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## **An analysis of the genetic implications of maternal and grandmaternal effects in beef cattle selection programs**

Dan Travis Brown

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To the Graduate Council:

I am submitting herewith a dissertation written by Dan Travis Brown entitled "An analysis of the genetic implications of maternal and grandmaternal effects in beef cattle selection programs." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Animal Science.

D.O. Richardson, Major Professor

We have read this dissertation and recommend its acceptance:

C.C. Melton, L.M. Josephson

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

To the Graduate Council:

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D. O. Richardson  
D. O. Richardson, Major Professor

We have read this dissertation  
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Vice Chancellor  
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Thesis

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AN ANALYSIS OF THE GENETIC IMPLICATIONS OF MATERNAL  
AND GRANDMATERNAL EFFECTS IN BEEF CATTLE  
SELECTION PROGRAMS

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Dan Travis Brown

December 1977

1346889



## ACKNOWLEDGMENTS

The author wishes to express his sincere thanks and appreciation to the following persons who have contributed to this dissertation:

To Dr. D. O. Richardson, major professor, for his sincere recommendations concerning the analysis of the data and constructive criticism of the manuscript. His assurance and trust contributed greatly toward the final manuscript.

To Drs. J. B. McLaren and W. T. Butts, Jr., for their friendship and support throughout the course of graduate study.

To Drs. C. C. Melton and L. M. Josephson for their participation on the graduate committee and helpful criticism of the manuscript.

To Mr. Gayle V. Parrish for his friendship and companionship both at work and the initiation of this study.

The author also wishes to express gratitude to The University of Tennessee Agricultural Experiment Station for providing partial support during the course of study.

And last but not least to my wife, Sophia, for her sincere love and patience throughout this graduate study and the loss of our son, Samuel Travis Leo.

## ABSTRACT

A study utilizing 3,220 performance records of Angus calves dropped over a 19-year period from 1957 to 1975 was undertaken in an attempt to estimate the importance of direct, maternal, and grandmaternal variances and to evaluate their interrelationship as causative factors in creating phenotypic variation in birth weight, gain from birth to weaning, weaning condition, and weaning weights. All of these records were obtained from cattle at the Ames Plantation in Tennessee and were from non-creep-fed calves. The data were adjusted by least squares procedures for the effects of year of birth, season of birth, and age of dam. These adjusted data were used to calculate the various covariances among relatives. The model for maternal effects utilized the covariances of the individual with itself and paternal half-sibs, maternal half-sibs, full-sibs, dam-offspring, and granddam offspring covariances. While the model for assessing grandmaternal genetic influences utilized, in addition to the above six, covariances between cousins, within cousins, and within paternal half-sibs. All of these were equated to their expected biological components, direct genetic variance, maternal genetic variance, grandmaternal genetic variance, covariances between direct and maternal, between direct and grandmaternal, between maternal and grandmaternal, direct environmental variance, maternal environmental variance, and the covariance between direct and maternal environmental effects.

The maternal model yielded positive effects for all estimates of variances with the direct environmental variance contributing the largest fraction of the total phenotypic variances for all traits except adjusted

weaning weight (6.6%). The estimates ranged quite high (up to 83.4% for birth weight); however, the heritability estimates are in line with accepted values for these traits. The direct estimates of variance, ranging from a low of 16.1% for weaning condition to a high of 41.5% for weaning weight, were, therefore, considered quite reasonable. Estimates of the maternal variance all tended to be low (from 1.4% to 4.5%); however, they are positive and do exist. The covariance between direct and maternal effects and the environmental covariances between direct and maternal effects exhibited negative signs except for the genetic covariance for birth weight (7.4% and 6.1%) and environmental covariance for weaning condition (16.4% and 17.0%). This negative covariance supports the theory of an antagonism existing between direct and maternal effects for the weaning and preweaning traits.

The grandmaternal model showed the variance estimates for all effects to be positive except adjusted weaning weight and adjusted gain (-1.2 and -1.2) for the maternal environmental variance. These estimates ranged from 20.2% for birth to 42.8% for weaning weight for direct effects, while the maternal variances were in the 6% to 16% range as to their influence upon the total phenotypic variance. The estimates of the grandmaternal variance were in the range of 5% to 10%, thus very evident as to their importance upon the total phenotypic variance. The estimates for grandmaternal genetic variance were all fairly large in magnitude and were thought to play an important role in validating the alternate generation phenomenon.



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## CHAPTER I

### INTRODUCTION

Most of the beef producers in Tennessee derive their returns from pounds of calf sold at weaning. Their goal is to obtain the maximum weaning weights on their calves in order to maximize net returns. They attempt to accomplish this by striving to improve the genetic potential of the herd by selection. Normally, selection is practiced with the intention of improving individually or collectively such traits as birth weight, gain from birth to weaning, or weaning weight. However, relatively little long-run progress has been made by individual selection for weaning weights.

The covariances between various related individuals may be utilized to estimate the genetic variances and to estimate heritability. However, the preweaning traits involve relationships which are not so easily separated and/or interpreted because they are influenced by maternal environment. In beef cattle, the cow influences these traits both by the genes she transmits and by the maternal environment she provides. Perhaps the most classic mammalian example of an indirect genetic effect is the maternal effect. The maternal genetic influence contributes an environmental effect to the offspring but is genetic in the sense that the genotypic differences among dams are expressed in the phenotypic measurements of their offspring.

Therefore, an understanding of the relationship between direct genetic effects and maternal effects is necessary for traits affected

by maternal influences. By definition, a maternal effect is a phenotypic value of a dam measurable only as a component part of her offspring's phenotypic value. There is the possibility that the maternal effect as expressed in the offspring could be influenced by the dam of the dam that is contributing the maternal effect--thus, a grandmaternal effect.

Producers for years have claimed an alternate generation phenomena--a fat dam, a thin calf, or a thin dam, a fat calf. Most of the time, milk production is credited for this effect; however, milk production is only one component of the total maternal effect and will be considered as such in this study. Recently, there is considerable evidence for an antagonism between direct genetic effects and maternal effects on weaning weights of beef cattle. This would tend to support the alternate generation theory. Thus, if, in fact, maternal genetic effects are important, selection could be modified to increase progress in the short run. However, a few non-theoretical studies have been reported concerning the relative importance of maternal effects or the relationships between maternal effects and other factors affecting performance. With this in mind, the objectives of this study were to (1) evaluate the importance of maternal effects and direct genetic effects on birth weight, gain from birth to weaning, weaning condition, and weaning weight; (2) evaluate the importance of a grandmaternal effect upon said traits; (3) evaluate genetic parameters associated with objectives 1 and 2; and (4) assert the validity of the alternate generation theory.

## CHAPTER II

### REVIEW OF LITERATURE

Maternal effects in animals have been studied in recent years both because of their economic importance in domestic mammals and because of their theoretical interest. In most mammals maternal effects are thought to be an important component of performance. However, few studies have been reported which attempt to quantitate the relative importance of maternal and/or grandmaternal effects or the relationships between these and other factors which affect performance in beef cattle. Most of the published reports concerning maternal effects in beef cattle have been theoretical in nature. Therefore, this review of literature will include research reported in several species and/or classes of livestock.

#### I. MATERNAL EFFECTS IN ANIMALS

##### Theory

The early theory and foundation for genetic control of maternal effects have been developed primarily by Koch and Clark (1955), Willham (1963 and 1972), and Van Vleck (1974 and 1977). Biometrical techniques for assessing the relative contributions of maternal and direct genetic effects on variation in growth for beef cattle have been developed by these authors. Procedures for partitioning the genotypic variance and covariance into direct and maternal components by using covariances between relatives were outlined by Willham (1963) for maternal effects. The magnitudes of direct genetic and maternal genetic variances and the



direct maternal genetic covariances for a quantitative trait often are inferred by comparing covariance estimates from different sets of relatives. This procedure may yield biased estimates of the causal components when the estimates of the genetic covariances are correlated (Osborn and Patterson, 1952). Willham's (1963) method, although useful, does not necessarily yield unbiased minimum variance estimates of the causal components. Thus, caution should be exercised in determining the appropriate set of genetic and environmental components of variance and covariance.

Willham (1963) explained that for some species in which family members are dependent on or are in close proximity to one another, a character may be composed of several conceptual components, some being contributed by related individuals. A general expression for the genotypic covariance between relatives can be synthesized for such characters when mating is random. The relationships between individuals contributing to a measure of the character are important in defining the genotypic variance and the response to selection. Partitioning the covariances makes it possible to estimate the maternal effect in cattle data.

In the model developed by Willham (1963), the phenotypic observation on animal X can be described as  $P_X = G_{D_X} + G_{M_W} + E_{D_X} + E_{M_W}$ , where  $G_{D_X}$  is the direct effect of X's genotype;  $G_{M_W}$  is the maternal effect on X caused by the genotype of the animal's dam, W;  $E_{D_X}$  is the direct effect of environment on X; and  $E_{M_W}$  is the effect of the environment on the maternal value of W. The G's are assumed to be independent of the E's.

One can consider the direct (D) and the maternal (M) effects to be two traits, which may be correlated. Trait M is measured one generation later than the direct effect D. Van Vleck (1974) describes the model for a record on animal X as  $P_X = G_{D_X} + E_{D_X} + G_{M_W} + E_{M_W}$  and the model for a record on animal Y as  $P_Y = G_{D_Y} + E_{D_Y} + G_{M_Z} + E_{M_Z}$ , where animal Z is the mother of Y and W is the mother of X.

Sometimes these relationships can be more easily visualized when they are depicted in a path coefficient diagram. The diagram illustrates that the maternal genetic ability of the mother is expressed only in her progeny (Figure 1) (Van Vleck, 1974).

Utilization of the procedures for determining the covariance of linear functions produces the genetic covariance between X and Y.

Van Vleck (1974) listed this covariance as:

$$\text{Cov}(P_X P_Y) = a_{XY} \sigma_{G_D}^2 + a_{WZ} \sigma_{G_M}^2 + (a_{XZ} + a_{WY}) \sigma_{G_D G_M},$$

where  $\text{Cov}(P_X P_Y)$  is the covariance between relatives;  $a_{XY}$  is the relationship coefficient between animals X and Y;  $a_{WZ}$  is the relationship coefficient between animals W and Z;  $a_{XZ}$  is the relationship between animals X and Z;  $a_{WY}$  is the relationship between animals W and Y;  $\sigma_{G_D}^2$  and  $\sigma_{G_M}^2$  are the additive genetic variances for the direct and maternal traits, respectively; and  $\sigma_{G_D G_M}$  is the covariance between direct and maternal traits. This covariance can be negative and thus mask the additive genetic variances for the direct and maternal traits. With the relationship coefficients and the covariances between relatives, it is possible to

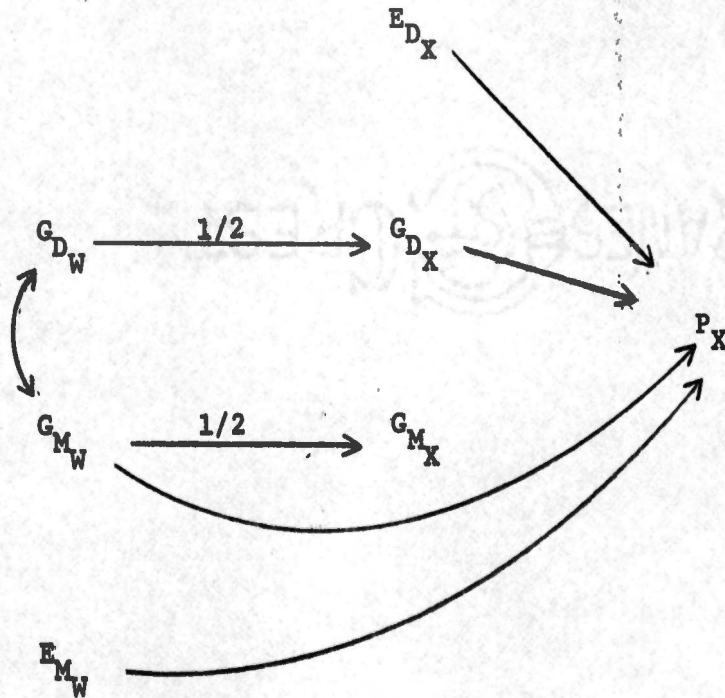


Figure 1. A Path Coefficient Describing a Phenotypic Value Influenced by a Maternal Effect.

Source: Van Vleck (1974).



solve by a series of simultaneous equations for the various genetic and maternal variances and covariances (Willham, 1963; Van Vleck, 1974).

### Milk Production

As stated earlier, it is conceded that milk production of the dam induces a large source of the variation in the traits gain from birth to weaning and weaning weight. However, milk production of the dam is but one component of the total overall aggregate effect of the maternal influence that a dam expresses over her offspring. Other factors include (1) cytoplasmic inheritance, (2) maternally provided intrauterine and early postnatal nutrition, (3) transmission of either antibodies or pathogens from dam to offspring, and (4) maternal behavior patterns. Thus, this study will consider the maternal effect as the aggregate maternal influence upon the offspring's performance and not any specific individual factor.

However, since milk production is generally assumed to be one important avenue of maternal influence, it was felt that a brief review would be in order. The amount of milk produced by a cow being used for beef production is really not the issue. The issue is the response of the calf at side to the total maternal environment created by the cow. But for weaning weight, Neville (1962) reports that 66% of the variation in weight at 8 months of age was due to milk consumption. Drewry, Brown and Honea (1959) found 60% of the variation of 6 months' weight to be due to difference in milk yield of dam. Gifford (1949) presented evidence that indicates that the maximum milk

production was normally attained during the first 6 weeks of lactation and was affected by the capacity of the young calves to consume the milk. Moore (1966), experimenting with sheep, stated that the actual amount of milk produced by a ewe is influenced both by her own potential to produce milk and by the potential of the lamb to obtain it. In contrast, Christian et al. (1965) reported that estimates of the dam's milk production appeared to be independent of the birth weight of her calf, suggesting that the total milk produced was not affected by the capacity of the calf to consume it.

Gifford (1953) reported correlations in Hereford cows ranging from .19 to .71 between the monthly milk production of the cows and the ability of the calf to consume and .65 between total milk production of the cow and gain of the calf up to 6 months of age. Total calf gain was positively correlated with weight of dam and negatively correlated with gain of dam during lactation in the study by Melton et al. (1966) involving three different breeds of cows.

Several researchers have indicated the existence of a negative relationship of dam's milk production and her pattern of growth across generations dealing with milk production. This was first pointed out by Koch and Clark (1955) who presented evidence in beef cattle for a negative genetic correlation between maternal environment and growth potential of the calf.

Besides natural selection against milk production operating through the reproductive performance of the cow herself, there exists another avenue whereby natural selection may be operating. This is



through the over fat heifer at weaning. Chambers et al. (1960) found that the full-fed heifers produced lighter calves at weaning. Totusek (1968) found a 9.1 kg advantage per calf from cows that were weaned at 140 days when compared with those weaned at 240 days which had been creep fed. Other workers have demonstrated that excess fat deposition in the mammary tissue lowers the milk production potential. This produces a negative environmental correlation between the weaning weight of a cow and the weaning weight of her calves as found by Mangus and Brinks (1971). Gould and Whiteman (1975) dealing with sheep stated that the change in correlation coefficients from  $-.13$  for lambs from 15-month-old dams to  $.28$  for 96-month-old dams suggests a possible negative relationship between ewe lamb nutrition and subsequent maternal influence that disappears as the ewe gets older. All of this suggests that possibly a genetic antagonism exists between the direct and maternal effect for weaning weights and gain.

Cartwright and Carpenter (1961) advanced the theory that milk production may be affected not only by the genotype of the dam but also by the genotype of the calf.

#### Parameters

The degree of maternal influence decreases with age of the calf as the dependency of the calf on its dam decreases. Therefore, traits evaluated or measured during the preweaning period would naturally be more affected by the maternal influence than the postweaning traits. Garwood et al. (1967) using swine data demonstrated that prenatal influences represented 10% of the total variance at 56 days of age, but

only 4% at 154 days of age. Postnatal maternal effects significantly affected mortality to both 21 and 56 days accounting for 5% and 7% of the variation respectively. Of the total variation in 21-day weight, postnatal maternal effects accounted for 27% and prenatal 17%. The 56-day weight was affected to the extent of 12% and 13%, respectively. Duroc and Yorkshire lines differed significantly in maternal influence on total litter weight and average pig weight at birth and at 21 and 56 days of age (Bereskin et al., 1974).

Gain in weight from 21 to 56 days was influenced more by prenatal effects (10%) than by postnatal maternal effects (8%) as reported by Harvey et al. (1961) in a rabbit study. A cross-nursing experiment in mice by Cox et al. (1959) found that the postnatal maternal influence to be the most important single factor in determining weight through weaning. It controlled 71.5% of the variance in 12-day weight.

Koch and Clark's (1955) analyses indicated that maternal environment was quite important for birth weight, gain from birth to weaning, and weaning score. In contrast, Sagebiel et al. (1973) said that there was no significant maternal effect on birth weight. Although Koch (1972) found that the genetic and permanent environmental components of maternal ability and covariance of individual and maternal effects accounted for 15% to 20% of variation in birth weight and 35% to 45% of variation in daily gain from birth to weaning. In the case of birth weight, maternal ability of dams did not have a significant direct effect on maternal ability in the next generation. Deese and Koger (1967) estimated the variances for additive genotypes for growth and for maternal effects, the covariance between the two, the variance of



permanent environmental influences on maternal effects and nonpermanent environmental variance. The respective values for these components, expressed as a percent of total phenotypic variance, were for Brahman cattle: 18, 15, 0, 8, and 59; and for crossbred cattle: 40, 46, -30, 7, and 38. Kuhlert et al. (1977) working with swine estimated the percentage of total variance which was ascribed to direct additive genetic variance as being low for birth weight (5%), slightly negative for 3-week weight (-2%), 24% for weight at 16 weeks of age, and 17% for 20-week weight. His estimates for the additive genetic maternal variance were negative in 5 of 12 situations.

As early as 1954, Dawson et al. (1954) determined from heritability estimates calculated by different methods that maternal abilities affect 6-month calf weights and suggested that they are heritable traits. Koch and Clark (1955) estimated heritabilities for birth weight, weaning weight, and gain taking maternal environment into account as .42, .19, and .12, respectively. In spite of high phenotypic correlations between type and condition, Butts (1966) showed type as possessing medium heritability (.40 at weaning) and low maternal estimates while condition score showed essentially no heritability and a greater response to maternal effects. Brown and Galvez (1969) published heritability estimates for maternal and non-maternal influences on birth weight for Hereford and Angus cattle as .30 and .56 and .25 and .14, respectively. Koch (1972) estimated heritability of maternal ability for gain to weaning was on the order of 30% to 36%.

Several workers have suggested negative correlations between dam performance and subsequent offspring performance (McDaniel et al., 1969;



Leonard et al., 1967; Blackmore et al., 1958; Christian et al., 1965). Specific evidence for negative correlations between direct and maternal effects was found by Ahlschwede and Robison (1971a,b) in swine. Values for birth weight, 56-day weight, and 140-day weight were -1.04, -1.06, and -.97 for Durcos. Yorkshire data showed -.97 for birth weight and -1.07 for 140-day weight. Koch (1969) also suggested that a negative relation between environment affecting dam's growth and maternal environment she provides her offspring exists. Results from Koch (1972) list the genetic correlation between direct and maternal effects on birth weight as being inconclusive (.07) while the average of literature values was -.44. The genetic correlation between maternal and individual effects on gain to weaning was negative in most solutions (about -.05), whereas negative values of -.30 to -.78 were indicated in the literature (Koch, 1972). Kuhlers et al. (1977) calculated correlations for weights at 12, 16, and 20 weeks of age of -.83, -.73, and -.66, respectively, between genetic and maternal genetic effects. Gains from 8 to 12, 12 to 16, and 16 to 20 weeks produced correlations of -.78, -.72, and .22, respectively, between the direct genetic and maternal genetic effects.

Whether the maternal effects are genetic or environmental has not been resolved (Koch, 1972; Hohenboken, 1973). These reports have attempted to explain why relatively little long-run progress has been made by individual selection for weaning weight. If, in fact, maternal genetic effects are important, selection could be modified to increase progress in the short run. Van Vleck (1977), using theoretical data, evaluated expected genetic progress from selection for direct and



maternal genetic effects. Two sets of standardized genetic variances and covariances were used, with one having an additional  $-.35$  environmental covariance between offspring and dam records. Results listed illustrated that genetic improvement is difficult to achieve with the large negative covariance. The breakdown of the total selection response showed that the additional gain in direct genetic value is counterbalanced by a decrease in the maternal component.

## II. GRANDMATERNAL EFFECTS IN ANIMALS

### Theory

Willham (1963) stated that phenotypic values composed of components contributed by ancestral relations such as maternal effects deserve special attention. Possibly a maternal effect is influenced by a maternal effect. Then the granddam of the offspring would exert a direct effect through the dam on the phenotypic value of her daughter's offspring. This is plausible if early environment of the dam influences her subsequent performance as a mother. In 1972, Willham, in a symposium on maternal effects on animal breeding, expanded the linear model to include an effect of the maternal granddam on the maternal effect of the dam. Beef cattle data examined by Totusek et al. (1971) and also by Koch (1972) suggested the existence of such a grandmaternal effect on weaning weight in beef cattle.

The economic cost of the grandmaternal effect is difficult to visualize since the grandmaternal effect for a trait such as weaning weight appears to influence the efficiency of the dam to produce milk



(Van Vleck, 1976). The expected correlated response in the individual components resulting from index selection which utilizes various combinations of economic values for direct, maternal, and grandmaternal effects would be of interest to determine whether selecting for grandmaternal or even maternal effects has important economic consequences.

The model as described by Willham (1972) can be written as:

$$P_i = G_{D_i} + G_{M_{i'}} + G_{N_{i''}} + E_i,$$

where  $P_i$  is the phenotypic performance of individual  $i$  and  $G_{D_i}$  is the direct effect of the genotype of  $i$ ;  $G_{M_{i'}}$  is the maternal effect on  $P_i$  caused by the genotype of the animal's dam,  $i'$ ;  $G_{N_{i''}}$  is the grandmaternal effect on  $P_i$  caused by the genotype of the dam of the dam of  $i$ ,  $i''$ ; and  $E_i$  is the remaining environmental effect which can also be partitioned into three components. Only selection for additive genetic value for the direct, maternal, and grandmaternal components will be considered since the additive effects make up a large part of long-term gain by selection (Van Vleck, 1976).

These relationships can be more easily visualized when they are depicted in a path coefficient diagram (Figure 2). The diagram illustrates that the maternal genetic ability of the mother is expressed only in her progeny. Similarly, the grandmaternal genetic effect is expressed only in the grandprogeny (Van Vleck, 1974). This grandmaternal effect may have a genetic basis in the maternal ability of the mother



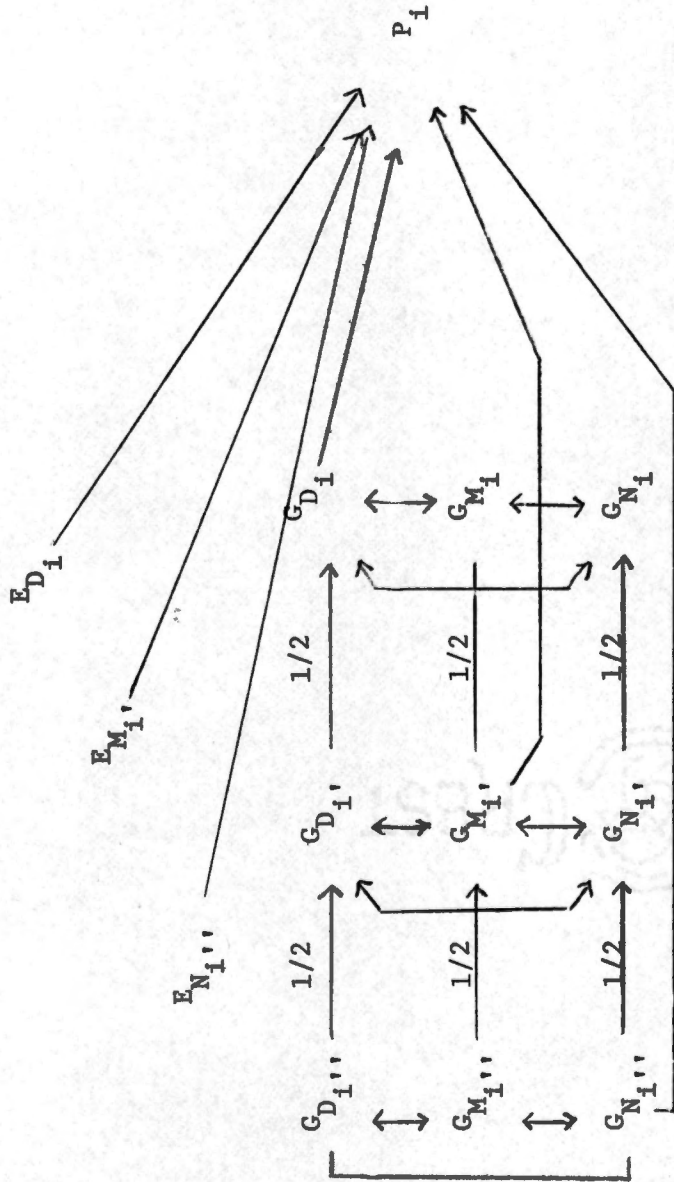


Figure 2. A Path Coefficient Describing a Phenotypic Value Influenced by a Grandmaternal Effect.

Source: Van Vleck (1974).

(i') and on the actual phenotype of the calf (i). Beef cattle breeders have reported that cows that were large themselves at weaning tend to wean calves that are lighter than cows that were not so heavy at weaning. Van Vleck (1974) postulated a grandmaternal effect as a cause of this phenomenon.

By expansion of the model, the covariances among relatives can be determined as before with maternal effects. Van Vleck (1974) using only additive genetic effects expressed this as:

$$\text{Cov}(G_X G_Y) = a_{XY} \sigma_{G_D}^2 + (a_{XY'} + a_{YX'}) \sigma_{G_D G_M} + (a_{XY''} + a_{YX''}) \sigma_{G_D G_N} + a_{X'Y'} \sigma_{G_M}^2 + (a_{X'Y'} + a_{Y'X''}) \sigma_{G_M G_N} + a_{X''Y''} \sigma_{G_N}^2,$$

where the  $a_{ii'}$ 's are the relationship coefficients existing between animals X and Y, their dams X' and Y', and granddams X'' and Y'';  $\sigma_{G_D}^2$  is the direct genetic variance;  $\sigma_{G_M}^2$  is the genetic variance for maternal effect; and  $\sigma_{G_N}^2$  is the genetic variance for the grandmaternal effect;  $\sigma_{G_D G_M}$  is the covariance between direct and maternal genetic effects;  $\sigma_{G_D G_N}$  is the covariance between maternal and grandmaternal genetic effects;  $\sigma_{G_M G_N}$  is the covariance between maternal and grandmaternal genetic effects. This model can also be expanded to include the environmental variance and covariance effects involved with the relationship covariance (Willham, 1972). If a more in-depth understanding of the grandmaternal theory is desired, Willham (1972) or Van Vleck (1974) should be consulted.

### Parameters

Kuhlers et al. (1977) provides the latest research dealing with grandmaternal influences upon the grandprogeny's phenotypic performance. A study of early-weaned pigs produced the following results. Weights were taken at birth, 3, 8, 12, 16, and 20 weeks of age. Five of the six weights had negative grandmaternal variances. Expressed as percentages of the total variance, these grandmaternal effects were 7, -7, -16, -10, -9, and -10, respectively. The covariance estimates between direct and grandmaternal effects were generally positive, -3, 13, 19, 14, 11, and 10, respectively, for the characters analyzed. Likewise, the estimates for gain produced a similar pattern with 4 of 6 gain measurements having negative grandmaternal effects and 5 of 6 producing positive covariances between maternal and grandmaternal effects. As with the weights, the estimates of grandmaternal variance for gains appeared to be close to zero. Genetic correlations between maternal and grandmaternal effects for gain from 8 to 12 and 16 to 20 weeks of age were calculated to be 1.71 and -.72, respectively.

Heritability estimates for weights at birth, 3, 8, 12, 16, and 20 weeks of age were 5, -2, 12, 17, 24, and 17% with the estimates for gains being -6, 16, 11, 23, and 3%. These results by Kuhlers et al. (1977) reflect little evidence of any additive grandmaternal influence for weights and gains in swine.



## CHAPTER III

### AN ANALYSIS OF THE GENETIC IMPLICATIONS OF MATERNAL EFFECTS IN BEEF CATTLE SELECTION PROGRAMS

#### I. SUMMARY

A study on 3,220 performance records of Angus calves dropped over a 19-year period from 1957 to 1975 was undertaken in an attempt to estimate the importance of maternal effects as a causal component in variance of preweaning and weaning traits of beef cattle. All of these records were obtained from cattle at the Ames Plantation in Tennessee and were from non-creep-fed calves. The objectives of this study were to determine the importance of direct and maternal variances and to evaluate their interrelationship as causative factors in creating phenotypic variation in birth weight, gain from birth to weaning, weaning condition, and weaning weights. The data were adjusted by least squares procedures for the effects of year of birth, season of birth, sex of calf, and age of dam. These adjusted data were used to calculate the various covariances among relatives. They included individual with himself, paternal half-sibs, maternal half-sibs, full-sibs, dam-offspring, and granddam-offspring. These were equated to their expected biological components, direct genetic variance, maternal genetic variance, covariance between direct and maternal, direct environmental variance, maternal environmental variance, and the covariance between direct and maternal environmental effects.



The variance estimates for all effects were positive in sign with the direct environmental variance contributing the largest fraction of the total phenotypic variance for all traits except adjusted weaning weight. The covariance between direct and maternal effects and the environmental covariances between direct and maternal effects exhibited negative signs except for the genetic covariance for birth weight and environmental covariance for weaning condition. Thus, in this study as other reported data, an antagonism existed between direct and maternal effects for the weaning and preweaning traits. (Key words: Beef Cattle, Genetics, Growth, Maternal Effects)

## II. INTRODUCTION

Beef cow-calf producer's return on investment is dependent upon the pounds of calf sold at weaning. Their selection programs are usually directed toward the improvement of preweaning traits such as birth weight, gain from birth to weaning, weaning condition and/or weaning weights of the calves. Yet with all of the selection pressure that is exerted on these traits, relatively little long-term progress has been realized by individual selection (Van Vleck, 1977). There is considerable evidence to support the thesis that an antagonism exists between maternal and direct genetic effects for these traits in beef cattle (Koch and Clark, 1955; Deese and Koger, 1967; Hohenboken and Brinks, 1970a, b); Mangus and Brinks, 1971). This has led to speculation concerning the nature and extent of the maternal influence upon the offspring's performance by the dam. Robison (1972) stated that direct and indirect genetic maternal influences may play an important role in

the expression of economically important traits. These effects may be genetic or environmental in a dam but are considered environmental in the progeny, and they apparently decrease with age (Willham, 1963).

The early theory and foundation for genetic control of maternal effects primarily has been developed by Koch and Clark (1955), Willham (1963 and 1972), and Van Vleck (1974 and 1977). Biometrical techniques for assessing relative contributions from maternal and direct genetic effects on variation in growth for beef cattle have been developed by these authors. Procedures for partitioning the genotypic variance and covariance into direct and maternal components by using covariances between relatives were outlined by Willham (1963) for maternal effects. The primary objectives of this study were to determine the relative magnitude of both direct and maternal variances and to determine their relationship to each other as causative factors inducing variation in birth weight, gain from birth to weaning, weaning condition, and weaning weight of beef calves.

### III. MATERIALS AND METHODS

Over a 19-year period, data were collected from the purebred Angus herd at Ames Plantation. The records were collected from 1957 to 1975 on 3,220 non-creep-fed calves and included identification of calf, dam and sire, birth dates of calf and dam, birth weight, sex, weaning age, weight, and condition scores of the calves. From these records, the gain from birth to weaning was calculated as the weaning weight minus birth weight.

All records were adjusted by using constants obtained by least squares procedures for year of birth, season of birth, and sex of calf to produce the following traits: birth weight (BWT), weaning weight (WWT), weaning condition (WCOND), and gain from birth to weaning (GAIN). Since it has been theorized that adjustment for age of dam might mask the effects of the maternal influence, a set of traits was also formalized in the following manner: Birth weight was additionally adjusted for effects of age of dam (ABWT) by using constants obtained by least squares procedures from a linear regression analysis; weaning condition was adjusted for age of dam and weaning age (AWCOND). Adjusted 205-day weights were calculated using the regression of calculated 205-day weight on weaning age. Adjustments were made for the effects of age of calf, age of dam, and sex of calf with an additional adjustment made for the overadjustment of younger and older calves (AWWT). Adjusted gain from birth to weaning was calculated as AWWT minus ABWT (AGAIN).

The general procedure used to estimate the genetic and environmental variances and covariances was to calculate covariances and variances among the members of the six relationships studied and then equate these to their expected biological components. The relationships used were the total phenotypic variance ( $\sigma_p^2$ ), paternal half-sibs ( $\sigma_{PHS}$ ), maternal half-sibs ( $\sigma_{MHS}$ ), full-sibs ( $\sigma_{FS}$ ), dam-offspring ( $\sigma_{D-O}$ ), and granddam-offspring ( $\sigma_{GD-O}$ ).

The theoretical expectations for the covariances and variances among relatives are shown in Table 1. The rationale for the theoretical expectations for the genetic causal components for any relationship was given by Willham (1972) and Van Vleck (1974).



Table 1. Contribution of Direct and Maternal Genetic Variance and Covariance to the Covariance Between Relatives

Covariance <sup>b</sup>	Causal Components <sup>a</sup>					
	$\sigma_D^2$	$\sigma_M^2$	$\sigma_{DM}$	$\sigma_{E_D}^2$	$\sigma_{E_M}^2$	$\sigma_{E_{DM}}$
$\sigma_P^2$	1	1	1	1	1	1
$\sigma_{PHS}$	1/4	0	0	0	0	0
$\sigma_{MHS}$	1/4	1	1	0	1	0
$\sigma_{FS}$	1/2	1	1	0	1	0
$\sigma_{D-O}$	1/2	1/2	1-1/4	0	0	1
$\sigma_{GD-O}$	1/4	1/4	5/8	0	0	0

<sup>a</sup>The subscripts on the causal components denote direct genetic effects (D), maternal genetic effects (M), direct environmental effects ( $E_D$ ), and maternal environmental effects ( $E_M$ ).

<sup>b</sup> $\sigma_P^2$ , the total phenotypic variance;  $\sigma_{PHS}$ , paternal half-sibs;  $\sigma_{MHS}$ , maternal half-sibs;  $\sigma_{FS}$ , full-sibs;  $\sigma_{D-O}$ , dam-offspring; and  $\sigma_{GD-O}$ , granddam-offspring.

Detailed analysis had to be performed in order to obtain values for the variances and covariances used in this study. The records described earlier were manipulated into three separate data sets, hereafter referred to as Ames 1, Ames 2, and Ames 3.

Ames 1 data set contained 3,220 performance records consisting of one generation of data. From Ames 1 data by the use of a nested analysis of variance procedure, the total phenotypic variance and paternal half-sibs relationships were calculated along with the maternal half-sibs and full-sibs relationships for all traits involved in the study. The latter two terms were calculated by a dam within sire nested hierarchy while the former two were derived from paternal half-sib analysis.

Ames 2 data set was created to form a two-generation data set (calf performance plus its dam's performance as a calf). This data set was necessary in order to breakout the covariance between dam and offspring. Seventeen hundred and forty-eight (1,748) two-generation records were available for analysis.

The third data set for formulated in order to assess the covariance between granddam and offspring. This was accomplished by fitting three generations of performance records together to formulate Ames 3 (calf performance plus its dam's performance as a calf plus her dam's performance as a calf (the granddam)). Ames 3 contained 687 three-generation records.

In the preliminary analyses performed on the data, each data set was used separately and independently of one another for all analyses performed in order to determine direct and maternal genetic effects.

However, since the preliminary results were in accord with each other from data set to data set, it was conducive to combine the various relationships from different data sets for greater degrees of freedom (Table 2) to enhance the validity of the final results. The covariances and variances among the members of the six relationship groups calculated are presented in Table 2.

In order to compare the effects of selection for direct and selection for direct and maternal genetic effects, heritability estimates were calculated from the original data by three different well-known methods: paternal half-sib, maternal half-sib, and full-sib. The estimates are presented in Table 3.

As there are six covariances and six unknowns (Table 1), six equations can be solved to obtain the values for these unknowns. It should be noted from Table 1 that there are some linear dependencies. Because of these dependencies, the equations were solved by using the Moore-Penrose generalized inverse method. It is computed using singular value decomposition. This method yields solutions that are not necessarily unique, but the relative relationship of the unknowns to each other should be valid. The scaling affect, however, does not appear to be a major problem in that estimates of direct genetic variance conform with the accepted range of values widely published for additive genetic variation for the traits. It was felt that the solutions obtained were very plausible.

The model included direct additive genetic variance ( $\sigma_D^2$ ), additive maternal variance ( $\sigma_M^2$ ), the covariance of direct with maternal ( $\sigma_{DM}$ ), the direct environmental variance ( $\sigma_{E_D}^2$ ), the maternal environmental variance



Table 2. Degrees of Freedom and the Covariance Among Relatives by Trait (Kg)

Source	df	Trait							
		BWT	WWT	WCOND <sup>a</sup>	GAIN	ABWT	AWWT	AWCOND <sup>a</sup>	AGAIN
$\sigma_P^2$	3219	9.70	783.85	190.48	734.99	8.86	804.18	181.65	777.16
$\sigma_{PHS}$	113	.60	91.61	15.59	80.29	.33	66.53	12.96	61.48
$\sigma_{MHS}$	2678	1.82	130.53	9.96	115.80	1.59	74.78	9.71	75.28
$\sigma_{FS}$	353	2.05	191.50	1.73	170.28	2.01	156.34	2.22	144.68
$\sigma_{D-0}$	1657	.52	-2.61	-.42	-5.25	.64	29.48	5.10	21.66
$\sigma_{GD-0}$	624	1.01	9.50	-15.84	1.56	.80	27.49	-12.92	16.18

<sup>a</sup>Weaning condition is a subjective scoring system.

Table 3. Heritability Estimates Calculated from Conventional Covariances Among Variances of Relatives

Trait	Method of Calculation		
	Paternal Half-Sib	Maternal Half-Sib	Full-Sib
BWT	.24	.80	.44
WWT	.47	.75	.51
WCOND	.33	.23	.08
GAIN	.44	.71	.48
ABWT	.14	.73	.44
AWWT	.33	.40	.38
AWCOND	.28	.23	.09
AGAIN	.32	.42	.37

$(\sigma_{EM}^2)$ , and the covariance between direct and maternal environmental sources of variation ( $\sigma_{EDM}$ ). Genetic correlations and estimates of heritability were calculated using the results of the solutions given by the generalized inverse of the model.

#### IV. RESULTS AND DISCUSSION

The adjusted means and standard deviations of the calf variables are presented in Table 4. The average calf's performance and the dam's performance as a calf are both shown in Table 5 broken down by dam-age. These means tended to illustrate an alternate-generation type of an affect. With the exception of birth weight, all of the variables, generally speaking, tend to fluctuate in the same direction. For example, if the dam, as a calf, had a low weaning weight, then her respective offspring was heavier at weaning. Weaning condition shows this situation to be the most dramatic in the 2-year-old dams where the calf's weaning condition score was 73.5 compared to the dam's score of 85.9; however, this predominately occurs regardless of the age of the dams. It is generally conceded that there is very little change in birth weight except across breeds by selection. This appears to also be true in this study.

Table 6 shows the covariance and variance component estimates for the traits studied in this analysis. For ease of discussion, the estimates of the causal components expressed as a percentage of the total phenotypic variance for the maternal model are shown in Table 7.

The estimates of the percentages of total phenotypic variance which were ascribed to direct genetic variance ( $\sigma_D^2$ ) were low for birth



Table 4. Means and Standard Deviations of Traits from Ames 1 by Dam Age (Kg)<sup>a</sup>

Trait	Age of Dam					
	2	3	4	5	6-10	11+
Number	283	466	432	390	1,243	406
BWT	23.8 <sup>†</sup> -2.4	24.7 <sup>†</sup> -2.9	26.0 <sup>†</sup> -2.8	26.5 <sup>†</sup> -3.1	27.0 <sup>†</sup> -3.0	26.9 <sup>†</sup> -3.0
WWT	171.2 <sup>†</sup> -28.0	183.0 <sup>†</sup> -26.6	191.2 <sup>†</sup> -26.2	197.8 <sup>†</sup> -25.1	203.0 <sup>†</sup> -26.5	196.3 <sup>†</sup> -24.7
WCOND <sup>b</sup>	73.6 <sup>†</sup> -14.7	80.6 <sup>†</sup> -13.1	83.4 <sup>†</sup> -13.4	83.6 <sup>†</sup> -12.7	84.6 <sup>†</sup> -13.6	82.6 <sup>†</sup> -12.6
GAIN	147.4 <sup>†</sup> -27.4	158.3 <sup>†</sup> -26.1	165.2 <sup>†</sup> -25.5	171.4 <sup>†</sup> -24.5	176.0 <sup>†</sup> -25.9	169.4 <sup>†</sup> -24.3
ABWT	25.8 <sup>†</sup> -2.4	25.8 <sup>†</sup> -2.9	25.8 <sup>†</sup> -2.9	25.8 <sup>†</sup> -3.1	25.8 <sup>†</sup> -3.0	28.0 <sup>†</sup> -3.0
AWWT	198.0 <sup>†</sup> -31.7	201.9 <sup>†</sup> -29.6	203.2 <sup>†</sup> -28.4	204.4 <sup>†</sup> -27.2	205.8 <sup>†</sup> -28.0	201.5 <sup>†</sup> -25.8
AWCOND <sup>b</sup>	81.3 <sup>†</sup> -14.9	81.3 <sup>†</sup> -13.1	81.3 <sup>†</sup> -13.4	81.5 <sup>†</sup> -12.7	81.5 <sup>†</sup> -13.8	83.7 <sup>†</sup> -12.6
AGAIN	172.2 <sup>†</sup> -31.2	176.1 <sup>†</sup> -29.0	177.4 <sup>†</sup> -27.8	178.6 <sup>†</sup> -26.7	180.0 <sup>†</sup> -27.5	173.5 <sup>†</sup> -25.5

<sup>a</sup> All means and standard deviations are adjusted as described on page 21.

<sup>b</sup> Weaning condition is a subjective scoring system.

Table 5. Means and Standard Deviations of Traits from Ames 2 by Dam Age (Kg)<sup>a</sup>

Trait	Age of Dam					
	2	3	4	5	6-10	11+
Number	241	309	243	234	597	124
BWT	23.7 <sub>±</sub> 2.3	24.8 <sub>±</sub> 2.9	25.8 <sub>±</sub> 2.6	26.4 <sub>±</sub> 3.1	27.2 <sub>±</sub> 2.9	26.6 <sub>±</sub> 3.1
WWT	169.0 <sub>±</sub> 27.9	182.1 <sub>±</sub> 26.7	190.4 <sub>±</sub> 24.8	197.1 <sub>±</sub> 24.8	204.9 <sub>±</sub> 26.4	198.1 <sub>±</sub> 24.3
WCOND <sup>c</sup>	73.5 <sub>±</sub> 11.5	80.5 <sub>±</sub> 12.1	82.1 <sub>±</sub> 10.5	83.4 <sub>±</sub> 11.8	85.2 <sub>±</sub> 11.3	84.0 <sub>±</sub> 9.8
GAIN	146.1 <sub>±</sub> 27.3	157.3 <sub>±</sub> 26.1	164.5 <sub>±</sub> 24.3	170.7 <sub>±</sub> 24.3	177.8 <sub>±</sub> 25.8	171.5 <sub>±</sub> 23.4
ABWT	25.7 <sub>±</sub> 2.3	25.9 <sub>±</sub> 2.9	25.6 <sub>±</sub> 2.6	25.8 <sub>±</sub> 3.1	25.9 <sub>±</sub> 2.9	27.7 <sub>±</sub> 3.1
AWWT	196.7 <sub>±</sub> 31.5	201.2 <sub>±</sub> 29.5	203.1 <sub>±</sub> 27.0	204.5 <sub>±</sub> 27.1	208.2 <sub>±</sub> 28.2	205.3 <sub>±</sub> 25.4
AWCOND <sup>c</sup>	81.1 <sub>±</sub> 11.5	81.1 <sub>±</sub> 12.1	80.0 <sub>±</sub> 10.5	82.2 <sub>±</sub> 11.3	82.2 <sub>±</sub> 11.3	85.1 <sub>±</sub> 9.8
AGAIN	170.9 <sub>±</sub> 31.0	175.2 <sub>±</sub> 28.9	177.5 <sub>±</sub> 26.6	178.7 <sub>±</sub> 26.8	182.2 <sub>±</sub> 27.6	177.6 <sub>±</sub> 24.6
DBWT <sup>d</sup>	26.6 <sub>±</sub> 2.9	26.6 <sub>±</sub> 3.1	26.8 <sub>±</sub> 2.9	26.6 <sub>±</sub> 2.9	26.5 <sub>±</sub> 2.9	25.9 <sub>±</sub> 3.0
DWWT	202.7 <sub>±</sub> 22.9	205.5 <sub>±</sub> 24.5	202.3 <sub>±</sub> 26.3	200.0 <sub>±</sub> 24.2	198.8 <sub>±</sub> 23.1	194.8 <sub>±</sub> 19.6
DWCOND <sup>c</sup>	85.9 <sub>±</sub> 13.2	82.8 <sub>±</sub> 19.1	82.7 <sub>±</sub> 18.8	81.6 <sub>±</sub> 18.2	81.5 <sub>±</sub> 17.6	81.3 <sub>±</sub> 11.9
DGAIN	176.1 <sub>±</sub> 22.0	178.8 <sub>±</sub> 24.0	175.6 <sub>±</sub> 25.7	173.4 <sub>±</sub> 23.5	172.3 <sub>±</sub> 22.5	168.9 <sub>±</sub> 19.3
DABWT	26.3 <sub>±</sub> 2.9	26.5 <sub>±</sub> 3.1	26.6 <sub>±</sub> 3.0	26.5 <sub>±</sub> 2.9	26.4 <sub>±</sub> 3.0	25.7 <sub>±</sub> 2.8
DAWWT	215.5 <sub>±</sub> 26.0	216.9 <sub>±</sub> 28.6	213.6 <sub>±</sub> 30.7	211.0 <sub>±</sub> 28.9	210.1 <sub>±</sub> 28.2	204.4 <sub>±</sub> 25.4
DAWCOND <sup>c</sup>	84.5 <sub>±</sub> 13.1	81.9 <sub>±</sub> 19.0	81.8 <sub>±</sub> 18.5	80.7 <sub>±</sub> 17.7	80.6 <sub>±</sub> 17.3	79.9 <sub>±</sub> 11.9
DAGAIN	189.2 <sub>±</sub> 25.7	190.5 <sub>±</sub> 28.2	187.0 <sub>±</sub> 30.1	184.5 <sub>±</sub> 28.2	183.7 <sub>±</sub> 27.5	178.7 <sub>±</sub> 25.1

<sup>a</sup>All means and standard deviations are adjusted as described on page 21.

<sup>b</sup>All variables beginning with the letter D are dam records when dam was a calf.

<sup>c</sup>Weaning condition is a subjective scoring system.

Table 6. Causal Component Estimates for Maternal Effects Model by Trait (Kg)

Trait	$\sigma_D^2$	$\sigma_M^2$	$\sigma_{DM}$	$\sigma_{KD}^2$	$\sigma_{EM}^2$	$\sigma_{EDM}$
BWT	1.90	.37	.72	8.09	.13	-1.50
WWT	325.59	30.50	-127.23	440.96	135.65	-21.62
WCOND <sup>a</sup>	30.59	2.72	-38.66	134.26	30.32	31.25
GAIN	286.74	28.78	-123.71	421.10	130.45	-8.37
ABWT	1.42	.40	.55	7.31	.31	-.97
AWWT	286.15	12.53	-75.49	535.27	71.21	-25.50
AWCOND <sup>a</sup>	24.59	2.73	-31.60	129.37	25.61	30.94
AGAIN	256.47	15.54	-82.91	517.58	81.18	-10.70

<sup>a</sup>Weaning condition is a subjective scoring system.



Table 7. Causal Component Estimates Expressed as Percentages of Total Phenotypic Variance for Maternal Effects Model by Trait

Trait	$\sigma_D^2$	$\sigma_M^2$	$\sigma_{DM}$	$\sigma_{E_D}^2$	$\sigma_{E_M}^2$	$\sigma_{E_{DM}}$
BWT	19.5	3.8	7.4	83.4	1.4	-15.5
WWT	41.5	3.9	-16.2	56.3	17.3	-2.8
WCOND	16.1	1.4	-20.3	70.5	15.9	16.4
GAIN	39.0	3.9	-16.8	57.3	17.7	-1.1
ABWT	15.8	4.5	6.1	80.9	3.4	-10.7
AWWT	35.6	1.6	-9.4	66.5	8.8	-3.2
AWCOND	13.5	1.5	-17.4	71.2	14.1	17.0
AGAIN	33.0	2.0	-10.7	66.6	10.4	-1.4

weight whether unadjusted or adjusted for age of dam, 19.5% and 15.8%, respectively, as were those of weaning condition, 16.1% and 13.5%, respectively, when compared to the other traits in this study.  $\sigma_D^2$  effects for weaning weight and gain from birth to weaning were quite large in comparison. In all of the estimates of  $\sigma_M^2$ , the genetic maternal variances were positive. This is somewhat different from Kuhlers et al. (1977) where only four of six were positive. When the values estimated for the genetic maternal variances are evaluated, there appears to be no significant differences between the traits unadjusted or adjusted for effects of age of dam. Although differences do exist, the magnitudes are not great, thus leading to a conclusion that adjustment for age of dam does not tend to mask the effects of the maternal influence. In fact, the trait weaning condition adjusted for age of dam actually exhibited a larger percentage (1.5%) than the unadjusted (1.4%) of total phenotypic variance (Table 7). Although the percentages are low for  $\sigma_M^2$ , by evaluating the covariance between direct and maternal genetic variances ( $\sigma_{DM}$ ), one can see that these covariances reflect a genetic antagonism between direct and maternal genetic effects for all traits except birth weight. The  $\sigma_{DM}$  for BWT was 7.4% and 6.1% for ABWT. Although the lowest direct and maternal genetic variances were exhibited by weaning condition, this trait proved to have the largest negative covariance between effects (-20.3%). This is thought to possibly be due to the milk production of the dam and the amount of milk received as a calf. It is known that excess fat in the mammary system decreases milk production. Therefore, a fat calf at weaning would in turn produce a thin calf at weaning. All of the covariances between direct and maternal genetic variances were

negative except for birth weight.

The estimates of the direct environmental variance ( $\sigma_{E_D}^2$ ) were quite large in magnitude, with the lone exception being that of AWWT (6.6%). This was as expected, due to the method of adjusting for environmental sources of variation. Birth weight showed the largest percentage of the total phenotypic variance contributed to  $\sigma_{E_D}^2$  with 83.4% and 80.9%, respectively, for unadjusted and adjusted for age of dam. The estimates of maternal environmental variances were also larger than those for maternal genetic variance. The estimates for the covariances between direct and maternal environmental effects once again points out the antagonism that exists between the direct effects and the maternal influences effect. All traits except weaning condition were negative (WCOND, 16.4% and AWCOND, 17.0%) for this causal component.

Since all of the variances calculated in the maternal model were positive, it was possible to express results as genetic correlations for the relationship of genetic and maternal genetic effects and as environmental correlations for the environmental effects. Table 8 contains the correlations between direct and maternal genetic variances ( $r_{DM}$ ) and the correlations between direct and maternal environmental variances ( $r_{E_{DM}}$ ). All of the  $r_{DM}$  correlations were highly negative except those for birth weight which were strongly positive, .86 and .73 for BWT and ABWT, respectively. Weaning condition exhibited the largest distorted negative values with -4.24 for WCOND and -3.86 for AWCOND. The correlation estimates for  $r_{E_{DM}}$  followed the same pattern as the causal components; whereas, the correlations for weaning condition were positive (.49 and .54, respectively), and all of the other traits negative in sign.



Table 8. Genetic Correlations and Estimates of Heritability of Causal Components for Maternal Effects Model by Trait

Trait	Correlations		Heritabilities	
	$r_{DM}^{genetic}$	$r_{EDM}^{causal}$	$h_D^2$	$h_M^2$
BWT	.86	-1.44	.20	.04
WWT	-1.28	-.88	.42	.04
WCOND	-4.24	.49	.16	.01
GAIN	-1.36	-.04	.39	.04
ABWT	.73	-.65	.16	.05
AWWT	-1.26	-.13	.36	.02
AWCOND	-3.86	.54	.14	.02
AGAIN	-1.31	-.05	.33	.02

Heritability estimates were calculated using the causal components as sources of uncontaminated genetic and maternal variances (Table 8). Estimates of heritability for the traits studied conform to other published sources. However, these estimates should be compared and a significant difference noticed between these and those listed in Table 3, page 26. The estimates for direct genetic effect ( $h_D^2$ ) are lower in magnitude. Estimates for maternal genetic improvement ( $h_M^2$ ) are relatively low, but they do exist; therefore, progress could be made by selection for maternal effects alone. Since the estimates of heritability are low and there is a negative correlation between direct and maternal effects, it is postulated that this is one reason why relatively little progress is actually made in improving these traits by selection. Brown (1976) using the sires-over-time technique calculated estimates of the phenotypic, genetic, and environmental trends in 205-day adjusted weaning weight as being 2.89, 2.58, and .31 pounds, respectively.

## CHAPTER IV

### AN ANALYSIS OF THE GENETIC IMPLICATIONS OF GRANDMATERNAL EFFECTS IN BEEF CATTLE SELECTION PROGRAMS

#### I. SUMMARY

A study of 3,220 performance records of Angus calves collected over a 19-year period from 1957 to 1975 was undertaken in an attempt to estimate the importance of grandmaternal effects as a causal component in variance of preweaning and weaning traits of beef cattle. All of these records were obtained from cattle at the Ames Plantation in Tennessee and were from non-creep-fed calves. The objectives of this study were to evaluate the importance of direct, maternal, and grandmaternal variances and to evaluate their interrelationship as causative factors in creating phenotypic variation in birth weight, gain from birth to weaning, weaning condition, and weaning weights. The data were adjusted by least squares procedures for the effects of year of birth, season of birth, and age of dam. These adjusted data were used to calculate the various covariances among relatives. The covariances included individual with itself, paternal half-sibs, maternal half-sibs, full-sibs, dam-offspring, granddam-offspring, cousins, and also within cousins and within paternal half-sibs covariances. These were equated to their expected biological components which were the direct, maternal, and grandmaternal genetic variance and the covariances between direct and maternal, direct and grandmaternal, maternal and grandmaternal



genetic effects. The components also included the direct environmental variance, maternal environmental variance, and the covariance between direct and maternal environmental effects.

The variance estimates for all effects were positive in sign with the exception of the environmental maternal variance for adjusted weaning weight (AWWT) and adjusted gain (AGAIN) (-1.2 and -1.2). The direct environmental variance contributed the largest fraction of the phenotypic variance for all traits ranging from a low of 58.4% for weaning weight to a high of 66.6% for adjusted gain. In this model, the variances attributed to the direct, maternal, and grandmaternal effects varied to some extent among various traits. Direct variances estimates were lowest for birth weight and weaning condition (20.8% and 20.2%) and highest for weaning weight and gain (42.8% and 40.2%); whereas, grandmaternal estimates were highest for weaning condition (10.3%). The estimates for grandmaternal genetic variance were all fairly large in magnitude and, therefore, appear to support the theory of an alternate generation phenomenon. (Key words: Beef Cattle, Genetics, Growth, Maternal Effects, Grandmaternal Effects)

## II. INTRODUCTION

Most of the beef cow-calf producers derive their income from pounds of calf sold at weaning. Their goal is to obtain the maximum weaning weights on their calves in order to maximize net returns. Normally, selection is practiced with the intention of improving individually or collectively such traits as birth weight, gain from birth to weaning, or weaning weight. However, relatively little long-term

progress has been made by individual selection for weaning weights (Van Vleck, 1977). Willham (1963) stated that traits whose phenotypic values are composed of components contributed by ancestral relations such as maternal effects deserve special attention. Robison (1972) stated that direct and indirect genetic maternal influences may play an important role in the expression of economically important traits. In 1972, Willham expanded the linear model to include an effect of the maternal granddam on the maternal effect of the dam. He asserted that there is the possibility that the maternal effect as expressed in the offspring could be influenced by the dam of the dam that is contributing the maternal effect. This grandmaternal effect may have a genetic basis in the grandmother but is an environmental effect on the maternal ability of the mother and on the actual phenotype of the calf (Van Vleck, 1974). Beef cattle breeders have reported that cows that were large themselves at weaning tend to wean calves that are lighter than cows that were not so heavy at weaning (Van Vleck, 1974). A grandmaternal effect can be postulated as a cause of this phenomenon. Beef cattle data examined by Totusek et al. (1971) and also by Koch (1972) suggested the existence of such a grandmaternal effect on weaning weight in beef cattle. Procedures for partitioning the genotypic variance and covariance into direct, maternal, and grandmaternal components by using covariances between relatives were outlined by Willham (1972) and Van Vleck (1974) for maternal and grandmaternal effects. The primary objectives of this study were to determine the relative magnitude of direct, maternal, and grandmaternal variances and to determine their relationship to each other as causative factors inducing variation in birth weight, gain from birth

to weaning, weaning condition, and weaning weight of beef calves.

### III. MATERIALS AND METHODS

Over a 19-year period, data were collected from the purebred Angus herd at Ames Plantation. The records were collected from 1957 to 1975 on non-creep-fed calves and included identification of calf, dam and sire, birth dates of calf and dam, birth weight, sex, weaning age, weight, and condition scores of the calves. From these records, the gain from birth to weaning was calculated as the weaning weight minus the birth weight. Available for this study were 3,220, 205-day records.

All records were adjusted by using constants obtained by least squares procedures for year of birth, season of birth, and sex of calf to produce the following traits: birth weight (BWT), weaning weight (WWT), weaning condition (WCOND), and gain from birth to weaning (GAIN). Since it has been theorized that adjustment for age of dam might mask the effects of the maternal and/or grandmaternal influence, a set of traits was also formalized in the following manner: Birth weight was additionally adjusted for effects of age of dam (ABWT) by using constants obtained by least squares procedures from a linear regression analysis, weaning condition adjusted for age of dam and weaning age (AWCOND). Adjusted 205-day weights were calculated using the regression of calculated 205-day weight on weaning age. Adjustments were made for the effects of age of calf, age of dam, and sex of calf with an additional adjustment made for the overadjustment of younger and older calves (AWWT). Adjusted gain from birth to weaning was calculated as AWWT minus ABWT (AGAIN).



Weaning condition score was a subjective scoring system that was used to evaluate the fat cover of a calf at weaning. The scores are based on a 100-point system, and the personnel who served as scorers have changed from time to time during the 19-year period.

The general procedure used to estimate the genetic and environmental variances and covariances was to calculate covariances and variances among the members of the nine groups of relatives studied and to equate the covariances to their expected biological components. The relationships used were the total phenotypic variance ( $\sigma_P^2$ ), paternal half-sibs ( $\sigma_{PHS}$ ), maternal half-sibs ( $\sigma_{MHS}$ ), full-sibs ( $\sigma_{FS}$ ), dam-offspring ( $\sigma_{D-O}$ ), granddam offspring ( $\sigma_{GD-O}$ ), between cousins ( $\sigma_{\text{cousins}}$ ), within cousins ( $\sigma_{\text{within cousins}}$ ), and within paternal half-sibs ( $\sigma_{\text{within PHS}}$ ).

The theoretical expectations for the covariances and variances among relatives are shown in Table 9. The rationale for the theoretical expectations for the genetic causal components for any relationship was developed by Willham (1972) and Van Vleck (1974).

Detailed preliminary analyses were performed in order to obtain estimates of the variances and covariances used in this study. The records described earlier were manipulated into three separate data sets hereafter referred to as Ames 1, Ames 2, and Ames 3.

Ames 1 data set contained 3,220 performance records consisting of one generation of data. From Ames 1 data, by the use of a nested analysis of variance procedure, the total phenotypic variance, paternal half-sibs, and the within paternal half-sibs relationships were calculated along with the maternal half-sibs and full-sibs relationships for all traits

Table 9. Contribution of Direct, Maternal, and Grandmaternal Genetic Variance and Covariance to the Covariance Between Relatives

Covariance <sup>b</sup>	Causal Components <sup>a</sup>								
	$\sigma_D^2$	$\sigma_M^2$	$\sigma_N^2$	$\sigma_{DM}$	$\sigma_{DN}$	$\sigma_{MN}$	$\sigma_{E_D}^2$	$\sigma_{E_M}^2$	$\sigma_{E_{DM}}$
$\sigma_P^2$	1	1	1	1	1/2	1	1	1	1
$\sigma_{PHS}$	1/4	0	0	0	0	0	0	0	0
$\sigma_{MHS}$	1/4	1	1	1	1/2	1	0	1	0
$\sigma_{FS}$	1/2	1	1	1	1/2	1	0	1	0
$\sigma_{D-O}$	1/2	1/2	1/2	1-1/4	5/8	1-1/4	0	0	1
$\sigma_{GD-O}$	1/4	1/4	1/4	5/8	1-1/16	5/8	0	0	0
$\sigma_{Cousins}$	1/16	1/4	1	1/4	1/2	1	0	0	0
$\sigma_{Within Cousins}$	15/16	3/4	0	3/4	0	0	1	0	0
$\sigma_{Within PHS}$	3/4	1	1	1	1/2	1	1	1	1

<sup>a</sup>The subscripts on the causal components denote direct genetic effects (D), maternal effects (M), grandmaternal effects (N), direct environmental effects ( $E_D$ ), and maternal environmental effects ( $E_M$ ).

<sup>b</sup> $\sigma_P^2$ , the total phenotypic variance;  $\sigma_{PHS}$ , paternal half-sibs;  $\sigma_{MHS}$ , maternal half-sibs;  $\sigma_{FS}$ , full-sibs;  $\sigma_{D-O}$ , dam-offspring;  $\sigma_{GD-O}$ , granddam-offspring;  $\sigma_{Cousins}$ , between cousins;  $\sigma_{Within Cousins}$ , and  $\sigma_{Within PHS}$ , within paternal half-sibs.

involved in this study. The latter two terms were calculated by a dam within sire nested hierarchy while the former three were derived from paternal half-sib analysis.

Ames 2 data set was created to form a two-generation data set (calf performance plus its dam's performance as a calf). This data set was necessary in order to breakout the covariances between dam-offspring, between cousins, and within cousins. Seventeen hundred and forty-eight (1,748) two-generation records were available for analysis.

The third data set was formulated in order to obtain the covariance between granddam and offspring. This was accomplished by fitting three generations of performance records together to formulate Ames 3 (calf performance plus its dam's performance as a calf plus her dam's performance as a calf (the granddam)). Ames 3 contained 687 three-generation records.

In preliminary analyses performed on the data, each set was used separately and independently to determine direct, maternal, and grandmaternal genetic effects. However, since the preliminary results were in such accord with each other from data set to data set, it was deemed to be conducive to combine the various covariances from different data sets to utilize the maximum degrees of freedom (Table 10) to enhance the validity of the final results. The covariances and variances among the members of the nine relationship groups are presented in Table 10.

In order to compare the effects of selection for direct, selection for direct and maternal genetic effects, and selection for direct, maternal, and grandmaternal genetic effects, heritability estimates were calculated from the original data by four different well-known methods:



Table 10. Degrees of Freedom and the Covariance Among Relatives by Trait (Kg)

Source	df	Trait									
		BWT	WWT	WCOND <sup>a</sup>	GAIN	ABWT	AWWT	AWCOND <sup>a</sup>	AGAIN		
$\sigma_P^2$	3219	9.70	783.85	190.48	734.99	8.86	804.18	181.65	777.16		
$\sigma_{PHS}$	113	.60	91.61	15.59	80.29	.33	66.53	12.96	61.48		
$\sigma_{MHS}$	2678	1.82	130.53	9.96	115.80	1.59	74.78	9.71	75.28		
$\sigma_{FS}$	353	2.05	191.50	1.73	170.28	2.01	156.34	2.22	144.68		
$\sigma_{D-0}$	1657	.52	-2.61	-.42	-5.25	.64	29.48	5.10	21.66		
$\sigma_{GD-0}$	624	1.01	9.50	-15.84	1.56	.80	27.49	-12.92	16.18		
$\sigma_{Cousins}$	120	.42	-14.55	-6.32	-18.29	.16	-33.32	-5.93	-35.36		
$\sigma_{Within Cousins}$	940	8.41	826.25	147.39	776.70	7.62	858.22	136.96	830.81		
$\sigma_{Within PHS}$	3106	9.11	692.24	174.89	654.70	8.70	737.65	168.69	715.68		

<sup>a</sup> Weaning condition is a subjective scoring system.

paternal half-sib, maternal half-sib, full-sib, and cousins. The estimates are presented in Table 11.

Since there were nine covariances and nine unknowns (Table 9), the equations can be solved to obtain the values for these unknowns. It should be noted from Table 9 that there are linear dependencies in this system of equations. Because of this dependency, the equations were solved by using the Moore-Penrose generalized inverse method. The solutions were computed using singular value decomposition. This method yields solutions that are not necessarily unique, but the relative relationship of the unknowns to each other should be valid. The scaling effect, however, does not appear to be a major problem in that estimates of direct genetic variance conforms with the accepted range of values widely published for additive genetic variation for the traits. It was felt that the solutions obtained were very plausible.

The model included direct additive genetic variance ( $\sigma_D^2$ ), additive maternal variance ( $\sigma_M^2$ ), additive grandmaternal variance ( $\sigma_N^2$ ), the covariances of direct with maternal ( $\sigma_{DM}$ ), direct with grandmaternal ( $\sigma_{DN}$ ), maternal with grandmaternal ( $\sigma_{MN}$ ), the direct environmental variance ( $\sigma_{E_D}^2$ ), the maternal environmental variance ( $\sigma_{E_M}^2$ ), and the covariance between direct and maternal environmental sources of variation ( $\sigma_{E_{DM}}$ ). Genetic correlations and estimates of heritability were calculated using the results of the solutions given by the generalized inverse of the model.

Table 11. Heritability Estimates Calculated from Conventional Covariances Among Various Relatives

Trait	Method of Calculation			
	Paternal Half-Sib	Maternal Half-Sib	Full-Sib	Cousins
BWT	.24	.80	.44	.76
WWT	.47	.75	.51	0
WCOND	.33	.23	.08	0
GAIN	.44	.71	.48	0
ABWT	.14	.73	.44	.33
AWWT	.33	.40	.38	0
AWCOND	.28	.23	.09	0
AGAIN	.32	.42	.37	0



## IV. RESULTS AND DISCUSSION

The adjusted means and standard deviations of the average calf's performance, the dam's performance as a calf, and the granddam's performance as a calf are all shown in Table 12 by granddam-age. These values were from the data set which had two generations of data. These means tended to illustrate an alternate generation pattern. With the exception of birth weight, all of the variables tend to fluctuate in the opposite direction for each type of animal, the calf, dam, or granddam. For example, if the dam, as a calf, had a high weaning weight, then her respective offspring was lighter at weaning. Van Vleck (1974) postulated a grandmaternal effect as a cause of this situation existing across generations; for age of granddam 2, granddam weaning condition (GWCOND) was 87.3, dam's weaning condition (DWCOND) plunged down to 77.5, and the calf then subsequently rose to 83.3. Table 13, which is also a table of means and standard deviations, has the variables broken into groups by dam-age and granddam-age. This table also illustrates the presence of maternal and grandmaternal influences on the traits studied. This is demonstrated generally for all of the traits by the presence of high values for younger-aged granddams and then decreasing as these granddams approach the mid-aged groups. For example, in the dam age 2 group, as the granddam becomes older, the corresponding weaning weights decrease dramatically from 181.3 kg to 167.1 kg.

Table 14 contains the covariance and variance component estimates for the traits studied in this analysis. For ease of discussion, the estimates of the causal components are expressed as a percentage of the



Table 12. Means and Standard Deviations of Traits from Ames 3 by Granddam Age (Kg)<sup>a</sup>

Trait	Age of Granddam					
	2	3	4	5	6-10	11+
Number	88	169	131	96	186	17
BWT	25.6 <sup>±</sup> 3.1	26.9 <sup>±</sup> 3.1	25.8 <sup>±</sup> 3.4	25.5 <sup>±</sup> 3.0	24.9 <sup>±</sup> 2.9	25.2 <sup>±</sup> 3.3
WWT	193.4 <sup>±</sup> 28.4	198.2 <sup>±</sup> 29.2	193.3 <sup>±</sup> 28.6	188.2 <sup>±</sup> 25.9	183.6 <sup>±</sup> 27.7	163.5 <sup>±</sup> 35.6
WCOND <sup>b</sup>	83.3 <sup>±</sup> 11.9	82.5 <sup>±</sup> 12.9	81.0 <sup>±</sup> 13.1	81.7 <sup>±</sup> 11.7	80.4 <sup>±</sup> 11.6	74.0 <sup>±</sup> 10.2
GAIN	167.8 <sup>±</sup> 27.4	171.3 <sup>±</sup> 28.4	167.5 <sup>±</sup> 27.3	162.7 <sup>±</sup> 25.1	158.7 <sup>±</sup> 26.6	138.3 <sup>±</sup> 34.4
ABWT	25.4 <sup>±</sup> 3.0	26.7 <sup>±</sup> 2.8	26.0 <sup>±</sup> 3.2	25.4 <sup>±</sup> 2.7	25.3 <sup>±</sup> 2.6	26.4 <sup>±</sup> 3.0
AWWT <sup>b</sup>	203.9 <sup>±</sup> 25.6	208.8 <sup>±</sup> 29.9	205.7 <sup>±</sup> 30.0	199.9 <sup>±</sup> 24.4	200.4 <sup>±</sup> 26.4	185.0 <sup>±</sup> 33.2
AWCOND	82.2 <sup>±</sup> 11.6	81.5 <sup>±</sup> 12.8	81.1 <sup>±</sup> 12.2	81.4 <sup>±</sup> 10.6	81.2 <sup>±</sup> 10.9	77.3 <sup>±</sup> 10.1
AGAIN	178.5 <sup>±</sup> 28.7	182.0 <sup>±</sup> 29.5	179.7 <sup>±</sup> 29.1	174.4 <sup>±</sup> 24.3	175.1 <sup>±</sup> 25.9	158.6 <sup>±</sup> 32.7
DBWT <sup>c</sup>	25.3 <sup>±</sup> 2.4	25.9 <sup>±</sup> 3.1	25.3 <sup>±</sup> 2.2	26.3 <sup>±</sup> 2.2	28.0 <sup>±</sup> 2.8	27.0 <sup>±</sup> 2.3
DWWT <sup>b</sup>	200.5 <sup>±</sup> 31.2	192.9 <sup>±</sup> 27.1	201.5 <sup>±</sup> 22.2	200.3 <sup>±</sup> 23.9	216.5 <sup>±</sup> 20.5	208.9 <sup>±</sup> 18.1
DWCOND	77.5 <sup>±</sup> 14.1	82.9 <sup>±</sup> 12.0	85.7 <sup>±</sup> 9.6	85.2 <sup>±</sup> 13.9	89.2 <sup>±</sup> 12.7	91.4 <sup>±</sup> 15.4
DGAIN	175.2 <sup>±</sup> 29.9	167.0 <sup>±</sup> 25.4	176.2 <sup>±</sup> 22.7	174.0 <sup>±</sup> 23.6	188.5 <sup>±</sup> 20.3	181.9 <sup>±</sup> 17.4
DABWT	27.3 <sup>±</sup> 2.4	27.0 <sup>±</sup> 3.1	25.1 <sup>±</sup> 2.2	25.6 <sup>±</sup> 2.2	26.8 <sup>±</sup> 2.8	28.1 <sup>±</sup> 2.3
DAWWT <sup>b</sup>	232.4 <sup>±</sup> 38.9	215.5 <sup>±</sup> 32.8	218.5 <sup>±</sup> 30.0	200.6 <sup>±</sup> 26.0	225.5 <sup>±</sup> 24.8	221.1 <sup>±</sup> 18.0
DAWCOND	85.2 <sup>±</sup> 14.1	83.6 <sup>±</sup> 12.0	83.7 <sup>±</sup> 9.6	83.0 <sup>±</sup> 13.9	86.1 <sup>±</sup> 12.7	92.5 <sup>±</sup> 15.4
DAGAIN	205.1 <sup>±</sup> 37.6	188.4 <sup>±</sup> 31.1	193.4 <sup>±</sup> 26.2	175.0 <sup>±</sup> 25.8	198.7 <sup>±</sup> 24.7	193.0 <sup>±</sup> 17.5
GBWT <sup>d</sup>	26.1 <sup>±</sup> 2.7	26.9 <sup>±</sup> 2.9	26.7 <sup>±</sup> 3.0	25.6 <sup>±</sup> 2.4	27.1 <sup>±</sup> 2.8	25.6 <sup>±</sup> 3.0
GWWT	200.2 <sup>±</sup> 26.4	202.4 <sup>±</sup> 25.7	194.6 <sup>±</sup> 27.0	193.9 <sup>±</sup> 26.1	194.9 <sup>±</sup> 26.3	194.7 <sup>±</sup> 17.1
GWCOND	87.3 <sup>±</sup> 9.1	83.2 <sup>±</sup> 13.8	80.0 <sup>±</sup> 13.2	72.8 <sup>±</sup> 27.2	82.8 <sup>±</sup> 14.4	78.8 <sup>±</sup> 6.8
GGAIN	174.2 <sup>±</sup> 25.7	175.5 <sup>±</sup> 26.3	167.8 <sup>±</sup> 26.4	168.4 <sup>±</sup> 25.7	167.8 <sup>±</sup> 26.4	169.1 <sup>±</sup> 17.9
GABWT	25.9 <sup>±</sup> 2.7	27.0 <sup>±</sup> 3.0	26.6 <sup>±</sup> 3.2	25.1 <sup>±</sup> 2.3	26.9 <sup>±</sup> 2.8	25.5 <sup>±</sup> 2.1
GAWWT	210.9 <sup>±</sup> 28.9	213.4 <sup>±</sup> 28.9	205.0 <sup>±</sup> 31.0	203.5 <sup>±</sup> 27.2	206.4 <sup>±</sup> 31.0	207.7 <sup>±</sup> 23.0
GAWCOND <sup>b</sup>	86.3 <sup>±</sup> 7.9	83.0 <sup>±</sup> 13.5	78.8 <sup>±</sup> 13.2	71.2 <sup>±</sup> 27.8	81.4 <sup>±</sup> 14.8	78.2 <sup>±</sup> 7.7
GAGAIN	185.0 <sup>±</sup> 28.4	186.4 <sup>±</sup> 29.7	178.4 <sup>±</sup> 30.6	178.4 <sup>±</sup> 26.5	179.5 <sup>±</sup> 30.8	182.1 <sup>±</sup> 24.1

<sup>a</sup>All means and standard deviations are adjusted as described on page 39.

<sup>b</sup>Meaning condition is a subjective scoring system.

<sup>c</sup>All variables beginning with letter D are dam records when dam was a calf.

<sup>d</sup>All variables beginning with letter G are granddam records when granddam was a calf.

Table 13. Means and Standard Deviations of Traits by Dam Age and Granddam Age (Kg)<sup>a</sup>

D-Age	GD-Age	No.	Trait			
			BWT	WWT	WCOND <sup>b</sup>	GAIN
2	2	9	24.9 <sup>+</sup> <sub>-3.4</sub>	181.3 <sup>+</sup> <sub>-25.5</sub>	72.3 <sup>+</sup> <sub>-8.4</sub>	156.4 <sup>+</sup> <sub>-24.0</sub>
	3	23	24.7 <sup>+</sup> <sub>-2.4</sub>	177.1 <sup>+</sup> <sub>-27.0</sub>	74.9 <sup>+</sup> <sub>-13.1</sub>	152.4 <sup>+</sup> <sub>-26.6</sub>
	4	35	23.7 <sup>+</sup> <sub>-2.7</sub>	179.3 <sup>+</sup> <sub>-30.2</sub>	71.7 <sup>+</sup> <sub>-12.9</sub>	155.6 <sup>+</sup> <sub>-29.7</sub>
	5	26	23.4 <sup>+</sup> <sub>-2.1</sub>	166.5 <sup>+</sup> <sub>-24.6</sub>	73.3 <sup>+</sup> <sub>-13.9</sub>	143.1 <sup>+</sup> <sub>-24.4</sub>
	6-10	111	23.7 <sup>+</sup> <sub>-2.1</sub>	166.2 <sup>+</sup> <sub>-27.3</sub>	73.7 <sup>+</sup> <sub>-10.5</sub>	142.5 <sup>+</sup> <sub>-26.7</sub>
	11+	37	23.3 <sup>+</sup> <sub>-2.3</sub>	167.1 <sup>+</sup> <sub>-28.7</sub>	74.1 <sup>+</sup> <sub>-11.5</sub>	143.8 <sup>+</sup> <sub>-28.3</sub>
3	2	30	23.8 <sup>+</sup> <sub>-3.0</sub>	183.7 <sup>+</sup> <sub>-25.3</sub>	83.4 <sup>+</sup> <sub>-12.3</sub>	160.0 <sup>+</sup> <sub>-24.4</sub>
	3	30	25.8 <sup>+</sup> <sub>-2.7</sub>	181.6 <sup>+</sup> <sub>-31.2</sub>	77.6 <sup>+</sup> <sub>-12.9</sub>	155.8 <sup>+</sup> <sub>-30.2</sub>
	4	38	24.9 <sup>+</sup> <sub>-2.8</sub>	185.8 <sup>+</sup> <sub>-31.2</sub>	80.2 <sup>+</sup> <sub>-13.1</sub>	160.8 <sup>+</sup> <sub>-30.4</sub>
	5	38	24.7 <sup>+</sup> <sub>-2.8</sub>	178.9 <sup>+</sup> <sub>-30.4</sub>	77.6 <sup>+</sup> <sub>-14.0</sub>	154.1 <sup>+</sup> <sub>-30.2</sub>
	6-10	129	24.8 <sup>+</sup> <sub>-2.9</sub>	180.8 <sup>+</sup> <sub>-24.0</sub>	80.9 <sup>+</sup> <sub>-11.0</sub>	156.0 <sup>+</sup> <sub>-23.7</sub>
	11+	44	24.9 <sup>+</sup> <sub>-3.3</sub>	184.7 <sup>+</sup> <sub>-25.3</sub>	82.0 <sup>+</sup> <sub>-11.6</sub>	159.8 <sup>+</sup> <sub>-24.0</sub>
4	2	20	25.8 <sup>+</sup> <sub>-2.7</sub>	192.6 <sup>+</sup> <sub>-27.6</sub>	85.1 <sup>+</sup> <sub>-12.2</sub>	166.7 <sup>+</sup> <sub>-27.2</sub>
	3	35	26.7 <sup>+</sup> <sub>-2.6</sub>	189.3 <sup>+</sup> <sub>-25.7</sub>	80.4 <sup>+</sup> <sub>-11.0</sub>	162.7 <sup>+</sup> <sub>-24.9</sub>
	4	28	25.4 <sup>+</sup> <sub>-2.9</sub>	187.7 <sup>+</sup> <sub>-24.6</sub>	83.6 <sup>+</sup> <sub>-11.2</sub>	162.2 <sup>+</sup> <sub>-22.9</sub>
	5	34	25.8 <sup>+</sup> <sub>-2.0</sub>	194.2 <sup>+</sup> <sub>-19.4</sub>	84.2 <sup>+</sup> <sub>-10.9</sub>	168.5 <sup>+</sup> <sub>-19.1</sub>
	6-10	97	25.7 <sup>+</sup> <sub>-2.8</sub>	189.2 <sup>+</sup> <sub>-26.3</sub>	81.0 <sup>+</sup> <sub>-10.1</sub>	163.4 <sup>+</sup> <sub>-26.1</sub>
	11+	29	25.5 <sup>+</sup> <sub>-2.2</sub>	192.1 <sup>+</sup> <sub>-23.3</sub>	81.4 <sup>+</sup> <sub>-8.3</sub>	166.6 <sup>+</sup> <sub>-23.2</sub>
5	2	19	26.3 <sup>+</sup> <sub>-3.8</sub>	192.3 <sup>+</sup> <sub>-26.0</sub>	86.8 <sup>+</sup> <sub>-11.5</sub>	165.9 <sup>+</sup> <sub>-25.3</sub>
	3	35	26.6 <sup>+</sup> <sub>-2.7</sub>	203.4 <sup>+</sup> <sub>-24.4</sub>	81.9 <sup>+</sup> <sub>-12.3</sub>	176.5 <sup>+</sup> <sub>-24.1</sub>
	4	24	26.1 <sup>+</sup> <sub>-2.9</sub>	195.3 <sup>+</sup> <sub>-24.4</sub>	83.9 <sup>+</sup> <sub>-11.9</sub>	169.2 <sup>+</sup> <sub>-23.4</sub>
	5	32	26.1 <sup>+</sup> <sub>-3.5</sub>	193.9 <sup>+</sup> <sub>-27.0</sub>	82.9 <sup>+</sup> <sub>-11.2</sub>	167.8 <sup>+</sup> <sub>-26.6</sub>
	6-10	95	26.2 <sup>+</sup> <sub>-2.9</sub>	199.3 <sup>+</sup> <sub>-22.8</sub>	84.6 <sup>+</sup> <sub>-11.9</sub>	173.0 <sup>+</sup> <sub>-22.6</sub>
	11+	29	27.2 <sup>+</sup> <sub>-3.5</sub>	190.6 <sup>+</sup> <sub>-27.9</sub>	79.0 <sup>+</sup> <sub>-11.2</sub>	163.4 <sup>+</sup> <sub>-26.6</sub>
6-10	2	43	26.2 <sup>+</sup> <sub>-2.6</sub>	204.1 <sup>+</sup> <sub>-30.6</sub>	85.0 <sup>+</sup> <sub>-10.7</sub>	177.8 <sup>+</sup> <sub>-29.8</sub>
	3	94	28.0 <sup>+</sup> <sub>-3.1</sub>	207.7 <sup>+</sup> <sub>-26.0</sub>	86.3 <sup>+</sup> <sub>-11.9</sub>	179.8 <sup>+</sup> <sub>-25.6</sub>
	4	72	27.1 <sup>+</sup> <sub>-3.7</sub>	204.9 <sup>+</sup> <sub>-28.4</sub>	84.4 <sup>+</sup> <sub>-13.2</sub>	177.9 <sup>+</sup> <sub>-27.2</sub>
	5	93	26.2 <sup>+</sup> <sub>-2.7</sub>	200.4 <sup>+</sup> <sub>-23.0</sub>	85.4 <sup>+</sup> <sub>-11.0</sub>	174.1 <sup>+</sup> <sub>-23.0</sub>
	6-10	217	27.4 <sup>+</sup> <sub>-2.6</sub>	206.7 <sup>+</sup> <sub>-25.4</sub>	85.5 <sup>+</sup> <sub>-10.8</sub>	179.3 <sup>+</sup> <sub>-24.8</sub>
	11+	78	27.2 <sup>+</sup> <sub>-2.7</sub>	202.9 <sup>+</sup> <sub>-29.0</sub>	83.3 <sup>+</sup> <sub>-11.0</sub>	175.7 <sup>+</sup> <sub>-28.1</sub>
11+	2	4	26.6 <sup>+</sup> <sub>-1.0</sub>	200.6 <sup>+</sup> <sub>-25.5</sub>	85.1 <sup>+</sup> <sub>-14.7</sub>	174.1 <sup>+</sup> <sub>-25.8</sub>
	3	20	27.6 <sup>+</sup> <sub>-2.6</sub>	197.0 <sup>+</sup> <sub>-22.0</sub>	81.4 <sup>+</sup> <sub>-9.0</sub>	169.4 <sup>+</sup> <sub>-20.9</sub>
	4	21	26.2 <sup>+</sup> <sub>-3.9</sub>	203.8 <sup>+</sup> <sub>-23.2</sub>	81.6 <sup>+</sup> <sub>-8.4</sub>	177.6 <sup>+</sup> <sub>-23.2</sub>
	5	21	25.3 <sup>+</sup> <sub>-3.1</sub>	195.0 <sup>+</sup> <sub>-28.2</sub>	86.3 <sup>+</sup> <sub>-11.3</sub>	169.7 <sup>+</sup> <sub>-26.3</sub>
	6-10	44	27.0 <sup>+</sup> <sub>-2.7</sub>	197.8 <sup>+</sup> <sub>-22.8</sub>	84.9 <sup>+</sup> <sub>-9.7</sub>	170.7 <sup>+</sup> <sub>-22.5</sub>
	11+	14	26.7 <sup>+</sup> <sub>-3.7</sub>	196.4 <sup>+</sup> <sub>-29.8</sub>	84.3 <sup>+</sup> <sub>-9.9</sub>	169.6 <sup>+</sup> <sub>-27.8</sub>

<sup>a</sup>All means and standard deviations are adjusted as described on page 39.

<sup>b</sup>Weaning condition is a subjective scoring system.



Table 14. Causal Component Estimates for Grandmaternal Effects Model by Trait (Kg)

Trait	$\sigma_D^2$	$\sigma_M^2$	$\sigma_N^2$	$\sigma_{DM}$	$\sigma_{DN}$	$\sigma_{MN}$	$\sigma_{E_D}^2$	$\sigma_{E_M}^2$	$\sigma_{E_{DM}}$
BWT	2.02	1.20	.80	-.79	1.18	-1.19	6.20	.57	.26
WWT	335.80	124.52	66.94	-53.52	-18.29	-111.09	458.19	17.37	-49.05
WCOND	38.53	12.67	19.54	-30.99	.87	-24.12	125.01	13.87	32.56
GAIN	295.34	120.95	61.37	-46.61	-21.04	-106.18	444.07	13.28	-39.94
ABWT	1.39	1.20	.57	-.54	1.02	-1.17	5.81	.71	.55
AWWT	281.14	127.21	40.52	-33.47	10.62	-120.16	524.34	-9.29	-9.56
AWCOND	31.41	11.97	16.72	-26.91	2.56	-22.15	118.72	13.28	34.78
AGAIN	253.83	129.39	40.53	-28.92	1.82	-117.79	517.49	-9.33	-7.96

<sup>a</sup>Weaning condition is a subjective scoring system.

total phenotypic variance for the grandmaternal model in Table 15.

The estimates of the percentages of total phenotypic variance which were ascribed to the various variance components were positive with the exceptions of adjusted weaning weight and adjusted gain for the maternal environmental variance ( $\sigma_{EM}^2$ ), -1.2 and -1.2, respectively. Grandparental variance,  $\sigma_N^2$ , appears to be of importance for all traits regardless of method of adjustment with the values for BWT, WWT, WCOND, GAIN, ABWT, AWWT, AWCOND, and AGAIN being 8.2, 8.5, 10.3, 8.4, 6.3, 5.0, 9.2, and 5.2%, respectively. This is in contrast to the findings of Kuhlert et al. (1977), who reported that five of six weights taken at various ages had negative grandmaternal variances ( $\sigma_N^2$ ) in pigs. Also estimates of grandmaternal variance for gains appeared to be close to zero in their study.

With the addition of grandmaternal influences to the model, both maternal and grandparental effects appear to be larger in magnitude and of more importance in affecting the total phenotypic variance for all traits including birth weight (refer to Chapter III, page 18).

When the values estimated for both the maternal genetic variance and the grandmaternal genetic variances are evaluated, there appears to be little difference between the magnitude of the causal components of variation whether adjusted or unadjusted for effects of age of dam; thus leading to the conclusion that adjustment for age of dam does not distort the variances due to the effects of the maternal and/or grandmaternal on the offspring. By evaluating the covariance between direct and maternal genetic variances ( $\sigma_{DM}$ ), one can see that these covariances reflect a genetic antagonism between direct and maternal effects for all traits.

Table 15. Causal Component Estimates Expressed as Percentages of Total Phenotype for Grandmaternal Effects Model by Trait

Trait	$\sigma_D^2$	$\sigma_M^2$	$\sigma_N^2$	$\sigma_{DM}$	$\sigma_{DN}$	$\sigma_{MN}$	$\sigma_{ED}^2$	$\sigma_{EM}^2$	$\sigma_{EDM}$
BWT	20.8	12.4	8.2	-8.1	12.1	-12.3	64.0	5.8	2.7
WWT	42.8	15.9	8.5	-6.8	-2.3	-14.2	58.4	2.2	-6.3
WCOND	20.2	6.7	10.3	-16.3	0.5	-12.7	65.6	7.3	17.1
GAIN	40.2	16.5	8.4	-6.3	-2.9	-14.4	60.4	1.8	-5.4
ABWT	15.4	13.3	6.3	-5.9	11.2	-13.0	64.4	7.8	6.1
AWWT	35.0	15.8	5.0	-4.2	1.3	-15.0	65.2	-1.2	-1.2
AWCOND	17.3	6.6	9.2	-14.8	1.4	-12.2	65.4	7.3	19.1
AGAIN	32.7	16.6	5.2	-3.7	0.2	-15.2	66.6	-1.2	-1.0



Weaning condition exhibited the largest negative covariance between direct and maternal effects (-16.3 for WCOND and -14.8 for AWCOND); whereas, the covariances between direct and grandmaternal genetic variances ( $\sigma_{DN}$ ) were all positive, except WWT and GAIN (-2.3 and -2.9). However, even these estimates were nearly zero. These results could be explained by the grandmaternal influence theory which suggests that excess fat in the mammary system decreases milk production. Therefore, a fat granddam at weaning would in turn produce a thin calf at weaning which (if a female) would produce a fat offspring at weaning.

The estimates of the direct environmental variance ( $\sigma_{ED}^2$ ) were large in magnitude as was to be expected. Kuhlert et al. (1977) also reported large environmental variances. Weaning condition (WCOND) and gain from birth to weaning (AGAIN) exhibited the largest estimates for this causal component (65.6% and 66.6%, respectively). The estimates for the covariance between direct and maternal environmental effects for the traits weaning weight and gain once again point out the antagonism that exists between selection for direct and the maternal influences effect.

Since most of the variances in the grandmaternal model were positive, it was possible to express results as genetic correlations for the relationship of genetic and maternal genetic effects, genetic and grandmaternal genetic effects, maternal and grandmaternal genetic effects, and as environmental correlations for the environmental effects. Table 16 contains the correlations between direct and maternal genetic variances ( $r_{DM}$ ), between direct and grandmaternal genetic variances ( $r_{DN}$ ), between maternal and grandmaternal genetic variances ( $r_{MN}$ ), and the correlations between direct and maternal environmental variances

Table 16. Genetic Correlations and Estimates of Heritability of Causal Components for Grandmaternal Effects Model by Trait

Trait	Correlations				Heritabilities		
	$r_{DM}^2$	$r_{DN}^2$	$r_{MN}^2$	$r_{E_{DM}}^2$	$h_D^2$	$h_M^2$	$h_N^2$
BWT	-.51	.93	-1.22	.14	.21	.12	.08
WWT	-.26	-.12	-1.22	-.55	.43	.16	.09
WCOND	-1.40	.03	-1.53	.78	.20	.07	.10
GAIN	-.25	-.16	-1.23	-.52	.40	.16	.08
ABWT	-.41	1.14	1.42	.27	.15	.13	.06
AWWT	-.18	.10	-1.67	0*	.35	.16	.05
AWCOND	-1.39	.11	-1.57	.88	.17	.07	.09
AGAIN	-.16	.12	-1.63	0*	.33	.17	.05

\*Negative maternal environmental variance.

( $r_{E_{DM}}$ ). All of the  $r_{DM}$  correlations were moderate to highly negative ranging from -.16 for AGAIN to -1.40 for WCOND. In contrast, all of the  $r_{DN}$  correlations were low to strongly positive for all but two of the traits (-.12 for WWT and -.16 for GAIN). Birth weight both adjusted and unadjusted for effect of age of dam were highly positive in sign (1.14 and .93, respectively). All traits except ABWT (1.42) were highly negative for  $r_{MN}$  estimates once again illustrating a two-generation alternate effect.

Heritability estimates were calculated using the causal components as sources of uncontaminated genetic and maternal and grandmaternal variances (Table 16). Estimates of heritability for the traits studied conform to other published values. However, these estimates should be contrasted with those listed in Table 11, page 45. The estimates for direct genetic effect ( $h_D^2$ ) are slightly lower in magnitude. However, the addition of  $h_D^2$  and  $h_M^2$  (the estimates for maternal genetic improvement) is much lower than the corresponding maternal half-sib estimates. The estimates of grandmaternal genetic improvement ( $h_N^2$ ) all tend to be low in magnitude; however, they are positive and do exist. Since the estimates of heritability for direct genetic effects and those of the maternal plus grandmaternal genetic effects are about equal in magnitude for some traits, it is postulated that this is one reason why relatively little progress is actually made in improving these traits by selection. Van Vleck (1977) in a theoretical study illustrated the importance of the covariance term in long-term response. With a large negative covariance, selection of males for direct and females for maternal genetic value would give greater expected response in progeny after the first generation than selection of females for direct genetic value.



## CHAPTER V

### SUMMARY

A study utilizing 3,220 performance records of Angus calves dropped over a 19-year period from 1957 to 1975 was undertaken in an attempt to estimate the importance of direct, maternal, and grandmaternal variances and to evaluate their interrelationship as causative factors in creating phenotypic variation in birth weight, gain from birth to weaning, weaning condition, and weaning weights. All of these records were obtained from cattle at the Ames Plantation in Tennessee and were from non-creep-fed calves. The data were adjusted by least squares procedures for the effects of year of birth, season of birth, and age of dam. These adjusted data were used to calculate the various covariances among relatives. The model for maternal effects utilized the covariances of the individual with itself and paternal half-sibs, maternal half-sibs, full-sibs, dam-offspring, and granddam-offspring covariances. While the model for assessing grandmaternal genetic influences utilized, in addition to the above six covariances, between cousins, within cousins, and within paternal half-sibs. All of these were equated to their expected biological components, direct genetic variance, maternal genetic variance, grandmaternal genetic variance, covariances between direct and maternal, between direct and grandmaternal, between maternal and grandmaternal, direct environmental variance, maternal environmental variance, and the covariance between direct and maternal environmental effects.

The maternal model yielded positive effects for all estimates of variances with the direct environmental variance contributing the largest fraction of the total phenotypic variances for all traits except adjusted weaning weight (6.6%). The estimates ranged quite high (up to 83.4% for birth weight); however, the heritability estimates are in line with accepted values for these traits. The direct estimates of variance, ranging from a low of 16.1% for weaning condition to a high of 41.5% for weaning weight, were, therefore, considered quite reasonable. Estimates of the maternal variance all tended to be low (from 1.4% to 4.5%); however, they are positive and do exist. The covariance between direct and maternal effects and the environmental covariances between direct and maternal effects exhibited negative signs except for the genetic covariance for birth weight (7.4% and 6.1%) and environmental covariance for weaning condition (16.4% and 17.0%). This negative covariance supports the theory of an antagonism existing between direct and maternal effects for the weaning and preweaning traits.

The grandmaternal model showed the variance estimates for all effects to be positive except adjusted weaning weight and adjusted gain (-1.2 and -1.2) for the maternal environmental variance. These estimates ranged from 20.2% for birth to 42.8% for weaning weight for direct effects, while the maternal variances were in the 6% to 16% range as to their influence upon the total phenotypic variance. The estimates of the grandmaternal variance were in the range of 5% to 10%, thus very evident as to their importance upon the total phenotypic variance. The estimates for grandmaternal genetic variance were all fairly large in magnitude and were thought to play an important role in validating the alternate generation phenomenon.



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CRANES  CREST



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## VITA

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On August 25, 1974, the author married Sophia R. Pappas of Anderson County, Tennessee. They were and are the proud parents of a son, Samuel Travis Leo, born June 9, 1977, deceased June 20, 1977.

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