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Effects of genetic and environmental variance on dairy sire evaluation

Ben Bereskin

Iowa State University
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ON DAIRY SIRE EVALUATION

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Ben Bereskin

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In Charge of Major Work

Signature was redacted for privacy.

Head of Major Department

Signature was redacted for privacy.

Dean of Graduate College

Iowa State University
Of Science and Technology
Ames, Iowa

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I. INTRODUCTION

For many centuries, man has attempted, by the means available during each period, to improve the breeding value of the dairy animal. During most of this period, these attempts were sporadic and necessarily very crude, as they were limited by man's meagre knowledge of mammalian reproductive physiology and genetics.

Only in this century the biological and related sciences have been developed to a point permitting a genuine scientific approach to the many intricate problems concerned with dairy cattle breeding.

Great strides have been made in recent years. Yet it seems safe to assume that we are on the threshold of further significant gains in our search for a clearer understanding of the genetics of the dairy animal. Only by continued research, both theoretical and applied, can we hope to attain this understanding. Research not only provides answers to some of the many unsolved problems we face, but also opens new pathways that may need further exploration.

In evaluating a dairy bull by a progeny test, we need to remove from his daughters' records any differences that would bias the estimate of his genetic merit, or breeding value. From a priori considerations, the sources of variance among daughters' records include: (1) the herd in which a daughter makes her record; (2) the year and season in which a record is started; (3) the daughter's genic merit; (4) permanent environmental effects peculiar to each daughter and the remainder of her genetic effects - those due to dominance and epistasis; and (5) temporary environmental effects and other random errors peculiar to each record of a daughter.
The approximate relative magnitudes of each of these effects may be determined by appropriate analyses of variance and related studies. The results then provide a guide to methods of solving the general problem of AI dairy sire evaluation, and indicate what might be expected in practice if those methods are adopted.

For example, previous studies indicate that environmental differences among herds contribute much to the variance among milk and fat records. If this herd effect is not eliminated or considerably reduced, it could bias seriously the estimate of the breeding value of a bull being evaluated. The use of deviation records, in which the herd average is deducted from the record of the daughter, is one method advocated to reduce, statistically, the bias contributed by that source.

Although some evidence indicates the herd effect may not be as important for test as it is for milk and fat production, further investigations would help determine whether the use of deviation records is practical for test, also. In addition, the relationships found for the factors affecting test may well apply in handling records for percent of total solids or protein, for example.

Previous research has indicated that the effects of year and season of freshening are worthy of consideration, although the variances from these sources are minor when compared with that contributed by the herd effect. However, herd averages need to be computed over some arbitrary time periods. These time periods may be specified as the seasons which reflect maximum differences between the time-separated groups of records within a herd. It seems reasonable to expect that we may largely eliminate the effects of both herds and seasons by using deviation records.
Usually some of the daughters will have more than one record at the time the sire is being evaluated. It is desirable to utilize all the available information on each daughter. Hence a way needs to be found to combine properly the several records of each daughter into a composite average which can be incorporated readily into the proof. This necessitates obtaining some measure of the repeatability of single records of a cow.

The bull's breeding value is manifested only through the records of his daughters, and each daughter carries only a sample half of her sire's genes. Each daughter alone is usually a poor indicator of her sire's breeding value. We need some means of combining records of several daughters to be able to place a figure on the sire's breeding value. This entails evaluating the heritability of production traits and the kind and amount of environmental correlations present among paternal sibs.

Another factor to consider is the role of the dam of each daughter. The daughter receives the other half of her genic effects from her dam and usually both daughter and dam are tested in the same herd. If the dam contributes an unusual sample of genes to her daughter, either above or below the population average in merit, and this effect is not discounted properly, the proof of the daughter's sire will contain some bias. Until recently, the equal-parent index has been relied upon to account for the dam's effect on daughter production records. However, this has not proven to be satisfactory, in many cases. It is possible that by use of deviation records, employing the herd-year-season averages contemporary with the daughters' records, a more accurate and efficient means of sire evaluation may be realized.
This outline describes, in a qualitative way, the effects of genetic and environmental variance and covariance on dairy sire proofs. It is evident that there are many facets to the problem defined by the title of this thesis. It is obviously impossible to evaluate all of them fully, here. A major difficulty is that most of the factors are closely related and it is hard to present a complete picture in any single analysis or discussion. However, the aim in the presentation to follow has been to consider these factors as they logically would be approached in any systematic research for devising a sound program of dairy sire evaluation. The primary specific purpose is to analyze those various effects and measure each in relation to the whole. The end product should be an improved plan for evaluating dairy sires that would be as simple as possible and yet be effective in producing the desired result, namely, the most accurate and efficient estimate of a sire's breeding value or, if desired, some function of that value.
II. REVIEW OF LITERATURE

A. Development of Sire Evaluation Methods

The domestication of the progenitors of modern cattle by ancient man led to primitive attempts at animal improvement through breeding (reviewed by Winters, 1948, Chapter 2). Apparently the early Egyptians, as long ago as 2500 B.C., were the first group of people who attempted, by control of parentage, to differentiate their cattle into different classes. Both the early Greeks and Romans of the pre-Christian and early Christian eras raised different types of cattle and made some progress in certain phases of animal breeding. Passages from the writings of various authors of the time indicate that planned selection of parents was practiced in breeding, based on the recognition of the importance of good parents of both sex. However, careful studies have indicated that in general, the cattle owners held largely erroneous ideas concerning the transmission of hereditary traits. As a result, the changes in animal characteristics were but slightly different from or more rapid than those occurring under natural selection.

Following the dissolution of the Roman Empire and the centuries of the Middle Ages, the gradual breakdown of feudalism and the onset of the Industrial Revolution opened the way for modern livestock improvement work. During the 16th and 17th centuries, northwestern Europe developed into an early center for such endeavors. But only in the latter 1700's were systematic, although usually crude, methods of livestock breeding first adapted. Robert Bakewell (1725-1795) is generally credited with being the founder of modern practical livestock improvement work (Pawson, 1957). It is likely that Bakewell actually made efficient use of many of the tools now available to modern breeders. He made a variety of crosses
among breeds and retained what he considered the best for foundation stock. He tested by methods that approached the complexity of some present-day performance tests. He developed a system of leasing and testing young sires and he used inbreeding with a success that few have achieved to this day. After the time of Bakewell and his immediate followers, breeders such as Tompkins, Bates and the Colling brothers, great strides were made in animal improvement methods. But it was not until some years after the rediscovery, in 1900, of Mendel's genetic work, that animal breeding was placed on a scientific basis, as we know it today.

In 1893, Branth, a Danish dairy cattle breeder, observed,

"The fact is that there is no trace of an external sign on the animals by which it is possible to know whether they will produce a fat or a poor milk. One has to judge exclusively from their pedigree, and the value of the sire in this respect will only become evident in the progeny." (Bonnier, 1936.)

Branth's investigations were known to Sederholm, who later made a more thorough investigation in his own herd in Sweden. He compared the daughters of a number of sires with their dams and was able to demonstrate that his various bulls had a distinctive influence upon the fat percentage in the milk of their respective daughters.

Still later the Sederholm herd was studied by Hansson, who, in 1913, suggested that the expected record of the daughter would be half way between that of her dam and the potential of her sire, with reference to the fat percentage of the milk. In other words, on the average, the yield of any daughter would be $D = \frac{S + M}{2}$, and $S = 2D - M$, where $S$ and $M$ represent sire and dam (Bonnier, 1936). Hansson was primarily concerned with nutrition in his studies. He introduced sire evaluation simply as a means of adjusting the records of the cows so as to more accurately judge the effects of feeding on the percentage of butterfat.
In 1919, Pearl et al. used as a measure of a sires' "transmitting quality" the index, \( S = D - M \), or the average difference of the daughters and their dams. They applied this same test to corrected yearly records of milk, fat yield and average test by Jersey cows. Milk production records were corrected to a basis equivalent to the production of an eight-year-old cow, while yearly average test was corrected to a basis equivalent to that of a two-year-old cow. The corrected fat yield was a product of the corrected values for milk and test for that record.

At the 1924 meetings of the American Society of Animal Production, Yapp, apparently unaware of Hansson's work, proposed that the transmitting ability of the sire is indicated by the index, \( S = 2D - M \), but with all values expressed in terms of 4 percent fat-corrected milk (FCM). This latter value is computed by the formula developed by Gaines and Davidson (1923), being \( FCM = 0.4 \text{ milk} + 15 \text{ fat} \), expressed in units of weight.

While these two men proposed the same basic index, one for percent butterfat and the other for FCM, it was also widely adapted to index sires for milk and butterfat production. In the United States, the index was given its greatest impetus by Goodale and Prentice (Prentice, 1935) stemming from their work at the Mount Hope Farm in Massachusetts. This index, with various slight modifications, came to be known as the Yapp-Hansson, equal-parent (EP), intermediate, modified Mount Hope or American index.

Both Hansson and Yapp presented their index before the development of what is presently known as quantitative genetics. Yet extensive later research work in the fields of population and quantitative genetics did not destroy the validity of the index under certain conditions. This research has clearly indicated that very large numbers of individual
pairs of genes affect a production trait such as milk or butterfat. This fact, coupled with the sampling nature of inheritance, where each offspring receives a sample half of the genes from each parent, creates a condition where the daughters of a bull tend toward an average production value midway between that of his potential and the average of the various dams. However, in order for this to be entirely true, the environmental effects must all be random.

One of the main criticisms directed at the EP index is that it supposedly assumes the heritability ($g^2$) of the trait being indexed to be unity (1.0) (Johansson and Robertson, 1952; Edwards, 1953; Hofmeyr, 1955). However, as Lush points out (Lush, 1945, p. 363) this criticism is important only when the daughters are considered one or a few at a time. The major reasons for not trusting this index completely arise from what are called Mendelian errors and errors of appraisal. The former come from chance at segregation which permits gametes coming from the same parent to contain different genes, so that some offspring are genetically superior to the average of their parents, while others are inferior. These variations are truly random, provided the daughters are an unselected sample. Therefore, they tend to cancel each other and their importance in an average diminishes as the number of daughters increases. Some of the errors of appraisal, such as corrections for length of lactation or age differences, tend to cancel each other also with an increase in number of daughter-dam pairs. Other errors of appraisal may not be random and thus do not cancel each other with an increase in number of pairs. These may include levels of environment to which the daughters and dams are exposed, selection of records for
daughters and/or dams, selection of daughters and/or dams used in the
index, and allowances for the effects of dominance and epistasis. The
latter are usually of only minor significance, but the other factors are
often of vital importance when comparing different bulls.

Graves, in 1926, suggested that sires be evaluated on the basis of:
(1) the average yield of their daughters; (2) the average increase (or
decrease) in the yield of the daughters over their dams; and (3) the
numbers of daughters that exceed their dams. His argument for (3) seemed
to be based on the presumption, without conclusive evidence, that uni­
formity in the superiority of the daughters of a sire over their dams
was a clear indication of the sire's merit. Johnson (1945) has shown
that this uniformity is, in general, related to environmental factors
rather than to the transmitting ability of the sire. However, the basic
features of Graves' method were later incorporated into the USDA system
of presenting information available for sire evaluation. Under this
system, periodic reports were issued which included: (1) the average
production of all reported records of tested daughters of a particular
sire; (2) the average records of daughters with tested dams along with
the average records of these dams; (3) the difference in production
between the daughter average and the average of their dams; and (4) the
numbers of daughters exceeding the production of their dams for milk and
butterfat yield and lactation average test. No rating or index, as such,
was published for a sire. The information was merely presented to be
used as the public saw fit. This system was supplanted in 1962 by a
new plan which will be discussed later.

Gifford (1930) compared dairy sires by various indexes including the
equal-parent \((S = 2\overline{D} - \overline{M})\), that of Pearl et al. (1919) \((S = \overline{D} - \overline{M})\), daughter average \((S = \overline{D})\), and one he had developed \((S = \overline{D} - .2\overline{M})\). In the latter index, the \(.2\)' was the intra-group regression of records of individual daughters on their dam's production, all computed on a 365 day--ME basis, and after all records were divided into \(\frac{1}{4}\) sire groups on the basis of the average production of daughters of the respective sires. The criterion Gifford used to compare the indexes was the average deviation of the proofs, computed when the mates of each sire were divided into three groups according to their production, from the proofs computed when all records were pooled for each sire. The simple daughter average had long been used as a measure of a bull's transmitting ability by some dairy breeders. Gifford was apparently one of the first workers to have analyzed actual dairy data specifically to compare different progeny testing schemes, and found that the simple daughter average compared favorably with other methods. However, this was true only when there was a considerable number of unselected daughters included in the progeny group. In the United States, the American Jersey Cattle Club bases some of its sire recognition programs on the principle of simple daughter average. The daughter average also plays a prominent role in the advertising of some artificial insemination (AI) companies in this country.

In a study of the effects of selection of dams on sire indexes, Lush et al. (1941) pointed out that more intense selection of the mates of some sires than of others biases the daughter-dam difference more than either the EP or daughter average indexes. Selection of the dams makes
the increase of daughters over dams too low by the quantity \((\bar{M} - \text{BA}) (1 - \frac{g^2}{2})\), where \(\bar{M}\) is the average of the dams, BA equals the breed population average and \(g^2\) is the heritability of the trait. The daughter average is biased in the opposite direction by the quantity \((\bar{M} - \text{BA}) \frac{g^2}{2}\) which favors the bull mated to the most highly selected dams. Since the EP index is simply the sum of the daughter average and the increase of the daughters over their dams \([S = 2\bar{D} - \bar{M} = \bar{D} + (\bar{D} - \bar{M})]\) these two biases tend partly to cancel each other in the index leaving the net bias equal to \((\bar{M} - \text{BA})(1 - g^2)\). The daughter average is most vulnerable and the daughter-dam difference is least vulnerable to errors from wrongly appraising differences in general environment from herd to herd, with the EP index again being intermediate but somewhat nearer to the daughter average.

The above authors, in the same study, suggested that, if the dams were selected solely on their past records in that herd, then for strict-est accuracy, the sire index should include the expression for the estimated breeding value of the dam rather than a simple average of each dam's records. The estimated breeding value of each dam, \(G_M\), is computed as

\[
G_M = \text{herd average} + \frac{ng^2}{1 + (n-1)r} (M - \text{herd average}). 
\]  

(Eq. 1)

Here \(n\) is the number of records by each dam, \(M\); \(g^2\) is the heritability of intraherd differences among cows on the basis of single lactations; and \(r\) is the intraherd repeatability of single lactations of the same cow. The sire index would then be:

\[ S = 2\bar{D} - \text{average } G_M. \]
If the dams were unselected in relation to the herd average, the last term in Equation 1 would tend toward zero, and it would not matter whether \( M \) or the herd average were used in the index.

In 1889, Galton presented his concept of regression as related to heredity,

"... by the law of universal regression, each peculiarity in man is shared by his kinsman, but on the average, in a less degree."

Pearson and Lee (1903), in a study of sons' heights in relation to their fathers' heights, found that the sons' average height deviated from the population mean slightly less than half as much as the deviation of the fathers.

Down through the ages, livestock breeders have found this same tendency of offspring to regress toward the population mean from the average level of their parents.

Norton in 1933 (Lush, 1933) incorporated a form of this concept of regression into dairy sire indexes. He substituted a value termed "Expectancy" or \( E \) in place of the average production of the dams in the EP index: \( S = \bar{Y} + (\bar{Y} - E) \). He calculated the average production of daughters out of cows producing at various levels of production from a large number of Holstein-Friesian A.R. records. He called these values the expectancy for daughters of dams at the various levels. For example, dams averaging 500 pounds of butterfat had daughters averaging 602 pounds of butterfat production, while dams producing at the 800 pound level had daughters which averaged 705 pounds production, etc. His expectancy figures correspond closely to the equation,

\[
E = BA + b_{DM} (\bar{Y} - BA), \tag{Eq. 2}
\]
where BA is the breed average and $b_{DM}$ is the regression of the records of individual daughters on the records of their respective dams, and was computed simply over the whole population sampled. The computed $b$ was close to .33. Thus $E = BA + \frac{1}{3} (\overline{M} - BA) = \frac{M + 2BA}{3}$ and $S = D + (D - E) = D + (D - \frac{M + 2BA}{3}) = D + \frac{1}{3} (D - M) + \frac{2}{3} (D - BA)$.

This proposed index was not put into practice but the regression concept attained increasing importance with the passage of time.

In 1944, Rice offered what he termed the NEW (or Regression) index in which $S = BA + (\overline{D} - E)$, where $BA =$ breed average. He computed his $E$, or expectancy value, from HIR data to be $\frac{M + BA}{2}$. This he derived from the regression equation, $E = BA + b_{DM} (\overline{M} - BA)$. Here $b_{DM}$ was computed as the regression of the average of the records of the daughters of each sire on the average of the records of their respective dams, and was close to the value of .5 which he adopted. Thus, $E = BA + \frac{1}{2} (\overline{M} - BA) = \frac{M + BA}{2}$. Rice also substituted breed average as a base in place of daughter average, which Norton had proposed. Therefore, $S = BA + (\overline{D} - E)$

$= BA + (\overline{D} - \frac{M + BA}{2}) = BA + \frac{1}{2} (\overline{D} - M) + \frac{1}{2} (\overline{D} - BA)$, or simply,

$S = \frac{(2\overline{D} - \overline{M}) + BA}{2}$. The last equation indicates that Rice's index was simply another form of the EP index, in that the latter was merely regressed half way toward the breed average. This exact form for a sire index was never adopted in actual practice, but its presentation served a useful purpose in stimulating thinking on various aspects of sire evaluation in general.

One other index proposal is worth mentioning. Wright (1932)
incorporated both a form of the regression concept plus a consideration for number of daughter-dam pairs. With \( n \) daughter-dam pairs,
\[
S = BA + \frac{n}{n+2} [2\bar{D} - \bar{M} - BA].
\]
When \( n \) is large this formula approaches the EP index: \( S = 2\bar{D} - \bar{M} \). While this index did allow for differences which small numbers would make in proofs\(^1\) where heritability was less than perfect, it did not allow for any nonrandomness among the nongenetic factors which affected the daughter average and the average of the dams. In this respect it was similar to the EP index.

In 1944, Lush pointed out that the amount of genetic improvement in the next generation by selecting on the basis of an index, \( I \), which incorporated the records of both the daughters, \( D \), and Dams, \( M \), is
\[
\frac{r_{GS}I}{r_{GS}D} \times \text{the improvement to be expected by selecting (with the same intensity) for } \bar{D}, \text{ the daughters' average, alone. } G_S \text{ is the sire's breeding value. If we assume } r_{GS}M \text{ is zero (it most likely is not far from zero), the above ratio reduces to } \frac{1}{\sqrt{1 - r_{DM}^2}}.
\]
From Rice's data (1944), which consisted entirely of records comprising 'natural' proofs, Lush calculated that this fractional increase amounted to from 12 to 20 percent in favor of an index incorporating averages of daughters and dams as compared to using the daughter average only.

According to Lush\(^2\), the principal use of including the records of

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\(^1\)The word 'proof' or 'proving', as commonly used in dairy cattle breeding literature, is simply a synonym for 'index' and refers specifically to a composite value placed on a bull on the basis of his progeny test, where the latter may take numerous forms.

the dams in proving a sire is to correct for environmental peculiarities of the herd in which those daughters made their production. For this purpose, the records of the contemporaries should be even better, by quite a margin. The main reason is that the environment changes from year to year in the same herd, and the dams will rarely have made their records in exactly the same years as their daughters. The dams' records do have a slight theoretical advantage in correcting for whether the dams' breeding values were above or below herd average, but heritability is low enough that this advantage is small.

All the previous indexes largely predate the introduction of artificial insemination (AI) into dairy cattle breeding. They apply mainly to so-called natural provings where a bull is used in only one or at most in a very few herds. We have seen that the two major sources of bias in evaluating dairy sires are: (1) the effects of unknown or uncorrected differences in the herd environment accorded the individuals in the same or in different proofs, and (2) differences in the merit of the dams mated to one bull as compared with those mated to a second bull. A new phase of dairy sire evaluation studies came with the introduction of AI into Western Europe and North America in the late 1930's and early '40's. Bulls could now be used in numerous herds covering the full range of herd environments found in any stud service area. Also the use of fresh semen precluded much selection of sires for use on specific cows, as the dairyman had, at most, only a limited choice of bulls available on the day the cow was ready for service. As a result, the two major biases noted above as limiting the effectiveness of natural service proofs were greatly reduced with AI proofs. In the late 1950's, frozen semen, along
with differential fees for different sires, became a new feature of AI service, thus permitting special, or nominated matings, as referred to by Robertson and Rendel (1951). This conceivably might become a factor for bias if the trend continues toward increased use of such service.

The rapid acceptance of AI has greatly stimulated interest in progeny testing, with numerous methods being employed throughout the world. Only those most pertinent to this thesis will be discussed here.

In Denmark, a station test for progeny of AI bulls was started in 1945 and continues to the present. The main features are: (1) the daughters of the bulls are chosen at random without considering the yield of their dams; (2) all daughters selected for test must freshen in the same season and at approximately the same age; (3) their records are made in the supposedly standardized environment of the testing stations; and (4) comparisons between progeny groups are based simply on their average records at the various stations. However, analyses from these stations have indicated that the attempts to eliminate various nongenetic differences between progeny groups have not been entirely successful (Touchberry et al., 1960; Johansson, 1961).

Since 1953, Swedish progeny testing has been centrally coordinated by the state with daughters now tested on the farms where they were raised. The average first lactation yield of milk and butterfat is calculated for all the daughters of the bull on test and corrected to an expected yield at a standard age of 28 months at first calving. The milk yield is also converted to a standard fat content of 4 percent. No daughter-dam comparisons are made. Instead the daughters' average yield of fat-corrected-milk is expressed as a percentage of the
corresponding yield of daughters of other bulls in herds at the same
production level as that where the members of the particular progeny
groups were raised and freshened. An adjustment is made for number of
daughters included in the summary.

Norway has incorporated many of the features noted for Sweden. With
the advent of their "Hedmark System" in 1955, the yields of first calf
heifers are recorded for actual and 4 percent FCM, along with fat and
protein content. As the daughters are purposely located in many herds
within a concentrated area and freshen within the same season, no
corrections for season of calving or herd environment are made. Only
the daughters' average goes into the bull index.

In Holland, on-the-farm testing is likewise the basis of the progeny
test, with daughter-dam comparisons computed for milk, butterfat, butter-
fat percentage and protein content of the milk.

Peters, in Germany, perhaps was the first to use herdmate comparisons
in progeny testing (Johansson, 1961). At the present time, methods
vary among the states of West Germany. The most common method is
daughter-dam comparisons, using the milk and butterfat yields relative
to their herd averages. The average fat percentage of the daughter
group is compared directly with that of their dams without reference
to the herd average.

The contemporary comparison has been the basic feature of progeny
testing work in Great Britain since 1953 (Edwards, 1953). The compu-
tational procedure, originally devised by Alan Robertson, compares the
average of the first 305-day yield of the daughters of a bull with the
average yield of their contemporary herdmates of the same age group but
sired by different bulls. The difference between the two averages is weighted for the number of heifers in each group. The weighting factor \((w)\) equals \(\frac{\frac{n_1}{n_1 + n_2}}{\eta}\), the inverse of the variance of the difference between the two groups or one-half of the harmonic mean of the number of daughters \(n_1\) and number of contemporaries \(n_2\) in the herd. The weighted differences for all herds with such comparisons are added and weighted, \(\sum w (D - HA) = D_w\), where \(HA\) is the average of the contemporary herdmates. This value is adjusted for the number of daughters by multiplication with the factor, \(b = \frac{\eta^2 \sum w}{\eta + (2w-1)g^2}\), which is one-half of the regression of the bull's breeding value on the average of his daughters, or the regression of future daughters on those tested. (The above value for \(b\) thus assumes random mating and zero environmental correlations between all paternal half sibs.) For a comparison with the population as a whole, \(0.2 (HA - BA)\) is included, where \(0.2\) is the estimated heritability of interherd variation and \(BA\) is the breed average for first calf heifers in the specified population. The relative breeding value (RBV) of the bull is then expressed as:

\[
RBV = \frac{[2b D_w + 0.2 (HA - BA) + BA] 100}{BA},
\]

being a percentage of the breed average. Two features associated with this method are: (1) no age correction factors are used although a few months of difference in age at first calving can have important effects on lactation production (Lush and Shrode, 1950); and (2) numerous herds do not provide comparisons due to a lack of contemporary first calf heifer herdmates by other bulls.
The method of progeny testing presently in effect in New Zealand likewise is based on the contemporary comparison principle, with several major differences from that in Great Britain (New Zealand Dairy Board, Annual Report, 1958-61). All records of cows are corrected to a mature-equivalent basis with ages 5 to 9 considered mature and with multiplicative factors now being applied. Each daughter's adjusted record is then compared with what is termed the expected daughter average. This latter value is computed as:

$$\text{Expected daughter average} = \text{district-season average} + 0.9 \left( \text{HA} - \text{district-season average} \right).$$

The district-season average is computed from the average of herd test records for the particular district and season by multiplying the actual average by 1.1 to convert it to a mature equivalent (ME) basis. The herdmate average, HA, is really the ME lactation average for contemporary cows, other than daughters of the bull in question, in the particular herd concerned. The factor 0.9 is the estimate of the fraction of environmental difference between the herd average and the district average that could be expected to be reflected in the daughter average. The deviations for all daughters from their respective expected values are then averaged and the bull's final rating is adjusted by the factor $\frac{n}{n + 15}$, which is comparable to the 'b' value employed in Great Britain. The bull's index is presented in terms of a deviation, either plus or minus, from expectancy.

In the United States, a major change in sire evaluation methods was inaugurated in 1962. Previous to that, as was discussed on page 9, the USDA simply presented daughter and dam production averages along with differences in these averages. No rating or index, as such, was published
for any bull. All records were corrected to a 305-day-2X-ME basis, which means the record is standardized to a lactation of 305 days, two times per day milking, and on a mature equivalent yield basis. Multiplicative factors were used in making these corrections.

The new system for testing AI bulls is quite similar to that described for New Zealand, with certain modifications. The major features of the present system are: (1) lactation records standardized to a 305-day-2X-ME basis are still being used; (2) dams are no longer considered; (3) 'adjusted' and 'regressed' contemporary herdmate averages have been incorporated; and (4) each bull is given a production rating, or index, which is published periodically.

The methods of computation are outlined in brief here, using to a large extent the terminology employed by Miller (1962), in describing this system of indexing AI sires in the United States. Certain aspects of the methods or reasoning may not be self-explanatory as presented and some duplication of formulas may appear to exist. However, a detailed discussion will be postponed until later in this thesis.

A moving five-month season grouping is used to determine the makeup of herdmates. For a particular record of a daughter, the production is averaged for all cows calving in the herd in the five-month period centered on the month in which the daughter has freshened. Neither the record of the daughter nor of any identified paternal half sib is included in this herdmate average (HA). The adjusted herdmate average (AHA) is then computed by the formula: 

$$AHA = breed\ season\ average + \frac{n}{n + 1} (HA - breed\ season\ average)$$

where $n$ = number of herdmates. Thus a herdmate average containing many records has a greater weight, when
adjusted, than one with few records. The breed season average is compiled from nation-wide DHIA standardized lactation averages of all cows of the same breed freshening in the same five-month season as this daughter. Records for the previous four years are used.

The average of the records for the daughters is then 'adjusted' as follows:

\[ \text{ADA} = \text{daughter average} - 0.9 \left[ \text{AHA} - \text{breed average (BA)} \right], \]

where ADA means adjusted daughter average. The breed average is the nation-wide breed DHIA standardized lactation production average for the preceding four-year period, over all the months in the year. Although seemingly used in a different capacity here as compared with its use in the New Zealand scheme, the factor 0.9 is applied for the same purpose in both computations - to adjust the daughter's record for the nongenetic effects of the herd in which the record is made.

The predicted AI daughter average for the sire is then computed as follows:

\[ \text{Predicted AI daughter average} = \text{BA} + \frac{n}{n + 12} (\text{ADA} - \text{BA}), \]

where \( n \) here is number of daughters. \( \frac{n}{n + 12} \) is the particular value that has been adopted in this country for the regression of future daughters on previous ones tested. It functions in a manner similar to the \( 'b' \) values used in Great Britain and New Zealand - to adjust the sire index for the number of daughters included. Under this system the predicted AI daughter average is the sire index, and is computed for milk and for butterfat yield. The final values are presented in pounds of milk and butterfat and are therefore comparable to lactation values for cows.
B. Seasonal Effects on Lactation Production

Numerous workers have investigated the effect of season or month of calving on subsequent lactation totals or averages. In general, under northern hemisphere temperate zone conditions, cows calving in the fall and winter months yield more milk and butterfat than those calving at other times of the year. However, in an area as large as the United States, significant divergences from these average effects have been noted, as might be expected.

Cannon (1933) studied 68,000 records from Iowa cow testing associations for the years 1925-1930 for the effect of month and season of freshening on total production by these cows during their subsequent 12 months on test. For milk production, cows freshening in November produced the top production totals (5.5 percent above the mean). The lowest 12 month production totals were made by cows freshening in June (9 percent below the population average). November was also the high month for subsequent butterfat production, while May, June, and July were equal as low months. For average butterfat test, however, cows calving in June produced the highest average lactation test, while cows calving in February and March were lowest in this respect.

Plum (1935) studied the effect of season of freshening on differences in production records as a part of a more extensive study, using sources of data similar to that employed by Cannon. He found that cows calving during November through January produced 13.6 percent more butterfat than cows calving from May through July. His analysis of variance indicated that only 3 percent of the total variance among records was due to season of calving.
Sundaresan and Freeman (1961) in a study of 12,623 records, corrected to a 305-day-2X-ME basis, made by Iowa Holsteins in 12 state-owned herds for the period 1940 through 1956, determined the relative importance of month and season of calving on lactation butterfat production. The variance components they found for month and season of freshening are as follows, expressed as a percentage of total variance:

<table>
<thead>
<tr>
<th>All records</th>
<th>First records</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Month</strong></td>
<td><strong>First records</strong></td>
</tr>
<tr>
<td></td>
<td><strong>3 months</strong></td>
</tr>
<tr>
<td><strong>Season</strong></td>
<td></td>
</tr>
</tbody>
</table>

The 3 month seasons were consecutive groups of months beginning with January, while the 6 month seasons were April through September and October through March. They also found that calving from October through December were the most favorable months for high fat production in that lactation, with July through September the least favorable.

Annis et al. reported in 1959 on month and seasonal effects upon lactation production in the state of Washington. March and April were the most favorable months of freshening for both milk and butterfat yield, while July and August were least favorable. The range in differences for milk and butterfat totaled 4.9 percent. They further found seasonal differences to be associated with age of cow and level of herd production.

Two reports from Georgia indicate that cows calving in the winter and spring produced significantly more milk and butterfat than cows calving during the summer months (Lee et al., 1961; Fosgate and Welch, 1960).
In a New Hampshire study, Morrow et al. (1945) reported the average milk yields by breeds for 4030 cows calving in different months. Production was calculated on a 305-day-ME basis corrected to 4 percent butterfat. December was the most favorable month for freshening with June least favorable, the difference in yields being 19.2 percent.

Frick et al. in 1947 reported that, in Connecticut, cows calving in February produced the most milk during that lactation, with those freshening in August producing the least. The difference here was 14.9 percent.

Carter and Henderson (1955) studied lactation butterfat records of AI-sired New York Holsteins, 22 to 34 months of age. Cows freshening in the period September through December produced on the average 40 pounds of butterfat more than cows freshening from April through August.

According to Van Vleck et al. (1961b), the seasonal breakdown in New York for use in their sire proving work is as follows: December through March, April through July, and August through November, which agrees well with the effects found in the previously cited reference.
III. SOURCE AND ADJUSTMENT OF DATA

Only records by grade and registered Holsteins in Iowa Standard DHIA and DHIR herds on central processing¹ were used. Holsteins were selected because over 2/3 of all records available were by cows of this breed. Each record was required to have been at least 90 days in length before it was terminated. Records thus qualifying but which were ended by death of the cow, sale of the cow for beef or dairy purposes, or legitimate use of the cow as a nurse cow were extended to a 305-day-equivalent basis. Madden's factors (Bureau of Dairy Industry, 1953) were used. Any record under 305 days in length and terminated by an abortion was extended to 305 days. The lactation started by this abortion was then discarded. However, if a new lactation record was started by an abortion in a dry cow or in a lactating cow at least 12 months after the start of the previous record, it was used, if qualifying otherwise. Also, if a cow had no other record available, one that had started with an abortion was used. Approximately one percent of the records of 90 days or more in length were started by an abortion. Records for cows going dry were not extended. All records were then converted to a 2X-ME basis using factors by Kendrick (1955).

All records were carefully screened for accuracy of identification and production data. By the time the final analyses were being made, over 39,000 usable lactation records from over 750 different Iowa herds were used.

¹Central processing refers to the method where herd test data are sent to a computing center each month for processing on digital computers instead of the former practice of having each herd's records computed by the tester on the farm.
had accumulated. Freshening dates extended from May of 1957 through September of 1960.

Of this total number of records, about 16,000 or 40 percent, were by registered cows with sire and dam identified. Of the 60 percent by grade cows, 62 percent had no sire identified, 36.5 percent had registered sires identified, and 1.5 percent had grade sires identified. Approximately 64 percent of records by grade cows had no dam identified, 34 percent had grade dams identified, and 2 percent had registered dams indicated. Of the grade cows with sire identified, 76 percent also had the dam identified. But among the grade cows with no sire identified, only 10 percent had the dam identified. Thus 37 percent of all records by Iowa Holsteins included in these studies had no sire identified, 38 percent had no dam identified and fully 33 percent had neither sire nor dam identified.

While a grand total of over 39,000 records were on hand by December of 1961, relatively few records were available during the early years after central processing of records commenced in Iowa in January of 1958. This may be seen in Table 1. A complete file of records for any individual month of freshening was generally not available for computational use until approximately 13 to 14 months later.
Table 1. Numbers of records available from different time periods of freshening

<table>
<thead>
<tr>
<th>Freshening period</th>
<th>Records available</th>
</tr>
</thead>
<tbody>
<tr>
<td>May, 1957, to April, 1958</td>
<td>3980</td>
</tr>
<tr>
<td>May, 1958, to April, 1959</td>
<td>9746</td>
</tr>
<tr>
<td>May, 1959, to April, 1960</td>
<td>16730</td>
</tr>
<tr>
<td>May, 1960, to Sept., 1960</td>
<td>8902</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>39368</strong></td>
</tr>
</tbody>
</table>
IV. METHODS, RESULTS AND DISCUSSION

A. Effects of Herds and Months or Seasons of Freshening on Lactation Production Records

1. Herds and months analysis

By the end of February, 1961, 24,259 usable lactation records with freshening dates from May, 1957, through December, 1959, a period of 32 months, were available for analysis. Averages were computed from all records commencing in each of the 12 months over all the years of data available. For example, records for cows freshening in May of 1957, 1958 and 1959 were pooled to get the average for May freshening. Only records for two years were available for the months of January through April in this study, while records for three years were on hand for the other eight months.

Analyses of variance were then computed so as to determine the relative importance of the effects attributable to herds, months of freshening, and their interaction, for the three production traits. The statistical model assumed for these analyses was a simple cross-classification with two effects plus their interaction:

\[ X_{ijk} = \mu + h_i + m_j + h_m_i_j + e_{ijkl} \]

Here, \( X_{ijk} \) is the lactation yield (on a 305-day-2X-ME basis) for the \( k \)th record which was started in the \( j \)th month and made in the \( i \)th herd;

\( \mu \) is a constant effect common to all records in this population and is estimated by the overall average yield;

\( h_i \) is the effect of the \( i \)th herd and includes all causes for the
average production in the \(i^{th}\) herd being different from that in other herds. It includes both an environmental and a genetic effect peculiar to the \(i^{th}\) herd;

\(m_j\) is the average effect of the \(j^{th}\) month of freshening which causes records started in that month to differ from records started in other months, among all herds;

\(hm_{ij}\) is the particular effect of the \(j^{th}\) month of freshening in the \(i^{th}\) herd. It represents the effect of the interaction of the \(j^{th}\) month of freshening with the conditions in the \(i^{th}\) herd in which the record is made;

\(e_{ijk}\) is a random effect attributable to the deviation of the \(k^{th}\) record from the mean of the \(ij^{th}\) herd-month group of records.

With this type of analysis, we are interested primarily in estimates of the variance components as parameters of the population. We have assumed that the main effects and interaction effects are randomly and independently distributed, and they are defined to have zero means and variances \(\sigma_n^2, \sigma_m^2, \sigma_{hm}^2, \text{ and } \sigma_e^2\). Thus \(\sigma^2_{(X_{ij}^k)} = \sigma_n^2 + \sigma_m^2 + \sigma_{hm}^2 + \sigma_e^2\) under the above assumptions. Perhaps the main question about the assumption of randomness concerns the effects of months. It was considered random here since it is only one of numerous time period divisions possible, which more than likely would have yielded similar results. These include, for example, a strict 30-day time period division, or one in which each time period extended from the 15th of one calendar month to the 15th of the next month, etc.

The assumption of independence of main effects is not likely to be entirely valid as a later analysis indicated a slight positive correlation
between level of herd production and season of freshening. If such a
correlation does exist then both herds and months get credited with any
term resulting from the covariance between them. This automatically
makes the interaction term too low if that correlation is positive. It
is believed, however, that, since only part of the data were used to
determine the correlation found, the biases were not of a serious nature
here. Thus the values obtained may be considered reasonably accurate.

The computational procedures used in this analysis are fully des-
cribed by Henderson (1953) under his Model I, and by Harvey (1960, p. 65).

Table 2 shows the analysis of variance. Because the data are not
completely orthogonal nor can be assumed to be normally distributed,

Table 2. Analysis of variance for herds and months

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>Degrees of freedom</th>
<th>Mean squares&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Milk</td>
</tr>
<tr>
<td>Herds (H)</td>
<td>648</td>
<td>966642</td>
</tr>
<tr>
<td>Months (M)</td>
<td>11</td>
<td>2700906</td>
</tr>
<tr>
<td>H x M</td>
<td>4300</td>
<td>64357</td>
</tr>
<tr>
<td>Within</td>
<td>19299</td>
<td>47005</td>
</tr>
<tr>
<td>Total</td>
<td>24258</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup>The original data were in 10 pounds for milk, in percent for test and in pounds for fat.

tests of significance are not exact. However, with so many degrees of
freedom, almost any real effect might be expected to appear statistically
significant. As was noted earlier, the components of variance are the
main concern in this type of analysis. These provide estimates of the relative importance of the effects in the population as a whole.

Table 3 presents the computed values for these components. We see that slightly over 30 percent of the variance present among all milk and butterfat production records is due to the average effect of the herd in which the record is made. This compares with only about 1.5 percent associated with the month of freshening and 5 percent due to the effect of the interaction of herd and month of freshening. The balance, about 60 percent, is accounted for by the variation among records within a herd-month subclass. The latter is almost wholly variance among records by different cows, in this analysis.

Table 3. Components of variance from analysis for herds and months

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>Milk Actual</th>
<th>Milk Percent</th>
<th>Test Actual</th>
<th>Test Percent</th>
<th>Fat Actual</th>
<th>Fat Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herds (H)</td>
<td>23962</td>
<td>31.5</td>
<td>.021</td>
<td>17.1</td>
<td>3456</td>
<td>32.7</td>
</tr>
<tr>
<td>Months (M)</td>
<td>1281</td>
<td>1.7</td>
<td>.001</td>
<td>1.1</td>
<td>143</td>
<td>1.4</td>
</tr>
<tr>
<td>H x M</td>
<td>3823</td>
<td>5.0</td>
<td>.004</td>
<td>3.1</td>
<td>554</td>
<td>5.3</td>
</tr>
<tr>
<td>Within</td>
<td>47005</td>
<td>61.8</td>
<td>.097</td>
<td>78.7</td>
<td>6401</td>
<td>60.6</td>
</tr>
</tbody>
</table>

Note: Components are in actual values and in percent of total variance. The original data were in 10 pounds for milk, in percent for test and in pounds for fat.

The herd effect is considerably less important as a source of variance in test, contributing 17 percent of the total, while month and interaction effects contribute slightly less of the variance for test.
than they do for milk or fat yield.

The relative magnitudes of the months and interaction effects would seem to indicate that adjusting records for the month in which they were commenced is hardly worth-while unless the herd can be considered as well.

2. Herds, months and seasons effects

The primary purpose of a seasonal grouping of records within a herd, at least so far as sire evaluation work is concerned, is to measure and remove this extraneous source of variation and thus facilitate a more exact appraisal of genetic merit. Subdividing seasonal variation into increments as small as months may be impractical because the numbers of records beginning in an average herd-month generally would be too small for a reliable contemporary comparison. By grouping months into appropriate seasons, this problem could be alleviated greatly. Various questions immediately arise: (1) How does one go about selecting the proper plan for such groupings? (2) What criteria shall be used to judge which plan is most desirable for a specific sire-proving program? (3) What are the consequences of using a less favorable scheme?

Two major types of seasonal groupings are possible in this situation - moving (or rolling) seasons and fixed seasons. The former refers to the type used by the USDA in its present sire proving program (see page 20) while the latter has specific consecutive months of freshening comprising a season, with generally 2 or 3 such seasons for the year. The former will be discussed further on page 43. In the present discussion we are concerned only with fixed seasons.

If two or more production traits such as milk, test and butterfat
are being considered, whether seasonal trends differ significantly among the traits must be determined. If so, a decision must be made as to which trait or traits will be given most consideration.

A study of the data showing trends in lactation production starting in the various months of the year and averaged over all of the years of data available will then allow at least a preliminary decision as to which grouping of months might be most appropriate. Perhaps more than one seasonal plan may appear to be satisfactory. Analyses of variance can then be computed as one means of evaluating the data further.

The most appropriate seasonal grouping (plan) presumably should have the following characteristics, as determined from the analyses of variance: (1) largest possible variance due to seasons, for the trait(s) being given primary consideration; (2) least possible variance among months within seasons; and (3) smallest possible variance components for the interactions, herds-by-seasons and herds-by-months-within-seasons. Other considerations of practical importance include: (4) largest number of records available within herd-year-season subgroups; and (5) most applicable to systematic operational procedures.

Any one seasonal grouping is unlikely to excel in all respects so that a less than optimum, or compromise, seasonal division may need to be adopted. Finally, seasonal trends must be kept under constant study so that, periodically, slight adjustments can be made, if needed, in the groupings of months. Such changes might be due to changes in weather conditions in an area or to a general adoption of new management practices that are related to seasonal effects.

In these studies, a meaningful seasonal division for test would be
quite different from one for milk and butterfat. Table 3 shows that month of freshening has less effect on test than on milk and butterfat production. Also, milk yield is more important commercially than test. It was therefore decided to disregard test and consider only milk and butterfat production in these analyses of seasonal effects.

Five different season plans were tested, using exactly the same data as were used in the analysis of herds and months (see previous section). These plans are presented in Table 4.

Table 4. Groupings of months into seasons

<table>
<thead>
<tr>
<th>Plan</th>
<th>Seasons</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>I</td>
<td>October-February (Five months)</td>
</tr>
<tr>
<td>II</td>
<td>November-April (Six months)</td>
</tr>
<tr>
<td>III</td>
<td>October-March (Six months)</td>
</tr>
<tr>
<td>IV</td>
<td>October-April (Seven months)</td>
</tr>
<tr>
<td>V</td>
<td>October-January (Four months)</td>
</tr>
</tbody>
</table>

The structure of the model assumed for this analysis was purely a cross-classification with respect to herds and seasons, and hierarchal with respect to months within seasons. The herds-by-months interaction effects were computed on an intraseason basis while the 'within subclass'
effects were confined to groups of records within the various herd-month subclasses, the same as in the herds and months analysis in the previous section. All effects were assumed to be randomly and independently distributed and were defined to have zero means and variances $\sigma_h^2$, $\sigma_s^2$, etc.

Of course the assumption that 'seasons' is a random effect is not an entirely valid one. The data were first examined and various seasonal divisions were made so that the subsequent seasons components would be expected to be maximized. As a result it is indeed surprising that the seasons components were as small as those actually found (see Table 5). It would seem, therefore, that a significant facet of this analysis is that no matter which season plan was adopted, among those tested here, only small differences were found among the season components for the various plans.

It is apparent from Table 5 that each of the above five plans has advantages and disadvantages, any of which might need to be considered in any particular situation. On the basis of the criteria noted above and additional information obtained when more records were available at a slightly later date, it was decided to use Plan IV in subsequent seasonal divisions of the data. This plan provides two seasons each year, October through April and May through September.

3. **Further analyses of effects of months and seasons of freshening**

Further studies of the effects of months and seasons of freshening on lactation production records were made at a later date when 38,435 records for cows freshening in the three-year period, October, 1957, through September, 1960 were available. Table 6 presents the numbers
Table 5. Herds, months and seasons analysis of variance for different season plans

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>Plan I</th>
<th>Plan II</th>
<th>Plan III</th>
<th>Plan IV</th>
<th>Plan V</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Milk yield</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Herds (H)</td>
<td>30.87</td>
<td>31.17</td>
<td>31.11</td>
<td>31.12</td>
<td>30.60</td>
</tr>
<tr>
<td>Seasons (S)</td>
<td>1.68</td>
<td>1.98</td>
<td>1.98</td>
<td>2.39</td>
<td>1.95</td>
</tr>
<tr>
<td>Mos./Seas.</td>
<td>.75</td>
<td>.56</td>
<td>.59</td>
<td>.40</td>
<td>.31</td>
</tr>
<tr>
<td>H x S</td>
<td>.74</td>
<td>.08</td>
<td>.13</td>
<td>.05</td>
<td>1.96</td>
</tr>
<tr>
<td>H x Mos./S</td>
<td>4.64</td>
<td>4.06</td>
<td>4.95</td>
<td>5.01</td>
<td>3.75</td>
</tr>
<tr>
<td>Residual</td>
<td>61.33</td>
<td>61.15</td>
<td>61.24</td>
<td>61.03</td>
<td>61.43</td>
</tr>
<tr>
<td><strong>Butterfat yield</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Herds (H)</td>
<td>32.36</td>
<td>32.47</td>
<td>32.37</td>
<td>32.35</td>
<td>32.45</td>
</tr>
<tr>
<td>Season (S)</td>
<td>1.72</td>
<td>1.16</td>
<td>1.79</td>
<td>1.93</td>
<td>1.52</td>
</tr>
<tr>
<td>Mos./Seas.</td>
<td>.38</td>
<td>.69</td>
<td>.36</td>
<td>.31</td>
<td>.29</td>
</tr>
<tr>
<td>H x S</td>
<td>.14</td>
<td>.42</td>
<td>.35</td>
<td>.51</td>
<td>.28</td>
</tr>
<tr>
<td>H x Mos./S</td>
<td>5.45</td>
<td>5.43</td>
<td>5.40</td>
<td>5.43</td>
<td>5.09</td>
</tr>
<tr>
<td>Residual</td>
<td>59.65</td>
<td>59.83</td>
<td>59.73</td>
<td>59.47</td>
<td>60.37</td>
</tr>
</tbody>
</table>

Components of variance are in percent of total variance within each plan.

For milk production, the extreme difference in lactation averages is 1109 pounds or 9.5 percent more by cows freshening in November than...
Table 6. Lactation production averages for different months of calving, pooled over all years available

<table>
<thead>
<tr>
<th>Month of calving</th>
<th>No. of records</th>
<th>Calving age (mos.)</th>
<th>Milk (lbs.)</th>
<th>Test (%)</th>
<th>Butterfat (lbs.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>3267</td>
<td>52.7</td>
<td>12631</td>
<td>3.59</td>
<td>453</td>
</tr>
<tr>
<td>February</td>
<td>2779</td>
<td>53.2</td>
<td>12692</td>
<td>3.59</td>
<td>454</td>
</tr>
<tr>
<td>March</td>
<td>2755</td>
<td>54.3</td>
<td>12462</td>
<td>3.60</td>
<td>447</td>
</tr>
<tr>
<td>April</td>
<td>2291</td>
<td>54.5</td>
<td>12455</td>
<td>3.60</td>
<td>447</td>
</tr>
<tr>
<td>May</td>
<td>1923</td>
<td>52.7</td>
<td>12355</td>
<td>3.57</td>
<td>440</td>
</tr>
<tr>
<td>June</td>
<td>2250</td>
<td>53.6</td>
<td>12053</td>
<td>3.60</td>
<td>433</td>
</tr>
<tr>
<td>July</td>
<td>2976</td>
<td>55.1</td>
<td>11789</td>
<td>3.62</td>
<td>427</td>
</tr>
<tr>
<td>August</td>
<td>321</td>
<td>51.7</td>
<td>11615</td>
<td>3.65</td>
<td>422</td>
</tr>
<tr>
<td>September</td>
<td>5883</td>
<td>50.6</td>
<td>11923</td>
<td>3.66</td>
<td>435</td>
</tr>
<tr>
<td>October</td>
<td>3366</td>
<td>51.9</td>
<td>12460</td>
<td>3.66</td>
<td>455</td>
</tr>
<tr>
<td>November</td>
<td>3253</td>
<td>52.1</td>
<td>12724</td>
<td>3.66</td>
<td>464</td>
</tr>
<tr>
<td>December</td>
<td>3371</td>
<td>52.6</td>
<td>12717</td>
<td>3.61</td>
<td>457</td>
</tr>
<tr>
<td>Total and averages</td>
<td>38435</td>
<td>52.68</td>
<td>12278</td>
<td>3.624</td>
<td>443.6</td>
</tr>
</tbody>
</table>

by those freshening in August. The comparative figures for butterfat yield are 42 pounds and 9.8 percent, also for the same months. However, it should be noted that these differences would be cut approximately in half if the average over the entire year were used as a base for comparison, which would be the normal practice if the standard deviation of monthly means were being computed.
Figure 1. Lactation production averages for each month of freshening (in percent of overall average yield for each trait)
4. **Year and season effects**

Table 7 presents averages for various groupings of records according to time periods. The averages are presented in actual values for each trait and in the percent of the overall average for the three-year period. Notable are: (1) the higher milk and fat production averages for the winter season over the summer season; and (2) the gradual decline in level of milk and fat production, but not in test, from one year to the next as an increasing number of herds participated in the voluntary central-processing program.

Table 7 is presented mainly to show certain peculiarities of the data used in these various studies which undoubtedly had some effect on some of the results throughout the thesis.

5. **Herds and year-season effects**

Studies concerning the role of herds with respect to month and season of freshening were discussed in Sections IV-A-1 and IV-A-2. In the present analysis, the time periods consisted of year-seasons. A total of 33,139 lactation records for cows freshening from May, 1957, through September of 1960 were used, comprising a total of seven year-seasons. That is, lactation records with freshening dates from May, 1957, through September, 1957, made up year-season 1, records with freshening dates from October, 1957, through April, 1958, were designated as year-season 2, etc., up to year-season 7 which included records with freshening dates from May, 1960, through September of 1960. (These 33,139 records were the same as those used in the analysis described on page 104.)

Table 8 shows the derived components of variance in actual values.
Table 7. Variation in lactation production records

<table>
<thead>
<tr>
<th>Months included</th>
<th>No. of records</th>
<th>Milk</th>
<th>Test</th>
<th>Butterfat</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pounds</td>
<td>Percent</td>
<td>Percent</td>
<td>Percent</td>
</tr>
<tr>
<td>Year-season lactation averages</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10-57:4-58</td>
<td>3057</td>
<td>12805</td>
<td>104.29</td>
<td>3.607</td>
</tr>
<tr>
<td>5-58:9-58</td>
<td>3124</td>
<td>12123</td>
<td>98.74</td>
<td>3.616</td>
</tr>
<tr>
<td>10-58:4-59</td>
<td>6622</td>
<td>12735</td>
<td>103.72</td>
<td>3.607</td>
</tr>
<tr>
<td>5-59:9-59</td>
<td>5327</td>
<td>11890</td>
<td>96.84</td>
<td>3.649</td>
</tr>
<tr>
<td>10-59:4-60</td>
<td>11403</td>
<td>12464</td>
<td>101.51</td>
<td>3.626</td>
</tr>
<tr>
<td>5-60:9-60</td>
<td>8902</td>
<td>11805</td>
<td>96.15</td>
<td>3.629</td>
</tr>
<tr>
<td>Season averages</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May-Sept.</td>
<td>17353</td>
<td>11888</td>
<td>96.82</td>
<td>3.632</td>
</tr>
<tr>
<td>Winter</td>
<td>21082</td>
<td>12598</td>
<td>102.61</td>
<td>3.617</td>
</tr>
<tr>
<td>Year averages</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10-57:9-58</td>
<td>6181</td>
<td>12460</td>
<td>101.48</td>
<td>3.611</td>
</tr>
<tr>
<td>10-58:9-59</td>
<td>11949</td>
<td>12358</td>
<td>100.65</td>
<td>3.626</td>
</tr>
<tr>
<td>10-59:9-60</td>
<td>20305</td>
<td>12175</td>
<td>99.16</td>
<td>3.627</td>
</tr>
<tr>
<td>Total and averages</td>
<td>38435</td>
<td>12278</td>
<td>3.624</td>
<td>443.6</td>
</tr>
</tbody>
</table>

*Percent of overall average for each trait (e.g., 104.29 = \( \frac{12805}{12278} \)).
and in percent of the respective totals.

We see further confirmation in Table 8 of the dominant role played by the herd in which a record is made, so far as concerns variance in milk and butterfat. However, for test, the importance of the herd is only about one-half that for milk or butterfat yield.

Table 8. Components of variance for herds and year-season analysis

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Milk Actual</th>
<th>Milk Percent</th>
<th>Test Actual</th>
<th>Test Percent</th>
<th>Fat Actual</th>
<th>Fat Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herds (H)</td>
<td>21178</td>
<td>28.1</td>
<td>.0177</td>
<td>14.7</td>
<td>3046</td>
<td>29.2</td>
</tr>
<tr>
<td>Year-Seas. (YS)</td>
<td>1703</td>
<td>2.3</td>
<td>.0002</td>
<td>.2</td>
<td>187</td>
<td>1.8</td>
</tr>
<tr>
<td>H x YS</td>
<td>2434</td>
<td>3.2</td>
<td>.0050</td>
<td>4.1</td>
<td>424</td>
<td>4.1</td>
</tr>
<tr>
<td>Within</td>
<td>50140</td>
<td>66.4</td>
<td>.0976</td>
<td>81.0</td>
<td>6764</td>
<td>64.9</td>
</tr>
</tbody>
</table>

Components are in terms of actual values and in percent of total variance for each trait.

In contrast with the herd effect, the year-season in which a record is started has a relatively minor effect on lactation milk and butterfat yields. The seasonal division employed here was made by a previous examination of a portion of the same data used in this study, with reference to milk and fat yields, so the components for year-seasons for these traits appear at least a little larger than would have been the case with a purely random selection of the seasonal division.

It was pointed out in Section IV-A-2 that a desirable seasonal division for test would have been quite different from that for milk or fat yield. As a result of the division into seasons employed here, the
component for year-seasons for test is negligible.

The components for interaction of herds and year-seasons appear to be high relative to the seasonal effect, being of the order of three to four percent. This suggests that even in as homogeneous an area as Iowa, a moderate amount of variation exists with respect to a proper alignment of year-seasons for all herds. The most recent estimate published for this effect was made for New York herds by Van Vleck et al. (1961b, see Table 17). After having removed the sire effect, they found the herd-by-year-season component to be 5.9 and 6.9 percent of the total variance for milk and 6.7 and 8.5 percent for butterfat yield in two separate analyses. These are considerably higher than the values found here. Those authors mention that differential reaction to drought conditions, especially with regard to purchased feedstuffs, by different herds may be a factor contributing to the magnitude of these effects. It is possible, too, that differences in weather and other management practices are more pronounced within the state of New York than in Iowa.

Perhaps the most significant conclusion that can be made from Table 8 is that we should be considerably more concerned with reducing the herd-by-time-period interaction effects than with year-season effects, per se. It is apparent that the fixed year-season method leaves much to be desired in this important respect.

Although no analysis was computed here to evaluate the herd-by-year interaction effects, it seems plausible that much of the herd-by-months and herd-by-year-seasons interaction effects noted are really herd-by-year interaction effects. Some herds are improving in management and
some are declining. Some have outbreaks of disease while others are overcoming its effects. These things are not properly a seasonal effect at all, but under the models in the above analyses of variance, they would contribute to the interaction effects.

6. The rolling season average

The USDA presently uses another approach to the problem of grouping months into seasons for use in their new sire proving program (see p. 20). In this method, herdmate comparisons are made with cows calving in the same herd as, say, cow A, and in the five-month period centered on the month in which cow A freshened. For example, if cow A freshened in May, her herdmate comparison would be made with records of cows in the same herd and freshening in the months of March, April, May, June and July of that same year. (Actually records from previous years for these same months are used in arriving at the final herdmate average, but this need not concern us at the moment.) This system may be referred to as the rolling season method.

Perhaps the major appeal of this method of seasonal grouping of months is that it allows for uniform handling of records from widely different areas in the country, where seasonal effects may vary considerably. Another advantage is that herdmate comparisons can be made at any time of the year and do not depend on fixed seasons. For example, in the Iowa data, if cow A has calved in May, we would need to wait until the records for cows freshening through July were in the files in order to make the desired herdmate comparison under the rolling season scheme. However, we would have to wait two months longer, until the September
records are completed and in the files, under a method of fixed seasons, where the summer season is May through September, for example.

Of far more importance, the rolling season method would merit adoption if it could be shown, along with the above advantages, that a significant reduction in the herd-by-year-season interactions as well as no loss of precision in the removal of year-season effects result when taking deviations from a fixed year-season herdmate average.

A method for testing accurately this precision of removal of season effects would entail using large numbers of records, with deviations computed for each record on the basis of the alternate season plans. Such data were not available or prepared for this study. A modified analysis was therefore devised to provide a simulated comparison of various methods of seasonal groupings.

In this analysis, approximately 39,000 records were used to compute the average production, over all herds, for each month of freshening from August, 1957, through July, 1960. Average production values were also computed for each grouping of months under the five different plans being compared. These were: (1) fixed year-seasons where records from May through September and October through April comprised the seasons for each of the three years; (2) rolling year-seasons where records from five consecutive months, centered on the month of freshening by the cow in question, comprised the year-season; (3) pooled fixed seasons in which records from the three years were averaged for the summer and winter seasons; (4) pooled rolling seasons in which the records from the particular five-month period were averaged for all three years of data available; and (5) years from fixed seasons, whereby records from two adjacent
fixed seasons (as in plan 1) were combined so that each 'season' was one year in length.

Deviations were then computed as follows: the month's average minus its particular season average, for each of the 36 months included and for each of the five season plans studied here. For example, say the particular month is June of 1959. The average production of all records commencing in that month is computed. Then, under plan (1), above, the production of all records starting in the months of May, 1959, through September of 1959, including June, were used to compute the appropriate season average. Under plan (2) all records starting in April, 1959, through August of 1959 were used to compute this season average. Under plan (3) all records starting in May through September for 1957, 1958, 1959 and 1960 were used to compute this season average. Under plan (4) all records starting in April through August in 1958, 1959 and 1960, along with the records started from May through August of 1957 were used to compute this season average. (No records were available prior to May of 1957.) Finally, under plan (5), records starting from October, 1958, through September of 1959 were used to compute this particular season average. The same process was followed for the other 35 months.

Appropriate season averages and deviations were computed for each of the 36 months, or three deviations for each calendar month. The 36 deviation records for each of the 5 plans were used to compute analyses of variance for effects between months and among years within months, with 11 and 24 degrees of freedom, respectively. Thus, for each of the 12 calendar months, the three deviation records were averaged and the
variance among the averages provided the mean square between months. The variance among years within months is really variation among, for example, the deviations for June, 1958, June, 1959, and June, 1960, within the average effect of June over all three years. This was computed similarly for the other 11 months. This variance is denoted as $\sigma^2_w$, and is the measure used here for comparing the various plans in their ability in removing seasonal effects when records are expressed as deviations from various seasonal averages.

Table 9 shows the values for $\sigma^2_w$ computed for milk and butterfat yield, as well as for average lactation test, when employing each of the five season plans. The actual components are presented along with the fraction which is the ratio of the $\sigma^2_w$ component for the fixed year-season plan, plan (1), to the $\sigma^2_w$ components for each of the other plans.

Table 9. A comparison of different season plans

<table>
<thead>
<tr>
<th>Season plan</th>
<th>Milk Actual</th>
<th>Milk Fraction</th>
<th>Test Actual</th>
<th>Test Fraction</th>
<th>Fat Actual</th>
<th>Fat Fraction</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1)</td>
<td>184</td>
<td>1.00</td>
<td>.000298</td>
<td>1.00</td>
<td>18</td>
<td>1.00</td>
</tr>
<tr>
<td>(2)</td>
<td>167</td>
<td>1.10</td>
<td>.000168</td>
<td>1.77</td>
<td>23</td>
<td>0.78</td>
</tr>
<tr>
<td>(3)</td>
<td>559</td>
<td>0.33</td>
<td>.000631</td>
<td>0.47</td>
<td>35</td>
<td>0.51</td>
</tr>
<tr>
<td>(4)</td>
<td>631</td>
<td>0.29</td>
<td>.000586</td>
<td>0.51</td>
<td>62</td>
<td>0.29</td>
</tr>
<tr>
<td>(5)</td>
<td>361</td>
<td>0.51</td>
<td>.000427</td>
<td>0.71</td>
<td>44</td>
<td>0.41</td>
</tr>
</tbody>
</table>

*aSee text for a description of these season plans.

The component for plan (1) is computed as a fraction of the components for each of the other plans; e.g., $\frac{184}{167} = 1.10; \frac{184}{559} = 0.33; \text{ etc.}$
We had noted earlier (Table 2) that the average level of production declined slightly but steadily as the data accumulated under the newly inaugurated central-processing program. This decline was more than would normally be expected under a situation where the number of herds participating remained relatively uniform. Therefore, when season averages were computed using all three years of data as under plans (3) and (4), we would automatically expect a slight inflation of the $\sigma^2_w$ components under these two plans. The use of monthly production averages, rather than the averages of individual records, further limited the interpretation of the results. However, it is believed that we can still get a very good indication of what might be expected when various seasonal averages are used in computing deviations.

There are a number of implications from the results in Table 9. We can only say briefly here that, considering all three production traits, the rolling year-season plan proved to be about equal to the fixed year-season plan as a means of removing year-season effects with deviation records. The pooling of records from more than one year into a season average appears to be considerably less efficient in removing year-to-year seasonal changes when records are expressed as deviations from their respective season average.

At the beginning of Section IV-A-2 the question was asked, "what are the consequences of using a less favorable scheme?" This referred to a scheme for grouping months into seasons. Table 9 provides some
information on this question, although the results are restricted in that (1) the only fixed season plan employed was that which was judged best suited to these data after a large portion of them were studied, and (2) no estimate was computed for the size of the herd-by-rolling-season interaction. We do see that using a year's average would remove only about one-half of the variation, for milk and butterfat, that is attributable to season of freshening, which could be removed by employing deviations from a seasonal average within the year. For test, it is less vital to consider seasonal differences within a year. Therefore, part of the answer is simply that the further a season plan deviates from the optimum in removing season effects, the less accurate will be the estimate of the genetic merit of sires, for example, from the deviation records of their daughters.

In order to view the picture in its proper perspective, it should be kept in mind that the year-season component is a relatively minor source of variance among records, contributing only about two to three percent of the total in these data. Also, the seasonal effect would generally be even less important in sire proving because usually the daughters are scattered over several months and seasons, so far as freshening dates are concerned. An extreme example of when it might be important to consider the seasonal effect is when one bull's daughters all freshened in a favorable season and he was compared with a bull all
of whose daughters freshened in an unfavorable season.

On the other hand, in evaluating cows, the month and seasonal effects are more important because all of a cow's records are usually bunched in one season of a year. This is true because on the average the calving interval is close to 13 months.

However, even with AI sire provings, as long as deviation records are to be used, with the primary consideration being the removal of herd environmental effects, it seems only logical to use a seasonal division that will remove, at the same time, as much of the month, season and year effects as is possible.

But this is only part of the answer, and the lesser part. As noted earlier, a major defect of the fixed season plan was the comparatively high herd-by-year-season interaction component accompanying its use. As the present analysis (Table 8) tested only the removal of seasonal effects when using deviations, no comparison is possible there between the two alternate season plans (rolling versus fixed) with regard to reduction of the herd-by-season interaction components. However, the rolling-year-season plan would appear to be quite promising in this respect, and surely merits further study.

Thus, each season plan needs to be judged on its utility in reducing both seasonal and herd-by-seasonal interaction components of variance.
B. Repeatability Estimates

1. Theoretical considerations

It is common knowledge that a cow will not produce exactly the same amount of milk or fat in two separate lactations. In other words, the repeatability of these records is not unity (1.0). By repeatability, in the present context, is meant simply the coefficient of correlation, $r$, between single records made by the same cow. Many factors may contribute to the differences in yield among lactations by the same cow. These include age of the cow, number of times milked per day, length of lactation, year and season conditions and management practices, to name only a few.

In studying production records we often seek to evaluate the real producing ability (RPA) of a cow. This might be defined as the producing ability of the cow under environmental conditions chosen as standard. As it is practically impossible to standardize the environment physically, statistical adjustment of records for certain measurable factors is common practice. Correcting records to a 305-day-2X-ME basis is such an attempt to correct for average differences in length of lactation, times milked per day and age at freshening. However, it is not possible to evaluate correctly all environmental sources of error. Neither is it practical nor desirable to correct the raw data too much. After making corrections for a few of the most important conditions which are not standard, it is preferable to compute the repeatability of these records and then take the incompleteness of repeatability into consideration when estimating the desired element, real producing ability, for
example. In order to compute the RPA, an estimate of \( r \) is needed.

One method of estimating repeatability is by the use of intraclass correlation with variance components derived from an analysis of variance. We can approach this method by the use of path diagrams (Wright, 1934).

Figure 2 shows the general intraherd relationships between two records by the same cow, with respect to the factors affecting their values. \( YS \) is the effect of the specific year-season of freshening on the respective records. \( E_{Ti} \) and \( E_{Tj} \) are any other random temporary environmental factors affecting records \( i \) and \( j \). By definition, \( E_{Ti} \) and \( E_{Tj} \) are uncorrelated. \( GT \) may be thought of as the sum total of the genetic (or genotypic) effects of this cow, including additive, dominance and epistatic, if they could be measured in a perfectly standardized environment.

Similarly, \( EP \) may be defined as the average effect of the permanent environmental factors affecting different records by the same cow but which are different from one cow to another. Examples might be stunted growth of a cow during the months prior to first calving or permanent udder injury prior to her first lactation. There also could be favorable permanent effects.

Therefore, from Figure 2, we have, \( r_{RiRj} = h^2 + e^2_p \), on an intraherd basis. Here, \( h^2 \) is defined as heritability in the broad sense (Lush, 1959). In terms of variances,

\[
    r_{RiRj} = \frac{\sigma_{GT}^2}{\sigma_{Ri} \sigma_{Rj}} + \frac{\sigma_{EP}^2}{\sigma_{Ri} \sigma_{Rj}} = \frac{\sigma_{GT}^2 + \sigma_{EP}^2}{\sigma_R^2},
\]

if we assume \( \sigma_{Ri} = \sigma_{Rj} \), \( R_i = R_j \) and no environment-genotype interactions.
Figure 2. Path diagram showing intraherd relationships between two records by the same cow.

YS = Year-season effect
ET = Temporary environmental effect
EP = Permanent environmental effect
GT = Genotypic or hereditary effect
R = Record or phenotype
Now, for the sake of convenience, let $Y_S$ be the variance of the year-season effects, $E$ be the variance of the other temporary environmental and random error effects, and $C$ be the variance of the 'cow effect', or the variance of the combined effects of $G_T$ and $E_p$. Then,

$$r_{R_i R_j} = \frac{C}{C + Y_S + E}.$$  

This is the intraclass correlation (repeatability) of different records of the same cow within herds. If we can measure the effect due to $Y_S$ and deduct it from the denominator, we have

$$r_{R_i R_j} = \frac{C}{C + E},$$  

the repeatability within herd-year-seasons. This value would be applicable to records which are expressed as deviations from their herd-year-season averages.

When a cow makes her separate records in different herds, what may be termed a repeatability ratio would be of the form $\frac{C + fH}{H + C + Y_S + E}$.

Here, $H$ is the variance of herd environmental effects, and $fH$ represents a function or fraction of this variance that would be included in the numerator. $f$ would range between zero and one, depending on how closely related in level of management practices were the different herds in which the separate records were made.

The repeatability ratio may also be thought of as expressing the fraction of the total variance among corrected records which is due to permanent differences among cows ($G_T + E_p$). More rigid control of the environment, i.e., making $E$ smaller, will naturally increase the value of $r$. Thus $r$ is a description of conditions in a particular situation and is not a fundamental biological constant (Lush, 1945, p. 175).

The above discussion leads directly into the model for the analysis of variance used in these studies to estimate repeatability.
2. Model and results

The biometrical model assumed for this analysis of variance is as follows:

\[ X_{ijk} = \mu + h_i + y_{ij} + c_{ik} + e_{ijk} \]

\( X_{ijk} \) is the lactation yield of the \( k^\text{th} \) cow freshening in the \( j^\text{th} \) year-season in the \( i^\text{th} \) herd.

\( \mu \) is the effect common to all observations in this specific population.

\( h_i \) is the effect of the \( i^\text{th} \) herd and the expectation, \( E \), of \( h_i^2 \),

\[ E(h_i)^2 = \sigma_h^2 = H. \]

\( y_{ij} \) is the effect of the \( j^\text{th} \) year-season of freshening in the \( i^\text{th} \) herd, and \( E(y_{ij})^2 = \sigma_{ys}^2 = YS. \)

\( c_{ik} \) is the effect of the \( k^\text{th} \) cow in the \( i^\text{th} \) herd and \( E(c_{ik})^2 = \sigma_c^2 = C. \)

\( e_{ijk} \) is the random error in evaluating the \( (ik)^{\text{th}} \) cow's production, with \( E(e_{ijk})^2 = \sigma_e^2 = E. \)

As the problem here is not to make tests of significance, but rather to estimate the variance components from the different effects in the model, no assumptions need be made concerning the form of the distribution of the several effects. All that must be assumed is that the effects which make-up each observation are random variables independently distributed (Crump, 1946). As is customary, these effects are defined to have zero means; i.e., each is defined as a deviation from its mean in that particular population.

A study of the model indicates that cows and year-seasons are confounded with each other to some extent, instead of being completely
independent, as the model states. Thus a cow may have records in more than one year-season, but no cow will have records in all year-seasons, while different cows commence records within each year-season. A clean separation of cow, year-season and error effects is desired.

Dr. Lush suggested a solution for a similar problem to Legates (Legates and Lush, 1954). The idea was to break down the intraherd variance in two ways simultaneously: (1) years within herds, and within years within herds; and (2) cows within herds, and within cows within herds. Under (1), and applying this method to the present model (which has year-seasons in place of years, which was used in the cited reference), the intra-year-season effect is composed of $c_{ik} + e_{ijk}$; while under (2), $y_{ij} + e_{ijk}$ make-up the effects within cows. The analysis of variance then yields five simultaneous equation with but four unknowns, $H$, $YS$, $C$ and $E$. The desired component values can be derived by solving any four of these equations.

The data used in this analysis, which is termed the 'Overall' analysis, covered a time period of three years of freshening. But only records from herds with 10 or more records and with records commencing in at least three year-seasons were included. All usable, corrected (305-day-2X-ME) records for all cows from these herds were used, whether a cow had only one, two or three records.

Table 10 presents the analysis of variance for the three production characters studied. Table 11 presents the components found for each character in actual values and in percent of total variance and of the variance within herds and Table 12 gives the various estimates of repeatability computed from the values in Table 11.
Table 10. "Overall" repeatability analysis of variance

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>Degrees of freedom</th>
<th>Mean squares&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Milk</td>
<td>Test</td>
</tr>
<tr>
<td>Herds (H)</td>
<td>399</td>
<td>1482534</td>
</tr>
<tr>
<td>YS/H</td>
<td>1379</td>
<td>96469</td>
</tr>
<tr>
<td>Within YS/H</td>
<td>23051</td>
<td>50356</td>
</tr>
<tr>
<td>Cows/H</td>
<td>15976</td>
<td>65728</td>
</tr>
<tr>
<td>Within C/H</td>
<td>8454</td>
<td>28830</td>
</tr>
<tr>
<td>Total</td>
<td>24829</td>
<td>75932</td>
</tr>
</tbody>
</table>

<sup>a</sup>Original data were in 10 pounds for milk, in percent for test and in pounds for fat.

Table 11. Components of variance for "Overall" repeatability analysis

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>Milk Actual</th>
<th>Milk Total</th>
<th>Milk Within herd</th>
<th>Test Actual</th>
<th>Test Total</th>
<th>Test Within herd</th>
<th>Fat Actual</th>
<th>Fat Total</th>
<th>Fat Within herd</th>
</tr>
</thead>
<tbody>
<tr>
<td>H</td>
<td>21784</td>
<td>28.7</td>
<td>.0168</td>
<td>13.8</td>
<td>3138</td>
<td>29.9</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>YS/H</td>
<td>3893</td>
<td>5.1</td>
<td>.0066</td>
<td>5.5</td>
<td>589</td>
<td>5.6</td>
<td>5.0</td>
<td>8.0</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>25420</td>
<td>46.8</td>
<td>.0700</td>
<td>57.8</td>
<td>3192</td>
<td>30.5</td>
<td>43.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>24936</td>
<td>46.0</td>
<td>.0278</td>
<td>22.9</td>
<td>3564</td>
<td>34.0</td>
<td>48.5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 12. 'Overall' repeatability estimates with approximate 95% confidence limits

<table>
<thead>
<tr>
<th></th>
<th>Milk</th>
<th>Test</th>
<th>Fat</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>.505</td>
<td>.716</td>
<td>.473</td>
</tr>
<tr>
<td>C + E</td>
<td>.691 - .521</td>
<td>.706 - .726</td>
<td>.457 - .488</td>
</tr>
<tr>
<td>C + YS + E</td>
<td>.689</td>
<td>.671</td>
<td>.435</td>
</tr>
<tr>
<td>H + C + YS + E</td>
<td>.334</td>
<td>.578</td>
<td>.305</td>
</tr>
</tbody>
</table>

*Computed by Fisher's z transformation (Snedecor, 1956, p. 173).

These estimated repeatability values agree well with most published figures, which range from .3 to .5 for milk and butterfat and are distinctly higher for test.

From Table 11 it can be seen that in terms of percent of total or intraherd variance, the cow component for milk is larger than that for fat yield, while that for lactation average test is considerably larger than either. Conversely, the error components are smallest for test and largest for fat yield. These relationships are reflected in the larger repeatability values for milk as compared with fat yield, while those for test are larger than for either milk or fat.

If the differences between herds are ignored and the records are treated as if the population were not subdivided into herds, what we may
term a form of repeatability would be computed, for example, as

$$\frac{H + C}{Total} = \frac{.287 + .334}{100} = .621$$

for milk as compared with

$$\frac{C}{Total} = .334$$

when the herd component is properly accounted for; that is, when repeatability is computed on an intraherd basis. The former is comparable to the methods used by a number of the early students of dairy records, who reported high repeatability figures. Although the cows usually stayed in the same herds, the data from many herds were treated as if they came from the same population. See, for example Gowen, 1930, p. 91.

3. **Repeatability analyses for daughters and dams**

Two additional repeatability analyses, using the same model as above, were computed from data used in connection with the heritability studies to be discussed in a later section, one for the dams and another for their daughters.

Table 13 summarizes some descriptive statistics concerning these three separate studies. It may be noted that more herds were represented in the analyses for daughters and dams than in the 'overall' repeatability study. This is due simply to the fact that only those herds with 10 or more records were selected for the overall repeatability study, while this restriction was not applied to the data for the daughter and dam analyses. Tables 14 and 15 contain the components of variance computed for the daughter and dam repeatability analyses. These are presented in actual component values and in percent of total variance. Table 16 lists the repeatability values computed from Tables 14 and 15.

Two points are of interest: (1) the cow components for the dams are slightly larger than for their daughters; and (2) among the dams,
Table 13. Miscellaneous statistics from three repeatability analyses

<table>
<thead>
<tr>
<th>Type of statistic</th>
<th>'Overall'</th>
<th>Dams</th>
<th>Daughters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total no. of records</td>
<td>24830</td>
<td>5311</td>
<td>6117</td>
</tr>
<tr>
<td>No. of cows</td>
<td>16376</td>
<td>3138</td>
<td>4178</td>
</tr>
<tr>
<td>Ave. no. records per cow</td>
<td>1.52</td>
<td>1.69</td>
<td>1.46</td>
</tr>
<tr>
<td>No. of herds</td>
<td>400</td>
<td>443</td>
<td>443</td>
</tr>
<tr>
<td>Ave. no. records per herd</td>
<td>62.1</td>
<td>12.0</td>
<td>13.8</td>
</tr>
<tr>
<td>No. of herd-year-seasons (HYS)</td>
<td>1779</td>
<td>1400</td>
<td>1355</td>
</tr>
<tr>
<td>Ave. no. records per HYS</td>
<td>14.0</td>
<td>3.8</td>
<td>4.5</td>
</tr>
<tr>
<td>Ave. no. YS per herd</td>
<td>4.4</td>
<td>3.2</td>
<td>3.1</td>
</tr>
<tr>
<td>Average age (mos.)</td>
<td>52.8</td>
<td>76.5</td>
<td>40.4</td>
</tr>
</tbody>
</table>

Table 14. Repeatability components of variance for dams

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>Milk</th>
<th>Test</th>
<th>Fat</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Actual</td>
<td>Percent</td>
<td>Actual</td>
</tr>
<tr>
<td>H</td>
<td>19765</td>
<td>26.3</td>
<td>.0222</td>
</tr>
<tr>
<td>YS/H</td>
<td>5874</td>
<td>7.8</td>
<td>.0046</td>
</tr>
<tr>
<td>C</td>
<td>26878</td>
<td>35.8</td>
<td>.0659</td>
</tr>
<tr>
<td>E</td>
<td>22609</td>
<td>30.1</td>
<td>.0277</td>
</tr>
</tbody>
</table>
Table 15. Repeatability components of variance for daughters

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>Milk Actual</th>
<th>Percent</th>
<th>Test Actual</th>
<th>Percent</th>
<th>Fat Actual</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>18748</td>
<td>26.3</td>
<td>.0195</td>
<td>17.7</td>
<td>2622</td>
<td>26.8</td>
</tr>
<tr>
<td>YS/H</td>
<td>2487</td>
<td>3.5</td>
<td>.0077</td>
<td>6.9</td>
<td>458</td>
<td>4.7</td>
</tr>
<tr>
<td>C</td>
<td>23319</td>
<td>32.7</td>
<td>.0583</td>
<td>52.7</td>
<td>3024</td>
<td>30.9</td>
</tr>
<tr>
<td>E</td>
<td>26808</td>
<td>37.5</td>
<td>.0251</td>
<td>22.7</td>
<td>3675</td>
<td>37.6</td>
</tr>
</tbody>
</table>

Table 16. Repeatability values for dams and daughters

<table>
<thead>
<tr>
<th>r</th>
<th>Milk Dams</th>
<th>Daughters</th>
<th>Test Dams</th>
<th>Daughters</th>
<th>Fat Dams</th>
<th>Daughters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>.543</td>
<td>.465</td>
<td>.704</td>
<td>.699</td>
<td>.487</td>
<td>.451</td>
</tr>
<tr>
<td>C + E</td>
<td>.486</td>
<td>.443</td>
<td>.672</td>
<td>.640</td>
<td>.430</td>
<td>.422</td>
</tr>
<tr>
<td>C + YS + E</td>
<td>.548</td>
<td>.527</td>
<td>.313</td>
<td>.309</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>.358</td>
<td>.326</td>
<td>.548</td>
<td>.527</td>
<td>.313</td>
<td>.309</td>
</tr>
</tbody>
</table>

the year-season components (YS) for milk and fat, but not for test, are larger than for their daughters.

While these analyses were not made with the specific purpose of checking on the effects of year-season of freshening on records of cows of different ages, such a comparison was possible here. From Table 13, we see that the average age at freshening was 76.5 months for the dams.
as compared with 40.4 for the daughters, which is a difference of 36 months. This age differential would, of course, be expected in data such as were used here, covering a period of only three years. It is of little concern here that these two groups of records were made by dams and their daughters. The important thing is that older cows are more subject to changes in seasonal effects than are younger cows, so far as concern milk and fat yield. This is indicated by the considerably larger year-season components (for milk and fat) for older cows (dams) than for the younger cows (daughters). A similar effect was noted by Annis et al. (1959) and by Sundaresan and Freeman (1961). Yet the seasonal effect worked in the opposite direction for test; i.e., the younger cows had a larger YS component for test than did the older cows. This is undoubtedly related to the negative genetic and phenotypic correlations between the traits of milk and test and simply indicates that the latter trait reacts differently to environmental effects such as year-season of freshening. However, this would not invalidate the conclusions noted above concerning factors affecting milk and fat responses.

A study of the lactation production averages for milk and fat for different months of freshening among both the dam and daughter groups indicated a more extreme dip for lactations following summer calving and a larger increase for lactations subsequent to winter calving among the dams than among their daughters. However, no changes in the groupings of months from those used here would be needed to maximize seasonal differences for the records of either the dams or the daughters, separately.
C. Heritability Analyses

1. Theoretical considerations

The literature contains many fine discussions on the meaning and estimation of what is termed the heritability of quantitative traits. See, for example, those by Lush (1940, 1945, 1948, 1949, 1961) and Falconer (1960). For the sake of simplicity we shall confine ourself in the main to the situation for a population mating at random. Random mating has been defined as the condition existing when, for any given kind of male gamete, the probability that it will unite with each kind of female gamete is the proportion of that kind of female gamete present in the population. Although mating is, of course, not absolutely random in all cases, this situation is closely approximated, within subgroups of a population, in most livestock breeding operations.

For each individual animal, its phenotype (P) is a function of its genotype, or heredity (H), and its environment (E). The term heritability, in its broad sense, designated here as $h^2$, concerns what fraction of the observed phenotypic variance is due to differences between the hereditary make-up of different individuals. If we assume additivity of E and H and no correlation between them, we have, simply,

$$h^2 = \frac{\sigma_H^2}{\sigma_P^2} = \frac{\sigma_H^2}{\sigma_H^2 + \sigma_E^2}.$$

Although the genotype functions as a unit, it is not transmitted as such. Instead the genes possessed by an individual segregate and recombine in new combinations for each separate offspring. In its simplest form, this process is that of Mendelian segregation and independent
assortment, with multiple alleles and linkage modifying the results.

Upon union of male and female gametes, a new zygote, or genotype, is formed. The effects of genes and gene interactions in this new genotype have been classified into arbitrary components. Thus,

\[ H = G + D + I, \]

where

- **H** is the hereditary or genotypic value;
- **G** is the sum of the effects ascribable to individual genes (additive or genic effect, denoted also as breeding value);
- **D** is the sum of the effects of interactions between allelic genes, or dominance deviations, over all loci; and
- **I** is the sum of the effects of interactions among non-allelic genes, or epistatic deviations, over all combinations of loci.

By definition and computation, these three effects are uncorrelated. Thus, in terms of variance,

\[ \sigma_H^2 = \sigma_G^2 (\text{or } \sigma_A^2) + \sigma_D^2 + \sigma_I^2. \]

Actually, one never knows exactly what effects a gene substitution would have in all kinds of genotypes in which it might occur. In fact we usually know very little about what particular genes are present and we are uncertain about the frequencies of those. Therefore, estimating what fractions of \( \sigma_H^2 \) are \( \sigma_G^2 \), \( \sigma_D^2 \), and \( \sigma_I^2 \) has to be done indirectly by methods which are based in one way or another on the resemblances between various kinds of relatives.

The correlation between parent and offspring of the various kinds of genetic effects is of primary importance in any consideration of heritability. This correlation comes directly from the fraction of the
effects of a given kind which are identical in parent and offspring. As a parent transmits only a sample half (within loci, and discounting sex-linkage) of its aggregate of genes through one of its gametes to any offspring, one-half of the genic effects, none of the dominance effects, and a small amount of the epistatic effects in the parent go in the gamete to its offspring. There are no dominance correlations between parent and offspring under random mating because the two genes in a pair at any locus cannot get into the same gamete in order to reach that particular offspring. This is the primary reason we separate dominance from other forms of gene interaction; i.e., it is a property of allelic as contrasted with non-allelic interaction. Departures from random mating will affect, in a complicated manner, the correlation of the above effects in parent and offspring (see Lush, 1948, Chapter 8).

Heritability in the narrow sense, designated as \( h^2 g^2 \), or simply as \( g^2 \), here, includes only as hereditary the variance due to the average effects of the genes; i.e., only the additive or genic variance \( \sigma_G^2 \):

\[
g^2 = \frac{\sigma_G^2}{\sigma_P^2} = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_D^2 + \sigma_I^2 + \sigma_E^2},
\]

assuming an additive combination of \( E \) and \( H \), and no correlation between them. That is, in our abstract or idealized definition, heritability in the narrow sense may be said to describe the fraction of the differences in parents which can be expected to be realized in the offspring. In actual practice, this fraction will include some epistatic effects even under random mating. When the two parents are related, more of the epistatic and some of the dominance deviation also will be realized in the offspring.
All methods of estimating \( g^2 \) rely basically on comparing the phenotypic likeness with the genetic likeness of relatives of some specified kind, with the later inferred from the relationship. To illustrate this, we see from Figure 3 that:

\[
 r_{P_1P_2} = h^2 r_{H_1H_2} + e^2 r_{E_1E_2}
\]

\[
 = h^2 g^2 r_{G_1G_2} + h^2 d^2 r_{D_1D_2} + h^2 i^2 r_{I_1I_2} + e^2 r_{E_1E_2} \quad \text{(Eq. 3)}
\]

The value of \( r_{G_1G_2} \) is the correlation between the gene aggregates of individuals 1 and 2. Under random mating, \( r_{G_1G_2} \) for daughter and dam is \( \frac{1}{2} \). The corresponding correlation among half sibs (\( t \)) is \( \frac{1}{2} \cdot \frac{1}{2} = \frac{1}{4} \). These are the relationships most frequently used in estimating heritability. We have noted that under random mating, \( r_{D_1D_2} \) for daughter and dam or for half sibs is zero. (Recall that \( D \), in the present context, refers to dominance deviations.)

Also \( h^2 i^2 \) equals \( \frac{\sigma_i^2}{\sigma_P^2} \).

Therefore, under random mating, and assuming that \( \sigma_P^2 \) is equal for daughters and dams, Equation 3 reduces to:

\[
2 h^2 g^2 = h^2 g^2 + 2 \frac{\sigma_i^2}{\sigma_P^2} r_{I_1I_2} + 2 \frac{\sigma_E^2}{\sigma_P^2} r_{E_1E_2} \quad \text{(Eq. 4)}
\]

or \( h^2 \) Half sibs = \( h^2 g^2 + 4 \frac{\sigma_i^2}{\sigma_P^2} r_{I_1I_2} + 4 \frac{\sigma_E^2}{\sigma_P^2} r_{E_1E_2} \quad \text{(Eq. 5)}
\]

In terms of covariance, the right hand side of Equation 4 would be
Figure 3. Composition of phenotypic correlation between different individuals (from Lush, 1948, p. 290)

G = Genic deviations
D = Dominance deviations
I = Epistatic deviations
H = Genotypic or hereditary deviations
E = Environmental deviations
P = Phenotype
\[ h^2 g^2 + \frac{2 \text{ Cov } I_1 I_2}{\sigma_p^2} + \frac{2 \text{ Cov } E_1 E_2}{\sigma_p^2}, \text{ and similarly for Equation 5.} \]

In both of the above cases, Equations 4 and 5, the estimate of heritability includes a portion of epistatic covariance. In general, however, this is of minor importance.

A major problem in estimating heritability with some degree of accuracy concerns the component for environmental correlations. That is especially serious for half sib relationships where any of the environmental contributions to \( r_{P_1P_2} \) that are not removed in the design and/or computations are multiplied by \( 4 \) (see Equation 5). Other sources of bias in the estimates of heritability arise when diverse selection goals are prominent in a population or where other deviations from the random mating pattern are present. In addition, possible discrepancies between the assumed coefficient of relationship and the real correlation between the genic values may reduce the accuracy of the estimate.

Many pitfalls and uncertainties accompany the estimation of heritability because heritability is a property not only of a trait but also of the breeding structure of the population and the environmental circumstances affecting that population.

The above difficulties are not equally prevalent in all kinds of relationships and will be discussed in more detail in the next two sections.

2. Sire, herd, year-season analysis

An analysis of variance was computed in an effort to measure:
(1) the sire's contribution to variance among production records; (2) the
possible effects of interaction between sires and herds; and (3) other related sources of variance. Several previous studies of this type have been reported, with results summarized in Table 17 for lactation butterfat production. All of these analyses utilized DHIA (or their equivalent) records made in numerous herds and with daughters of many sires included in each analysis. The data were therefore similar to those studied here. Numbers of records included in each study ranged from 3900 by Hickman and Henderson to 43,000 by Barr. The models used were not quite the same in all analyses, but the deviations were minor. A dash indicates that the corresponding component was not computed. Residual values include all variances not listed above each.

Table 17. Components of variance for sires, herds, year-seasons and their interactions for lactation butterfat yield

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>Workers and component values in percent of total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Henderson^a</td>
</tr>
<tr>
<td>Sires (S)</td>
<td>7.0</td>
</tr>
<tr>
<td>Herds (H)</td>
<td>33.0</td>
</tr>
<tr>
<td>Year-Seasons (YS)</td>
<td>5.0</td>
</tr>
<tr>
<td>S x H</td>
<td>2.0</td>
</tr>
<tr>
<td>S x YS</td>
<td>-</td>
</tr>
<tr>
<td>H x YS</td>
<td>15.0</td>
</tr>
<tr>
<td>Residual</td>
<td>38.0</td>
</tr>
</tbody>
</table>

^aHenderson, 1956; Legates et al., 1956; Barr, 1962; Van Vleck et al., 1961b.
In selecting the present data from among those available, the only restriction stipulated was that each sire must have daughters in at least two different herds.

The model assumed was as follows:

$$X_{ijkl} = \mu + s_i + h_j + y_k + (sh)_{ij} + (hy)_{jk} + e_{ijkl}$$

$X_{ijkl}$ represents the 305-day-2X-ME lactation production of the $i^{th}$ daughter of the $i^{th}$ bull, in the $j^{th}$ herd, and calving in the $k^{th}$ year-season.

$\mu$ is the population mean and thus is common to all observations.

The other terms are defined briefly as follows, with fuller descriptions following:

- $s_i$ is the effect of the $i^{th}$ sire on this particular record;
- $h_j$ is the effect of the $j^{th}$ herd in which the record was made;
- $y_k$ is the effect of the $k^{th}$ year-season of freshening;
- $(sh)_{ij}$ is the effect of the interaction between the $i^{th}$ sire and the $j^{th}$ herd;
- $(hy)_{jk}$ is the effect of the interaction of the herd and the $k^{th}$ year-season of freshening;
- $e_{ijkl}$ is the error term.

Included in $s_i$ is the total of all influences which make the sire's progeny different from the mean of all progeny groups, after allowing for the average effects of herd and year-season. The direct influence of the sire is in the sire component which contains one-fourth of the additive variance plus a small portion of the epistatic variance. However, the sire component will vary from this theoretical composition.
in proportion to how far removed the data are from satisfying the conditions stipulated in the model. This is especially true with regard to departures from random mating, environmental correlations between paternal half sibs, and correlations of sires with other components in the model.

The herd effect \( h_j \) is the sum of the effects which cause the \( j^{th} \) herd average to differ genuinely from the mean of all herds. These include variations both in breeding value and in environment, but evidence indicates it is mostly the latter.

The year-season effect \( y_{hk} \) is due largely to environmental factors prevailing during the \( k^{th} \) year-season of freshening, but not in other year-seasons.

An interaction effect is the deviation of a particular subclass from the sum of the simple effects involved. Thus the sire-by-herd interaction effect would measure the failure of the sire differences to be the same under different herd conditions. The herd-by-year-season effect is almost wholly an environmental type of interaction.

Effects included in \( e_{ijkl} \) are probably of numerous kinds. There are genetic effects due to differences in genic merit of the dams of the daughters in question (the dams were not included in the model), sampling effects from Mendelian segregation, and nearly all of the dominance and epistatic effects. Also included are the effects of second and third order interactions not defined in the model; i.e., the sire-by-year-season and the three-way interaction effects. There are also other random and measurement errors affecting the particular lactation.

All elements of the model except \( \mu \) were assumed to be randomly and
independently distributed and are defined to have zero means and variances \( \sigma^2_s, \sigma^2_h, \) etc. The variance components were estimated by equating the mean squares to their expectations and solving for the estimates by Method 1 of Henderson (1953).

Table 18 gives the degrees of freedom and the derived components of variance in actual values and in percent of total variance.

Table 18. Degrees of freedom and components of variance for sires, herds and year-season analysis of variance

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>Degrees of freedom</th>
<th>Components of variance Milk</th>
<th>Components of variance Butterfat</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Actual</td>
<td>Percent</td>
</tr>
<tr>
<td>Sires (S)</td>
<td>612</td>
<td>5487</td>
<td>7.3</td>
</tr>
<tr>
<td>Herds (H)</td>
<td>581</td>
<td>20061</td>
<td>26.8</td>
</tr>
<tr>
<td>Year-Season (YS)</td>
<td>5</td>
<td>1435</td>
<td>1.9</td>
</tr>
<tr>
<td>S x H</td>
<td>2684</td>
<td>3331</td>
<td>4.4</td>
</tr>
<tr>
<td>H x YS</td>
<td>1122</td>
<td>1930</td>
<td>2.6</td>
</tr>
<tr>
<td>Residual</td>
<td>7206</td>
<td>42743</td>
<td>57.0</td>
</tr>
<tr>
<td>Total</td>
<td>12213</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

On the whole the results from this study agree well with those by other workers as was shown in Table 17. The slightly lower herd components here might possibly reflect more uniformity among the Iowa herds sampled. The results further confirm the position of relatively minor importance for year-seasons and herd-by-year-season interactions as sources of variance among production records in the Iowa herds sampled.
Both the sire and sire-by-herd interaction components appear to be slightly high in view of the results by other workers as shown in Table 17. One factor contributing to the former is that all available records by each daughter were included separately in the analysis. There was a weighted average of approximately 20 records included for each bull. These were treated as though they were by 20 separate daughters. No count was kept of how many records each daughter had. However, from Table 13 in Section IV-B-3, we see they were approximately 1.5 records per cow in the entire group of records from which the present data were selected ('Overall' analysis). If we assume this figure is applicable here, we may conjecture that, on the average, each bull had 13 daughters with a total of 20 records. If we further assume that one of these daughters had 3 records, 5 others had 2 records each, and the other 7 had only single records, we would have an average correlation of genic effects among these daughters, assuming random mating, of .2816, instead of .25. Thus, the sire components, as they stand, are inflated somewhat not only by extra genic covariance, but by some dominance and extra epistatic covariances, not ordinarily present when only a single record or an average of all records by each daughter are included in the analysis.

Another factor contributing to the inflated sire components is that a number of sires had a large majority of their daughters in only one or two herds. As a result, environmental correlations within some groups of paternal sibs might be expected to contribute to a larger than normal sire component.
Barr (1962; see Table 17), in his paternal sib analysis, also included all records of each daughter but calculated them as was done in the present study. He found the sire components for fat and milk to be 5.2 and 2.7 percent, respectively, thus indicating that the resultant bias is probably very small when considering each record separately. Hence, the environmental correlations would appear to be the major source of any inflation of the sire components in the present analysis.

No explanation is apparent for the size of the sire-by-herd interaction components. They may in fact be a true representation of this effect in the Iowa data.

Hence, the estimates of heritability computed from this analysis would appear to be at least slightly biased. However, part of this bias may be reduced by multiplying the sire components by 3.55 (= \( \frac{1}{.2816} \)), yielding \( g^2 \) for milk = .259 and \( g^2 \) for fat = .298. These values compare with .292 and .336, respectively, when we use 4.0 instead of 3.55 as the value for \( \frac{1}{r_{G_iG_j}} \). The standard errors for these estimates, although not computed, might be expected to be low, due to the volume of data. However, the errors resulting from the biases are not correspondingly reduced.

Some further aspects of this analysis are discussed in the next section.

3. Daughter-dam regression

If the data cover a long enough period, time trends could contribute to daughter-dam correlations. This is because each daughter-dam pair would be treated more alike than would animals from more widely separated
time periods. This, of course, assumes that time periods are not included as an effect in the analysis. Also, if the environment of the offspring is partly determined by the merit of the dam, some increase in the daughter-dam correlation might result (Lush, 1949). An example of this might be the case where the herdsman might feed a certain cow better just because he knew her dam was a high producer and he hoped the daughter would be, also. However, this would not be of much importance, generally. Insofar as such preferential treatment is due to the real or supposed merit of the sire, computing the correlation of daughter and dam on an intrasire basis would remove this effect. This method also would largely bypass the problem of time trends because the progeny of a sire are usually contemporaries, to a large extent. Thus most of the variance attributable to management trends would be eliminated with the differences among the sire groups. (Of course, if the resultant sire component was used to estimate heritability, the latter would be proportionally increased.)

If each sire was used largely on only one farm, the intrasire analysis would tend to eliminate the herd environmental component contributing to the covariance between daughter and dam. In addition, the intrasire analysis, where each sire again is used largely in only one herd, would eliminate the variance from any difference in the average merit of females mated to different sires. Of course, these components would merely be transferred to the sire in such a situation.

The data available for this analysis were from a period of only three years, so time trends were of no practical importance. With the increased use of artificial insemination (AI), many sires have daughter-
dam pairs in numerous herds. In the present data, about 3.4 percent of the daughters were sired by bulls which were, at the time of service, or eventually became AI sires. For these daughters and their dams, being in several to many different herds, an intraherd analysis would be preferred to an intrasire analysis for eliminating environmental correlations contributed by differences among herds. The increased use of AI would also tend to decrease, if not eliminate, differences in the merit of females mated to different sires but, at the same time, increase the differences in the merit of females mated to the same sire. The advantages of an intrasire analysis would be proportionally lessened in data where most of the cows were produced by AI.

The advantages of an intraherd analysis, therefore, outweighed those for an intrasire analysis in the present situation. Consequently, the intraherd regression of daughter on dam was used.

Only those daughter and dam pairs making their records in the same herd were used in this study. All pairs, so qualifying, were included. No further selection was practiced. A total of 13,178 pairs from 443 different Iowa DHIA and DHIR herds were represented. All records had been corrected to a 305-day-2X-ME basis.

The average of all available records for both the daughters and dams were used. The dam's average was repeated for each of her daughters. Kempthorne and Tandon (1953) found little if any advantage in using an unweighted or weighted regression of means of daughters on their dams as compared with repeating the record of the dam with each daughter's record. An important factor, of course, is the number of daughters per dam in the population. They had an average of 1.39 daughters per dam while each
dam in the present study had an average of 1.33 daughters, with a range of 1 to 6.

Further descriptive statistics were presented in Table 13.

Under random mating and no environmental correlation between daughter and dam, the regression (b) of daughters on their dams is:

\[ b(\text{Daughters on Dams}) = \frac{\text{Covariance (Daughters, Dams)}}{\text{Variance (Dams)}} = \frac{1}{2} \frac{\sigma^2_G}{\sigma^2_P}, \]

where \( \sigma^2_G \) is the genic variance and \( \sigma^2_P \) is the phenotypic variance. An estimate of \( \frac{1}{2} \sigma^2_G \) may be obtained from a suitable analysis of covariance for daughters and dams, while an estimate of \( \sigma^2_P \) is derived from an analysis of variance for the records of the dams.

The models and computational procedures applied here follow closely those used by Harvey (1949) and Legates (1949) in their analyses of heritability.

The linear model to describe the average production of a dam (M) for the variance analysis is as follows:

\[ \frac{M_{i,k}}{n_{i,k}} = \mu + h_i + \frac{\sum n_{ij,k} y_{ij}}{n_{i,k}} + e_{ik} \quad (\text{Eq. 6}) \]

\( M_{i,k} \) = sum of all records (over all year seasons) of the \( k^{th} \) dam in the \( i^{th} \) herd;

\( n_{i,k} \) = number of records for the \( k^{th} \) dam in the \( i^{th} \) herd;

\( \mu \) = a constant, representing the population mean, and thus is common to all observations;

\( h_i \) = effect of the \( i^{th} \) herd;
\( n_{ijk} \) = number of records for the \( k \)th dam in the \( j \)th year season, in the \( i \)th herd and would be either 0 or 1;

\( y_{ij} \) = effect of the \( j \)th year-season in the \( i \)th herd; and

\[
\sum_{j} \frac{n_{ijk} y_{ij}}{n_{i.k}} = \text{year-season effect remaining in the average of all records of the } k \text{th dam in the } i \text{th herd.}
\]

\( e_{ik} = c_{ik} + \frac{1}{n_{i.k}} \sum_{j} e_{ijk} \)

\( c_{ik} = \text{the 'cow' effect, or the effect of the } k \text{th dam in the } i \text{th herd. This includes both the genotypic plus permanent environmental effects for each cow, thus having the same connotation as that described for the cow effects in the repeatability analysis, Section IV-B.} \)

\( e_{ijk} = \text{random error effects including temporary environmental effects not accounted for elsewhere in the model, and associated with each record.} \)

By using the average production of each dam, the error component, \( \sigma^2 \), which is derived from the \( e_{ik} \) effect, contains variance from the effects of all real differences among cows plus a portion, \( \frac{1}{n_{i.k}} \), of the variance of temporary environmental and random error effects associated with each of the dam's \( n_{i.k} \) records. In terms of the variance

\[
\sigma^2 = \sigma^2_c + \frac{\sigma^2_{E_T}}{n_{i.k}}.
\]

We have assumed that all effects in the model are randomly and
independently distributed, and are defined to have zero means and
variances $\sigma^2_H$, $\sigma^2_{YS/H}$, and $\sigma^2_E$.

The analysis of variance consisted of a simple one-way classification, among herds and within herds. As a result, the desired component, $\sigma^2_E$, is confounded in the mean square within herds with a fraction of the year-season component. This can be seen under the coefficients for the expected mean squares in Table 19 which summarizes the analysis of variance for the dams. An analysis of variance for the daughters also

Table 19. Analysis of variance for dams

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>d/f</th>
<th>Mean squares$^a$</th>
<th>Coefficients for expected mean squares</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Milk Test Fat</td>
<td>$\sigma^2_H$ $\sigma^2_{YS/H}$ $\sigma^2_E$</td>
</tr>
<tr>
<td>Total</td>
<td>3137</td>
<td>67197 .1118 9045</td>
<td>.996 .706 1</td>
</tr>
<tr>
<td>Among herds</td>
<td>442</td>
<td>196869 .2577 27452</td>
<td>7.067 2.557 1</td>
</tr>
<tr>
<td>Within herds</td>
<td>2695</td>
<td>45930 .0879 6026</td>
<td>0 .102 1</td>
</tr>
</tbody>
</table>

$^a$Original data were in 10 pounds for milk, in percent for test and in pounds for fat.

was computed with the same model as above. This analysis is summarized in Table 20. Table 21 contains the derived components of variance for
Table 20. Analysis of variance for daughters

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>df</th>
<th>Mean squares</th>
<th>Coefficients for expected mean squares</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Milk</td>
<td>Test</td>
</tr>
<tr>
<td>Total</td>
<td>4177</td>
<td>65718</td>
<td>.1039</td>
</tr>
<tr>
<td>Among herds</td>
<td>442</td>
<td>225245</td>
<td>.2947</td>
</tr>
<tr>
<td>Within herds</td>
<td>3735</td>
<td>46840</td>
<td>.0813</td>
</tr>
</tbody>
</table>

Table 21. Summary of components

<table>
<thead>
<tr>
<th>Component values</th>
<th>Dams</th>
<th></th>
<th></th>
<th>Daughters</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Milk</td>
<td>Test</td>
<td>Fat</td>
<td>Milk</td>
<td>Test</td>
<td>Fat</td>
</tr>
<tr>
<td>$\sigma^2_{YS/H}$</td>
<td>5874</td>
<td>.0046</td>
<td>873</td>
<td>2187</td>
<td>.0077</td>
<td>458</td>
</tr>
<tr>
<td>$\sigma^2_E$</td>
<td>43566</td>
<td>.0861</td>
<td>5675</td>
<td>45693</td>
<td>.0777</td>
<td>5949</td>
</tr>
<tr>
<td>$\sigma_E$</td>
<td>2087</td>
<td>.293</td>
<td>75</td>
<td>2138</td>
<td>.278</td>
<td>77</td>
</tr>
</tbody>
</table>

$\sigma^2_{YS/H}$ components were taken from Tables 14 and 15.

$\sigma^2_E$ and $\sigma_E$ along with those for $\sigma^2_{YS/H}$ obtained from the repeatability analyses in Section IV-B-3. Although the analysis of variance among daughters was not needed for computing the regression of daughters on dams, it provided additional useful information for the present discussion. The $\sigma_E$ values for daughters and dams are nearly the same, with the daughters having slightly higher values for milk and fat yield, but
a lower value for test. In other words, the variability among the average records of daughters is little different from that of their dams. Thus the correlation between daughter and dam would be only slightly different from the regression, in this population. This further suggests a negligible effect of selection among dairy cows so far as concerns the present data.

As noted earlier, the component desired from the covariance analysis is that for estimating \( \sigma_G^2 \), the additive or genic variance. It is therefore necessary to modify the models for daughters and dams so as to include this effect.

The model for the average production of a dam \((M)\) then becomes:

\[
\frac{M_{i\cdot k}}{n_{i\cdot k}} = \mu + h_i + \frac{1}{n_{i\cdot k}} + g_{ik} + \text{error}.
\]

All subscripts have the same meaning here as in the original model (Equation 6, p. 75). \( g_{ik} \) is defined as the transmissible genetic effects of the \(k^{th}\) dam in the \(i^{th}\) herd. It thus includes the average genic effect plus a small portion of the epistatic effects. The error term includes all permanent and \( \frac{1}{n_{i\cdot k}} \) of the temporary environmental effects plus all the effects of dominance and the balance of the epistatic effects on the records of this particular dam.

Similarly, the model describing the average production of the \(l^{th}\) daughter of the \(k^{th}\) dam is:

\[
\frac{D_{i\cdot kl}}{n_{i\cdot kl}} = \mu + h_i + \frac{1}{n_{i\cdot kl}} + g_{ik} + \frac{1}{2} + \text{error}.
\]
μ in this case refers to the general mean of the population of daughters. It is not necessary to assume that μ for the dams and daughters are the same, since this component of covariance goes out with the correction term.

Since a daughter receives a sample half of the genes at each locus which her dam has, the dam's genic effects will, on the average, be only 1/2 as large on the daughter's records as on her own records.

Tables 22 and 23 present a summary for the analysis of covariance. No error covariance component is indicated. For this to be accurate, the respective error terms for daughter and dam must not be correlated. This assumption appears to be valid here, for all practical purposes.

Estimates of $\sigma_{YS/H}^2$ must be available before values for $\frac{\sigma_G^2}{2}$ can be derived from the equations for the intraherd mean crossproducts. A similar problem was encountered when estimating $\sigma_E^2$ in the analysis of variance for the dams (p. 77). There may be some question as to the appropriate values of $\sigma_{YS/H}^2$ to apply here. The estimates obtained in the 'Overall' repeatability analysis (Table 11) may be used, or it might be preferable to use estimates derived from the separate dams' and daughters' repeatability analysis (Tables 14 and 15). If the latter are to be applied, weighted estimates of $\sigma_{YS/H}^2$ for the covariance equations would be advisable. These were computed and an example for fat is shown in Table 24.

Table 25 presents values for $\sigma_E^2$, $\frac{\sigma_G^2}{2}$ and the regression of daughters on dams (bDM) computed with the various estimates for $\sigma_{YS/H}^2$. 

Table 22. Covariance of daughters and dams (analysis of covariance table)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degrees of freedom</th>
<th>Mean crossproducts (covariance)</th>
<th>Coefficients for expected covariance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Milk</td>
<td>Test</td>
</tr>
<tr>
<td>Total</td>
<td>14176.4</td>
<td>2459.4</td>
<td>.0446</td>
</tr>
<tr>
<td>Among herds</td>
<td>639.9</td>
<td>129135</td>
<td>.1539</td>
</tr>
<tr>
<td>Within herds</td>
<td>3536.5</td>
<td>5679</td>
<td>.0249</td>
</tr>
</tbody>
</table>

Table 23. Summary of components of covariance

<table>
<thead>
<tr>
<th>Description of component</th>
<th>Milk</th>
<th>Test (%)</th>
<th>Fat</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma^2_{YS/H}$</td>
<td>4061</td>
<td>.0062</td>
<td>651</td>
</tr>
<tr>
<td>$\sigma^2_G$</td>
<td>5603</td>
<td>.0247</td>
<td>602</td>
</tr>
<tr>
<td>$\sigma^2_G$</td>
<td>1059</td>
<td>.222</td>
<td>35</td>
</tr>
</tbody>
</table>

$^a$ $\sigma^2_{YS/H}$ component values were taken from Table 24.
Table 24. Statistics for estimating a weighted $\sigma^2_{YS/H}$ for the covariance analysis (fat yield$^a$)

<table>
<thead>
<tr>
<th>Source of estimate</th>
<th>$\sigma^2_{YS/H}$</th>
<th>Total no. of records (n)</th>
<th>(n)•($\sigma^2_{YS/H}$)</th>
<th>Weighted $\sigma^2_{YS/H}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dams</td>
<td>873</td>
<td>5311</td>
<td>4636503</td>
<td></td>
</tr>
<tr>
<td>Daughters</td>
<td>458</td>
<td>6117</td>
<td>2801586</td>
<td></td>
</tr>
<tr>
<td>Sum</td>
<td>11428</td>
<td>7438089</td>
<td>651</td>
<td></td>
</tr>
</tbody>
</table>

$^a$Weighted components for milk and test, computed as above, were .061 and .0062, respectively.

Table 25. Estimates for variance components and regression of daughters on dams, using different values of $\sigma^2_{YS/H}$

<table>
<thead>
<tr>
<th>Source of $\sigma^2_{YS/H}$</th>
<th>Milk$^a$</th>
<th>Test</th>
<th>Fat</th>
<th>&quot;Overall&quot; analysis</th>
<th>Dams' analysis</th>
<th>Weighted (From Table 23)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma^2_{YS/H}$</td>
<td>$\sigma^2_{G}$</td>
<td>$\sigma^2_{E}$</td>
<td>$b_{DM}$</td>
<td>$\sigma^2_{G}$</td>
<td>$\sigma^2_{E}$</td>
<td>$b_{DM}$</td>
</tr>
<tr>
<td>'Overall'</td>
<td>5606</td>
<td>.127</td>
<td>.0247</td>
<td>.0853</td>
<td>.290</td>
<td>603</td>
</tr>
<tr>
<td>Dams'</td>
<td>43566</td>
<td>.128</td>
<td>.0861</td>
<td>5675</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weighted (From Table 23)</td>
<td>5603</td>
<td>.128</td>
<td>.0247</td>
<td>602</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^a$Original data were in 10 pounds for milk, in percent for test and in pounds for fat.
Practically no differences are noted in the $\frac{g^2}{2}$ component values or in the regression coefficients. Only minor deviations are present in the $\sigma^2_E$ estimates. Use of the values in the lower two rows is preferred for this analysis, however, because the estimate of $\sigma^2_{YS/H}$ used in deriving the $\sigma^2_E$ from the dams' analysis was obtained from the dams' repeatability analysis. For the sake of uniformity the same dams' estimate should be incorporated into the derivation of $\sigma^2_G$. This implies use of the weighted $\sigma^2_{YS/H}$ estimate from Table 24.

We now can compute various regressions of daughter on dam from the results of the above analyses. Table 26 contains three such regressions: (1) total regression of daughter on dam; (2) intraherd regression of daughter on dam, ignoring the effects of year-seasons; and (3) intraherd regression after correcting for the year-season effects. For example, the total regression of daughter on dam for average fat yield is $\frac{3291}{9045} = .364$. An example of regression (2), above, is $\frac{614}{6026} = .102$ for average fat yield, while regression (3) is computed as $\frac{602}{5675} = .106$, also for average fat yield. These values were taken from Tables 19 and 21.

The contrast between regressions of type (1) and those of types (2) and (3) clearly emphasize the importance of removing the herd differences when using daughter-dam regression or correlation to estimate heritability.

The minor differences between the regressions of type (2) and (3) indicate at least two things: (1) much of the confusing influence of the year-season environmental changes on the daughter-dam regressions
Table 26. Three regressions of daughters on dams using average lactation yields

<table>
<thead>
<tr>
<th>Type of regression(^a)</th>
<th>Milk</th>
<th>Test</th>
<th>Fat</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Total</td>
<td>.366</td>
<td>.399</td>
<td>.364</td>
</tr>
<tr>
<td>(2) Intraherd,</td>
<td>.124</td>
<td>.283</td>
<td>.102</td>
</tr>
<tr>
<td>ignoring seasons</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(3) Intraherd, correcting</td>
<td>.128</td>
<td>.287</td>
<td>.106</td>
</tr>
<tr>
<td>for seasons</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) See text for full explanation of computation methods.

is averaged out by using the average yield for each cow; and (2) year-season effects have a minor role in contributing to daughter-dam covariances, at least in these data. It should be added that the above differences would be expected to be small also because in only a fraction of the cases would the daughter and dam have made their records in the same year-season. That fraction is the only portion where year-seasons would contribute to the covariance.

A further point of interest is the relatively small drop in the regressions for test when going from a 'total' basis to a computation on an intraherd basis.

The regressions given above are based on averages of \(n\) records for each dam (\(n\) varies from 1 to 3 in this study). As a result the regressions calculated are larger than those to be expected when using a single random record of each dam. Lush and Straus (1942) give a formula developed by Cochran to adjust a regression calculated on an average of \(n\)
records of the dam to the basis of a regression on a single record (see also Laben, 1950). The formula is as follows:

\[ b = b' \left[ \frac{1 + (\bar{n} - 1)r}{\bar{n}} + \frac{\sigma^2_n (1-r)}{\bar{n}^3} \right] . \]

Here \( b' \) is the regression calculated using averages, while \( b \) is the regression on a single record. \( \bar{n} \) is the mean number of records for the dams and \( r \) is the appropriate value of repeatability of records by the same cow. This formula was applied to the intraherd regression values shown in Table 26. The resultant regressions were multiplied by 2 to estimate the heritability of differences in single lactation records for the three production traits studied. The results are given in Table 27.

Table 27. Regression coefficients and heritability estimates on a single record basis

<table>
<thead>
<tr>
<th>Type of estimatea</th>
<th>Production trait</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Milk</td>
<td>Test</td>
<td>Fat</td>
</tr>
<tr>
<td>A. Regression coefficients = b</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>.105</td>
<td>.255</td>
<td>.085</td>
</tr>
<tr>
<td>2</td>
<td>.110 ± .020b</td>
<td>.263 ± .016</td>
<td>.090 ± .021</td>
</tr>
<tr>
<td>B. Heritability (( g^2 )) estimates = 2b</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>.210</td>
<td>.510</td>
<td>.170</td>
</tr>
<tr>
<td>2</td>
<td>.220 ± .040b</td>
<td>.526 ± .036</td>
<td>.180 ± .042</td>
</tr>
</tbody>
</table>

\( ^a \)Type 1 refers to the regression computed on an intraherd basis but ignoring effects of year-seasons. Type 2 is computed on an intraherd basis after correcting for effects of year-seasons.

\( ^b \)Standard errors computed by usual method (Snedecor, 1956, p. 135).
The records for the paternal sib and for the daughter-dam analyses both came from the same basic source. In fact many of the same records were included in both analyses. Yet the estimates of heritability were widely different, especially for fat yield. These are shown in Table 28.

Table 28. Estimates of heritability from paternal sib and daughter-dam analyses

<table>
<thead>
<tr>
<th>Source of estimate</th>
<th>Milk</th>
<th>Fat</th>
<th>Test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Paternal sib correlation</td>
<td>.259</td>
<td>.298</td>
<td>--</td>
</tr>
<tr>
<td>Daughter-dam regression</td>
<td>.220</td>
<td>.180</td>
<td>.526</td>
</tr>
</tbody>
</table>

The possible sources of error in the paternal sib analysis were discussed in the last section. It was surmised that environmental correlations and bias due to some dominance and extra epistatic effects had inflated the paternal sib correlations, mostly the former. The fact that numerous sires had most of their daughters in one or a very few herds was suggested as contributing to the possibly inflated sire component, especially noticeable for fat yield. Failure of the model to account for any correlation between effects further contributed to the bias.

If herd-related correlations were of importance in a paternal sib analysis, the expected results might be similar to those actually found here. By computing the daughter-dam regression on an intraherd basis, the problem of correlation from common herd effects is largely bypassed,
thereby resulting in more dependable estimates of heritability. It seems logical that, if much herd-related environmental correlations might be suspected in a paternal-sib analysis, the computation on an intraherd basis would be of considerable benefit. Of course, it should be noted that when computing the daughter-dam regression on an intraherd basis, we are estimating heritability of intraherd variance among the dams rather than heritability of variance among dams in the whole population. Therefore, the relative merits of the different estimates depend to some extent on the application of the estimates so obtained.

D. Relative Importance of Different Factors Affecting Production Records

After considering all the previous analyses in this study, including the herds-and-time-periods, repeatability, and heritability analyses, the estimates shown in Table 29 were judged to be most appropriate to the

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>Components for traits (in % of total)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Milk</td>
</tr>
<tr>
<td>Herd</td>
<td>28</td>
</tr>
<tr>
<td>Year and season of freshening</td>
<td>4</td>
</tr>
<tr>
<td>Additive genetic effect</td>
<td>24</td>
</tr>
<tr>
<td>Balance of genetic effects and permanent environment</td>
<td>11</td>
</tr>
<tr>
<td>Temporary environment, random and other effects</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>100</td>
</tr>
</tbody>
</table>
present data. The effects for year-seasons are considered to be those attributable to the particular year-seasons that are most appropriate for each trait separately. The other effects are largely self-explanatory. The various applications of these results will be described in subsequent sections of this thesis.

E. The Role of Herd Averages in Dairy Sire Evaluation

1. Introductory theoretical aspects, including general model

The breeding value of an animal was defined in a previous section as the sum of the average effects of all of the individual genes possessed by that animal. This average effect may be expressed in relation to the average value of the specified population of which that particular animal is a member, and in this form it is expressed as a deviation, plus or minus, from that base level.

Breeding value is synonymous with transmitting ability. Thus the mean value of an animal's progeny offers a useful method of estimating its breeding value. For a dairy sire, which cannot express production traits itself, this is the most promising method for estimating its breeding value. Just as the average effect is the property of a gene and the population, so the breeding value is a property of the individual and the population from which his or her mates are drawn. If the mates are a random sample of the population and the progeny are exposed to the average environment of the population, the breeding value measured is referred to as general breeding value, or simply, breeding value, here. However, if the mates deviate from the average of the population and/or
the progeny are exposed to environmental conditions that are not standard for that population, we introduce biases into the estimate of breeding value.

In reality, the conditions for unbiasedness are rarely, if ever, completely fulfilled. The problem resolves to one of reducing or eliminating, if possible, the biases and errors that accompany the estimation of breeding value.

The approach we will take here is similar to the general method finding increasing favor during the last 10 years; namely, considering the production average of contemporary herdmates of the daughters of the bull being evaluated. Lush (1947) pointed out that (substituting 'herd' for 'family'):

"the herd average contains two different kinds of information. First, it gives some indication of the average breeding value of the herd. Second, it indicates the special environmental conditions to which the whole herd was exposed. Information of the first kind is useful positively since the individual's own breeding value is likely to be somewhere between its own phenotype and the average phenotype of its herd. Information of the second kind makes the herd average useful negatively as a means of correcting partially for some nongenetic circumstances which affected the whole herd. The net usefulness of the herd average depends upon the balance between the two kinds of information it contains."

We can get a closer look at the factors involved in sire evaluation by a study of appropriate biometrical models describing the various records. Thus, for a record of a daughter of a bull used in more than one herd, a record of her dam, and their respective contemporary herd-mate averages, we have the following:

\[ \text{Daughter's record} = D_{ijklm} = D \]
\[ D = \mu + h_i + \frac{s_j}{2} + \frac{d_k}{2} + y_l + e_{ijklm} \]  
(Eq. 7)
Contemporary herdmate average for the daughter's record = $H_A^D$

$$H_A^D = \mu' + h_i + \frac{\sum s_{ij'}}{2p} + \frac{\sum d_{ik'}}{2p} + \frac{\sum e_{ij'k'lm'}}{p}$$

(Dam's record = $M_{ikl'n} = M$

$$M = \mu'''' + h_i + d_k + y_{il'} + e_{ikl'n}$$

Contemporary herdmate average for the dam's record = $H_A^M$

$$H_A^M = \mu'''' + h_i + \frac{\sum s_{ij'}}{2p} + \frac{\sum d_{ik'}}{2p} + \frac{\sum e_{ij'k'lm'}}{p}$$

In the above equations:

- $\mu' = \mu + y_1$, where $\mu$ = overall breed mean for the region concerned and for a specified time period, and $y_1$ = effect of the 1st year-season of freshening in that particular region.

- $\mu'''' = \mu'' + y_{1'}$, where $\mu''$ = an overall breed mean for the region concerned and for a specified time period; $\mu''$ may or may not = $\mu$, and $1'$ may or may not = 1.

- $\mu'$ and $\mu''''$ are constants estimated by the breed mean for the specified region and for the particular year-season of freshening to which they refer; $\mu'$ may or may not = $\mu''''$.

- $h_i$ = effect of the $i^{th}$ herd in which all the above records are made. In the above models, $h_i$ is strictly a herd management and environmental effect. Both daughter and dam are assumed, for these studies, to make their records within the same herd, as is in fact the usual case.

- $s_j$ = breeding value of the $j^{th}$ sire which is used in more than one herd.
$d_k =$ breeding value of the $k^{th}$ dam.

$y_{ij} =$ particular effect of the $i^{th}$ year-season of freshening within the $i^{th}$ herd.

$e_{ijklm} =$ random error effects of the $m^{th}$ record of this daughter. This error is composed of temporary environmental and other random error effects plus the errors resulting from the Mendelian sampling of both the sire's and dam's gene aggregates. In this model, the error effect for the dam, $e_{ijkl'n}$, does not contain errors resulting from Mendelian sampling, as her breeding value is taken simply as $d_k$. The error terms for the herdmate averages are composed of the averages of the errors for all records making up the respective herdmate averages.

$s_{ij}$ is the breeding value of the $j^{th}$ sire which was used in the $i^{th}$ herd and is assumed to be unrelated to either the daughter or her dam, so $j'$ does not equal $j$.

$d_{ik'}$ is the genic effects of the $k'th$ dam, a present or former member of the $i^{th}$ herd, and is assumed to be unrelated to either the daughter or her dam, so $k'$ does not equal $k$.

All effects in the models, except $\mu'$ and $\mu'''$ are considered to be randomly and independently distributed, and are defined to have zero means and variances $\sigma_h^2$, $\sigma_s^2$, etc. In addition, $s_j$ and $d_k$ are assumed to be uncorrelated with the herd environmental effects, $h_i$, and the errors for a cow (either a daughter or a dam) and her respective herdmate average are assumed to be uncorrelated. Finally, it is assumed that each herdmate has a different sire and dam, and that both daughter and dam have the same number, $p$, of herdmates. Some of the above assumptions may appear to be presumptuous, but the errors resulting in their not
being entirely accurate are not believed to be serious for the kind of data used here (see Heidhues et al., 1960, and Van Vleck et al., 1961a). If these assumptions are not made, the expressions become impossible to handle.

Subtracting Equation 8 from Equation 7 and multiplying by 2 yields:

\[
2(D-H_A) = s_j + d_k + 2 e_{ijklm} - \frac{\Sigma s_{ij}^' k}{p} - \frac{\Sigma d_i^k}{p} - \frac{2 \Sigma e_{ijklm}^i}{p} \quad (Eq. 11)
\]

(The summations are the same as in Equation 8.)

Further,

\[
(M-H_{AM}) = d_k + e_{ikl'M} - \frac{\Sigma s_{ij}^' k}{2p} - \frac{\Sigma d_i^k}{2p} - \frac{\Sigma e_{ijklm}^i}{p} \quad (Eq. 12)
\]

(The summations are the same as in Equation 10.)

Hence,

\[
2(D-H_A) - (M-H_{AM}) = s_j - \frac{\Sigma s_{ij}^' k}{2p} - \frac{\Sigma d_i^k}{2p} + \text{errors} \quad (Eq. 13)
\]

Equation 13, therefore, yields an estimate of the breeding value of the jth sire, s_j, but it is a biased estimate, as the average effects of the other breeding in this herd still remain. However, this equation may be said to provide a comparison for the breeding value of the jth sire in relation to the average breeding value of this particular herd.

Now if the dam is a representative sample of the genetic make-up of this herd, i.e.,

\[
d_k = \frac{\Sigma s_{ij}^' k}{2p} + \frac{\Sigma d_i^k}{2p},
\]

Equation 12 reduces to zero, except for errors, and contributes nothing to the estimate of s_j.
If the latter is true, we then can express the daughter's record as follows:

\[ D_{ijklm} = D = \mu' + h_i + \frac{s_i}{2} + \frac{g_i}{2} + y_{il} + e_{ijlm}, \]  

(Eq. 14)

where each term is the same as in Equation 7, except for \( g_i \). Here \( g_i \) expresses the average breeding value of the \( i \)th herd, of which \( D \) has received a sample half. Similarly,

\[ H_A = \mu' + h_i + g_i + y_{il} + \frac{\sum e_{ilm}}{n}, \]  

(Eq. 15)

where there are \( n \) records included in the herdmate average. Therefore,

\[ 2(D - H_A) = 2 \left[ \frac{s_i}{2} + \frac{g_i}{2} - g_i + \text{errors} \right] \]

\[ = s_i - g_i + \text{errors} \]  

(Eq. 16)

If the average breeding value of the \( i \)th herd is equal to that of the population mean; that is, if \( g_i = 0 \), Equation 16 gives an unbiased estimate of \( s_j \). However, if \( g_i \neq 0 \), the equation contains a bias proportional to the amount that \( g_i \) deviates, either plus or minus, from the population average.

It should be added that, although not yet mentioned, the most serious source of bias in estimating a sire's breeding value is that caused by selection of either the daughter or her record, or both, for use in the sire's proof. (See, for example, Lush and McGilliard, 1955.)

2. The adjusted herdmate average

Various random errors are associated with any estimate of breeding value. The sources of these errors may be classified as follows:
(1) First, there are errors concerned with the particular record of a daughter. These are of a temporary environmental nature, varying from record to record for the same daughter. An increase in the number of records per daughter provides a partial means for reducing this error.

(2) Second, there are errors concerned with the particular daughter being tested. As each daughter receives a sample half of the genes possessed by her sire, her particular sample may not be entirely representative of the genes possessed by the sire. Increasing the number of daughters in a proof automatically reduces this source of error.

The above two sources of error will be discussed more fully in later sections of this thesis.

(3) A third source of error, and the one we are concerned with here, is directly related to the number of records comprising the contemporary herdmate average for a particular record of a daughter. The primary purpose for using the contemporary herdmate average at all is to provide a more accurate estimate of the environmental factors affecting a daughter's (or a dam's) record, so that these extraneous effects may be deducted.

Equations 8 and 10, for the herdmate averages, each contain error terms of the general form,

\[ \frac{\sum (\text{individual errors})}{n} = \frac{\sum W}{n} \]

While the expected value of this error term is zero, its presence reduces the accuracy of the sample estimate of the other real effects present in the herdmate average; namely, herd environmental and genic effects, and year-season effects within the herd. The size of \( \frac{\sum W}{n} \) is inversely pro-
portional to the size of n. We can have more confidence in the estimates of the other real effects if they are measured from a large number of herdmates rather than from only a few. In fact, if the herdmate group was infinite in size, these random errors would average to zero: \( \frac{e_w}{\infty} = 0 \).

The problem is, exactly how much reliance can we place on \( H_A^D \) (or \( H_A^M \)) if it is computed from, say, n records? Heidhues et al. (1960) have indicated one solution, while Barr (1962) presented this solution in a slightly different form. Following the latter interpretation and expanding on it further, we have:

Equation 15 expressed the herdmate average for a daughter as follows:

\[
H_A^D = \mu_i + h_i + g_i + y_{ij} + \frac{e_{ilm}}{n}.
\]

Therefore, under certain assumptions,

\[
\sigma_{H_A^D}^2 = \sigma_h^2 + \sigma_g^2 + \sigma_y^2/h + \frac{\sigma_e^2}{n} \quad \text{(Eq. 17)}
\]

If we combine the herd environmental (\( h_i \)), herd genic (\( g_i \)), and the intraherd year-season effects (\( y_{ij} \)) into a single effect, \( b_i \), we can express \( H_A^D \) simply as (dropping the D):

\[
H_A = \mu' + b_i + \frac{\sum_{j=1}^{J} e_{ij}}{n}.
\]

Here, \( \mu' = \mu + y_1 \), as before (Eq. 7);

\[
b_i = h_i + g_i + y_{ij}; \quad \text{and}
\]

\( e_{ij} \) = random error of each of n records included in HA.

The linear regression estimate of the true mean of a group of cows
Freshening in the same herd-year-season may be written as:

\[
\hat{HA} = \mu + f(\hat{HA} - \mu), \quad \text{(Eq. 18)}
\]

where: \( \hat{HA} \) = linear regression estimate of the true herdmate-year-season average;

\[\mu = \text{true mean of all cows in this particular population}; \text{ and} \]

\[f = \text{the linear regression of the } \hat{HA} \text{ on the sample average of the cows in the herdmate group.} \]

The covariance between \( \hat{HA} \) and the sample average is \( \sigma_b^2 \) and the variance of the sample average is

\[
\sigma_w^2 = \frac{\sigma_b^2}{n}. \quad \text{Hence, } f = \frac{\sigma_b^2}{\sigma_b^2 + \sigma_w^2} = \frac{n}{n + a}, \text{ where } a = \frac{\sigma_w^2}{\sigma_b^2}.
\]

If we denote \( \hat{HA} \) by \( AHA \), the Adjusted Herdmate Average, and specify that \( \mu' \) (as defined above) = \( \mu \), we have,

\[
AHA = \mu' + \frac{n}{n + a} (HA - \mu') \quad \text{(Eq. 19)}
\]

as the regression estimate of the true herdmate average.

In terms of our full model (Equation 15), Equation 19 is:

\[
AHA = \mu' + \frac{n}{n + a} (\mu' + h_i + g_i + y_{i1} + \frac{\sum e_{ilm'}}{n} - \mu'), \quad \text{or} \quad AHA = \mu' + \frac{n}{n + a} (h_i + g_i + y_{i1} + \frac{\sum e_{ilm'}}{n}) \quad \text{(Eq. 20)}
\]

\[
AHA = \mu' + \frac{n}{n + a} (\text{effects of HA}), \quad \text{and}
\]

\[
\sigma_{AHA}^2 = \left( \frac{n}{n + a} \right)^2 \sigma_{HA}^2. \quad \text{(Eq. 21)}
\]

Now, \( \frac{n}{n + a} = \frac{\sigma_b^2}{\sigma_b^2 + \sigma_w^2} = \frac{\sigma_b^2}{\sigma_h^2 + \sigma_g^2 + \frac{\sigma_y^2}{h}} \).  

\[
\frac{\sigma_b^2 + \sigma_w^2}{n} = \frac{\sigma_b^2}{\sigma_h^2 + \sigma_g^2 + \frac{\sigma_y^2}{h}} + \frac{\sigma_w^2}{n} \quad \text{(Eq. 22)}
\]
and \(1 - \frac{n}{n + a} = \frac{\sigma_w^2}{\sigma_n^2 + \sigma_g^2 + \sigma_{y/h}^2 + \sigma_w^2/n}\) (Eq. 23)

Thus the amount of the variance included in HA that is retained in AHA (see Equation 19) is proportional to the ratio of the variance of the 'true' HA effects to the total variance of HA (Equation 17). Conversely, Equation 23 show that the amount by which the variance of HA is reduced is proportional to the ratio of the average intra-herdmate-year-season variance to the total HA variance. In other words, the reduction in variance is a function of the relative magnitudes of the various components making up a herdmate-year-season average, and comes from the fact that the herdmate group is finite in size, causing \(\frac{\sigma_w^2}{n}\) to be larger than zero.

In the adjustment factor, \(\frac{n}{n + a}\), there are only two component parts, \(n\), the number of herdmates (= the number of records) and \(a\), the ratio of intraherd-year-season variance to the variance between herd-year-seasons. If the variance among records within the herd-year-season group is large relative to that between groups, we need more records to provide an accurate estimate of the average herd-year-season effects. Conversely, if there is very little variance among records within a herd-year-season group, fewer records are required to estimate accurately the average herd-year-season effects. The ratios for a specific population and trait need to be calculated from an appropriate analysis of variance.

A total of 33139 records were available for this analysis. The
model was a simple 1-way classification, between herd-year-season groups and within them. Table 30 presents the analysis and the estimates of the components of variance.

Table 30. Analysis of variance for herd-year-season effects

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>Degrees of freedom</th>
<th>Expected mean squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between HYS</td>
<td>2259</td>
<td>$\sigma_w^2 + 12.941 \sigma_b^2$</td>
</tr>
<tr>
<td>Within HYS</td>
<td>30579</td>
<td>$\sigma_w^2$</td>
</tr>
<tr>
<td>Total</td>
<td>33138</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Components of variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Milk</td>
</tr>
<tr>
<td>$\sigma_b^2$</td>
</tr>
<tr>
<td>$\sigma_w^2$</td>
</tr>
</tbody>
</table>

From Table 30, we can compute the ratios of $\frac{\sigma_w^2}{\sigma_b^2}$ to be:

Milk: 1.98 to 1; test: 4.27 to 1; fat: 1.85 to 1.

Reducing these ratios to their nearest whole numbers, we get the following values for $\frac{n}{n+a}$:

Milk and fat: $\frac{n}{n+2}$  
Test: $\frac{n}{n+4}$.

The milk and fat value for $\frac{n}{n+a}$ being used at present by both Cornell University and the USDA is $\frac{n}{n+1}$, in contrast to $\frac{n}{n+2}$ found here.
Barr (1962) also found a value of \( \frac{n}{n + 2} \) to be applicable to Canadian herd test data.

Table 31 contains both the values of \( \frac{n}{n + a} \) and their square roots, for various \( n \).

**Table 31. Values for \( \frac{n}{n + a} \) and \( \sqrt{\frac{n}{n + a}} \) for various \( n \)**

<table>
<thead>
<tr>
<th>Trait</th>
<th>1</th>
<th>2</th>
<th>4</th>
<th>8</th>
<th>14</th>
<th>18</th>
<th>22</th>
<th>32</th>
<th>56</th>
</tr>
</thead>
<tbody>
<tr>
<td>Milk, fat</td>
<td>.33&lt;sup&gt;b&lt;/sup&gt;</td>
<td>.50</td>
<td>.67</td>
<td>.80</td>
<td>.86</td>
<td>.90</td>
<td>.92</td>
<td>.94</td>
<td>.97</td>
</tr>
<tr>
<td></td>
<td>(.58)</td>
<td>(.71)</td>
<td>(.82)</td>
<td>(.90)</td>
<td>(.93)</td>
<td>(.95)</td>
<td>(.96)</td>
<td>(.97)</td>
<td>(.98)</td>
</tr>
<tr>
<td>Test</td>
<td>.25</td>
<td>.33</td>
<td>.50</td>
<td>.67</td>
<td>.78</td>
<td>.82</td>
<td>.85</td>
<td>.89</td>
<td>.93</td>
</tr>
<tr>
<td></td>
<td>(.50)</td>
<td>(.58)</td>
<td>(.71)</td>
<td>(.82)</td>
<td>(.88)</td>
<td>(.91)</td>
<td>(.92)</td>
<td>(.94)</td>
<td>(.97)</td>
</tr>
</tbody>
</table>

<sup>a</sup> \( a = 2 \) for milk and fat, 3 for test, which was used here.

<sup>b</sup> \( \frac{n}{n + a} \) is in top line and its square root is immediately below in parentheses.

While \( \frac{n}{n + a} \) represents the regression of 'true' herdmate average on the sample average, for purposes of comparing the accuracy of the estimate of the 'true' herdmate average, one should compare the square roots of the regressions rather than the regressions themselves. The square root of the regression is the correlation between the sample average of the herdmates based on \( n \) records and the 'true' herdmate average. Therefore, setting an arbitrary figure of .90, for example, as the desired accuracy of estimate, we see from Table 31 that 8 herdmates would be needed with milk or fat while 16 would be required with test.
The only remaining item related to computing the adjusted herdmate average, AHA, which concerns us here, is the proper \( \mu' \) to use in the formula (Equation 19). That equation implied that \( \mu' \) was the proper value. As noted, \( \mu' \) was the regional (or state) breed mean of records, commenced in the same year-season in which the particular daughter started her record. This compares with use of the nation-wide breed average of the previous four years for this particular season, under the present USDA system. Implications concerned with use of different \( \mu \) values will be discussed later.

3. The regressed adjusted herdmate average

   a. Theoretical considerations  The problem of biases in sire evaluation is a difficult one to solve. We have seen that by using deviations of the daughter's record from her contemporary herdmate average, the biases ascribable to herd and year-season effects can be eliminated, at least in theory. There remain the biases associated with the breeding value of the dam which, like the sire, contributes one-half of the genes to the daughter's gene aggregate. We will postpone the analysis of the dam's specific contribution to this bias until later. However, if the dam is a random sample of the breeding in the herd, we may disregard the specific contribution of the dam. Instead, we may then consider the average breeding value of the herd as a source of possible bias in sire evaluation.

   In this section we are concerned primarily with differences among herds in their average breeding value and their effects on sire evaluation.
In Equation 16, p. 92, we saw that 2 times the deviation of a daughter's record (D) from her contemporary herdmate (HA_D) provided an estimate of the sire's breeding value:

\[ 2(D-HA_D) = 2 \left[ \frac{s_j}{2} + \frac{g_i}{2} - g_i + \text{errors} \right] = s_j - g_i + \text{errors} \]

In this equation for a single daughter we have assumed that the breeding value of the dam is exactly equal to that of the herd average (g). As a simple illustration, suppose we have two herds with different average breeding values, g:

- in herd A: \( g_i = +20 \) units; in herd B: \( g_i = -20 \) units.

Now suppose we have a bull that is used in the above two herds, with one daughter in each herd. Let us further assume, for the sake of illustration, that both herdmate averages have been adjusted as in the previous section so that any differential effect of differences in numbers within a herd will be minimized. In other words, let us work with the adjusted herdmate averages, AHA. We then have, in herd A,

\[ 2(D-AHA_D) = 2 \left[ \frac{s_j}{2} + \frac{g_i}{2} - g_i + \text{errors} \right] = s_j + 2 \left[ \frac{(+20)}{2} - (+20) + \text{errors} \right] = s_j - 20 + \text{errors} \]

Likewise, in herd B,

\[ 2(D-HA_D) = s_j + 2 \left[ -\frac{(-20)}{2} - (-20) + \text{errors} \right] = s_j + 20 + \text{errors} \]

In other words, there is an apparent difference of 40 units, disregarding
errors, in the breeding value of this same bull in these two herds, but neither estimate is correct for his general breeding value. The estimate in the herd with the higher average breeding level is biased downward while that in the herd with the lower breeding value is biased upward.

This type of bias can be reduced in only three ways: (1) test the bull in a perfectly representative sample of herds in the population; (2) correct the herd averages so as to eliminate or at least reduce the bias statistically; or (3) adjust each daughter's record to account for the difference between the breeding value of her herd and the average breeding value of the whole population. Method (1) is close to the philosophy guiding some programs of sampling young sires for possible use in AI. Thus by testing a bull in a large number of representative herds in a particular population, this type of bias will tend toward zero. For instance, in the purely hypothetical example above, the average bias in the estimate of $s_j$ from the two herds is zero.

Concerning the latter two methods above, they are, in effect, simply 'two sides of the same coin'. Pursuing method (2), the correction needed to eliminate this source of bias is one which would reduce the adjusted herdmate average value by an amount equal to one-half of its average breeding value, i.e., by an amount equal to $\frac{-g_i}{2}$. This amount is equal to \[
\frac{\sigma^2_{HE}}{2 \left( \sigma^2_{HE} + \sigma^2_{HG} + \sigma^2_{YS/H} \right)}
\]
of the adjusted herdmate average, for which we have assumed that the average intraherd-year-season variance $\frac{\sigma^2_W}{n}$, has been removed. In the above fraction, $\sigma^2_{HE}$ equals the environmental
variance among herd averages, or $\sigma^2_h$ in the models of the previous section; $\sigma^2_{HG}$ equals the genic variance among herd averages, or $\sigma^2_g$ in the models of the previous section; and $\sigma^2_{YS/H}$ equals the variance of the effects of year-seasons within herds, or $\sigma^2_y/h$, of the previous section. The amount of effects retained in the adjusted herdmate average is therefore

$$1 - \frac{\sigma^2_{HG}}{\sigma^2_{HE} + \sigma^2_{HG} + \sigma^2_{YS/H}}$$

of the adjusted herdmate average, in relation to the population average. This latter is equal to

$$\frac{\sigma^2_{HE} + \sigma^2_{HG} + \sigma^2_{YS/H}}{\sigma^2_{HE} + \sigma^2_{HG} + \sigma^2_{YS/H}}$$

of the adjusted herdmate average, in relation to the population average. Let us now call the new herdmate average the **Regressed Adjusted Herdmate Average (RAHA)** because the adjusted herdmate average (AHA), from which it is derived, is regressed (1-b) of the way toward the population mean,

$$b = \frac{\sigma^2_{HE} + \sigma^2_{HG} + \sigma^2_{YS/H}}{\sigma^2_{HE} + \sigma^2_{HG} + \sigma^2_{YS/H}}$$

(Eq. 24)

In other words,

$$\text{RAHA} = \mu + b(\text{AHA} - \mu).$$

(Eq. 25)

What is needed for the solution to this problem is a means of evaluating the genic fraction, $\sigma^2_{HG}$, of the differences between herd averages. Method (3) presented on p. 101 provides us with one approach to the
solution of this problem, i.e., to evaluate \( b \) of Equation 24.

The reasoning behind that method is as follows: Considered in terms of purely additive effects, the ME production of a home-raised cow would be expected to follow very closely the average ME production of all cows in the herd because the same factors affect her records as theirs - i.e., the same herd effect of feeding and management practices and the same general climatic and weather conditions. If these were the only factors affecting her record, the latter would be expected to be equal to the herd average. However, the factor of genetic effects must be accounted for. Under random mating, one-half of the cow's gene aggregate comes from the herd gene pool, \( g_i \) (when considering the breeding value of her dam as equal to that for the herd average), and the other half from her sire. Thus the cow's production might be expected to vary somewhat from that of her herdmate average. The expected difference of the cow's record from the adjusted average of her contemporary herdmates would be equal to

\[
\begin{bmatrix}
\frac{2}{\sigma_{HE}^2} \\
\frac{2}{\sigma_{HG}^2} \\
\frac{2}{\sigma_{YS/H}^2}
\end{bmatrix}
\]

of the adjusted herdmate average, and of course,

\[
1 - \frac{2}{\sigma_{HE}^2 + \sigma_{HG}^2 + \sigma_{YS/H}^2} = b.
\]

(Eq. 26)

\( 'b' \), here, is defined as the regression of a daughter's record on her contemporary adjusted herdmate average, AHA, and is the desired value to be estimated.
b. Computation and interpretation of regressions

The entire deck of over 39,000 useable records was screened to select those bulls which had at least one daughter in each of at least two different herds. A total of 716 bulls qualified with 15,749 records by daughters in 705 different herds. The remaining records in these herds (by other bulls, or with sire not identified) were collated into the selected deck, giving a grand total of 33,139 records available for computing the various herdmate averages and related information. All major calculations here, as well as for all other studies in this thesis, were made on IBM equipment, including the 650 computer.

Two basic types of herdmate averages were calculated for all the records of each daughter of the 716 bulls and for all records of the dams of these daughters. Type 1 herdmate averages contained all records of the cows freshening in the same herd-year-season (HYS) except those for the daughter (or dam) herself, her dam (or daughter), and any paternal or maternal sibs of that particular daughter, that were identified.

Type 2 herdmate average (HA) contained all records in the same HYS except that for the daughter (or dam) herself. Records of dams, as such, were used only if they were made in the same herd as the daughter. Of course, many dams were also daughters of some of the 716 bulls and their records were also used as such.

Records from seven year-seasons were included. These correspond to the divisions noted previously, i.e., May through September and October through April for each year for the period May, 1957, through September, 1960. The population averages for the first season, May through September of 1957 were: milk, 12.2 (in 10 lbs.); test, 3.60%; and butterfat, 4.6 pounds. The averages for the other seasons were presented previously.
in Table 7, p. 40. All computations for herdmate averages, deviations, variances, covariances, etc., were made with milk expressed to the nearest 10 pounds, test to two decimal places, and fat to the nearest pounds.

The respective adjusted herdmate averages, AHA, were computed by the formulas:

\[
\text{for milk and fat yield, } AHA = \mu_1 + \frac{n}{n + 2} (HA - \mu_1)
\]

\[
\text{for test, } AHA = \mu_1 + \frac{n}{n + 3} (HA - \mu_1),
\]

where \(\mu_1\) is the population average for the particular year-season of freshening corresponding the freshening date for each record, and HA is the simple average of the records going into each herdmate average.

Table 32 contains a few simple statistics concerning the numbers of records in the various groups.

When only the record of the cow herself is excluded from her HA (type 2), the number of records in each HA group is increased by from two to three records, on the average, as compared with the type 1 herdmate groups, where the dam (or daughter) and any sibs (of the daughter) are also excluded.

A total of 155 type 1 records for daughters, out of the total of 15749 available, had no contemporary herdmates for a herdmate average (HA). This was due largely to the fact that all the herdmates of these daughters were paternal and/or maternal sibs, or the dam. Only 45 such records (i.e., with no contemporary herdmates) were in the type 2 daughter group, however. These were from small herds where this daughter was the only cow freshening in a particular herd-year-season. Neither of the above groups of zero herdmate records was included in Table 32 nor in any further computations. The small loss of information from this source
Table 32. Enumeration statistics concerning contemporary herdmate analyses

<table>
<thead>
<tr>
<th>HAa type</th>
<th>Subgroup</th>
<th>Number of Records</th>
<th>Ave. no. rec. perb</th>
<th>Ave. no. rec. per HAc</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>HYS Herds</td>
<td>HYS Herd</td>
<td>Indiv. basis</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Herd basis</td>
</tr>
<tr>
<td>1</td>
<td>Daus.</td>
<td>15594 2115 705</td>
<td>7.3 22.1</td>
<td>18.6 11.5</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Dam</td>
<td>1417 1420 147</td>
<td>3.1 10.0</td>
<td>18.4 12.8</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

AHA types were described on p. 104.

b These refer to the numbers of records for daughters and dams within each HYS or herd, rather than to the total number of records contained in each such group.

c Individual basis: simple overall average of number of records in the herdmate average groups; herd basis: the average number of records in each HA group within each herd was computed and this number was then used to compute the average for all herds, each with an equal weight.

is of little practical importance in AI sire evaluation.

Sums of squares and crossproducts were then computed for all the records with usable herdmate averages. The numbers of records involved were shown in Table 32. Tables 33 and 34 present the pertinent covariances and variances, on an individual record basis.

Table 35 gives the sample coefficients for the regression of records of daughters and dams on their respective herdmate averages, as computed from the values in Tables 33 and 34. Also included are the coefficients for the regression of AHA on HA using the type 1 records of daughters.
Table 33. Covariances of records and herdmate averages

<table>
<thead>
<tr>
<th>HA type</th>
<th>Record groups</th>
<th>Milk</th>
<th>Test</th>
<th>Fat</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>D:HA</td>
<td>23168</td>
<td>.0200</td>
<td>3376</td>
</tr>
<tr>
<td></td>
<td>D:AHA</td>
<td>19391</td>
<td>.0154</td>
<td>2817</td>
</tr>
<tr>
<td>2</td>
<td>D:HA</td>
<td>23791</td>
<td>.0221</td>
<td>3480</td>
</tr>
<tr>
<td></td>
<td>D:AHA</td>
<td>20680</td>
<td>.0178</td>
<td>3012</td>
</tr>
<tr>
<td>1</td>
<td>M:HA</td>
<td>22434</td>
<td>.0241</td>
<td>3325</td>
</tr>
<tr>
<td></td>
<td>M:AHA</td>
<td>19065</td>
<td>.0188</td>
<td>2827</td>
</tr>
<tr>
<td>2</td>
<td>M:HA</td>
<td>22410</td>
<td>.0241</td>
<td>3326</td>
</tr>
<tr>
<td></td>
<td>M:AHA</td>
<td>19728</td>
<td>.0195</td>
<td>2918</td>
</tr>
</tbody>
</table>

*D:HA* = covariance of a daughter's record and her herdmate average.

*D:AHA* = covariance of a daughter's record and her adjusted herdmate average.

*M:HA* = covariance of a dam's record and her herdmate average.

*M:AHA* = covariance of a dam's record and her adjusted herdmate average.

Table 34. Variances of records and herdmate averages

<table>
<thead>
<tr>
<th>HA type</th>
<th>Record groups</th>
<th>Milk</th>
<th>Test</th>
<th>Fat</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Daughters</td>
<td>74134</td>
<td>.1143</td>
<td>10420</td>
</tr>
<tr>
<td></td>
<td>HA</td>
<td>29694</td>
<td>.0315</td>
<td>4299</td>
</tr>
<tr>
<td></td>
<td>AHA</td>
<td>20449</td>
<td>.0194</td>
<td>2961</td>
</tr>
<tr>
<td>2</td>
<td>Daughters</td>
<td>- - same as for daughters, above - -</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>HA</td>
<td>28695</td>
<td>.0319</td>
<td>4136</td>
</tr>
<tr>
<td></td>
<td>AHA</td>
<td>21287</td>
<td>.0197</td>
<td>3056</td>
</tr>
<tr>
<td>1</td>
<td>Dams</td>
<td>73630</td>
<td>.1219</td>
<td>10299</td>
</tr>
<tr>
<td></td>
<td>HA</td>
<td>27518</td>
<td>.0333</td>
<td>3970</td>
</tr>
<tr>
<td></td>
<td>AHA</td>
<td>19524</td>
<td>.0191</td>
<td>2824</td>
</tr>
<tr>
<td>2</td>
<td>Dams</td>
<td>- - same as for dams, above - -</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>HA</td>
<td>26323</td>
<td>.0305</td>
<td>3822</td>
</tr>
<tr>
<td></td>
<td>AHA</td>
<td>19966</td>
<td>.0191</td>
<td>2890</td>
</tr>
</tbody>
</table>
Table 35. Regression coefficients computed on an individual record basis

<table>
<thead>
<tr>
<th>HA Sub-type group</th>
<th>Herdmate average (HA)(^a)</th>
<th>Adjusted herdmate average (AHA)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Milk</td>
<td>Test</td>
</tr>
<tr>
<td>1 Daughter</td>
<td>.780</td>
<td>.580</td>
</tr>
<tr>
<td>AHA</td>
<td>.815</td>
<td>.729</td>
</tr>
<tr>
<td>2 Daughter</td>
<td>.829</td>
<td>.692</td>
</tr>
<tr>
<td>1 Dam</td>
<td>.815</td>
<td>.722</td>
</tr>
<tr>
<td>2 Dam</td>
<td>.851</td>
<td>.791</td>
</tr>
</tbody>
</table>

\(^a\)For example, .780 pounds is the regression of records of daughters on their respective type 1 herdmate averages for milk yield.

With reference to Tables 33 through 35, we may note briefly the following: (1) The regression coefficients increase substantially when going from those for a cow (daughter or dam) or her herdmate average (HA) to those for the cow on her adjusted herdmate average (AHA). (2) There is a marked increase in the regression coefficients when going from those of type 1 to type 2 herdmate groups. This is true for both daughters and dams and with either HA or AHA as the independent variable. Affecting this latter change among the daughters is the fact that the covariances increased from type 1 to type 2 herdmate groups. This probably reflected the fact that a larger number of close relatives of the daughter were included in the type 2 herdmate average. However, the covariance for the dams changed only slightly, or not at all, from type 1 to type 2 herdmate groups. This reflected the very slight changes in average genetic merit among herdmate cows for the dams when going from
type 1 to type 2 herdmate groups. The composition of the herdmate group for a dam was determined by the relatives of her daughter rather than by the relatives of the dam, herself. Thus a dam's herdmate groups of type 1 and 2 both may have contained the dam's paternal and/or maternal sibs and possibly her own dam. Changes in the composition of these herdmate groups by the presence or absence of the more distant relatives which were related through her daughter would then not have produced as large of a change in the herdmate average, and in turn, the covariance would have changed but little, also.

The regression coefficients shown in Table 35 are probably not directly usable as 'b' values primarily because of correlation both among the daughters and among the herdmate groups within a single herd-year-season (HYS). Table 32 showed an average of 7.27 records per HYS group among the daughters and 3.13 among the dams of the type 1 HA groups. A further breakdown indicated an average of 1.77 records per bull per HYS group and an average of 4.1 different bulls represented among the 7.27 records within each average HYS group. Thus, both the covariance of daughter and herdmate average and variance among herdmate averages were biased downward. Many of the same records contributed to all of the herdmate averages within a HYS group, while only about one-fourth of the daughters within each such group were by the same bull. For this reason it seems logical that the variances among the herdmate group averages were reduced substantially more than were the covariances, thereby tending to inflate the sample regression coefficients.

Among the dams, an additional factor tended to raise still further the regression coefficients. Dams with more than one daughter by one
of the 716 bulls included in the study had a separate herdmate average card prepared so that the dam might have a suitable herdmate average and deviation card to go with each daughter in subsequent analyses. Hence, for a dam with more than one daughter, while the composition of her respective herdmate groups varied slightly from daughter to daughter, these different herdmate groups for each record included basically the same records. For example, if a dam had two daughters, two separate herdmate average and deviation cards were prepared for each of the dam's records. If the daughters were full sibs, each set of records for the dam was identical. However, if the daughters were half sibs, as was the usual case, the composition of the herdmate groups for the dam's records was slightly different for each daughter, depending on the relationship of the herdmate cows with each daughter. As all records by dams were included in the dams' regression analysis, some duplication of herdmate groups resulted, thereby depressing the variance among the herdmate groups and increasing the regression coefficients slightly.

As a consequence of the above, perhaps the major benefit from the regression coefficients shown in Table 35 is that they provide an estimate of the upper limit for the \( b \) values applicable to this population. If only one randomly selected record per herd-year-season group had been used in the regression analysis, undoubtedly more reliable \( b \) values might have been obtained. Unfortunately, this was not done.

In view of the many qualifications accompanying the preceding calculations and estimates, the values for the regression of cow on adjusted herdmate average, \( b_{c \text{ AHA}} \), were adjusted downward and set at the values shown in Table 36.
Table 36. Adjusted values for $b_c$ AHA

<table>
<thead>
<tr>
<th>Trait</th>
<th>Type 1 HA</th>
<th></th>
<th>Type 2 HA</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Daughters</td>
<td>Dams</td>
<td>Daughters and dams</td>
<td></td>
</tr>
<tr>
<td>Milk</td>
<td>.90</td>
<td>.92</td>
<td>.92</td>
<td></td>
</tr>
<tr>
<td>Test</td>
<td>.77</td>
<td>.87</td>
<td>.93</td>
<td></td>
</tr>
<tr>
<td>Fat</td>
<td>.91</td>
<td>.94</td>
<td>.93</td>
<td></td>
</tr>
</tbody>
</table>

It is unlikely that the exact values needed for any specific group or situation can ever be determined perfectly, in view of the many factors involved, only a few of which were discussed here. The best we can hope is to be close enough to the correct values so that we are removing much more of the biases than we are adding. It may be added that the USDA, Cornell and New Zealand groups are using $b$ values of .9 for daughters' records for both milk and fat, with no RAHA's being computed for test.

The RAHA's were then computed for all records to be used here in subsequent analyses. The appropriate values for $b$ were taken from Table 36, depending on which type of RAHA record was being computed. For example, for fat, .91 was used for daughters with type 1 herdmate average group, .94 for dams with type 1 herdmate average group, and .93 for daughters and dams of type 2 herdmate average group, etc.

An important question is the choice of $\mu$ to use in this operation. This will be discussed in more detail presently, but we may note that we have used the same herd-year-season average here as was employed in
computing the AHA previously. In other words, under the present method for computing the RAHA, and if estimates of $b'$ are available, the regressed adjusted herdmate average (RAHA) could be computed in one operation from the individual lactation records, as follows:

$$\text{RAHA} = \mu' + \frac{bn}{n + a} (HA - \mu')$$  \hspace{1cm} (Eq. 27)

Here, $\mu'$ is the state or regional breed average for the particular year-season of freshening and $n$ is the number of cows making up the contemporary herdmate average, HA.

During the operation for computing the RAHA, two deviations also were computed for each record:

1. cow's record minus AHA and
2. cow's record minus RAHA.

These were computed for milk to the nearest 10 pounds, for test in percent to 2 decimal places and for butterfat to the nearest pound, to be used in subsequent analyses.

4. Handling multiple records of cows

In the section on repeatability (page 149), we have seen that temporary environmental and random error effects may have a large influence on a single record of a cow. These effects do not carry over from one lactation to the next as do the cow's average genotypic and permanent environmental effects. With each succeeding freshening, the cow is faced with a new set of conditions which influence that particular record, making it either higher or lower than her 'true' lactation yield.

By 'true' lactation yield we mean the real producing ability (RPA) of that cow, which may in turn be defined as the producing ability of
the cow under environmental conditions chosen as standard (Lush, 1945, p. 170). One method for estimating an animal's real producing ability is:

\[
RPA = \mu_1 + \frac{n r}{1 + (n-1) r} (\bar{C} - \mu_2),
\]

(Eq. 28)

where: \(\mu_1\) and \(\mu_2\) are specified population averages, \(r\) is the repeatability of a cow's record, or the average coefficient of correlation between two records by the same cow, and \(\bar{C}\) is the average of \(n\) records by the cow. (See Lush et al., 1933, and Kempthorne, 1957, p. 230, for separate derivations of the formula for \(RPA\).)

Estimates of repeatability were obtained from various analyses that were discussed in Section IV-B. The \(r\) values applicable to records expressed as deviations from their respective contemporary herdmate averages were shown in Table 12 to be as follows: for lactation milk yield, \(r = .51\); fat yield, \(r = .47\); and for lactation average test, \(r = .72\). Table 37 presents values for \(\frac{nr}{1 + (n-1) r} = R\), when \(r\) equals the above figures and when \(n\) goes from 1 to 5. These values (\(R\)) represent the regression of \(RPA\) on the average of \(n\) records by the cow, or the fraction of what one expects to get of what is reached for. However, for purposes of comparing what one gains by selecting on the basis of one or more records, one should compare the square roots of the regressions rather than the regressions themselves (see Lush, 1948, p. 173). The square root of the regressions is the correlation between the average record of the cow based on \(n\) records and her real producing ability. These also are shown in Table 37.

Table 38 shows the gains one might expect by selecting cows on an
Table 37. The relationships between the average record of a cow and her real producing ability (RPA) for different number of records, $n$, in the average (regressions and correlations $^a$)

<table>
<thead>
<tr>
<th>Trait</th>
<th>$r$</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Milk</td>
<td>.51</td>
<td>.510</td>
<td>675</td>
<td>.757</td>
<td>.806</td>
<td>.839</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(71)</td>
<td>(82)</td>
<td>(87)</td>
<td>(90)</td>
<td>(91)</td>
</tr>
<tr>
<td>Test</td>
<td>.72</td>
<td>.720</td>
<td>837</td>
<td>.885</td>
<td>.911</td>
<td>.928</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(85)</td>
<td>(91)</td>
<td>(93)</td>
<td>(95)</td>
<td>(96)</td>
</tr>
<tr>
<td>Fat</td>
<td>.47</td>
<td>.470</td>
<td>639</td>
<td>.727</td>
<td>.780</td>
<td>.816</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(69)</td>
<td>(80)</td>
<td>(85)</td>
<td>(88)</td>
<td>(90)</td>
</tr>
</tbody>
</table>

$^a$Values in parentheses are correlations to go with the regressions immediately above.

Table 38. Gains expected for milk with increased $n^a$

<table>
<thead>
<tr>
<th>$n_1$</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.15</td>
<td>1.23</td>
<td>1.27</td>
<td>1.28</td>
</tr>
<tr>
<td>2</td>
<td>1.06</td>
<td>1.10</td>
<td>1.11</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>1.03</td>
<td>1.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td></td>
<td>1.01</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^a$See text for full description of table.

average of $j$ records as compared with selecting on only $i$ records, for milk yield. For example, this gain with 2 records over 1 equals $1.15 = \frac{0.82}{0.71}$ from Table 37. That is, by selecting on an average of two records, one would expect to gain about 1.15 times as much in milk yield as he would by selecting on one record only.
From the values in Tables 37 and 38, we see that appreciable increases in information on a cow are achieved by using a second record for all three traits, with the least increase achieved for test. Very little is gained by using a third record for test or by using a fourth record for milk or fat. These correlations also indicate that one lactation record for test gives as much information about the real producing ability of a cow as we get from approximately 2.5 records for milk and 3 records for fat.

However, other considerations enter when weighing the gains achieved with an increased number of records by a cow. One is the important question of costs. That is, does the cost of securing a second or additional record offset the gains expected in a selection program when using more than one record?

Also, if we wait for additional records on a cow before deciding whether to keep her or dispose of her, we may increase the length of generation more than enough to offset the additional accuracy attained. Dickerson and Hazel (1944) pointed out that the criterion by which any breeding program must be judged is the genetic improvement per year rather than per generation. This criterion applies to proofs for sires as well as for the estimated real transmitting ability for cows. While the latter is not the same as real producing ability, although they are closely related (Berry, 1945), the same type of reasoning applies to the use of RPA.

In sire proving, we usually have the additional factor of varying numbers of daughters per sire to contend with. While this topic will be taken up in more detail later, we may note here that, under certain
conditions, it may be easier and more desirable to increase the number of daughters in a bull proof than to increase the number of records per daughter. However, adding another record by a previous daughter is not equivalent to adding another daughter. A new record is merely new evidence on that previous daughter and does nothing to reduce the errors from Mendelian sampling which occurred when that daughter was conceived nor those from dominance, epistasis, and permanent environment in her.

Most dairy cows have more than one lactation record during their lifetime. Voelker (1950) found that, in Iowa DHIA herds, the average productive life for a cow in any one herd was 3.22 years. Thus each cow had an average of about three lactations, which is close to the number required if the cow population is to be maintained. Original proofs for a dairy sire may include only single records of daughters, but in a year or two most of these daughters will have additional records. In the meantime, additional daughters are being tested. Hence, subsequent proofs for the sire will include daughters with varying numbers of records. These later proofs are useful not only during the productive life of many AI bulls, but also in pedigree evaluation. Therefore, later proofs form an integral part of any complete breeding program. There appears to be no valid reason for not including all available production information on all tested daughters in a sire proof. Possibly the only exception is when sires are purposely compared on the basis of single records of each daughter. For that case, each daughter would simply be given an equal weight with every other daughter in the proofs.

Equation 28 for RPA indicates that values for $\mu_1$ and $\mu_2$ are needed. The RAHA for each record of a cow is well suited as a proper value for
\( \mu_2 \) when the cow is to be used in an AI sire proof. We would compute the deviation of a single record from its RAHA, multiply the result by its appropriate \( r \), then add the value of the RAHA. This gives an estimate of the RPA for a cow with a single record. In this case, the RAHA served as both \( \mu_1 \) and \( \mu_2 \). However, when more than one record per cow is to be used, complications arise. These concern mainly what value shall be used as \( \mu_1 \) for each cow. Several possibilities are available but none has found general acceptance. The decision as to which value to apply largely depends on the use to be made of the records.

As we are concerned here primarily with applications to bull proofs, we have adopted the following procedure: Instead of computing for each cow an expression for her real producing ability (RPA), we simply bypass the question of \( \mu_1 \) until later. Instead, we will designate the computed value, \( R(\bar{C} - \bar{\mu}_2) \), as the real producing deviation (RPD) for that cow. Tyler (1958) has substituted, for the \( \mu_2 \) term, above, the herd averages for the respective years in which the records were made. He used the resultant RPD values in indexing cows in the Wisconsin station herds.

Thus, for our situation, we have:

\[
\text{RPD} = \frac{nr}{1 + (n-1)r} (\text{cow's average} - \text{average of her RAHA's}). \quad (\text{Eq. 29})
\]

All deviation records available for each cow were then combined according to the formula in Equation 29, with \( r \) values being obtained from Table 37. The resultant RPD is termed the "weighted average of deviations from the regressed adjusted herdmate average", or simply "Wt. Av. Dev. RAHA". In addition, the unweighted average of deviations from the RAHA (Unwt. Av. Dev. RAHA) was computed for each cow. This is
the simple average of the respective deviations. Finally, the 'actual' (i.e., 305-day-2X-ME) records for each cow simply were averaged, with no weighting factors for number of records being applied. The above were computed for all type 1 records for daughters and dams, and type 2 records for daughters only, to be used in subsequent analyses.

5. Further notes on the use of population averages

As was described in Section IV-E-3-c, the RAHA associated with each production record used in a bull proof may be computed by the formula:

$$RAHA_{ij} = \mu_j + \frac{bn}{n+a} (HA_{ij} - \mu_j).$$

\(\mu_j\) was the year-season average over all herds in the available Holstein data from Iowa, with the year-season of freshening being the same as that for the \(j^{th}\) record of the \(i^{th}\) daughter, and all other terms have been defined previously. By using the same \(\mu\) to both adjust and regress each herdmate average (HA), each RAHA may be computed from the original records in one simple operation and the deviation taken at the same time.

This is in sharp contrast to the method currently in use by the USDA in its computational procedures (see p. 19). They use a nation-wide breed average for the preceding four years in correcting the records for the daughters and herdmates comprising each bull proof. The major points in question here concern:

(1) using a season average extending back over four years but not including even the current year-season; and

(2) using a nation-wide population average in correcting these records instead of an average for the particular state or region in which each cow makes her record.
Concerning (1), we saw in the analysis presented in Section IV-A-6 that using a pooled season average comprising several years was only about one-half as efficient in removing year-season effects as was accomplished when only the average of the particular year-season associated with a particular record was used in computing the deviations.

Regarding point (2), this revolves on the question of how many herds are needed to provide a reliable estimate of $\mu$ in a specific population. Our approach is as follows:

Following Cochran (Snedecor, 1956, p. 501), suppose that $L$ is the allowable error in the sample mean, and that we are willing to take a five percent chance that the error will exceed $L$.

The 95 percent confidence limits computed for a sample mean, $\bar{y}$, are: $\bar{y} \pm \frac{2\sigma}{\sqrt{N}}$, where $\sigma$ is the population standard deviation, in this case for the herdmate average, $HA$; and $N$ is the sample size making up $\bar{y}$. We then may set $L = \frac{2\sigma}{\sqrt{N}}$. Therefore, the required sample size ($N$) is:

$$N = \frac{4\sigma^2}{L^2}.$$

From the present data $\sigma^2_{HA}$ was estimated to be 2.94, 3.61, and 0.02278 for milk, fat and test, respectively (see Table 30, p. 97). (The original units of measurement were 10 pounds for milk, percent for test and pounds for fat.) If we set the allowable error, $L$, at 1/10 of a standard deviation for each trait, we then have $L^2 = 250, 36$ and $0.000228$ for milk, fat and test. $N$ is then estimated as 399, 402 and 400 for these three traits, respectively.

In other words, we have a 95 percent assurance that 400 herd
averages, within a single year-season, will provide an estimate of the population mean, \( \mu \), within \( \frac{1}{10} \) of a standard deviation of its true value. In Iowa, this number is far exceeded for the Holstein breed. When there are not approximately 400 herds within a particular relatively homogeneous region, two alternatives are available:

1. Enlarge the region so that more herds are included; or
2. Accept a larger error in the estimate of the true herdmate average.

However, to include herds from widely differing regions in the value for \( \mu \) is likely to introduce a bias in the resulting deviation record. (See, for example, Thompson et al., 1962.)

The only conclusion possible in view of the above is that as long as a sufficient number of herds are within a region that is quite uniform in climate and management practices, there seems little justification for including other regions and/or extra year-seasons in the estimate of \( \mu \), used in computing the RAHA for each record.

In the previous section, the RFD for each daughter was computed by first taking the deviation of the respective RAHA from each record by that cow. However, no concrete evidence was presented to justify its use in place of a different population average. This question is closely related to the fact that one of the more desirable features for a bull proof is that it contain the least possible amount of extraneous (non-genetic) variance among the daughters making up that proof.

To study this problem, and in connection with other analyses of bull proofs to be presented later, three separate proofs consisting of unweighted averages of 10, 25 and 75 different daughters were computed.
for each of the 13 AI bulls having at least 110 tested daughters. Only the first available records for each daughter were used in these proofs. The 'actual' production and corresponding deviations from RAHA were used in the computations for milk and test. The pooled intrasire variances were computed for each of the proofs containing the three different numbers of daughters, as well as the pooled variances over all proofs for each bull. Table 39 presents a summary of the variance among daughters within sire groups, $\sigma^2_w$, for the different classification of proofs, along with F tests.

Table 39. A comparison of the variances within proofs when using 'actual' and deviation records

<table>
<thead>
<tr>
<th>Class of records</th>
<th>Milk</th>
<th>Test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\sigma^2_w$</td>
<td>d.f.</td>
</tr>
<tr>
<td>10 records</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Actual records</td>
<td>1.082</td>
<td>1.107</td>
</tr>
<tr>
<td>Dev. from RAHA</td>
<td>.1054</td>
<td>1.082</td>
</tr>
<tr>
<td>25 records</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Actual records</td>
<td>1.107</td>
<td>1.107</td>
</tr>
<tr>
<td>Dev. from RAHA</td>
<td>.1058</td>
<td>1.107</td>
</tr>
<tr>
<td>75 records</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Actual records</td>
<td>1.096</td>
<td>1.096</td>
</tr>
<tr>
<td>Dev. from RAHA</td>
<td>.0978</td>
<td>1.096</td>
</tr>
<tr>
<td>Pooled, all proofs</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Actual records</td>
<td>1.098</td>
<td>1.098</td>
</tr>
<tr>
<td>Dev. from RAHA</td>
<td>.0978</td>
<td>1.098</td>
</tr>
</tbody>
</table>

*a* d.f. = degrees of freedom.

b* = significant at 5 percent level; ** = significant at 1 percent level.
For milk, statistically significant reductions are accomplished in the $\sigma_w^2$ components when deviation records are used. The variance among daughters equals the variance among $(D - \mu)$; hence the variance among the daughters' 'actual' records would be the same as if each daughter's record were first taken as a deviation from the overall population average, $\mu$. However, the deviation records for the exact same 'actual' records were computed as $D_{ij} - \text{RAHA}_{ij}$ where $D_{ij}$ is the $j^{th}$ record of the $i^{th}$ daughter and $\text{RAHA}_{ij}$ is the $j^{th}$ RAHA associated with the $j^{th}$ record of the $i^{th}$ daughter. The RAHA is equivalent to a variable $\mu$ and is generally closer to the expected value of $D$ than is the overall population average, $\mu$. It then follows that the variance among deviation records within sires would be smaller than the variance of the 'actual' records. As a result we have the desirable feature that a milk proof using deviation records computed from an appropriate $\mu_2$, which in this case is the RAHA, has a smaller error. The results for fat yield surely would follow closely the pattern for milk yield. For test, the intra-sire variance when using deviation records is reduced consistently, but the reduction is not statistically significant at the 5 percent level of probability. However, the gains in efficiency are consistent enough to merit considering using the deviations from RAHA in any bull-proving proving even for a trait such as test. We then may conclude that the regressed adjusted herdmate average (RAHA), or something closely related to it, is well suited to serve as $\mu_2$ in Equation 28, when those records are to be used in bull proofs.
6. Testing the efficiency of deviation records in removing herd-year-season effects

a. Intrasire HYS analysis In this and the next section we will discuss the results of several studies designed to evaluate how effectively the use of deviation records removes the extraneous sources of variance due to herds, years and seasons, in comparison with use of 'actual' production records. These studies should provide some basis for determining the gains that might be expected from the use of deviation records in various applied problems of dairy cattle breeding, to be discussed in the final sections.

For the first analysis to be discussed here, a random record of type 1 herdmate group was selected for each daughter of the 75 bulls having the most daughters in the data for which deviation records were computed. As noted previously, all bulls included here had daughters in more than one herd, and all but 12 of the 75 were AI sires. Each bull had at least 25 daughters and the number ranged up to 374 daughters. A simple hierarchical model was used: herd-year-seasons within sires and within herd-year-seasons. A total of 5081 records were included in the analysis. Table 10 shows the degrees of freedom and the expected composition of the mean squares.

In this analysis we are not interested in the sire's contribution to the variance among records, but only in that of the herd-year-season (HYS). By designing the analysis within sires, we are able to bypass the latter effect. So, in essence, we have a simple one-way classification: among herd-year-seasons, and within herd-year-seasons, the sire differences having been bypassed. To the extent that the deviations
Table I40. Degrees of freedom and expected mean squares for HYS/S analysis

<table>
<thead>
<tr>
<th>Source of variance</th>
<th>d/f</th>
<th>Expected mean squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sires (S)</td>
<td>74</td>
<td>$\sigma_W^2 + 3.695 \sigma_{HYS/S}^2 + 67.046 \sigma_S^2$</td>
</tr>
<tr>
<td>Herd-year-seasons</td>
<td></td>
<td></td>
</tr>
<tr>
<td>within sires, HYS/S</td>
<td>3401</td>
<td>$\sigma_W^2 + 1.413 \sigma_{HYS/S}^2$</td>
</tr>
<tr>
<td>Within HYS/S</td>
<td>1605</td>
<td>$\sigma_W^2$</td>
</tr>
<tr>
<td>Total</td>
<td>5080</td>
<td></td>
</tr>
</tbody>
</table>

from the corrected herdmate averages succeed in removing the HYS effects, the F values for testing the significance of HYS/Sires should approach 1.0. The results for 'actual' records and for deviations from both the AHA and RAHA values for milk, test and butterfat are shown in Table 41.

With so many degrees of freedom, all F tests are significant. However, the F values for the AHA and the RAHA are markedly lower than those for 'actual' records.

The F ratios are, of course, affected by the coefficients of the mean squares, but the ratios of the components $\frac{\sigma_{HYS/S}^2}{\sigma_W^2}$ are free of this encumbrance. Thus, the latter present a clearer picture of the relationship between the two effects, not confused by the amount of evidence on each. For example, the ratio,$$
\frac{\sigma_{HYS/S}^2}{\sigma_W^2},
$$for milk is only .21 as large with deviations from RAHA.
Table 41. Analysis of herd-year-seasons within sires

<table>
<thead>
<tr>
<th>Class of record</th>
<th>Components</th>
<th>( \sigma^2_S )</th>
<th>( \sigma^2_{HYS/S} )</th>
<th>( \sigma^2_W )</th>
<th>( \frac{\sigma^2_{HYS/S}}{\sigma^2_W} )</th>
<th>F values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Actual record</td>
<td>5230</td>
<td>16474</td>
<td>46428</td>
<td>.354</td>
<td>1.501</td>
<td></td>
</tr>
<tr>
<td>Milk</td>
<td>Dev. AHA</td>
<td>3321</td>
<td>3741</td>
<td>46795</td>
<td>.080</td>
<td>1.113</td>
</tr>
<tr>
<td></td>
<td>Dev. RAHA</td>
<td>3330</td>
<td>3571</td>
<td>46750</td>
<td>.076</td>
<td>1.108</td>
</tr>
<tr>
<td>Actual record</td>
<td>.01056</td>
<td>.02129</td>
<td>.08060</td>
<td>.264</td>
<td>1.373</td>
<td></td>
</tr>
<tr>
<td>Test</td>
<td>Dev. AHA</td>
<td>.01076</td>
<td>.01052</td>
<td>.08124</td>
<td>.130</td>
<td>1.183</td>
</tr>
<tr>
<td></td>
<td>Dev. RAHA</td>
<td>.01024</td>
<td>.01004</td>
<td>.08104</td>
<td>.124</td>
<td>1.175</td>
</tr>
<tr>
<td>Actual record</td>
<td>857</td>
<td>2429</td>
<td>6125</td>
<td>.396</td>
<td>1.560</td>
<td></td>
</tr>
<tr>
<td>Fat</td>
<td>Dev. AHA</td>
<td>690</td>
<td>655</td>
<td>6159</td>
<td>.106</td>
<td>1.150</td>
</tr>
<tr>
<td></td>
<td>Dev. RAHA</td>
<td>676</td>
<td>626</td>
<td>6154</td>
<td>.102</td>
<td>1.144</td>
</tr>
</tbody>
</table>

F values are the ratio of the mean squares for HYS/S and W.

as with 'actual' records. That is, \( \frac{\sigma^2_{HYS/S}}{\sigma^2_W} = .21 \) of \( \frac{\sigma^2_S}{\sigma^2_W} = .21 \). Or, in other words, for milk yield, the HYS component, as a fraction of the variance within HYS groups, has been reduced 79 percent, by expressing each record as a deviation from its RAHA. The comparable reduction for fat yield is 74 percent and for test is 53 percent.

The results in Table 41 indicate that much, but not all of the herd-year-season effects have been removed by the use of deviations. Had deviations from the uncorrected herdmate average (HA) also been studied.
in such an analysis, a more complete picture would have been available, especially for judging the effectiveness of the adjustments used in computing the AHA and RAHA. Unfortunately this was not done. However, the deviations from RAHA seem to be slightly more effective in removing the HVS effects, for all three traits, than were the AHA deviations. However, the results for these two types of deviation records were so close that the actual effects of the two separate corrections, \( \frac{n}{n+a} \) and \( b \), cannot be clearly differentiated with this analysis.

A brief review of the models may help to clarify some of the aspects involved. It may be recalled from Sections IV-E-2 and IV-E-3 that the adjusted herdmate average (AHA) was computed as

\[
AHA = \mu' + \frac{n}{n+a} (HA - \mu'),
\]

while the regressed adjusted herdmate average (RAHA) was computed as

\[
RAHA = \mu' + b(AHA - \mu'),
\]

which is equivalent to

\[
RAHA = \mu' + \frac{bn}{n+a} (HA - \mu').
\]

In terms of additive models, we have:

- Daughter's record = \( D = \mu' + h_i + \frac{s_j}{2} + g_i + y_{i1} + e_{ij1m} \)
- Herdmate average = \( HA = \mu' + h_i + g_i + y_{i1} + \frac{\sum e_{ij1m}}{n} \)
- Adjusted herdmate average (AHA) = \( \mu' + \frac{n}{n+a} (h_i + g_i + y_{i1} + \frac{\sum e_{ij1m}}{n}) \)
- Regressed adjusted herdmate average (RAHA) = \( \mu' + \frac{bn}{n+a} (h_i + g_i + y_{i1} + \frac{\sum e_{ij1m}}{n}) \)

In the present analysis, deviations were considered within sires, so we
may disregard the sire effect, s_i. Therefore,

\[ D - HA = - \frac{g_i}{2} + \text{daughter error} + \text{average HA error} \]

\[ D - AHA = \left(1 - \frac{n}{n + a}\right) (h_i + y_{ii}) + \left(\frac{1}{2} - \frac{n}{n + a}\right) g_i + \text{error} - \left(\frac{n}{n + a}\right) (\text{HA error}) \]

\[ D - RAHA = \left(1 - \frac{bn}{n + a}\right) (h_i + y_{ii}) + \left(\frac{1}{2} - \frac{bn}{n + a}\right) g_i + \text{error} - \left(\frac{bn}{n + a}\right) (\text{HA error}) \]

The purpose of the corrections, \( \frac{n}{n + a} \) and b, on the herdmate average were to remove the average herdmate error and g_i effects, respectively, where g_i is the average additive genetic effect of the i^(th) herdmate group. In so doing, it is possible that some biases connected with herd environmental (h_i) and year-season effects within that herd (y_{ii}) were not removed. Also, the sum of the various intraherd effects surely are not uniform from herd to herd, so the \( \frac{n}{n + a} \) adjustment factor used undoubtedly was not equally appropriate for all herdmate groups. Likewise, the value for b was surely not applicable to all herds, being an average value. And finally, we had seen previously (Section IV-A-5) that some interaction of herd and year-season effects was present with the year-season divisions adopted for the present data.

The above and other factors no doubt contributed to creating a situation where not all the herd-year-season (HYS) effects might be expected to be removed when records, expressed as deviations, are employed in such analyses as those made here. This result is perhaps the key factor restricting the usefulness of deviation records in sire evaluation.
and related studies, as we shall see in subsequent sections. It is extremely doubtful if any scheme of computation can ever remove all HYS effects. However, on the basis of theoretical considerations and the results obtained with the present analysis, it appears that, taken as a whole, deviation records are an effective means and perhaps the most effective means available, of removing most of the HYS effects from dairy production records.

b. Daughter-dam analyses These studies concern comparisons between: (1) the intrasire regressions of daughter on dam computed from 'actual' records and those computed from deviation records; and (2) the corresponding intrasire correlations of daughter and dam.

The sole criterion used in the selection of data for these studies was that each bull was required to have at least two daughter-dam pairs so as to contribute to the intrasire components.

Three types of averaged records were used for each daughter and her dam in the analysis. These were described in Section IV-E-4, and were as follows: (1) unweighted average of all 'actual' records available for each cow, (2) unweighted average of deviations from RAHA (Unwt. Av. Dev. RAHA), and (3) weighted average of deviations from RAHA (Wt. Av. Dev. RAHA). All the above were records of type 1 HA in which not only the record of the daughter (or her dam) but also those of certain close relatives of the daughter were excluded from the respective herd-mate averages. A total of 3129 daughter-dam pairs for 351 sires were included, with an average of approximately 8.9 pairs per sire.

Table 1 presents the intrasire mean crossproducts (covariances) and mean squares ($\sigma^2_{W}$ components) computed from the analyses of covariance
Table 42. Intrasire analysis; covariances of daughters and dams and variances of each

<table>
<thead>
<tr>
<th>Trait</th>
<th>Covariance or variance</th>
<th>'Actual' records</th>
<th>Unwt. av. dev. RAHA</th>
<th>Wt. av. dev. RAHA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Daus.</td>
<td>Dams</td>
<td>Daus.</td>
</tr>
<tr>
<td>Milk</td>
<td>Covariance</td>
<td>15682</td>
<td>66284</td>
<td>43353</td>
</tr>
<tr>
<td></td>
<td>Variance</td>
<td>51488</td>
<td>56284</td>
<td>43353</td>
</tr>
<tr>
<td>Test</td>
<td>Covariance</td>
<td>.0366</td>
<td>.1035</td>
<td>.0277</td>
</tr>
<tr>
<td></td>
<td>Variance</td>
<td>.0835</td>
<td>.1325</td>
<td>.0752</td>
</tr>
<tr>
<td>Fat</td>
<td>Covariance</td>
<td>2200</td>
<td>7619</td>
<td>876</td>
</tr>
<tr>
<td></td>
<td>Variance</td>
<td>7252</td>
<td>7619</td>
<td>5976</td>
</tr>
</tbody>
</table>

Table 43. Correlation and regression coefficients with approximate 95 percent confidence limits computed from 'actual' and deviation records

<table>
<thead>
<tr>
<th>Trait</th>
<th>Coefficient</th>
<th>'Actual' records</th>
<th>Unwt. av. dev. RAHA</th>
<th>Wt. av. dev. RAHA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Milk</td>
<td>( r_{\text{Dau. Dam}} )</td>
<td>.291</td>
<td>.155</td>
<td>.166</td>
</tr>
<tr>
<td></td>
<td>( b_{\text{Dau. Dam}} )</td>
<td>(.259 - .323)</td>
<td>(.120 - .189)</td>
<td>(.132 - .200)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(.246 - .312)</td>
<td>(.112 - .182)</td>
<td>(.116 - .182)</td>
</tr>
<tr>
<td>Test</td>
<td>( r_{\text{Dau. Dam}} )</td>
<td>.394</td>
<td>.330</td>
<td>.332</td>
</tr>
<tr>
<td></td>
<td>( b_{\text{Dau. Dam}} )</td>
<td>(.366 - .425)</td>
<td>(.299 - .361)</td>
<td>(.301 - .363)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(.323 - .385)</td>
<td>(.264 - .326)</td>
<td>(.260 - .322)</td>
</tr>
<tr>
<td>Fat</td>
<td>( r_{\text{Dau. Dam}} )</td>
<td>.296</td>
<td>.142</td>
<td>.152</td>
</tr>
<tr>
<td></td>
<td>( b_{\text{Dau. Dam}} )</td>
<td>(.263 - .328)</td>
<td>(.108 - .176)</td>
<td>(.118 - .190)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(.255 - .321)</td>
<td>(.103 - .173)</td>
<td>(.108 - .174)</td>
</tr>
</tbody>
</table>
and variance for daughters and dams using the above data. From the results shown in Table 42, we can compute the intrasire correlations of daughter and dam and intrasire regressions of daughter on dam. These are presented in Table 43. Examples of the computations are as follows:

\[ r_{\text{Dau. Dam}} \text{ using actual milk records} = \frac{15682}{\sqrt{51488 \times 56284}} = 0.291; \]

\[ b_{\text{Dau. Dam}} \text{ using Wt. Av. Dev. RAHA records} = \frac{290}{2058} = 0.141. \]

Also shown in Table 43 are the approximate 95 percent confidence limits for the various coefficients. For the correlations, Fisher's z transformation was used (Snedecor, 1956, p. 173). In this situation,

\[ z = \frac{1}{2} \left[ \log_e(1 + r) - \log_e(1-r) \right] \text{ and } \sigma_z = \sqrt{\frac{1}{N-3}}, \]

where \( r \) is the sample correlation and \( N \) is the number of daughter-dam pairs less the number of sires in the analysis, or 2778 in this case. For the variance of the regression coefficients, the formula of Falconer (1960, p. 179)

\[ \sigma_b^2 = \frac{1}{N-2} \left[ \frac{\sigma_{\text{Dau}}^2}{\sigma_{\text{Dam}}^2} - b^2 \right]. \]

As noted above, the comparisons of interest here are between the intrasire correlations/regressions of daughter and/or dam computed from 'actual' records and the corresponding correlations or regressions computed from deviation records. For the correlations, significances were tested with Student's t using the z values for each of the two correlations being compared and the variance of z. The variances for all z values in this analysis were the same, as they depend only on the degrees of freedom, 2778 here. Thus,
$$t = \frac{z_A - z_D}{\sqrt{2\sigma_z^2}},$$

where $z_A$ and $z_D$ are the $z$ values corresponding to the correlation for the 'actual' and deviation records, respectively. For the comparisons between the regressions, Students' $t$ test likewise was used, where here,

$$t = \frac{b_A - b_D}{\sqrt{\sigma_{b_A}^2 + \sigma_{b_D}^2}},$$

and $b$ is the sample regression coefficient. The correlations and regressions computed from 'actual' records were significantly larger than the corresponding correlations and regressions computed from the deviation records with a probability of <0.01 for each of the three production traits.

For milk and fat, the coefficients computed from deviation records were only about half as large as those computed from the 'actual' records for the same daughter-dam pairs. The reduction was slightly more for fat than for milk yield. However, for test, the reductions in the correlations and regressions were only about 15 percent when going from 'actual' to deviation records. These reductions are undoubtedly due to the removal of much of the herd environmental covariances between daughters and dams when deviation records are used. As the herd-year-season components are smaller among records for test than for milk or fat, their removal resulted in less change in the coefficients for test.

However, the lower limit for the correlation and regression coefficients for daughter and dam is $\frac{g^2}{2}$, under random mating, and not zero.
When approximately 1.5 to 1.7 records are included in the average for each cow (as was the case for the daughters and dams here), the value of $\frac{\sigma^2}{2}$ is probably in the range of .10 to .14 for milk, .09 to .13 for fat, and .24 to .29 for test. For the most part, the coefficients computed from the deviation records approach these values closely. This would reflect favorably on the efficiency of the deviation records in removing the extraneous environmental variances.

In no case was there a significant difference in the correlation or regression coefficients computed from the two types of deviation records used here. In fact, in every case it is the regression which is the lower. From Table 42 one can see that this is because the dams are more variable than their daughters. This analysis thus provides an example which tends to refute the contention that selection among the dams will make the correlation between daughter and dam lower, but will not alter the regression. Rather, the underlying factors do not seem to operate in so simple a manner.

c. Paternal sib correlation analyses Two separate but related analyses are discussed here. Both concern the intraclass correlations among paternal sibs. This correlation, $r$, is computed as

$$r = \frac{\sigma^2_{\text{sires}}}{\sigma^2_{\text{sires}} + \sigma^2_{\text{within sires}}} = \frac{\sigma^2}{\sigma^2_{\text{sires}} + \sigma^2_{\text{within sires}}}.$$

In one study, values for $r$ were computed using the same records for the daughters as were employed in the daughter-dam analyses described in the previous section. As noted there, the averaged records for a total of 3129 daughters by 351 different sires were included, or an average
of 8.86 daughters per sire. Each sire was represented by at least two daughters and each daughter had an average of about 1.5 records.

The analysis was computed as a simply one-way classification, between sires and within sires, using, for each daughter, three types of averaged records: (1) 'actual'; (2) the unweighted average of deviations from the respective regressed adjusted herdmate averages (Unwt. Av. Dev. RAHA); and (3) the weighted average of deviations from the regressed adjusted herdmate averages (Wt. Av. Dev. RAHA).

In addition to the above analysis, r values were computed from data described in connection with the study in Section IV-E-6-a. In that study, a single randomly selected record for each daughter was used. There were 5081 records by daughters of the 75 bulls having the largest number of daughters in the available data, or an average of 67.05 daughters per sire. Each of these sires had records for at least 25 daughters, and all but 12 of the bulls were in AI service, with daughters scattered over numerous herds. The remaining 12 bulls each had daughters in at least 2 herds. This latter analysis also was computed as a simple one-way classification as was described above for the analysis with the averaged records.

Table 44 presents the values for the correlations among paternal sibs, r, computed for both analyses. Also included are the 95 percent confidence limits for the r's. The confidence limits and tests of significance were computed by using Fisher's z transformation (Fisher, 1958, Section 39) and referred to by Clark and Touchberry (1962). For the present situation,
Table 4. Checking the effectiveness of deviation records by the correlations among paternal sibs

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Type of records</th>
<th>Correlations among paternal sibs (r)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Milk</td>
</tr>
<tr>
<td>I</td>
<td>'Actual'</td>
<td>.193</td>
</tr>
<tr>
<td></td>
<td>( .158 - .231)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Unwt. av.</td>
<td>.119</td>
</tr>
<tr>
<td></td>
<td>dev. RAHA</td>
<td>(.090 - .151)</td>
</tr>
<tr>
<td></td>
<td>Wt. av.</td>
<td>.120</td>
</tr>
<tr>
<td></td>
<td>dev. RAHA</td>
<td>(.091 - .152)</td>
</tr>
<tr>
<td>II</td>
<td>'Actual'</td>
<td>.087</td>
</tr>
<tr>
<td></td>
<td>(.061 - .120)</td>
<td>(.072 - .140)</td>
</tr>
<tr>
<td></td>
<td>Dev. AHA</td>
<td>.065</td>
</tr>
<tr>
<td></td>
<td>(.044 - .091)</td>
<td>(.076 - .149)</td>
</tr>
<tr>
<td></td>
<td>Dev. RAHA</td>
<td>.065</td>
</tr>
<tr>
<td></td>
<td>(.044 - .091)</td>
<td>(.075 - .140)</td>
</tr>
</tbody>
</table>

a) Analysis I used averaged records for each daughter. 
Analysis II used single records for each daughter.

b) 95 percent confidence limits for r value immediately above each parenthesis.

\[ z = \frac{1}{2} \log_e \left( \frac{1 + (K-1)r}{1-r} \right) = \frac{1}{2} \log_e F, \text{ where} \]

\[ F = \frac{\text{mean square between sires}}{\text{mean square within sires}} = \frac{1 + (K-1)r}{1-r}. \]

Also \( \sigma^2_z = \frac{K}{2(K-1)(n-2)} \). In these formulas, \( K \) is the coefficient of \( \sigma^2_S \) in the expected mean square between sires, \( n \) is the number of sires in the analysis of variance, and \( r \) is the sample intraclass correlation coefficient. Tests of significance for the \( r \) values were tabulated by
Student's 't' test (Snedecor, 1956), using the transformed values; e.g.,

\[ t = \frac{z_A - z_D}{\sqrt{2\sigma^2_z}} \]

where \( z_A \) and \( z_D \) are the z values corresponding to the r's computed from 'actual' and deviation records, respectively, in the formula shown above. Within each analysis, \( \sigma^2_z \) was alike for all types of records and for all traits, as may be seen from the formula for \( \sigma^2_z \).

The sum of the effects of all of the factors which cause the records to be alike for the daughters of a particular sire are reflected in the r values. Under random mating, this sum includes the correlation among the genic effects of his various daughters, a small portion of the epistatic effects, and any environmental effects which affect their records alike but differ from sire to sire.

By using the average of the records by each daughter, the temporary environmental and other random error effects are reduced. As a result, the variance among the daughters' averaged records is reduced. However, the averaging of each daughter's records does nothing toward reducing the environmental correlations among separate daughters of a sire. These include mainly those classified as herd and year-season effects. They remain in their entirety in the 'actual' records and thus tend to inflate both the sire components and the resulting r values. By using deviation records, we are able to reduce these extraneous correlations and thereby cause a reduction in the r values, as may be seen in the top half of Table H4.

However, in this analysis, many sires had only two or slightly more
daughters, and often all of these daughters of a sire were in a single herd. This was true despite the fact that all of these sires actually had daughters in at least two herds, when all of the daughters of each sire were considered. Here, only those daughters were included which had dams with records in the same herd. Any bull having at least two such daughter-dam pairs was included in this particular group of data, regardless of the distribution of the pairs. As a result, the effects of numerous sires were completely confounded with herd effects, thus accounting for the high r values for 'actual' records, especially for milk and fat yields.

When deviation records were used for the same daughters, there was a statistically significant reduction in the r values for both milk and fat, with $P < .01$ for milk and near .015 for fat. While a reduction was produced in the r for test by using deviation records, it was not statistically significant in the present analysis. These data provided a severe test for the effectiveness of deviation records in reducing environmental correlations, due to the distribution of records. The above results, shown in the top half of Table 1, would surely attest to the merit of deviation records in this respect.

In the lower half of Table 1 are shown the r values computed in the analysis where only a single randomly selected record was used for each daughter of the 75 bulls having the most daughters. As noted earlier, these bulls were mostly AI sires with daughters scattered over many herds. As a result, the environmental correlations among the daughters of any sire would be considerably less than those among the daughters of a bull in the previous analysis (top half of Table 1).
Thus, the sire components and $r$ values reflect little more than the genic correlations among the daughters within any sire group. The lower limit for $r$, the paternal sib correlation, is not zero, of course, but $\frac{g^2}{4}$, under random mating, and for milk and fat it is probably not much, if any, below .05, and about .10 to .14 for test. As a result of the particular distribution of records in these data, the $r$ values for 'actual' records are much closer to these lower limits than in the previous analysis, where averaged records were used. Hence, neither did deviation records have many environmental correlations to contend with and the resultant $r$ values were not appreciably lower for deviation records than they were with 'actual' records. The reduction in $r$ for fat was not significant; there was no reduction for test; while for milk, the reduction was statistically significant at about the .15 level of probability.

However, even these latter results do not detract much from the overall efficiency shown by deviation records in reducing, by a significant amount, certain environmentally-related effects from production records.

F. The Dam's Role in AI Sire Proofs

1. Selection of bulls for use on dams

Before the introduction of artificial insemination (AI) into the dairy cattle breeding picture about 1940 to 1945, most bulls were used in only one or, at most, in just a few herds. Hence, the proof of each bull reflected, to a large extent, the environmental conditions to which each group of daughters was subjected. Besides the substantial
differences in environment among herds, there was usually some difference in the average genetic merit of the cows from one herd to the next. Under these circumstances great emphasis developed in dairy sire breeding work for including the records of the dams in a bull proof, as exemplified by the equal-parent (EP) index. The records of the dams presumably would correct for differences in the average breeding values of the mates of different bulls and also for such environmental effects as were alike for the mates and daughters of a sire, but differed from one sire to another.

After the introduction of AI and even up to the present day, the EP index has been used extensively to compute proofs for bulls going into AI service. However, the performance of AI daughters of these bulls was often disappointing in view of the expectations based on their EP 'natural' proofs (Bayley and Heizer, 1955). In other words, the repeatability of the proofs was often low. Many factors may account for this condition, including: (1) the changed environmental conditions under which the original and later proofs of a bull were made; (2) selection of daughter-dam pairs and/or records of the same; and (3) drastically different environmental conditions for the daughters as compared with those for the dams within a proof.

Of course, the three factors mentioned here were true in the days before AI as they are since, but the influence of factor (1) was greatly accentuated with the introduction of AI into the breeding picture. Actually, the repeatability of the proofs was about what one should have expected. But the people were not prepared for the regression which comes from having selected for further use only those bulls whose early
proofs were high for any reason whatever. Thus, for the most part, only those bulls with high initial proofs were tried out long enough to measure their repeatabilities. Then too was the fact that the bulls generally came out of purebred herds where their daughters received good care, but their subsequent AI daughters were more nearly in a general sample of herds and care. The AI results did shock a number of people by getting so many bulls tried out in herds with poorer environmental conditions than had happened before. Earlier, under strictly natural service conditions, a bull which had a very high initial proof rarely got into a herd where his daughters didn't get good treatment. He was regarded as too valuable for that, and if he made a second proof, it also was in a herd where conditions were good.

This general topic will be discussed further in a later section of this thesis. For the present we are primarily concerned with certain aspects of points (2) and (3).

With the increased attention to the EP index and the tremendous early growth of AI, extra demand was created for 'favorably' proved bulls for use in AI. High prices were being offered for such bulls. As a result, undoubtedly a number of bulls went into AI on the basis of so-called 'favorable' natural service proofs that were biased because of the selection of daughters going into the proofs (the dams, thereby, also would, in effect, be selected) or by relying on unsound measures of a bull's merit. These include, for example, emphasizing individually high producing daughters and/or records. When the AI daughters from such bulls came into production, some three or more years later, the results frequently were disappointing. The above conditions were, of
course, the exception rather than the rule.

However, even under normal, average dairy farm conditions, the environmental regimes under which daughters and dams made their records were, in general, largely dissimilar. This is due to the fact that, while daughter and dam usually make their records in the same herd, the daughters make their records two to four years later, on the average, than do their dams. Changes in herdsmen, the adoption of new feeding and management practices, the outbreak or control of disease, and severe changes in the weather and economic conditions are some of the factors contributing to a dissimilarity of the environments, even within the same herd, to which daughters and dams are subjected.

Hence, in the situations of changed environmental conditions for daughters and dams, inclusions of the dams in the proofs would be of little value, or even misleading, for the purpose of correcting for environmental effects which were alike for daughter and dam but differed from one bull to another.

Of course, we sometimes do find cases where both the daughter and dam make records in the same year or even in the same year and season. However, this is the exception rather than the rule. For example, in the data available for the present studies, which covered only about a 3 1/2 year period, and much less for many herds, the dam had a record concurrent with a record of one of her daughters in only about 1/3 of the cases. Where records are available for a longer span of years, this proportion would be even lower.

On the other hand, where conditions change slowly or imperceptibly over a period of several years within a herd, inclusion of the dams in
an EP index would be of considerable value in fulfilling their assigned role as outlined at the start of this section. Yet, in either event, by using records expressed as deviations from the contemporary herdmate average, we should be able to correct for herd and year-season effects far more effectively than by using the daughter-dam difference with 'actual' records. In addition, in numerous cases, no records for the dam are available, due to number of reasons. Thus, the daughter's record would not be included in the bull's equal-parent index. Except in very rare instances (see p. 105), this difficulty would not be a problem with the contemporary herdmate comparison, thereby resulting in a considerably increased use of records by tested daughters in sire evaluation. Therefore, we see that the main respect in which the dams' records would be superior to the records of the herdmates is to correct for differences in the average breeding value of the mates of different bulls.

While one of the reasons dams are used in the EP proofs is to correct for differences in the breeding value of mates of different bulls, we will work here with the production records of the dams (mates) as indicators of their breeding values. We then seek an answer to the question of how much, if any, and what kind of stratification was practiced in breeding different bulls to cows of different levels of production. In other words, were the top-indexed bulls bred to the top-producing cows and were the lower-indexed bulls bred to the 'tail-enders' among the cows? This would be positive assortive mating. Or was some other plan followed? In essence, we seek to determine the correlation of the bull's breeding value with the average producing ability of his mates. Such an estimate would be very hard to determine accurately, but, if available,
it would be helpful in evaluating the emphasis that should be placed on dams' records in bull proofs. This will be discussed further in the next section.

If any type of an assortive mating plan were generally and consistently followed by dairymen, and if their appraisal both of the bulls and their cows was accurate, we would then expect some genetic bias to be present in subsequent proofs containing the records of daughters resulting from these matings. However, it is likely that the above conditions are not remotely approached, even with AI service which uses frozen semen, let alone under the conditions of fresh semen in both AI and natural service that prevailed when the cows in this study were conceived. In the first place, no dairyman deliberately selects a poorer bull if a presumably better one is available; second, the dairyman usually does not have an accurate estimate of the breeding value of his cows, especially for his heifers and young cows; and third, with AI, cows are generally bred to whichever bull the technician had or wished to use for reasons that were usually other than assortive mating considerations. The latter is largely true even with frozen semen service. Thus, from purely theoretical considerations we should find little effective assortive mating being practiced within the average run of DHIA herds. Yet, we cannot rule out such a possibility, entirely.

In order to estimate, with any accuracy, the degree and amount of assortive mating practiced, a considerable amount of time and special kinds of data would be required. These include reliable estimates of the bulls' breeding values at the time of service to these mates. The data and the time were not available here, so a simple analysis was
substituted which was designed to determine whether the average of the records of a bull's mates varied more than randomly from one bull to the next. This would, in fact, indicate if any stratification of the mates took place and would provide one step in the complete assessment of assortive mating practices. If the evidence indicated that, on the average, there was a real difference in the productive ability of mates bred to different bulls, we would have a good argument for the inclusion of the dams' records in bull proofs. However, if the variance among mates within bulls was equal to or larger than that between bulls, we may conclude that on the average no such stratification of mates had occurred.

The test of statistical significance in such a comparison would be the F test of the mean squares between and within bulls. However, with data containing very large numbers of degrees of freedom, almost any source of variance would appear to be significant, statistically. Therefore, use of the intraclass correlations, which are free of the encumbrance of degrees of freedom, would define more clearly the relationships involved.

We shall denote the intraclass correlation of the records of the mates of a bull by 'r' and it is computed by the formula:

$$ r = \frac{\sigma^2_{\text{Bulls}}}{\sigma^2_{\text{Bulls}} + \sigma^2_{\text{Within}}} = \frac{\sigma^2_{\text{B}}}{\sigma^2_{\text{B}} + \sigma^2_{\text{W}}}.$$  

However, in the present case, $\sigma^2_{\text{B}}$ would not reflect the genic correlation among daughters of each of the separate bulls, as was the case for the sire component, $\sigma^2_{\text{S}}$, in the paternal sib analysis of the previous section.
The component labelled here as $\sigma_B^2$ would be the variance from the genetic and environmental effects which different mates of one sire have in common but which vary from the mates of one sire to another. Theoretically, it is possible that $\sigma_B^2$ could approach zero rather than $\frac{\sigma^2}{4}$, which is the lower bound of $\sigma_S^2$ in a paternal sib analysis. For $\sigma_B^2$ to be zero would require strict random mating and no environmental correlations among mates of the same bull. Neither of these conditions could be expected with field-collected data as were used here. The analysis of variance gives a measure of this aspect of the data as they actually do exist.

The records of the dams used in the daughter-dam analysis in Section IV-E-6-b also provided the data for the present study. A total of 3129 dams, but considered here as mates for 351 bulls, were included, or an average of about 8.9 mates per sire. Each mate had approximately 1.7 records included in her average production. For each mate, three kinds of averaged records were used: (1) 'actual' average; (2) Unwt. Av. Dev. RAHA; and (3) Wt. Av. Dev. RAHA. These were described fully in Section IV-E-4. Table 45 summarizes the pertinent results of the analysis.

In interpreting the results shown in Table 45, we must remember that the only restriction on the particular set of data selected for use in these different analyses was that each bull must have at least two daughter-dam pairs. Only the dams were used in the present analysis and are considered here as mates of the 351 bulls represented. Consequently, numerous bull groups contained less than five mates each, and some of these groups of mates were in only one herd. This could be due to several causes, among which are: (1) while a bull may have been used in more
Table 45. Variance among mates, between and within bulls

<table>
<thead>
<tr>
<th>Trait</th>
<th>Type of record</th>
<th>Mean square between bulls</th>
<th>$\sigma_w^2$</th>
<th>$\sigma_B^2$</th>
<th>$r^a$</th>
<th>$F^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Milk</td>
<td>'Actual' average</td>
<td>153855</td>
<td>56284</td>
<td>11015</td>
<td>.164</td>
<td>2.73</td>
</tr>
<tr>
<td></td>
<td>Unwt. av. dev. RAHA</td>
<td>59582</td>
<td>48176</td>
<td>1288</td>
<td>.026</td>
<td>1.24</td>
</tr>
<tr>
<td></td>
<td>Wt. av. dev. RAHA</td>
<td>21821</td>
<td>17979</td>
<td>434</td>
<td>.024</td>
<td>1.21</td>
</tr>
<tr>
<td>Test</td>
<td>'Actual' average</td>
<td>.1917</td>
<td>.1035</td>
<td>.0100</td>
<td>.088</td>
<td>1.85</td>
</tr>
<tr>
<td></td>
<td>Unwt. av. dev. RAHA</td>
<td>.1053</td>
<td>.0940</td>
<td>.0013</td>
<td>.013</td>
<td>1.12</td>
</tr>
<tr>
<td></td>
<td>Wt. av. dev. RAHA</td>
<td>.0662</td>
<td>.0585</td>
<td>.0009</td>
<td>.015</td>
<td>1.13</td>
</tr>
<tr>
<td>Fat</td>
<td>'Actual' average</td>
<td>22579</td>
<td>7619</td>
<td>1689</td>
<td>.181</td>
<td>2.96</td>
</tr>
<tr>
<td></td>
<td>Unwt. av. dev. RAHA</td>
<td>8310</td>
<td>6359</td>
<td>220</td>
<td>.033</td>
<td>1.31</td>
</tr>
<tr>
<td></td>
<td>Wt. av. dev. RAHA</td>
<td>2741</td>
<td>2058</td>
<td>77</td>
<td>.036</td>
<td>1.32</td>
</tr>
</tbody>
</table>

$a_r = \text{correlation among mates} = \frac{\sigma_B^2}{\sigma_B^2 + \sigma_w^2}$

$b_F(350, \infty \text{ d.f.}) = 1.14$ for $P = .05$.

than one herd, with daughters in each, records for the dams may have been available from only one herd in these data; and (2) a bull may have been used in only one herd but some of his daughters may have been sold or otherwise transferred into other herds. A number of the bulls included here were not AI sires although all had daughters in at least two herds.

When only one bull is used in a single herd, he is mated to all
cows in that herd. As a result, no stratification of mates is effected in that herd. On the other hand, under AI, and especially where frozen semen is available, more opportunities for stratification of mates would exist.

The effect of environmental correlations among mates also is included in the $\sigma_B^2$ and $r$ values, tending to inflate both. This is especially true when all the mates of a sire are found in only one herd, in which case the bull effects, so far as their mates are concerned, would be completely confounded with herd effects. However, the large majority of bulls in the present analysis had mates in more than one herd, so that the distribution of records included here did not deviate far from that normally existing in Iowa data at the time these studies were made.

While the $F$ tests were all statistically significant, or close to it, this was not surprising in view of the many degrees of freedom. The size and changes in the intraclass correlations are more illuminating. Thus, the relatively high $r$ values, from 'actual' records, and the extremely low $r$ values from deviation records indicate at least three things: (1) Most of the factors affecting alike the various mates of a bull are related to environmental conditions; (2) deviation records are a very effective means of reducing environmental correlations among mates; and (3) very little, if any, choosing of different bulls to mate to cows of different levels of production was done. When the herd and year-season effects were reduced by deviation records, the very small residuals included only the genetic correlations among the mates and any remaining environmental effects. As some of the latter surely remained, it is then safe to conclude that these data indicate substantially no
stratification in the direction of mating cows with different levels of production to different bulls.

2. **Correlation of daughter and dam averages**

   Another approach to the question of the use of dams' records in dairy sire evaluation was defined by Lush (1944). Although he was referring primarily to natural provings of sires, the method is equally as applicable to our present data, which include deviation records for daughters of AI bulls.

   The real accuracy of a bull index (I) is measured by its correlation with the true transmitting ability (say, G) of the sire for which it is computed. The amount of genetic improvement made in the offspring by selecting bulls with equal intensity but according to $I_1, I_2, \ldots, I_n$, is strictly in proportion to $r_{GI_1}, r_{GI_2}, \ldots, r_{GI_n}$.

   Lush found that the optimum emphasis to place on $Y$ as compared with $X$ is

   $$
   \frac{\sigma_X}{\sigma_Y} \cdot \frac{r_{GX} r_{GY} - r_{GY}}{r_{GX} - r_{GY} r_{XY}},
   $$

   where $X$ is the average of the records of the daughters and $Y$ is the average of the records of the dams of those daughters. Using this value, when considering both daughters and dams in computing the index, we obtain

   $$
   \text{maximum } r_{IG} = \frac{\sqrt{r_{GX}^2 - 2r_{GX} r_{GY} r_{XY} + r_{GY}^2}}{1 - r_{XY}^2}
   $$

   (Eq. 30)
\( r_{GY} \) is the correlation of the breeding value of the bull and the average production of his mates. This is generally a small positive value, based on the assumption that the dairyman who has good cows would take more trouble in picking a bull and could afford to pay more than the dairyman who has ordinary or poor cows. Also we assume that the extra care he would take actually would yield him some degree of success, even though small. Yet, the smallness or \( r_{GY} \) is almost inevitable from the fact that nobody is deliberately trying to find a poor bull for his poor cows. With AI, there is probably slightly less of a difference in the merit of bulls available to any dairyman than was the case with natural service.

The correlation of the breeding value of a bull and the average production of his mates, \( r_{GY} \), was discussed briefly in the last section with a related study. However, no estimate of \( r_{GY} \) was available from the present data.

On the other hand, \( r_{GX} \), the correlation of the breeding value of a bull and the average production of his daughters, would surely be larger than \( r_{GY} \). \( r_{GX} \) has in it much that is real and genetic, regardless of the wisdom or diligence with which the breeders choose their bulls. A more exact evaluation and discussion of \( r_{GX} \) will be postponed until the next section, but even for traits with heritabilities as low as .2, one would hardly expect this correlation to be less than .4 to .6 where at least several daughters are included in \( X \).

If we assume \( r_{GY} \) is zero, maximum \( r_{GI} \), Equation 30, then reduces to
In view of the above discussion, Equation 31 would be a slightly larger value than that for the full equation, Equation 30.

The amount of improvement made in the next generation by selecting on the basis of I (Index) is \( \frac{r_{GI}}{r_{GX}} \) times the improvement to be made by selecting (with the same intensity) for \( X \), the daughters' average, alone. When \( r_{GY} \) is zero,

\[
\frac{r_{GI}}{r_{GX}} = \frac{r_{GX}}{\sqrt{1 - r_{XY}^2}} = \frac{1}{\sqrt{1 - r_{XY}^2}} \quad \text{(Eq. 32)}
\]

As \( r_{GI} \) is slightly larger than if we had not assumed \( r_{GY} \) to be zero, the above proportion,

\[
\frac{r_{GI}}{r_{GX}} = \frac{1}{\sqrt{1 - r_{XY}^2}},
\]

expresses the upper limit of gain normally expected by including the records of the mates in sire proofs.

Lush found, from his study of Rice's data, that something like 12 to 20 percent faster gains in genetic improvement could be achieved by using the dams' records, when the latter were weighted by the proper 'b' in the proofs. The value, 12 to 20 percent, referred to effects for proofs in which 'actual' records were used for daughters and dams and bulls were used largely in only one or a few herds (natural proofs).
We then may apply this simple but powerful test to the data in the present study, as follows: The required values were obtained from a previous daughter-dam analysis discussed in Section IV-E-6-b in connection with some other studies. The analysis was a simple one-way classification, between and within sires. Table 46 summarizes the mean squares and mean crossproducts between sires which are needed here. From these results we may compute $r_{XY} =$ the correlation of daughter average and dam average, as:

$$\sqrt{\text{Mean squares for sires in daughter analysis}} \cdot \sqrt{\text{Mean squares for dams in dam analysis}}$$

Table 46. Mean squares and crossproducts between sires for correlation of daughter and dam averages

<table>
<thead>
<tr>
<th>Trait</th>
<th>Type of record</th>
<th>Mean squares Daus.</th>
<th>Mean squares Dams</th>
<th>Mean crossproducts Daus.-Dams</th>
</tr>
</thead>
<tbody>
<tr>
<td>Milk</td>
<td>'Actual' average</td>
<td>160793</td>
<td>153855</td>
<td>91100</td>
</tr>
<tr>
<td></td>
<td>Wt. av. dev. RAHA</td>
<td>32263</td>
<td>21821</td>
<td>5484</td>
</tr>
<tr>
<td>Test</td>
<td>Actual average</td>
<td>.2106</td>
<td>.1917</td>
<td>.0858</td>
</tr>
<tr>
<td></td>
<td>Wt. av. dev. RAHA</td>
<td>.1064</td>
<td>.0662</td>
<td>.0161</td>
</tr>
<tr>
<td>Fat</td>
<td>'Actual' average</td>
<td>23246</td>
<td>22579</td>
<td>13311</td>
</tr>
<tr>
<td></td>
<td>Wt. av. dev. RAHA</td>
<td>4306</td>
<td>2741</td>
<td>752</td>
</tr>
</tbody>
</table>
For example, for fat, using 'actual' records,

\[
\begin{align*}
    r_{XY} &= \frac{13311}{\sqrt{23245} \sqrt{22579}} = .581 \\
    r_{XY}^2 &= .3378; \quad \sqrt{1 - r_{XY}^2} = .8137 \\
    \sqrt{1 - r_{XY}^2} &= \sqrt{1 - .3378} = 1.229.
\end{align*}
\]

This was done similarly for milk, test, and butterfat for the 'actual' average and weighted average of deviations from the regressed adjusted herdmate averages (Wt. Av. Dev. RAHA). The pertinent results are presented in Table 47.

Table 47. Correlations of daughter-dam averages and genetic gains expected from including dams in proofs

<table>
<thead>
<tr>
<th>Trait</th>
<th>Type of record</th>
<th>(r_{XY})</th>
<th>(\frac{1}{\sqrt{1 - r_{XY}^2}})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Milk</td>
<td>'Actual' average</td>
<td>.579</td>
<td>1.227</td>
</tr>
<tr>
<td></td>
<td>Wt. Av. Dev. RAHA</td>
<td>.118</td>
<td>1.007</td>
</tr>
<tr>
<td>Test</td>
<td>'Actual' average</td>
<td>.427</td>
<td>1.106</td>
</tr>
<tr>
<td></td>
<td>Wt. Av. Dev. RAHA</td>
<td>.192</td>
<td>1.019</td>
</tr>
<tr>
<td>Fat</td>
<td>'Actual' average</td>
<td>.581</td>
<td>1.229</td>
</tr>
<tr>
<td></td>
<td>Wt. Av. Dev. RAHA</td>
<td>.219</td>
<td>1.025</td>
</tr>
</tbody>
</table>
From the results in Table U9, we see, once more, the striking effects in reducing environmental correlations when using deviation records. For example, with averages of 'actual' records, the genetic progress that might be expected by including the dams in the proofs over and above that expected when only the daughters are included in the proofs, amounts to about 23 percent for milk and fat yields. This compares with only .7 and 2.5 percent, respectively, when using the averages of deviation records. Even for test, the comparable reduction is highly significant, from 11 down to 2 percent genetic gain.

Therefore, on the whole, it would appear safe to assume, from this analysis and the one in the previous section (see Table k7), that, if deviation records are used, little additional information on the sire is to be gained by including the dams' records in dairy bull proofs.

We are now ready to examine some of the remaining considerations related to the final computation of bull indexes composed only of the records of daughters of the bulls. These considerations comprise the subject matter for the next and concluding sections of this thesis.

G. Determining the Breeding Value of Dairy Sires

1. Theoretical considerations
   a. Neglecting environmental correlations between daughters From the discussion in Section IV-E-1 we saw that

   \[ \hat{G}_s = 2(D - \mu) + \text{errors of appraisal} \]  

   (Eq. 33)

   provides an estimate of the breeding value of the sire, \( G_s \), for a given level of production of a daughter, \( D \), expressed as a deviation from the
population mean. The accuracy of the prediction of $G_S$ is determined by $r_{GS_D}$, the correlation of the breeding value of the sire and the record of the daughter. For only one daughter, $r_{GS_D} = \frac{\sigma}{2}$. Thus the record of a single daughter generally does not provide an accurate expression of her sire's breeding value, as shown in Equation 33, for two reasons: (1) the sampling nature of Mendelian inheritance (the denominator of $r_{GS_D}$ is $12^\frac{1}{2}$); and (2) imperfect heritability ($g < 1.0$). In addition, the estimate may be subject to systematic errors of appraisal, such as the effects of herd and season of freshening, which could bias the proof.

By increasing the number of daughters included in a proof, the random sources of error in the estimate of $G_S$ decrease, but the systematic errors may not be affected. The use of a regression or prediction equation, which includes a factor to adjust or weight the proof for the number of daughters included, serves primarily to minimize the random errors of appraisal.

However, the simple regression equation is not the perfect answer either. For example, when we predict, say, $Y$ from $X$, the predicted value of $Y$ for a given level of $X$ is unbiased, but the predicted $Y$'s for a given level of true $Y$'s are biased in the direction of being nearer the mean than are the true values. This bias is related to the imperfectness of the correlation between predictor and the thing predicted. Thus, for the sire-daughter relationship, $\sigma^2_{G_S} \neq \sigma^2_{G_S}$, where $G_S$ is the true measure of the sire's breeding value and $\hat{G}_S$ is its estimate from the data. Rather, $\sigma^2_{G_S} = r^2_{GS_D} \cdot \sigma^2_G = \frac{\sigma^2}{4} \cdot \sigma^2_G$. Here, $\sigma^2_{G_S}$ can be called the variance of $G_S$ "due to" the regression of $G_S$ on $D$. 
For only one daughter, $b_{GsD} = r_{GsD} \frac{\sigma_S}{\sigma_D}$. If the scale of measurement chosen for $G_S$ is such that $\sigma_S$ equals $\sigma_D$, which is reasonable, then $\frac{\sigma_S}{\sigma_D} = g$. As $r_{Gs} = \frac{g}{2}$, the prediction equation then takes the form:

$$\hat{G}_s = \frac{g^2}{2} (D - \mu),$$

in terms of deviations from the population average.

When we have more than one daughter of a bull, we obtain:

$$r_{GsD} = \frac{ng}{2} \sqrt{\frac{1}{n[1 + (n-1)r_{DjDj}]}}, \quad \frac{g}{2} \sqrt{\frac{n}{1 + (n-1)r_{DjDj}}}, \quad \text{(Eq. 34)}$$

$$r_{DjDj} = \frac{g^2}{4} + e_i e_j, \quad \text{which equals } \frac{g^2}{4}, \quad \text{if we assume } r_{EiEj} = 0 \text{ and random mating conditions. Under those conditions,}$$

$$r_{GsD} = \sqrt{\frac{ng^2}{4 + (n-1)g^2}} \quad \text{(Eq. 35)}$$

Now, $b_{GsD} = r_{GsD} \frac{\sigma_S}{\sigma_D}$. Likewise, here, the scale of $G_S$ is chosen so that $\sigma_S = \sigma_D$;

$$\sigma_S = g \sigma_D, \quad \frac{\sigma_S}{\sigma_D} = \sqrt{\frac{ng^2}{4 + (n-1)g^2}},$$

and $b_{GsD} = \frac{2ng^2}{4 + (n-1)g^2}. \quad \text{(Eq. 36)}$

This gives:

$$\hat{G}_s = \frac{2ng^2}{4 + (n-1)g^2} (D - \mu) \quad \text{(Eq. 37)}$$

in terms of deviations from the population average, $\mu$. 
The basic principles presented thus far in this section, for the most part, are common knowledge in animal breeding theory and are included here primarily to provide the necessary background and starting point for the discussion to follow.

Of significance is the fact that the use of this regression equation allows the comparison of bulls with varying numbers of daughters on a basis which is more 'equitable' to the observer than to the bulls. Thus, bulls with only a very few daughters are never estimated either very high or very low, being bunched about the population mean. This is the inevitable result despite the fact that the bulls with few daughters (specifically, young bulls with few daughters in their initial proofs) actually do vary as much in their breeding value as do the older bulls with many daughters which thus can have high or low regression proofs.

Another important consideration with regard to Equation 37 is that as \( n \) approaches infinity, \( b_{G_S} \) approaches 2. That is,

\[
\lim_{n \to \infty} \frac{2ng^2}{4 + (n-1)g^2} = 2.
\]

This says that if we have an infinite number of daughters for a bull and no bias (systematic errors; i.e., nothing in common among the paternal sibs except their sire), \( G_S \) then would be estimated accurately by \( 2(\bar{D} - \mu) \) or \( 2\bar{D} \), regardless of the value for heritability, \( g^2 \). This points out the fact that it is not primarily imperfect heritability, but rather the low correlation of \( r_{G_S\bar{D}} \) which keeps the functional-type equation (see Williams, 1959, Chapter 11), \( G_S = 2(\bar{D} - \mu) \), from being the same as the regression estimate of \( G_S \) from sample data, \( G_S = \frac{2ng^2}{4 + (n-1)g^2}(\bar{D} - \mu) \).
However, within the normal range of numbers of daughters, as from 3 to 60, the heritability value, $g^2$, also has a considerable influence on the size of $b_{GS}$. 

Thus far we have referred to a situation where 'actual' (305-day-$2X$-$ME$) production records are used in computing a proof and under the arbitrary assumptions of random mating and no environmental correlations among paternal sibs. The results when environmental correlations are a factor will be considered in the next subsection. First, however, let us consider the case when records consisting of deviations from contemporary herdmate averages make-up the proofs.

Figure 4 represents the path diagram for the situation assumed here for deviation records. Touchberry (1961) has indicated that

$$r_{GS(D-HA)} = \frac{\sqrt{n kg^2}}{\sqrt{h(1-s)(k+1) + (n-1)kg^2}} \quad (Eq. 38)$$

and

$$b_{GS(D-HA)} = \frac{2n kg^2}{h(1-s)(k+1) + (n-1)kg^2} \quad (Eq. 39)$$

In their derivation, $k$ is the number of contemporary herdmates and is assumed to be the same for each daughter in a proof; $g^2$ is the estimated heritability of the trait concerned; $n$ is the number of daughters; and $s$ is the phenotypic intraclass correlation among cows in the same herd-year-season (HYS) group, including the daughter in question. A value for $s$ may be obtained from an analysis of variance between and within HYS groups, where

$$s = \frac{\sigma^2_{between HYS groups}}{\sigma^2_{between HYS groups} + \sigma^2_{within HYS groups}}.$$
Figure 1. Path diagram showing relationship between $G_5$ and (D-HA) (modified from Touchberry, 1961)
\[ GD_1 \] = Breeding value of the sire
\[ GD_2 \] = Breeding value of a daughter
\[ D \] = Phenotype of a daughter
\[ HM_{ij} \] = \( j^{th} \) heterozygote of the \( i^{th} \) daughter
\[ (HA)_i \] = Herdmate average for the \( i^{th} \) daughter

\[ GS \]
\[ GD_1 \]
\[ GD_2 \]
\[ GD_n \]

\[ r_{E_1 E_2} \]
\[ E_1 \]
\[ E_2 \]
The results of one such analysis were presented in Table 30 in Section IV-E-2. It is further assumed that there is only one daughter by each bull in each herd and that the dams of the daughters are not related to each other nor to the sires of the daughters. These latter conditions were also assumed in the previous discussion concerning 'actual' records. In fact, in both cases, i.e., with 'actual' and with deviation records, it is assumed for the present that all that the daughters of a bull have in common is their sire. Thus, all environmental correlations between paternal sibs are assumed to be zero.

However, the variance due to herds and seasons will affect the proofs with 'actual' records, but not so, theoretically, at least, the records expressed as deviations from their contemporary herdmate averages. It is precisely this latter difference between the two types of records which is reflected in their relative accuracy in providing an estimate for Gs, in the present discussion.

As was noted previously, the real accuracy of any bull index is measured by its correlation with the transmitting ability or breeding value of the sire, Gs, for which it is computed. When the index is composed of the average of the daughters' 'actual' records, Equation 35 applies, while when the average of the deviation records comprises the index, Equation 38 applies. Those expressions really are the expected correlations of indexes and breeding values, under the assumptions of random mating and zero environmental correlations among paternal sibs. If we further assume that the heritability, g^2, is .25, and the phenotypic correlation among herdmates, s, is .35, we can express the
correlations $r_{GS(D-HA)}$ and $r_{GS}$, in terms of $n$, the number of daughters, for a given $k$, the number of herdmates. These might be the conditions applicable for milk production proofs, and are shown in Table 48. If we assume $g^2$ to be .50 and $s$ to be .20, conditions that might well be expected for test (i.e., percent butterfat), the corresponding values are found in Table 49.

From Table 48 for milk yield, we see that, theoretically, we need about 2 herdmates for each daughter to achieve as much accuracy in estimating $G_S$ by using deviation records, as if we had used 'actual' records, for an equal number of daughters. An approximately similar relationship would be expected with fat yield. But, for test, from Table 49, we see that, in theory, four herdmates per daughter are needed, when using deviation records, to estimate $G_S$ as accurately as may be done with actual records.

Under present Iowa dairying conditions, the average number of herdmates per daughter is over 10, so in this respect, the advantage lies clearly with deviation records for all three traits considered here. For example, with 10 herdmates per daughter, 20 daughters with deviation milk records are as reliable an indicator of $G_S$ as are 29 daughters using 'actual' milk production records in the proof. This may be computed as follows: when the number of herdmates, $k$, equals 10, we use

$$r_{GS(D-HA)} = \sqrt{\frac{n}{n + 10,44}}$$

from Table 48. With $n = 20$, $\sqrt{\frac{n}{n + 10,44}} = .810$.

For actual records, Table 48 indicates that $r_{GS} = \sqrt{\frac{n}{n + 15}}$. Equating $\sqrt{\frac{n}{n + 15}}$ to .810, and solving, yields $n = 29$. By a similar method, but
Table U8. Expected correlations between breeding values of sires and two indexes, $D$ and $D-HA$, with $g^2 = .25$; $s = .35$; $n =$ number of daughters; $k =$ number of herdmates (Touchberry, 1961)

<table>
<thead>
<tr>
<th>$n$</th>
<th>$D$</th>
<th>$k=1$</th>
<th>$k=2$</th>
<th>$k=5$</th>
<th>$k=10$</th>
<th>$k=20$</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>.50</td>
<td>.45</td>
<td>.51</td>
<td>.55</td>
<td>.57</td>
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</tr>
<tr>
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<tr>
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<td>.88</td>
<td>.91</td>
<td>.93</td>
<td>.93</td>
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</tr>
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<td>.91</td>
<td>.93</td>
<td>.95</td>
<td>.95</td>
<td>.95</td>
</tr>
</tbody>
</table>

Table U9. Expected correlations between breeding values of sires and two indexes, with $g^2 = .50$; $s = .20$; $n =$ number of daughters; $k =$ number of herdmates

<table>
<thead>
<tr>
<th>$n$</th>
<th>$D$</th>
<th>$k=1$</th>
<th>$k=4$</th>
<th>$k=7$</th>
<th>$k=10$</th>
<th>$k=20$</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
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<td>.66</td>
<td>.67</td>
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</tr>
<tr>
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<td>.68</td>
<td>.77</td>
<td>.78</td>
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<tr>
<td>20</td>
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<td>.95</td>
<td>.96</td>
<td>.97</td>
<td>.97</td>
<td>.97</td>
</tr>
</tbody>
</table>
using Table 49, we see that actual test records of only 23 daughters are needed to be equivalent to deviation test records for 20 daughters in predicting a sire's breeding value.

Estimates of their breeding value are useful for comparing different bulls. For instance, say we have two bulls, A and B, with estimated regressed breeding values of +60 and +80 pounds of butterfat, respectively, expressed in terms of deviations of the daughters from their RAHA's. If other considerations were equal, such as transmitting ability for type, bloodlines, and breeding fee, bull B would be selected for use by a dairyman. However, the +80 pounds does not represent the expected gain in production that the dairyman might realize in his own herd by using bull B. This is so because +80 in this example represents the full complement of the sire's breeding value, or essentially his additive genetic effect, s_j, while only a sample half of these effects is transmitted to each of the bull's daughters. In other words, a dairyman might expect that the daughters of bull B would, on the average, produce at a level roughly 1/2 of 80, or 40 pounds, above their respective herdmate averages.

By applying the factor of 1/2 to a bull's estimated breeding value (EBV), we are not changing the order or rank of bull indexes. We are merely reducing the standard deviation among the indexes by one-half. In view of this, we may adjust our proof calculations so that the index for each bull is expressed as 1/2 of its estimated breeding value. We denote this new index as the Estimated Producing Value or EPV of the bull, and use P_s to represent the predicted production of the bull's
daughters, where \( P_S = \frac{1}{2} G_S = \frac{s_j}{2} \). It should be emphasized, however, that we are, in reality, still estimating the breeding value of the sire, or rather, a function of his breeding value. We are merely changing the scale of the measure so that it will have approximately the same standard deviation as lactation production records and hence be more directly comparable to them.

Therefore, we have:

Index for estimated breeding value of a bull, using 'actual' records:

\[
EBV = b_{PS}(D - \mu) = \frac{2ng^2}{4 + (n-1)g^2} (D - \mu).
\]

Index for estimated 'producing value' of a bull:

\[
EPV = b_{PS}(D - \mu) = \frac{1}{2} b_{SG}(D - \mu) = \frac{ng^2}{4 + (n-1)g^2} (D - \mu) \quad \text{(Eq. 40)}
\]

The above are expressed in terms of deviations from the population mean. Similarly, for deviation records,

\[
b_{PS(D-HA)} = \frac{1}{2} b_{SG(D-HA)} = \frac{nkg^2}{4(1-s)(k+1) + (n-1)kg^2}, \quad \text{(Eq. 41)}
\]

where the letters have the same meaning as in Equation 39.

The weighting or regression factors also may be thought of as the regression of future daughters on those already tested. For example, in Figure 5, we have two groups of daughters, \( D_{11} \ldots D_{1n} \) and \( D_{21} \ldots D_{2m} \), each sired by the same bull with breeding value \( G_S \). From Figure 5, we have,

\[
b_{D_2D_1} = r_{D_2D_1} \cdot \frac{G_{D_2}}{D_1}; \quad r_{D_2D_1} = r_{G_SD_2} \cdot r_{G_SD_1}.
\]

Let us assume, for the present, that all environmental correlations
Figure 5. Path diagram for the correlation of the average production of separate groups of daughters by a single bull.
among the daughters, both within and between groups are zero.

Then it can be shown that

\[ r_{D_2 D_1} = \sqrt{\frac{ng^2}{4 + (n-1)g^2}} \cdot \sqrt{\frac{mg^2}{4 + (m-1)g^2}} \]  

(Eq. 42)

and \( b_{D_2 D_1} = \frac{ng^2}{4 + (n-1)g^2} \).  

(Eq. 43)

Hence, \( b_{D_2 D_1} = b_{P S} = \frac{1}{2} b_{G S} \).

Here we see that in predicting the average production of \( m \) future daughters of a bull, based on the average of \( n \) previously tested daughters, the number of future daughters, \( m \), is of no concern at all, as \( m \) cancels out completely in the derivation. No matter whether we are predicting 5 or 500 future daughters, the index is based entirely on past performance. This is true so long as random mating is in effect and there are no environmental correlations between daughters in the separate proofs, which is the situation assumed for the present.

However, if we are computing the correlation between the average of \( n \) past daughters and the average of \( m \) future daughters, the number, \( m \), of future daughters is a vital factor, as may be seen in Equation 42.

Now if \( m = n \), if all environmental correlations between paternal sibs are zero and random mating is in force, then

\[ b_{D_2 D_1} = b_{P S} = b_{G S} + r_{G S} \]  

Similarly, for deviation records under these assumptions and when all parameters are uniform from one proof to the next for a bull,

\[ b_{(D-HA)_2(D-HA)_1} = b_{P S(D-HA)} = \frac{1}{2} b_{G (D-HA)} = r_{G S(D-HA)}^2 \]  

The values for
\[ b_{PS} = b_{D_2 D_1} \] and \[ b_{PS(D-HA)} = b_{(D-HA)^2(D-HA)_1} \], under all the assumptions noted above, of course, can be expressed in terms of \( n \), the number of daughters included in the proofs. These factors may be derived from Table 48 and 49 simply as the squares of the respective correlations shown there.

Still another approach to the derivation of the weighting factor, \( b_{PS} = b_{D_2 D_1} \), is by the method of variance components. The regression of future daughters of a bull on those previously tested is

\[
\frac{\sigma_S^2}{\sigma_S^2 + \sigma_W^2}, \text{ where } \sigma_S^2 \text{ is the variance component among sires and } \sigma_W^2 \text{ is the variance within sires, or the variance among the } n \text{ tested daughters of a sire, computed over all sires in a suitable analysis of variance.}
\]

Under the conditions of random mating and zero environmental correlation,

\[
\frac{\sigma_S^2}{\sigma_S^2 + \sigma_W^2} = \frac{g^2}{4} = t, \text{ the correlation among paternal half sibs. This algebraic relationship may be manipulated as follows:}
\]

\[
\frac{\sigma_S^2}{\sigma_S^2 + \sigma_W^2} = \frac{g^2}{4} = \frac{g^2}{g^2 + 4 - g^2} = \frac{g^2}{\frac{4}{4} + g^2 - g^2} = \frac{g^2}{4} + \frac{4 - g^2}{4} \quad (Eq. 44)
\]

Now, if we consider \( \frac{\sigma_S^2}{\sigma_S^2 + \sigma_W^2} \) as the proportion of the total variance, which equals \( \sigma_S^2 + \sigma_W^2 \), i.e.,

\[
\frac{\sigma_S^2}{\sigma_S^2 + \sigma_W^2} = \frac{\sigma_S^2}{\sigma_{\text{Total}}} = \frac{\sigma_S^2}{1},
\]
then, \( \frac{\sigma^2}{1} = \frac{\sigma^2}{t} = t \), and \( \sigma^2_w = 1-t = \frac{\mu-g^2}{\mu} \).

As \( \frac{\mu-g^2}{\mu} \) is the right hand term in the denominator of Equation 41,

\[
\frac{\sigma^2}{h} = \frac{\mu-g^2}{4n}, \quad \text{and} \quad \frac{\sigma^2}{s} = \frac{\sigma^2}{g} = \frac{\mu-g^2}{4n} = \frac{\mu-g^2}{4(n-1)g^2}.
\]

The latter of course = \( b_{D_2D_1} = b_{P_sD} = \frac{1}{2} b_{GSD} \).

b. The effects of environmental correlations between paternal sibs

In all the discussion and computations of the previous section we have assumed that there were no environmental correlations between paternal sibs. As a result, all of the regression and correlation factors were considerably simplified. However, that some degree of environmental correlations do in fact exist among daughters of an AI bull is much easier to visualize than the assumption that none exist. This problem is an exceedingly difficult one to cope with in the present context of sire proofs. This is due primarily to the fact that varying environmental conditions may exist relating to a single bull proof, to separate proofs of a bull, and to the proofs of different bulls that may be compared.

We may approach this problem by the use of a path diagram as in Figure 5. As noted earlier, this diagram shows the relationship of the breeding value of a bull, \( G_S \), with the average of two groups of daughters, \( D_1 \) and \( D_2 \), which constitute separate proofs for the bull. Also shown are the relationships of environmental effects among the various daughters, both within and between proofs. Each daughter is
represented by her 'actual' production record. We have, for simplicity sake, shown only the relationship of environmental effects of two daughters in each proof. However, \( r_{E_i E_j} \) represents the environmental correlations between any two daughters in proof 1, while \( r_{E_k E_l} \) represents those between any two daughters in proof 2. In addition, \( r_{E_i E_k} \), \( r_{E_i E_l} \), \( r_{E_j E_k} \), and \( r_{E_j E_l} \) represent environmental correlations between a daughter in proof 1 and another daughter in proof 2. Thus, in essence, we have two different kinds of environmental correlations, i.e., those between separate daughters included in the same proof, and those between separate daughters in separate proofs. These environmental correlations can of course include the full range of effects possible — herds, regions, years, and seasons, and in every conceivable combination. Within a single proof there are \( \frac{n!}{2!(n-2)!} \) or \( \frac{m!}{2!(m-2)!} \) separate environmental correlations between different daughters, while between the two proofs there are \( n \times m \) different such correlations, some or all of which may be zero.

First, we will consider only those environmental correlations between daughters within a single proof of a bull, \( r_{E_i E_j} \). We have seen previously that the correlation of the breeding value of a bull, \( G_b \), and the average of his daughters, \( \bar{D} \), using actual records, is

\[
r_{G_b \bar{D}} = \sqrt{\frac{ng^2}{4[1 + (n-1)r_{D_i D_j}]}} , \text{ where } r_{D_i D_j} = \frac{g^2}{4} + e_{i} r_{E_i E_j},
\]

where

\[
r_{E_i E_j} = \frac{g^2}{4} + e_{i} r_{E_i E_j} \quad \text{Eq. (45)}
\]

If \( r_{E_i E_j} = 0 \), then \( r_{G_b \bar{D}} = \frac{ng^2}{\sqrt{4 + (n-1)g^2}} \).
However, if over all daughter pairs, the average $r_{EiEj}$ is not 0, we may represent $e_i r_{EiEj} e_j$ by $e^2$ which can be considered either as an expression of environmental covariances and variances or as an environmental correlation derived from common elements. In the literature, $c^2$ is generally used to express the sum of $e^2$ from common environmental effects and an additional portion resulting from deviations from random mating. As we are assuming no selection of mates in these discussions, $e^2$ is the appropriate term here. Then, for 'actual' records,

$$r_{G_{SS}} = \frac{ng^2}{\sqrt{\mu + (n-1)(g^2 + \mu e^2)}}$$

(Eq. 46)

Similarly, when deviation records are used, and $r_{EiEj} = 0$,

$$r_{G_{SS}(D-HA)} = \frac{nk^2}{\sqrt{\mu(1-s)(k+1) + (n-1)k^2 g^2 + \mu e^2}}$$

(Eq. 47)

While, in theory, deviation records are designed to eliminate all environmental effects related to herd and year-season of freshening, we have seen (in Section IV-E-6-a, for example) that this is actually not the case in the average run of data. Specifically, when more than one daughter of a single bull is included in a particular herd-year-season (HYS) group, then some correlation will remain between their deviation records. This is also true, but to a lesser degree, for records made in the same herd, but in different year-seasons. In addition, there are other items, including perhaps some of the individual record or herd average adjustment factors used which cause an incomplete removal of environmental effects. Hence, while environmental correlations are indeed considerably reduced with deviation records, they are rarely zero. In that case,

$$r_{G_{SS}(D-HA)} = \frac{nk^2}{\sqrt{\mu(1-s)(k+1) + (n-1)k^2 g^2 + \mu e^2}}$$

(Eq. 48)
(All the letters in Equation 4.8 have been identified previously.)

In the derivation of $r_{G_S(U-HA)}$, we had assumed that only one daughter of any one bull was to be found in each HYS group, and that no environmental correlations existed between separate daughters of the bull. The letter 's' represented the average phenotypic correlation among cows with a HYS group, which included the single daughter, in relation to the average phenotypic correlation among cows in the population as a whole. By introducing environmental correlations between separate daughters of a bull we are, in effect, reducing the value of $s$ in the population. However, for the purposes of this discussion, we assume throughout that $s$ is unchanged from its value when the environmental correlations between separate daughters are zero. Thus $e^2$ may be introduced to reflect a departure from the base value of $s$ in the population as determined by the distribution of the daughters among the various herds represented in a single proof of a bull. In this way, $e^2$, referred to as the average environmental correlation or covariance among daughters in a single bull proof, may be considered when evaluating both 'actual' and deviation record proofs.

We may express both correlation factors, $r_{G_S}$ and $r_{G_S(U-HA)}$, in terms of $n$ for specific values of $g^2$, $s$, $e^2$, and $k$. This was done for $g^2 = .25$, $s = .35$, $k = 10$, and $e^2 = .01$, .02, .04, and .06. The general formulas as well as the computed values for different $n$ are shown in Tables 50 and 51. The values when $e^2 = 0$ also are included for comparison purposes. Of significance is the result that it is not possible, theoretically, to achieve a correlation of 1.0 for the breeding value, $G_S$,
Table 50. Expected correlations between the breeding value of a sire and the average of his daughters' 'actual' records \( (r_{GS}) \) with \( g^2 = .25 \) and different \( e^2 \)

<table>
<thead>
<tr>
<th>n</th>
<th>.00</th>
<th>.01</th>
<th>.02</th>
<th>.04</th>
<th>.06</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>.50</td>
<td>.49</td>
<td>.48</td>
<td>.47</td>
<td>.46</td>
</tr>
<tr>
<td>10</td>
<td>.63</td>
<td>.61</td>
<td>.60</td>
<td>.57</td>
<td>.55</td>
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<tr>
<td>20</td>
<td>.76</td>
<td>.73</td>
<td>.70</td>
<td>.65</td>
<td>.61</td>
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<td>.74</td>
<td>.69</td>
<td>.64</td>
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<td>50</td>
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</tr>
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<td>100</td>
<td>.93</td>
<td>.87</td>
<td>.83</td>
<td>.75</td>
<td>.69</td>
</tr>
<tr>
<td>∞</td>
<td>1.00</td>
<td>.93</td>
<td>.87</td>
<td>.78</td>
<td>.71</td>
</tr>
</tbody>
</table>

\[ \sqrt{\frac{n}{n+15}} \] \[ \sqrt{\frac{n}{1.16n+14.84}} \] \[ \sqrt{\frac{n}{1.32n+14.68}} \] \[ \sqrt{\frac{n}{1.64n+14.36}} \] \[ \sqrt{\frac{n}{1.96n+14.04}} \]

Table 51. Expected \( r_{GS(D-HA)} \) with \( g^2 = .25 \), \( s = .35 \), \( k = 10 \), and different \( e^2 \)

<table>
<thead>
<tr>
<th>n</th>
<th>.00</th>
<th>.01</th>
<th>.02</th>
<th>.04</th>
<th>.06</th>
</tr>
</thead>
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<tr>
<td>5</td>
<td>.57</td>
<td>.56</td>
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<td>20</td>
<td>.81</td>
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<tr>
<td>30</td>
<td>.86</td>
<td>.82</td>
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<tr>
<td>50</td>
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<td>.74</td>
<td>.68</td>
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</tr>
<tr>
<td>100</td>
<td>.95</td>
<td>.89</td>
<td>.84</td>
<td>.76</td>
<td>.70</td>
</tr>
<tr>
<td>∞</td>
<td>1.00</td>
<td>.93</td>
<td>.87</td>
<td>.78</td>
<td>.71</td>
</tr>
</tbody>
</table>

\[ \sqrt{\frac{n}{n+10.44}} \] \[ \sqrt{\frac{n}{1.16n+10.28}} \] \[ \sqrt{\frac{n}{1.32n+10.12}} \] \[ \sqrt{\frac{n}{1.64n+9.80}} \] \[ \sqrt{\frac{n}{1.96n+9.48}} \]
with either the daughter average of 'actual' records or the average of deviation records when \( e^2 > 0 \). As the size of \( e^2 \) increases, the curves for \( r_{GS} \) (where \( I = D \) or \( D-HA \)) become increasingly flat, asymptoting at a progressively lower level. As a result, the advantage of increased numbers of daughters in a proof is reduced after the first relatively few daughters are included. Lush (1931 and 1935) and Johnsson (1961) previously have discussed some of the above and related topics.

Therefore, it is evident that environmental correlations between the daughters of a bull vitally affect the correlation of the breeding value of the bull and his daughter average, whether using actual or deviation records.

It further can be shown that, when \( m = n \) and \( e_1^2 = e_2^2 = e^2 \),

\[
r_{D_2D_1} = \frac{nq^2}{4 + (n-1)(g^2 + le^2)} \quad \text{(Eq. 49)}
\]

In which case,

\[
r_{D_2D_1} = b_{D_2D_1} = b_{PS} = \frac{1}{2} b_{GS} = r_{GS} \quad \text{(Eq. 50)}
\]

Similarly, if we use deviation records, we can show that, when \( m = n \) and the other parameters are equal for the separate proofs,

\[
r_{(D-HA)}_2(D-HA)_1 = \frac{nkg^2}{4(1-s)(k+1) + (n-1)k(g^2 + le^2)} \quad \text{(Eq. 51)}
\]

In which case,

\[
r_{(D-HA)}_2(D-HA)_1 = b_{(D-HA)}_2(D-HA)_1
\]

\[
= b_{PS}(D-HA) = \frac{1}{2} b_{GS}(D-HA) = r_{GS}^2 \quad \text{(Eq. 52)}
\]
The preceding indicates that when environmental correlations between the daughters are zero or concern only daughters within a single proof, the regression factor applicable to that proof reflects accurately the expected correlation or repeatability of separate proofs of the bull. This is true, however, only if the same number of daughters are included in each proof, random mating is in effect and all parameters in the formulas are equal for both groups of daughters.

These regressions may be expressed in terms of \( n \), the number of daughters in the bull's previous proof, and are exactly the squares of the corresponding values for \( r_{GS} \) and \( r_{GS(D-HA)} \) in Tables 50 and 51. This, of course, was implied in Equations 50 and 52.

When we introduce the element of environmental correlations between daughters in the separate proofs of a bull, which we shall denote by \( \epsilon^2 \), the picture is changed, however. Figure 5 shows that \( \epsilon^2 \) actually represents a relationship of the type \( e_i^r e_k e_k \), which like \( \epsilon^2 \), may vitally affect the predictability or repeatability of a proof. (Here, too, as with \( \epsilon^2 \), \( \epsilon^2 \) may be expressed either in terms of environmental covariances and variances or as an environmental correlation.) Thus, we need to consider not only where the bull was used previously, but also where his future daughters will make their records. For example, if a sizable portion of the daughters comprising one proof are in the same or very similar herds, so far as concern their general environment, \( \epsilon^2 \), as defined previously, would be \( > 0 \), probably even with deviation records. Likewise, if the same or similar herds were represented by daughters in the separate proofs of a bull, \( \epsilon^2 \) also would be \( > 0 \).

We saw that when \( \epsilon^2 > 0 \), only the denominator in the expression for the expected correlation of separate proofs of a bull is affected (see...
Equations 49 and 51). In other words, $r_{D_1D_j}$ now equals $\frac{g^2}{4} + e^2$, instead of simply $\frac{g^2}{4}$. This has the effect of reducing the correlation between separate proofs. However, when we have $e^2 > 0$, we affect directly the numerator in the correlation coefficient; i.e., the covariance between the separate proofs. This is accomplished by creating another pathway, other than through $G_S$, between the daughter averages. Hence when $e^2 > 0$, the effect is to increase the correlation between the separate proofs of a bull. But, whenever $e^2 > 0$, $e^2$ is of necessity also $> 0$. In fact, and perhaps this is a key point, while $e^2$ may possibly equal $e^2$, the former can never exceed the latter. Consequently, it does not necessarily follow that when $e^2 > 0$, $r_{D_2D_1}$ and $r_{(D-HA)_2(D-HA)_1}$ automatically increases, but instead the correlations depend on the relative magnitudes of both $e^2$ and $e^2$, among other things.

Formulas for the expected correlations of separate proofs of a bull may be derived from Figure 5 for 'actual' records. Corresponding formulas for deviation records may be derived from a diagram representative of those conditions, and composed of relationships such as shown in Figure 5. These correlation values were shown previously and discussed for the cases of zero $e^2$ and $e^2$ and $e^2 > 0$. Now, when $e^2$ and $e^2$ both $> 0$, we have, for actual records,

$$r_{D_2D_1} = \frac{n(g^2 + 4e^2)}{4 + (n-1)(g^2 + 4e^2)}$$  \hspace{1cm} (Eq. 53)

and for deviation records,

$$r_{(D-HA)_2(D-HA)_1} = \frac{nk(g^2 + 4e^2)}{4(1-s)(k+1) + (n-1)(g^2 + 4e^2)}$$  \hspace{1cm} (Eq. 54)
In both of the above expressions, we assume $m = n$ and $s$ and $k$ are equal for the separate proofs. Further, it can be shown that, under the above conditions,

$$r_{D_2D_1} = b_{D_2D_1} \quad \text{and} \quad r_{(D-HA)_2(D-HA)_1} = b_{(D-HA)_2(D-HA)_1}.$$ 

We may now compute the theoretical correlations between separate proofs of a bull for any prescribed combination of population parameters. Of interest is the result that when $\epsilon^2$ and $\xi^2$ are greater than zero and equal to each other, the net effect is to cancel each other, producing a situation comparable to that prevailing when both $\epsilon^2$ and $\xi^2$ are zero. In these instances (i.e., when $\epsilon^2$ and $\xi^2 = 0$), the 'n' in the denominator of the general formula has a coefficient of unity. However, with each successive increase of both $\epsilon^2$ and $\xi^2$, we have a progressively higher expected correlation than for the corresponding $n$ when $\epsilon^2$ and $\xi^2$ are both zero. This may explain why some of the early investigators of the extent to which later daughters of a bull performed the same as past daughters, found rather high figures. They were working with natural service material, and the later daughters, for the most part, produced in the same herd as the early daughters. Therefore, whatever characterized the environment of that herd permanently, contributed to the numerator of the repeatability. A similar effect would be noted if $g^2$ were increased.

The preceding discussions illustrate the complexity of the problems concerned with the application of proper weighting or regression factors to bull proofs. The main difficulty is that conditions usually vary from proof to proof and from bull to bull. While attention should be
given to where a bull will be used subsequently after an initial proof, practical considerations dictate that primary emphasis be placed on the information already available; i.e., his previously tested daughters. Thus, bulls proved in a single or in very few herds need to be regressed considerably towards the population mean. Bulls proved in numerous herds, representative of the general population, such as in an ideal AI situation, can be taken largely at their 'face value'. This calls for a larger regression factor.

In former years, bull indexes were not generally weighted for the number of daughters included. However, the present trend seems to be toward a widespread application of weighting factors with proofs. As a result, considerable further research is needed so that more equitable weighting factors may be applied in practice. Of particular concern are the complicated interrelationships of $g^2$, $s$, $e^2$ and $\epsilon^2$, so far as they affect sire evaluation. A few, simple, exploratory studies in that general area will be discussed in the next section.

2. The sample correlations of separate proofs of bulls
   a. Study I: Daughters in high and low level herds All herds containing records for daughters by bulls with at least 30 daughters each were separated into a low and high half based on the average of all butterfat records within each herd. Two groups of daughters were selected for each bull so that the daughters in one group came from the high level herds and the other group came from the low level herds. Daughters were selected so that a maximum number of herds from those available were included in each proof for any one bull. Since only
about 40 of the bulls had more than 50 daughters, in order to have a more uniform number of daughters included in the proofs of the various bulls, no more than 25 daughters were included in any one proof of a bull. However, no bull was included if fewer than 15 daughters were available for each of his proofs.

In the first round of selection herds containing daughters of a particular bull were selected at random within a herd level. Then a single daughter of that bull was selected at random from among the daughters available within that herd and was added to the proof for that bull. In a considerable number of cases, a bull would be represented by daughters in 25 different herds within each herd level. Thus 50 different herds would be represented in his two proofs. However, the daughters in one proof always came from high level herds while the daughters in the second proof came from the low level herds. In other cases, a second round of selection was needed to make up the required complement of daughters for each of the two proofs for any one bull. As a result some bulls had proofs with more than one daughter from separate herds within a herd level. Yet, within the limits of available herds and daughters within herds, both herds and daughters were selected at random for each proof of each bull. A total of 60 bulls had sufficient daughters to qualify for this study. Table 52 contains some descriptive statistics describing the average number of herds, daughters and records contained in each proof of the bulls.

Simple daughter averages were then computed for the separate proofs of each of the 60 bulls. Several types of records were used in computing these proofs. These included: (1) the first available record for each
Table 52. Descriptive statistics from study I

<table>
<thead>
<tr>
<th>Source of proof</th>
<th>No. of herds</th>
<th>No. of daughters</th>
<th>No. of records</th>
<th>Rec. per daughter</th>
<th>Daus. per herd</th>
</tr>
</thead>
<tbody>
<tr>
<td>High herds</td>
<td>14</td>
<td>19.9</td>
<td>30.4</td>
<td>1.5</td>
<td>1.4</td>
</tr>
<tr>
<td>Low herds</td>
<td>16</td>
<td>19.8</td>
<td>27.8</td>
<td>1.4</td>
<td>1.2</td>
</tr>
</tbody>
</table>

daughter; (2) all available records for each daughter, but treating each record as if it were made by a separate daughter; and (3) an average of all records by each daughter. 'Actual' production records as well as the exactly corresponding deviation records were used in each of the above categories. In addition, with deviation records, the unweighted average and also the weighted average, described earlier (see p. 117) were used. Finally, with deviation records, Type 1 and Type 2 herdmate groups were used in computing the daughter averages for each bull. It may be recalled that the Type 1 herdmate groups contained neither the records of the daughter nor any maternal or paternal sibs, nor the contemporary record of the dam. The Type 2 herdmate group average excluded only the record of the daughter herself. Proofs consisting of daughter averages were computed for milk, test, and fat yield, but to conserve space and simplify the discussion, only milk and test are considered here.

The product-moment correlations between the separate proofs of each of the 60 bulls were computed for each type of record noted above. Table 53 contains the results. In addition to the sample correlations between the separate proofs, the expected regression coefficients were
Table 53. Study I: The correlation between separate proofs of bulls in high and low level herds

<table>
<thead>
<tr>
<th>Type of record used</th>
<th>Milk</th>
<th>Test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$r$</td>
<td>$z$</td>
</tr>
<tr>
<td>&quot;Actual&quot; production</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st available record</td>
<td>.174</td>
<td>.176</td>
</tr>
<tr>
<td>All records separately</td>
<td>.190</td>
<td>.192</td>
</tr>
<tr>
<td>Average for each daughter</td>
<td>.238</td>
<td>.243</td>
</tr>
</tbody>
</table>

Deviations from RAHA

<table>
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<th>Test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st available record</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type 1 herdmates</td>
<td>.235</td>
<td>.239</td>
</tr>
<tr>
<td>Type 2 herdmates</td>
<td>.218</td>
<td>.222</td>
</tr>
<tr>
<td>All records separately</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type 1 herdmates</td>
<td>.207</td>
<td>.210</td>
</tr>
<tr>
<td>Type 2 herdmates</td>
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<td>.170</td>
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</tbody>
</table>

Unwtd. av. dev. RAHA

<table>
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<tr>
<td>Type 1 herdmates</td>
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<tr>
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<td>.254</td>
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</tbody>
</table>

Wt. av. dev. RAHA

<table>
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<th>Test</th>
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<td></td>
<td></td>
</tr>
<tr>
<td>Type 1 herdmates</td>
<td>.247</td>
<td>.253</td>
</tr>
<tr>
<td>Type 2 herdmates</td>
<td>.182</td>
<td>.183</td>
</tr>
</tbody>
</table>

Number of bull pairs = 60

$s_{z_1} - z_2 = .187$

\(^a\)See text for description of table values.
computed for each proof. These of course depended on the number of
records and type of records included in each proof. For 'actual' records,
\( b_{PS}^{D} \) was computed, where
\[
\frac{ng^2}{4 + (n-1)g^2}
\]
and \( g^2 \) was .25 for milk
and .55 for test, and \( n \) was the number of daughters (or records, when
all records by a daughter were considered as being by separate daughters).

For deviation proofs, \( b_{PS}^{D}(O-HA) \) was used,
\[
\frac{nkg^2}{4(1-s)(k+1) + (n-1)kg^2}
\]
with \( g^2 \) = .33 for milk and .57 for test, \( k \) = the harmonic mean number of
herdmates for each daughter within a single proof, \( g^2 \) = the same as for
'actual' records, and \( n \) was the number of daughters (or records, in the
one case) included in each proof. These regression factors were computed,
therefore, from formulas which considered all environmental correlations
to be zero (see previous section). The expected correlation between the
separate proofs of a bull were then computed as follows:

\[
\mathbb{P}_{12} = \frac{N}{\sum_{i=1}^{N} \left[ b_{PS}^{Proof 1} \right]_{i} \left[ b_{PS}^{Proof 2} \right]_{i}}
\]

(Eq. 55)

\( P_1 \) and \( P_2 \) are proofs 1 and 2 for a bull and \( N \) is the number of bulls
included in the study. These expected correlations are shown in Table 53
alongside each corresponding sample \( r \) value. To provide tests of sig-
nificance, each sample \( r \) value was transformed to its \( z \) equivalent
(Snedecor, 1956, p. 173). These are also presented in Table 53 alongside
the respective sample \( r \) values. The standard deviation of the difference
between any two \( z \) values for this study, \( z_{1} - z_{2} \), is computed as
\[
\sqrt{\frac{1}{N_1-3} + \frac{1}{N_2-3}}, \text{ where } N_1 \text{ and } N_2 \text{ are the number of bull proof pairs comprising } \\
r_1 \text{ and } r_2, \text{ each being 60 in this case. Thus } s_{z_1 - z_2} = \sqrt{\frac{2}{s^2}} = .187. \text{ The } \\
\text{statistical significance of the difference between any two correlations } \\
\text{can be tested by the usual Student's 't' test, where } \\
t = \frac{z_{r_1} - z_{r_2}}{s_{z_1} - s_{z_2}}, \text{ with degrees of freedom equal to } \infty \text{ in the t table.}
\]

The following points may be noted from the results shown in Table 53 for Study I:

1. The correlations between separate daughter averages for each bull are significantly higher for test than are the corresponding correlations for milk yield.

2. Daughter averages from Type 1 deviation records have consistently higher correlations than 'actual' record averages, within a particular class of records. For example, considering milk production, the sample correlation between daughter averages, using the first available 'actual' record for each daughter, is .174, but is .235 for the corresponding deviation records. When all records of each daughter are considered separately in the proofs, the comparable correlations are .190 and .207.

3. The use of Type 1 deviation records produces higher correlations among the separate proofs of a bull that do Type 2 deviation records.

Of course, we see that when the z values for the r's are compared statistically, none of the correlations within a production trait are significantly different from one another, considering the number of bull pairs included. However, the differences actually noted are consistent
enough in all such comparisons to indicate that the statements made in paragraphs (2) and (3), above, probably indicate the true relative merits of the types of records considered.

(4) One of the most striking effects noted in Table 53 is that the sample correlations, $r$, between separate proofs of a bull, fall far short, in all cases, of the corresponding expected correlations, $\hat{r}$. There is far less of a discrepancy for test then for milk, however. This is undoubtedly due to the fact that the expected correlations were computed from formulas that did not allow for environmental correlations among paternal sibs within the separate proofs ($e^2$). Such environmental correlations automatically were induced by the manner in which the daughters of a bull were allocated to the separate proofs; i.e., one proof contained daughters from high level herds only, while low level herds contributed the daughters to the second proof of each bull. In addition there was an average of 1.2 to 1.4 daughters from each herd within each proof which tended to increase slightly the value of $e^2$.

This study furnishes a good example of what environmental correlations can do to affect the repeatability of a proof. For example, if bulls are proved in high level herds, the chances are that their daughter averages, even with deviation records, would not be very indicative of what these bulls might do in low level herds, so far as predicting the actual level of daughter production.

b. Studies II and III: Other distributions of daughters

For Study II, two proofs were computed for each bull, with herds and daughters allocated as follows: For each bull, approximately 10 herds were selected from the entire available deck (these were the very same records that
were used in Study I). Herds were selected at random with the only qualification being that herds with at least four daughters of a particular bull were given priority. This was done so that each of the separate proofs for a bull might contain two daughters, selected at random from among those available from that herd. Due to the limitations of the data available, some bulls had more than two daughters from a single herd in each proof, while other bulls received only one daughter from some herds for each of their proofs. However, each of the two proofs for every bull was, in all cases, allocated the same number of daughters from each herd selected. The number of daughters in a single proof for the bulls varied from a minimum of 15 to a maximum allowed of 25.

Table 54 contains some descriptive statistics concerning Study II.

Proofs consisting of daughter averages were computed using the 'actual' production and Type 1 deviation records for each daughter. The correlations between the two proofs of each bull were then calculated for the total of 61 bulls represented. Table 55 contains the sample correlations and related results for milk and test.

The results from Study II are in sharp contrast to those in Study I. The sample correlations between separate proofs of a bull have shown a $\frac{1}{2}$ to 4-fold increase for milk yield and statistically significant increases in all categories for test. This would seem to confirm the contention that the repeatability of a proof for a bull depends largely on where he was proved in relation to where he is used subsequently. If he is to be re-used in the exact same few herds where he was originally proved, 'actual' production records apparently are adequate in predicting
Table 54. Descriptive statistics from study II

<table>
<thead>
<tr>
<th>Proof</th>
<th>No. of herds</th>
<th>No. of daughters</th>
<th>No. of records</th>
<th>Rec. per daughter</th>
<th>Daus. per herd</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>10</td>
<td>18.5</td>
<td>29.5</td>
<td>1.6</td>
<td>1.85</td>
</tr>
<tr>
<td>2</td>
<td>10</td>
<td>18.5</td>
<td>29.7</td>
<td>1.6</td>
<td>1.85</td>
</tr>
</tbody>
</table>

Table 55. Study II: the correlation between separate proofs of bulls with the same herds represented in both proofs

<table>
<thead>
<tr>
<th>Type of record used</th>
<th>Milk</th>
<th>Test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(r)</td>
<td>(z)</td>
</tr>
<tr>
<td>Actual production</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st available record</td>
<td>.774</td>
<td>1.031</td>
</tr>
<tr>
<td>All records separately</td>
<td>.797</td>
<td>1.091</td>
</tr>
<tr>
<td>Average for each daughter</td>
<td>.805</td>
<td>1.112</td>
</tr>
</tbody>
</table>

Deviations from RAHA

<table>
<thead>
<tr>
<th></th>
<th>(r)</th>
<th>(z)</th>
<th>(r)</th>
<th>(z)</th>
<th>(r)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st available record</td>
<td>.653</td>
<td>.789</td>
<td>.615</td>
<td>.689</td>
<td>.847</td>
</tr>
<tr>
<td>All records separately</td>
<td>.636</td>
<td>.751</td>
<td>.709</td>
<td>.718</td>
<td>.904</td>
</tr>
<tr>
<td>Unw. av. dev. RAHA</td>
<td>.674</td>
<td>.819</td>
<td>.617</td>
<td>.716</td>
<td>.964</td>
</tr>
<tr>
<td>Wt. av. dev. RAHA</td>
<td>.666</td>
<td>.803</td>
<td>.617</td>
<td>.756</td>
<td>.985</td>
</tr>
</tbody>
</table>

Number of bull pairs = 61

\(s^2_{z1} - s^2_{z2} = .186\)

\(^a\)See text for description of table values.
the production level of future daughters.

Another result of significance is that the sample correlations now exceed the expected correlations in all cases, save one, for milk yield, and are very close to the expected values for test. Surely this is due to an increase in both $e^2$ and $\xi^2$ among the daughters of the bulls. The expected correlations were computed here as in Study I on the assumption of zero environmental correlations between paternal sibs, using Equation 55.

However, the distribution of daughters in both studies I and II are not representative of the situation usually prevailing when both early and later proofs of a bull are made under AI conditions. Hence, Study III was designed to simulate as closely as the data allowed the latter situation. Using the same basic record deck, herds were selected at random from among all those available that had daughters for a particular bull. Daughters were allocated to the proofs so that a maximum number of herds were represented in each proof of a bull. If any herd was represented in proof 1 of a bull, it was excluded from representation in proof 2 of that bull. From 15 to 25 daughters per bull were used in each of his proofs and a total of 58 bulls met the requirements so as to be included in this study.

Table 56 presents the usual descriptive statistics, while Table 57 presents the computed sample correlations and related information. However, the comparatively small amount of data available for this kind of study imposed certain restrictions on the interpretation of the results.

Very few of the differences in the correlations for milk yield,
### Table 56. Descriptive statistics from study III

<table>
<thead>
<tr>
<th>Proof</th>
<th>No. of herds</th>
<th>No. of daughters</th>
<th>No. of records</th>
<th>Rec. per daughter</th>
<th>Daus. per herd</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>16</td>
<td>19.1</td>
<td>27.9</td>
<td>1.1*6</td>
<td>1.2</td>
</tr>
<tr>
<td>2</td>
<td>16</td>
<td>19.0</td>
<td>27.1</td>
<td>1.43</td>
<td>1.2</td>
</tr>
</tbody>
</table>

### Table 57. Study III: the correlation between separate proofs of bulls with different herds, otherwise chosen at random, represented in each proof

<table>
<thead>
<tr>
<th>Type of record used</th>
<th>Milk(^a)</th>
<th></th>
<th>Test</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>r</td>
<td>z</td>
<td>(\hat{r})</td>
<td>r</td>
</tr>
<tr>
<td>'Actual' production</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st available record</td>
<td>.202</td>
<td>.205</td>
<td>.557</td>
<td>.503</td>
</tr>
<tr>
<td>All records separately</td>
<td>.317</td>
<td>.362</td>
<td>.636</td>
<td>.521</td>
</tr>
<tr>
<td>Average for each daughter</td>
<td>.310</td>
<td>.321</td>
<td>.557</td>
<td>.517</td>
</tr>
<tr>
<td>Deviations from RAHA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st available record</td>
<td>.300</td>
<td>.309</td>
<td>.617</td>
<td>.531</td>
</tr>
<tr>
<td>All records separately</td>
<td>.396</td>
<td>.412</td>
<td>.694</td>
<td>.533</td>
</tr>
<tr>
<td>Unwt. av. dev. RAHA</td>
<td>.398</td>
<td>.419</td>
<td>.620</td>
<td>.556</td>
</tr>
<tr>
<td>Wt. av. dev. RAHA</td>
<td>.408</td>
<td>.434</td>
<td>.620</td>
<td>.561</td>
</tr>
</tbody>
</table>

Number of bull pairs = 58

\(s_{z_1 - z_2} = .191\)

\(^a\)See text for description of table values.
expressed in terms of $z$, are larger than the standard error of their differences. Yet, once again, we have a consistent pattern of results which hints strongly at the true state of the relationships involved. Several points stand out:

(1) When averaged records for each daughter are used we have a substantially and consistently higher repeatability value for bull proofs over that noted when only a single record is used for each daughter. This is the case for both actual and deviation records for milk yield, while for test, the differences are in the same direction, but smaller.

(2) Deviation records show a sizable advantage over 'actual' records of the same type for milk yield but to a lesser degree for test.

(3) The use of all records of each daughter separately raises the correlations for both 'actual' and deviation records, confirming the method of increasing the number of daughters in a proof as a means of increasing the repeatability.

(4) The sample correlations in Study III fall significantly short of the expected correlations, although not nearly as short as was the case in Study I. This may be due to one or the other of the following: we have a sizable degree of environmental correlations between daughters within a proof; that the heritability or other parameter estimates used in determining the expected correlation factors are incorrect; or that we have a combination of both of these influences present.

The daughters of the various bulls were allocated quite differently in Studies II and III. In the former, the same few herds were represented in both proofs of each bull so that the environmental correlations between proofs ($\xi^2$) is much above average for AI bulls. In Study III, different
herds, but otherwise randomly selected from among those available here, 
are represented in the separate proofs for each bull, resulting in a 
much lower environmental correlation between proofs. In fact $\epsilon^2$ should 
be not far from zero in Study III. Therefore, the changes in sample 
correlations from Study II to Study III, as shown in Table 58, should 
give some indication of the relative merits of the three types of averages 
of individual daughter records in removing environmental correlations 
between separate proofs of a bull. The values for fat are also included 
here although the separate correlations were not shown previously.

Table 58. Differences in sample r and z values for studies II and III

<table>
<thead>
<tr>
<th>Type of record</th>
<th>Milk Differences in r</th>
<th>Milk Differences in z</th>
<th>Test Differences in r</th>
<th>Test Differences in z</th>
<th>Fat Differences in r</th>
<th>Fat Differences in z</th>
</tr>
</thead>
<tbody>
<tr>
<td>'Actual' average</td>
<td>.495*</td>
<td>.791</td>
<td>.282</td>
<td>.525</td>
<td>.340</td>
<td>.580</td>
</tr>
<tr>
<td>Unwt. av. dev. RAHA</td>
<td>.276</td>
<td>.400</td>
<td>.190</td>
<td>.337</td>
<td>.198</td>
<td>.318</td>
</tr>
<tr>
<td>Wt. av. dev. RAHA</td>
<td>.258</td>
<td>.369</td>
<td>.195</td>
<td>.352</td>
<td>.191</td>
<td>.308</td>
</tr>
</tbody>
</table>

a. .805 minus .310 = .495; 1.112 minus .321 = .791; etc.

The differences noted in Table 58 for 'actual' records are undoubt-
edly close to being significantly different from the differences noted 
for deviation records. With the deviation records, the weighted average 
shows to a slight advantage over the unweighted average for milk and fat, 
while the opposite is true for test. These results no doubt were in-
fluenced by the fact that each daughter had an average of only about 1.5 
records available in this sample of data.
3. **Applying the index weighting factor for AI bulls**

In the selection of a weighting or regression factor for AI bull indexes, the guiding principles should be:

1. allow a simple computation of the index;
2. be consistent with basic animal breeding precepts; and
3. be realistic with regard to conditions as they actually exist in practice.

When the environmental correlations between paternal sibs is zero, our problem is relatively simple. With 'actual' production records of daughters, the daughter values simply are averaged, the difference of that average from a specific population mean is computed, and the weighting or regression factor is applied. Thus, the estimated breeding value of a bull, expressed in terms of the estimated producing value of his daughters, is \( \text{EPV} = b_{PS}(\bar{D} - \mu) \), in terms of deviations from the population mean. Here \( b_{PS} \) has the value \( \frac{ng^2}{4 + (n-1)g^2} \), where \( n \) is the number of daughters, and \( g^2 \) is the heritability of the trait concerned. When deviation records are used, the progeny regression factor has the value of \( b_{PS(D-HA)} = \frac{nkg^2}{4(1-s)(k+1) + (n-1)kg^2} \). This is not exactly true because we actually are using deviations of the type \( D-RAHA \), which is not quite the same as \( D-HA \), but the discrepancy surely is not serious.

However, \( \frac{nkg^2}{4(1-s)(k+1) + (n-1)kg^2} \) is probably considered too complicated to be adapted for any large scale computation of bull proofs, so we will attempt to derive a simpler form to apply in practice.
Both the Cornell and New Zealand groups, which use deviation records computed somewhat similarly to the methods described here, use \( \frac{n}{n + 15} \) as the weighting factor for milk and fat yield, as of the latest reports.

This is equal to the value of \( b_{PSJ} = \frac{ng^2}{4 + (n-1)g^2} \) when \( g^2 = .31 \).

The question really reduces to: what is the effective value of \( g^2 \) that can be applied with the factor \( b_{PSJ} \) when deviation records are used in the proof? Heritability is computed as \( \frac{\sigma_G^2}{\sigma_T^2} \), where \( \sigma_G^2 \) is the genic variance and \( \sigma_T^2 \) is the total variance among records of different cows. From Table 29 on page 86, we see that with 'actual' records,

\[
\frac{\sigma_G^2}{\sigma_T^2} = \left( \frac{.21}{.68} \right) = .353
\]

for milk, \( .52 \) for test, and .21 for fat yield. If we assume that deviation records remove all herd-year-season (HYS) effects, then, from Table 29,

\[
\frac{\sigma_G^2}{\sigma_T^2} = \frac{.21}{.68} = .353
\]

\[
\frac{.52}{.83} = .626
\]

for test, and \( \frac{.21}{.66} = .318 \) for fat. We previously found that in the present data under the methods of computation employed here, deviation records actually removed .79 of the HYS effects for milk, .53 of the HYS effects for test and .74 of the HYS effects for fat. Effective heritability would then be computed as

\[
\frac{.21}{.75} = .280
\]

\[
\frac{.52}{.87} = .597
\]

\[
\frac{.21}{.82} = .256
\]

for fat yield.
the latter are then the theoretical values that may be applied for $g^2$ in the factor $\frac{ng^2}{4 + (n-1)g^2}$ when regressing bull proofs for varying numbers of daughters included in the proofs, and using deviation records.

Another approach to this problem and one which utilizes typical values of $k$ and $s$ found in actual data is as follows: We wish to determine those values of $\frac{ng^2}{4 + (n-1)g^2} = b_{PS}$ that are equivalent, on the average to $b_{PS(D-HA)} = \frac{nkg^2}{4(1-s)(k+1) + (n-1)kg^2}$. The average progeny weighting factors were computed from Studies I - III in the previous section for 'actual' and deviation records. These were computed by formulas that assumed the environmental correlations to be zero. Table 59 presents a summary of the factors.

From Table 59 we see that, for milk, the average computed value of $\frac{ng^2}{4 + (n-1)g^2}$ for actual records over all proofs was .558. Equating $\frac{ng^2}{4 + (n-1)g^2}$ to .558 and solving for $g^2$ when $n$ is 19.2, the overall average number of daughters per bull, we get $g^2 = .25$. This was the value actually used in the computations. When these same records, but expressed as deviations, were used, $\frac{nkg^2}{4(1-s)(k+1) + (n-1)kg^2}$ was the factor applied in computing $b_{PS(D-HA)}$ for each proof. For milk yield, $g^2$ was set at .25, $s$ at .33, and $k$ was the harmonic mean number of herd-mates for the $n$ daughters of each bull. The average computed value for
Table 59. Average progeny weighting factors from Studies I - III

<table>
<thead>
<tr>
<th>Study</th>
<th>Average no. of daughter per bull</th>
<th>Milk Actual records</th>
<th>Milk Deviation records</th>
<th>Weighting factors Test Actual records</th>
<th>Weighting factors Test Deviation records</th>
<th>Weighting factors Fat Actual records</th>
<th>Weighting factors Fat Deviation records</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>20.0</td>
<td>.568</td>
<td>.629</td>
<td>.755</td>
<td>.767</td>
<td>.513</td>
<td>.582</td>
</tr>
<tr>
<td>II</td>
<td>18.5</td>
<td>.548</td>
<td>.617</td>
<td>.739</td>
<td>.758</td>
<td>.493</td>
<td>.570</td>
</tr>
<tr>
<td>III</td>
<td>19.0</td>
<td>.557</td>
<td>.617</td>
<td>.746</td>
<td>.758</td>
<td>.502</td>
<td>.570</td>
</tr>
<tr>
<td>Means</td>
<td>19.2</td>
<td>.558</td>
<td>.621</td>
<td>.747</td>
<td>.761</td>
<td>.503</td>
<td>.574</td>
</tr>
<tr>
<td>$\bar{g}^2$</td>
<td></td>
<td>.25</td>
<td>.31</td>
<td>.55</td>
<td>.57</td>
<td>.20</td>
<td>.26</td>
</tr>
</tbody>
</table>

*aSee text for meaning of these values.*

This factor over all proofs was .621 for milk yield. Hence by equating

$$\frac{ng^2}{l + (n-1)g^2}$$

to .621, using 19.2 as n, and solving for $g^2$, we get

$$g^2 = .31.$$ Now, if we use $g^2 = .31$ in the factor $b_p g^5 = \frac{ng^2}{l + (n-1)g^2}$, we get $\frac{n}{n + 11.9}$ in terms of number of daughters. Therefore, on the average, within this population and using deviation records, we would expect to compute approximately the same regressed proof for an AI bull by using $\frac{ng^2}{l + (n-1)g^2} = \frac{n}{n + 11.9}$ as if we had used $b_p S_D N$ as the regression factor with the above defined values for $g^2$, $k$, and $s$.

We can go through the same process for test as was done for milk,
above. A value of \( g^2 = .55 \) was applied to \( \frac{ng^2}{4 + (n-1)g^2} \) for proofs using actual test records. But if this same form of regression factor were to be used with deviation records, a \( g^2 \) of .57 would be needed, equivalent to \( \frac{n}{n + 6.6} \) in terms of number of daughters. (In the formula for \( b_{PS(D-HA)} \) applied to the data, \( s \) was set at .19 as derived from the analysis shown in Table 30, p. 97.)

For butterfat yield, proofs were computed with \( g^2 = .20 \) and \( s = .35 \) in the respective formulas. If the factor \( b_{PS} = \frac{ng^2}{4 + (n-1)g^2} \) is to be used with deviation records for fat, \( g^2 \) would need to be set at .26 to allow the above factor to equal the average value of \( b_{PS(D-HA)} \) actually computed, .57l. Then \( \frac{ng^2}{4 + (n-1)g^2} \) would reduce to \( \frac{n}{n + 14.4} \). All three values of \( g^2 \), applicable for deviation records found in the actual data, agree exceedingly well with the theoretical values found on page 189. However, if we allow for the fact that .20 may represent a slightly conservative estimate of \( g^2 \) for fat yield, we may assume a value of .28 for \( g^2 \) with deviation records. Then \( \frac{ng^2}{n + (n-1)g^2} \) would have a value of \( \frac{n}{n + 13.3} \) in terms of \( n \).

The above factors then would be applicable to deviation records under the conditions of zero environmental correlations. However, there undoubtedly are some environmental correlations remaining among progeny of AI sires even when deviation records are used. The nature and extent of these correlations will of course vary widely from proof to proof,
as we have seen in Studies I - III of the previous section. These may consist largely of correlations within a single proof, represented by $e^2$, or they may consist of some $e^2$ in combination with correlations between daughters in separate proofs of a bull, with this correlation represented by $e^2$.

Under ideal AI conditions of an almost unlimited population of different herds where a bull may be used, both $e^2$ and $e^2$ undoubtedly would be very close to zero when deviation records are used. In Study III of the previous section, conditions most closely simulating average AI situations were attained in making up the separate proofs of the bulls. Due to the limited amount of data available, however, the resultant proofs were not as completely free of environmental correlations as was desired. Nevertheless, we had a clear indication of the prevalence of environmental correlations of the $e^2$ type, resulting in lower correlations between the separate proofs than might be expected under conditions of strictly zero environmental correlations. Therefore, in evaluating bulls whose subsequent daughters are to be the result of artificial insemination, and thus scattered over many herds with a minimum of environmental correlations between them, the emphasis most logically should be placed on the information presently available. This calls for the use of some form of the factor $b_{PS}$, the regression of the coded breeding value of the bull on the average of his daughters already tested. Therefore, we need to concern ourselves only with environmental correlations of the $e^2$ type, with the proper amount to be included in the regression factor dependent on such things as the number of daughters included per herd or per season, etc., in a particular proof.
Until such time as further research can determine the precise amount of $e^2$ to include in the regression factor for a specific proof, the evidence now available from the present studies indicates that we are safe to assume a minimum amount of $e^2$ correlation in the average AI proof. As a result, the regression factor $b_{PSO}$ would have the form

$$\frac{ng^2}{4 + (n-1)(g^2 + he^2)}.$$ We then would be fulfilling conditions (2) and (3) specified at the start of this section; i.e., we would be more consistent with basic animal breeding precepts and be realistic with regard to conditions as they actually exist in the field. Allowing .01 for $e^2$ would seem to be a bare minimum for each production trait under present conditions. Then, with effective heritability, $g^2$, of .31, .57 and .28 for milk, test, and fat, respectively, when deviation records are used, we would have the following rounded values for $b_{PSO}$, expressed in terms of $n$:

Milk: $\frac{n}{1.1n + 12}$; Test: $\frac{n}{1.1n + 6}$; Fat: $\frac{n}{1.1n + 13}$.

These factors probably would be applicable to the average AI deviation proof under present field conditions.

4. The final form of the AI sire index

On the basis of the analyses and discussions presented in this thesis, we may now stipulate that, when daughters with varying numbers of records are included, the final form of the AI sire index should as follows:

$$EPV = \mu + b_{PSO}(RRI)$$

(Eq. 56)
Here, EPV is the estimated breeding value of the bull expressed in terms comparable to lactation production records; μ is a specified overall population average; \( b_{PS} \) is an appropriate regression or weighting factor discussed in the preceding sections; and RPD is the estimated real producing deviation for a daughter of the bull in question.

As the first step in compiling the index, the RAHA for each record of a daughter is used to compute the deviation record. All such deviation records for each daughter then are combined by means of an appropriate weighting process to account for the number of records included for each daughter. One such process was outlined in Section IV-E-4. This weighted average of deviation records is denoted by RPD for each daughter.

The RPD values for all daughters of the bull then are averaged. To this average another weighting factor, \( b_{PS} \), is applied to adjust the index for the number of daughters included and for the estimated average relationship among those daughters. For the average AI bull, \( b_{PS} \) probably would take a form similar to that recommended at the close of the previous section, such as \( \frac{n}{1.1n + 12} \) for milk yield.

Where only single or otherwise equal numbers of records per daughter are included, the index would take the form:

\[
EPV = \mu + b_{PS}(D-RAHA)
\]  
(Eq. 57)

Thus the final consideration here concerns the addition of an overall mean, μ, in Equations 56 and 57, to compute the index for the bull.

It may be recalled (see Section II-A) that under the present New Zealand method, each bull proof is presented simply in terms of the average deviation of the bull's daughters from their respective regressed
herdmate averages. In Britain, the proof is computed in terms of a percentage of the population average, resulting in what is termed the Relative Breeding Value, RBV, for each bull.

Both the Cornell group and the USDA now present proofs in terms of lactation production by adding a population average value to the weighted average of daughter deviations. This method is preferred because it provides an index for each bull that is directly useable in the several functions of bull proofs. The most important of these functions are:

(1) provide a comparison of different bulls for selection by dairymen in their breeding programs; and

(2) allow the use of the bull's index in evaluating pedigrees for selecting young sires and in other long range breeding studies and programs.

The USDA uses as $\mu$, the nation-wide breed DHIA standardized lactation production average for the preceding four-year period, over all months of the years. The generation interval for dairy cows is something of the order of four to five years. By confining the estimate of $\mu$ to a period of approximately this length, each bull would be rated in the particular period in which he was used most. This problem is complicated slightly by the fact that a few AI bulls are now in service for a longer period of time due to the freezing of semen. As new proofs for these bulls are recomputed, the number of years included in their respective population averages may need to be extended somewhat, but should be confined as much as possible to the period of maximum service.
V. SUMMARY AND CONCLUSIONS

A number of exploratory analyses were computed to measure the relative effects of herds, time periods of freshening and their respective interactions on lactation production records.

The model for one such study included effects of herds, month of freshening, herd-by-month interaction, and effects within subclasses. The herd effect contributed about 30 percent of the total variance among records for milk and fat yield, but only 17 percent for lactation average test. The variance component for month of freshening was 1.7 percent of the total for milk, 1.4 percent for fat and 1.1 percent for test. The interaction effects contributed from 3 to 5 percent of the total variance.

Production averages, using all available records for milk, test, and fat were computed for each month of freshening. Lactation production trends related to season of freshening were then studied from these averages. Adjacent months were combined into five different seasonal groupings or plans which appeared to be representative of seasonal effects on lactation milk and fat yields.

Analyses of variance were then computed to determine which plan yielded the largest component for seasons and the smallest component for months within seasons and for herds-by-seasons interaction.

The seasons of freshening judged most appropriate for Iowa conditions included the months of May through September in one season and October through April in the other season. These were the fixed seasons employed in all subsequent analyses. This division maximized the differences in lactation yields of milk and fat but resulted in no difference of any
consequence in lactation average test. Production trends for average test of lactations started in the different months of the year indicated that the seasonal difference for lactation test would have been maximized if the two seasons were composed of January through June and July through December. However, while the effects for month of freshening were of minor importance for all three traits, they were less significant for test than for milk or fat. Also, as the main concern was with milk and fat yield, these two traits were given primary consideration in the grouping of months into fixed seasons of freshening.

The peak average lactation yields of both milk and fat were by records with November freshening, while the low month for both traits was August. The difference was 1109 pounds of milk and 42 pounds of butterfat, or a gain of 9.5 and 9.8 percent, respectively, from August to November.

In another analysis, the components of variance for herds were 28, 29, and 15 percent of the total for milk, fat, and test. Components for year-seasons were 2.3, 1.8 and .2 percent of the total variance for these same traits, while the herd-by-year-season interaction components were 3.3, 4.1 and 4.1 percent for milk, fat and test, respectively. Thus, not all herds, even within a region such as Iowa, where the climate and management practices are relatively uniform, react similarly to year-season effects. This was attributed largely to year-to-year changes in production levels within herds.

The rolling year-season plan for the grouping of months was tested in comparison with the fixed season plan, which was used in the above analyses, to determine which method of grouping of months into seasons
was more efficient in removing year-season effects by the use of deviation records. The two methods proved to be practically equal in this respect. However, the effect of herds-by-rolling-year-seasons interaction was not determined.

The repeatability of single records of a cow was computed as the intraclass correlation of separate records, with variance components derived from an appropriate analysis of variance. Repeatabilities applicable to deviation records as computed in these studies were: for milk yield, 0.505; for fat yield, 0.473; and for test, 0.716. The intraherd repeatability coefficients, ignoring year-season effects, were: for milk yield, 0.489; for fat yield, 0.435; and for test, 0.671.

Repeatability coefficients also were computed for daughters and dams separately in connection with a heritability study. The average age of dam at freshening was 76 months, while for the daughters it was 40 months. These two groups of cows differed mainly in their components for year-season effects. The older cows (dams) had year-season components of 7.8 percent of the total variance within herds for milk and 8.4 percent for fat yield, as compared with 3.5 and 4.7 percent for the younger cows (daughters). The results suggest that older cows are more subject to the effects of year-season changes than are younger cows. A further breakdown indicated that older cows, freshening in generally favorable seasons, produced more, and those freshening in generally unfavorable seasons produced less milk and fat than did their younger contemporaries, on a mature-equivalent basis.

Included in the model for a paternal sib analysis were the effects of sires, herds, year-season of freshening, sire-by-herd interaction,
herd-by-year-season interaction, and residual variance. Components of variance were derived for each effect for milk and fat production. Those of major interest were the components for sires and sire-by-herd interaction. The sire components were 7.3 and 8.4 percent of the total variance for milk and fat yield, respectively, while the sire-by-herd interaction components were 4.4 and 3.8 percent for the two traits.

The proportion of differences among records of different cows attributable to genic effects, or heritability, was computed by the intraherd regression of daughter on dam. After correcting for year-season effects, the estimates of heritability, in the narrow sense, and expressed on a single record basis, were as follows: milk yield, \( .200 \pm .010 \); fat yield, \( .180 \pm .012 \); and test, \( .526 \pm .036 \). The standard deviation of genic effects among individual cows, \( \sigma_G \), was: for milk yield, 1059 pounds; for fat yield, 35 pounds; and for test, .222 percent.

The use of deviation records was studied in an attempt to assess their effectiveness in reducing certain environmental correlations, principally from herds and year-seasons, so that sire evaluation might be made more accurate and efficient.

Herdmate averages, contemporary to daughters of the sires being evaluated, were first adjusted for (1) finite number of herdmates, and (2) possible differences in the average breeding value among herds. The adjusted herdmate average, AHA, is the result of the first adjustment. It is computed as:

\[
AHA = \mu + \frac{n}{n + a} (HA - \mu),
\]
where \( \mu \) is the mean value for each trait in the specified population; HA is the simple average of herdmate
production; \( n \) is the number of herdmates; and \( a \) is the fraction,

\[
\frac{\sigma^2_{\text{within herd-year-season groups}}}{\sigma^2_{\text{between herd-year-season groups}}}.
\]

Values of \( a \) that were used were obtained from an analysis of variance. Rounded to the nearest whole number, \( a = 2 \) for milk and fat, and \( 3 \) for test.

The factors for correcting herdmate averages for differences in the average breeding value among herds were calculated from the regression \( (b) \) of records of daughters on their respective contemporary adjusted herdmate averages. Values used for \( b \) were: for milk, .90; for fat, .92; and .80 for test. The resultant herdmate averages are called the regressed adjusted herdmate averages, RAHA, where RAHA = \( \mu + b(AHA - \mu) \).

The RAHA may be computed in one operation from 305-day-2X-ME records as follows:

\[
\text{RAHA} = \mu + \frac{bn}{n + a} (HA - \mu).
\]

The specific population mean, \( \mu \), used in computing the RAHA, was the average production of all cows (these were from Iowa Holstein herds, only, in this study) which freshened in the same year and season as those in the particular herdmate group. In general, the region from which \( \mu \) is estimated, should contain approximately 400 different herds.

Computing the real producing deviation (RPD) value for each daughter is one way of handling multiple records for an individual cow, especially for use in AI deviation proofs. This is a weighted average of the cow's deviation records and is computed as follows:

\[
\text{RPD} = \frac{nr}{1 + (n-1)r} (\overline{C} - \overline{RAHA}),
\]

where \( r \) is the repeatability of single records of a cow, \( \overline{C} \) is the average of the cow's \( n \) records, and \( \overline{RAHA} \) is
the average of the contemporary regressed adjusted herdmate averages associated with each of the cow's records. RPD is expressed as a deviation, either plus or minus. However, sample results indicated that use of a simple average of the daughter's deviation records provided almost the same precision in evaluating sires. This result may have been affected by the fact that only about 1.5 records were available, on the average, for each daughter of the sires studied here.

Analyses of variance were computed to determine how much of the herd and year-season effects had been removed by the use of deviations from the RAHA's. In one study, using a single random deviation record for each cow, the herd-year-season effects were reduced by 79 percent with milk records, 74 percent with fat records, and 53 percent with records for test.

The role of the dams' records in AI proofs was investigated by two analyses. The first concerned whether mates (dams) of different levels of production were chosen for breeding to specific sires. Averaged records of each mate were used and the correlation among these mates for each sire was computed. When actual (305-day-2X-ME) production records were used, the correlations were: for milk, .161; for fat, .181; and for test, .088. When the corresponding deviation records were used, the respective correlations were: .024, .036, and .015. These results indicate that (1) deviation records are an effective means of reducing environmental correlations, and (2) very little, if any, choosing different sires for cows of different levels of production was done when deciding which bulls to use.

The second analysis was based on the fact that the amount of genetic
improvement expected in the next generation by selecting on the basis of bull proofs which included dams' records as compared with the improvement expected when the proofs included only the daughters' records, was proportional to \( \frac{1}{\sqrt{1 - r_{XY}^2}} \). Here, \( r_{XY} \) is the correlation of the daughters' average and their dams' average production. The gain in genetic merit expected by considering the dams was 23 percent for milk and fat yields and 11 percent for test when using actual records. When deviation records were used, the expected gains by including the dams' records were only .7 percent for milk, 2.5 percent for fat, and 1.9 percent for test. Thus the dams' records enhance the accuracy of proofs very little when deviation records are used, at least under conditions reflected in the data available here.

The important question of the correlation of a bull's breeding value, \( G_S \), and his daughter average, \( r_{GS} \), was approached from both the theoretical and applied angles. When 'actual' production records are used, under conditions of random mating and with zero environmental correlations among paternal sibs, \( r_{GS} \) was shown to equal

\[
\frac{\sqrt{ng^2}}{h^2 + (n-1)g^2}, \text{ with } n \text{ being the number of daughters and } g^2 \text{ the heritability in the narrow sense. Under the same conditions, but using deviation records, i.e., the deviation of a daughter's record from her contemporary herdmate average, } D-HA, r_{GS(D-HA)} = \frac{nkg^2}{h(1-s)(k+1) + (n-1)kg^2}.
\]

Here \( k \) is the average number of herdmates per daughter and \( s \) is the
phenotypic correlation among contemporary cows in a herd.

In order to adjust or weight a bull proof for the number of daughters contained therein, we use the expected regression, $b$, of the bull's breeding value on his daughter average, $b_{GS}$. However, we wish to scale the index so that it is comparable with cow production values, so we use, instead of $b_{GS}$, the factors $\frac{1}{2} b_{GS} - \frac{1}{2} b_{GS(D-HA)}$, which we have denoted here as $b_{PS}$ and $b_{PS(D-HA)}$. Under random mating and zero environmental correlations, these factors are

$\frac{ng^2}{h + (n-1)g^2}$ and $\frac{nkg^2}{h(1-s)(k+1) + (n-1)kg^2}$, for 'actual' and deviation record proofs, respectively.

When there are environmental correlations between paternal sibs included within a single proof for a bull, $b_{PS}$ becomes

$\frac{ng^2}{h + (n-1)(g^2 + 4e^2)}$, and $b_{PS(D-HA)}$ becomes

$\frac{nkg^2}{h(1-s)(k+1) + (n-1)kg^2}$, thus reducing the regression of a bull's coded breeding value, $P_{S}$, on his daughter average. Also reduced is the advantage of large numbers of daughters in a proof, so far as concerns estimating the bull's breeding value.

In connection with the above, the correlation of separate proofs of a bull also was studied. This correlation is affected not only by the environmental correlation, $e^2$, among the daughters comprising each
proof, but also by any environmental correlation, \( \varepsilon^2 \), between daughters in the separate proofs. Assuming no selection of mates, the expected correlation of separate proofs of a bull, using 'actual' records, has the form,

\[
\rho_{D_1D_2} = \frac{n(g^2 + 4\varepsilon^2)}{1 + (n-1)(g^2 + 4\varepsilon^2)},
\]

and with deviation records,

\[
\rho_{(D-HA)_1(D-HA)_2} = \frac{nk(g^2 + 4\varepsilon^2)}{4(1-s)(k+1) + (n-1)k(g^2 + 4\varepsilon^2)},
\]

assuming further that \( n_1 = n_2 \) and \( k_1 = k_2 \) in the formulas. As \( \varepsilon^2 \) increases and \( \varepsilon^2 \) is small or zero, the net effect is to reduce substantially the correlation between the separate proofs of a bull. However, when \( \varepsilon^2 \) increases along with \( \varepsilon^2 \), the correlation attains a higher value.

From three separate studies it was shown how the two kinds of environmental correlation between paternal sibs, \( \varepsilon^2 \) and \( \varepsilon^2 \), affected the correlations of the separate proofs of bulls. By the use of deviation records, the correlations of separate proofs of a bull, under average field conditions, were consistently and substantially increased over the correlations realized when using the corresponding 'actual' records. However, the correlations realized between proofs fell significantly short of their theoretical values computed with the assumption of zero environmental correlations among the daughters included therein.

From both theoretical and practical considerations, plus the evidence from the above studies, it was concluded that the regression factors applicable to AI proofs using deviation records should include a minimum amount of environmental correlations of the \( \varepsilon^2 \) type. When
reduced to terms of \( n \), the number of daughters included in a proof, the following regression factors, \( b_{PSU} \), are recommended for the average AI proofs:

\[
\text{milk: } \frac{n}{1.1n + 12} ; \text{ test: } \frac{n}{1.1n + 6} ; \text{ and fat: } \frac{n}{1.1n + 13}.
\]

The index of the AI bull in its final form should be expressed in terms of lactation production values regressed to the population average, \( \mu \). The latter would include approximately four to five years of records contemporary, as much as is practical, with the majority of the daughters in the proof. In other words, the bull's index should be of the form:

\[
\text{EPV} = \mu + b_{PSU}(D-RAHA), \text{ where only single or otherwise equal numbers of records per daughter are included; or}
\]

\[
\text{EPV} = \mu + b_{PSU}(RPD), \text{ where variable numbers of records per daughter are included. Here EPV is the bull's coded estimated breeding value and all other terms have been defined previously in the summary.}
\]

The final conclusions from this dissertation are:

The major source of identifiable nongenetic variance in dairy production records is the herd in which each cow makes her records. The year and season of freshening also contribute a measurable, although minor, effect on production records.

In setting up procedures for computing dairy sire indexes, these extraneous environmental effects need to be accounted for before a reasonably accurate evaluation of a bull is possible. The use of deviation records, whereby each daughter's record is expressed as a deviation from its contemporary herdmate average, was tested for effectiveness in removing these environmental factors. By removing upwards of three-
fourths of these effects for milk and fat yield and over half for test, deviation records have amply demonstrated their utility in sire proving work. This applies to traits such as test, as well as for milk and fat yield.

It is hard to pinpoint the exact reasons why more of the herd and season effects are not removed with deviation records. But evidence indicates that they concern principally two factors: (1) The delimitation of year-seasons within the separate herds. The sizable herd-by-year-season interaction component found infers that much is to be desired in present methods of grouping records by herd-year-seasons. Perhaps the most flexible and effective plan yet proposed is use of rolling year-seasons within herds. However, it appears advisable to use only the concurrent, regional year-season average if the herdmate average or deviation record is to be adjusted. (2) Adjustment factors. These include mature equivalent and record extension factors for individual records, and the factors used in computing the regressed adjusted herdmate average. Further work is needed in these areas.

One of the main consequences of the use of deviation records is that herdmate averages can be effectively substituted for records of dams in bull proofs. If dams are used, in addition to deviation records in proofs, they generally provide little added information on the bull.

Methods of combining more than one deviation record by a cow into a composite average need to be defined more clearly so that daughters with different numbers of records can be utilized more equitably in bull proofs. Neither a simple average nor the real producing deviation (RPD), as computed here, appears to be wholly satisfactory.
At present, one of the major unsolved problems in dairy sire evaluation methods probably is the proper use of weighting or regression factors to adjust daughter averages for the number of daughters included in the proof. In the first place, a simple regression factor is not entirely satisfactory because it penalizes too much the really top bulls and not enough the really poor bulls. In the second place, if environmental correlations among the daughters are not considered in the factor, as is common practice, gross inaccuracies are likely to be present in the estimated breeding value of some bulls.

We have seen that deviation records do not remove all environmental variance. When paternal sibs make their records in the same herd and/or season, it is doubtful if the deviation records can reduce this source of environmental correlation between daughters in a proof to such a degree that it can be ignored. It is therefore recommended that, for each proof, consideration should be given to the number of paternal sibs making their records in the same herd and/or season and allot a value to $e^2$ in the regression factor to allow for this source of environmental correlation between the daughters.

True, we have made substantial progress in recent years, but many difficult problems remain to be solved before sire indexes can merit a greater degree of confidence and esteem than they now hold with the average dairyman, in whose herds the final judgments are generally made.

While it is acknowledged that certain peculiarities of the data used in the studies presented here may have influenced the results somewhat, for the most part the data were a representative sample of those currently available from DHIA-tested herds. For this reason these
findings should provide additional concrete evidence on the questions considered, with special emphasis on dairy sire evaluation.

A quotation from Yates (1951) seems particularly appropriate in conclusion:

"Research workers, therefore, have to accustom themselves to the fact that in many branches of research the really critical experiment is rare, and that it is frequently necessary to combine the results of a number of experiments dealing with the same issue in order to form a satisfactory picture of the true situation."
VI. LITERATURE CITED


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