The importance of bull X herd-year-season interaction in milk production

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KELLEHER, Denis Joseph Louis, 1934–
THE IMPORTANCE OF BULL X HERD–YEAR–SEASON INTERACTION IN MILK PRODUCTION.

Iowa State University of Science and Technology
Ph.D., 1964
Agriculture, animal culture

University Microfilms, Inc., Ann Arbor, Michigan
THE IMPORTANCE OF BULL X HERD-YEAR-SEASON INTERACTION IN MILK PRODUCTION

by

Denis Joseph Louis Kelleher

A Dissertation Submitted to the Graduate Faculty in Partial Fulfillment of The Requirements for the Degree of DOCTOR OF PHILOSOPHY

Major Subject: Animal Breeding

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1964
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GLOSSARY OF ABBREVIATIONS

2X = Milked twice daily.

305-day = Lactation-length cut off at, or adjusted to, 305 days.

A.I. = Artificial Insemination.

d.f. = Degrees of freedom.

D.H.I.A. = Dairy Herd Improvement Association.


I.B.M. 88 = Card-collating machine built by I.B.M.

I.B.M. 650 = Drum-storage computer built by I.B.M.

I.B.M. 7074 = Core-storage transistorized computer built by I.B.M.

M.E. = Mature Equivalent.

U.S.D.A. = United States Department of Agriculture.
INTRODUCTION

Non-additivity of the genetic and environmental effects in biometrical analyses of plants and animals is a constant source of discussion among research workers, geneticists and biometricians. In many cases, particularly in survey-analyses, interaction among the main-effects is assumed, on insufficient supporting evidence, to be equal to zero. An assumption of this nature is made because (a) in that particular situation it may not appear too unreasonable, based on one's knowledge of the experimental material and because (b) one hopes that the true value of the interaction is equal to zero because this simplifies the mathematical computations greatly.

In designed experiments, one can ensure that the treatments are applied in such a way that they are orthogonal with other sources of variation. This orthogonality precludes correlation between the main-effects in the sample and permits "clean" separation of interaction-effects from the main-effects.

On the other hand, in survey analyses, as, for example, in the analysis of D.H.I.A. milk-production data, which have been collected in many herds and year-seasons, the assumption which is frequently made that there is no real interaction
between bulls and herd-year-seasons (or between bulls and herds) is rarely, if ever, supported by reliable statistical evidence. The reason for this is that survey-material is highly non-orthogonal with respect to bulls and herd-year-seasons. This non-orthogonality prevents "clean" separation of the interaction-effects from the main-effects and, in this way, precludes "exact" testing of hypotheses and placing of confidence limits on the interaction component of variance.

It is easy to see, therefore, why research-workers, when they are analyzing survey-material, do not place confidence-limits on the interaction-component of variance when the study of this interaction-component is not a major part of the operation in hand. The present author believes that it is desirable to investigate the feasibility of a technique which would enable one to do this (place confidence-limits on the bull X herd-year-season interaction-component of variance) for non-orthogonal data.

Following that, having obtained an estimate of the interaction-component and a measure of the probable amount of error in the estimate, it is considered worth-while to measure the degree to which this component is likely to influence the
accuracy of selecting dairy bulls using D.H.I.A. records. Both of these operations are described in greater detail in later chapters.
DISCUSSION ON GENETIC-ENVIRONMENTAL INTERACTION

General Discussion

Lush (1960) stated that;

Genetic environmental interactions exist whenever the phenotypic differences among 2 or more genotypes are genuinely different from environment to environment. Another less specific way to say this is that some genotypes excel in some environments but other genotypes excel in other environments. Another way, somewhat closer to the terms the naturalist uses, is that genotypes or breeds or local races or species, vary in their adaptability to different ecological niches. Expressing it somewhat more statistically: The actual phenotype is not simply the sum of the genotype and the environment; that is, environment and genetic variations do not combine their effects additively.

Elaborating somewhat on this statistical concept, let us consider the differences in "response" or "yield" in a conceptual population among a number of genetic materials (denoted by the subscript i; i=1, 2, ......., a) which are each placed in a number of environments (denoted by the subscript j; j=1, 2, .......,b). Some genetic materials have higher average yields (that is, "average" over all environments) than others. Similarly, some environments have higher average yields (that is, "average" over all genetic materials) than others.

Let $Y_{ij}$ denote the yield of the $i^{th}$ genetic material in the $j^{th}$ environment.
Then, \( \bar{Y}_{..} \) = the over-all mean = \( \frac{\sum \sum \bar{Y}_{ij}}{ij} \) (1). \( \bar{Y}_{..} \) may be symbolized by \( \mu \).

\( \bar{Y}_{i.} \) = the mean of the \( i^{th} \) genetic material over all environments = \( \frac{\sum \bar{Y}_{ij}}{j} \) (1),

\( \bar{Y}_{.j} \) = the mean of the \( j^{th} \) environment over all genetic materials = \( \frac{\sum \bar{Y}_{ij}}{i} \) (1).

\( \bar{Y}_{i.} - \bar{Y}_{..} \) is regarded as the average effect of the \( i^{th} \) genetic material. \( \bar{Y}_{i.} - \bar{Y}_{..} \) may be symbolized by \( b_i \).

\( \bar{Y}_{.j} - \bar{Y}_{..} \) is regarded as the average effect of the \( j^{th} \) environment and \( \bar{Y}_{.j} - \bar{Y}_{..} \) may be symbolized by \( t_j \).

\( \bar{Y}_{ij} - \bar{Y}_{i.} - \bar{Y}_{.j} + \bar{Y}_{..} \) is regarded as the effect of interaction between the \( i^{th} \) genetic material and the \( j^{th} \) environment. \( \bar{Y}_{ij} - \bar{Y}_{i.} - \bar{Y}_{.j} + \bar{Y}_{..} \) may be symbolized by \( (bt)_{ij} \).

The "response" or "yield" of the \( i^{th} \) genetic material in the \( j^{th} \) environment can then be written as,

\[
\bar{Y}_{ij} = \bar{Y}_{..} + (\bar{Y}_{i.} - \bar{Y}_{..}) + (\bar{Y}_{.j} - \bar{Y}_{..}) + (\bar{Y}_{ij} - \bar{Y}_{i.} - \bar{Y}_{.j} + \bar{Y}_{..})
= \mu + b_i + t_j + (bt)_{ij}.
\]

Let us imagine a diagram in which the genetic materials are listed along one \( (L_1) \) axis, the environments along another \( (L_2) \) and production or yield along the third \( (L_3) \) axis.
Let the genetic materials be positioned along $L_1$ in such a way that the $\bar{Y}_i$-values ($i = 1, 2, \ldots, a$) in the $L_3$-direction are in a straight line. Similarly, let the environments be positioned along $L_2$ in such a way that the $\bar{Y}_j$-values ($j = 1, 2, \ldots, b$) are also in a straight line. This is achieved by giving each genetic material (or environment) the value of its average effect. Then the $Y_{ij}$-values can be plotted, with respect to the $i^{th}$ genetic material and the $j^{th}$ environment ($i = 1, 2, \ldots, a; j = 1, 2, \ldots, b$), and will form a surface which is termed a "response-surface". Similarly, the values for $\bar{Y}_{..} + (\bar{Y}_i - \bar{Y}_{..}) + (\bar{Y}_j - \bar{Y}_{..})$ will form a surface; the surface in this case is a plane. Since the sum of the deviations of the $Y_{ij}$-values from the corresponding values of
\( \bar{Y}_{..} + (\bar{Y}_{i.} - \bar{Y}_{..}) + (\bar{Y}_{.j} - \bar{Y}_{..}), \text{ that is, } \sum_{ij} (y_{ij} - \bar{y}_{i.} - \bar{y}_{.j} + \bar{y}_{..}), \) equals zero, this plane is the best-fitting plane for the \( Y_{ij} \)-response-surface.

Any deviations of the response-surface from the best-fitting flat plane represent the effects of interaction between the genetic materials and the environments.

This response-surface can be regarded as analogous to the topography of a particular geographical area. The hills and the valleys, respectively, can be thought of as representing the favorable and unfavorable effects of interaction. These hills and valleys vary in intensity from one area (mountainous) to another (prairie-country or other flat areas). Likewise, in biological material, the importance of interaction can vary from one set of genetic-environmental conditions to another. This precludes generalizing on the importance of interaction from one situation to another.

When we analyze a sample of data, we never have complete information on the true response-surface of the population from which the data came. There are at least two reasons for this.

(a) It may be impossible, for one reason or another, to test all genetic materials in all environments. For example, this is true for the D.H.I.A. milk-
production data with which this dissertation deals; it is impossible for all bulls to have daughters in all herd-year-seasons.

(b) In the sample, the surface, in addition to being poorly represented, may be covered above and below by a zone of random error-effects \( (e_{ijk}) \) which prevent it from being "seen" and measured.

In estimating the importance of genetic-environmental interaction, it is desirable that as much information as possible is available on a particular "area" because this enables one to estimate the true surface more precisely. This precision is greatest (but frequently impossible to attain) when all the genetic classes which are tested in one environmental class are tested also in all other environmental classes, with many observations per subclass. Information on interaction-effects and interaction components of variance can be obtained only from interaction-comparisons (see Snedecor, 1956). Therefore, if a particular genetic material is tested in only one environment, since it can not be included in any interaction-comparison, it contributes nothing to the estimation of the interaction-component. For a genetic material to contribute information on interaction-components,
it should be tested in at least two environments and, similarly, for an environment to contribute information on interaction-components it should have at least two genetic materials tested in it.

Genetic-Environmental Interaction in Farm Animals

When we discuss farm animals and their ability to produce under particular environments, we are focusing our attention on a particular region of the $Y_{ij}$ response-surface discussed in the last section. Phillips (1948) discussed the wide differences in the abilities of animals to thrive and perform efficiently under a given set of conditions. Some animals are adapted to cold climates, others to temperate climates, still others are more suited to tropical conditions. Certain types of animals, such as the yak and the vicuna, thrive at high altitudes while others cannot survive satisfactorily there. Animals vary also in their grazing ability. Some can obtain a satisfactory living while grazing over extensive rangelands, while others require lush pastures and supplementary feeding if they are to perform efficiently.

For example, the Holstein-Friesian breed of cattle was developed in the temperate zone and under conditions of intensive farming. It is well adapted to areas where pastures
are good, where it is possible to grow ample supplemental feed, and where there is a market for a sizable volume of milk. But it is not suited to many areas in the tropics or to areas of scanty feed in the temperate zones. By contrast, the yak is admirably suited to high elevations and extensive grazing conditions such as are found on the Tibetan highlands of central Asia, but it does not produce at a sufficiently high level to use large amounts of good-quality feed efficiently.

Still another contrasting type is the water-buffalo. These are huge feeders, and less discriminating than cattle in foraging, which makes them suitable for exploiting the coarse natural pastures and other forages of the tropics. Because of the absence of an efficient perspiring mechanism, these animals are likely to suffer from hot temperatures but are capable of counteracting this inefficiency by their natural tendency to wallow in water.

Neither the yak nor the water-buffalo would be suited to areas where intensive dairying is practiced, such as the Netherlands, or Wisconsin and New York, for they are not adapted to the climatic and other conditions prevailing there, and do not have sufficient inherent milk-producing capacity to utilize the available feed efficiently.
The more distantly related the genetic materials are, the more likely they are to require different environmental conditions in order to express themselves fully. Members of different breeds, inbred lines, strains or family-groups are more likely to require differential treatment and different environmental conditions than are members of the same breed, line, strain or family-group. Closely-related genotypes tend to be adapted to similar environments. Even then, interaction may be still so great that individuals may not be mutually interchangeable between their particular environments.

Specific and General Genetic Merit

We can assume that a random sample of one half of a bull's genes are transmitted to its offspring at the moment of fertilization. The total effect of these genes on the production of the progeny is defined as the effect of that bull. If mating is random, the effect of the bull is expected to include 1/2 of the additive portion, 1/4 of the additive X additive portion, 1/8 of the additive X additive X additive portion, etc., of the total effects of the genes which that animal possesses. The genetic merit of the individual is defined as all of the additive portion, 1/2 of the additive X additive portion, etc., of the total effects of the genes which that
animal possesses. Thus, if $b_i$ is the effect of the $i$th bull and $G_i$ is its genetic merit, $G_i = 2b_i$.

If the $i$th bull is mated to females selected at random within a particular environment, one may write a mathematical model describing the factors affecting the phenotype of the $k$th daughter as

$$X_{ik} = \mu + b_i + e_{ik},$$

(or, if $x_{ik} = X_{ik} - \mu$, $x_{ik} = b_i + e_{ik}$) where $b_i$ is the effect of the $i$th bull and $e_{ik}$ is the remainder or difference between $X_{ik}$ and $\mu + b_i$. Then the genetic merit of the individual, in relation to the population of individuals within this environment, is estimated as

$$nh^2 \times \frac{2[1 + (n - 1)t]}{2[1 + (n - 1)t]}$$

times the deviation of the progeny mean from the population mean. ($h^2$ is the heritability of the trait in that environment, $n$ is the number of offspring and $t$ is the average phenotypic correlation between the offspring). $h^2$, as it is used here, is defined as the ratio of the genetic variance [i.e., variance among the genetic merits (defined above)] over the phenotypic variance. Since genetic merit includes a fraction of the epistatic effects as well as all of the additive effects of the genes, this heritability is expected to be intermediate between heritability in
the "narrow" and the "broad" senses as they are defined by Lush (1948).

If there is no genetic-environmental interaction and if the progeny are scattered over several environments, the mathematical model is

\[ x_{ijk} = b_i + t_j + e_{ijk} \]

where \( t_j \) is the effect of the \( j^{th} \) environment. Then, the bull-effect, \( b_1 \), can be estimated as \( \hat{b}_1 \) by the least-squares procedure of fitting constants, described by Kempthorne (1952), and the genetic merit estimated as

\[ \frac{2\text{Cov}(b_1, \hat{b}_1)}{\hat{V}(\hat{b}_1)} \cdot \hat{b}_1 \]

If, in the sample, the effects of the bulls are correlated with the effects of the environments, the estimate of \( b_1 \) will include some influence due to the environments in which this bull is used and, vice versa, the estimate of \( t_j \) will include some influence due to the bulls which were used in that environment. (However, this discussion does not apply to the computations in this dissertation because, as can be seen in Analysis I later, we deliberately select the data so that all bulls have an equal number of daughter-records in each environment (herd-year-season). We do this because we wish to get the interaction-component free from any bias which may result from
covariance between the main-effects.)

If there is interaction between the $i^{th}$ bull and the $j^{th}$ environment in this trait, the model is no longer $x_{ijk} = b_i + t_j + e_{ijk}$, but rather,

$$x_{ijk} = b_i + t_j + (bt)_{ij} + e_{ijk}$$

$(bt)_{ij}$ is the effect of interaction between the $i^{th}$ bull and the $j^{th}$ environment which results from some real physiological advantage or disadvantage specific to the daughters of this bull in this environment.

When $(bt)_{ij}$ is real, the concept of genetic merit must be redefined because the meaning of "genetic merit" is no longer the same in one environment as it is in another. Instead, genetic merit now depends upon the environment. The genetic merit of the $i^{th}$ individual in the $x^{th}$ environment, denoted by $G_{ix}$, is the expected value of $2[b_i + (bt)_{ix}]$.

It is convenient to term the genetic merit of an individual in a specific environment as its specific genetic merit and its average genetic merit over all environments (denoted by $G_i$) as its general genetic merit. Thus, $G_{ij}$ is the specific genetic merit of the $i^{th}$ individual in the $j^{th}$ environment and $G_i$ is its general genetic merit over all environments. These definitions of general and specific
genetic merits are not analogous to the definitions of general and specific combining abilities used by Sprague and Tatum (1942). These authors, in discussing the results of crossing inbred lines of corn, divided the gene action concerned with combining ability between lines into two categories, general and specific combining abilities. General combining ability was regarded as being due predominantly to additive gene action. Specific combining ability involved "all effects which cannot be accounted for by the additive scheme. These may be the result of dominance, epistasis, genotypic-environmental interactions, etc."

Thus, Sprague and Tatum (1942) defined "specific combining ability" as not including "general combining ability" whereas we define specific genetic merit as including general genetic merit. Other differences, of course, exist; Sprague and Tatum are concerned with the interactions between genetic lines whereas we are concerned with interactions between genetic factors (bulls) and environmental factors (herd-year-seasons).

Estimation of specific genetic merit is of interest when selection among individuals is made within the environment in which its descendants are to live. If the offspring are to live in an environment different from that in which an individual is tested, the genetic merit of the individual which is
specific to that test-environment is of no interest in itself because the interaction-effect is not available to the offspring in other environments. Since the genetic-environmental interaction-effects peculiar to one environment are not available to the offspring which live in another environment, one must be cautious in comparing individuals which were tested in two different environments. This statement becomes more and more meaningful in situations where the bull x environment interaction-effect, \((bt)_{ij}\), is large relative to the bull-effect, \(b_i\).

In commercial production, even when the genetic "ingredients" are available and one has reason to believe that genetic-environmental interaction is real, further conditions must exist before it is considered worth-while to select and breed for adaptability to a specific environment;

(1) The environment must be controllable or, at least, predictable.

(2) The genetic-environmental interaction-effect must be sufficiently large that the time, effort and expense involved in breeding specifically for adaptation to that environment are justified.

The Kerry breed of dairy cattle is claimed to be specifically adapted to the high rainfall and sparse feeding in
South-West Ireland and Wales and they are bred specifically to meet the demands of these areas. The Jersey breed is specifically adapted to supply the demands of people who like high-test milk. The Holstein breed is capable of extremely high milk production of 3.5% - 4.0% fat on the rich, level, low-lying pastures in temperate regions of the world. In warm humid areas where European breeds either find it difficult to survive or show considerable distress, genetic-environmental interaction is so large that genetic improvement is based on the native genotype which, although extremely low in milk-producing ability, is adapted to this environment through natural selection for survival ability for many generations.

When for one or more reasons there is insufficient justification for breeding for adaptability to particular environments, the selection program is aimed at selecting for general genetic merit, $G_i$, rather than specific merit, $G_{ij}$. In that case, $(bt)_{ij}$ is regarded as a source of error to be minimized or eliminated rather than a factor to be selected for.

Interaction as a Source of Error in Experiments

Genetic-environmental interaction, as a source of variation among performance records of individuals, can cause serious
difficulties in statistical analyses, either when the primary object of inquiry is environmental (e.g. nutritional) or when it is genetic.

In nutritional experiments, where the detection of true differences among treatments is the object of study, the procedure is to apply each of the treatments to several plants or animals, as the case may be, which are otherwise treated alike environmentally and which are, it is hoped, moderately uniform genetically. Here the nutritional treatments are controllable and it is hoped that any other factors which are causing variation are random.

Having the experimental material genetically uniform is desirable if it is representative of that population to which one intends to extrapolate the results. This uniformity is purely a means of reducing the background variation so that the effects of treatments may be measured with greater confidence. It is permissible only if the population to which inference will be made is not so variable genetically that different genotypes within that population would respond differently (genetic-environmental interaction) to these nutritional treatments.

For example, one may wish to compare the effects of two types of roughage when fed to dairy cattle. If the results
are intended for application to one breed (e.g. Holstein), the experiment should be conducted on individuals from that breed. However, if the results are intended for application to Jerseys as well as Holsteins, the treatments should be compared on both breeds, if there is reason to suspect that the comparisons may not be the same in both cases. If interaction exists between the treatments under investigation and the genetic factors, one hopes that it can be demonstrated in the analysis of variance.

When a test of significance makes one confident that the interaction-component is real, the interpretation is that the effects of the nutritional treatments depend upon the specific genetic material to which they are applied. A well-designed experiment allows for the possible existence of such interactions. The real difficulty arises when interaction exists but cannot be separated from the main-effects because of non-orthogonality between the treatments and the genetic materials and/or because of too few observations in the subclasses.

Frequently, in the course of an analysis, a worker suspects that interaction between the treatments under investigation and the other factors is real but, because of poor experimental design, he is unable to make any statement with
confidence concerning it. A situation like this would exist if the roughage-treatments, mentioned above, were applied to one breed only or if one treatment were applied to each breed. In such a case, even if interaction does exist between these breeds and environments, one could not measure it. Obviously, such an experiment is of limited value and does little more than indicate the necessity to re-run the whole experiment using orthogonal conditions.
REVIEW OF LITERATURE

Theoretical Considerations

In the introduction to a series of articles on "The inheritance of egg production in the domestic fowl", Munro (1936) stated that;

(1) Phenotypes are not solely the expression of genetic potentiality but result from a gene-environment interaction.
(2) Environmental differences affecting a whole population, as a rule, modify only the absolute expression of given characters, i.e., overlapping or reversal of phenotypes is not the rule.
(3) When, however, the same genotypes occur under different environments, the situation outlined under (2) may cause phenotypic variability between populations.
(4) Different phenotypes may be obscured under certain uniform environments.
(5) When different genotypes occur under different environments the situations outlined under (2), (3) and (4) make phenotypic expressions of certain traits almost completely unreliable as indicators of relative genetic potentialities. In fact, it is quite possible to witness a reversal of phenotypes a second season, even when the environment is common to the same genotypes within each season.

As Lerner (1950) pointed out in discussing the foregoing, Munro (1936) used gene-environment interaction in a different sense from that in which subsequent workers use it. From the context of his discussions, Munro (1936) seems to regard the actual phenotype of the individual as the expression of interaction between the genotype and the environment to which it
is exposed.

This can be termed "interaction in the biological sense" to avoid confusion with non-additivity of genetic and environmental effects which is the more general definition of what is meant when one speaks of genetic-environmental interaction.

Haldane (1946) discussed in detail the nature of interaction and gave numerous examples to illustrate his discussion. He considered two genetically different populations, A and B, which may be pure lines, clones, inbred lines, etc., and two different environments, X and Y. He illustrated four different types of genotype-environment interaction between these two environments and genotypes. McBride (1958) illustrated Haldane's examples in a graphical manner which may be more meaningful to some people. He also went to the extent of classifying environmental differences between individuals into two types, micro- and macro-environments, and also considered intra- and inter-population genotypic differences separately.

Comstock and Moll (1963) discussed micro- and macro-environments in relation to plants,

....the potential number of different single plant environments [in a restricted location and period of time] is infinite (even within a very restricted area) and the probability that two plants in the same field at the same time have had precisely the same environment is infinitesimal. It is this unique complex of forces in development that we call the micro-environment (of a single plant
organism). We visualize on the other hand that organisms encounter a different class of environment in one area than in another, in one period of time than in another. The environments that are potential or realised within a given area and period of time are referred to collectively as macro-environment.

This method of classifying the environments was a step in the right direction. However, it seems to be a rather vague procedure of classification and does not appear to be guided by any rigid statistical or economic considerations.

Falconer (1952), in a classic paper, approached the problem of genetic-environmental interaction, and its effect on the selection of breeding-stock, from an entirely new direction. He examined the importance of the interaction component, not by considering its absolute value per se, but by considering its effect on the estimated genetic product-moment correlation, $r_G$, between the same genetic material exposed to two different environments. He reasoned that, if there is no genetic-environmental interaction, the same genetic basis exists for the expression of the phenotypes in both environments. Therefore, in the absence of genetic-environmental interaction, the genetic product-moment correlation between these expressions should equal unity.

Robertson (1959) extended this approach further when he discussed the distribution of the genetic correlation-
coefficient and some of the problems involved in testing the significance of its deviation from unity. However, he explained that the computation of the standard error of the genetic product-moment correlation and statements concerning the possible amount of error involved in estimating the true correlation are based on conditions which are not always present. Firstly, the heritability of this trait should be essentially the same in both environments. This may not be true, especially when interaction is real. Secondly, the genetic correlation is not normally distributed when the true value is close to unity and error is likely to be introduced in transformation procedures.

The intra-class correlation, $r_I$, is used frequently in place of the product-moment correlation. Both can be used to measure the degree to which the response-slopes in the two environments tend to vary with one another. These correlations are not equal, however, unless certain assumptions are true. This point is emphasized in a discussion on the relationship between the true values of $r_G$ and $r_I$ in Appendix III.

Small-Animal Experiments

Many research-workers in the "small-animal" field have allowed for the possible existence of genotype-environmental
interaction in designing and analyzing their experiments. Generally, characters in small animals (e.g., egg-production in poultry) are of little direct interest, per se, to dairy cattle breeders. However, the general results are interesting and it is considered worthwhile to review some of them briefly here.

Gutteridge and O'Neil (1942) reported evidence of a highly significant interaction (P<.01) between genotype and location in poultry for maximum body-weight but no interaction for production, egg-weight, days to first egg or body-weight at first egg.

Gowe and Wakeley (1954) reported little evidence of strain X location interaction with respect to hen-housed egg-production or survivor egg-production from four different strains tested at five locations in Canada. However, Gowe (1956) observed a highly significant interaction between strain and environment (floor vs. battery) with respect to survivor egg-production and March body-weight.

Nordskog and Kempthorne (1960) studied the results from the Iowa Multiple Unit Poultry Test carried out in 1957-1958. Results indicated that strain-farm interactions are important (P<.01) in such traits as age at sexual maturity (9%), rate of egg-production (9%), mortality (31%) and egg-weight (10%).
(The values in parentheses are the fractions of the total variance among pen means due to such interactions.)

The nature of the interactions was discussed. The farm test units had been operated under two general types of management, floor-pens and cages. This "managemental" difference was then incorporated into the model and each farm-effect separated into (a) managemental effect and (b) farm-effect within type of management. In the same way the interaction-effect was separable into two parts—strain x management and strain x farm within management. Analysis of the data with regard to these two sources of interaction showed that only in the case of egg-production was there statistical significance between strains and types of management (floor-pens vs. cages). On the other hand, interaction between strains and farms within "management" was highly significant statistically.

Young (1953) from an experiment conducted on mice, reported that the three strains used responded differently to dietary environmental influences but the interaction component remained insignificantly small until extreme dietary stress was administered. These results appear to support the argument that interaction always exists but is not demonstrated until
different genetic materials are compared in more than one environment. In fact, it (interaction) can be demonstrated more clearly when the environments are chosen in such a way that the different genetic materials are specifically adapted to them. The question, which generally requires to be answered, is not, "Does interaction exist?", but rather, "Does interaction exist under the ranges of genetic and environmental conditions in which we are particularly interested at the present moment?"

In another experiment on mice, Falconer and Latyszewski (1952) selected for six-week body weight, under two different environments, high and low planes of nutrition. In that experiment, it appeared that, in fact, they were selecting for two genetically different "characters"; (1) ability to produce fat and (2) ability to produce muscle, bone and other body tissues. Falconer (1952) used this experiment in discussing the practical implications of the genetic correlation as a measure of the importance of genetic-environmental interaction. He pointed out that when the genetic-environmental interaction is important the genetic basis for the phenotypic expression under one environment differs from the genetic basis for expression under other environments. Consequently,
selection of breeding sires under an environment which differs from that in which the offspring are to live cannot be as efficient as selection under the environment in which they will live, if both heritability and intensity of selection are the same under both environments. This is so because selection is operating on different genes in each case. When selection is carried out in an environment (X) which differs from the environment (Y) in which it is desired to keep the offspring, the genetic response experienced in environment Y due to selection in environment X can be termed "correlated" response as opposed to the "direct" response, i.e. the response obtainable had selection been done under the same environment (Y) in which the offspring were to live.

Lerner (1950) and Falconer (1952 and 1960), showed that the correlated response in Y due to selection in X, may be written as:

\[ i_Y h_Y r_G \sigma_{GY}, \]

and the direct response in Y, due to selection in Y, as:

\[ i_X h_X \sigma_{XY}, \]

where \( i_Y = \frac{\bar{Y}_S - \bar{Y}}{\sigma_{PY}} \) and \( i_X = \frac{\bar{X}_S - \bar{X}}{\sigma_{PX}} \),

\( \bar{Y}_S = \) mean of the selected individuals in environment Y,
\( \bar{Y}_S - \bar{Y} = \) selection differential in environment Y,
\( \bar{X}_S = \) mean of the selected individuals in environment X,
\[ X_S - X = \text{selection differential in environment X}, \]

\[ \sigma_{PX}, \sigma_{PY} \text{ are phenotypic standard deviations in X and Y respectively,} \]

\[ \sigma_{GX}, \sigma_{GY} \text{ are genetic standard deviations in X and Y respectively, and} \]

\[ h_Y = \frac{\sigma_{GY}}{\sigma_{PY}}, \quad h_X = \frac{\sigma_{GX}}{\sigma_{PX}}. \]

Then the relative merit of indirect selection to direct selection may be expressed as the ratio:

\[
\frac{\text{Correlated response}}{\text{Direct response}} = \frac{i_X h_X r_G \sigma_{GY}}{i_Y h_Y \sigma_{GY}} = r_G \frac{i_X h_X}{i_Y h_Y}
\]

For a particular value of \( h_Y, \sigma_{GX} \) and \( i_Y \), which can be considered fixed for any one selection program, the response in Y due to selection in X depends on \( r_G \), the genetic correlation between the phenotypic expressions in environments X and Y.

Thus, in general, one should not select under a correlated environment unless \( r_G \) is close to unity, or unless \( r_G h_X > h_Y \) if \( h_X > h_Y \). Many instances occur in dairy cattle where there is no alternative but to select in environments which differ from the one in which the offspring are to live. The most obvious are the cases in which the future environment is not entirely
predictable; a good example of this is where the environment varies with time, e.g. seasons or managemental systems.

Often selection is done under a different environment even though the future environment is predictable. One example is the selection of bulls based on the production of their daughters or other female relatives in herds with a high level of feeding and management and the use of these bulls under other levels of feeding and management. A more extreme case of selection under a different environment is where breeding stock is brought from one climatic situation to another, as, for example, from one country to another.

Bull X Herd and Bull X Herd-Year-Season Effects

There is little direct evidence pertaining to the importance of genetic-environmental interaction in milk production in dairy cattle. This results from the absence of controlled experiments specifically designed to investigate these interactions. This, in turn, results from the difficulty and expense in setting up such experiments. Much of the available information comes from (a) survey analyses, (b) observations made in the course of investigating other factors or (c) indirect reasoning from unequal heritability estimates in two
environments and from unexpectedly low genetic correlation estimates between performances of related genetic material exposed to different environments.

D.H.I.A. milk-production records (305-day, 2X, M.E.) from New York State were analyzed by Hickman and Henderson (1955), who used a within-year, sire-herd classification to provide estimates of sire, herd, sire X herd, and residual variances for milk-production (first lactation), fat production, age, etc. The component of variance for herd X sire-interaction in milk-production was so large (13.2% of the total variation) that more detailed investigation was considered necessary. The data were then analyzed in a three-factorial classification (herds, sires and year-seasons). In analyzing in this way, the sire X herd-component was reduced to 1.7% of the total variance while a herd X year-season component of 14.3% was obtained.

Mason and Robertson (1956) collected milk-production records of daughters of Red Danish A.I. bulls in Denmark with a view to studying the value of Danish bull-testing stations in the improvement of milk-production in commercial herds. At each A.I. center, the herd-years were divided into three roughly-equal groups in order of average yield. Then the sums of squares and d.f., within stations, for sires, herds, sire X
herd-interaction and residual were pooled over stations within levels of production to provide weighted estimates of the components of variance for those effects. For high, medium and low levels respectively, milk production having been coded in tens of kg, the components of variance for sire effects were 73.2, 196.5, and 412.9; the components of variance for sire X herd interaction effects were -461.8, 54.6, and -333.6. The authors argue that these results are due in a large part to the non-orthogonality of the data and that there is no real evidence in the data to indicate that the true component for sire X herd-interaction is any different from zero.

Legates, Verlinden and Kendrick (1956) studied 305-day, 2X, M.E. records produced in the period 1946-1950 by the daughters of dairy sires from three different breeds (Guernsey, Holstein and Jersey) used in A. I. throughout the United States. Values for the components of variance of herd, sire, herd X sire and residual effects were obtained for each of the three breeds in milk, test and fat. The variance-components for sire X herd interaction show much change of sign from one trait to another within a particular breed and from one breed to another within a particular trait. This is interpreted by those authors as what "might be anticipated from fluctuation
about a population value of near zero".

Wadell and McGilliard (1959), in a study on milk and fat records from Michigan dairy herds, obtained large negative values for the estimates of the components of variance for bull X herd interaction effects (within breed) and concluded that there was no herd-sire interaction present.

On the other hand, Specht and McGilliard (1960) analyzing somewhat similar material from Michigan, but involving only one breed (Holstein), report that "7% of the total variation was found to be interaction between herds and sires".

Touchberry, Rottensten and Andersen (1960) studied first-lactation milk and butterfat records of daughters of 305 Red Danish Milkrace sires tested at the Danish bull-testing stations and of daughters of 110 of these same sires tested in farmer herds. The estimates of heritability based on sire-components for milk and butterfat respectively were, (1) .66 (calculated by Robertson and Mason (1956)) and .61 within stations and year, (2) .29 and .27 among the field data when herd differences were removed and (3) .23 and .22 when the records were expressed as deviations from the contemporary herd averages. These large differences in heritability-estimates between station-data and field-data resulted principally from a greatly "inflated" sire-component in the
test-station data. If genetic-environmental interaction were equal to zero, one would expect that the sire-components should be the same under all environments. Consequently, the estimates of heritabilities for milk (and for butterfat) should be the same (apart from variation due to errors of measurement) in (1), (2), and (3). The estimates of the genetic correlations between the station-tests and field-tests were .68 for milk and .75 for butterfat. These results suggest either that there is a large interaction between sires and the levels of management of test-stations as opposed to farmer-herds or that the components of variance for sire-effects from test-station data are inflated with environmental factors.

The latter cause seemed more logical to these authors because (a) the data indicated that sire x herd-interaction was small and (b) there was some evidence that the environments within the stations were correlated with the genetic merits of the sires. The authors believe that competition among the test-stations, which resulted in high groups being "pushed" more than lower groups at a particular station, could have caused the correlation mentioned in (b).
Monozygous Twin Experiments

In twin-analyses, it is the whole genotype of the individuals rather than one-half of a bull's genes which is the genetic material exposed to two or more environments. Therefore, it is more appropriate to speak of genotype-environmental interaction in twin-analyses rather than genetic-environmental interaction which is more descriptive when half-sibs (or full sibs) are exposed to different environments.

Bonnier, Hansson and Skjervold (1948) used 14 pairs of monozygous twins to study the influence of environment on growth and lactation characteristics in dairy cattle. The ancestry of most of the animals was not known so it is difficult to determine how variable they were genetically. (Judging from type, it was assumed that they were of the Swedish Red and White Breed). The pairs were split into low and high levels of feeding (Bonnier and Hansson, 1946). In studying the interaction of heredity and environment within lactation, it was found that the interaction between genotype and environment was marked through all lactations but diminished progressively from the first to the second to the third lactation.
Ramsay* (1963), working with monozygous Holstein twins, studied the effects of two levels of feeding on 1st, 2nd, and 3rd lactation milk production (adjusted to 305-day, 2x, ME). Within each pair, one member was fed a ration of high grain-content while the other was fed a ration of low grain-content. In order to estimate the component for pair x ration-interaction, the "error"-variance was estimated from a simultaneous experiment in which both members of each pair were kept on the same ration (high or low).

The following results were obtained for the components of variance due to rations, pairs, pairs x rations and error-variance in this experiment.

Components of variance (in lb.²)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>1st lactation (15 pairs)</th>
<th>2nd lactation (11 pairs)</th>
<th>3rd lactation (5 pairs)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rations</td>
<td>965,405</td>
<td>485,444</td>
<td>-78,320</td>
</tr>
<tr>
<td>Pairs</td>
<td>5,907,583</td>
<td>4,667,532</td>
<td>3,616,999</td>
</tr>
<tr>
<td>Rations X pairs</td>
<td>770,739</td>
<td>-2,747,646</td>
<td>1,856,248</td>
</tr>
<tr>
<td>Error</td>
<td>1,223,689</td>
<td>5,065,866</td>
<td>1,400,753</td>
</tr>
</tbody>
</table>

The estimates of the components for each source of variation vary from one lactation to another. Ramsay believed that it would be desirable to have at least three times as many

---

pairs of twins before a reliable statement could be made con-
cerning the importance of interaction between rations and
pairs.

Discussion

The review of literature shows that estimates of the
components of variance due to interaction of bull x herd and
bull x herd-year-season, which have been obtained from analyses
of experiments and survey-data, varied considerably from one
situation to another. In essentially all cases it was con-
cluded that the true parameters, of which these components
were estimates, were probably equal to zero. Although the
true value may not have been actually equal to zero, we agree
that it may be of minor importance because, in most cases, the
analyses were carried out within a limited range of environ-
ments and genotypes.

Usually, more confident statements are expected as a
result of analyses of variance than one generally witnesses
from the analysis of non-orthogonal data. One can guess in
most cases, before any analysis is carried out, that the
component of variance due to interaction between bull and herd-
year season is probably small. Therefore, it is not an
exaggeration to state that the results of analyses of non-
orthogonal data quoted in the Review of Literature do not increase one's knowledge of the true parameter very much compared with what one should be able to guess from one's general knowledge of the data.

Not only are the estimates obtained from the analysis of variance in non-orthogonal data likely to be biased, but confidence-intervals, which denote the possible degree of error in a particular estimate, cannot be calculated from this type of analysis. How much faith can one put in a particular estimate or how does one compare the estimate of a parameter obtained from one analysis with estimates obtained from other analyses, if no confidence-intervals are given? The author considers it important to investigate a procedure which will circumvent the non-orthogonality of the data and enable one to make a more valid statement concerning the possible amount of error involved in the estimates obtained.
INVESTIGATION

Material

The data used in the investigation were obtained from D.H.I.A. milk-production records of dairy cattle which are stored and kept at Iowa State University and made available for research through the courtesy of the Dairy Extension Service. These records were in turn obtained from production information which is being sent routinely each month under the D.H.I.A. milk-recording program for processing at the Central Processing Service at that university. The geographical area from which the records were drawn includes nine midwestern states in the U.S.—Minnesota, Iowa, Missouri, Arkansas, North Dakota, South Dakota, Nebraska, Kansas and Oklahoma (see Fig. 1). This information is constantly accumulating and provides material for a wide variety of investigations on dairy cattle production.

Only records which were more than 90 days in length, and which were produced by Holstein-Friesian cows which were daughters of registered bulls, were used. This latter restriction was applied, firstly, to avoid complicating the results with breed differences and, secondly, because the investigation had as its primary consideration the importance
of bull X herd-year-season interaction component in sire-ranking programs. Since each sire-ranking program in a particular A.I. stud generally involves a limited range of genotypes, (e.g. registered bulls of a particular breed), it is considered reasonable to limit the analysis to a similar range of genotypes.

Similarly, in the case of environments, since the daughters of A.I. bulls are expected to produce milk over a range of herd-year-seasons similar to those from which the available data were collected, it was considered desirable not to alter the ranges of these herd-year-seasons in the analysis of the data. In this way inference may be made to bull-testing situations. A total of 37,701 milk-production records, adjusted to 305-day, 2X, M.E. (Kendrick, 1955), were available for the study. As they were made over a three-year period from 1958 to 1961, they were classified into six different year-seasons (see Table 1)—the year-season to which a particular record belonged was the year-season in which it was begun. The definition of year-seasons was based on investigations by Bereskin and Freeman (1961) and Bereskin, Freeman and Lush (1962) on similar material.
Table 1. Definition of the six year-seasons used, plus the number of records in each

<table>
<thead>
<tr>
<th>Year-season</th>
<th>Months (inclusive)</th>
<th>Number of records</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>May 1958 - Sept 1958</td>
<td>337</td>
</tr>
<tr>
<td>2</td>
<td>Oct 1958 - Apr 1959</td>
<td>5,755</td>
</tr>
<tr>
<td>3</td>
<td>May 1958 - Sept 1959</td>
<td>5,815</td>
</tr>
<tr>
<td>4</td>
<td>Oct 1959 - Apr 1960</td>
<td>12,787</td>
</tr>
<tr>
<td>5</td>
<td>May 1960 - Oct 1960</td>
<td>10,856</td>
</tr>
<tr>
<td>6</td>
<td>Oct 1960 - Apr 1961</td>
<td>2,151</td>
</tr>
</tbody>
</table>

Histographical distribution of the data with respect to year-seasons is shown in Fig. 2. Only 337 records were classified into year-season 1. This was because the Central Processing of dairy-production records was organized only recently in the midwest U.S. and, though expanding, the number of cows on Central Processing before October, 1958 was still small.

There are relatively few records in year-season 6. Many records which will ultimately be in year-season 6 were not yet available when
this study was begun.

The bull X herd-year-season interaction component is the prime object of study. The difficulty of deriving valid tests of significance for this component may be appreciated by a more detailed description of the data. The histogram in Fig. 3 shows the frequencies of the herds which have daughters of 1, 2, 3, 4, ..., bulls over the three-year period. Many of the herds from which these records came were using natural service. This partly explains the relatively large number of one-bull herds.

Fig. 4 depicts the frequencies of the bulls which have daughters in 1, 2, 3, 4, etc. herds. There were 2,909 bulls who had daughters in just one herd (i.e., there were 2,909 single-herd bulls). The majority of these are bulls which are used in natural service while others were used in outside areas and their daughters were imported to herds in this area.

A brief summary of the description of the total data used in the study can be presented in tabular form, as follows:

<table>
<thead>
<tr>
<th>Description</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of records</td>
<td>37,701</td>
</tr>
<tr>
<td>Number of bulls</td>
<td>3,836</td>
</tr>
<tr>
<td>Number of herds</td>
<td>1,383</td>
</tr>
<tr>
<td>Number of year-seasons</td>
<td>6</td>
</tr>
<tr>
<td>Number of herd-year-seasons</td>
<td>4,694</td>
</tr>
</tbody>
</table>
Fig. 1. Histogram, showing the number of records obtained from different states.
Fig. 2. Histogram, showing the numbers of records in year-seasons 1, 2, 3, 4, 5, and 6.
Fig. 3. Histogram, showing the numbers of the herds each of which has daughters of \( i \) (\( i = 1, 2, \ldots, 28 \)) bulls.
Fig. 4. Histogram, showing the number of bulls which have daughters in $i$ ($i = 1, 2, \ldots, 28$) herds
Model

The linear model which describes a cow's production (305-day, 2X, M.E. milk) is written as

$$X_{ijk} = \mu + b_i + h_{sj} + (bhs)_{ij} + e_{ijk}.$$ 

$X_{ijk}$ is the production of the $k^{th}$ daughter of the $i^{th}$ bull in the $j^{th}$ herd-year-season.

$\mu$ is the true population mean.

$b_i$ is the effect of the $i^{th}$ bull.

$h_{sj}$ is the effect of the $j^{th}$ herd-year-season.

$(bhs)_{ij}$ is the effect of the interaction between the $i^{th}$ bull and the $j^{th}$ herd-year-season.

$e_{ijk}$ is the random error affecting the record of the $k^{th}$ daughter of the $i^{th}$ bull in the $j^{th}$ herd-year-season.

$b_i$: The effect of the $i^{th}$ bull, $b_i$, believed to be entirely genetic in nature, is the total of all influences which make the progeny of the $i^{th}$ bull different from the mean of all progeny-groups. This is mainly due to additive effects of genes but it also includes some effects of non-allelic gene interaction (see page 11).

$h_{sj}$: The effect of the $j^{th}$ herd-year-season, $h_{sj}$, is the sum of all the effects, genetic and environmental, which make the $j^{th}$ herd-year-season different from the mean of all other
herd-year-seasons. Herd-year-season-effect is a "mixture" of a herd-effect, a year-season-effect and the interaction between the herd and year-season. Genetic differences among herd-year-seasons include (a) genetic differences among herds due to selection, random drift, etc., and (b) genetic differences among animals which freshen in different year-seasons in the same herd. Environmental differences among herd-year-season-effects include effects due to climatic, nutritional, pathological, and managemental causes, plus some interaction between climate and disease-factors, climate and nutrition, nutrition and disease-factors, etc.

Two different herd-year-season-effects are correlated if they have a herd-effect or a year-season-effect in common. (This situation exists when one is dealing with data from two year-seasons within the same herd or from two herds within the same year-season). To circumvent the effect of correlation due to herd-effects as much as possible, data from only one randomly-selected year-season were used from each herd in each group. [As will be explained later, in Analysis I, the data were divided into 129 groups (with some data in all bull-herd-year-season-subclasses) for analysis]. Much of the remaining data were from different herds within the same year-season. However, to make all herd-year-season-effects independent
within each group would require selecting only one herd from each year-season. This would mean discarding approximately 80% of the remaining data. This was not done because the loss of information through discarding these data seemed unlikely to be justified by an increase in accuracy of variance-component-estimates after removing the relatively minor correlation caused by particular year-season-effects. That the year-season-effect is a minor source of variation is supported by observations by other workers who reported the percentages of total variance in milk and fat caused by year-season components of variance (see Table 2). It should be noted that the data used by Krehbiel and Brown (1962) included much of the data used in this analysis.

\[(bhs)_{ij}\]: This is the effect of a real physiological advantage or disadvantage which is specific to the daughters of the \(i\)th bull in the \(j\)th herd-year-season. (A more general statistical discussion on the nature of interaction is presented earlier, beginning on page 4). \((bhs)_{ij}\) is the result of (a) interaction between this bull \((i)\) and the factors responsible for the environmental portion of the herd-year-season-effect, (b) interaction between the bull and the factors responsible for the genetic portion of the herd-year-season-effect and (c) "three-way" interaction between the bull, the genetic and the environmental factors responsible for the herd-year-season-effect.
Table 2. Observations made by various research-workers on the importance of year-season-effects

<table>
<thead>
<tr>
<th>Observations made by:</th>
<th>Number of records</th>
<th>Percent of total variance attributable to year-season-effect</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Milk</td>
</tr>
<tr>
<td>Barr (1962)</td>
<td>43,498</td>
<td>0.3%</td>
</tr>
<tr>
<td>Bereskin and Freeman (1961)</td>
<td>24,259</td>
<td>1.7% - 2.4%</td>
</tr>
<tr>
<td>Lee, Fosgate and Carmon (1961)</td>
<td>2,364</td>
<td>3.5%</td>
</tr>
<tr>
<td>Plum (1935)</td>
<td>2,316</td>
<td>3.0%</td>
</tr>
<tr>
<td>Sundaresan and Freeman (1961)</td>
<td>12,623</td>
<td></td>
</tr>
<tr>
<td>VanVleck, Wadell and Henderson (1961)</td>
<td>39,728</td>
<td>2.7%</td>
</tr>
<tr>
<td></td>
<td>1st lact.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>37,218</td>
<td>2.1%</td>
</tr>
<tr>
<td></td>
<td>2nd lact.</td>
<td></td>
</tr>
</tbody>
</table>
The effect of interaction between the bull and the factors responsible for the environmental portion of the herd-year-season-effect is believed to be truly genetic-environmental in nature and to be responsible for the largest portion of \((bhs)_{ij}\). The effect of interaction between the bull and the factors responsible for the genetic portion of the herd-year-season-effect, discussed in (b), is due to (i) dominance-effect (interaction between allelic genes in the gametes of the bull and the gametes of the cows with which it is mated) and (ii) interaction between genes which are not allelic in the gametes of the bull and its mates.

\(e_{ijk}\): The effect of \(e_{ijk}\) includes all those factors which can cause the record produced by the \(k^{th}\) daughter of the \(i^{th}\) bull in the \(j^{th}\) herd-year-season to deviate from \(\mu + b_i + hs_j + (bhs)_{ij}\). It includes temporary and permanent environmental effects affecting this particular record and/or all records during this cow's lifetime. It also includes genetic effects which are due to differences in genetic merit of the dams of the daughters of this \(i^{th}\) bull in the \(j^{th}\) herd-year-season and to Mendelian segregation in formation of the gametes from both the sire and the dam.

The \(b_i\), \(hs_j\), \((bhs)_{ij}\) and \(e_{ijk}\) are assumed to have zero
means and to be independently distributed;

\[ E[\mathbf{b}_i \mathbf{b}_i'] = E[\mathbf{h}_{ij} \mathbf{h}_{ij}'] = E[(\mathbf{bhs})_{ij} (\mathbf{bhs})_{ij}'] = \]

\[ E[\mathbf{e}_{ijk} \mathbf{e}_{ijk}'] = E[\mathbf{b}_i \mathbf{h}_{ij}] = E[\mathbf{b}_i (\mathbf{bhs})_{ij}] = E[\mathbf{b}_i \mathbf{e}_{ijk}] = \]

\[ E[\mathbf{h}_{ij} (\mathbf{bhs})_{ij}] = E[\mathbf{h}_{ij} \mathbf{e}_{ijk}] = E[(\mathbf{bhs})_{ij} \mathbf{e}_{ijk}] = 0. \]

They are defined to have variances \( \sigma_b^2, \sigma_{hs}^2, \sigma_{bhs}^2 \) and \( \sigma_e^2 \) respectively. The validity of the statistical inferences made from the investigation which follows are conditional upon the accuracy of the model in describing the factors affecting production and upon the accuracy of the assumptions made concerning the distributions of these factors. Any inaccuracy present in the assumptions is believed to be of only minor importance. However, it is nearly always there to some extent. For example, the \( \mathbf{e}_{ijk} \) are almost never completely homogeneous in their variances. If this were to occur, the theoretical assumption that one would find exactly \( \sigma_e^2 \) in all mean-squares would not be fulfilled and the tests of significance which one makes would not be completely exact.

It must be emphasized that the assumption that bulls and herd-year-seasons are uncorrelated is not meant to apply to the data as they are collected "in the field". An assumption of that nature would be difficult to defend because of the disproportionality of bull-herd-year-season-subclass numbers.
The assumption that bulls are uncorrelated with herd-year-seasons applies to the conceptual population from which we believe the sample we are studying has been randomly drawn. It also applies to the data used in the computations in Analysis I. It is precisely because we wish to ensure that this assumption holds in the computations that we go to the trouble of "arranging" completely balanced situations among bulls and herd-year-seasons in Analysis I.

Analysis of Data with Unequal Subclass-Frequencies

It bears repeating that the importance of interaction between bulls and herd-year-seasons, rather than the main effects themselves, is the object of study in this investigation. It also bears repeating that the first phase of the investigation involves

(a) obtaining the best possible estimate of the interaction component, \( \sigma_{bhs}^2 \),
(b) carrying out a valid F-test on the hypothesis that \( \sigma_{bhs}^2 = 0 \),
(c) placing 95% confidence limits on \( \sigma_{bhs}^2 \).

The method of analysis used was decided upon because (i) it satisfied these three requirements and (ii) it was, at the same
time, capable of application to the volume of data available for investigation.

An alternative method which would satisfy (a), (b) and (c) above is to calculate the sum of squares due to interaction as \( R(\mu, b, hs, (bhs)) - R(\mu, b, hs) \). \( R(\mu, b, hs, (bhs)) \) is the reduction in the sum of squares due to fitting \( \mu, b_i, hs_j, (bhs)_{ij} \).

\[
R(\mu, b, hs, (bhs)) = \sum_{ij} \frac{X_{ij}^2}{N_{ij}}
\]

\( X_{ij} \) is the sum of the observations in the \( j \)th herd-year-season for the \( i \)th bull. \( N_{ij} \) is the number of those observations in \( X_{ij} \). \( R(\mu, b, hs) \) is the reduction in the sum of squares due to fitting \( \mu, b_i \) and \( hs_j \) under the null hypothesis that \( (bhs)_{ij} = 0 \) and under the assumptions listed on pages 51-53.

\[
R(\mu, b, hs) = i \hat{\mu} X_i^2 + \sum_{i} b_i \hat{X}_i^2 + \sum_{j} hs_j \hat{X}_j^2.
\]

However, it is not possible to evaluate \( R(\mu, b, hs) \) because of the amount of computing-time necessary and the expense involved in evaluating the \( \hat{b}_i \)s and \( \hat{hs}_j \)s. Calculation of these effects necessitates setting up \( 1 + \sum_{i} (1) + \sum_{j} (1) \) normal equations. These equations may be solved (a) simultaneously in a single operation or (b) by first absorbing the \( (\hat{\mu} + \hat{b}_i) \)-equations into the \( \hat{hs}_j \)-equations, solving for the \( \hat{hs}_j \), and
then substituting these $\hat{h}_{sj}$-values back into the original equations and solving for $\hat{u}$ and the $\hat{b}_i$'s, or vice versa (Kempthorne, 1952).

A matrix of this magnitude cannot be solved by an I.B.M. 650 at a single machine-loading because of the limited storage capacity. Even on a machine equipped with auxiliary tape-storage and which is also considerably faster (e.g. I.B.M. 7074), the time-element becomes the limiting factor. The computing-time necessary for an operation of this magnitude is of the order of 5,000 hours on an I.B.M. 7074.

The method of analysis which was used was based on the "standard" form of Analysis of Variance in which the total variance is partitioned into four parts with respect to bulls, herd-year-seasons, bull X herd-year-season-interaction and remainder or error (see Fig. 5).

This method of analysis had to be modified in a manner which will be described in the following paragraphs to provide completely balanced conditions between bulls and herd-year-seasons.


### Sums of Squares

<table>
<thead>
<tr>
<th>Source</th>
<th>Algebraic Notation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulls</td>
<td>$\sum_{i} (X_{i} \ldots - \bar{X} \ldots)^2$</td>
</tr>
<tr>
<td>Herd-Year-Seasons</td>
<td>$\sum_{j} (\bar{X}_{.j} \ldots - \bar{X} \ldots)^2$</td>
</tr>
<tr>
<td>Interaction</td>
<td>$\sum_{ij} (\bar{X}<em>{ij} \ldots - \bar{X}</em>{i} \ldots - \bar{X}_{.j} \ldots + \bar{X} \ldots)^2$</td>
</tr>
</tbody>
</table>

**Fig. 5.** Algebraic notation for the expected values of seasons and interaction, in unbalanced data
Expected values of the sums of squares

\[
\begin{align*}
\sigma_e^2 &+ \left[ \sum_{i,j} N_{ij}^2 - \sum_{i} N_{i}. \sum_{j} N_{.j} \right] \sigma_{bhs}^2 + \\
&\quad \left[ \sum_{i,j} \frac{N_{ij}^2}{N_{i}.} - \sum_{j} \frac{N_{.j}^2}{N_{.j}} \right] \sigma_{hs}^2 + \\
&\quad \left[ \frac{N_{..} - \sum_{j} \frac{N_{.j}^2}{N_{.j}}}{N_{..}} \right] \sigma_{b}^2
\end{align*}
\]

\[
\begin{align*}
\sigma_e^2 &+ \left[ \sum_{j} \frac{N_{ij}^2}{N_{ij}} - \sum_{i} \frac{N_{ij}^2}{N_{ij}} \right] \sigma_{bhs}^2 + \\
&\quad \left[ \sum_{j} \frac{N_{ij}^2}{N_{..}} - \sum_{i} \frac{N_{ij}^2}{N_{ij}} \right] \sigma_{hs}^2 + \\
&\quad \left[ \frac{N_{..} - \sum_{j} \frac{N_{.j}^2}{N_{.j}}}{N_{..}} \right] \sigma_{b}^2
\end{align*}
\]

\[
\begin{align*}
\sum_{i,j} N_{ij}^2 - \sum_{i} \frac{N_{i}. \sum_{j} N_{ij}}{N_{i}.} \sigma_{bhs}^2 + \\
&\quad \sum_{i} \frac{N_{i}. \sum_{j} N_{ij}}{N_{i}.} \sigma_{hs}^2 + \\
&\quad \sum_{i} \frac{N_{i.} \sum_{j} N_{ij}}{N_{i.}} \sigma_{b}^2
\end{align*}
\]

Sums of the sums of squares due to bulls, herd-year-data
In this "standard" form of the analysis of variance, non-orthogonality, involving missing subclasses and disproportionality of subclass numbers, prevents one from obtaining the sum of squares due to interaction-effects free or "clean" from the influence of the main-effects. For example, from Fig. 5, the expected value of the sum of squares due to the interaction of bulls X herd-year-seasons is:

\[
\begin{align*}
\sigma^2_e & + \left[ N - \sum_{i} \frac{\sum_{j} N_{ij}^2}{N_i} - \sum_{j} \frac{\sum_{i} N_{ij}^2}{N_j} + \sum_{i} \frac{N_{ij}^2}{N} \right] \sigma^2_{bhs} \\
+ \left[ \frac{\sum_{j} N_{.j}^2}{N} - \sum_{i} \frac{\sum_{j} N_{ij}^2}{N_i} \right] \sigma^2_{hs} & + \left[ \frac{\sum_{i} N_{i.}^2}{N} - \sum_{j} \frac{\sum_{i} N_{ij}^2}{N_j} \right] \sigma^2_b
\end{align*}
\]

If the coefficients of \(\sigma^2_b\) and \(\sigma^2_{hs}\), respectively, are not zero, tests of significance of the interaction component, \(\sigma^2_{bhs}\), are not expected to be "exact". (The values of these coefficients are equal to zero only when the subclass frequencies are equal or proportional.) Thus, when we speak of "exactness" of test here we mean that the mean-square, which is being tested, is
"expected", after the assumptions in the Null Hypothesis have been made (in addition to those listed on page 52), to be equal to the mean-square which is used as the error-term. (It is assumed that the model, which is used, correctly describes the factors affecting production.)

To circumvent the difficulty of confounding caused by non-orthogonality, it was decided to search through the data for groups of observations in which all bull-herd-year-season-subclasses were filled. If these could be found, and if the numbers of observations per subclass made equal by a procedure of random-selection, the validity of tests of significance would be satisfied and a more reliable statement could be made concerning the importance of bull x herd-year-season-interaction.

At the beginning of the investigation it was hoped that large groups could be obtained involving many bulls and herd-year-seasons. However, the distribution of the data, with so few subclasses filled (less than 1%), discouraged searching for these groups.
Finding Sections of Data in Which all
Bull-Herd-Year-Season Subclasses are Filled

If there were a limited number of data (say, less than 1,000) and if a large percentage of the subclasses were filled, one could pick out these groups using pencil and paper or some other "visual aid". Since the data at hand involved 37,701 records from the daughters of 3,836 bulls in 1,383 herds and six year-seasons, attempts to obtain these groups by pencil and paper are tedious, time-consuming and discouraging. In data of this nature with a very large volume of material but only a minute fraction of the subclasses "filled", the only really practical approach would seem to be in the use of electronic machine facilities (when available). The simplest type of filled-subclass-groups are those in which two bulls have data simultaneously in a number of herd-year-seasons.

A program was written for the I.B.M. 650 so that it would check through the data and list out those situations in which two bulls were represented simultaneously in more than one herd-year-season. This procedure proved inadequate mainly because only a fraction of the data could be scanned at any one machine-loading due to its limited storage-capacity (4,000 ten-digit locations). Scanning the data in sections
is undesirable because, strictly speaking, all possible pair-
combinations of the bulls should be taken and all the data
scanned with respect to each pair. This is not possible unless
all the data could be loaded into the storage-memory of the
machine at the same time. (This statement applies less readily
to machines which have auxiliary tape-storage but, even in
these, storage capacity is limited.) Consequently, an alterna-
tive procedure was sought.

On investigation, the I.B.M. 088 collator proved much
more satisfactory than the I.B.M. 650, particularly because its
efficiency was not affected by the volume of data. It had
the advantages also of being much less expensive and did not
require the writing of complex programs. In addition, machine-
operations were performed in a manner which could be checked
easily by the operator whereas computer operations are done
internally and are not checked so easily. Consequently,
except in cases where the scanning operation is done routinely
on a large scale, the I.B.M. 088 collator, in the author's
opinion, is much more satisfactory than a computer. A more
detailed account of the operational aspects of this scanning
is presented in Appendix II.

There were 129 groups of data involving 2,784 records
obtained in this way. Each group was a 2-bull X n-herd-year-
season cross-classification with all $2n$ subclasses filled. $n$ (the number of herd-year-seasons per group) varied from one group to another. The average value of $n$ for the 129 groups was 7.2. A graphical presentation of these groups is given in Fig. 6. The relatively small average value of $n$, 7.2, results from the fact that no attempt was made to scan firstly for pairs of bulls that were used in the same period of time or in the same areas. Doing so would provide groups with larger $n$-values but may introduce a bias in estimating genetic variance.

We expect that bulls with high genetic merit have more daughters than bulls with low genetic merit. If the A.I. manager knows that one bull is of lower genetic merit than another, he tends to get rid of that one with lower genetic merit as quickly as possible. On the other hand, bulls of high genetic merit tend to be used for a longer period of time and therefore are expected to have more daughters' records appearing in the data. If the order in which the bulls are compared depends on the frequency in which they were used, the danger exists that bulls of like genetic merit are compared with each other, thus reducing the chances of comparing bulls of unlike genetic merit. To avoid this bias as much as possible, the bulls were
Fig. 6. Tabular presentation of the nature of the groups of data which were taken for analysis from the total distribution of data. (The figure in a particular bull X herd-year-season subclass denotes the number of daughters that that bull has in that herd-year-season.)

paired without consideration of their age, the year-seasons or the areas in which they were used.
Estimation of $\sigma_e^2$

Though risking undue repetition, it may be worthwhile to recall that a total of 37,701 records were originally available for study and that, from these, we selected 2,874 records in order to estimate and place confidence limits on the bull x herd-year-season interaction-component ($\sigma_{bhs}^2$). $\sigma_e^2$ can be estimated from the selected sample of 2,874 records, since many of the bull x herd-year-season subclasses in this selected sample have more than one record. However, we hope that a more precise estimate of $\sigma_e^2$ can be obtained if we include also the estimate of $\sigma_e^2$ calculated from the data "discarded" in "selecting" these 2,874 records. The estimate of $\sigma_e^2$ from the "discarded" data was 45,996.5 with 4,775 degrees of freedom, while the estimate from the "selected" sample was 46,317.5 with 1,020 degrees of freedom. An F-test, made by calculating the ratio of the larger over the smaller estimate, suggests that $\hat{\sigma}_e^2$ in the sample and $\hat{\sigma}_e^2$ in the discarded data do not differ enough (at a probability level of 10%) to convince one that they estimate different parameters. Therefore, both were combined into a weighted average, weighted by the degrees of freedom.

Weighted estimate of $\sigma_e^2$,

$$\hat{\sigma}_e^2 = \frac{(45,996.5) (4,775) + (46,317.5) (1,020)}{4,775 + 1,020} = 46,053$$
Analysis I

It was stated on pages 48 and 49 that records made in two different herd-year-seasons in the same herd are correlated through the herd-effect. To overcome this, it is necessary to use data from only one year-season in each herd. The year-season selected from each herd was that which had most data.

It was also stated (page 57) that, in order to obtain the sum of squares due to the interaction-effects free or "clean" from the influence of the main-effects, the numbers of observations in the subclasses must be equal (or proportional). To obtain this situation in the present analysis, a computer program was written which would randomly select an equal number of observations from each bull-herd-year-season-subclass in each of the 129 groups described in the last section. (This selection procedure is described in Appendix I.) The lowest subclass-frequency of each group pre-determines the number of observations which will be selected from all subclasses in that group; in the sample being analyzed the lowest subclass frequency in all groups is equal to one. The data were analyzed five times; each time, one observation was selected at random from each subclass and the sums of squares due to bulls, herd-year-seasons, and remainder were obtained within each
group. Since it is reasonable to assume that the data in all
groups are drawn from the same population, "pooled" sums of
squares were obtained by summing the sums of squares due to
bulls, herd-year-seasons and remainder over all 129 groups.
Because the data were analyzed five times, five pooled sums
of squares were obtained. These are given in Table 3. The
expectations of these sums of squares, expressed as functions
of the components of variance, are presented in Fig. 7 and
Table 3. These expectations are based on the assumptions and
definitions listed on page 52.

The variances or mean-squares (Table 4) differ somewhat
from one analysis to another; the dissimilarity is due to the
"background" or error variance among the observations within
bull-herd-year-season-subclasses \( \sigma_e^2 \) and to the probability
of obtaining different observations in successive analyses.
This latter is a function of the subclass frequencies. Because
a large number of subclasses had only one observation, one
expects that the five successive mean-squares for each source
of variation in the present data are highly correlated.

Estimation of components of variance

Each of the five pooled mean-squares for bulls, herd-
year-seasons and remainder has the same expectation. Conse-
quently, and conversely, there are five estimates each for the
Table 3. Sums of squares, and their expectations, from Analysis I

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Sums of squares (in 10 lb)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Bulls</td>
<td>9,396,359</td>
</tr>
<tr>
<td>Herd-year-seasons</td>
<td>78,152,875</td>
</tr>
<tr>
<td>Remainder</td>
<td>37,685,210</td>
</tr>
</tbody>
</table>
from five successive analyses of 129 groups of data -

<table>
<thead>
<tr>
<th>10 lb milk$^2$</th>
<th>analyses</th>
<th>Mean value</th>
<th>Expected values of the sums of squares</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>4</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>7,702,701</td>
<td></td>
<td>8,935,467</td>
<td>9,294,101 129\sigma_e^2 + 129\sigma_{bhs}^2 + 926\sigma_b^2</td>
</tr>
<tr>
<td>8,493,306</td>
<td></td>
<td>80,450,549</td>
<td>79,030,650 798\sigma_e^2 + 798\sigma_{bhs}^2 + 1,596\sigma_{hs}^2</td>
</tr>
<tr>
<td>3,205,505</td>
<td></td>
<td>37,633,984</td>
<td>37,962,900 798\sigma_e^2 + 798\sigma_{bhs}^2</td>
</tr>
</tbody>
</table>


<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Sums of squares</th>
<th>Expectations of the sums of squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulls</td>
<td>$\sum_{ri}(\bar{X}<em>{ri..} - \bar{X}</em>{r...})^2$</td>
<td>$\sum(1)[\sigma_e^2 + \sigma_{bhs}^2] + \sum_{r} n_r \sigma_b^2$</td>
</tr>
<tr>
<td>Herd-year-seasons</td>
<td>$\sum_{rj}(\bar{X}<em>{r.j.} - \bar{X}</em>{r...})^2$</td>
<td>$\sum(n_r-1)[\sigma_e^2 + \sigma_{bhs}^2] + 2\sum(n_r-1)\sigma_{hs}^2$</td>
</tr>
<tr>
<td>Remainder</td>
<td>$\sum_{rijk}(X_{rijk} - \bar{X}<em>{ri..} - \bar{X}</em>{r.j.} + \bar{X}_{r...})^2$</td>
<td>$\sum(n_r-1)[\sigma_e^2 + \sigma_{bhs}^2]$</td>
</tr>
</tbody>
</table>

\( \bar{X}_{ri..} = \text{Mean for the } i^{th} \text{ bull in the } r^{th} \text{ group,} \\
\bar{X}_{r.j.} = \text{Mean for the } j^{th} \text{ herd in the } r^{th} \text{ group,} \\
\bar{X}_{r...} = \text{Mean for the } r^{th} \text{ group,} \\
\sigma_e^2 \text{ Variance of error,} \\
\sigma_{bhs}^2 \text{ Variance of herd-year-seasons,} \\
\sigma_b^2 \text{ Variance of bull,} \\
n_r \text{ Number of herd-year-seasons in the } r^{th} \text{ group.} \\

Fig. 7. Algebraic notation for the expectations of the pooled sums of squares among bulls, herd-year-seasons, and remainder within groups when there is one observation per subclass.
Table 4. Mean-squares and their expected values from balanced data - Analysis I

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>d.f.</th>
<th>Mean-squares (in (10 lb. milk)$^2$)</th>
<th>Expected values of the Mean-squares</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><strong>Five successive analyses</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Bulls</td>
<td>129</td>
<td>72,840</td>
<td>70,876</td>
</tr>
<tr>
<td>Herd-year-seasons</td>
<td>798</td>
<td>97,936</td>
<td>98,175</td>
</tr>
<tr>
<td>Bull X herd-year-seasons</td>
<td>798</td>
<td>47,225</td>
<td>46,770</td>
</tr>
<tr>
<td>Error*</td>
<td>5,795</td>
<td>46,053</td>
<td>46,053</td>
</tr>
<tr>
<td>F - value**</td>
<td></td>
<td>1.025</td>
<td>1.016</td>
</tr>
</tbody>
</table>

*Calculated from the total volume of data as described on page 63.

**$F(0.01) = 1.135$

$F(0.05) = 1.094$

$F(.1) = 1.073$
expectations of these mean-squares. The average values of these five are taken as the best estimates of these expectations. These average values are given in Table 4. The best estimates of the components, $\sigma^2_b$, $\sigma^2_{hs}$, $\sigma^2_{bhs}$ and $\sigma^2_e$ are therefore obtainable from the averages of the mean-squares by equating them (the average mean-squares) to their expected values and solving for $\sigma^2_b$, $\sigma^2_{hs}$, $\sigma^2_{bhs}$ and $\sigma^2_e$. These estimates are presented in Table 5.

Table 5. Estimates of $\sigma^2_b$, $\sigma^2_{hs}$, and $\sigma^2_{bhs}$ obtained from balanced data - Analysis I

<table>
<thead>
<tr>
<th>Parameter</th>
<th>d.f.</th>
<th>Estimate</th>
<th>% of total</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma^2_b$</td>
<td>129</td>
<td>3,520.0</td>
<td>4.58</td>
</tr>
<tr>
<td>$\sigma^2_{hs}$</td>
<td>798</td>
<td>25,713.7</td>
<td>33.49</td>
</tr>
<tr>
<td>$\sigma^2_{bhs}$</td>
<td>798</td>
<td>1,519.6</td>
<td>1.98</td>
</tr>
<tr>
<td>$\sigma^2_e$</td>
<td>5,795</td>
<td>46,053.0*</td>
<td>59.95</td>
</tr>
</tbody>
</table>

*Calculated from the total volume of data as described on page 63.
Confidence limits on the variance components

The point estimate of $\sigma^2_{\text{bhs}}$ is more informative if accompanied by some measure of its possible error of estimation. Stated in another way, the point estimate is more informative when it is accompanied by an interval with some measure of assurance that the true parameter, $\sigma^2_{\text{bhs}}$, does lie within the interval.

In general, little is known about the distribution of $\hat{\sigma}^2_{\text{bhs}}$. However, in a special situation, as in the present case, in which the sample is large and the variance-component is estimated with a large number of degrees of freedom (798), $\hat{\sigma}^2_{\text{bhs}}$ can be assumed to be normally distributed. Justification for this is based on the central limit theorem and the reproductive property of $\chi^2$. The central limit theorem (Anderson and Bancroft, 1952) states that "if an arbitrary population distribution has a mean $\mu$ and finite variance $\sigma^2$, then the distribution of the sample mean approaches the normal distribution with mean $\mu$ and variance $\sigma^2/n$ as the sample size, $n$, increases".

The reproductive property of $\chi^2$ states that the sum of $n$ sample values of $\chi^2$, each of which is distributed with $k_r$ degrees of freedom, is itself distributed as $\chi^2$ with $\sum k_r$ degrees of freedom. Since the mean-square due to interaction
(V_i) from each of the 129 groups is the mean of squared linear functions of NID variates, it is independently distributed as \( \chi^2_{(\sigma_{bhs}^2 + \sigma_e^2)} \) with d.f. equal to the interaction d.f. (k_i) from that particular group. Also, \( \sum_{i=1}^{129} k_i V_i \) (that is, the "pooled" interaction mean-squares from all 129 groups) is distributed as \( \chi^2_{(\sum k_i)} \) with \( \sum k_i \) degrees of freedom.

The two theorems quoted may be then combined to state that, "If an arbitrary population of squared interaction comparisons has an expected value of \( \sigma_{bhs}^2 + \sigma_e^2 \) and a finite variance of \( 2[\sigma_{bhs}^2 + \sigma_e^2] \), then the distribution of the mean of a number (\( \sum k_i \)) of squared comparisons approaches the normal distribution, with mean \( \sigma_{bhs}^2 + \sigma_e^2 \) and variance \( 2[\sigma_{bhs}^2 + \sigma_e^2]^2 \)."

Thus, (a) the mean-square for interaction is approximately normally distributed with true mean \( \sigma_{bhs}^2 + \sigma_e^2 \) and variance \( 2[\sigma_{bhs}^2 + \sigma_e^2]^2 \), interaction d.f.

(b) the mean-square for error is approximately normally distributed with true mean \( \sigma_e^2 \) and variance \( 2[\sigma_e^2]^2 \), error d.f.

and (c) since these mean-squares are independently
distributed, and since a linear function of normal variables is itself normally distributed, the difference between these mean squares (which estimates \( \sigma_{bhs}^2 \)) is approximately normally distributed with true value \( \sigma_{bhs}^2 \) and variance \( \frac{2[\sigma_{bhs}^2 + \sigma_e^2]^2}{\text{Interaction d.f.}} + \frac{2[\sigma_e^2]^2}{\text{Error d.f.}} \).

Since \( \sigma_{bhs}^2 \) and \( \sigma_e^2 \) are unknown, \( V(\hat{\sigma}_{bhs}^2) \) and \( V(\hat{\sigma}_e^2) \) are also unknown. They can be estimated, however, using the procedure described in Kempthorne (1957), as:

\[
\hat{V}(\hat{\sigma}_{bhs}^2) = \frac{2[\text{Interaction Mean-square}]^2}{\text{Interaction d.f.}} + 2
\]

\[
\hat{V}(\hat{\sigma}_e^2) = \frac{2[\text{Error Mean-square}]^2}{\text{Error d.f.}} + 2
\]

The interaction-mean-square and error-mean-square from each of the five analyses or "runs" (see Table 4) can be used in deciding upon an interval for which we can have 95% confidence that \( \sigma_{bhs}^2 \) lies in that interval. [It is not legitimate to use the average of the five mean-squares in calculating \( \hat{V}(\hat{\sigma}_{bhs}^2) \) because they are not independently distributed and the covariances between them are unknown.] \( V(\hat{\sigma}_{bhs}^2) \) can be estimated from the five "individual" mean-squares and, therefore, confidence intervals may be calculated from these. In this way five confidence intervals are obtained.
Since $\hat{\sigma}_{bhs}^2$ is approximately normally distributed and since $V(\hat{\sigma}_{bhs}^2)$ is estimated (in each of the five cases) with such a large number of degrees of freedom, we will use the standard normal distribution in placing the confidence-limits on $\sigma_{bhs}^2$. Thus, for example,

$$\sigma_{bhs}^2 = \hat{\sigma}_{bhs}^2 \pm T_{0.05} \sqrt{\hat{V}(\hat{\sigma}_{bhs}^2)}$$

where $T_{0.05} = 1.96$.

The 95% confidence-limits on $\sigma_{bhs}^2$ for each of the five "runs" are presented in Table 6.

<table>
<thead>
<tr>
<th>Run</th>
<th>95% confidence intervals on $\sigma_{bhs}^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$1,171 \pm 4,923 = -3,751$ to $6,094$</td>
</tr>
<tr>
<td>2</td>
<td>$717 \pm 4,881 = -4,164$ to $5,598$</td>
</tr>
<tr>
<td>3</td>
<td>$2,634 \pm 5,058 = -2,423$ to $7,692$</td>
</tr>
<tr>
<td>4</td>
<td>$1,968 \pm 4,996 = -3,028$ to $6,964$</td>
</tr>
<tr>
<td>5</td>
<td>$1,107 \pm 4,917 = -3,809$ to $6,024$</td>
</tr>
</tbody>
</table>

Confidence limits were not placed on $\sigma_b^2$ and $\sigma_{hs}^2$ because,
(a) there was no real reason for doing so,
(b) $\sigma_{bhs}^2$ was the object of study and attention was focused specifically on this parameter, and
(c) there is reason to question the true number of degrees of freedom for mean-squares due to bulls and herd-year-seasons respectively because some bulls and some herd-year-seasons are found in more than one group.

Testing the hypothesis that $\sigma_{bhs}^2 = 0$

In the last section, five different confidence intervals were placed on $\sigma_{bhs}^2$. Zero was included in all five intervals. Testing the hypothesis that $\sigma_{bhs}^2 = 0$ is an operation closely related to the fitting of confidence intervals. The information obtained from testing this hypothesis is therefore not expected to differ greatly from the information obtained from the placing of confidence intervals. However, it is not quite the same in that it focuses attention on a specific value of $\sigma_{bhs}^2$ (zero in this case) and enables us to make a definite statement concerning the probability of getting the estimate which we did get, by a purely random process, if the true value is really equal to the hypothesized value.

F-values from the sample are calculated as:

**Interaction-mean-square** for each of the five successive "runs".
**Error-mean-square**
These F-values are presented in Table 4. The "critical points" \( F(.1), F(.05), \) and \( F(.01) \) cannot be obtained from an F-table because the numbers of degrees of freedom involved are too large. They are calculated using the relationship between F and Fisher's (1928) z-value.

Fisher (1928) defined z as \( \frac{1}{2} \log_e \frac{1 + (k-1)r}{1-r} \). In the present case, \( k = 2, r = \frac{\sigma^2_{\text{bhs}}}{\sigma^2_{\text{bhs}} + \sigma^2_{\text{e}}} \) and \( z = \frac{1}{2} \log_e \frac{\sigma^2_{\text{bhs}}}{\sigma^2_{\text{bhs}} + \sigma^2_{\text{e}}} \).

The 10%, 5% and 1% "critical points" for z are calculated for 798 and 5,795 degrees of freedom using the extrapolation-formulae given by Fisher and Yates (1953). These z-values and their corresponding F-values are:

<table>
<thead>
<tr>
<th>z-values</th>
<th>F-values</th>
</tr>
</thead>
<tbody>
<tr>
<td>( z(.1) = .03488 )</td>
<td>( F(.1) = 1.0727 )</td>
</tr>
<tr>
<td>( z(.05) = .04478 )</td>
<td>( F(.05) = 1.0935 )</td>
</tr>
<tr>
<td>( z(.01) = .06348 )</td>
<td>( F(.01) = 1.1348 )</td>
</tr>
</tbody>
</table>

All five observed F-values in Table 4 are less than \( F(.1) \). The interpretation is that the probability of obtaining F-values of the observed magnitudes by a purely random process,
when $\sigma_{bhs}^2 = 0$, is at least greater than 10%. In other words, one is "quite likely" to obtain values as large as these when $\sigma_{bhs}^2 = 0$. There is, therefore, insufficient justification for rejecting the null hypothesis that $\sigma_{bhs}^2 = 0$.

It should be pointed out that, if the five interaction mean-squares had been independent, the hypothesis would be tested on a "pooled" or "average" mean-square rather than on five separate mean-squares. This, if it were "legitimate", would give a much more powerful test than could be obtained from the five individual tests. However, since they are not independent, this procedure cannot be followed.

Analysis II

In estimating components of variance in non-orthogonal or unbalanced data, one of the assumptions made is that the effects of bulls are uncorrelated with effects of herd-year-seasons. The expectation of the correlation between bulls and herd-year-seasons may be zero but the actual correlation in the data may be real, even if only due to chance. The fact that the correlation is zero in the population does not make it zero in the sample and ignoring it in the computations will bias the estimates obtained for the components of variance. Therefore, estimates from non-orthogonal data are not expected
to be the same as those obtained by the procedure used in the previous section, unless this correlation is zero.

The data used in Analysis II were the same as those used in Analysis I (which involved 129 groups in which all bull-herd-year-season-subclasses had some data in them). The only difference was that, in Analysis II, the orthogonalizing procedure of randomly selecting one observation per subclass was not done. The sums of squares for bulls, herd-year-seasons, and bull X herd-year-season interaction-effects within groups were calculated, and pooled sums of squares for these three sources of variation were obtained by summing the sums of squares over all 129 groups. These pooled sums of squares and their expectations are presented in Table 7.

As in the previous analysis, a weighted estimate of $\sigma^2_e$ is used instead of the estimate obtained in the "selected" sample (of 2,874 observations). Estimates of $\sigma^2_b$, $\sigma^2_{hs}$ and $\sigma^2_{bhs}$ were obtained by equating the sums of squares due to bulls, herd-year-seasons and bull X herd-year-season-interaction to their expected values, substituting the weighted estimate of $\sigma^2_e$ (46,053) and solving the resulting equations simultaneously. The estimates of these components obtained in this analysis are presented in Table 8.
Table 7. Sums of squares, with their expected values, in terms of the components of variance - Analysis II

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Sums of squares</th>
<th>Expected values of the sums of squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulls</td>
<td>10,969,333</td>
<td>(129\sigma_e^2 + 204.40\sigma_{\text{bhs}}^2 + 23.68 \sigma_{\text{hs}}^2 + 1,197.77\sigma_b^2)</td>
</tr>
<tr>
<td>Herd-year-seasons</td>
<td>91,151,794</td>
<td>(798\sigma_e^2 + 1,088.37\sigma_{\text{bhs}}^2 + 2,037.84 \sigma_{\text{hs}}^2 + 68.57\sigma_b^2)</td>
</tr>
<tr>
<td>Bulls X Herd-year-seasons</td>
<td>38,193,177</td>
<td>(798\sigma_e^2 + 925.79\sigma_{\text{bhs}}^2 - 23.68 \sigma_{\text{hs}}^2 - 68.57\sigma_b^2)</td>
</tr>
</tbody>
</table>
Table 8. Estimates of $\sigma_b^2$, $\sigma_{hs}^2$, and $\sigma_{bhs}^2$ obtained from unbalanced data - Analysis II

<table>
<thead>
<tr>
<th>Parameter</th>
<th>d.f.</th>
<th>Estimate</th>
<th>% of total variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma_b^2$</td>
<td>129</td>
<td>3,278.1</td>
<td>4.3%</td>
</tr>
<tr>
<td>$\sigma_{hs}^2$</td>
<td>798</td>
<td>25,278.0</td>
<td>32.8%</td>
</tr>
<tr>
<td>$\sigma_{bhs}^2$</td>
<td>798</td>
<td>2,447.8</td>
<td>3.2%</td>
</tr>
<tr>
<td>$\sigma_e^2$</td>
<td>5,795</td>
<td>46,053.0*</td>
<td>59.8%</td>
</tr>
</tbody>
</table>

*Calculated from the total volume of data as described on page 63.

These estimates are similar to, but not quite the same as, the estimates obtained in Analysis I. It is believed that the differences are due to some bias occurring in the estimates in Analysis II because of dis-proportionality of subclass numbers.

Apart altogether from this bias, which may or may not be present, the salient feature in this analysis is that it does not enable us to place confidence intervals on the estimate of $\sigma_{bhs}^2$ or to test the hypothesis that $\sigma_{bhs}^2 = 0$. (The same remarks may be made concerning Analysis III which follows in the next section.) This point should be emphasized because this is the real reason why we went to so much trouble to
ensure a completely balanced situation among bulls and herd-year-seasons. (It may be recalled that this was done by (a) finding sections of data in which all bull-herd-year-season subclasses were filled and (b) by randomly selecting one observation from each of the subclasses in each of the five successive "runs" in Analysis I.)

Many estimates of $\sigma^2_{bhs}$ have been recorded in animal-breeding literature but, as far as the author is aware, no work has been done to indicate the probable error in these estimates or to test hypotheses concerning $\sigma^2_{bhs}$. Because Analysis I enables us to place confidence limits on $\sigma^2_{bhs}$, it is more informative with regard to $\sigma^2_{bhs}$ (which is the parameter we are interested in) than Analysis II (or Analysis III).

Analysis III

Other estimates of the variance components were obtained from the data (2,874 observations) which were discussed on pages 60 and 61, (and which were used also in Analyses I and II). These data were analyzed with respect to the four sources of variation (bulls, herd-year-seasons, bull x herd-year-season-interaction and error) without dividing them (the data) into groups (as was done in Analyses I and II). The sums of squares and their expectations, in terms of the
components of variance, due to bulls, herd-year-seasons and interaction, are presented in Table 9. The estimates of $\sigma_b^2$, $\sigma_{hs}^2$ and $\sigma_{bhs}^2$ were obtained by equating the sums of squares to their expected values, substituting in the weighted estimate of $\sigma_e^2 (46,053)$, and solving the resulting equations simultaneously. These estimates are as follows:

<table>
<thead>
<tr>
<th>Variance component</th>
<th>Estimate</th>
<th>% of total variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma_b^2$</td>
<td>3,667.52</td>
<td>4.61%</td>
</tr>
<tr>
<td>$\sigma_{hs}^2$</td>
<td>27,839.13</td>
<td>35.00%</td>
</tr>
<tr>
<td>$\sigma_{bhs}^2$</td>
<td>1,992.65</td>
<td>2.50%</td>
</tr>
<tr>
<td>$\sigma_e^2$</td>
<td>46,053*</td>
<td>57.89%</td>
</tr>
</tbody>
</table>

The estimates of the components of variance in Analysis III are more likely to be biased than are the estimates in Analysis I, because of the unbalanced nature of the data. As in Analysis II, one cannot place confidence-limits on $\sigma_{bhs}^2$ or test the hypothesis that $\sigma_{bhs}^2 = 0$. Therefore, this analysis is not expected to increase our knowledge of bull X herd-year-season-interaction in A.I.-data more than those methods which have been used before now by other research-workers.

*Calculated from the total volume of data as described on page 63.
Table 9. Sums of squares, with their expected values, in terms of the components of variance - Analysis III

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Sums of squares</th>
<th>Expected values of the sums of squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulls</td>
<td>17,531,799</td>
<td>$86\sigma_e^2 + 164.03\sigma_{bhs}^2 + 160.64\sigma_{hs}^2 + 2,391.89\sigma_b^2$</td>
</tr>
<tr>
<td>Herd-year-seasons</td>
<td>105,580,590</td>
<td>$691\sigma_e^2 + 1,001.75\sigma_{bhs}^2 + 2,453.70\sigma_{hs}^2 + 936.55\sigma_b^2$</td>
</tr>
<tr>
<td>Bulls X Herd-year-seasons</td>
<td>43,942,984</td>
<td>$1,070\sigma_e^2 + 1,291.32\sigma_{bhs}^2 - 160.64\sigma_{hs}^2 - 936.55\sigma_b^2$</td>
</tr>
</tbody>
</table>
Discussion

The results obtained from this investigation are informative concerning the importance of bull x herd-year-season interaction in A.I. data. This was the major purpose of the study. Even though the estimates of $\sigma_{bhs}^2$ differ among Analyses I, II and III, in all three cases the estimate was less than 3.5% of the total variance.

In the next section we will discuss how much influence this interaction is likely to have on the accuracy of selecting dairy bulls, using records produced in farmer-herds (and affected by the same sources of variation as the records studied here).

As we discussed earlier, one should be cautious in applying results to situations which differ from the situation studied. For example, the results do not tell us how much genetic-environmental exists between breeds and managemental systems. Even within a particular breed, if the bulls came from several highly inbred lines, bull x environment interaction would be expected to be a greater source of variation than if they came from a "more or less" freely interbreeding population.
This is merely stating in another way that answers are applicable only to a particular set of conditions. To get answers for another set of conditions, an experiment or survey should be carried out under that specified situation.
APPLICATION OF THE RESULTS

Successful dairy-farming is regarded, in this thesis, as a dynamic equilibrium in the adaptation of environments and genetic materials to each other in the most efficient manner to give maximum economic return.

How is it decided to which environments particular strains or breeds should be adapted? Some environments (e.g., levels of feeding and management) can be controlled and changed at will by the herd-owners. Other environments, such as disease (e.g., foot and mouth disease) or changes in market-prices (which can seriously affect the value of a product), are largely outside the control of the herd-owner as an individual, though some of these factors may be changed by a group of herd-owners as a body. When the herd-owner cannot change the environment easily, he may be able to make progress by altering the genetic material to suit the environment rather than by altering the environment to suit the genetic material.

Many different genetic materials are available to dairy farmers to satisfy particular economic or environmental conditions which may be peculiar to individual herds. In the nine midwestern states of the U.S., from which these data came, at least six breeds of dairy-cattle (Holsteins, Shorthorns,
Brown-Swiss, Guernseys and some Jerseys and Ayrshires) are used. One can assume that, in general, each of these breeds is adapted better than any other to some particular economic-environmental niche. (Otherwise there would be no real reason for the continued existence of different breeds.) These niches are not localized but are scattered over the entire area. (One frequently finds two dairy-farmers living across the road from each other keeping different breeds. It is also quite common to find two or three different breeds in the same herd.)

The herd-owners choose the genetic material:

(1) by choosing a particular breed, and

(2) by routine-selection of cows and bulls of high genetic merit in so far as this is possible.

Although, in recent times, much of the breeding is done artificially, many dairy-men still prefer to do their own breeding, using natural service. Even in A.I., where the bulls used are selected by those who manage the A.I.-studs, the herd-owners, as a body, ultimately control the selecting of these bulls. They express their approval (or disapproval) of the ability of the A.I.-managers to select in the direction in which they themselves (the herd-owners) would like to go
(a) by the degree to which they use the services of the A.I.-
stud and (b) through conferences and discussions among farmer-
organizations, A.I.-managers, representatives of extension-
services, etc.

In the dairy-industry, particular breeds are adapted to a
relatively broad geographic and climatic niche with less
tendency towards specialization than we find, for example, in
sheep. One of the main reasons in that it has been more
economical to house and care for dairy-cattle to a greater
degree than it would be for sheep. In other words, it appears
to have been generally more economical to make progress by
changing (in effect, insofar as it influences the dairy-cattle).
adverse climatic conditions to suit the genetic material (by
proper housing, feeding and management) whereas, in sheep, it
appears to have been generally more economical to change the
genetic material to suit the different environments. The
degree of attention devoted to controlling and adapting the
environment to suit the genetic material by housing and man-
age ment in the case of dairy-cattle can be realized by con-
sidering that any particular breed can be found in areas which
are really very different in their prevailing climatic condi-
tions.

Speaking specifically of the Holstein breed (although the
same remarks apply to other breeds also), this breed extends as
a relatively freely interbreeding group throughout much of the
Northern and Southern temperate regions. Any barriers against
interbreeding within this area (which would result in the devel-
opment of "regional" strains) are set up more by distance and
political boundaries than by environmental-economic factors.
The ability of the herd-owners to control many of the environ­
mental factors which affect dairy-cows (thus precluding the
necessity for animals to be genetically specialized to suit
particular climatic conditions), has many practical advantages
from a breeder's point of view. Among other things, it permits
greater flexibility in selection and in moving breeding stock
from one area into another. It also means less wastage of
breeding-effort resulting from particular breeds or strains
(which were developed to take advantage of specific environ­
ments) becoming extinct if these environments were to change.

As Lush (1960) stated, in referring to adaptation of
species to environments:

... too perfect and rigid adaptation to one special set
of conditions (that is, being extremely specialized so as
to make the very most out of the conditions in a certain
locality or climate), is likely sooner or later to lead
to extinction as those conditions change, even if the
changes are rare and only cyclical or irregular.
Genetic Merit on Which the Bulls Involved in the Study are Selected

Within the "environmental niche" from which the data came, we assume that Holsteins are selected for general or average genetic merit for the entire area. Bull x herd-year-season interactions are considered as factors whose influence should be minimized or eliminated rather than something to be selected for. [As indicated by the discussion in the previous section, the decision as to whether particular controllable environments should be changed to suit the available genetic material or whether the genetic material should be changed to suit the environments is something that is decided by the farmers themselves (with the aid of extension services, etc.) and is not something that is decided by us, the research-workers.] As far as estimation of the breeding value for the whole region is concerned, these interaction-effects are put in the same category as herd-year-season and residual error-effects.

Expressed mathematically, if the model describing the factors affecting production is

\[ X_{ijk} = \mu + b_i + h_s j + (bhs)_{ij} + e_{ijk}, \]  

(see page 47)

the genetic merit of the \( i^{th} \) bull is \( G_i \) rather than \( G_{ij} \) (see pages 9 and 10).
\[ G_i = 2 b_i \]
and \[ G_{ij} = 2(b_i + (bhs)_{ij}). \]

On the other hand, if the interaction-effects were large enough and if the environments were fixed or, at least, controllable, so that breeding for adaptability to specific environments could be worth-while, the interaction-effect would then be considered as part of the genetic merit. Under those conditions one would need to specify the environment in order to define genetic merit. In the case of bull X herd-year-season interaction, the genetic merit of the \(i^{th}\) bull in the \(j^{th}\) herd-year-season is \(G_{ij}\) rather than \(G_i\).

**Influence of Genetic and Non-Genetic Factors on the Accuracy of Selection**

Selecting individuals which are superior in genetic merit (for a particular trait, for a particular environment) is the basic idea behind selection indexes. The "best" or most accurate index (relative to other indexes) is defined as that index which is most likely to lead us to select individuals with the most superior genetic merit. The index with this desirable property is that index which is most highly correlated with the true genetic merit. The term "accuracy", when applied to an index, therefore, is defined as "the true
correlation between the index and the true genetic merit of the bull". If we could really measure the true genetic merit of each individual exactly, the accuracy of that measurement as a selection index would be unity. We cannot measure the genetic merit directly, however, but must do so indirectly through observing the phenotypes of related individuals. As a result, many factors, genetic and non-genetic, influence the accuracy of the index. Generally, the degree to which these factors are detrimental to the accuracy is more or less proportional to how small is their correlation with the genetic merit. On the other hand, looking at the problem from another point of view, these factors can be used as aids to selection if they are at all correlated with $G_i$. Occasionally, one can find some factors which are used as aids to selection, even though they are uncorrelated with the genetic merit of the individual in the trait being selected for. This could happen if these factors are correlated with other factors in such a way that they serve as helps in increasing the correlation between the selection index and the genetic merit for which one is selecting.

Hazel (1943) showed that there could even be situations in which one should select against a trait (e.g., type-score), even though it is positively correlated with genetic merit (e.g., aggregate genotype, including weight and type-score), merely
because it is still more highly correlated with some uncontrolled environmental circumstance for which correction should be made.

If one knows the distribution of the offspring of the \(i^{th}\) bull among herd-year-seasons, and if one has estimates of the components of variance for \(b_i, h_s, (bhs)_{ij}\) and \(e_{ijk}\), one can estimate the true correlation between the genetic merit and any index compiled from information distributed in any particular manner. This estimate provides a "measure" of the accuracy of the index. Also, by the same means, one can "measure" the influence which a particular factor has on the accuracy in any particular situation.

Many indexes have been proposed for ranking A.I. sires using records of their progeny. VanVleck, O'Bleness and Henderson (1961) compared 17 procedures for ranking A.I. sires with the method which is currently being used by the New York Dairy Processing Laboratory (and by the U.S.D.A. in its D.H.I.A. sire-ranking program). They concluded from that study that the "New York" method is more likely to rank the bulls according to their true genetic merits than any of those with which it was compared. Henderson (1963) and Harris (1964) presented procedures for calculating the best selection index ("best" in terms of correlation with genetic
merit) when an equal amount of information is not available on all individuals.

In the pages which follow, we will investigate the influence of interaction, $\sigma_{bhs}^2$, on the accuracy of selection, assuming that we have equal information on all individuals. Furthermore, we will use a selection index which is computationally simpler than the "New York" index (but which is not expected to be quite as accurate). This index, or selection criterion, $I_f$, has been discussed by Touchberry (1961) and by Bereskin (1963) as the "daughter-stablemate comparison".

$I_f$ is the average of the intra-herd-year-season differences between the average production of the daughters of the $f^{th}$ bull and the average production of their stablemates.

$r_{Gf}I_f$, that is, the estimated correlation between the index and genetic merit, $\frac{\hat{\sigma}_b}{\sqrt{\hat{V}(I_f)}}$ (Equation 1)

$$\hat{V}(I_f) = \left[1 + \frac{1}{(\sum_1^J)^2} \sum_s \left\{ \frac{\sum_j \left( \frac{N_{sj}}{e_{sj}} \right)}{\sum_s e_{sj}} \right\}^2 \right]^{\frac{2}{\hat{V}(I_f)}}$$

$$\left[ \frac{1}{\sum_j (\sigma_e^2)} \sum_j \sum_s \left\{ \frac{N_{sj}}{e_{sj}} \right\}^2 \right]^{\frac{2}{\hat{V}(I_f)}}$$

$$\left[ \frac{1}{\sum_j N_{fj}} + \sum_j \frac{1}{\sum_s e_{sj}} \right]^{\frac{2}{\hat{V}(I_f)}}$$

$(\text{For derivation of this}$
equation see Appendix IV). $N_{fj}$ and $N_{sj}$ respectively, are the numbers of offspring which the $f^{th}$ (test-bull) and the $s^{th}$ bull have in the $j^{th}$ herd-year-season. $\Sigma(1)$ is the number of daughter-stablemate comparisons which are made (and which are then averaged) to provide the index. ($\Sigma(1)$ is, therefore, equal to the number of herd-year-seasons in which stablemate-comparisons are made.)

Influence of Factors Unrelated to the Genetic Merit of the Bull on the Accuracy of the Index

The genetic merit of the test-bull is assumed to be uncorrelated with the genetic merits of stablemate-bulls, with interaction-effects and with residual error-effects. ("Stablemate-bulls" are defined as those bulls which are sires of the stablemates, i.e., sires of other cows in the same herd-year-season.) The effects of all these factors, because they are uncorrelated with the genetic merit of the test-bull, tend to decrease the accuracy of the index. Their influence is expressed only through $\sqrt{\hat{\nu}(I_f)}$. The effect of the test-bull, $b_f$, is the cause of covariance, and therefore correlation, between the index and the genetic merit of the $f^{th}$ bull. (In other words, the index is related to the genetic merit of the bull because (due to the daughters' records) it (the index) is
a function of the bull-effect, \( b_1 \).

Under the assumptions which have been made above,

\[
\hat{V}(I_f) = \frac{\hat{\sigma}_b^2}{\sqrt{\hat{V}(I_f)}} + \text{(effects of unrelated factors)}.
\]

\( r_{GfI_f} \), which equals \( \frac{\hat{\sigma}_b}{\sqrt{\hat{V}(I_f)}} \), approaches unity as \( \hat{\sigma}_b \)

increases or as the effects of unrelated factors decrease.

The genetic variation among the stablemate-bulls affects

\[
\hat{V}(I_f) \text{ through } \frac{1}{[\Sigma(1)]^2} \sum_j \left\{ \sum_s \left( \frac{N_{si}}{\Sigma N_{sj}} \right) \right\}^2 \hat{\sigma}_b^2.
\]

The bull x herd-year-season interaction affects \( \hat{V}(I_f) \) through

\[
\left[ \frac{1}{\Sigma(1)} + \frac{1}{(\Sigma(1))^2} \sum_j \sum_s \left( \frac{N_{si}}{\Sigma N_{sj}} \right)^2 \right] \hat{\sigma}_{bhs}^2.
\]

while the random elements (\( e_{ijk} \)) affect \( \hat{V}(I_f) \) through

\[
\frac{1}{(\Sigma(1))^2} \left[ \sum_j \frac{1}{N_{sj}} + \sum_j \frac{1}{\Sigma N_{sj}} \right] \hat{\sigma}_e^2.
\]

For a particular situation, it is assumed that the true values of \( \hat{\sigma}_b^2 \), \( \hat{\sigma}_{bhs}^2 \) and \( \hat{\sigma}_e^2 \) are constant. Then the accuracy of the index for a particular test-bull is determined by the coefficients of these components, that is, by the manner in which the test-bull's daughters and the daughters of stablemate-bulls are distributed among the various herd-year-seasons.
Influence of $\sigma^2_b$ and $\sigma^2_{bhs}$

The influence of the true values, $\sigma^2_b$ and $\sigma^2_{bhs}$ respectively, on the true accuracy of the index depends upon their coefficients,

$$1 + \frac{1}{(\Sigma(1))^2} \sum_s \left\{ \sum_j \left( \frac{N_{sj}}{\Sigma N_{sj}} \right) \right\}^2$$

and

$$\left[ \frac{1}{\Sigma(1)} + \frac{1}{(\Sigma(1))^2} \sum_{sj} \left( \frac{N_{sj}}{\Sigma N_{sj}} \right)^2 \right].$$

These two coefficients are highly correlated with each other because any variation in the distribution of the offspring will cause both of them to change in the same direction. This hinders measuring the influence of $\sigma^2_b$ or $\sigma^2_{bhs}$ free from confounding with the influence of the other. Referring strictly to the influence of $\sigma^2_b$ and $\sigma^2_{bhs}$, the accuracy of the index is enhanced when:

(a) the bulls are tested in a large number of herd-year-seasons, and (b) the total number of different stablemate-bulls is large, and (c) the number of daughters which each stablemate-bull has in each herd-year-season is small, relative to the total number of stablemates in that herd-year-season. Point (c) depends upon (1) having many different stablemate-bulls in each herd-year-season and (2) having the numbers of daughters per stablemate-bull as close as possible to being equal in each herd-year-season.
Influence of $\sigma_e^2$

The influence of $\sigma_e^2$ on the accuracy of the index depends on the coefficient,

$$\frac{1}{(\sum_1^n)^2} \left[ \sum_j \frac{1}{N_{fj}} + \sum_s \frac{1}{\sum N_{sj}} \right]$$

Referring strictly to $\sigma_e^2$, the accuracy of the index tends to be enhanced when (a) the bull is tested over a large number of herd-year-seasons and (b) when both the test-bull and the stablemate-bulls have a large number of daughters in each herd-year-season.

Influence of $\sigma_{bhs}^2$ on the Accuracy of the Index

In an earlier section the term "accuracy" of an index was defined as the true correlation between the index and the breeding value of the bull. This true correlation cannot be calculated directly. It is estimated by $r_{GI}$. Similarly, the influence of $\sigma_{bhs}^2$ on the true accuracy cannot be calculated directly but it can be estimated by observing or measuring the influence of its estimate ($\hat{\sigma}_{bhs}^2$) on the estimate ($r_{GI}$) of the true correlation. In order to do this (estimate the influence of $\sigma_{bhs}^2$ on the "accuracy" of the index) $r_{GI}$ is calculated, substituting different values for $\hat{\sigma}_{bhs}^2$ in Equation 1 on page 93. (The values for $\hat{\sigma}_b^2$ and $\hat{\sigma}_e^2$ are held constant at
\[ \hat{\sigma}_{b}^2 = 3,520 \]
\[ \hat{\sigma}_{e}^2 = 46,053 . \]

If \( \hat{\sigma}_{bhs}^2 = 0 \), genetic environmental interaction has no influence on \( r_{GI} \); the deviation of \( r_{GI} \) from unity is then attributable to

\[
\left[ \frac{1}{(\Sigma(1))^2} \sum_s \left\{ \sum_j \frac{N_{sj}}{\Sigma N_{sj}} \right\}^2 \right] \hat{\sigma}_{b}^2 + \\
\frac{1}{(\Sigma(1))^2} \left[ \sum_j \frac{1}{N_{fj}} + \sum_j \frac{1}{\Sigma N_{sj}} \right] \hat{\sigma}_{e}^2,
\]

that is, attributable to the influence of genetic variation among stablemate-bulls and to the influence of error-variation.

To help us in our discussion here, let us define the following symbols.

When \( \hat{\sigma}_{bhs}^2 = M \), denote \( r_{GI} \) by \( r_M \).

When \( \hat{\sigma}_{bhs}^2 = 0 \), denote \( r_{GI} \) by \( r_0 \).

When \( \hat{\sigma}_{bhs}^2 = 1,520 \), denote \( r_{GI} \) by \( r_{1,520} \).

When \( \hat{\sigma}_{bhs}^2 = 8,000 \), denote \( r_{GI} \) by \( r_{8,000} \).

Then, speaking generally for a moment, the "influence" of \( \hat{\sigma}_{bhs}^2 \) on \( r_{GI} \), when \( \hat{\sigma}_{bhs}^2 = M \), can be measured as

\[
\frac{r_0 - r_M}{1 - r_M} \times 100
\]
where $r_0 - r_M$ is the decrease in $r$ caused by $\hat{\sigma}_{bhs}^2$ alone, $1 - r_M$ is the decrease in $r$ caused by all sources of error combined (when $\hat{\sigma}_{bhs}^2 = M$).

This decrease in $r$ due to $\hat{\sigma}_{bhs}^2$ is expressed in this way because it seems more reasonable to portray it as a relative thing (that is, relative to the decrease in $r$ due to all factors) than to express it in absolute value (e.g., $r_0 - r_M$).

If our "best estimate" of $\sigma_{bhs}^2 = 1,520$ (see Analysis I and Table 5), the "best estimate" of the influence of $\sigma_{bhs}^2$ on the accuracy of selection in a particular situation (if the daughters of all bulls being tested are distributed in the same manner as those of the bull under consideration) is obtained as

$$\frac{r_0 - r_{1,520}}{1 - r_{1,520}} \times \frac{100}{1}$$

Furthermore, since $\sigma_{bhs}^2$ is not expected to be larger than 8,000, the maximum amount of influence which it ($\sigma_{bhs}^2$) is expected to have on the accuracy of selection in a particular situation is measured as

$$\frac{r_0 - r_{8,000}}{1 - r_{8,000}} \times \frac{100}{1}$$

It can be shown that, even if interaction is responsible for 10% of the total variance, it is still not a major source
of error in selecting bulls. To show this, that is, that the influence of interaction is small relative to the influence of other sources of error, the influence of $\sigma_{bhs}^2$ on $r_{GI}$ can be examined in many different situations. The numbers of herd-year-seasons in which a bull is tested, the number of stablemate-bulls present and the numbers of daughters per test-bull and per stablemate-bull, are all different from one situation to another. Analyzing several situations, therefore, should enable us to obtain more reliable answers concerning the importance of interaction which are applicable to A.I. data.

As an example, Bull 1019538 has 72 daughters in 43 different herd-year-seasons, with an average number of 4.7 stablemate-bulls per herd-year-season.

In calculating $r_{GI}$ for the index on this bull, the coefficients of $\sigma_{b}^2$, $\sigma_{bhs}^2$ and $\sigma_{e}^2$, respectively, have the following values:

$$1 + \frac{1}{(\Sigma(1))^2} \sum_{s} \left\{ \frac{\sum_{j} \left( \frac{N_{sij}}{\Sigma N_{sij}} \right) }{s} \right\}^2 = 1.03097$$

$$\frac{1}{\Sigma(1)} + \frac{1}{(\Sigma(1))^2} \sum_{j} \sum_{s} \left\{ \frac{N_{sij}}{\Sigma N_{sij}} \right\}^2 = .03050$$
The values of $V(I)$, $r_{GI}$, etc., are presented in Table 10. In this table we see that, when $\hat{\sigma}_{bhs}^2 = 0$, $r_{GI} = .859$; decrease in the value of $r_{GI}$ from unity = .141 points. When the effect of $\hat{\sigma}_{bhs}^2$ is included, it causes little additional decrease in $r_{GI}$.

The "best estimate" of the influence of interaction on the true correlation between the index and the genetic merit of the bull is got by setting $\sigma_{bhs}^2$ equal to 1,520. When $\sigma_{bhs}^2 = 1,520$, $r_{GI} = .855$. $\frac{r_0 - r_{1,520}}{1 - r_{1,520}} \times \frac{100}{1} = 2.85\%$, that is, expressed as $\%$ of $1 - r_{1,520}$ (which is the total decrease from all sources) the additional decrease in $r_{GI}$ due to $\sigma_{bhs}^2$ is only 2.58\%. Our best estimate is that 97\% of the error in the index is due to sources of variation other than interaction.

When $\sigma_{bhs}^2 = 8,000$, which is as large as the true component is likely to be, $r_{GI} = .838$. $\frac{r_0 - r_{8,000}}{1 - r_{8,000}} \times \frac{100}{1} = 13.04\%$. 

\[
\frac{1}{(\Sigma(1))^2} \left[ \sum_{j} \frac{1}{N_{fj}} + \sum_{j} \frac{1}{\Sigma N_{sj}} \right] = 0.02481
\]

Then, $r_{GI} = \sqrt{\frac{\hat{\sigma}_{b}^2}{1.03097\hat{\sigma}_{b}^2 + .03050\hat{\sigma}_{bhs}^2 + .02481\hat{\sigma}_{e}^2}}$ (see page 93)
Table 10. Values of $\hat{V}(I)$, $r_{GI}^2$ and $r_{GI}$ for bull "1019538"
($\hat{\sigma}_{bhs}^2 = 0, 1,000, \ldots, 8,000.$)

<table>
<thead>
<tr>
<th>Actual value</th>
<th>Expressed as % of the total variance</th>
<th>$\hat{V}(I)$</th>
<th>$r_{GI}^2$</th>
<th>$r_{GI}$</th>
<th>$1 - r_{GI}$</th>
<th>Additional decrease in $r_{GI}$ due to $\hat{\sigma}_{bhs}^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>4.772</td>
<td>.738</td>
<td>.859</td>
<td>.141</td>
<td>0</td>
</tr>
<tr>
<td>1,000</td>
<td>1.35%</td>
<td>4.802</td>
<td>.733</td>
<td>.856</td>
<td>.144</td>
<td>.003</td>
</tr>
<tr>
<td>1,520</td>
<td>2.03%</td>
<td>4.818</td>
<td>.731</td>
<td>.855</td>
<td>.145</td>
<td>.004</td>
</tr>
<tr>
<td>2,000</td>
<td>2.66%</td>
<td>4.833</td>
<td>.728</td>
<td>.853</td>
<td>.147</td>
<td>.005</td>
</tr>
<tr>
<td>3,000</td>
<td>3.93%</td>
<td>4.863</td>
<td>.724</td>
<td>.851</td>
<td>.149</td>
<td>.008</td>
</tr>
<tr>
<td>4,000</td>
<td>5.17%</td>
<td>4.894</td>
<td>.719</td>
<td>.848</td>
<td>.152</td>
<td>.011</td>
</tr>
<tr>
<td>5,000</td>
<td>6.39%</td>
<td>4.924</td>
<td>.715</td>
<td>.845</td>
<td>.155</td>
<td>.013</td>
</tr>
<tr>
<td>6,000</td>
<td>7.57%</td>
<td>4.955</td>
<td>.710</td>
<td>.843</td>
<td>.157</td>
<td>.016</td>
</tr>
<tr>
<td>7,000</td>
<td>8.72%</td>
<td>4.985</td>
<td>.706</td>
<td>.840</td>
<td>.160</td>
<td>.019</td>
</tr>
<tr>
<td>8,000</td>
<td>9.60%</td>
<td>5.016</td>
<td>.702</td>
<td>.838</td>
<td>.162</td>
<td>.021</td>
</tr>
</tbody>
</table>
The additional decrease in $r_{GI}$ due to $\hat{\sigma}_{bhs}^2$ is still only 13.04% of that due to errors from all sources.

**Other situations**

The relative importance of genetic-environmental interaction on the accuracy (measured through $r_{GI}$) of the index can be evaluated from other situations also. As we discussed in pages 94 to 97, increasing the accuracy by reducing the influence of the residual error-effects may be accomplished by increasing the number of offspring per bull. In A.I. data, increasing the number of offspring tends to reduce the influence of genetic-environmental interaction ($\sigma_{bhs}^2$) as well as that of $\sigma_b^2$. This happens, because increasing the number of offspring of A.I. bulls will, "automatically" (unless a deliberate effort is made to prevent it), (a) tend to involve many different herd-year-seasons and (b) tend to include stablemates from many different bulls.

In fact, it can be shown that the conditions which cause bull X herd-year-season interaction to be important (in affecting the accuracy of selection) rarely occur in A.I. data. When A.I. bulls have several offspring, these offspring are ordinarily found in several herd-year-seasons. The only case in which $\sigma_{bhs}^2$ is likely to cause trouble is when the informa-
tion comes from a single herd-year-season where the test-bull has a large number of daughters and these have many stablemates which are daughters of one or two other bulls. As an example of such a case consider a hypothetical situation in which the test-bull has 10 daughters and two other bulls also have 10 daughters each, in a single herd-year-season. Values of $\hat{\gamma}(I)$, $r_{GI}$, etc., were calculated for this situation and are presented in Table 11. $r_{GI}$ drops from .537 to .489 as $\sigma^2_{\text{bhs}}$ varies from 0 to 1,520. Expressing this change in $r_{GI}$ as a percent of $1 - r_{GI}$, $\frac{r_0 - r_{1,520}}{1 - r_{1,520}} \times 100 = 9.48\%$. When $\sigma^2_{\text{bhs}} = 8,000$, $\frac{r_0 - r_{8,000}}{1 - r_{8,000}} \times 100 = 26.4\%$. (A situation as extreme as this is not expected to occur in A.I. data and is presented here merely as an example.)

Dealing with A.I. data, it can be shown that, even if the test-bull has as few as 10 offspring distributed in as few as seven herd-year-seasons, the relative importance of interaction is very small (see Table 12).

When $\sigma^2_{\text{bhs}} = 0$, $r_{GI} = .537$,

When $\sigma^2_{\text{bhs}} = 1,520$, $r_{GI} = .529$, $\frac{r_0 - r_{1,520}}{1 - r_{1,520}} \times 100 = 1.73\%$. 


Table 11. Values of $\hat{V}(I)$, $r^2_{GI}$ and $r_{GI}$ for a hypothetical situation in which the test-bull and each of two stablemate-bulls have 10 daughters each in a single herd-year-season ($\sigma^2_{bhs} = 0, 1,000, \ldots , 8,000$.)

<table>
<thead>
<tr>
<th>Value of $\sigma^2_{bhs}$</th>
<th>Absolute value</th>
<th>Expressed as % of total variance</th>
<th>$\hat{V}(I)$</th>
<th>$r^2_{GI}$</th>
<th>$r_{GI}$</th>
<th>1 - $r_{GI}$</th>
<th>Actual decrease in $r_{GI}$ due to $\sigma^2_{bhs}$</th>
<th>Expressed as % of 1 - $r_{GI}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>0.35%</td>
<td>12,188</td>
<td>.289</td>
<td>.537</td>
<td>.463</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1,000</td>
<td>1,520</td>
<td>2.03%</td>
<td>13,855</td>
<td>.254</td>
<td>.504</td>
<td>.496</td>
<td>.033</td>
<td>6.73%</td>
</tr>
<tr>
<td>2,000</td>
<td>3,000</td>
<td>2.66%</td>
<td>14,721</td>
<td>.239</td>
<td>.489</td>
<td>.511</td>
<td>.048</td>
<td>9.48%</td>
</tr>
<tr>
<td>3,000</td>
<td>4,000</td>
<td>3.93%</td>
<td>15,521</td>
<td>.227</td>
<td>.476</td>
<td>.524</td>
<td>.061</td>
<td>11.68%</td>
</tr>
<tr>
<td>4,000</td>
<td>5,000</td>
<td>5.17%</td>
<td>17,188</td>
<td>.205</td>
<td>.453</td>
<td>.547</td>
<td>.085</td>
<td>15.50%</td>
</tr>
<tr>
<td>5,000</td>
<td>6,000</td>
<td>6.39%</td>
<td>18,855</td>
<td>.187</td>
<td>.432</td>
<td>.568</td>
<td>.105</td>
<td>18.55%</td>
</tr>
<tr>
<td>6,000</td>
<td>7,000</td>
<td>7.57%</td>
<td>20,521</td>
<td>.172</td>
<td>.414</td>
<td>.586</td>
<td>.123</td>
<td>21.04%</td>
</tr>
<tr>
<td>7,000</td>
<td>8,000</td>
<td>8.72%</td>
<td>22,188</td>
<td>.159</td>
<td>.398</td>
<td>.602</td>
<td>.139</td>
<td>23.12%</td>
</tr>
<tr>
<td>8,000</td>
<td></td>
<td>9.60%</td>
<td>23,855</td>
<td>.148</td>
<td>.384</td>
<td>.616</td>
<td>.153</td>
<td>24.89%</td>
</tr>
</tbody>
</table>
Table 12. Values of $\hat{V}(I)$, $r^2_{GI}$ and $r_{GI}$ for an A.I. bull which has 10 daughters in seven herd-year-seasons ($\sigma^2_{bhs} = 0, 1,000, \ldots, 8,000$).

<table>
<thead>
<tr>
<th>Values of $\sigma^2_{bhs}$</th>
<th>Actual value</th>
<th>Expressed as % of the total variance</th>
<th>$\hat{V}(I)$</th>
<th>$r^2_{GI}$</th>
<th>$r_{GI}$</th>
<th>$1 - r_{GI}$</th>
<th>Additional decrease in $r_{GI}$ due to $\sigma^2_{bhs}$</th>
<th>Actual decrease expressed as % of $1 - r_{GI}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>12,195</td>
<td>.289</td>
<td>.537</td>
<td>.463</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1,000</td>
<td>1.3%</td>
<td>12,444</td>
<td>.283</td>
<td>.532</td>
<td>.468</td>
<td>.005</td>
<td>1.16%</td>
<td></td>
</tr>
<tr>
<td>1,520</td>
<td>2.03%</td>
<td>12,574</td>
<td>.280</td>
<td>.529</td>
<td>.471</td>
<td>.008</td>
<td>1.73%</td>
<td></td>
</tr>
<tr>
<td>2,000</td>
<td>2.66%</td>
<td>12,694</td>
<td>.277</td>
<td>.527</td>
<td>.473</td>
<td>.011</td>
<td>2.25%</td>
<td></td>
</tr>
<tr>
<td>3,000</td>
<td>3.93%</td>
<td>12,943</td>
<td>.272</td>
<td>.521</td>
<td>.479</td>
<td>.016</td>
<td>3.29%</td>
<td></td>
</tr>
<tr>
<td>4,000</td>
<td>5.17%</td>
<td>13,192</td>
<td>.267</td>
<td>.517</td>
<td>.483</td>
<td>.021</td>
<td>4.29%</td>
<td></td>
</tr>
<tr>
<td>5,000</td>
<td>6.39%</td>
<td>13,442</td>
<td>.262</td>
<td>.512</td>
<td>.488</td>
<td>.026</td>
<td>5.23%</td>
<td></td>
</tr>
<tr>
<td>6,000</td>
<td>7.57%</td>
<td>13,691</td>
<td>.257</td>
<td>.507</td>
<td>.493</td>
<td>.030</td>
<td>6.13%</td>
<td></td>
</tr>
<tr>
<td>7,000</td>
<td>8.72%</td>
<td>13,941</td>
<td>.252</td>
<td>.502</td>
<td>.498</td>
<td>.035</td>
<td>6.99%</td>
<td></td>
</tr>
<tr>
<td>8,000</td>
<td>9.60%</td>
<td>14,190</td>
<td>.248</td>
<td>.498</td>
<td>.502</td>
<td>.039</td>
<td>7.81%</td>
<td></td>
</tr>
</tbody>
</table>
When $\sigma^2_{bhs} = 8,000$, $r_{GI} = .498$, \[ \frac{r_0 - r_{8,000} \times 100}{1 - r_{8,000}} = 7.81\% . \]

Although the foregoing discussion applies specifically to the "daughter-stablemate" comparison index, it is assumed that the results are true, in general, for other indexes of this nature, that is, indexes which are designed for selecting bulls using A.I. survey-data. (Evidence to support this assumption would require calculating $\frac{r_0 - r_{1,520}}{1 - r_{1,520}}$ for many different indexes using information on many different bulls.)

From the results of the study, therefore, it seems that there is little need to focus attention on, or waste resources on, seeking methods which would be primarily useful for reducing bull X herd-year-season interaction-effects. These effects will always cause some error as long as $\sigma^2_{bhs} \neq 0$ but the magnitude of the error is not serious unless $\sigma^2_{bhs}$ is responsible for at least 10% or more of the total variance. Other factors (genetic, environmental and error-effects) are more important than interaction-effects both as percent of the total variance and in the degree to which they influence accuracy of selection. It seems that, under A.I. conditions, reducing the loss of accuracy caused by these other factors
will also tend to reduce the influence of interaction because, as we said previously, increasing the numbers of daughters of A.I. bulls will "automatically" involve several herd-year-seasons and several stablemate-bulls.
SUMMARY

The purposes of this study were (1) to evaluate the importance of genetic-environmental interaction as a source of variation in milk-production and (2) to determine whether this interaction is likely to be important as a source of error in sire-selection.

A total of 37,701 milk-production records, adjusted to 305-day, 2x, M.E. (Kendrick, 1955), were available for the study. The records were from farmer-herds in nine midwestern states in the U.S.—Minnesota, Iowa, Missouri, Arkansas, North Dakota, South Dakota, Nebraska, Kansas and Oklahoma.

The model assumed to describe the factors affecting a particular record was:

\[ X_{ijk} = \mu + b_i + h_s + (bhs)_{ij} + e_{ijk} \]

\( X_{ijk} \) is the production (in units of 10 lbs) of the \( k \)-th daughter of the \( i \)-th bull in the \( j \)-th herd-year-season,

\( \mu \) is the true population mean,

\( b_i \) is the effect of the \( i \)-th bull,

\( h_s \) is the effect of the \( j \)-th herd-year-season,

\( (bhs)_{ij} \) is the effect of interaction between the \( i \)-th bull and the \( j \)-th herd-year-season,

\( e_{ijk} \) is the remainder or difference between \( X_{ijk} \) and
\[ \mu + b_i + h s_j + (b h s)_{i j} \].

The factors \( b_i \), \( h s_j \), \( (b h s)_{i j} \) and \( e_{i j k} \) are assumed to have been randomly and independently drawn from their respective populations which have variances equal to \( \sigma^2_b \), \( \sigma^2_{h s} \), \( \sigma^2_{b h s} \) and \( \sigma^2_e \).

To obtain an estimate of the bull X herd-year-season interaction-component, it is desirable to analyze situations in which the same bulls are represented together in a number of herd-year-seasons. Furthermore, in order to obtain "exact" tests of significance and in order to set confidence limits on the interaction component, \( \sigma^2_{b h s} \), the sum of squares due to interaction must be obtainable free or clean from the main effects. This can be done only when there is complete orthogonality among the main effects, that is, when all bull-herd-year-season-subclasses have equal numbers of observations.

To provide the desired orthogonality, the data were searched for those situations in which bulls, taken in pairs, had daughters together in several herd-year-seasons. There were 129 groups of data involving 2,874 records obtained in this way. To obtain a situation with equal subclass-frequencies a computer-program was written which would randomly select an equal number of observations from each subclass in each of the 129 groups. The lowest subclass-frequency of each group pre-determined the number of observations to be selected from
all subclasses in that group; the lowest subclass-frequency in all groups was equal to 1. The data were analyzed five times; each time one observation was selected at random from each subclass and the sums of squares due to bulls, herd-year-seasons and remainder were obtained within each group. Assuming that all of the data came from the same population, "pooled" sums of squares were obtained by summing these sums of squares over all 129 groups. Because the data were analyzed five times, five pooled sums of squares were obtained. These sums of squares and their expectations are shown in Table 3. The corresponding mean-squares are presented in Table 4. The average values of the five mean-squares due to bulls, herd-year-seasons and remainder were taken as the best estimates of the expectations in these three sources of variation. (Background or error-variation within the subclasses, \( \sigma^2_e \), was estimated both from the sample of 2,874 records and from the "discarded" data.)

The estimates of the components of variance were as follows:
<table>
<thead>
<tr>
<th>Parameter</th>
<th>d.f.</th>
<th>Estimate</th>
<th>% of Total Variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma^2_b$</td>
<td>129</td>
<td>3,520.0</td>
<td>4.58</td>
</tr>
<tr>
<td>$\sigma^2_{hs}$</td>
<td>798</td>
<td>25,713.7</td>
<td>33.49</td>
</tr>
<tr>
<td>$\sigma^2_{bhs}$</td>
<td>798</td>
<td>1,519.6</td>
<td>1.98</td>
</tr>
<tr>
<td>$\sigma^2_e$</td>
<td>5,795</td>
<td>46,053.0</td>
<td>59.95</td>
</tr>
</tbody>
</table>

The 95% confidence-intervals on $\sigma^2_{bhs}$ were computed from each of the five "runs" described in Analysis I.

<table>
<thead>
<tr>
<th>Run</th>
<th>95% confidence-intervals on $\sigma^2_{bhs}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$1,171 \pm 4,923 = -3,751$ to $6,094$</td>
</tr>
<tr>
<td>2</td>
<td>$717 \pm 4,881 = -4,164$ to $5,598$</td>
</tr>
<tr>
<td>3</td>
<td>$2,634 \pm 5,058 = -2,423$ to $7,692$</td>
</tr>
<tr>
<td>4</td>
<td>$1,968 \pm 4,996 = -3,028$ to $6,964$</td>
</tr>
<tr>
<td>5</td>
<td>$1,107 \pm 4,917 = -3,809$ to $6,024$</td>
</tr>
</tbody>
</table>

It is not legitimate to use the average of the five mean-squares from these "runs" to compute confidence limits because these mean-squares are not independently distributed and the covariances between them are unknown.

F-values to test the hypothesis that $\sigma^2_{bhs} = 0$ were obtained as

$$ F = \frac{\text{Interaction Mean-square}}{\text{Error Mean-square}} $$

from each of the five successive "runs". None of these F-values was significant, even at the 10% level of probability (see Table 4).

The importance of interaction, as a source of error (or
confusion) in selection, can be studied in a meaningful way by estimating to what degree its presence decreases the accuracy of any particular index which one wishes to use.

The accuracy of an index is defined as the true correlation between it (the index) and the true genetic merit of the individual. The estimate of this correlation, $r_{GI} = \frac{\hat{\sigma}_b^2}{\hat{V}(I)}$.

If one knows the distribution of the offspring among herd-year-seasons and if one has estimates of the variance-components for the different sources of variation (bull-effects, herd-year-season-effects, interaction-effects and residual error-effects), one can estimate the accuracy of any index for a given situation. Also, one can estimate the amount of influence which a particular factor has on the accuracy in that situation.

The index (I) which was considered, as an example, was the average of the intra-herd-year-season differences between the average production of the daughters of the test-bull and their stablemates.

For a particular situation, it is assumed that the true values, $\sigma_b^2$, $\sigma_{bhs}^2$ and $\sigma_e^2$ are constant. Then, the accuracy of the index is determined by the distribution of the bulls' daughters and their herdmates among herd-year-seasons. The
bull which was studied (as an example in evaluating $r_{GI}$) had 72 daughters in 43 herd-year-seasons with an average of 4.7 stablemate bulls per herd-year-season.

$$r_{GI} = \sqrt{\frac{\hat{\sigma}^2}{\sigma_b^2}}$$

Clearly, when $\hat{\sigma}^2_{bhs} = 0$, interaction has no influence on $r_{GI}$; the deviation of $r_{GI}$ from unity is attributable to the other sources of error. When $\hat{\sigma}^2_{bhs} = 0$, $\hat{\sigma}^2_b = 3,520$ and $\hat{\sigma}^2_e = 46,053$ and $r_{GI} = .859$.

The "best estimate" of the influence of interaction on the accuracy of the index is got by setting $\hat{\sigma}^2_{bhs}$ equal to 1,520. When $\hat{\sigma}^2_{bhs} = 1,520$, $r_{GI} = .855$. This difference between .859 and .855 (.004 points) is our best estimate of the loss of accuracy due to bull X herd-year-season interaction ($\hat{\sigma}^2_{bhs}$) alone. This estimated loss of accuracy (due to $\hat{\sigma}^2_{bhs}$) is only 2.85% of that due to all sources.

Furthermore, even when $\hat{\sigma}^2_{bhs} = 8,000$, which is as large as the true component is likely to be, bull X herd-year-season interaction is still responsible for only an estimated 13.04% of the total "inaccuracy" in the index.

Since $\hat{\sigma}^2_{bhs}$ seems to be of such minor importance as a percent of the total variance and in the degree to which it
is likely to affect the accuracy of an index, it seems that this interaction can be ignored when designing bull-testing programs using data of this nature. Other factors ($\sigma_{b}^{2}$, $\sigma_{hs}^{2}$ and $\sigma_{e}^{2}$) have much more influence than $\sigma_{bhs}^{2}$ on index-accuracy. We are justified in giving these other factors more attention not only because of this greater influence which they have on the accuracy of the index but also, as was pointed out on pages 94 and 97, because reducing the influence of these factors will tend, "automatically", to reduce the influence of $\sigma_{bhs}^{2}$.
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ACKNOWLEDGEMENTS

I am deeply grateful to Dr. J. L. Lush, and to Mrs. Lush, for the innumerable favors and kindnesses which they have bestowed on me since I came to Ames in 1959. Without Dr. Lush's direction and criticism this thesis would not have been possible in its present form.

A special "Thank you" is due to Dr. A. E. Freeman for his willing counsel and assistance which were a tremendous help during the analysis of the data.

Dr. D. L. Harris was a friend as well as a teacher and his interest and enthusiasm were very stimulating.

Dr. J. O'Mara deserves more than a passing word of thanks. I shall always remember his kindness, sincerity and understanding and the encouragement which he gave me on many occasions.

Thanks are due to Dr. J. B. Ruane of University College Dublin for permitting leave of absence during the final writing and presentation of the thesis and for advice which he has given me when I was an undergraduate at that college.

Lastly, I wish to thank Mr. Wallace Taylor (who, I hope, will soon be Dr. Taylor) of the Dairy Extension Service for supplying the data and for explaining much about the systems of milk-recording, etc., which have been used in the U. S. and which were new to me at that time.
APPENDIX I

A convenient method which can be used for selecting one or more observations from a number of observations within a subclass is as follows: Set up a procedure to generate a random variable and use this variable to select each observation, using a different random variable for each selection made. In the present study, the "power residue" method was used to generate these random variables. The background theory, statistical considerations and programming procedures for this method are discussed in detail by International Business Machines Corporation (1959). The procedure, when used on a computer with word size of 10 positions (e.g. IBM 650), gives random integers of 10 digits, which, when divided by $10^{10}$, gives random variables between 0 and 1 with uniform distribution.

Having selected a random variable, the particular individual between 1 and $n$ ($n$ being the number in the subclass) which corresponds to the random variable between 0 and 1, is identified by simply multiplying the random variable by $n$, adding 1 and dropping the digits after the decimal point. Thus, if the random integer obtained by the power residue procedure equals $X$, it is a random variable between 0 and $10^b$. 

where \( b \) = the number of digits in the variable. It is converted from a random variable between 0 and \( 10^b \) to random variable between 0 and 1 by dividing by \( 10^b \). As an example, if \( X = 4 \) when \( b = 1 \), the random variable between 0 and 1 = .4 and the corresponding randomly selected individual in a subclass of size 17 = 7. In that case the seventh individual would be chosen.

This procedure is convenient from the point of view of computer programming and from the point of view of varying numbers of observations within the subclasses.
APPENDIX II

The 3,836 bull-groups were compared, each group with all of the others in turn, with respect to the herd-year-seasons in which they were represented. The control-panel for the collator was wired as shown in Fig. 8. The data-cards were sequenced with respect to herd-year-seasons within bull and then sequence-checked prior to the operation. No method could be found to sequence-check the cards as they passed through the machine while the desired operation was being performed.

A master-card was placed immediately behind each bull-group, separating it from the following group. Each master-card was punched with 9's in the herd-year-season-field and an X-punch in column 70. The purpose of the 9's in the herd-year-season-field was to delay the introduction of the next bull-group to the comparing unit until the master-card on the opposite side had also reached the comparing unit. Then, when the master-card, also punched with 9's, entered the comparing unit on the opposite side, an equal comparison caused both master-cards to be fed simultaneously, thus causing the introduction of the next two bull-groups into both sides of the comparing unit simultaneously. The purpose of the X-70 was to
Fig. 8. Control-panel wiring for I.B.M. 088 collator
cause selective stacking of the master-cards. An impulse from the "normal" hubs of the "equal-comparison"-section of the comparing unit caused the "equal-comparison" detail-cards, since they were non-X-cards, to be fed simultaneously into pocket 3.

However, master-cards, even though they were "equal" (being punched with 9's), could not be stacked in pocket 3 because they would be needed again as master-cards for the next run and therefore must be stacked in pockets 2 and 4 with the low secondaries and low primaries respectively. This was accomplished by selective stacking using the X-70 punch.

The master-cards having been inserted, the data cards were divided into two decks with half of the bull-groups in each deck.

As an example of the scheme which was followed in order to compare each bull group with every other bull group in turn, assume that bull groups A-G were in deck 1 and bull groups H-N in deck 2. These are stacked in the collator as shown in Fig. 9.

Comparisons were made as follows. (↔ reads "is compared with").
In run's 2, 4, 6..., two groups do not figure in the comparing procedure. If the number of groups were an "odd" number then only one would have been removed for runs 2, 4, 6, 8... .

In order to compare each bull group with each other bull group in turn n-1 runs must be made, where n is the number of bull groups.
Pocket 3 receives Non-X, "equal-comparison" cards.

Pocket 2 receives (a) Non-X, low primaries.

(b) X-punched-master cards from primary feed.

Pocket 4 receives (a) Non-X, low secondaries.

(b) X-punched master-cards from secondary feed.

Fig. 9. Schematic diagram of I.B.M. 088 collator set-up for comparing bull-groups (Details of this diagram are discussed by International Business Machines Corporation (1960).)
APPENDIX III

Falconer (1952 and 1960) suggested using "the genetic correlation" in interpreting the importance of genetic-environmental interactions. He stated that "When so formulated [in terms of the genetic correlation] the genetic aspect of the situation [that is, influence of interaction on selection under an environment different from that in which the offspring are to live] becomes clear, and a quantitative evaluation of the efficacy of different methods of selection may be easily obtained by the procedures already devised for dealing with genetic correlation".

The genetic correlation figured in the mathematics used by Dickerson and Hazel (1944) and Lerner (1950) when discussing the genetic progress expected in a particular trait through selection in a related trait. It is assumed that the genetic correlation referred to above is the product-moment genetic correlation (denoted here by $\rho_G$). Lerner (1958), Falconer (1952 and 1960), Robertson (1959), Kidwell et al. (1964) used the intra-class genetic correlation (denoted here by $\rho_I$) when discussing the genetic progress one expects to attain in a particular "trait" in one environment through selection in another.
We wish to emphasize two points in this appendix:

(a) \( p \) need not be equal to \( P \), (although usually they are not very different) and (b) even though \( p \) may be useful as a measure of the magnitude of genetic-environmental interaction, it is not the best measure of association.

Let us assume that the model describing the factors affecting the true production of the \( i^{th} \) genetic material in the \( j^{th} \) environment is

\[
Y_{ij} = G_{ij} + t_j, \quad (i = 1, 2, \ldots, a; j = 1, 2)
\]

where \( G_{ij} \) = genetic effect of the \( i^{th} \) genetic material in the \( j^{th} \) environment,

\( t_j \) = effect of the \( j^{th} \) environment.

\[
E[G_{ij} t_j] = E[t_j G_{ij}] = 0.
\]

Product-moment genetic correlation is defined as

\[
\frac{\sigma_{G_{ij}'}}{\sigma_{G_{ij}}} = E[G_{ij} G_{ij}'] = \text{expected value of the covariance between the genetic effects of the } i^{th} \text{ genetic material in two different environments, } j \text{ and } j'.
\]

\[
\sigma^2_{G_j} = E[G_{ij}^2 | j] = \text{expected variance among genetic effects, } G_{ij} \quad (i = 1, 2, \ldots, a), \text{ within the } j^{th} \text{ environment}.
\]

Let us assume, further, that \( G_{ij} = g_i + (gt)_{ij} \).
\( g_i \) is the average genetic merit of the \( i^{th} \) genetic material, averaged over all environments in which it is represented.

\((gt)_{ij}\) is the effect of interaction between the \( i^{th} \) genetic material and the \( j^{th} \) environment.

If, as \( i \) varies from 1 to \( a \), (i) \( E[g_i(gt)_{ij}] = E[g_i(gt)_{ij}'] = 0 \) (ii) \( E[g_i^2] = \sigma_G^2 \) and (iii) \( E[(gt)^2_{ij}] = E[(gt)^2_{ij}] = \sigma_{GE}^2 \), \( E[G_{ij}^2] \) and \( E[gt_{ij}] = \sigma_G^2 + \sigma_{GE}^2 \).

Then, \( \sigma_{Gj}^2 \) would be equal to \( \frac{\sigma_G^2}{\sigma_G^2 + \sigma_{GE}^2} \), which is defined as the intra-class genetic correlation. The product-moment correlation need not be equal to the intra-class correlation unless these assumptions are true. Assuming that they are true does not make them true and ignoring them can result in one using, incorrectly, \( \rho_I \) as a measure of association.

It is entirely possible for interaction to be real and, at the same time, it is possible for the degree of association between the genetic merits in both environments to be perfect (positively or negatively). For example, in illustrations A and B below, the "surfaces" which portray the responses in the trait under consideration (when the different genetic materials are placed in environments \( E_1 \) and \( E_2 \) respectively) are straight lines.
In A, and also in B, the degree of association between the genetic merits in $E_1$ and $E_2$, respectively, is $-1$ and $+1$. In both cases, $\rho_G$ (in absolute value) = 1 but $\rho_I$ (in absolute value) is less than unity.

Obviously, in these cases the assumptions that $E[g_i(gt)_{ij}]$, $E[g_i'(gt)_{ij}]$ and $E[(gt)_{ij}(gt)_{ij}] = 0$ are not true. Under this situation, $\rho_G$ and $\rho_I$, as they are defined above, are not equal.

For this reason, one should be cautious in using $\rho_I$ as a measure of association without regard for possible errors in the assumptions. In most cases where one would ordinarily use these methods, the difference between $\rho_G$ and $\rho_I$ is small.
On the other hand, where degree of association is the basis of a particular concept, the assumptions involved in \( p_I \) must certainly be borne in mind.
APPENDIX IV

Referring to the discussion on pages 93 and 94,

\[ I_f = \frac{1}{\Sigma(1)} \sum_j \left[ \overline{Y_{fj}} - \overline{SA_{fj}} \right] \]

\( \overline{Y_{fj}} \) = daughter-average for the \( f \)th bull in the \( j \)th herd-year-season,

\[ = \mu + b_f + hs_j + (bhs)_{fj} + \Sigma e_{fjk} \frac{k}{N_{fj}} \]

\( \overline{SA_{fj}} \) = stablemate-average for the \( f \)th bull in the \( j \)th herd-year-season, that is, average production of cows in the \( j \)th herd-year-season that are not daughters of the \( f \)th bull.

\[ = \mu + \Sigma N_{s_j} b_s + hs_j + \Sigma N_{s_j} (bhs)_{s_j} + \Sigma \Sigma e_{sjk} \frac{k}{s_{s_j}} \]

\( N_{fj} \) is the number of offspring which the \( f \)th (test) bull has in the \( j \)th herd-year-season.

\[ \overline{Y_{fj}} - \overline{SA_{fj}} = b_f - \sum_s \frac{N_{s_j} b_s}{\Sigma N_{s_j}} + (bhs)_{fj} - \sum_s \frac{N_{s_j} (bhs)_{s_j}}{\Sigma N_{s_j}} \]
\[
I_f = \frac{1}{\Sigma(1)} \sum_j \left[ V_{fj} - \frac{1}{N_{fj}} \sum_s \frac{e_{sjk}}{N_{sj}} \right] = b_f - \frac{1}{\Sigma(1)} \sum_j \sum_s \frac{N_{sj}b_s}{N_{sj}} + \\
\frac{1}{\Sigma(1)} \sum_j (bhs)_{fj} - \frac{1}{\Sigma(1)} \sum_j \sum_s \frac{N_{sj}(bhs)_{sj}}{N_{sj}} + \\
\frac{1}{\Sigma(1)} \sum_j \sum_s \frac{e_{fjk}}{N_{fj}} - \frac{1}{\Sigma(1)} \sum_j \sum_s \frac{e_{sjk}}{N_{sj}}
\]

\[
\hat{V}(I) = \hat{V}(b_f) + \sum_s \left\{ \frac{1}{\Sigma(1)} \sum_j \frac{N_{sj}}{N_{sj}} \right\}^2 \hat{V}(b_s) + \\
\sum_j \left\{ \frac{1}{\Sigma(1)} \right\}^2 \hat{V}((bhs)_{fj}) + \sum_s \sum_j \left\{ \frac{N_{sj}}{\Sigma(1)N_{sj}} \right\}^2 \hat{V}((bhs)_{sj}) + \\
\sum_j \sum_k \left\{ \frac{1}{\Sigma(1)N_{fj}} \right\}^2 \hat{V}(e_{fjk}) + \\
\sum_s \sum_j \sum_k \left\{ \frac{1}{\Sigma(1)N_{sj}} \right\}^2 \hat{V}(e_{sjk})
\]

whence,
\[
\hat{V}(I) = \left[ 1 + \frac{1}{(\Sigma(1))^2} \sum_j \left\{ \sum_s \left( \frac{N_{sj}}{N_{sj}} \right) \right\}^2 \right]^2 \sigma_b^2 + 
\]
\[
\left\{ \frac{1}{\Sigma (l)} + \frac{1}{(\Sigma (l))^2} \sum_{j} \frac{\Sigma N_{sj}^2}{j (\Sigma N_{sj})^2} \right\} \sigma_{bhs}^2 + \\
\frac{1}{(\Sigma (l))^2} \left[ \sum_{j} \frac{1}{N_{fj}} + \sum_{j} \frac{1}{\Sigma N_{sj}} \right] \sigma_{e}^2.
\]

As the number of stablemates in each herd-year-season increases,

\[
\Sigma \left\{ \sum_{j} \left( \frac{N_{sj}}{\Sigma N_{sj}} \right)^2 \right\}, \quad \sum_{j} \frac{\Sigma N_{sj}^2}{(\Sigma N_{sj})^2} \quad \text{and} \quad \frac{1}{(\Sigma (l))^2} \sum_{j} \frac{1}{\Sigma N_{sj}}
\]

become very small. If the test-bull has n daughters "tested" in each of k herd-year-seasons, 
\[ \hat{V}(I) \text{ approaches } \hat{\sigma}_b^2 + \frac{\hat{\sigma}_{bhs}^2}{k} + \frac{\hat{\sigma}_e^2}{nk} \]

and \( r_{GI} \) approaches 
\[
\frac{\hat{\sigma}_b}{\sqrt{\hat{\sigma}_b^2 + \frac{\hat{\sigma}_{bhs}^2}{k} + \frac{\hat{\sigma}_e^2}{nk}}}.
\]