ABSTRACT

INTERACTIONS OF SIRE WITH MATERNAL GRANDSIRE IN MICHIGAN HOLSTEINS

by Basil Ralph Eastwood

First available Michigan DHIA lactations from 3798 Holstein-Friesian cows whose sire and maternal grandsire were in artificial service were studied to measure interactions between sire and maternal grandsire for productive traits. Records used were deviations of 305 day-2X-mature equivalent lactations from the 305-2X-ME lactation herd average. There were represented 225 sires and 229 maternal grandsires. Components of variance were calculated from the model:

$$Y_{j\ell m} = \mu + c_j + f_\ell + (cf)_{j\ell} + \gamma_{j\ell} + \theta_{j\ell} + T_{j\ell} + e_{j\ell m}$$

where c is sire, f is maternal grandsire, (cf) is the interaction of sire with maternal grandsire, γ is a reciprocal interaction effect, θ is a specific inbreeding effect, T is a general effect of inbreeding, and e is an error term. All components are uncorrelated random variables. Components were also calculated for a model which eliminated the inbreds ($\theta_{j\ell}$ and $T_{j\ell}$) and for a model with only simple interaction.

The standard deviations for milk and fat production were 2,100 and 77 lbs. Sire and maternal grandsire effects accounted for 5.7 and 1.9 percent of the variation in milk production and 5.9 and 2.5 percent of the variation in fat production.

Negative components of variance were obtained for reciprocal effect and for both inbreeding effects. A large positive estimate was obtained for the interaction of sire with maternal grandsire. This component became negative, however, when the three negative components were set equal to zero and the sire, maternal grandsire, and interaction components were re-estimated. The best estimate of the contribution of the variance components γ, θ, T, and (cf) to the overall variation in these data is zero.

The unbalanced nature of these data with only 5 percent of the subclasses filled has apparently prevented an interaction from being detected if one truly exists.

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INTRODUCTION

The genetic contribution to the variation in any trait may be divided into additive and non-additive fractions. Sprague and Tatum (43) suggested in 1942 that in any previously unselected population the genes with additive effects are more common or produce greater effects than genes with dominance or epistatic effects. After many generations of selection, however, the relative importance of the non-additive fraction increases. As differences in additive effects are eliminated, dominance and epistatic effects become relatively more important.

It is doubtful that any measurable decrease in the additive genetic variation for productive traits of dairy cattle will occur for many generations. Although selection procedures are becoming constantly improved, the long generation interval and small selection differential hold the average rate of genetic improvement at a rather low level. If non-additive genetic effects are important, however, maximum progress may be obtained only through use of specific combinations of individuals or lines.

Present sire evaluation procedures are more effective if the mates of a sire are a random sample of the cow population for that breed. It is improbable that many dairymen select their sires at random, and most dairymen use only one or a few sires each year. Therefore, the mates of some sires could be highly related to each other and very atypical of the population. A genetic correlation of the sire with his mates could greatly bias the evaluation of that sire and lead to an incorrect decision regarding his future use. Such correlations may be referred to as specific combining ability or nicking. If these correlations are important, sire evaluations would need to consider the genetic make-up of the group of mates that produced the progeny, and recommendations for future use of that sire would need to specify the relative groups to which he should be mated.

The Genetic Basis of Specific Combining Ability

Sprague and Tatum (43) first used the term "specific combining ability" in 1942 in their discussion of single crosses of corn. These workers used specific combining ability to designate "those cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved". The term "general combining ability" was used to designate the "average performance of a line in hybrid combinations".

The observed differences in specific combining abilities between individuals or lines may come from several sources. Dominance deviations are one source. If the favored gene is dominant, the heterozygote

Aa will produce better offspring when mated to AA than when mated to Aa and much better than when mated to aa.

Larger differences in specific combining ability may be caused by overdominance. The aa individuals will then appear superior when used on AA mates, but inferior when used on aa mates. The contribution to specific combining ability due to overdominance may become more extreme as the number of genes increases.

Another source of differences in specific combining abilities is epistasis. Epistasis has been defined as interaction between non-allelic genes. Examples of non-additive combinations of the effects of genes such as inhibiting genes, threshold effects, and the case in which the phenotypic optimum is a genetic intermediate may contribute to specific combining ability. (31)

When specific combining ability is estimated in small populations confusion may arise due to other causes of variation contributing to the estimate. Chance at Mendelian segregation does not cause differences in specific combining ability, however it may contribute to the estimate of specific combining ability. Since the effects of chance at Mendelian segregation would be reduced with greater numbers of observations, chance has less effect on estimates of general combining ability than on estimates of specific combining ability.

The estimate of specific combining ability can also include differences caused by uncontrolled variations in the environment.

These environmental variations may cause the phenotypes of the offspring from a cross to average higher or lower than that which corresponds to their average genetic values. Both genotype-environment interactions and random environmental variations may contribute to an estimate of specific combining ability.

The Present Study

This study was undertaken to ascertain whether a sire produces superior offspring when mated to daughters of certain other sires than would be expected from the average performance of daughters of the sires involved. More specifically, a good estimate of specific combining ability was sought from the component of variance for interaction of sire by maternal grandsire in production of milk and fat.

REVIEW OF LITERATURE

Much of the research on specific combining ability has been with plants. Some laboratory work with rats, mice, Tribolium, and Drosophila has been done to evaluate combining abilities. Only relatively recently, however, have breeding experiments with dairy cattle been attempted to estimate the size of the "specific" effects commonly known as "nicking".

General and specific combining ability among inbred lines of dairy cattle are being studied at the Ohio and Minnesota stations in cooperation with the United States Department of Agriculture. The South Dakota and Wisconsin stations are studying the effects of inbreeding on economic traits in eight inbred lines of Holstein cattle. These inbred lines will be crossed and combining abilities measured. Crossbreeding experiments are being engaged in at Illinois, Indiana, and the Beltsville, Maryland, Station of the United States Department of Agriculture.

Each of these studies should provide needed data on specific combining ability for productive traits in dairy cattle in addition to other breeding information. Each is closely controlled but must necessarily deal with relatively few animals.

Larger numbers of dairy cattle may be utilized to study specific combining ability by using existing records. Several studies, including the present one, are of this nature.

Research with Plants

Many workers have studied specific combining ability in various species of plants. In general, they have found varying (but presumably real in many cases) amounts of specific effects.

Carnahan *et al*. (8) in studying combining abilities in alfalfa for seedling vigor and fall growth habit in the year of establishment found the variance from general combining ability was much higher than variance from specific combining ability. They concluded that evaluation for interactions of genotype with location for these traits should receive as much or more attention than that devoted to determining specific combining ability.

Morley *et al*. (38) found the component of variance for specific combining ability was approximately equal to that for general combining ability in their study of summer production of hybrids between 10 alfalfa varieties. For winter production, however, the variance for general was considerably greater than that for specific.

In a study of orchard grass, Oldemeyer and Hansen (40) noted considerable variation among the single crosses for the respective parents and suggested that this indicated the expression of specific combining ability.

Allard (1) has described four general types of tests for combining ability in plants: the open-pollinated progeny test, top-cross test, polycross test, and the single-cross test. The first three of these measure general combining ability while the single-cross test measures the combining ability of particular pairs of parents (clones, lines, etc.). The single-cross is the most sophisticated of the four and also lends itself to animal breeding experiments.

If all of the possible single crosses among n selected parents are made, the resulting set of crosses is called a diallel cross. The average combining ability of any parent may be calculated from single-cross data as the mean performance of that parent in its crosses. Average combining ability becomes more and more similar to general combining ability as the number of single crosses involving that parent is increased.

Recurrent Selection. - Hybrid varieties of cross pollinated crops have been universally developed by selection of desirable plants from heterozygous sources, inbreeding the progenies of these plants to increase homozygosity, and producing F_1 hybrids by crossing the most productive of these inbreds. The early maize hybrids were produced by isolating inbred lines directly from the old open-pollinated varieties. Later, "second-cycle" hybrids were produced which utilized inbreds isolated from crosses between superior inbred lines.

This eventually led to development in the 1940's of the breeding system commonly referred to as recurrent selection. In recurrent selection in maize, plants from a heterozygous source are self-pollinated and are evaluated for some trait. Superior plants are selected, all possible intercrosses are made, and the resulting intercross population serves as source material for recurrent cycles of selection and intercrossing.

Four types of recurrent selection generally recognized are: simple recurrent selection, recurrent selection for general combining ability, recurrent selection for specific combining ability, and reciprocal recurrent selection.

In simple recurrent selection no test crosses are made; the plants are discarded or propagated on the basis of their phenotypes or phenotypic scores on their selfed progeny. This system is not effective in selecting for combining ability for yield. The other three types of recurrent selection utilize test crosses to measure combining ability. In recurrent selection for general combining ability a tester with a broad genetic base is used to rate the plants on their general combining ability. A tester with a narrow genetic base (an inbred line) is employed to rate a group of plants on specific combining ability in recurrent selection for specific combining ability. Reciprocal recurrent selection allows for selection for both general and specific combining abilities and utilizes two heterozygous source populations -- each being the tester for the other. An excellent discussion of these systems is given by Allard (1).

Recurrent selection for specific combining ability was proposed in 1945 by Hull (22) to take advantage of that part of heterosis resulting from nonlinear interactions of both allelic and non-allelic genes, i.e.

dominance and epistasis. The outcome of this selection program would presumably be to develop a line which approaches the opposite extreme in gene frequency from the inbred line used as a tester. The line thus produced would then be crossed with the tester to produce commercial hybrids.

The other recurrent selection system which places some emphasis on specific combining ability is reciprocal recurrent selection, proposed by Comstock *et al*. in 1949 (9). These workers compared the efficiency of reciprocal recurrent selection with that of recurrent selection for general combining ability and recurrent selection for specific combining ability on a theoretical basis. The assumptions were that only two alleles per locus were possible, that no epistasis was present, and that the relative frequencies of genotypes at linked loci were at equilibrium.

In general, the conclusion reached from this theoretical analysis of efficiencies was that reciprocal recurrent selection is at least as effective as recurrent selection for general combining ability and recurrent selection for specific combining ability for all situations considered. Where overdominance is important, reciprocal recurrent selection and recurrent selection for specific combining ability are clearly superior to recurrent selection for general combining ability. In the case of partial or incomplete dominance, reciprocal recurrent selection and recurrent selection for general combining ability are superior to recurrent selection for specific combining ability. The presence of epistatic interaction, multiple alleles, or linkage disequilibrium would favor reciprocal recurrent selection and recurrent selection for specific combining ability (9). From this study reciprocal recurrent selection is superior to the other recurrent selection methods for use on populations where both general and specific effects are expected to be present.

In a population of lines previously unselected for combining abilities, genes with additive effects may be more common or produce larger effects than genes with dominance or epistatic effects. In material previously selected for genes having additive effects, genes with dominance and epistatic effects become relatively more important as differences in additive effects are eliminated (43).

Lonnquist and Rumbaugh (30) presented data in 1958 from their work with corn to support the common practice of testing new lines first for general combining ability and following this with tests for specific combining ability. Population improvement was greater when selection was based on a tester having a broad genetic base.

Laboratory Experiments

Several experiments with rats and mice have provided information from diallel crosses on the relative importance of general and specific effects for growth characteristics in these animals.

Using four inbred lines of rats, Kidwell *et al*. (28) made all sixteen possible mating combinations including inbreds and reciprocal crosses. The effects of sex, lines, and maternal ability on body weight were highly significant at 70 days but not at 90. There was no evidence of specific combining ability or sex linkage effects; however, an interaction between maternal effects and mating system was indicated for 28 day weight. Differences in general combining ability were highly significant at 28 days but not significant at 70 days. The authors concluded that preweaning differences in maternal ability and a post weaning compensating effect might also account for these results.

In a somewhat similar experiment with mice, Carmon (7) used weights of 1824 individuals from 312 first litters of all possible crosses among 4 lines of mice. Heterosis measured as a comparison between linebreds and crossbreds was highly significant. General combining ability, maternal effects, and sex linkage effects were significant, but specific combining ability was not.

The 72 possible single crosses among nine inbred lines of mice were made and studied by Eaton _et al_. (12). They found that specific combining ability effects were important though not significant for total litter weight but unimportant for individual mouse weights. Line differences were important only for mouse weight. Line differences in maternal influence were important for both litter size and mouse weight but because of a -.85 correlation between these components, were non-existent for total litter weight at 45 days. Ratios of variances from specific and general cross performance, assuming epistasis negligible, suggested superiority of the heterozygote for viability and total litter weight but little dominance for genes influencing mouse weights. Regressions of F_1 on inbred parent within common parent lines indicated much dominance for 45 day weight, however.

Poultry Breeding Experiments

Many experiments have been conducted with poultry to determine the relative importance of general and specific effects and also to study the effectiveness of various systems of selection.

Bell and co-workers (3) in their discussion of poultry breeding systems concluded that recurrent selection for nicking would increase the frequencies of desirable genes more rapidly than would reciprocal selection but would have a somewhat lower theoretical limit of improvement. Reciprocal selection would probably be more practical since superior strain and breed crosses could be utilized as foundation stocks.

A number of experiments crossing inbred and non-inbred lines have been carried out with poultry. Goto and Nordskog (15) estimated variances of general and specific combining abilities, maternal effects, and reciprocal effects for inbred linecrosses. General combining ability was more important than specific effects for all nine characters studied with the possible exceptions of percent brooder house mortality, percent hatch of all eggs, and percent laying house mortality.

Hill and Nordskog (21) studied nine factors in linecrosses and found an appreciable amount of specific combining ability present only for March body weight and broodiness.

Another study of linecrosses in poultry, conducted by Hutt and Cole (23), utilized two strains of Leghorns with low inbreeding coefficients of thirteen and eight percent. The resulting crosses consistently excelled both parent strains in hatchability, early maturity, egg production, size of eggs, and size of birds. The reciprocal crosses were equally as good. These workers suggested that enough heterosis might be achieved from crosses between lines of low inbreeding to eliminate the necessity of developing highly inbred lines.

Wyatt (47) found little relationship between topcross performance and inbred performance for the five traits studied. Since the relationship between topcross and inbred performance is a function of heritability, this indicates a relatively small contribution by additive genes to the variance between lines.

The different testers used failed to rank the inbred lines in the same order as measured by the average performance of the topcross progeny. This was further evidence that genes with additive effects contributed little to the variance between lines. Evidence of an important contribution by dominance and non-linear gene interactions was given by a significant line x tester interaction for hatchability and weight at six weeks. Since inbreeding decline is evidence of some kind of genetic variance, Wyatt concluded that non-additive genetic variance was probably important in these lines.

If heritability of individual differences is one hundred percent, the linear regression of topcross on inbred parents would be five-tenths. Glazener and Blow (14) found a regression value of three-tenths for weight in broiler production and reasoned that this difference between five-tenths and three-tenths could be due to interline non-additive genetic variance and intraline genetic and environmental variance. With large numbers of chicks in each line, the differences would reflect largely interline non-additive genetic effects. They concluded that since heritability of weight was high, a large portion of the variance between line means was the result of genes acting in an additive manner. However, since the inbred line x tester interaction was significant, dominance and gene interactions may also play an important role.

An analysis of variance to determine the types of gene action involved in the inheritance of ten-week body weight and breast angle in broilers was carried out by Brunson *et al*. (5). Approximately 43 percent of the total variance in body weight was due to genetic differences. This was subdivided into 41 percent for additive and 2 percent for non-additive genes. Sex linked genes accounted for 10 percent of the total variance and maternal effects for 2 percent.

Maw (35) found that the crossing of unrelated inbred lines for seeming lower mortality and increased egg production appeared superior to topcrosses, related inbred crosses, and random-bred leghorns kept as controls.

To separate the total phenotypic variance into additive genetic, non-additive genetic, and environmental variance, Kan *et al*. (27) utilized an analysis of variance components on six broiler traits from a series of diallel matings. The non-additive genetic effects were then studied by a test of significance of the interaction mean square and by estimating the interaction component. Of the six traits studied, non-additive gene effects contributed to the variation in shank length, heel length, body depth, and possibly gain in weight but had no apparent influence on 4 and 9 week body weight.

Another study of diallel matings using eight week body weight was made by Kan *et al*. (26). A significant interaction component was found but was overestimated due to small families of 12 hens per pen.

Jerome *et al*. (24) utilized Henderson's method I for variance component analysis with the following model:

$$Y_{hijk} = \mu + a_h + s_i + d_j + (sd)_{ij} + e_{hijk}$$

where "a" is hatch; "s" is sire; "d" is dam; and "e" is a random error term. A large amount of dominance variance was found for total egg production and fall body weight. The portions of genetic variance in the different components were as follows where "10" signifies additive, "01" -- dominance, "20" -- additive by additive, "11" -- additive by dominance, and "02" -- dominance by dominance:

TABLE 1. Fractions of Genetic Variance Contained (Jerome *et al.*, 24)

Components	σ^2_{10}	σ^2_{01}	σ^2_{20}	σ^2_{11}	σ^2_{02}	
Sire	1/4		1/16			Between full sib groups
Dam	1/4		1/16			
Sire x Dam		1/4	1/8	1/8	1/16	
Full Sibs	1/2	3/4	3/4	7/8	15/16	Within full sibs
	1	1	1	1	1	

Hazel and Lamoreux (17) studied three sets of diallel matings to estimate the importance of nicking. About five percent of the variation in body weight was due to maternal effects; however, sexual maturity was not influenced at all by maternal effects. Nicking was a minor factor in this study and seemed likely to be unimportant generally in non-inbred matings. The method used in this study was an analysis of variance to separate the total variation in each series of matings into three parts: I. differences within families, II. differences between dams mated to the same sire, and III. differences between sires. To examine the importance of the three sources of variation as they relate to differences between individual birds, the mean squares from the combined data were reduced to components of variation. The variance among unrelated birds was W + D + I + S, and the variance among paternal half-sisters which have different dams but the same sire was W + D + I where W is the variance expected between full sisters, D is the variance associated directly with the dams, I is the variance attributed to nicking between sires and dams, and S is the contribution from sires. In a group of birds some of which are related, correction must be made for the average number of full sibs or half sibs.

Research with Swine

A large volume of information is available on crossbreeding of swine and heterosis and its converse, inbreeding degeneration. A considerable amount of commercial application has been made of the general principles elucidated by these reports. The research reported here, however, will be limited to studies of line crosses within breeds and attempts to study specific combining ability.

Some of the early work in this area of investigation was done by Henderson (19) in 1949. Single crosses among 12 inbred lines of Poland China swine were studied for litter number and weight at 0, 21, 56, and 154 days. Specific effects (dominance and epistasis) accounted for five to fifteen percent of the variation among the crosses. The relative efficiencies of line cross and topcross tests for estimating general combining ability were studied. The line cross not only estimates general combining ability more efficiently, but it also furnishes information concerning maternal, specific, and sex-linked effects.

Bradford *et al*. (4) studied two-line crosses of inbred lines of swine and found maternal effects were more important than general combining ability for 56-day pig weights. The opposite was true, however, for five-month pig weights. Specific combining ability was not important for either 56-day or 5-month pig weights. If maternal effects are present, certain lines should be used only as female parents and certain others as male parents. There appeared to be a negative genetic association between the additive effects in the pig and maternal effects of the lines. This type of association could explain the ineffectiveness of selection for overall performance and would give support to the practice of selecting for cross performance.

Magee and Hazel (32) in 1959 estimated differences in the general combining abilities and the general maternal effects from 2137 three-line cross pigs of 12 Poland China inbred lines. Differences in general combining ability were statistically significant and accounted for 4 percent of the variation among pigs of the same season and farm. The maternal effects of the lines and the interactions involving specific effects were not statistically significant. The ratio $\frac{G}{E + L + G} = \frac{27}{450 + 228 + 27} = .04$ indicated that pigs from the same three-way cross (but from different litters) will vary 4 percent less in their weights than unrelated pigs of the same season-farm group. In this ratio G = general combining ability; L = litters within subclasses; and E = pigs within litters.

Two hundred eighteen litters from crosses among six inbred lines of swine were studied by Hetzer et al. (20) to determine differences in general and specific combining abilities. Differences in general combining ability were significant for only one pre-weaning trait, litter weight at 56 days. They were significant, however, for all post-weaning growth traits and for all carcass traits measured except dressing percentages, accounting for from 5 to 7 and 6 to 16 percent of the variation in these two sets of traits. Maternal effects were not significant for litter and pig weight at 56 days, pig weight at 140 days, daily gain, dressing percentage, yield of bacon, and yield of fat cuts, accounting for 7 to 21 percent of the variation in the latter five characteristics. Specific combining ability was significant only for yield of bacon.

Wilson et al. (46) obtained a significant line x season interaction in their study of the influence of sire and line of breeding on sow productivity but attributed this to the small number (2.8 to 3.5) of daughters per sire.

Beef Cattle Research

The long generation interval and the expense involved in breeding experiments with beef cattle greatly limit the volume of information available on specific combining ability. O'Bleness et al. (39)

studied the weaning weights of single cross animals from 13 inbred lines crossed with each other and crossed with an outbred control group. The differences between lines of sire and between lines of dam were significant at the 0.01 level. Least square estimates were used to rank the lines used as sires and as dams. The low rank correlation coefficient of 0.11 showed that some lines in this study performed better as sire lines than they did as dam lines and vice versa.

Damon *et al*. (10) studied beef crossbreeding data with a rather sophisticated model. The data studied were 180 day weight, slaughter calf grade, slaughter grade, rate of gain on feed, and weight per day of age. General combining ability was significant for all five traits (1.3 to 18.7 percent). Heterosis and specific combining ability effects were significant for all but slaughter calf grade. Specific combining ability was especially important for rate of gain on feed and weight per day of age accounting for 21.0 percent and 27.4 percent of the variance among crosses. Maternal effects were significant for all except slaughter grade; however, sex-linked effects appeared to have little influence on these traits.

Another detailed model was used by Beal and Martin (2) in their study of crossbreeding dual purpose cattle. These workers used Red Dane, Red Poll, and Milking Shorthorn sires and dams. Breed of dam and breed of sire were highly significant for total milk production, persistency, and part-lactation production. The sire x dam (breeds) interaction was highly significant for total milk, persistency, and the early months of the lactation but tailed off to no significance the last two months of lactation.

Research with Dairy Cattle

An early study of specific combining ability in dairy cattle in this country was made in 1933 by Fohrman and Graves (13). These workers used Ayrshire A. R. records from daughters of 51 different sires that had each been used in at least two herds.

Only one bull had daughters significantly higher in one herd than in the other, leading to the conclusion that there was essentially no "nicking" present.

Heizer et al. (18) in 1938 studied records of two Holstein-Friesian sires used in one herd and three Guernsey sires used in another. Daughter-dam comparisons were calculated for each sire x maternal grandsire group to determine whether any nicking had occurred. Since considerable differences were found in the apparent success of the matings, it was concluded that some nicking had occurred in the sires and herds used in this study. Since some sires appeared to work best on closely related families, it was concluded that the results were probably the effect of complementary effects of genes (epistasis) rather than heterosis.

In 1940, Johnson et al. (25), using Register of Merit records of daughters of 17 Jersey sires having daughters in more than one herd, studied both daughter-dam comparisons and daughter averages to get at the question of nicking in dairy cattle. These workers found four sires to have large differences in production between herds, but after studying the situation further, they concluded that these differences were largely environmental.

Seath and Lush (41), also in 1940, used an analysis of variance on daughters of Kansas DHIA proven sires to determine whether nicking had occurred between sire and maternal grandsire. It was concluded that with the kind of data usually found in proving sires, nicking is not often important enough that the pedigrees of the daughters need consideration if the records of the dams are taken into account.

Wisconsin workers (37) using data from 187 Holstein heifers representing six sire lines and four systems of mating, found that sire line and system of mating significantly affected the age at which an animal reached puberty. The interaction of sire line with systems of mating, however, was not significant. In another study (33), these same workers found conception rate was significantly affected by the interaction of sire line with system of mating, suggesting the presence of non-additive gene action among the lines on conception rate.

A third study by these same workers, (34) using an analysis of variance of the first estrual-cycle length following calving in outbred and inbred cows, showed a significant interaction of sire line and system of mating, again indicating non-additive genetic effects.

Dickinson and Touchberry (11), in a study of the broader aspect of non-additive genetic effects involved in crossbreeding, found a considerable influence of heterosis on livability and concluded that crossbreeding dairy cattle may provide a means for immediate and marked improvement in herd health and longevity.

Verley and Touchberry (44), however, in the same year, studied seven measures of reproductive performance and found no significant differences between the purebred and crossbred animals for any of the seven. These measures of reproductive performance, therefore, did not seem to be greatly affected by non-additive gene action.

An authors' summary on Swedish research by Hansson et al. (16), using data from 12,897 Swedish Red and White and 10,926 Swedish Friesian heifers sired by 939 and 764 bulls, respectively, reported that nicking had no significant effect on the genetic improvement of first lactation milk yield.

Shreffler and Touchberry (42), in a study of the effects of crossbreeding on rate of growth in dairy cattle, found little evidence to suggest that the effects of crossbreeding on size are dependent on mating a specific sire of one breed to dams of another breed. Since the effects of system of mating, breed of sire, and breed of dam were relatively large, additive genetic factors were the predominant genetic influences upon rate of growth.

Several studies have been conducted to ascertain the importance of genotype -- environment interactions in dairy cattle. These studies have concentrated mainly on attempting to measure any sire by herd or sire by type of herd environment interaction that may have been present (6, 29, 45). The component for this interaction was nearly zero or negative in all cases. It was concluded that sires will be ranked about the same regardless of the herds or environments in which their daughters are located.

Although these studies with dairy cattle show results which vary from no interaction between sire and maternal grandsire to significant interaction, no evidence of a conclusive nature has been presented. Each study was hampered by lack of a sufficient number of animals or a definitive technique for measuring a sire by maternal grandsire interaction.

Non-additive genetic effects have been demonstrated for certain traits in many different plants and animals. In some cases breeding schemes have been devised to take advantage of this variation. The inconclusive results, high cost, relatively small numbers available, and long generation interval inherent in cattle breeding have made it generally unfeasible to develop a scheme for utilizing non-additive genetic effects.

SOURCE OF DATA

First available lactations from the Michigan Dairy Herd Improvement Association on 3798 Holstein-Friesian cows sired by bulls in artificial service and from dams who were also sired by A. I. bulls were utilized. The records were on a 305 day, twice-a-day milking, mature equivalent basis and were deviations from the 305-2X-ME lactation herd average.

A total of 225 sires and 229 maternal grandsires was involved in the study with the average number of daughters per sire being 16.88 (ranging from 1 to 268), and the average number of granddaughters per maternal grandsire being 16.58 (ranging from 1 to 176). There were 2555 sire by maternal grandsire subclasses filled, the average number of animals in each being 1.49 with a range of 1 to 19. A generalized representation of the data may be seen in Table 2.

TABLE 2. A generalized representation of the data.

	f_1	f_2	$\cdots$	f_ℓ	$\cdots$	$f_{q'}$	
c_1	$Y_{111}\ Y_{112}\cdots Y_{11t}$ $\Sigma = Y_{11\cdot}$	$Y_{121}\ Y_{122}\cdots Y_{12t}$ $\Sigma = Y_{12\cdot}$	$\cdots$	$Y_{1\ell 1}\ Y_{1\ell 2}\cdots Y_{1\ell t}$ $\Sigma = Y_{1\ell\cdot}$	$\cdots$	$Y_{1q'1}\ Y_{1q'2}\cdots Y_{1q't}$ $\Sigma = Y_{1q'\cdot}$	$\Sigma = Y_{1\cdot\cdot}$
c_2	$Y_{211}\ Y_{212}\cdots Y_{21t}$ $\Sigma = Y_{21\cdot}$	$Y_{221}\ Y_{222}\cdots Y_{22t}$ $\Sigma = Y_{22\cdot}$	$\cdots$	$Y_{2\ell 1}\ Y_{2\ell 2}\cdots Y_{2\ell t}$ $\Sigma = Y_{2\ell\cdot}$	$\cdots$	$Y_{2q'1}\ Y_{2q'2}\cdots Y_{2q't}$ $\Sigma = Y_{2q'\cdot}$	$\Sigma = Y_{2\cdot\cdot}$
$\vdots$	$\vdots$	$\vdots$		$\vdots$		$\vdots$	$\vdots$
c_j	$Y_{j11}\ Y_{j12}\cdots Y_{j1t}$ $\Sigma = Y_{j1\cdot}$	$Y_{j21}\ Y_{j22}\cdots Y_{j2t}$ $\Sigma = Y_{j2\cdot}$	$\cdots$	$Y_{j\ell 1}\ Y_{j\ell 2}\cdots Y_{j\ell t}$ $\Sigma = Y_{j\ell\cdot}$	$\cdots$	$Y_{jq'1}\ Y_{jq'2}\cdots Y_{jq't}$ $\Sigma = Y_{jq'\cdot}$	$\Sigma = Y_{j\cdot\cdot}$
$\vdots$	$\vdots$	$\vdots$		$\vdots$		$\vdots$	$\vdots$
c_q	$Y_{q11}\ Y_{q12}\cdots Y_{q1t}$ $\Sigma = Y_{q1\cdot}$	$Y_{q21}\ Y_{q22}\cdots Y_{q2t}$ $\Sigma = Y_{q2\cdot}$		$Y_{q\ell 1}\ Y_{q\ell 2}\cdots Y_{q\ell t}$ $\Sigma = Y_{q\ell\cdot}$		$Y_{qq'1}\ Y_{qq'2}\cdots Y_{qq't}$ $\Sigma = Y_{qq'\cdot}$	$\Sigma = Y_{q\cdot\cdot}$
	$\Sigma = Y_{\cdot 1\cdot}$	$\Sigma = Y_{\cdot 2\cdot}$	$\cdots$	$\Sigma = Y_{\cdot\ell\cdot}$	$\cdots$	$\Sigma = Y_{\cdot q'\cdot}$	$\Sigma = Y_{\cdots}$

c_j	are sires	$j = 1 \cdots$ maximum of q
f_ℓ	are maternal grandsires	$\ell = 1 \cdots$ maximum of q'
$Y_{j\ell m}$	are daughters (granddaughters)	$m = 1 \cdots$ maximum of t

MODEL AND ANALYSIS

The method used to calculate the components of variance was a modification of Henderson's method I described by McGilliard (36). The components of variance were calculated from the data in this study using the following model:

$$Y_{j\ell m} = \mu + c_j + f_\ell + (cf)_{j\ell} + \gamma_{j\ell} + \theta_{j\ell} + T_{j\ell} + e_{j\ell m}$$

Where:

μ is the overall population mean.

c_j is the amount the jth sire causes the average of his daughters to deviate from the average of daughters of all sires. $j = 1 \cdots q$

f_ℓ is the amount the ℓth maternal grandsire causes the average of his granddaughters to deviate from the average of granddaughters of all grandsires. $\ell = 1 \cdots q'$

$(cf)_{j\ell}$ is the amount the particular combination of sire $j(\ell)$ and maternal grandsire $\ell(j)$ causes the average of their daughters (granddaughters) to deviate from the average of all daughters (granddaughters) of c_j and f_ℓ and is such that $(cf)_{j\ell} = (cf)_{\ell j}$. $(cf)_{j\ell} = 0$ for $j = \ell$.

$\gamma_{j\ell}$ is the amount the particular combination of sire j and maternal grandsire ℓ causes the average of their daughters (granddaughters) to deviate from the average of all daughters (granddaughters) of the combinations $j\ell$ and ℓj and is such that $\gamma_{j\ell} = -\gamma_{\ell j}$.

$\theta_{j\ell}$ = 0 for $j \neq \ell$ and for $j = \ell$ is the amount that inbreeding to sire j (maternal grandsire ℓ) causes the average of these inbreds to deviate from the average of inbreds from all sires (maternal grandsires).

$T_{j\ell}$ = 0 for $j \neq \ell$ and for $j = \ell$ is the amount that inbreeding (sire x daughter matings) causes the average of all inbreds to deviate from μ. $T_{11} = T_{22} = \cdots T_{qq'}$

$e_{j\ell m}$ is a random effect assumed to be normally and independently distributed with a mean of zero and variance, σ_e^2. $m = 1 \cdots t$

All components of the model are uncorrelated random variables with zero expectation and with variances σ_c^2, σ_f^2, σ_{cf}^2, σ_γ^2, σ_θ^2, σ_T^2, and σ_e^2, respectively. The sums of squares and mean squares obtained in the analysis are found on the following pages.

TABLE 3. Expected coefficients of variances from the complete model in uncorrected sums of squares for milk.

Source	μ^2	σ_c^2	σ_f^2	σ_{cf}^2	σ_γ^2	σ_θ^2	σ_T^2	σ_e^2	S. S.
Grand Total	3798	3798	3798	3743	3743	55	3798	3798	411,394,929
c	3798	3798	341.3930	340.2997	340.2997	6.5001	1937.0002	225	248,633,053
f	3798	389.6692	3798	388.1426	388.1426	7.2417	1328.4587	229	241,653,200
(cf)	3743	3541.9218	3541.9218	3743	3541.9218	0	0	2267	329,509,231
(cf) C. T.	3743	88.9121	55.4953	3.3858	3.0850	0	0	1	223,696,110
θ	55	55	55	0	0	55	55	38	5,942,553
θ C. T.	55	1.9091	1.9091	0	0	1.9091	55	1	4,024,093
T	3798	90.8212	57.4044	3.3858	3.0850	1.9091	3798	2	227,720,204
γ	0	201.0782	201.0782	0	201.0782	0	0	250	5,382,992
General C. T.	3798	89.9713	55.8689	3.3368	3.0403	.0276	3689.5929	1	227,683,493

TABLE 4. Expected coefficients of variances from the complete model in corrected sums of squares for milk.

Source	σ_c^2	σ_f^2	σ_{cf}^2	σ_γ^2	σ_θ^2	σ_T^2	σ_e^2	S.S.
Grand Total	3708.0287	3742.1311	3739.6632	3739.9597	54.9724	108.4071	3797	183,711,436
c	3708.0287	285.5241	336.9629	337.2597	6.4725	-1752.5927	224	20,949,560
f	299.6979	3742.1311	384.8058	385.1023	7.2141	-2361.1342	228	13,969,707
(cf)	-554.7169	-541.2287	3017.8455	2816.4748	-13.6866	4113.7269	1814	70,893,854
θ	53.0909	53.0909	0	0	53.0909	0	37	1,918,460
T	.8499	1.5355	.0490	.0447	1.8815	108.4071	1	36,710
γ	201.0782	201.0782	0	201.0782	0	0	250	5,382,992
Residual	0	0	0	0	0	0	1243	70,560,153

TABLE 5. Expected coefficients of variances from the complete model in mean squares for milk.

Source	σ_c^2	σ_f^2	σ_{cf}^2	σ_γ^2	σ_θ^2	σ_T^2	σ_e^2	M.S.
c	16.5537	1.2747	1.5043	1.5056	.0289	-7.8241	1	93,524.8214
f	1.3145	16.4129	1.6877	1.6890	.0316	-10.3559	1	61,270.6447
(cf)	-.3058	-.2984	1.6636	1.5526	-.0075	2.2678	1	39,081.5072
θ	1.4349	1.4349	0	0	1.4349	0	1	51,850.2702
T	.8499	1.5355	.0490	.0447	1.8815	108.4071	1	36,710.0000
γ	.8043	.8043	0	.8043	0	0	1	21,531.9680
Residual	0	0	0	0	0	0	1	56,766.0121

TABLE 6. Expected coefficients of variances from the complete model in mean squares for fat.

Source	d. f.	M. S.
c	224	12,813.0045
f	228	9,010.5089
(cf)	1814	5,296.3192
θ	37	7,778.6486
T	1	129.0000
γ	250	2,733.1040
Residual	1243	7,412.8705

RESULTS AND DISCUSSION

Solution of the simultaneous equations gave estimates of the variance components for the complete model as shown in Tables 7 and 8.

TABLE 7. Variance components for milk (10 lbs.) from the complete model.

Component	Variance	Standard Deviation	Percent
σ_c^2	3,273	57.2	3.4
σ_f^2	1,308	36.2	1.4
σ_{cf}^2	35,447	188.3	36.6
σ_γ^2	-48,388	--	--
σ_θ^2	-8,007	--	--
σ_T^2	-86	--	--
σ_e^2	56,766	238.3	58.6

TABLE 8. Variance components for fat (in lbs.) from the complete model.

Component	Variance	Standard Deviation	Percent
σ_c^2	419	20.5	3.2
σ_f^2	177	13.3	1.4
σ_{cf}^2	4,912	70.1	38.0
σ_γ^2	-6,414	--	--
σ_θ^2	-341	--	--
σ_T^2	-67	--	--
σ_e^2	7,413	86.1	57.4

Since there were only 55 inbred daughters of 38 sires in the study, a model which excluded the inbreds (diagonal elements) was also applied to the data for comparison with the results of the complete model.

TABLE 9. Expected coefficients of variances from the off-diagonal model in uncorrected sums of squares for milk.

Source	μ^2	σ_c^2	σ_f^2	σ_{cf}^2	σ_γ^2	σ_e^2	S.S.
Off-Diag. Total	3743	3743	3743	3743	3743	3743	404,265,746
c	3743	3743	340.2997	340.2997	340.2997	222	243,976,658
f	3743	388.1426	3743	388.1426	388.1426	227	237,396,814
(cf)	3743	3541.9218	3541.9218	3743	3541.9218	2267	329,509,231
γ	0	201.0782	201.0782	0	201.0782	250	5,382,992
Corr. Term	3743	88.9121	55.4953	3.3858	3.0850	1	223,696,110

TABLE 10. Expected coefficients of variances from the off-diagonal model in corrected sums of squares for milk.

Source	σ_c^2	σ_f^2	σ_{cf}^2	σ_γ^2	σ_e^2	S.S.
Off-Diag. Total	3654.0879	3687.5047	3739.6142	3739.9150	3742	180,569,636
c	3654.0879	284.8044	336.9139	337.2147	221	20,280,548
f	299.2305	3687.5047	384.7568	385.0576	226	13,700,704
(cf)	-500.3087	-485.8826	3017.9435	2816.5645	1819	71,831,869
γ	201.0782	201.0782	0	201.0782	250	5,382,992
Residual	0	0	0	0	1226	69,373,523

TABLE 11. Expected coefficients of variances from the off-diagonal model in mean squares for milk.

Source	σ_c^2	σ_f^2	σ_{cf}^2	σ_γ^2	σ_e^2	M.S.
c	16.5343	1.2887	1.5245	1.5259	1	91,767.1855
f	1.3240	16.3164	1.7025	1.7038	1	60,622.5840
(cf)	-.2750	-.2671	1.6591	1.5484	1	39,489.7576
γ	.8043	.8043	0	.8043	1	21,531.9680
Residual	0	0	0	0	1	56,585.2553

TABLE 12. Expected coefficients of variances from the off-diagonal model in mean squares for fat.

Source	d.f.	M.S.
c	221	12,476.5023
f	226	8,863.4513
(cf)	1819	5,371.9544
γ	250	2,733.1040
Residual	1226	7,383.6868

With the inbreds (diagonal elements) eliminated from the data and, therefore, no $\theta_{j\ell}$ and $T_{j\ell}$ in the model, estimates of the variance components are obtained as shown in Tables 13 and 14.

TABLE 13. Variance components for milk (10 lb.) with inbreds eliminated.

Component	Variance	Standard Deviation	Percent
σ_c^2	3,206	56.6	3.3
σ_f^2	1,324	36.4	1.4
σ_{cf}^2	35,342	188.0	36.6
σ_{γ}^2	-48,112	---	---
σ_e^2	56,585	237.9	58.7

TABLE 14. Variance components for fat (in lbs.) with inbreds eliminated.

Component	Variance	Standard Deviation	Percent
σ_c^2	433	20.8	3.3
σ_f^2	216	14.7	1.7
σ_{cf}^2	4,897	70.0	37.9
σ_γ^2	-6,432	----	---
σ_e^2	7,384	85.9	57.1

The variance components are shown in tables 7 and 8 for the complete model and in 13 and 14 for the off-diagonal model. The estimates of σ_γ^2, σ_θ^2, and σ_T^2 for the complete model and σ_γ^2 for the off-diagonal model were negative.

The estimates of σ_c^2 and σ_f^2 are not larger than might be expected, however,the intra-cell variance, σ_e^2 is somewhat higher than generally accepted for this parameter. This is true for both milk and fat production in both models.

The interaction of sire with maternal grandsire, σ_{cf}^2, is extremely large and accounts for from 36.6 to 38.0 percent of the total variation when these two models are used.

The simplest analysis of production data to estimate interaction between sires and maternal grandsires would utilize the following model: $Y_{j\ell m} = \mu + c_j + f_\ell + I_{j\ell} + e_{j\ell m}$

This model, in which $I_{j\ell}$ is a simple interaction between sire c_j and maternal grandsire f_ℓ , was used to determine what effect the negative values for σ_γ^2, σ_θ^2, and σ_T^2 in the original model might be having on the interaction term (cf). If σ_I^2 is not positive and relatively large, the size of σ_{cf}^2 might be assumed due largely to the model and method of analysis rather than to a real interaction. The sums of squares, mean squares, and variance components obtained from this analysis are shown in Tables 15 through 20.

TABLE 15. Expected coefficients of variances from the simple interaction model in uncorrected sums of squares for milk.

Source	μ^2	σ_c^2	σ_f^2	σ_I^2	σ_e^2	S.S.
Grand Total	3798	3798	3798	3798	3798	411,394,929
c	3798	3798	341.3930	341.3930	225	248,633,053
f	3798	389.6692	3798	389.6692	229	241,653,200
I	3798	3798	3798	3798	2555	340,834,776
C. T.	3798	89.9713	55.8689	3.0679	1	227,683,493

TABLE 16. Expected coefficients of variances from the simple interaction model in corrected sums of squares for milk.

Source	σ_c^2	σ_f^2	σ_I^2	σ_e^2	S.S.
Grand Total	3708.0287	3742.1311	3794.9321	3797	183,711,436
c	3708.0287	285.5241	338.3251	224	20,949,560
f	299.6979	3742.1311	386.6013	228	13,969,707
I	-299.6979	-285.5241	3070.0057	2102	78,232,016
Residual	0	0	0	1243	70,560,153

TABLE 17. Expected coefficients of variances from the simple interaction model in mean squares for milk.

Source	σ_c^2	σ_f^2	σ_I^2	σ_e^2	M.S.
c	16.5537	1.2747	1.5104	1	93,524.82
f	1.3145	16.4129	1.6956	1	61,270.64
I	-.1426	-.1358	1.4605	1	37,217.90
Residual	0	0	0	1	56,766.01

TABLE 18. Expected coefficients of variances from the simple interaction model in mean squares for fat.

Source	d.f.	M.S.
c	224	12,813.00
f	228	9,010.51
I	2102	5,032.70
Residual	1243	7,412.87

TABLE 19. Variance component estimates for milk (10 lbs.) using the simple interaction model.

Component	Variance	Standard Deviation	Percent
σ_c^2	3,297	57.4	5.4
σ_f^2	1,347	36.7	2.2
σ_I^2	-12,937	----	---
σ_e^2	56,766	238.3	92.4

TABLE 20. Variance components for fat (in lbs.) from the simple interaction model.

Component	Variance	Standard Deviation	Percent
σ_c^2	452	21.3	5.6
σ_f^2	223	14.9	2.8
σ_I^2	-1,565	----	---
σ_e^2	7,413	86.1	91.7

As can be seen from tables 19 and 20, the interaction σ_I^2 is negative for both milk and fat production. The sire and maternal grandsire components account for a slightly larger percentage of the total variance in the simple interaction model than with either the complete or off-diagonal models. These components account for 5.4 and 2.2 percent of the variation for milk and 5.6 and 2.8 percent for fat production.

The error variance for the simple interaction model is of the same magnitude as that for the other models; however, it accounted for 92.4 and 91.7 percent of the variation for milk and fat production, respectively. If the negative values are included in the total variance, the sire and maternal grandsire components account for approximately the same percentage of the total variance for each of the three models. The percentages for fat from the complete, off-diagonal, and simple models were 6.9, 6.7, and 6.9 for sire and 2.9, 3.3, and 3.4 for maternal grandsire.

Table 21 shows a comparison of the magnitude and relative importance of the variance components for fat production for each of the three models used. Negative values were not included in the total variance since this would force the error variance over 100 percent. These relationships are similar to those for milk production.

TABLE 21. Comparison of fat production variance components for three models.

Component	Complete Model Variance	Complete Model Percent	Off-Diag. Model Variance	Off-Diag. Model Percent	Simplified Model Variance	Simplified Model Percent
σ_c^2	419	3.2	433	3.3	452	5.6
σ_f^2	177	1.4	216	1.7	223	2.8
σ_{cf}^2	4,912	38.0	4,897	37.9	---	---
σ_I^2	---	---	---	---	-1,565	---
σ_γ^2	-6,414	---	-6,432	---	---	---
σ_θ^2	-341	---	---	---	---	---
σ_T^2	-67	---	---	---	---	---
σ_e^2	7,413	57.4	7,384	57.1	7,413	91.7
Total	12,921	100	12,930	100	8,088	100

Since a variance is a squared term, it cannot truly be negative although negative estimates of variance often arise in variance component analyses. Several alternatives exist in evaluating negative variance components. Among these are:

1. Present the estimates as they are on the basis that a negative estimate is strong evidence that the corresponding parameter is zero. If a variance is zero, both positive and negative estimates would be expected. The negatives may be presented to counter the bias toward the positive if only negative values are called zero.
2. Equate to zero all components having negative estimates and leave the positive estimates unchanged.
3. Equate to zero all components having negative estimates and pool those mean squares whose altered expectations are now the same.
4. Question the validity of the model.

The first two alternatives could satisfactorily solve the problem of the negative estimates obtained with the complete and off-diagonal models. This, however, would leave unexplained the exceptionally large estimate of σ_{cf}^2 which was obtained. It is doubtful that σ_{cf}^2 could in reality be large when a simple interaction, σ_I^2, applied to the same data is negative. The third alternative is not applicable in this case.

In discussing the validity of the assumed model, it should first be noted that this model is effective in obtaining unbiased estimates of the parameters built into a simulated, balanced set of data. It also has the capability of providing unbiased estimates of the population parameters with unbalanced data. These estimates, although unbiased, may differ greatly from the true population parameters.

To determine what effect the negative estimates have on the magnitude of the rest of the components, the negative components were assigned a zero value in both the complete model and the off-diagonal model. This was accomplished by deleting the negative components from the model and allowing these equations to be absorbed into the equation for residual. The remaining components were then re-estimated. The results are shown in tables 22 through 27.

The large positive estimate of σ_{cf}^2 became negative when the components γ, θ, and T in the complete model and γ in the off-diagonal model were set equal to zero.

As a final check on the magnitude of the sire and maternal grandsire components, σ_c^2 and σ_f^2, the sire by maternal grandsire interaction term (cf) was also set equal to zero and σ_c^2, σ_f^2, and σ_e^2 were re-estimated. The results are shown in tables 28 through 31.

TABLE 22. Expected coefficients of variances in corrected sums of squares for milk and fat from the complete model with γ, θ, and T assigned zero values.

Source	σ_c^2	σ_f^2	σ_{cf}^2	σ_e^2	S.S.	
					Milk	Fat
Grand Total	3708.0287	3742.1311	3739.6632	3797	183,711,436	24,717,445
c	3708.0287	285.5241	336.9629	224	20,949,560	2,870,113
f	299.6979	3742.1311	384.8058	228	13,969,707	2,054,396
(cf)	-554.7169	-541.2287	3017.8455	1814	70,893,854	9,607,523
Residual	255.0190	255.7046	.0490	1531	77,898,315	10,185,413

TABLE 23. Expected coefficients of variances in mean squares for milk and fat from the complete model with γ, θ, and T assigned zero values.

Source	σ_c^2	σ_f^2	σ_{cf}^2	σ_e^2	M.S.	
					Milk	Fat
c	16.5537	1.2747	1.5043	1	93,524.8214	12,813.0045
f	1.3145	16.4129	1.6877	1	61,270.6447	9,010.5089
(cf)	-.2750	-.2671	1.6591	1	39,489.7576	5,371.9544
Residual	.1666	.1670	0	1	50,880.6760	6,652.7845

TABLE 24. Variance components for milk (10 lbs.) from the complete model with γ, θ, and T set equal to zero.

Component	Variance	Standard Deviation	Percent
σ_c^2	3,076	55.5	5.7
σ_f^2	1,038	32.2	1.9
σ_{cf}^2	-5,929	----	---
σ_e^2	50,195	224.0	92.4

TABLE 25. Variance components for fat (in lbs.) from the complete model with γ, θ, and T set equal to zero.

Component	Variance	Standard Deviation	Percent
σ_c^2	423	20.6	5.9
σ_f^2	182	13.5	2.5
σ_{cf}^2	-644	----	---
σ_e^2	6,552	80.9	91.5

TABLE 26. Variance components for milk (10 lbs.) from the off-diagonal model with γ set equal to zero.

Component	Variance	Standard Deviation	Percent
σ_c^2	2,971	54.5	5.5
σ_f^2	1,003	31.7	1.9
σ_{cf}^2	-5,745	----	---
σ_e^2	50,107	223.8	92.7

TABLE 27. Variance components for fat (in lbs.) from the off-diagonal model with γ set equal to zero.

Component	Variance	Standard Deviation	Percent
σ_c^2	402	20.0	5.7
σ_f^2	173	13.2	2.4
σ_{cf}^2	-596	----	---
σ_e^2	6,518	80.7	91.9

TABLE 28. Variance components for milk (10 lbs.) from the complete model with γ, θ, T, and (cf) set equal to zero.

Component	Variance	Standard Deviation	Percent
σ_c^2	2,884	53.7	6.0
σ_f^2	772	27.8	1.6
σ_e^2	44,810	211.7	92.5

TABLE 29. Variance components for fat (in lbs.) from the complete model with γ, θ, T, and (cf) set equal to zero.

Component	Variance	Standard Deviation	Percent
σ_c^2	402	20.0	6.2
σ_f^2	153	12.4	2.4
σ_e^2	5,967	77.2	91.5

TABLE 30. Variance components for milk (10 lbs.) from the off-diagonal model with γ and (cf) set equal to zero.

Component	Variance	Standard Deviation	Percent
σ_c^2	2,782	52.8	5.8
σ_f^2	744	27.3	1.5
σ_e^2	44,805	211.7	92.7

TABLE 31. Variance component estimates for fat (in lbs.) from the off-diagonal model with γ and (cf) set equal to zero.

Component	Variance	Standard Deviation	Percent
σ_c^2	382	19.6	5.9
σ_f^2	146	12.1	2.3
σ_e^2	5,968	77.3	91.9

Essentially no further change in either the magnitude or relative importance of the remaining components can be seen by setting (cf) equal to zero. A comparison of fat production components for the complete and off-diagonal models with those same models after the negative components have been set equal to zero can be seen in tables 32 and 33.

TABLE 32. Comparison of fat production variance components for the complete model with those of the complete model after γ, θ, and T, and γ, θ, T, and (cf) have been set equal to zero.

	Complete Model		γ, θ, and T = 0		γ, θ, T, and (cf) = 0	
Component	Variance	Percent	Variance	Percent	Variance	Percent
σ_c^2	419	3.2	423	5.9	402	6.2
σ_f^2	177	1.4	182	2.5	153	2.4
σ_{cf}^2	4,912	38.0	-644	---	---	---
σ_γ^2	-6,414	----	---	---	---	---
σ_θ^2	-341	----	---	---	---	---
σ_T^2	-67	----	---	---	---	---
σ_e^2	7,413	57.4	6,552	91.5	5,967	91.5
Total	12,921	100	7,157	100	6,522	100

TABLE 33. Comparison of fat production variance components for the off-diagonal model with those of the off-diagonal model after γ; and γ and (cf) have been set equal to zero.

	Off-Diag. Model		With $\gamma = 0$		With γ and (cf) = 0	
Component	Variance	Percent	Variance	Percent	Variance	Percent
σ_c^2	433	3.3	402	5.7	382	5.9
σ_f^2	216	1.7	173	2.4	146	2.3
σ_{cf}^2	4,897	37.9	-596	---	---	---
σ_γ^2	-6,432	----	----	---	---	---
σ_e^2	7,384	57.1	6,518	91.9	5,968	91.9
Total	12,930	100	7,093	100	6,496	100

To better illustrate the relationship of the models to each other, the distribution of the degrees of freedom for each model is shown in table 34. As can be seen in this table, the degrees of freedom for (cf), γ, θ, and T all come from the simple interaction I. Also, (cf) is calculated the same with or without γ, θ, and T in the model.

It appears that the large negative estimate of σ_γ^2 has been the major cause of the large positive estimate of σ_{cf}^2 in both the complete model and the off-diagonal model. The negative estimates of σ_θ^2 and σ_T^2 are probably not of a great enough magnitude to have much influence on the other estimates.

TABLE 34. Distribution of the degrees of freedom for each model used in this study.

Source	Complete Model			Off-Diagonal Model			Simple Interaction Model
		Υ, θ, T=0	+(cf)=0		Υ=0	Υ,(cf)=0	
Total	3797	3797	3797	3742	3742	3742	3797
c	224	224	224	221	221	221	224
f	228	228	228	226	226	226	228
I	---	---	---	---	---	---	2102
(cf)	1814	1814	---	1819	1819	---	---
Υ	250	---	---	250	---	---	---
θ	37	---	---	---	---	---	---
T	1	---	---	---	---	---	---
e	1243	1531	3345	1226	1476	3295	1243

The reciprocal effect, σ_{γ}^{2}, is that contribution to the variance which is due to the position of any pair of bulls in the pedigree of the animals in question.

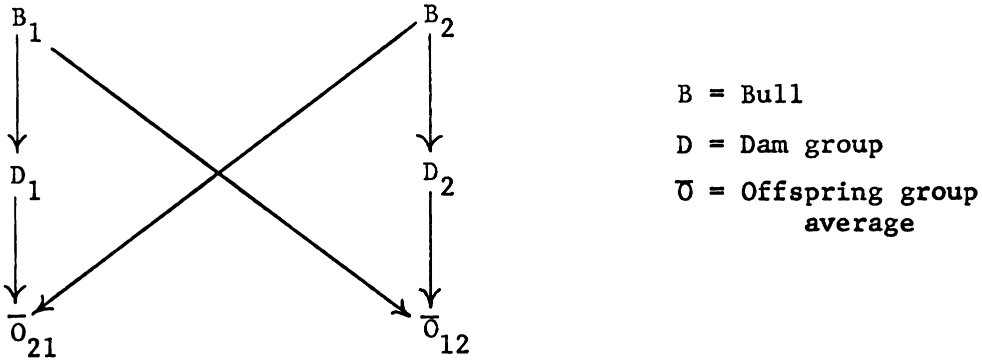


FIGURE 1. Diagram showing reciprocal offspring groups.

In this example σ_{γ}^{2} would measure the difference between the two offspring groups which is associated with the difference in position of the bulls in the pedigree, i.e. as sire versus maternal grandsire. Contributing factors to this component are prenatal maternal environment, postnatal maternal influence and non-randomness of dams. Chance at Mendelian segregation and uncontrolled environmental variation may contribute to the mean square but not to the variance component.

The estimates of σ_{γ}^{2} were -48,388 and -6,414 for milk and fat production, respectively when all animals were included in the study, and -48,112 and -6,432 when the inbred animals and the θ and T components were eliminated. Because of the negative estimates obtained, the best estimate from these data of the contribution of reciprocals to the overall variation is zero for both milk and fat production.

As described in the mathematical model the θ and T effects are associated with the inbred animals in the study. These inbreds are the result of sire x daughter matings (where c_j and f_ℓ are the same bull) and, therefore, have an inbreeding coefficient of at least 25 percent. The σ_θ^2 is that contribution to the total variance which is associated with differences among the inbred subclasses (those on the main diagonal). The contribution to the overall variance from any general inbreeding degeneration or that difference derived from a comparison of all inbreds with all non-inbreds is denoted by σ_T^2. The 55 inbred animals in this study averaged 260 lbs. of milk and 2 lbs. of fat less per lactation than the off-diagonal animals.

The estimates of σ_θ^2 and σ_T^2 in the complete model were -8,007 and -86 for milk and -341 and -67 for fat. Although there was some difference between the means of the diagonal and off-diagonal elements, the contribution of θ and T to the total variance is essentially zero.

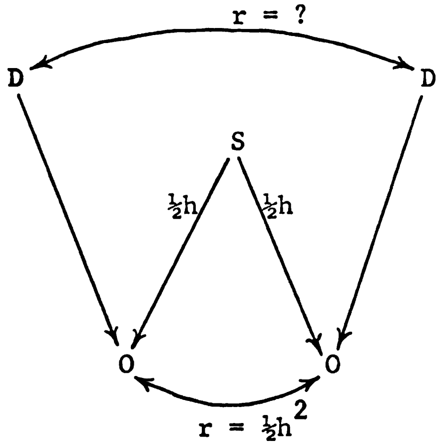
Genetic factors contributing to σ_{cf}^2 are non-additive in nature. Although the estimate of σ_{cf}^2 was extremely large in the complete and off-diagonal model, accounting for 36.6 to 38.0 percent of the variation, this term became negative when γ was set equal to zero. This indicates that the large interaction effect was probably due to the model and analysis and indirectly to the unbalanced nature of the data in this study.

The best estimate of the contribution of σ_{cf}^2 to the overall variation in these data is zero.

The portions of the variance in milk production associated with sires and maternal grandsires in the complete model were 3.4 and 1.4 percent, respectively, the corresponding figures for fat being 3.2 and 1.4. Table 32 shows what effect setting γ, θ, T, and γ, θ, T, and (cf) from the complete model equal to zero has on the sire and maternal grandsire components for fat production. Setting γ, θ, and T equal to zero increases the relative importance of the sire and maternal grandsire components to 5.7 and 1.9 percent for milk and 5.9 and 2.5 percent for fat for σ_c^2 and σ_f^2, respectively. Setting (cf) equal to zero in addition to γ, θ, and T made little difference in the relative importance of sires and maternal grandsires.

The relative importance of σ_c^2 for milk and fat production is 5.7 and 5.9 percent. The corresponding figures for σ_f^2 are 1.9 and

2.5 percent. General combining ability, therefore, accounted for 7.6 and 8.4 percent of the variation in the milk and fat production of the cows in this study. The heritability estimates for milk and fat based on σ_c^2 are .23 and .24, respectively.



S = Sire
D = Dam
O = Offspring
r = Correlation
h^2= Heritability

FIGURE 2. Heritability of milk production based on the sire component of variance.

The σ_f^2 is expected to be half as large as σ_c^2 because of the extra Mendelian segregation involved. The fact that the contribution of σ_f^2 to the total variance is considerably less than half as large as that of σ_c^2 may be an indication of some non-randomness of mates of the sires in this study. This would lead to a higher correlation between offspring of the same sire than is warranted due to the actual additive effects of that sire. The estimate of σ_c^2 is no larger than might be expected, however.

Although any attempt to measure nicking must make use of some type of interaction, it is doubtful that any conventional measure of interaction would have the ability to detect nicking in present dairy cattle populations. Most approaches to the problem have utilized a simple interaction model. A simple interaction, however, cannot consider the fact that two separate cells may have the same interacting genetic material in common, i.e., the members of a reciprocal pair.

By measuring differences between the reciprocal members of a pair of cells (γ in this study) separately from the remainder of the interaction, it is possible to measure differences between pairs of cells having different interacting genetic combinations (cf). To avoid possible contributions to the interaction due to differences between cells composed of inbreds (θ) and any general inbreeding degeneration (T), these were measured separately.

Dairy cattle breeders that try to take advantage of any nicking in their breeding programs do so in one or a combination of two ways. They may believe that certain relative groups nick with each other, or they may believe that regardless of the relationship of the animals involved, selection of mates according to some phenotypic characteristics produce extraordinary results.

If either or both of these methods are commonly practiced and are usually effective in producing nicking, almost any measure of interaction should be able to detect this nicking given a sufficient number of observations. However, if nicking is not actively pursued by a high proportion of dairymen or if nicking occurs only rarely, it would be impossible to measure it statistically in present dairy cattle populations.

The data used in the present study did not lend itself to an effective measurement of interaction since only 2,555 of the 51,525 cells were filled (about 5 percent) and the average number of animals in each cell was only 1.49. The conclusion that a sire by maternal grandsire interaction did not make a measurable contribution to the overall variation in these data is justifiable, however more extensive data are needed to obtain conclusive results.

The practical significance of an inability to find a measurable interaction between sire and maternal grandsire is that present sire evaluations are probably not often biased by an interaction of the sire with his mates.

SUMMARY

This study was conducted to determine if sire by maternal grandsire interactions exist for the productive traits in dairy cattle. First-available Michigan DHIA lactations on 3,798 Holstein Friesian cows whose sire and maternal grandsire were both in A. I. service were utilized. All records were 305 day, twice-a-day milking, mature equivalent deviations from the 305-2X-ME lactation herd average.

A variance component analysis was performed on the data using the following model:

$$Y_{j\ell m} = \mu + c_j + f_\ell + (cf)_{j\ell} + \gamma_{j\ell} + T_{j\ell} + e_{j\ell m}$$

where c represents sire; f, maternal grandsire; (cf), the sire by maternal grandsire interaction; γ is a reciprocal effect; θ, a specific sire inbreeding effect; T, a general effect of inbreeding, and e, an error term. All components of the model were assumed to be uncorrelated random variables with mean zero and variance σ_c^2, σ_f^2, σ_{cf}^2, σ_γ^2, σ_θ^2, σ_T^2, and σ_e^2, respectively.

The analysis of the data provided negative estimates of σ_γ^2, σ_θ^2, and σ_T^2 and a large positive estimate of σ_{cf}^2. Since there were only 55 animals resulting from sire-daughter matings involving 38 sires, these were eliminated and the model again

applied to the data. This second model, which eliminated the θ and T components gave results for the sire, maternal grandsire, interaction, and reciprocal effects similar to the complete model.

Variance components were also calculated using a third model which contained only a simple interaction term:

$$Y_{j\ell m} = \mu + c_j + f_\ell + I_{j\ell} + e_{j\ell m}$$

This analysis produced a negative estimate of the simple interaction component.

To investigate the possible effect of the negative estimates of σ_γ^2, σ_θ^2, and σ_T^2 on the large positive estimate of σ_{cf}^2 obtained with the original model, the negative components were set equal to zero and those remaining re-estimated. This produced negative estimates of σ_{cf}^2 for both the complete model and the off-diagonal (inbreds eliminated) model.

It was concluded that the large interaction effect obtained with the original model is due directly to the model and analysis and indirectly to the unbalanced nature of these data. Only 2,555 or about 5 percent of the 51,525 cells were filled in this study with the average number of animals in each being 1.49.

The best estimate of the contribution of σ_{cf}^2, σ_γ^2, σ_θ^2, and σ_T^2 to the total variation in these data is zero. It would apparently be quite difficult if not impossible for an interaction to be measured with very much accuracy with so few observations per cell and so few cells filled.

The estimates of the relative importance of the sire component of variance for milk and butterfat production with γ, θ, and T set equal to zero are 5.7 and 5.9 percent of the total variation. The corresponding figures for maternal grandsire are 1.9 and 2.5 percent.

The standard deviation of milk and butterfat production with all negative components set equal to zero was about 2,100 lbs. of milk and 77 lbs. of fat. This is somewhat higher than might be expected for milk but is close to the commonly accepted standard deviation for butterfat.

The heritabilities of milk and butterfat production as calculated from the sire component of variance were .23 and .24, respectively.

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