) age, 2) length of lactation period-305-day, and 3) times of milking per day - 3X.

Since the methods and calculation procedures were exactly similar to those already outlined in the previous sections, the repetition here has been avoided, and only the final tables of analysis of variance for each breed and the corresponding "F"-tests have been given in the following tables.

TABLE XCVIANALYSIS OF VARIANCE OF BUTTERFAT PRODUCTION<br/>FOLLOWING FRESHENING IN HOLSTEIN HERD

Source of Variance	Degrees of Freedom	Sum of Squares	Mean Squa <b>re</b>	F <b>-v</b> alue
Total	122	1462333		
Between Months	11	175402	15946	1.38
Within Months (or ERROR)	111	1286931	11594	

F-test for between months was not significant.

TABLE XCVIIANALYSIS OF VARIANCE OF BUTTERFAT PRODUCTIONFOLLOWING FRESHENING IN JERSEY HERD

S <b>ource of</b> Variation	Degrees of Freedom	Sum of Squares	Mean Square	F <b>-v</b> alue
Total	74	617822		
Between Months	. 11	51954	4723	0.53
Within Months (or ERROR)	63	565868	8982	

F-test for between months was not significant.

TABLE XCVIIIANALYSIS OF VARIANCE OF BUTTERFAT PRODUCTION<br/>FOLLOWING FRESHENING IN GUERNSEY HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Squar <b>e</b>	F-value
Total	54	366074		
Between Months	11	62617	5693	0.81
Within Months (or ERROR)	43	303457	7057	

F-test for between months was not significant.

TABLE XCIXANALYSIS OF VARIANCE OF BUTTERFAT PRODUCTION<br/>FOLLOWING FRESHENING IN AYRSHIRE HERD

Source of Variation	Degrees of Freedofi	Sum of Squares	Mean Square	F-value
Total	41	252876		
Between Months	11	55562	5051	0.77
Within Months (or ERROR)	30	197314	6577	

F-test for between months was not significant.

TABLE CANALYSIS OF VARIANCE OF BUTTERFAT PRODUCTION<br/>FOLLOWING FRESHENING IN BROWN SWISS HERD

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F-value
Total	36	329781		
Between Months	10	56941	5694	0.54
Within Months (or ERROR)	26	272840	10494	

F-test for between months was not significant.

F-test in all the five breeds was found to be insignificant. It would be of value to run a "t"-test if the F-test had been significant, to determine in which month or months the significant increase in production occurred. But since there was no significant F-test, it was thought that no useful purpose would be served by carrying out "t"-test.

From this study, it was thus concluded that the month of freshening has no appreciable and significant influence on the yearly butterfat production following it, in the several breeds of Michigan State College dairy herd. As pointed out by Olson (1938) the planning of breeding and freshening times in dairy herds are generally matters of management practices and marketing economics for the dairy products. Those closer to cities, where there would be an all the year round demand for the dairy products, breeders would have to gear up their production to meet these demands by a program of calving system throughout the year. In rural farming, one plans calving seasons on the basis of availability and the time of pasture, labor facilities, and the local demands.

### PART IV

## SEX RATIO AMONG DAIRY CATTLE

Differentiation of the living organism from its unicellular state of development to two different and distinct sexes embedded within the mosaic of the complex multicellular organism is the greatest contribution of evolution to the world. With increase in the quest for knowledge, man's attention was turned to measure the relationship and the frequency of the male and female sexes. Work in this field has been very voluminous and covers almost all phases of it, extending anywhere from control of sexes, to sex determination and development in the extra-uterine stages.

Among animals, studies in sex ratio generally relate to either statistical analysis of available data or to various attempts to control or modify by experimental means. Gowen (1917) and again in (1942) analysing a large number of births among cattle showed the sex ratio to be 50.5 for male and 49.5 for females. He also concluded that age of the sire or the dam has no material effect on the sex ratio. Works on the continent have also been fairly close to Gowen's work. Among the investigators who attempted to control sex ratio, mention should be made of some of the outstanding works to illustrate the trend in this particular field. These workers have generally used rats, rabbits, and swine for their work. Lush (1925) attempted by utilizing dimorphism in sperms, that is, the XY type of sex inheritance, to separate them by centrifugation, as a possible method to control sex in artificial insemination. He worked on both rabbits and swine, though the results were not of any significance.

Later, with Unterberger (1930) in Germany, while in the course of human medical practice accidnetally found that use of 5% sodium bicarbonate solution as a vaginal douche would result in male births and use of about 3% lactic acid solution as acid douche would result in female births. However, in all 53 cases he treated, he reported the birth of boys. Later works by others on humans have not supported his theory. This rather astounding work was replicated in animals notably in rats and rabbits by Roberts (1940), Cole et al (1940), Cuisenberry and Chandiramani (1940, 1945) McPhee and Eaton (1942) and Casida and Murphree (1942). In all these works the results have failed to show any significant modification of the normal sex ratio.

While the dairy cattle breeder is primarily interested in sex ratio from an economic point of view, that is, whether or not it would open a new avenue if the frequency of the male or female stock is controlled, the above works point out the inherent limitations in this adventure.

Sex ratio could be expressed as the number of males

per hundred females or the percentage of male births among all the births studied. Gardner (1950) studying sex ratio resulting from artificial insemination reported his results on the basis of the former, that is, 100 females to 105.89 males. The disadvantage of this method is that it magnifies any source of error that would affect any one sex. The latter method, which has been generally used by workers, has been, therefore, applied in the present study.

While one regards sex ratio to be equal--50 - 50, any effects of lethal genes, and environmental influences during the intra-uterine development resulting in embryonic mortality would affect considerably the sex ratio at birth. For any study involving sex ratio at birth, it is necessary therefore, to possess large number of data on births.

During the life span of an animal, sex ratio could be studied at three different stages, namely, 1) at conception - primary, 2) at birth - secondary, and 3) at maturity - tertiary. Gowen (1942) while reporting on sex ratio in cattle, reviewed the work of Jewell, who had reported the intra-uterine sex ratio or also called the sex ratio at the primary stage to be 55.2% in cattle. But the study of sex ratio at conception is commonly limited to laboratory animals. In dairy cattle and other larger mammals, the

study has been generally based on the number of offspring born i.e. at secondary stage.

Since the present study relates to the secondary sex ratio, it will be referred to hereafter as merely sex ratio. Still-born calves have also been included in the study.

All the male and female calves born in the Michigan State College dairy herd irrespective whether born single or in twins have been summarized in the Table CI as a basis of preliminary study.

Breed	Under Twins		Unde	Under Singles Total				
	Male	Female	Male	Female	Male	Female	Total	
Holstein	41	41	367	368	408	409	817	
Jersey	5	5	222	215	227	220	447	
Guerns <b>ey</b>	3	5	224	173	227	178	405	
Ayrshire	1	7	87	94	88	101	189	
Brown Swiss	0	0	104	101	104	101	205	
Total	50	58	1004	951	1054	1009	2063	

TABLECALVES BORN IN THE MICHIGAN STATE COLLEGE DAIRYCIHERD FROM 1919 - 1950

Sex	Number	Percentage Observed	Percentage Expected	Standard Error
Male	1054	51.1	50.00	1.1
Female .	1009	48.9	50.00	1.1
Total	2063	100.00	100.00	

TABLE CII CALCULATION OF SEX RATIO - ALL FIVE BREEDS

Standard error was calculated by the use of the formula:

Standard error of percentage  $=\sqrt{PQ/N}$  where N is the total births  $=\sqrt{(0.511 \times 0.489/2063)}$  $=\sqrt{.00012} = 0.011$ 

It means that if samples are drawn at random two-thirds of the time one would get the percentage of the male to be between the range of 52.2% to 50.0%.

To test the significance of the frequency of the male percentage Chi-Square test  $(X^2)$  was applied:

Chi-Square \_ S  $(0-C)^2$  with (n - 1) degrees of freedom, where 0 is the observed and C is the expected percentage of male and female births.

Chi-Square = 
$$\frac{(1054 - 1031 - 5)^2}{1031.5} + \frac{(1009 - 1031.5)^2}{1031.5}$$

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<u>-</u> 0.962 -- not significant. D.F. <u>-</u> 2-1 <u>-</u> 1

Thus, from a total of 2063 births of dairy calves in all the five breeds of the Michigan State College dairy herd, the percentage of male calves was found to be  $0.511 \pm 0.01$  which by Chi-Square test was found to be not significantly different from .5.

## TWINNING IN DAIRY CATTLE

Twins in dairy cattle are a special case of fertility. As a supplement to the study of sex ratio in the present work it was thought to be valuable to include a discussion on the frequency of twins in dairy cattle. Twinning is very rare and its occurrence has evoked interest mostly among scientists from a research point of view but has little or no importance to the average dairy cattle breeder.

Lush (1925) reported that twinning was more common among Holstein breed than other dairy breeds at Kansas State College and that there was some tendency to occur more frequently in particular families in the breed than the others. This indicates the inheritance of the characteristic. He reported the frequency of the twins to be 0.90% of the births of dairy cattle and 8.84% among the Holstein breed. Hewitt (1934) an Australian worker, observed the incidence of twins among Red Poll to be 2.1% and among Friesians to be 2.6% of the total births. The gestation period was shorter by 8 - 10 days and the twins and their dams showed to be heavier producers. He concluded that a close genetic relationship exists between twinning, high milk and butterfat yields and longevity of life and fertility. Pfau (1948) reported twins to be 3.95% in dairy cattle.

In regards to relationship of age of the dam to twinning, Jones and Rouse (1920), Hewitt (1934) and Pfau et al (1948), all agreed that it is rare in the first parturition, rises to a peak in the fifth to the seventh parturition and then declines with the advancing age.

As to the general nature of the inheritance there is considerable lack of agreement among the workers. Pfau et al (1948) agreeing with the findings of Hewitt (1934) stated that the twinning exhibits Mendelian segregation and that it seems to be under the control of genes. Some workers believe that it is a simple Mendelian recessive factor.

Apart from the genetic factors, environment does play a part in the causation of twinning, such as, age, size, physiological conditions, amangement and nutritional practices. While Hewitt (1934) agreed with the effect of

age on twinning, he pointed out that season has no influence on twinning.

Since dairy cattle, are classed as strictly uniparous animals, according to the development of their reproductive organs, the incidence of twins among them could be regarded as cases of atavism or reversion. It is considered as an undesirable character in dairy cattle.

Twins are generally classified into two groups on the basis of fertilization and embryonic differentiation, namely:

1) Monozygotic - Twins resulting from the splitting of a single fertilized ovum in the blastodermic stage and development. These are commonly referred to as "identical" twins. As they are genotypically the same, any variation within the identical twins must be considered to be wholly environmental. Genetically their coefficient of relationship is 100 per cent. They are of more common occurrence in humans than in farm animals. Scientists are particularly on the lookout for them as they contribute an important source of information on the study of environmental effects, particularly in nutritional investigations, etc.

2) Dizygotic - Twins that result from independent but nearly simultaneous fertilization of two separate ova, and they are the same as ordinary full sibs in genetic

variability, except that they develop at the same time under identical intra-uterine environment. It could also be said that the extra-uterine conditions to some extent would be similar. The coefficient of relationship is 50% in dizygotic twins, as it would be in full-sib relationships.

The first and the classical study on the diagnosis of monozygotic twins in domestic animals on the same methods as those applied to humans was done by Kronacher (1932), who based the diagnosis on the correlation of, a) physical characteristics, b) physiological characteristics, and c) on the concordance or otherwise of psychic properties. Kronacher later (1936), proposed a new approach to identify monozygotic twins in cattle. The method was based on similarity quotients on growth, production and physical characteristics, the post-mortem measurements of stature, and analysis of blood and hormonal secretions.

Lush, 1937, while reviewing the work of Kronacher (1936) further elucidated that diagnosis of the identical (monozygotic) twins, which are of the same genotype, depends upon the similarity of long series of characteristics. Whereas in the case of fraternal (dizygotic) twins, who although they are similar in one or few characteristics, become more and more divergent as the number of comparisons of the characteristics increase.

With the help of the available data, the present study has been directed to determine the frequency of the different sex combinations of twins and to test the significance from the expected frequencies.

As the data from all the five breeds of Michigan State College dairy herd were small, it was thought desirable to include the data that were available on the State Institution herds, which are primarily composed of the Holstein breed. Table CIII shows the number of twins in different breeds.

TABLE	CIII	TWIN	SEX	RATIO	IN	DIFFERENT	BREEDS

Breed	Twin Combination						
	Both Males	Male and Female	Both Females				
MICHIGAN STATE COLLEGE DAIRY HERD							
Holstein	10	21	10				
Jersey	1	3	l				
Ayrshire	0	3	l				
Guernsey	0	1	3				
Brown Swiss	0	0	Ο				
STATE (GOVERN- MENT) HERD							
Holstein	35	94	53				
lotal	46	122	68 23				

The total number of twins born in the College herd from all five breeds was 54, which was found to be 2.62% of the total number of calves born. This figure compares favourably with those reported by Kronacher (1932) and Hewitt (1934), which were 2.7% and 2.1% to 2.6% respectively.

Further statistical treatment consisted in testing whether or not the frequency of twin combinations was to a large extent a phenomenon of dizygotic nature; the tests were made under two different hypotheses.

1. It was assumed that the sex ratio was equal to 50 male calves to 50 female calves or in other words the frequency of male calves (q) to be 0.50. The total number of twins of all combinations being 236, the expected numbers were calculated by use of the formula,  $N \left[q + (1-q)\right]^2$  as suggested by Johansson (1932), where N is the total number of all twins and (q) and(1-q) is the frequency of the males and females. The (q) having been assumed to be 0.50, the expected values were calculated and shown in Table CIV, along with the observed (actual) values.

	Twin Combinations					
	Both Males	Male and Female	Both Femal	es		
Observed	46	122	68	236		
Expected	59	118	59	236		
Deviation	-13	+4	+9			

TABLE CIV OBSERVED (ACTUAL) AND EXPECTED (CALCULATED) NUMBER OF TWINS OF DIFFERENT SEX COMBINATIONS

The Chi-Square test on the above values was found to be insignificant, indicating the hypothesis to be correct. That is, the observed twin combinations do not significantly deviate from those expected combinations under the hypothesis in which q was equal to 0.50.

2. Under the second hypothesis the sex ratio of 51.1% male and 48.9% female obtained from the data under study was assumed to be the frequency in the population. The expected number of different twin combinations was calculated by the same bionomial formula,  $N[q + (1-q)]^2$ , where N is the total number of all twins which is 236 and q is equal to 0.511 and 1-q is equal to 0.489. The calculated expected values and the observed values have been shown in Table CV.

		TWIN	COMB	COMBINATIONS				
	- Both	Males	Male	and	Females	Both	Females	5
Observed	46	.C		122	•0	68	3.0	236
Expected	61	6		117	•9	50	6.4	235.9 or 236
De <b>vi</b> ation	-15	i <b>.</b> 6		+4.	.1	+11	L.6	

TABLE CV OBSERVED AND EXPECTED NUMBER OF TWINS OF DIF-FERENT SEX COMBINATIONS

Again the Chi-Square test for the above values was carried out and was found to be not significant. The hypothesis that they do not deviate from expected is correct.

Thus, it could be concluded that if there was preponderance of the monozygotic twins, there should have been a noticeable frequency of the same-sexed twins. Instead there is a slight increase in the opposite-sexed twins, which is not only not significant but also similar to the binomial distribution of q = 0.5. From this it could be concluded that the twins born in the Michigan State College dairy herd and that of the State (Government) herd, were mostly dizygotic twins, though one would not rule out the possibility of the occurrence of few monozygotic (identical) twins.

From the present study, the twin sex ratio among the dairy cattle was found to be: 4667:12259:6899.

## PART V

## GENERAL CONCLUSIONS AND SUMMARY

## GENERAL DISCUSSION OF RESULTS

The present study covers a range of varied characteristics, which have been dealt with as independent economic factors in the dairy herd of the Michigan State College at East Lansing. While discussions concerning these specific characteristics have been examined at length in the respective sections, only overall consideration of the resulting effects on the dairy cattle breeding has been stated here.

The heritability estimates are all based on the lifetime averages, which was 2.6 lactation records per cow for the whole herd. In view of the relatively smaller number of samples in some of the breeds, no attempt was made to transform and express these findings in terms of what they would be if each cow had only one record.

The heritability values in the present study, on an intra-sire basis for the whole herd was found to be,  $-0.01 \pm .08$  for milk,  $0.20 \pm .08$  for butterfat, and  $0.56 \pm .047$  for butterfat test. These are the weighted averages of 3 methods and 5 breeds in the herd. The corresponding estimates based only on intra-sire regression method were,  $-0.08 \pm .12$  for milk,  $0.09 \pm 0.123$  for butterfat and 0.47 ± .06 for the butterfat test. In comparing the results by the former method with that of the latter method it could be seen that in the case of milk and butterfat, the sampling errors (standard errors of heritability) have been partly reduced by weighting the average estimates of the different methods, which could be considered as of some advantage. Further, the sampling errors by the regression method in the case of milk and butterfat show values greater than the heritability estimates themselves, which was discounted in part by the weighted average. The occurrence of negative values of heritability in some of the individual breeds and methods, the weighted averages have been obviously smaller than weighted averages of the five breeds, as well as those of the three methods.

Under the hypothesis that there is a population difference which obviously presupposes that the difference must vary between certain limits, the fiducial limits at 99 per cent were calculated. These limits, however, provide one with the amount of confidence that one can place in these various heritability estimates:

Limit =  $h \pm t$  .01 x s<sub>h</sub> The "t" value at 1 per cent level should be taken for (n-2) degrees of freedom, where "n" is equal to the number of pairs of daughter-dams. Here, n = 271, and

the "t" value at 1 per cent level is 2.592.

By use of the above formula the confidence limits were found to be,  $-0.01 \pm .21$  for milk,  $0.20 \pm .21$  for butterfat and  $0.56 \pm .047$  for butterfat test. Therefore the 99 per cent confidence limits are:

> Milk = +0.20 and -0.22 Butterfat = 0.41 and -0.01 Butterfat test = +0.69 and + 0.43

These figures indicate that the heritability estimates under the present study in 99 out of 100 could lie within these limits. Since a negative heritability estimate is meaningless, the negative values and limits have thus been rejected from consideration. It seems, therefore, the peculiarities in these estimates, including negative values could be due to sampling variations.

The heritability estimate of milk yield by regression of daughter on dam method was found to be 0.11 which value is within the above fiducial limits of milk and closely approaches the positive limit.

According to the Galton's law of inheritance, the sire and the dam contribute almost equally to the genetic make up of the offspring. Therefore, the expected gain per generation in each of the traits, milk, butterfat, and butterfat test would be proportional to half the product of the percentage of heritability, the standard deviation and the total selection differential. The standard deviation for the whole herd inclusive of all breeds for each of these traits was calculated by use of the following formula:

$$\hat{\mathbf{G}} = \sqrt{\frac{n_1 s_1^2 + n_2 s_2^2 + \dots + n_k s_k^2}{n_1 + n_2 + \dots + n_k - k}}$$

where  $n_1 \ldots n_k$  is equal to the number of animals in each breed,  $s_1^2 \ldots s_k^2$  is the variance of each of the component breeds, and k is equal to the number of breeds. Thus the combined standard deviation in each instance was:

> Milk = 232 pounds Eutterfat = 92 pounds

Butterfat test = 0.5 per cent

According to Lush (1945), if one considers the percentage of replacements needed in a static population are about 55 per cent in the case of dairy cows and about 5 per cent in the case of dairy bulls, the corresponding maximum selection differential in terms of the standard deviations would be 0.70 and 2.06 respectively, in a normally distributed population. If the heritability estimate for milk is considered to be 0.11 (regression of daughter on dam method) and the standard deviation to be 232 pounds, then the expected average gain per generation would be (0.11) (232) (0.70 + 2.06)/2 = 35.2 pounds, provided the selection is directed only towards increasing the milk yield. Similarly, for the butterfat, with the heritability factor (intra-sire method) and the standard deviation being 0.20 and 92 pounds respectively, theexpected average gain per generation would be (0.20) (92) (0.70+2.06)/2 = 25.4 pounds, granting that the selection is directed only towards improving the butterfat production. In the case of butterfat test, the expected average gain per generation would be (0.56) (0.5)(0.70+2.06)/2 = 0.39 per cent or 0.004, assuming that the selection would be practiced only in one direction, i.e. butterfat test. Judging from these various expected values that could be attained under the conditions stated above, the improvement that one would make in respect of butterfat yield seems to secure for the breeder a greater source of income in comparison to the other two traits.

Since the average gains are expressed in terms of each generation, the maximum improvement or gain that could be attained in any one year would be one over the average of the cows times the average gain per generation. Lush (1945) has estimated that the average age of cows when their offspring are born (i.e. average interval between generations) is between 4 and  $4\frac{1}{2}$  years. On the basis of this estimate the average gain per year would be about 7.6 pounds of milk, 6 pounds of butterfat and about 0.14 per cent or 0.001 of butterfat test. When selection
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is practiced for more than one character and when those characters (n) are such that no correlation exists, while being equally important, the possible gain in any one character would be only  $1/\sqrt{n}$  times as great as if all selection were directed towards improving one characteristic alone. Thus, in any balanced breeding program where the breeder attempts to improve several traits at one time and where allowances must be made for any intensity of selection in one of these, the actual gain would evidently be much lower than the expected values obtained above.

## REPEATABILITY:

The repeatability for the whole herd, for milk and butterfat was found to be 0.49 and 0.50 respectively, which values compare favourably with the figures of other investigators. Since the greatest advantage of these estimates to a breeder is that they serve him as an important tool in practicing culling in his herd they could be profitably used in predicting the most probable future producing ability of a cow from the formula:

> Y = Herd average + nr x (X - Herd average). 1+(n-1)r

where Y = a cow's most probable future producing ability X = a cow's actual production,

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n = number of lactation records of the cow,

r = the repeatability.

The formula  $\frac{nr}{l+(n-1)r}$  gives the real ability

of the cow.

Repeatability estimates in combination with the heritability estimates could also be used to predict most probable breeding value of an animal in a given herd, if one practices culling on this basis, instead of on the producing ability. The breeding value could be obtained from the formula:

 $Y = \frac{hn}{1+(n-1)r}$  as far above or below the average

of the other members of the herd as the animals own actual records average.

where Y - the expected breeding value

h - heritability estimate.

The formula is similar to the one stated above, except that the "r" has been replaced by "h".

EFFECT OF MONTH OF CALVING ON MILK AND BUTTERFAT PRODUCTION:

Since no significant relation between these two factors and the month of calving was found, it could be concluded that the planning of any system of freshening of cows in one or the other month or months is one that mostly concerns management and production practices in a herd. The results found in this study compare well with several other similar studies.

# SEX RATIO AND TWIN RATIO:

The sex ratio shows no significant deviation from the normal proportion of 50 males to 50 females in the general population.

The twins among dairy cattle are extremely rare and no useful purpose would be served by practicing selection for them.. Many workers consider the occurrence as an undesirable character in dairy cattle, which in several instances has been reported to have been attended with untoward effects on the cows as well as on the twins themselves. Therefore breeders should attempt to eliminate such of those animals which are capable of potentially transmitting these undesirable genes.

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### SUMMARY

1. A statistical study was made on the lactation records from 1919 through 1950 of milk yield, butterfat production and the percentage of butterfat (or butterfat test) of the Michigan State College dairy herd, which comprises of all the five breeds, namely, Holsteins, Jerseys, Guernseys, Ayrshires, and Brown Swiss. The herd is a part of the Michigan Agricultural Experiment Station.

2. The estimates of heritability on an intra-sire basis for the 3 most important economic characteristics of the dairy herd as a whole was found to be,  $-0.01 \pm$ .08 for milk,  $0.20 \pm .08$  for butterfat and  $0.56 \pm .05$  for HF test, which are the weighted averages of three methods and five breeds.

3. The estimate of heritability for milk yield by regression of daughter on dam method was found to be 0.11.

4. Repeatability estimates for milk and butterfat production were shown to be 0.49  $\pm$  .272 for milk and 0.50  $\pm$  .269 for butterfat.

5. The study of the effect of the month of calving on the production of butterfat showed no significant difference between the two under the climatic conditions that exist at East Lansing, Michigan.

6. The analysis of the calving records covering the above period of study showed that there were a total of 2063 births and the percentage of male calves was found to be 0.511  $\pm$  0.01 which was not significantly different from the normal ratio of 50 male births to 50 female births.

7. The study, which included the data from the Michigan State Institution dairy herd on the frequency of the twins in dairy cattle showed that there was a ratio of 46667:12209:6899. The nature of the binomial distribution of these twins appears to indicate that the occurrence of identical twins in dairy cattle is a rare phenomenon.

8. The frequency of twins in the Michigan State College dairy herd was 2.62% of the total number of calves born.

#### BIBLIOGRAPHY

- Arnold, P. T. Dix, and Becker, T.B. 1935 The Effect of Season of the Year and Advancing Lactation Upon Milk Yield of Jersey Cows. Jour. Dairy Science, 18: 621-628
- Bonnier, Gert
  - 1927 Correlations Between Milk-yield and Butterfat Percentage in Ayrshire Cattle. I. Individual Correlation. Hereditas, 10: 230-236.
- Berry, J. C. and Lush, J. L. 1939 High Records Contrasted With Unselected Records and With Average Records as a Basis for Selecting Cows. Jour. Dairy Science, 22: 607-617, Illus.
- Briquet, Raul Jr., and Lush, J. L. 1947 Heritability of Amount of Spotting in Holstein-Friesian Cattle. Journal of Heredity, 38: 99-105, Illus.
- Brody, S., Ragsdale, A. C., and Turner, C. W. 1923 The Rate of Decline of Milk Secretion With the Advance of the Period of Lactation. Jour. General Physiology, 5: 441-444, Illus.
- Brody, S. 1924 The Rate of Growth of the Dairy Cow. IV. Growth and Senescence as Measured by Rise and Fall of Milk Secretion With Age. Jour. Gen. Fhysiology., 6: 31-40.
- Beardsley, John P., Bratton, R. W., and Salisbury, G. W. 1950 The Curvilinearity of Heritability of Butterfat Production. Jour. Dairy Science, 33: 93-97.
- Cannon, C. Y. 1933 Seasonal Effect on Yield of Dairy Cows. Jour. Dairy Science, 16: 11-15, Illus.
- Casida, L. E., and Murphree, R. L. 1942 Fertility and Sex Ratios in the Rabbit. Jour. Heredity, 33: 434-438.

Chai, Chen Kang 1951 The Relative Importance of Genetic and Environmental Factors on the Butterfat Production of Holstein-Friesian Cattle. PhD. Thesis, M.S.C. East Lansing.

Cole, Leon J. Letzky, Emmanuel and Shackelford, Max. 1940 Test of Sex Control by Modification of the Acid-Alkaline Balance. Jour. Heredity, 31: 501-502.

Copeland, Lynn

1927 Inheritance of Butterfat Percentage in Jersey Cows. Jour. Dairy Science, 10: 344-352.

- Darwin, Charles 1868 <u>The Variation of Animals and Plants Under</u> <u>Domestication</u>. John Murray, London.
- Darwin, Charles
  - 1875 <u>The Origin of Species by Means of Natural</u> <u>Selection, etc. 6th Edn. John Murray, London.</u>
- Dickerson, G. E.

1940 Estimates of Producing Ability in Dairy Cattle. Jour. Agric. Research, 61: 561-586.

- Eckles, Clarence H.
  - 1939 <u>Dairy Cattle and Milk Production</u>. (3rd. ed.). The Macmillan Co. New York.
- Edwards, Joseph 1932 The Progeny Test as a Method of Evaluating the Dairy Sire. Jour. Agri. Science, (England) 22: 811-837.
- 1936 Effect of Breed, Size , Yield of Milk, and Stage of Lactation Upon Efficiency of Milk Production. Jour. Dairy Research, (England) 7: 211-222.

Fisher, R. A.

1934 <u>Statistical Methods for Research Workers</u>. (5th ed.). Illus. Oliver and Boyd, Edinburg and London.

Gaines, W. L.

1927 Persistency of Lactation in Dairy Cows. University of Illinois, Agri. Expt. Stn. Bull. 288.

1931 Size of Cow and Efficiency of Milk Production. Jour. Dairy Science. 14: 14-25.

- 1936 Age and Size of Cow Affect Milk Yields About Equally. Ill. Agr. Expt. Sta., 48th Ann Report, 1934-35: 144-47.
- 1936 Fat Percentage and Milk Yield. Holstein-Friesian World. 33:579-580.
- Gardner, K. E.

1950 The Sex Ratio in Calves Resulting From Artificial Insemination. (Abstract). Jour. Dairy Science. 33:391.

- Gifford, Warren
  - 1930 The Value of a Sire. Guernsey Breeders' Jour. 38: 259-261 and 303.
- Gowen, John W.

1920 Studies in Milk Secretion. V. On the Variation and Correlation of Milk Secretion with Age. Genetics, 5: 111-188.

- 1924 <u>Milk Secretion</u>. Williams and Wilkins Co. Baltimore, Md.
- 1934 The Influence of Inheritance and Environment on the Milk Production and Butterfat Percentage of Jersey Cattle. Jour. Agri. Res. 49: 433-465.
- 1942 On the Sex Ratio in Cattle. Jour. Heredity, 33: 299-301.
- Harrish, G. M., Lush, J. L., and Shultz, E. N.
  1934 Progress Report on Comparison of Lactation and Yearly Records. Jour. Dairy Science, 17: 737-742.
- Hazel, L. N., and Lush, J. L. 1942 The Efficiency of Three Methods of Selection. Jour. Heredity, 33:393-399.

Hazel, L. N. 1943 Genetic Basis for Constructing Selection Indexes. Genetics, 28: 476-490.

Hazel, L. N., and Terrill, C. E. 1945 Heritability of Weaning Weight and Staple Length

in Range Rambouillet Lambs. Jour. Animal Science., 4: 347-358. Hewitt, A. C. T. Twinning in Cattle. Jour. Dairy Res., (England) 1934 5: 101-107. Huxley, Julian Evolution: The Modern Synthesis. Harper and 1942 Brothers, New York and London. Johannsson, Ivar Multiple Births in Sheep. Amer. Soc.An. Prod. 1932 Proc., pp. 285-291. Johannsen, W. 1926 Elemente der Exakten Erblichkeitslehre (Jena). (Elements of the Exact Hereditary Science) Jones, Sarah V. H., and Rouse, J. E. The Relation of Age of Dam to Observed Fecund-ity in Domesticated Animals. Part I. Multiple 1920 Births in Cattle and Sheep. Jour. Dairy Science, 3: 260-290. Kendrick, J. F. Standardising Dairy-Herd-Improvement Association 1941 Records in Proving Sires. U. S. Dept. Agri., B.D.I.M. 925. Kronacher, C., and Sanders, D. Neué Ergebnisse der Zwillingsforschung beim Rind. Zeitschrift Fur Zuchtung. Reihe B. 1936 Band XXIV. (Recent Results of the Investigation of Twins in Cattle. 34: 1-172). Lindquist, E. F. Statistical Analysis in Educational Research. 1940 Houghton Mifflin Co. New York. Lush, Jay L. Inheritance of Twinning in a Herd of Holstein 1925 Cattle. Jour. Heredity, 16: 273-279. 1925 The Possibility of Sex Control by Artificial Insemination With Centrifuged Spermatozoa. Jour. Agric. Res. 30: 893-913.

\_\_\_\_, and Schultz, F. S. 1936 Heritability of Butterfat Production in Dairy Cattle. Jour. Dairy Science, 19: 429-430.

and Arnold, Floyd 1937 Differences Between Records, Real Productivity and Breeding Values of Dairy Cows. (Abstract). Jour. Dairy Sci., 20: 440-441.

- 1937 Identical Twins in Cattle. (A Review of C. Kronacher's "Neue Ergebnisse der Zwillingsforschung beim Rind") Jour. Heredity, 28: 415-418.
- Lush, Jay L.
  - 1940 Intra-sire Correlation or Regression of Offspring on Dam as a Method of Estimating Heritability of Characteristics. Amer Goc. An. Prod., Proc., 293-301.
- Norton, H.W., and Arnold, Floyd 1941 Effects Which Selection of Dams May Have on Sire Indexes. Jour. Dairy Sci., 24: 695-721.
- and Straus, F. S. 1942 The Heritability of Butterfat Production in Dairy Cattle. Jour. Dairy Sci. 25: 975-982.
- Animal Breeding Plans. 3rd. Edition. The 1945 Collegiate Press. Ames, Iowa.
- 1949 Heritability of Quantitative Characters in Farm Animals. Heriditas, Suppl. Vol.
- Mather, K.
  - Biometrical Genetics. Dover Publications Inc. 1949 New York.
- M'Candlish, A. C.

1921 The Use of Cottonseed Meal to Increase the Percentage of Fat in Milk. Jour. Dairy Sci. 4: 310-333.

- M'Candlish, A. C., and Struthers, J. P. 1935 Feeding Butterfat to Dairy Cows. Jour. Dairy Res., (England) 6: 303-306.

McPhee, Hugh C., and Eaton, Orson, N. Experimental Attempts to Modify the Sex Ratio 1942 Jour. Heredity 33: 429-433.

Morrow, K.S., Keener, H.A. and Hall, C. N. 1945 Analysis of Certain Factors Involved in Dairy Herd Management in New Hampshire. N. H. Agri. Expt. Sta. Tech. Bull. 86.

Nelson, R. H.

The Effects of Inbreeding on a Herd of Hol-1943 stein-Friesian Cattle. Ph. D. Thesis. Iowa State College Library. Ames, Iowa. pp. 89.

Oloufa, Mohamed M., and Jones, I. R.

1948 The Relation Between the Month of Calving and Yearly Butterfat Production. Jour. Dairy Sci., 31: 1029-1031.

- Olson, T. M.
- 1938 Elements of Dairying. The Macmillan Co. New York.
- Pearl, Raymond 1914 On the Law Relating Milk Flow to Age in Dairy Cattle. Proc. Soc. Exp. Biol. and Med. 11: 18-19.
- 1915' Modes of Research in Genetics. The Macmillan Co. New York.
- Pearl, Raymond, and Patterson, S. W.
- 1917 The Changes of Milk Flow With Age as Determined From Seven-day Records of Jersey Cows. Maine Agric. Expt. Sta. Bull. 262.
- , Gowen, J. W., and Miner, J. R. 1919 Studies in Milk Secretion. VII. Transmitting Qualities of Jersey Sires for Milk Yield, Butterfat Percentage and Butterfat. Maine Agr. Expt. Sta. Bull. 281.
- Pfau, K. O., Bartlett, J. W., and Shuart, C. E. 1948 A Study of Multiple Births in a Hostein-Friesian Herd. Jour. Dairy Sci. 31: 241-254.

Quisenberry, J. H. and Chandiramani, S. V.

- An Experimental Attempt to Modify the Sex Ratio 1940 in Rats and Rabbits. Jour. Heredity, 31: 503-505.
- 1945 Additional Data on Sex Control in Rabbits. Jour. Heredity 36: 160.

Ragsdale, A. C., Brody, S., Thompson, H. J. and Worstell, 1948 D. M. Environmental Physiology: II. Influence of Temperature, 500 to 105° F., on Milk Production and Feed Consumption in Dairy Cattle. Mo. Agric. Exp. Sta. Res. Bull. 425.

Road, A. O.

1938 Some Observations on the Response of Pure Bred Bos taurus and Bos indicus Cattle and Their Cross Bred Types to Certain Conditions of Environment. Amer Soc. An. Proc., 284-295.

Roberts, E.

1940 The Effect of Lactic Acid and Sodi. Bicarbonate on the Sex Ratio. Jour. Heredity, 31: 499-500.

- Rice, V. A.
  - 1942 Breeding and Improvement of Farm Animals. 3rd. Edn. McGraw-Hill Book Co. New York, pp. 750, Illus

Sanders, H. G.

- 1927 The Variations in Milk Yields Caused by Season of the Year, Service, Age, and Dry Period and Their Elimination. Part I. Season of the Year. Jour. Agric. Sci. (England) 17: 339-379., Illus.
- Seath, D. M. 1947 Heritability of Heat Tolerance in Dairy Cattle. Jour. Dairy Science. 30: 137-144.
- Snedecor, G. W. 1946 <u>Statistical Methods</u>, 4th Edn. The Iowa State College Press. Ames, Iowa. pp. 485.

Stewart, H. A.

1945 The Inheritance of Prolificacy in Swine. Jour. An. Sci., 4: 359-366.

"Student"

1908 Probable Error of a Correlation Coefficient. Biometrika, (England), 6: 302-310.

1934 A Calculation of the Minimum Number of Genes in Winter's Selection Experiment. Annals of Eugenics (England), 6: 77-82.

Swett, W. W., Miller, F. W., Graves, R. R. Black, W. H., 1937 and Creech. Comparative Conformation, Anatomy and Udder Characteristics of Cows of Certain Beef and Dairy Breeds. Jour. Agric. Res. 55: 259-287.

- 1939 Relation Between Conformation and Anatomy of Cows of Unknown Producing Ability. Jour. Agric. Res., 58: 199-235.
- Turner, C. W., Ragsdale, A. C., and Brody, S. The Relation Between Age, Weight, and Fat Production in Dairy Cows. Mo. Agric. Expt. 1924 Sta. Bull. 221.
- Turner, C. W. The Mode of Inheritance of Yearly Butterfat 1927 Production. An Analysis of the Progeny per-formance of Jersey Sires and Dams. Mo. Agric. Exp. Sta. Res. Bull., 112.
- 1929 The Relation of Conformation and Anatomy of the Dairy Cow to Her Milk and Butterfat Production. Mo. Agric. Exp. Sta. Bull. 272.
- 1930 The Inheritance of Body Weight in Relation to Milk. Mo. Agric. Exp. Sta. Res. Bull. 147.
- Woodward, T. E. Factors Influencing Percentage of Fat in Milk. 1923 Jour. Dairy Sci., 6: 466-478.
- Wright, Sewall Systems of Mating. Genetics, 6:111-178. 1921
- 1934 The Method of Path Coefficients. Annals of Math. Statistics., 5: 161-215.
- 1939' Genetic Principles Governing the Rate of Progress of Livestock Breeding. Amer. Soc. An. Prod., 18-26 pp.

Unterberger, F. 1930 Voluntary Modification of Sex in Man. Dautsche Kalender Schwarzer Medizinische Wochenschrift, Berlin. 56: 304 Abstract: Jour. Amer. Med. Ass. 94: 1451.

Venkatachalam, G 1949 Estimates of Heritability of Birth Weight and Weaning Weights of Lambs, Ph. D. Thesis. Michigan State College, East Lansing, pp. 68.

Wylie, C. E. 1925 TI

The Effect of Season on the Milk and Fat Production of Jersey Cows. Jour. Lairy Sci., 127.

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