I. CORRELATIONS BETWEEN GROWTH TRAITS OF PATERNAL HALF-BROTHERS AND MATERNAL TRAITS OF PATERNAL HALF-SISTERS

Data from the USDA Livestock and Range Research Station, Miles City, MT collected between 1962 and 1975 were used in this study. Records involved five inbred Hereford lines that produced straight-line and linecross calves in an experiment of three phases. Growth traits including birth weight (BWT), weaning score (WNS), preweaning daily gain (PDG) and 205-day weight (205WT), all adjusted for year effects, dam age and, as appropriate, inbreeding of calf and dam were considered in 243 paternal half-brothers. Maternal traits including most probable producing ability for birth weight (MPPA-BWT), for preweaning daily gain (MPPA-PDG) and for 205-day weight (MPPA-205WT), all adjusted for the same effects as were the growth traits in males, were considered in 176 paternal half-sisters. Between and within sex least-squares analyses were the main analytical
procedures. Genetic correlations \((r_g)\) between direct genetic effects on growth traits and total genetic effects (direct, maternal and joint effects) on maternal traits were estimated in two ways: Yamada's (1962) technique and by calculating the correlation between sires' breeding values for each trait. Genetic correlations between direct genetic effects on growth traits of paternal half-brothers and total genetic effects on maternal traits of paternal half-sisters were large and had standard errors associated with them as large or larger than the estimates. These \(r_g\)'s were considered invalid. However, valid \(r_g\) estimates were obtained directly from correlations among sires' estimated breeding values for each trait. The \(r_g\)'s were all positive, ranging from .16 to .45. In this study, evidence of genetic antagonism between direct genetic effects and maternal genetic effects on preweaning growth in Herefords was not found.

II. DIRECT GENETIC EFFECTS AND MATERNAL GENETIC EFFECTS ON PREWEANING GROWTH TRAITS AND THEIR RELATIONSHIPS IN HEREFORD LINES

Data from the USDA Livestock and Range Research Station, Miles City, MT collected over two phases (II and III) of an experiment were used in this study. Phase II involved Hereford lines 1,4,6,9 and 10 as sources of inbred dams and linecross dams mated to two-way cross bulls for the production of three-way cross calves (250) between 1965 and 1968. Phase III involved lines 1,4,6 and 10 as sources of straightline and linecross dams mated to straightline
bulls to produce inbreds plus two-way, three-way and rotational line-cross calves (1009) between 1967 and 1975. Expectations for direct genetic \(g_I\) and maternal genetic effects \(g_M\) for each calf were worked out for both phases. In addition, expected individual \(h_I\) and maternal \(h_M\) heterosis as well as expected recombination losses, individual \(r_I\) and maternal \(r_M\), were determined for the linecross calves produced in Phase III. Preweaning traits included birth weight (BWT), preweaning daily gain (PDG), 205-day weaning weight (205WT) and weaning score (WNS) all adjusted for age of dam and sex of calf effects. The model contained year, \(g_I\) and \(g_M\) for each of the five lines and inbreeding of the dam (FD) effects in Phase II, while in Phase III it contained inbreeding of calf (FC) in addition to these effects. Another model that contained \(h_I\), \(h_M\), \(r_I\) and \(r_M\) was also used in Phase III. The correlations between line constants for \(g_I\) and \(g_M\) on BWT were \(-.29\) and \(.85\) in phases II and III, respectively. Estimates of \(r_g I g_M\) on PDG and 205WT were \(-.73\) and \(-.79\), respectively in Phase II and \(.14\) and \(.24\), respectively in Phase III. For WNS these correlations were \(-.58\) and \(.66\) in phases II and III, respectively. For all the traits, \(r_g I g_M\) changed from negative in Phase II to positive in Phase III. Possible contributing factors for this discrepancy are discussed, and it is concluded that estimates in Phase III probably are more reliable. Therefore compelling evidence of antagonism between line constants for \(g_I\) and \(g_M\) effects on the traits considered was not found. It was also observed that \(r_I\) and \(r_M\) were not significant sources of variation for any of the traits. Individual heterosis had a significant positive effect on
any of the other traits. Effects from FC and FD were either significantly negative or not significantly different from zero on all traits in both phases.
DIRECT-MATERNAL GENETIC CORRELATIONS FOR PREWEANING GROWTH IN HEREFORD CATTLE

by

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To my parents, whose love has always been inspiring, I dedicate this piece of work.
RESULTS AND DISCUSSION

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Maternal effects are an important source of variation in pre-weaning traits in beef cattle (Koch and Clark, 1955b; Koch, 1972), but some investigators have reported genetic antagonism between direct and maternal genetic effects on such traits (Deese and Koger, 1967; Brown and Galvez, 1969; Hohenboken and Brinks, 1971a). Knowledge of the genetic correlation between direct genetic effects and maternal genetic effects is necessary for the development of sound breeding programs (Hanrahan, 1975; Barlow, 1978).

The relative magnitudes of line direct additive and line maternal additive genetic effects as well as non-additive genetic effects on some traits of economic importance are a basis to determine whether a particular line should be used preferentially as male parent or female parent in an outcrossing system. Dickerson (1969, 1973) has shown the potential contribution of each of these effects in any crossbreeding system in terms of expectations.

The objectives of studies reported herein were: 1) To examine the direction and magnitude of relationships between growth traits in paternal half-brothers and maternal traits in paternal half-sisters using two biometrical techniques. In one, genetic correlations between growth in males and maternal traits in females were computed as functions of sire and sire x sex interaction variance components from analyses of variance (Yamada, 1962). In the other,
correlations were computed among estimated breeding values of sires for growth and maternal traits, estimated from progeny tests of sons and daughters, respectively. 2) To estimate line additive (direct) and maternal genetic effects while also looking at non-additive genetic effects. 3) To determine the relationship between line constants for additive genetic and maternal genetic effects on birth weight, preweaning daily gain, 205 day weaning weight and weaning score in Hereford cattle.
LITERATURE REVIEW

In beef cattle preweaning growth is influenced by genes at many loci in the manner common to other quantitative traits. There are many factors that can mask the inheritance of such traits. Included are non-additive genetic effects, environmental effects such as climate, nutrition and management and maternal effects. These factors can cause inaccuracy in the prediction of response to selection and can lead to biased estimation of heritabilities of traits and the genetic interrelationships among them. In fact Hanrahan (1976) showed that ignoring maternal effects in particular could lead to the choice of an inefficient selection scheme.

Of factors known to complicate estimation of genetic merit for economically important traits, maternal effects are of widespread importance. Legates (1972) defined maternal effects as phenotypic expressions arising from influences of the mother measured on her offspring apart from the direct influence of the genes she transmits (known as direct genetic effects). Maternal effects arise from the dam's own genotype (the maternal genetic effect) and associated environmental factors. However, maternal effects, insofar as their influences on the offspring are concerned, are environmental by nature (Koch and Clark, 1955b; Willham, 1963; Falconer, 1964; Young and Legates, 1965; Koch, 1972; Legates, 1972). Actually Koch (1972) defines maternal effects in beef cattle as differences in birth weight, rate of gain from birth to weaning and
other traits caused by differences in maternal environment provided by cows during gestation and (or) lactation.

Two main kinds of maternal effect are recognized: prenatal and postnatal maternal effects. Prenatal maternal effects are associated with the uterine environment which in turn is determined partly by the genotype of the dam. Postnatal maternal effects result from lactational output and (or) mothering ability and (or) maternal instinct, though the former plays a more important role in the development of the young (Dickerson, 1947; Cox et al., 1959; Drewry et al., 1959; Neville et al., 1962; Al-Murrani and Roberts, 1978). Hohenboken (1981) discusses additional types of maternal effects. These include cytoplasmic effects not involving extra-nuclear DNA and cytoplasmic inheritance that does involve extranuclear DNA, mainly through the mitochondria of the cell.

Prenatal maternal effects have been studied using cross-fostering experiments in mice (Cox et al., 1959; Al-Murrani and Roberts, 1978) and swine (Robison, 1972), but these have not been feasible in beef cattle. However, differences between reciprocal cross offspring from crossbreeding experiments do provide evidence on maternal effects in cattle. Some workers using cross-nursing experiments with mice have indicated that prenatal maternal effects account for a higher percentage of the total variation in 12-day weight than postnatal maternal effects (Brumby, 1960 and Bateman, 1954), while Cox et al. (1959) reported contrary results for the same trait.

In cattle, reciprocal cross progeny of the homogametic sex should differ at birth only in the uterine environment to which they were
subjected during gestation (Hohenboken, 1981). In studies reported by Gregory et al. (1965) and Gaines et al. (1966), significant differences between reciprocal crosses involving Angus, Hereford and Shorthorn cattle were found for gain from birth to weaning but not for birth weight. Reciprocal crosses among breeds differing greatly in size, such as the Holstein, Jersey and Ayrshire reported by Donald et al. (1962), however, showed significant differences among birth weights of reciprocals. This suggests that differences in prenatal environment may arise from differences in body size of the dams between certain breeds or genotypes. Brumby (1960), working with selected and unselected mice for body weight, found that fertilized eggs of the unselected strain when implanted into the large strain females, developed into mice with larger body weights up to 8 weeks of age than mice developing from fertilized eggs of the unselected strain implanted into small strain females. Also, the small strain fertilized eggs, when implanted in large strain mothers, developed into mice with heavier weights than the large strain fertilized eggs implanted into small strain mothers.

Among causes of postnatal maternal effects, milk yield of the dam has been found to be most important. Studies relating milk production of beef cows with weight gain of calves from birth to weaning have generally indicated a significant association. Dam's milk yield, however, has usually been found to be lowly related with the birth weight of the calf (Christian et al., 1965; Gleddie and Berg, 1968). Gifford (1953), however, reported a significant increase in milk production of dam with increased birth weight. Drewry et al. (1959) reported correlations between average daily milk
production of the dam and birth weight of the calf to be 0.43, 0.29 and 0.12 for the first, third and sixth month of lactation, respectively. This may indicate that heavier calves at birth provide a better nursing stimulus and cause greater milk production by the dam.

Gleddie and Berg (1968) studied milk production in range beef cows and its relationship to calf gains. Correlations between milk yield estimates and average daily gain of calves were 0.62, 0.75, 0.56 and 0.51 for first, second, third and fourth test periods, respectively. The lower correlation in early lactation was interpreted to mean that the calf had insufficient capacity to consume all the potential milk of the dam which resulted in decreased milk yield and a lowered correlation between milk yield and gain. By the second month, the calf would still be heavily dependent on its mother's milk, and its capacity would more equally match its mother's potential for milk production. This would cause a higher correlation. Later as the calf started consuming more and more solid feed, its dependency on its mother's milk would decrease to the extent that the correlation between milk yield and calf gain would be lowered. In this same study it was shown that 73% of the phenotypic variance in average daily gain from birth to weaning was attributable to average milk yield of the dam, while in studies by Klett et al. (1965) and Robison et al. (1978), 40% of the variability in weaning weights and gains of calves was attributable to variation in dams' milk yield. Williams et al. (1979) reported correlations between calf average daily gain and milk yield estimates to be 0.27, 0.46 and 0.45
depending upon whether milk production was estimated following a 4, 8, or 16 hour separation of cow and calf.

An increase in milk yield during the preweaning period has been shown to be associated with increased weaning weights of Hereford calves (Neville et al., 1962). Robison et al. (1978) presented correlations of birth weight with measures of milk yield in Hereford cattle ranging from 0.09 to 0.10, while these correlations ranged from 0.44 to 0.63 between weaning weight and measures of milk yield. Similarly, Winstrand and Riggs (1966) found a correlation of 0.68 between milk yield and 120-day weight in Santa Gertrudis. These relationships emphasize the importance of maternal effects as sources of variation in preweaning calf traits. In addition they suggest the need for more critical genetic evaluation of those maternally influenced traits.

Milk production and mothering ability of a cow as expressed in the preweaning gain and weaning weight of the calf have been found to change in a curvilinear fashion with age of dam (Hohenboken and Brinks, 1969). Various workers in beef cattle have concluded that younger cows produce less milk (therefore lighter calves at weaning) than intermediate age group cows (generally 5-8 year-olds) which in turn produce more milk than older cows (Gifford, 1953; Hock and Clark, 1955; Kleet et al., 1965; Mangus and Brinks, 1971; Tewolde, 1976; Robison et al., 1978). In addition, effects such as sex of calf, year, season of birth and levels of inbreeding have been found to be directly or indirectly related to mothering ability (Clark et al., 1958; Stonaker, 1963; Pahnish et al., 1961; Robison et al., 1978).
Genetic Significance of Maternal Effects. As indicated previously, maternal effects are important sources of variation in beef cattle. The genetic significance of maternal effects should therefore be considered.

Genetic parameter estimation for maternally influenced traits is complicated by the possible association between direct genetic effects (genotype of the individual for the trait) and maternal genetic effects (the genotype of the dam for maternal ability). Hanrahan (1976) has given the theoretical development of how the size and magnitude of the covariance or association between additive direct genetic effects and additive maternal genetic effects could influence genetic progress from selection for a maternally influenced trait in sheep. He assumed the absence of non-additive genetic effects, complete autosomal inheritance and independence of all effects in the model except for direct and maternal genetic effects. Hanrahan’s (1976) model was actually an extension of Willham’s (1963) model for maternal effects.

Deese and Koger (1967), working with purebred Brahman and Brahman-Shorthorn crossbreds, found that the magnitudes of the additive genotypic variance for growth and maternal effects for growth were approximately the same in both herds (18% vs. 15% in the Brahmans and 40% vs. 46% in the crossbreds). The covariance between these effects was near zero for the Brahmans but was -30% for the crossbred herd. The difference in covariance terms was reflected in the heritability estimates. In the Brahman herd, the heritability of combined direct and maternal effects on weaning weight was 0.25, while in the crossbreds it was 0.18.

Hill et al. (1966) showed that the calf's genotype for 180-
day weight and the dam's genotype for maternal effects had almost equal influences on the variance of 180-day weight. The variance for additive genetic effects was 100, while the variance for maternal genetic effects was 91. In Hohenboken and Brinks' (1971a) study, the variances due to the direct genetic effects and maternal genetic effects on weaning weight of Hereford calves were 177 kg$^2$ and 172 kg$^2$, respectively. This indicates that maternal effects contributed slightly more to weaning weight than did direct genetic effects in their population. The heritability estimates of direct genetic effects and maternal genetic effects on weaning weight ranged from 0.23 to 0.27 and 0.34 to 0.40, respectively.

Brown and Galvez (1969) studied maternal effects on birth weight of beef calves. The heritability estimates of maternal effects on the trait were 30% and 25% in Hereford and Angus, respectively. The heritability estimate of maternal effects on birth weight was found to be in the range of 4 to 15% in Holsteins (Everett and Magee, 1965). Heritability estimates of 30 to 36% for maternal effects on gain to weaning were also reported by Koch (1972). So, maternal effects on most preweaning traits are heritable, though some are low, suggesting that genetic progress could be possible from direct selection.

The possibility of a direct influence of dams on the maternal ability of their daughters cannot be ignored. This relationship is generally reported to be negative. Mangus and Brinks (1971), for example, found that heifers out of young dams subsequently produced heavier calves at weaning than heifers out of mature aged cows. They interpreted this to mean that high levels of milk in
dams had a detrimental effect on a heifer's future productivity. Conversely, a lower level of milk from young cows was beneficial to the daughter's future productivity. Cundiff et al. (1974) attributed a reciprocal cross difference in preweaning growth of beef calves from crossbred dams to the potential effect of maternal grand-dam (relative to offspring of the reciprocal cross cows). That is, heifers that had heavy weaning weights because of favorable mothering ability of their dams provided a poorer maternal environment and produced lighter calves at weaning in the subsequent generation.

Genetic Covariance Between Growth and Maternal Traits. Most of the selection response in beef cattle is derived from sire selection. Therefore, it would be useful to select sires that would improve both their sons' performance for traits of economic importance and their daughters' maternal performance as well. The potential to accomplish this, however, is dependent on whether and how such traits are genetically related. Knowledge of genetic correlations ($r_g$) therefore is important to design effective selection programs.

The genetic correlation between two traits is the correlation between gene effects influencing them (Pirchner, 1969) or it is the correlation between an individual's breeding values for the traits (Lush, 1948; Falconer, 1960). This correlation is caused by pleiotropy of genes and(or) by linkage. The former is characteristic of the gene itself in terms of its capacity to cause simultaneous variation in the traits. The latter may cause transient correlations between traits (Lush, 1948; Falconer, 1960; Pirchner,
Direct selection for one trait should cause correlated response in genetically correlated traits (Falconer, 1960; Pirchner, 1969).

Dickerson (1947) was led to believe there was antagonism between direct and transmitted maternal influences on growth in swine, since the variance component for dams was much smaller than the variance component for sires. Hohenboken and Brinks (1971a) reported a negative covariance (-9%) between direct genetic and maternal genetic effects on weaning weights in Hereford cattle. This suggests that some genes which cause individual calves to gain more rapidly also cause heifers to be poorer mothers. Deese and Koger (1967) found zero and negative covariances between additive genetic effects and maternal genetic effects for preweaning growth in straightbred Brahmins and Brahman x Shorthorn crossbreds. From this they concluded that selection of calves on individual growth rate and culling of cows on the basis of the preweaning gain of their calves should complement each other and increase progress since the real genetic correlation would be close to zero. Such a claim is not supported by Koch and Clark (1955b) who found antagonistic genetic correlations of -.55 between additive genetic effects and maternal genetic effects on weaning weight. However, Hohenboken and Brinks (1971a), based on $r_g = -28\%$, implied, as did Deese and Koger (1967), that the negative correlation did not differ significantly from zero.

In a study to investigate genetic progress from selection at Miles City, Montana, Hereford cows were mated contemporaneously with semen from sires born several years apart (Urick et al., 1977). Early sires
from line 1 (3 in number) were born in 1953 and 1955, while the later generation sires (2 in number) from that line were born in 1962 and 1963. Two early generation sires from line 10 were born in 1951 and 1955, and two later generation sires were born in 1963 and 1965. Data from these matings showed that in both lines, the later generation sires produced heavier calves at weaning (180.2 kg in line 1 and 179.6 kg in line 10) than the early generation sires (168.9 kg in line 1 and 164.0 kg in line 10). However, females that were produced by the early generation line 1 sires weaned heavier calves than those from later generation line 1 sires (167.1 kg vs. 163.5 kg, respectively) though this advantage was not significant. This was not true for line 10, however (162.3 kg for daughters of early sires vs. 180.6 kg for daughters of later sires, P < .01). What was observed in line 1 might be attributable to antogonism between direct and maternal effects; sires selected for faster growth might not have been the same sires that would have produced daughters with good maternal performance.

Suess et al. (1968) studied the relationship between carcass characteristics of Holstein steers and their estimated genetic merit for milk production. In that study, estimated breeding values for milk production of sires of the steers were estimated as weighted deviations of daughter records from contemporary herd mates. Sires with above average breeding values for milk production were considered the high group, while sires with below average breeding values were considered the low group. The difference between the high and low group was 328 kg of milk. Carcass traits were measured on the steers. Results of this study showed several significant negative correlations between
carcass traits and estimated breeding values in the low group; but although not different from the low group correlations, the same relationships in the high group were not different from zero. From these results, Suess et al. (1968) concluded that the negative relationship of estimated breeding value for milk with several carcass traits may not be important above some threshold level of milk production but that the correlations might become important as milk production dropped to lower levels. Mason (1964) also reported negative (but not significantly different from zero) genetic correlations between milk production and beef characters of steer progeny in dual-purpose cattle.

Hohenboken and Brinks (1971b) examined the covariance of paternal half-brother and sister performance in Hereford cattle. In the sons they considered weaning weight (WWT), average daily gain (ADG) and feed efficiency (FE) during a postweaning gain test and grade. In the daughters, most probable producing ability (MPPA) for weaning weight was considered. The genetic correlations between MPPA in sisters and ADG, FE, Grade and WWT in the brothers were -.22, -.23, -.17 and 0.49, respectively. The correlation value of 0.49 between MPPA and WWT differed in magnitude from that reported earlier by the same workers ($r_g = -.28$) estimated by partitioning of covariances among relatives. However, $r_g = 0.49$ was believed to examine, according to Hohenboken and Brinks (1971b), the correlation between the total genetic contribution to growth (from MPPA) and direct effects on growth (from weaning weight).
Langlet (1965) examined genetic correlations between beef and milk production in European cattle populations. Based on 236 sons and 2450 daughters from 25 Friesian sires, he reported a correlation of 0.22 between milk production and daily gain of half-sibs. The positive correlation indicates that favoring sires with high values for beef traits would lead to increased milk yield of their daughters.

Dim (1977) also studied the genetic correlation between growth rate and milk yield potential in Swedish bulls that were performance tested for beef traits and subsequently progeny tested for milk traits (daughters) and beef traits (sons). In his study, the correlations between estimated breeding value for growth traits in sons and estimated breeding value of milk yield in daughters ranged from -0.12 to 0.06.

Similar results were reported by Andersen and Andersen (1975, referenced in Dim, 1977) who found correlations of 0.02 and 0.01 between growth index and expected milk breeding value for two dual purpose breeds in Denmark. There was no explanation of what growth index and expected milk breeding values were used. Samson-Himelstjerna von (1965, also referenced in Dim, 1977) reported genetic correlations of zero between milk production of females and growth of half-sibs. Tyler (1970) also found low genetic correlations in his study of the relationship between growth traits and production of milk and meat. These correlations were between 0.05 and 0.27 between the progeny test of daughters for milk yield and progeny test of sons for daily gain. Similarly Soller et al. (1966) found a low genetic correlation.
between milk production as 12-month body weight in Israeli Friesian cattle. In Friesian cattle, Langlet (1965) found a correlation of 0.13 between dam's milk production and carcass weight per day of age of sons.

Calo et al. (1973) analysed 8412 body weight records of 504 bulls that were tested for their beef performance. These bulls were by 120 sires that were selected for progeny testing for milk yield. Body weights were taken at different ages after parturition and maternal effects on growth were treated as random, since the calves were removed from the dams three days after birth. The average genetic correlations between milk production and body weights at various ages were low but all were positive, ranging from 0.02 to 0.28. Higher correlations between body weights at earlier ages (9-24 months) and milk production than between body weights at 36 and 60 months and milk production were observed.

These results, in agreement with studies reviewed previously, suggest low but positive genetic correlations between beef traits and milk production. Therefore, selection for one trait should automatically bring some improvement in the other. More importantly the foregoing studies indicate that there may be no distinct antagonism between milk production and beef traits. This may also imply that there are no serious negative genetic correlations between direct genetic effects and maternal genetic effects.

Transmitted, Maternal Genetic and Non-additive Genetic Effects on Maternally Influenced Traits. Increased interest in beef cattle
crossbreeding has generated several questions concerning the productivity of various mating types using specialized breeds or lines. Among the possible reasons for differences among breeds include:

1) differences in the mean gene frequencies and hence in transmitted effects in breed crosses due to divergence in selection for particular traits, 2) differences in average heterozygosity relative to each other and 3) differences in epistatic effects of genes on performance (Dickerson, 1973). If lines within a breed have been selected for a long period of time for specific performance, then the between line divergence could also be attributed to those reasons postulated by Dickerson (1973) above. Those factors that cause differences may behave in different ways when one tries to combine breeds or lines through crossing.

Many workers have reported differences in performance between mating types in beef cattle. Turner and McDonald (1969) analyzed data from 1270 beef calves (straightbred, single crosses, backcrosses and three breed crosses) involving Angus, Brahman, Brangus, Charolais and Hereford breeds. They found mating type of calf to be a significant source of variation in birth weight, preweaning daily gain, slaughter score, type score and weaning weight. Also various workers have reported significant reciprocal cross differences in beef cattle for maternally influenced traits (Leonard et al., 1967; Turner, 1969; Gregory et al., 1965; Gregory et al., 1966; Gregory et al., 1978). Leonard et al. (1967) for example studied differences in birth weight, preweaning daily gain and 205 day weight among reciprocal crossbred
cows between Angus (A), Hereford (H) and Shorthorns (S). He found mean differences in birth weight, preweaning daily gain and 205 day weight of calves from cows of the three pairs of reciprocal crosses to be SA (sire breed first) minus AS (2.2 ± .7, .03 ± .01, 7.3 ± 3.2); AH minus HA (-1.3 ± 1.6, .09 ± .02, 16.8 ± 3.8); SH minus HS (-.5 ± 1.0, .09 ± .01, 17.2 ± 4.7), respectively. Feedlot gains following weaning, however, were generally in reverse order to preweaning growth indicating compensatory growth. These results were interpreted to mean that there was a negative phenotypic relationship between a cow's own weaning weight and her maternal performance. This is contrary to results of Kress and Burfening (1972) who found a significant positive correlation (r = .15) between 180 day weight and subsequent probably producing ability for 180-day weight (MPPA-180 WT) of the same cow.

In the long history of beef cattle crossbreeding programs, various workers have studied the crossbred advantage (heterosis) for some traits of economic importance such as preweaning growth of calves. Several positive estimates of heterosis for such traits have been reported (Ellis et al., 1965; Gregory et al., 1966; Turner, 1969; Cundiff et al., 1974; Koger et al., 1975; Crocket et al., 1978; Gaines et al., 1978; Gregory et al., 1978; Dillard et al., 1980; Knapp et al., 1980). Much work has also been done in developing inbred lines within a breed for eventual crossing, and generally positive heterosis estimates have been reported for growth traits (Brinks et al., 1967 and 1972; Kress et al., 1979).
Some workers have indicated that calves by superior breeds (lines) of sires mated to breeds (lines) of dams with superior maternal ability outperformed their reciprocal cross contemporaries. Gaines et al. (1978) reported that cows resulting from matings involving Hereford dams excelled their reciprocals for weaning weights of calves produced by them. Angus, Hereford and Shorthorns were involved in their study. Gregory et al. (1966) found greater heterosis for the Hereford-Angus and for the Hereford-Shorthorn combinations than their reciprocals even though these differences were not significant. Later, Gregory et al. (1978) worked with Red Poll, Brown Swiss, Hereford and Angus. They found heavier crossbred calves at birth ($P < .01$) and at weaning ($P < .01$) and faster growing calves ($P < .01$) from the Red Poll and Brown Swiss dams than their reciprocal crosses with Hereford and Angus dams. England et al. (1963) compared four mating systems involving Brahman, Brangus, Angus and Hereford breeds. They found that purebred and backcross Brahman and Brangus calves were superior to purebred and backcross Angus and Hereford calves but that first cross and three-breed cross calves sired by Angus and Hereford bulls were as heavy as those sired by Brahman and Brangus bulls. The heavier weaning weights of purebred and backcross Brahman and Brangus calves appeared to be due to the superior mothering ability of the Brahman-type dams. The suitability of the Brahman as a dam breed was later confirmed by Koger et al. (1975), as will be indicated later. Reciprocal differences in crosses for growth traits, therefore, include maternal effects as well as any differences in genetic merit for transmitted
effects between the sample of sires and dams represented in their respective crosses (Gregory et al., 1978).

The existence of reciprocal differences between breeds (lines) also signifies differential contributions of breeds (lines) to progeny performance when they are used as dams rather than sires or vice versa. To use such a diversity in any crossbreeding or line crossing systems, Dickerson (1969) pointed out the importance of considering factors such as 1) reproductive rate of the species, which is characteristically low in beef cattle; 2) magnitudes of heterosis for individual \( h^I \) and maternal \( h^M \) effects and recombination loss \( r \) which is a loss of epistatic superiority of purebreds due to recombination of gametes produced by crossbred parents, 3) size of breed differences in individual and paternal vs. maternal performances of purebreds \( g^I \) and \( g^P \) vs. \( g^M \), respectively) and 4) importance of interactions of genetic components with management or marketing systems. Of the factors mentioned above, the second and third seem to be the most important from the genetic standpoint. Knowledge of the parameters \( g^I, g^M, g^I, h^M, \) and \( r \) can be helpful to characterize beef cattle breeds in use today. As a consequence appropriate crossing systems can be recommended for specific purposes.

Recombination loss \( r \) can be individual \( r^I \) or maternal \( r^M \) if the dam is crossbred (linecross) from at least one crossbred parent. This was defined as the deviation from the linear association of heterosis with the degree of heterozygosity (Dickerson, 1973). Kinghorn (1980) indicated the dependence of \( r \) on the nature of gene action.
He proposed two hypotheses, and under each hypothesis the expectations of $r_I^I$ and $r_M^M$ were different. Some workers, however, have indicated that recombination loss may not be important in beef cattle (Koger et al., 1975; Dillard et al., 1980). Teehan et al. (1980) also found generally unfavorable but statistically nonsignificant recombination effects in sheep.

Little research has been done to evaluate breeds or lines in terms of the parameters mentioned above for purposes of achieving efficient crossing and selection systems. Koger et al. (1975) used Dickerson’s (1969) approach to characterize Brahmans (B), Shorthorns (S) and various crosses between them (F1, 3/4B 1/4S, 1/4B 3/4S). They estimated the magnitudes of $g_I^I$, $g_M^M$, $h_I^I$ and $h_M^M$ on birth weight, calf survival, weaning weight, 205 day weight and condition score. Results showed $g_I^I$ for Brahman to be negative for weaning score, zero for weaning rate and positive for growth while $g_M^M$'s for the same breed were positive for all traits. For the Shorthorn, $g_I^I$ and $g_M^M$ were opposite in sign to those for the Brahmans.

Dillard et al. (1980) used linear regression techniques to estimate the contributions of breed additive ($g_I^I$), heterozygosity ($h_I^I$), breed maternal ($g_M^M$) and average maternal heterosis ($h_M^M$) effects to differences in birth weight, preweaning daily gain, weaning weight and type score of different groups. These groups were generated from Hereford, Angus and Charolais. Charolais $g_I^I$'s were significantly different from zero and positive for birth weight and preweaning daily gain and highly significant and positive for weaning weight. The $g_M^M$ coefficients for the same breed were positive for all traits. Angus $g_I^I$ negatively
influenced birth weight \((P < .01)\) but increased type score \((P < .05)\), while \(g^M\)'s for the same breed were positive \((P < .01)\) for birth weight, preweaning daily gain and weaning weight. In the same study, heterosis levels were much larger when Charolais was used as a dam than as a sire.

Gregory et al. (1978) analyzed data from a diallel cross involving Red Poll, Brown Swiss, Hereford and Angus breeds to estimate heterosis \((h^I)\), breed maternal \((g^M)\) and transmitted effects \((g^I)\) for calf performance and cow reproductive traits. Breed maternal effects \((g^M)\) showed the Brown Swiss breed with the lowest level of calving difficulty. Breeds did not differ in \(g^I\) for calf crop but differed significantly from each other in \(g^M\) for preweaning daily gain and 200 day weight in the order of Brown Swiss, Red Poll, Angus and Hereford. Brown Swiss was heaviest at birth, had the highest preweaning daily gain and 200 day weight \(g^I\) and was superior for preweaning daily gain and 200 day weight \(g^M\) compared to the other four breeds.

Holtman and Bernard (1969) also estimated \(g^I\) in sheep involving purebred progeny, two-breed crosses, back crosses and three-breed crosses from Suffolk, Oxford and North Country Cheviot breeds. They found that the Suffolks were significantly superior to the Oxfords and Cheviots in \(g^I\) for 120 day body weight. They also found important interactions between mating system and maternal ability of the breed. From such interactions they concluded that Suffolk was the most outstanding in terms of mothering ability except in the backcross mating system.
Once $g^I$ and $g^M$ in any breeding system are estimated as components, it becomes quite important to look into the relationship between the two. This relationship would estimate the between breed or line genetic correlation between direct additive genetic effects ($g^I$) and maternal additive genetic effects ($g^M$) on traits of economic importance. Kress et al. (1979) for example estimated $g^I$'s and $g^M$'s for inbred lines of Herefords for birth weight and 180-day weight. From these they estimated genetic correlations between direct and maternal effects on birth weight and 180-day weight of -.58 and -.80, respectively.
LITERATURE CITED


Andersen, B. and Andersen, G.S. 1975. Samman haengen mellem maelkeprodukitionsevne, kodproduktionsevne of kropsmal hos RDM of SDM. Statens Husdynbrugsforsog. Danmark. Medd. 71 (Referenced in Dim (1977)).


Lush, J.L. 1948. The genetics of populations. Copyright Ames, Iowa.


Data from the USDA Livestock and Range Research Station, Miles City, MT collected between 1962 and 1975 were used in this study. Records involved five inbred Hereford lines that produced straight-line and linecross calves in an experiment of three phases. Growth traits including birth weight, prewean daily gain, weaning score and 205 day weaning weight, all adjusted for year effects, dam age and, as appropriate, inbreeding of calf and dam, were considered in 243 paternal half-brothers. Maternal traits including most probable producing ability for birth weight, for prewean daily gain and for 205 day weight, all adjusted for the same effects as were the growth traits in males, were considered in 176 paternal half-sisters. Genetic correlations ($r_g$) between direct genetic effects on growth traits and total genetic effects (direct, maternal and joint genetic effects) on maternal traits were estimated in two ways: Yamada's (1962) technique and by calculating the correlation between sires' breeding values for each trait. Genetic correlations between direct genetic effects on growth traits of paternal half-brothers and total genetic effects on maternal traits of paternal half-sisters were large and had standard errors associated
with them as large or larger than the estimates. These $\hat{r}_g$'s were
considered invalid. However, valid estimates were obtained direct-
ly from correlations among sires' estimated breeding values for
each trait. These $\hat{r}_g$'s were all positive, ranging from .16 to .45.
In this study, evidence of genetic antagonism between direct gene-
tic effects and maternal genetic effects on preweaning growth in
Herefords was not found.

(Key Words: Genetic correlations, maternal effects, cattle, Herefords.)
INTRODUCTION

Maternal effects are an important source of variation in pre-weaning traits in beef cattle (Koch and Clark, 1955b; Koch, 1972), but some investigators have reported genetic antagonism between direct and maternal genetic effects on such traits (Deese and Koger, 1967; Brown and Galvez, 1969; Hohenboken and Brinks, 1971a). Knowledge of the genetic correlation between direct genetic effects and maternal genetic effects is necessary for the development of sound breeding programs (Hanrahan, 1976; Barlow, 1978).

Objectives of this study were to examine the direction and magnitude of relationships between growth traits of bulls from birth to weaning and maternal traits (MPPA) of their paternal half-sisters. Data from the USDA Livestock and Range Research Station, Miles City, MT were examined using two biometrical techniques. In one, genetic correlations between growth in males and maternal traits in females were computed as functions of sire and sire x sex interaction variance components from analyses of variance (Yamada, 1962). In the other, correlations were computed among estimated breeding values of sires for growth and maternal traits, estimated from progeny tests of sons and daughters, respectively.

MATERIALS AND METHODS

Populations. Data for this study were obtained from the USDA Livestock and Range Research Station herds, Miles City, MT. Records
involved five inbred Hereford lines (1, 4, 6, 9 and 10) that participated in the production of straightline and linecross calves between 1962 and 1975 in a three phase experiment.

Phase I of the experiment involved the production of straightline and linecross F1 calves by lines 1, 4, 6, 9 and 10 from 1962 through 1965. Results concerning individual heterosis for preweaning weight gains and weaning weights were reported by Brinks et al., (1967).

Phase II involved the production of linecross calves from 1965 through 1968. Phase II females, produced in Phase I, were inbred from the five lines and all possible two-way crosses among them. All cows were mated in two successive years to two-way cross bulls, also produced in Phase I, to produce three-way cross calves. Heifers born in 1962 and 1963 were bred to calve initially as 3-year-olds, and heifers born in 1964 and 1965 were bred to calve initially as 2-year-olds. The objective of this experiment (Brinks et al., 1972) was to evaluate maternal heterosis.

Phase III involved the production of straightline, two-way cross, three-way cross and rotational linecross calves from 1967 to 1975. Foundation animals used to initiate this phase were lines 1, 4, 6 and 10 inbreds plus F1 females involving lines 1, 4, 6 and 10. They were produced in Phase I but also used in Phase II of the experiment. Here, straightline bulls were mated to straightline dams to produce straightline calves, as well as to linecross dams to produce two-line and three-line rotational cross calves. The objective of
Phase III (Urick et al., 1981) was to study the maintenance of heterosis for preweaning traits and weights in different linecrossing systems.

The physical environment and climate were described in detail by Hunt (1951). There is a 45 to 60 day regular breeding season at the station beginning on June 15. This breeding season fits grass conditions in the range area because during a normal year, forage is expected to be at its best during April, May and June.

Breeding bulls were selected mainly on yearling weight. However, they were also checked for fertility, feet and legs, testicle size and semen characteristics. Approximately 15 to 20% of the bull calves were selected in this way each year. Replacement heifers (about 80% of those available annually) were selected on the basis of their yearling weight. Older cows culled were mainly those open two consecutive seasons or unsound.

Data Management. Preweaning daily gain (PDG) for each calf was calculated as the difference between the actual weaning weight and actual birth weight (BWT) dividing by weaning age. The 205 day weight (205WT) was calculated for each calf as \((\text{PDG} \times 205) + \text{BWT}\). These traits together with BWT and weaning score (WNS) were then adjusted for age of dam (to a six year old basis (Urick et al., 1981)), sex of calf (to a heifer basis (Urick et al., 1981)), inbreeding of calf and inbreeding of dam (Brinks and Knapp, 1975). This adjusted data set was used to calculate the most probable producing ability (MPPA) based upon BWT, PDG and 205WT of all calves.
in phases II and III that were born to females produced in Phase I. The formula used to calculate MPPA was:

\[
MPPA = \frac{nr}{1+(n-1)r} \times \frac{1}{n} \sum_{i=1}^{n} (X_i - \bar{X}_i)
\]

where:

- \(X_i\) = phenotype of the dam's \(i^{th}\) calf for adjusted BWT, PDG or 205WT, with \(i\) ranging from one through \(n\), the number of calves produced by that cow,
- \(\bar{X}_i\) = average BWT, PDG or 205WT of calves born within the appropriate birth year and phase and
- \(r\) = repeatability of the trait (\(r = .27\) for BWT, \(r = .31\) for PDG and \(r = .23\) for 205WT from Woldehawariat et al., 1977).

Each adjusted BWT, PDG or 205WT was expressed as a deviation from the birth year-phase mean to avoid possible year and phase effects in the subsequent analyses. MPPA for BWT (MPPA-BWT), PDG (MPPA-PDG) and 205WT (MPPA-205WT) were calculated for 176 females born in Phase I that produced calves in phases II and III. The average number of calves produced per female was approximately three (ranging from 1 to 8). Then BWT, PDG, weaning score (WNS) and 205WT of the paternal half-brothers and MPPA's for BWT, PDG and 205WT of their paternal half-sisters born in Phase I were adjusted for age of dam (Koch and Clark, 1955a), inbreeding of dam and inbreeding of calf (Brinks et al., 1965; Brinks and Knapp, 1975). These records were expressed as deviations from the mean of all like-sexed
calves born in a given year and not paternal half-sibs to the calf in question (Harvey, 1981, personal communication). This was necessary in order to remove the year effect from the analyses since year effect was completely confounded with the sire within line effect. This was because only one sire per line per year was used in Phase I.

Statistical Analyses. The idea of studying genotype by environment interactions (GxE) using genetic correlations ($\hat{r}_g$) was first proposed by Falconer (1952). In this approach the same trait in the same genetic groups is measured in two different environments as if it were two distinct traits. If $\hat{r}_g$ among "traits" approaches unity, then it is assumed that the same sets of genes influence the trait in both environments and there is no GxE interaction. If, however, $\hat{r}_g$ is closer to zero, then different sets of genes probably influence the trait in different environments, and significant GxE interactions exist. Later, Dickerson (1962) presented a method of estimating $\hat{r}_g$ from results of two-way analyses of variance.

Yamada (1962) showed that Falconer's and Dickerson's methods could also be used to estimate genetic correlations among different traits. He also discussed random versus mixed models and their consequences in the estimation of $\hat{r}_g$'s. When the model is mixed (sires random and traits fixed), Yamada (1962) proposed the following estimation formula:
where:

\[ \sigma^2_G = \text{genetic variance component across environments (the variance component for sires within lines in this study)}, \]

\[ \sigma^2_{GE} = \text{genotype by environment interaction variance component (the sire within line by sex variance component in this study)} \]

and

\[ \hat{\sigma}_{G_1} \text{ and } \hat{\sigma}_{G_2} = \text{the square roots of the genetic group (sire) variance components in the environment shown in each subscript.} \]

The \( \frac{1}{2} (\hat{\sigma}_{G_1} - \hat{\sigma}_{G_2})^2 \) term is a correction to prevent bias from different genetic scales for the two traits or in the two environments.

This approach of estimating \( \hat{r}_g \) has been used in a variety of circumstances (Hohenboken and Brinks, 1971b; Brinks et al., 1978; Nunn et al., 1978; Benyshek, 1979).

In the present study the approach for estimating \( \hat{r}_g \) proposed by Yamada (1962) was used to obtain genetic correlation estimates between maternal traits in females (MPPA-BWT, MPPA-PDG and MPPA-205WT) and growth traits in their paternal half-brothers (BWT, WNS, PDG and 205WT) that were born in Phase I.
Using the adjusted male and female records that were expressed as deviations, the following mathematical model was employed:

\[ Y_{ijklm} = u + LS_i + S_{ij} + C_k + (SxC)_{ijk} + LD_1 + (LSxLD)_{i1} + (LDxC)_{kl} + (LSxC)_k \pm e_{ijklm} \]  

where:

- \( Y_{ijklm} \) = MPPA-BWT, MPPA-PDG or MPPA-205WT when the calf is female and BWT, WNS, PDG or 205WT when the calf is male.
- \( u \) = the general mean,
- \( LS_i \) = the effect of the \( i \)th line of sire \((i = 1,2,\ldots,5)\),
- \( S_{ij} \) = the effect of the \( j \)th sire within the \( i \)th line of sire \((j = 1,2,\ldots,4)\),
- \( C_k \) = the effect of the \( k \)th sex of calf, which is a means of coding for the male growth trait or female maternal trait as appropriate \((k = 1,2)\),
- \( (SxC)_{ijk} \) = sire within line of sire by sex interaction effect,
- \( LD_1 \) = the effect of the \( 1 \)th line of dam,
- \( (LSxLD)_{i1} \) = the interaction effect between the \( i \)th line of sire and the \( 1 \)th line of dam,
- \( (LDxC)_k \) = the interaction effect between the \( k \)th sex and the \( 1 \)th line of dam,
(LSxC)_{ik} = \text{the interaction effect between the } i^{\text{th}} \text{ line of sire and the } k^{\text{th}} \text{ sex and}

\varepsilon_{ijklm} = \text{the random error peculiar to the individual observation.}

S_{ij}, (SxC)_{ijk} \text{ and } \varepsilon_{ijklm} \text{ were assumed to be random while all other effects were considered to be fixed. Least-squares mixed model analyses utilizing model type 7 of Harvey (1975) were performed using the above equation. This model type permitted the interaction between a random effect (sires) and a fixed effect (the character or sex) to be fitted. The main purpose of this analysis was to obtain estimates of the sire and the sire by sex variance components and their coefficients for use in Yamada's (1962) formula for the } \hat{\rho}'s.

Another set of least-squares analyses was run for each trait within each sex using the mixed model type 3 of Harvey (1975) in order to obtain the genetic group standard deviation of each trait \( \hat{\sigma}_{G_i} \). The model used was:

\[ Y_{ijkl} = \mu + LS_i + S_{ij} + LD_k + (LSxLD)_{ik} + \varepsilon_{ijkl} \quad (4) \]

where the symbols are defined as before.

After this series of analyses was performed, genetic correlations between the maternal traits and growth traits were calculated using Yamada's (1962) formula, as presented earlier.

The sampling variance of the calculated \( \hat{\rho} \) was estimated using the formula:
\[ V(r_g) = \frac{\{nt(1-r_g^2) + (1-t)\}^2}{(N-1)n^2 t^2} + \frac{r_g^2 (1-t)^2}{N(n-1)n^2 t^2} \] (5)

as presented by Robertson (1959) involving two environments. In the above formula:

- \( n = \) the k-value (or coefficient) for the sire by sex interaction variance component \( \sigma^2_{S/LS \times sex} \) (k = 9.01),
- \( N = \) the number of sires (N = 20) and
- \( t = \) the intraclass correlation, \( \sigma^2_{S/LS}/\sigma^2_T \) (Falconer, 1960), where \( \sigma^2_{S/LS} \) is the sire variance component (across the sexes) while \( \sigma^2_T = \sigma^2_\epsilon + \sigma^2_{S/LS \times sex} + \sigma^2_{S/LS} \).

A second procedure was also used to obtain estimates of \( \hat{r}_g \). The estimated breeding value of each sire for each trait was first calculated using the formula:

\[ \text{EBV} = \frac{h^2}{2} \left( 1 + \frac{n}{1 + (n-1)h^2} \right) (\bar{P} - \bar{P}) \] (6)

where:

- \( \text{EBV} = \) the expected breeding value of each sire for either the growth or maternal trait,
- \( h^2 = \) the heritability of the trait being considered,
- \( n = \) the number of progeny per sire and
- \( (\bar{P} - \bar{p}) = \) the difference between the sire's progeny mean (\( \bar{P} \)) and the population average (\( \bar{p} \)).

The \( h^2 \) values were estimated from results of earlier analyses (formula 4). To obtain \( (\bar{P} - \bar{p}) \), a fixed model containing line of sire, sires within line of sire, line of dam and line of sire by line of dam interaction effects was utilized. Product moment
correlations were calculated between the breeding values for maternal traits and growth traits in all possible pairs. Such a correlation between breeding values is by definition an estimate of the genetic correlation between the maternal traits in the daughters and growth traits in the sons (Falconer, 1960).

RESULTS AND DISCUSSION

Within-Sex Analyses of Variance. Table 1 shows the analyses of variance for growth traits in males and maternal traits in females. The main objective of this analysis was to obtain the sire within line of sire variance component \( \sigma^2_{S/LS} \) for each trait within each sex. Genetic group standard deviations \( \sigma_{G_i} \) for each trait were generated from these values by taking the square roots of the components. Hohenboken and Brinks (1971b) also studied the covariance of paternal half-brother and sister performance. They considered the most probable producing ability for weaning weight (MPPA) in the paternal half-sisters, while weaning weight (WnWt) was considered in the paternal half-brothers. They reported \( \sigma^2_{S/LS} \) of 5.87 kg and 34.0 kg for MPPA and WnWt, respectively. Corresponding \( \sigma^2_{S/LS} \) components in the present study were 5.68 kg and 45.0 kg, respectively (Table 2).

From the same analyses, heritabilities \( (h^2) \) and genetic correlations \( (r_g) \) between growth and maternal traits were estimated (Table 3). The \( h^2 \) estimates were \( .23 \pm .18, .16 \pm .16, .15 \pm .16, .17 \pm .17, .29 \pm .25, .25 \pm .24 \) and \( .35 \pm .26 \) for BWT, WNS, PDG,
205WT, MPPA-BWT, MPPA-PDG and MPPA-205WT, respectively. The heritability estimate of MPPA for a trait is greater in each case than $h^2$ for the same trait. This is expected since MPPA is the weighted average production based on $n$ records, and the heritability of an average should increase as $n$ increases (Pirchner, 1969, page 159). These $h^2$ estimates are biased upwards by some undetermined amount because they were estimated on the assumption that the relationship among half-sibs was .25. This was not true in the present study because there were inbred as well as linecross calves produced by inbred dams.

### Analysis of Growth Traits in Males and Maternal Traits in Females.

The objective of these analyses was to obtain the sire within line of sire and sire within line of sire by sex interaction variance components ($\sigma^2_{S/LS}$ and $\sigma^2_{S/LS \times sex}$, respectively) for use in the estimation of $\hat{\rho_g}$. Results are shown in Table 4. The $\sigma^2_{S/LS \times sex}$ component was less than $\sigma^2_{S/LS}$ except for PDGMPPA-BWT, WNSMPPA-205WT and PDGMPPA-BWT. This component was negative for BWTMPPA-BWT, PDGMPPA-PDG and 205WTMPPA-205WT (-.02, -.0001 and -1.41). The negative interaction variance components were assumed to equal zero in the estimation of $\hat{\rho_g}$ using Yamada's (1962) technique. Hohenboken and Brinks (1971b) reported components for $\sigma^2_{S/LS}$ and $\sigma^2_{S/LS \times sex}$ of 7.71 kg and 9.14 kg for MPPA-WnWt, respectively. In their study, $\sigma^2_{S/LS \times sex}$ was always larger than $\sigma^2_{S/LS}$ for each trait analyzed contrary to what was observed in the present study.
Using the variance components from the between and within sex analyses, genetic correlations between growth traits in males and maternal traits in females were estimated using formula 2. Results are presented in Table 5. It should be pointed out that the maternal traits (MPPA's) were influenced by direct genetic effects, maternal genetic effects, direct x maternal interaction effects and other associated permanent environmental effects on the same trait. Therefore, any correlation between growth traits in males and maternal traits in females in this study should estimate the correlation between direct genetic effects on growth traits and total genetic effects on the maternal traits. Such correlations do not estimate solely the correlation of direct and maternal genetic effects on preweaning growth - the parameter that would be of greatest interest.

The \( r_g \)'s between BWT and MPPA-BWT; 205WT and MPPA-BWT; all growth traits (direct genetic effects) and MPPA-PDG; 205WT and MPPA-205 WT all were outside the theoretical limits (-1 to +1) for a genetic correlation. Generally, however, the standard errors were equal to or greater than the estimates themselves. Apparently the variance components were being estimated with such low precision that Yamada's (1962) technique was incapable of providing valid estimates. This becomes more apparent when the great change in \( \hat{r}_g \) between growth traits and MPPA-PDG or MPPA-205WT is observed. Correlations of any other trait with both of these should be similar but this is not the case in the present study (Table 5).
Correlations between Estimated Breeding Values. For comparison with the $\hat{r}_g$'s obtained by formula 2, breeding values (EBV) of each of the 20 sires for each of the traits (growth traits in sons and maternal traits in daughters) were estimated. Then product-moment correlations between EBV's for growth traits and maternal traits were calculated (Table 5). Most correlations were low, but all were positive, contrary to the earlier results. But with only 20 sires, none of the correlations was significantly different from zero. The correlations estimated using this technique ranged from 0.16 to 0.45.

Discussion. Hohenboken and Brinks (1971b) reported an $\hat{r}_g$ of .49 between 205 weaning weight in paternal half-brothers and MPPA for weaning weight in paternal half-sisters. In the present study this estimate was .23 (Table 5) from correlations among EBV's. Dim (1977) worked with Swedish Friesian cattle and found the $\hat{r}_g$ between performance test values for growth rate and breeding values for milk yield to be .06 for performance tested sires, while for performance tested sons of sires the correlation was .01. He concluded that no genetic relationship existed between growth rate and milk yield in paternal half-sib groups. A negative relationship between direct and maternal effects on growth rate in beef cattle was reported by Koch and Clark (1955b) and Hill et al., (1966). Deese and Koger (1967) also reported a negative covariance between direct genetic effects and maternal genetic effects on weaning weights in a Brahman x Shorthorn population. In the present study, correlating the EBV's
for each trait, all $\hat{r}_g$ estimates between direct genetic effects on growth traits and total genetic effects on maternal traits were positive. Other workers such as Brown and Galvez (1969) and Hill et al. (1966) reported negative $\hat{r}_g$'s between direct and maternal genetic effects on birth weight while Koch (1972) reported an $\hat{r}_g$ of .07 for the same effects. This correlation in the present study was positive (.32 using breeding values). Langlet (1965) reported a correlation of .22 between milk production and daily gain of half-sibs based on 236 sons and 2450 daughters from 25 Friesian sires. In the present study, the $\hat{r}_g$ between EBV for PDG and EBV for MPPA-205WT was .18. Mason (1964) studied data from Danish progeny test stations in which daughters and sons from the sires were tested for milk and beef production, respectively. The correlation was .23 but was believed to have been caused by environmental differences.

Even though there are conflicting results in the literature regarding the genetic correlation between direct genetic effects and maternal genetic effects on maternally influenced traits, the general conclusion seems to be that there is little genetic antagonism between these effects. The present study generally leads to the same conclusion. Therefore, continued selection of sires for growth traits should not reduce the maternal performance of their daughters. However, this tentative conclusion might be contradicted if larger sets of data were used and also if postweaning growth traits were considered in the paternal half-brothers (Brinks, 1980, personal communication).
<table>
<thead>
<tr>
<th>Source</th>
<th>Mean squares for growth traits D.F.</th>
<th>BWT</th>
<th>WNS</th>
<th>PDG</th>
<th>205WT</th>
<th>Mean squares for maternal traits</th>
<th>MPPA-BWT</th>
<th>MPPA-PDG</th>
<th>MPPA-205WT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Line of sire</td>
<td>4</td>
<td>119.8</td>
<td>181.7</td>
<td>.05</td>
<td>2414.9</td>
<td>13.5*</td>
<td>.01*</td>
<td>221.4^*</td>
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</tr>
<tr>
<td>Sire/line sire</td>
<td>15</td>
<td>49.3^+</td>
<td>142.4</td>
<td>.03</td>
<td>1512.3</td>
<td>3.0</td>
<td>.004^+</td>
<td>101.9*</td>
<td></td>
</tr>
<tr>
<td>Line of dam</td>
<td>4</td>
<td>178.8**</td>
<td>141.7</td>
<td>.02</td>
<td>705.3</td>
<td>6.5**</td>
<td>.0006</td>
<td>28.3</td>
<td></td>
</tr>
<tr>
<td>Line of sire x</td>
<td>16</td>
<td>21.30</td>
<td>70.4</td>
<td>.03</td>
<td>689.6</td>
<td>2.0</td>
<td>.01**</td>
<td>110.3*</td>
<td></td>
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<tr>
<td>Line of Dam</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Residual a</td>
<td>204</td>
<td>29.2</td>
<td>96.2</td>
<td>.02</td>
<td>1002.1</td>
<td>--</td>
<td>--</td>
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<tr>
<td>Residual b</td>
<td>136</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>1.9</td>
<td>.002</td>
<td>59.6</td>
<td></td>
</tr>
</tbody>
</table>

a - Residual degrees of freedom for growth traits
b - Residual degrees of freedom for maternal traits
*(P < .05)
**(P < .01)
^+(P < .10)
TABLE 2. WITHIN SEX VARIANCE COMPONENT ESTIMATES FOR GROWTH AND MATERNAL TRAITS

<table>
<thead>
<tr>
<th>Source</th>
<th>Growth Traits</th>
<th>Maternal Traits</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>BWT</td>
<td>WNS</td>
</tr>
<tr>
<td>$\sigma^2_{S/LS}$</td>
<td>1.76$^a$</td>
<td>4.03</td>
</tr>
<tr>
<td>$\sigma^2_E$</td>
<td>29.29</td>
<td>96.24</td>
</tr>
<tr>
<td>$\sigma^2_T$</td>
<td>31.06</td>
<td>100.27</td>
</tr>
</tbody>
</table>

$^a$All variance components are measured in $k^2_g$ except those for WNS which are in points.
TABLE 3. GENETIC PARAMETERS FOR GROWTH AND MATERNAL TRAITS

<table>
<thead>
<tr>
<th></th>
<th>Growth Traits</th>
<th>Maternal Traits</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>BWT</td>
<td>WNS</td>
</tr>
<tr>
<td>BWT</td>
<td>0.23 ± 0.18</td>
<td>0.85 ± 0.25</td>
</tr>
<tr>
<td>WNS</td>
<td>0.16 ± 0.16</td>
<td>0.93 ± 0.18</td>
</tr>
<tr>
<td>PDG</td>
<td>0.15 ± 0.16</td>
<td>1.0 ± 0.02</td>
</tr>
<tr>
<td>205WT</td>
<td>0.17 ± 0.17</td>
<td></td>
</tr>
</tbody>
</table>

*Values on the diagonals are the heritability of the trait while off-diagonal values represent the genetic correlations between respective traits.*
TABLE 4. BETWEEN SEX VARIANCE COMPONENT ESTIMATES

<table>
<thead>
<tr>
<th>Source</th>
<th>BWT</th>
<th>WNS</th>
<th>PDG</th>
<th>20SWT</th>
<th>BWT</th>
<th>WNS</th>
<th>PDG</th>
<th>20SWT</th>
<th>BWT</th>
<th>WNS</th>
<th>PDG</th>
<th>20SWT</th>
</tr>
</thead>
<tbody>
<tr>
<td>MPPABWT</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>MPPBWT</td>
<td>.84a</td>
<td>1.52</td>
<td>.04</td>
<td>14.61</td>
<td>0.58</td>
<td>1.01</td>
<td>.0004</td>
<td>13.18</td>
<td>3.00</td>
<td>8.83</td>
<td>1.51</td>
<td>17.35</td>
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<tr>
<td>MPPABWT</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>-</td>
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<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>MPPAPDG</td>
<td>-.02</td>
<td>0.90</td>
<td>.13</td>
<td>1.78</td>
<td>.32</td>
<td>0.83</td>
<td>-.0001</td>
<td>4.76</td>
<td>2.67</td>
<td>21.48</td>
<td>4.65</td>
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</tr>
<tr>
<td>MPPAPDG</td>
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<td>-</td>
<td>-</td>
<td>-</td>
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<td>-</td>
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<td>-</td>
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</tr>
<tr>
<td>MPPA205WT</td>
<td>18.00</td>
<td>60.63</td>
<td>.78</td>
<td>566.82</td>
<td>17.12</td>
<td>56.49</td>
<td>.012</td>
<td>585.96</td>
<td>43.83</td>
<td>186.18</td>
<td>26.00</td>
<td>613.88</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>MPPA205WT</td>
<td>18.82</td>
<td>63.05</td>
<td>.95</td>
<td>603.21</td>
<td>18.02</td>
<td>58.33</td>
<td>.012</td>
<td>603.90</td>
<td>49.50</td>
<td>216.50</td>
<td>32.16</td>
<td>629.82</td>
</tr>
</tbody>
</table>

\(^a\) All variance components are measured in \(kg^2\) except those involving WNS, which are in points x pound units.
<table>
<thead>
<tr>
<th>GROWTH TRAITS</th>
<th>MATERNAL TRAITS</th>
<th>Correlations Between Breeding Values</th>
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<tr>
<td></td>
<td>Using Yamada's Approach</td>
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<tr>
<td></td>
<td>MPPA-BWT</td>
<td>MPPA-PDG</td>
</tr>
<tr>
<td>BWT</td>
<td>2.20 ± 1.31</td>
<td>-3.32 ± 3.15</td>
</tr>
<tr>
<td>WNS</td>
<td>0.82 ± 1.43</td>
<td>-1.12 ± 2.20</td>
</tr>
<tr>
<td>PDG</td>
<td>-0.52 ± 0.74</td>
<td>1.47 ± 1.60</td>
</tr>
<tr>
<td>205WT</td>
<td>-3.05 ± 3.39</td>
<td>-1.57 ± 2.06</td>
</tr>
</tbody>
</table>
LITERATURE CITED


Harvey, W.R. 1975. Users Guide for LSML76. Ohio State University, Columbus, Ohio.


CHAPTER III

DIRECT GENETIC EFFECTS, MATERNAL GENETIC EFFECTS AND THEIR RELATIONSHIPS ON PREWEANING GROWTH TRAITS IN HEREFORD LINES

SUMMARY

Data from the USDA Livestock and Range Research Station, Miles City, MT collected over two phases (II and III) of an experiment were used in this study. Phase II involved Hereford lines 1,4,6,9 and 10 as sources of inbred dams and linecross dams mated to two-way cross bulls for the production of three-way cross calves (260) between 1965 and 1968. Phase III involved lines 1,4,6 and 10 as sources of straight-line bulls to produce inbreds plus two-way, three-way and rotational linecross calves (1009) between 1967 and 1975. Expectations for direct genetic ($g^I$) and maternal genetic effects ($g^M$) for each calf were derived for both phases. In addition expected individual ($h^I$) and maternal ($h^M$) heterosis as well as expected recombination losses, individual ($r^I$) and maternal ($r^M$), were determined for the linecross calves produced in Phase III. Preweaning traits included birth weight (BWT), preweaning daily gain (PDG), 205 day weaning weight (205WT) and weaning score (WNS), all adjusted for age of dam and sex of calf effects. The model contained year, $g^I$ and $g^M$ for each of the five lines and inbreeding of the dam (FD) effects in Phase II, while in Phase III it contained inbreeding of calf (FC) in addition to these effects. Another model that contained $h^I$, $h^M$, $r^I$ and $r^M$ was also used.
in Phase III. The correlations between line constants for \( g^I \) and \( g^M \) on BWT were -.29 and .85 in phases II and III, respectively. Estimates of \( r_{gIgM} \) for PDG and 205WT were -.73 and -.79, respectively, in Phase II and .14 and .24, respectively, in Phase III. For WNS these correlations were -.58 and .66 in Phases II and III, respectively. For all the traits, \( r_{gIgM} \) changed from negative in Phase II to positive in Phase III. Possible contributing factors for this discrepancy are discussed, and it is concluded that estimates in Phase III probably are more reliable. Therefore compelling evidence of antagonism between line constants for \( g^I \) and \( g^M \) effects on the traits considered was not found. It was also observed that \( r^I \) and \( r^M \) were not significant sources of variation for any of the traits. Individual heterosis had a significant positive effect on PDG and 205WT. Otherwise, \( h^I \) and \( h^M \) did not have significant effects on any of the other traits. Effects from FC and FD were either negative or not significantly different from zero on all traits in both phases.

(Key Words: direct genetic effects, maternal genetic effects, lines, Herefords.)
INTRODUCTION

Animal breeders have long recognized the importance of estimating effects such as direct genetic merit ($g_I$) and maternal genetic merit ($g^M$) of lines or breeds and, in crossbred or linecross populations, the magnitude of individual ($h^I$) and (or) maternal ($h^M$) heterosis. Epistatic loss for individual ($r^I$) and (or) maternal ($r^M$) effects due to recombination of genes originally fixed by selection has come under investigation more recently. Dickerson (1969, 1973) has shown the potential contribution of each of these effects in any crossbreeding system in terms of expectations.

Some workers have evaluated inbred lines and have estimated heterosis effects for economically important traits in beef cattle (Flower et al., 1963; Brinks et al., 1967, 1972; Humes et al., 1973; Kress et al., 1979), but only Kress et al. (1979) used line constants for $g^I$ and $g^M$ to estimate the genetic relationship between these two effects. In their study, correlations among line constants for $g^I$ and $g^M$ all were negative.

The objectives of this study were 1) to estimate line additive (direct) and maternal genetic effects while also looking at non-additive genetic effects, and 2) to determine the relationship between line constants for additive genetic and maternal genetic effects on birth weight, preweaning daily gain, 205 day weaning weight and weaning score in Hereford cattle.
MATERIALS AND METHODS

Data for this study were from inbred and linecross Hereford calves produced during the latter two phases of a long-term experiment conducted by the USDA Livestock and Range Research Station of Miles City, MT. In Phase II (1965-1968), five inbred lines (1,4,6,9 and 10) were involved in producing three-way linecross calves from straight line and first cross dams, while only lines 1,4,6 and 10 were involved to produce straightline and linecross calves in Phase III. History and origin of these lines were described by Urick et al. (1966).

Description of the physical environment, management of the breeding herd, selection of replacement heifers and calf management from birth to weaning are described elsewhere (Hunt, 1951; Brinks et al., 1972; Urick et al., 1981). The traits examined in this study were birth weight (BWT), preweaning daily gain (PDG), weaning score (WNS) and 205 day weaning weight (205WT). Records were adjusted for age of dam and calf sex by values derived from the report by Urick et al. (1981).

Data Analyses. Analyses were conducted separately for Phase II and Phase III records. This was necessary because Phase II had five lines while in Phase III only four lines were represented.

The traits considered here are maternally influenced (Koch, 1972), and therefore their evaluation must include consideration of both individual and maternal effects. A single offspring record can be
influenced by direct genetic effects (g_I) attributable to the line or lines contributing genes to the offspring, by maternal genetic effects (g_M) attributable to the line or lines contributing genes to the dam, by heterosis effects, both individual (h_I) and (or) maternal (h_M), and by recombination loss, individual (r_I) and (or) maternal (r_M), as described by Dickerson (1969, 1973).

In this study, expectations of g_I and g_M for each calf produced in Phase II and III were derived. Also expectations of h_I, h_M, r_I and r_M were worked out for linecross calves produced in Phase III. As an example, for a calf produced by mating a line 1 sire to a line 4 x line 6 cow, the expectations would be .5, .25 and .25 for g_1, g_4 and g_6, .5 and .5 for g_4 and g_6, 1.0 and 1.0 for h_I and h_M and .25 and 0 for r_I and r_M, respectively. In this study separate h and r terms were not fitted for each combination of two lines. Rather h_I, for example, represented the deviation from overall phenotypic average for all calves with maximum potential heterozygosity (two-line or three-line crosses) regardless of the lines contributing to the cross. A backcross calf (line 1 sire and line 1 x line 6 dam, for example) would have a coefficient for h_I of .5, while the coefficient for h_M would be 1.0. All other expectations were determined in a similar manner. These coefficients were considered as covariates together with the inbreeding of dam and calf. Similar techniques were used by Dillard et al. (1980) to study breed differences and heterosis effects on weaning traits in beef cattle and by Robison et al. (1981) in a study involving straightbred and crossbred dairy cows.
The data were analyzed by the method of least-squares for unequal subclass numbers (Harvey, 1975). The mathematical model used for Phase II data was:

\[ Y_{ij} = \mu + T_i + g_1 I_1 + g_4 I_4 + g_6 I_6 + g_9 I_9 + g_{10} I_{10} + g_1^M M_1 + g_4^M M_4 + g_6^M M_6 + g_9^M M_9 + g_{10}^M M_{10} + b_1 FD + \varepsilon_{ij} \]  

where:

- \( Y_{ij} \) = observation of the \( j^{th} \) calf in the \( i^{th} \) year,
- \( \mu \) = general mean,
- \( T_i \) = the effect of the \( i^{th} \) year \( (i = 1,2,3,4) \),
- \( I_1, I_4, I_6, I_9, I_{10} \) = percent of genes contributed to the calf by lines 1,4,6,9 and 10, respectively,
- \( g_1, g_4, g_6, g_9 \) and \( g_{10} \) = line additive genetic effects for lines 1,4,6,9 and 10, respectively where \( \Sigma g^I = 0 \),
- \( M_1, M_4, M_6, M_9, M_{10} \) = percentage of genes contributed to the dam by lines 1,4,6,9 and 10, respectively,
- \( g_1^M, g_4^M, g_6^M, g_9^M \) and \( g_{10}^M \) = maternal genetic effects for lines 1,4,6,9 and 10, respectively, where \( \Sigma g^M = 0 \),
- \( b_1 \) = the partial linear regression coefficient associated with the inbreeding of the dam (FD) and
- \( \varepsilon_{ij} \) = the random error peculiar to each observation.

Expectations for direct genetic and maternal genetic effects for lines 1,4,6 and 9 were expressed as deviations from that of line 10. This was done to impose a restriction to the equations and to avoid the occurrence of a zero determinant and hence a singular matrix.
A similar model was used for Phase III data, but FC was included as a covariate (since inbred calves were produced in this phase) and line 9 was not represented.

From analyses of records from both phases, product-moment correlations were computed between the direct genetic effect \( (g_I) \) and the maternal genetic effect \( (g^M) \) for each line for each trait.

Using Phase III linecross data, effects of \( h_I, h^M, r_I, \) and \( r^M \) on BWT, PDG, WNS and 205WT were studied using a model that contained partial regressions representing these effects with \( g_I \)'s or \( g^M \)'s excluded.

**RESULTS AND DISCUSSION**

Least-squares means and standard deviations for birth weight, pre-weaning daily gain, 205 day weaning weight and weaning score in phases II and III are presented in Table 1. Years were a highly significant source of variation for all traits in both phases (Tables 2 and 3).

**Birth Weight.** This trait is subject to influence by differences in prenatal maternal environment among lines or genotypes. The direct genetic effect \( (g_I) \) attributable to line 9 and the maternal genetic effect \( (g^M) \) attributable to line 6 were significant negative influences on birth weight in Phase II (Tables 2 and 4). In Phase III, however, \( g_4^I, g_6^I \) and \( g_6^M \) were significant sources of variation (Table 3). The line 4 \( g_I \) had a positive effect while \( g_6^I \) and \( g_6^M \) both had negative effects on birth weight (Table 5). Also, \( g_1^M \) approached significance in Phase III with a positive effect. The negative effects
of $g_6^I$, $g_6^M$ and $g_9^I$ on birth weight in Phase II are in general agreement with results of Brinks et al. (1967). Inbreeding of the dam (FD) was not a significant source of variation in either phase (Tables 2 and 3), in agreement with Brinks and Knapp (1975). Inbreeding of the calf (FC), however, had a significant negative effect in Phase III. Similar FC effects on BWT were shown by Brinks and Knapp (1975).

The correlations between $g^I$ and $g^M$ effects on BWT were -0.29 and 0.85 in phases II and III, respectively (Tables 4 and 5). Kress et al. (1979) reported a correlation of -0.58 between $g^I$ and $g^M$ effects on inbred Hereford lines for birth weight, in agreement with results for Phase II but contrary to results in Phase III in the present study. Speculations upon reasons for the difference in sign for $r_{gIgM}$ in the two phases will be made after this statistic has been presented for the other preweaning traits.

From separate analyses of Phase III data, heterosis effects ($h^I$ and $h^M$) and recombination effects ($r^I$ and $r^M$) on birth weight were not significantly different from zero. Very low but positive heterosis effects on birth weight were reported by Brinks et al. (1967, 1972), Flower et al. (1963) and Kress et al. (1979) in Hereford lines, in agreement with results in the present study, while Humes et al. (1973) reported significant positive heterosis in Hereford line crosses.

**Preweaning Daily Gain and 205 Day Weaning Weight.** These two traits are of great economic importance to the livestock producer. In the present study for Phase II records, the effects of $g_6^M$ and FD were highly significant sources of variation in PDG and 205WT, while $g_6^I$
approached significance (Table 2). In Phase III, $g_1^I$, $g_1^M$, $g_6^I$ and FC were significant sources of variation in PDG and 205WT (Table 3). Maternal genetic effects attributable to line 6 also approached significance for PDG. It is interesting to note that $g_1^I$ and $g_1^M$ were not significant in Phase II but became important sources of variation for both traits in Phase III. The effects of $g_1^I$ and $g_1^M$ on PDG and 205WT in Phase III were positive (Table 5), in agreement with Brinks et al. (1967, 1972); whereas in Phase II $g_1^I$ was positive while $g_1^M$ was negative for both traits. Direct genetic effects for line 6 were negative for both PDG and 205WT. The $g_6^M$ effect in Phase II exceeded that of the other lines in PDG and 205WT. In Phase III, $g_6^M$ was positive but lower than $g_1^M$. Brinks et al. (1967) reported that line 6 ranked lowest for preweaning gain and weaning weight by line of sire but was among the best for these traits as shown by the line of dam means. In their study, the difference for line 6 between line of sire and line of dam means was significant for PDG and weaning weight in both male and female calves. Humes et al. (1973) reported a highly significant negative influence of FD on the PDG of bull calves in Hereford lines, while Brinks and Knapp (1975) also concluded that inbreeding of the dam had a significant negative impact on PDG and 205WT. Inbreeding of dam, even though negative, was not important in the present study.

The correlations between direct genetic and maternal genetic effects ($r_{g_1gM}$) on PDG and 205WT were -.79 and -.79 in Phase II and .14 and .24 in Phase III, respectively. The Phase II estimate of -.79 for
205WT is in close agreement with that reported by Kress et al. (1979), -.80 for 180 day weight.

Of the non-additive genetic effects, individual heterosis ($h^I$) had a significant positive effect on PDG and 205WT, while maternal heterosis, though positive, did not have a significant effect on either of the traits in Phase III. This is in agreement with results of Flower et al. (1963). Neither of the recombination loss effects ($r^I$ and $r^M$) was a significant source of variation for either trait, though $r^I$ was negative. This agrees with Teehan et al. (1980) who reported negative but non-significant recombination loss effects among breed crosses in sheep. Similarly, Koger et al. (1975) and Dillard et al. (1980) concluded that recombination loss effects did not appear to be important in beef cattle. Neither group of investigators, however, measured recombination loss directly. Dillard et al. (1980) for example compared the coefficients of determination ($R^2$) of a model whose objective was to compare breed groups with that of another model that included $g^I$, $g^M$, $h^I$ and $h^M$. The $R^2$ values were similar, from which they concluded that recombination loss effects were not important, at least in their population. Similarly, Robison et al. (1981) ruled out the possibility that epistasis could cause differences among breed groups.

Weaning Score. This trait may reflect to some degree thrift and vitality under unfavorable environmental conditions (Koger et al., 1975). It is based upon subjective evaluation of calves' conformation at weaning. In this study weaning score was influenced by $g^I_9$ and $g^M_6$ in Phase II (Table 2). The direct genetic effect of line 9 was negative,
while $g_6^M$ was positive (Table 4). In Phase III, however, only FD and FC were significant sources of variation (Table 3). Both had negative influences.

The correlations between the effects of $g^I$ and $g^M$ on weaning score were -.58 and .66 in phases II and III, respectively. Of the non-additive genetic effects, $r^I$ and $r^M$ had non-significant but negative influences on weaning score while $h^I$ and $h^M$ effects were positive but non-significant as obtained from the line-cross analyses in Phase III.

**Comparison of Phase II and III Results.** For all the preweaning and weaning traits considered, the correlation between line constants for $g^I$ and $g^M$ changed from negative in Phase II (Table 4) to positive in Phase III (Table 5). Several factors could have contributed to this change. These include:

1) Difference in population size between the two phases. There were 260 records in Phase II and 1009 records (547 inbreds and 462 line-crosses) in Phase III. Phase III estimates of $r_{gIgM}$ should therefore be more reliable than Phase II estimates. Since, however, a minimum of 52 calves contributed information to the $g^I$ and $g^M$ estimates per line in Phase II, $r_{gIgM}$'s from that phase should be reasonably accurate.

2) Difference in population structure between phases. In Phase II straightline as well as F1 linecross dams from all possible two-line combinations of the five lines (1,4,6,9,10) were mated to two-way cross bulls to produce all three-way cross calves. In Phase III, straightline and F1 (two-line cross) females were initially mated to straightline bulls to establish a continuous program resulting in the production of
straight-line animals plus two-line and three-line rotational crosses. The fact that linecross bulls were used in Phase II and inbred bulls were used in Phase III may have contributed to the difference in $r_{gIgM}$ between the two phases. Bowman (1960) reported that the estimated genetic merit of a sire for some traits depended upon whether a progeny test were based on straightbred or crossbred progeny, and McNew and Bell (1971) showed theoretically that certain types of epistasis could cause negative covariances of an individual's straightbred vs. linecross progeny. There is no evidence to support an effect such as this in the current study, but it could be a factor contributing to the difference in $r_{gIgM}$ between phases II and III.

3) Absence of line 9 in Phase III. In Phase II all five lines (1,4,6,9,10) were involved while only four lines (1,4,6,10) were involved in Phase III. However, when the $r_{gIgM}$'s were re-computed excluding line 9 in Phase II, the estimates did not change materially (Table 4). Therefore, absence of line 9 from Phase III does not account for the change in signs of $r_{gIgM}$ coefficients.

4) Possible line by age of dam interactions. In Table 6, correlations between $g^I$ in Phase II and $g^I$ in Phase III ($r_{g^Ig^I}$) and between $g^M$ in Phase II and $g^M$ in Phase III ($r_{g^Mg^M}$) are presented. The $r_{g^Mg^M}$ coefficients for both PDG and 205 day weight were low (.58 and .37) in comparison to $r_{g^Ig^I}$ correlations for the same traits (.84 and .85). Thus, effects attributable to differences in $g^M$ line effects probably were more important than differences in $g^I$ line effects in causing the change in $r_{gIgM}$ correlations between phases. Adjustment for age of dam
at calving was made to both phase II and III records using constants from Urick et al. (1981). Phase II was based entirely on young females calving at 2 to 5 years of age and Phase III on females calving at 2 to 10 years of age, and with a higher proportion of mature or old cows. For example, all Phase III cows born in Phase I were mature before Phase III began. Some lines could have been more mature and others less mature physiologically at a given chronological age. Dickerson and Glimp (1975) found this to exist for reproductive traits among breeds of sheep; curvilinear regressions of fertility on age for the various breeds were not parallel in that study. If that were true in the present population, some lines would have been over-adjusted for age of dam and some would have been under-adjusted, causing changes in relative merit of lines for $g^M$ with time and across experimental phases. (This would be an interesting issue to pursue in the data, but such investigations were beyond the scope of this study.) If age of dam x line interactions for $g^M$ effects were important, then $r_{gIgM}$ coefficients from Phase III should be the more reliable since all degrees of maturity were represented in that phase.

5) Difference in the range of coefficients for the g terms. Coefficients for the $g^I$ terms (formula 1) ranged from 0 to .5 while $g^M$ coefficients ranged from 0 to 1.0 in Phase II. These ranges were from 0 to 1 for both $g^I$ and $g^M$ in Phase III, since there were more types of mating represented in the experimental design. Because of the mathematical characteristics of regression coefficients, there is therefore greater precision in the estimation of line constants for $g^I$ in Phase III than in Phase II (Brunk, 1975).
6) Possible changes in criteria for weaning score. Weaning score was based upon subjective evaluation. If criteria upon which the evaluations were based changed over time, greater emphasis on conformation in Phase III than in Phase II, for example, this could contribute to changes in $r_{I,I}$ to be -.75 and $r_{M,M}$ to be .65.

If the above tentative explanations, mainly those indicated in points 1, 2, 4 and 5, are justifiable, then estimates obtained from Phase III should be more representative of the among line relationship between direct genetic effects and maternal genetic effects on the traits examined.

Discussion. Line effects for $g^I$ on birth and weaning weight were plotted against line effects for $g^M$ for the same traits from Phase III of this study and from other experiments reported in the literature (Brinks et al., 1967; Humes et al., 1973; Grapevine et al., 1975; Kress et al., 1979) all involving Hereford lines. Brinks et al. (1967) and Humes et al. (1973) gave line of sire (LS) and line of dam (LD) least-squares means from diallel linecrossing studies for these traits. Such line of sire and line of dam means are expected to include $g^I$ and $g^I + g^M$, respectively, so LD-LS gave an estimate of $g^M$ for each line. Grapevine et al. (1975) presented general combining ability estimates (GCA's) of lines for weaning weight as an estimate of $g^I$. In their study, line of sire of dam (LSD) had the expectation $g^M + \frac{1}{2}g^I$. Therefore, LSD - $\frac{1}{2}$GCA gave an estimate of $g^M$ for weaning weight. Kress et al. (1979) presented line $g^I$ and $g^M$ effects for BWT and 180-day weaning weight.
Distribution of line $g_I$ and $g_M$ effects (converted to percentages of and deviations from appropriate least-square means) in Phase III and all the above sources are shown in Figure 1 for BWT and in Figure 2 for weaning weight, respectively. Examination of these figures indicates that little association existed between $g_I$ and $g_M$ for either BWT or weaning weight. In fact, the correlations between $g_I$ and $g_M$ considering all the values were .11 and -.32 for birth weight and weaning weight, respectively. From the results of this experiment and from comparisons with other evaluations of inbred line effects in Hereford cattle, we conclude that evidence is lacking to support the existence of genetic antagonism between direct and maternal effects on preweaning growth on a between line basis.
### TABLE 1. LEAST-SQUARES MEANS AND STANDARD DEVIATIONS OF THE PREWEANING TRAITS.

<table>
<thead>
<tr>
<th>TRAITS</th>
<th>PHASE II</th>
<th>PHASE III</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of calves</td>
<td>260</td>
<td>1009</td>
</tr>
<tr>
<td>Birth weight (kg)</td>
<td>34.4 (4.80)</td>
<td>35.0 (4.03)</td>
</tr>
<tr>
<td>Preweaning daily gain (kg)</td>
<td>.81 (.16)</td>
<td>.79 (.10)</td>
</tr>
<tr>
<td>205-day weaning weight (kg)</td>
<td>201.5 (31.40)</td>
<td>197.0 (21.00)</td>
</tr>
<tr>
<td>Weaning score (pt.)</td>
<td>82.1 (5.00)</td>
<td>82.7 (3.50)</td>
</tr>
</tbody>
</table>
TABLE 2. LEAST-SQUARES ANALYSIS OF VARIANCE FOR PREWEANING TRAITS IN PHASE II.

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>DF</th>
<th>BIRTH-WEIGHT MS</th>
<th>PREWEANING DAILY GAIN MS</th>
<th>205-DAY WEANING WEIGHT MS</th>
<th>WEANING SCORE MS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>3</td>
<td>109.6**</td>
<td>0.05**</td>
<td>3657.**</td>
<td>145.0**</td>
</tr>
<tr>
<td>9_1</td>
<td>1</td>
<td>.3</td>
<td>.03</td>
<td>1232.</td>
<td>4.0</td>
</tr>
<tr>
<td>9_4</td>
<td>1</td>
<td>39.9</td>
<td>.02</td>
<td>961.</td>
<td>30.1</td>
</tr>
<tr>
<td>9_6</td>
<td>1</td>
<td>0.0</td>
<td>.04^</td>
<td>1548.^</td>
<td>.47</td>
</tr>
<tr>
<td>9_9</td>
<td>1</td>
<td>55.1^</td>
<td>.02</td>
<td>1314.</td>
<td>69.4*</td>
</tr>
<tr>
<td>9_10</td>
<td>1</td>
<td>3.9</td>
<td>.002</td>
<td>107.</td>
<td>2.5</td>
</tr>
<tr>
<td>9_M</td>
<td>1</td>
<td>17.5</td>
<td>.004</td>
<td>123.</td>
<td>5.0</td>
</tr>
<tr>
<td>9_M</td>
<td>1</td>
<td>9.7</td>
<td>.03</td>
<td>1469.</td>
<td>17.7</td>
</tr>
<tr>
<td>9_6</td>
<td>1</td>
<td>62.3^</td>
<td>.13**</td>
<td>3882.**</td>
<td>75.3*</td>
</tr>
<tr>
<td>9_9</td>
<td>1</td>
<td>7.6</td>
<td>.0006</td>
<td>8.</td>
<td>13.2</td>
</tr>
<tr>
<td>9_10</td>
<td>1</td>
<td>12.2</td>
<td>.01</td>
<td>218.</td>
<td>26.0</td>
</tr>
<tr>
<td>FO</td>
<td>1</td>
<td>23.1</td>
<td>.11**</td>
<td>5320.**</td>
<td>28.1</td>
</tr>
<tr>
<td>Residual</td>
<td>245</td>
<td>12.1</td>
<td>.01</td>
<td>513.</td>
<td>13.2</td>
</tr>
</tbody>
</table>

*(P < .05)
**(P < .01)
^*(P < .01)
^*(P < .01)
TABLE 3. LEAST-SQUARES ANALYSES OF VARIANCE FOR PREWEANING TRAITS IN PHASE III.

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>DF</th>
<th>BIRTH-WEIGHT MS</th>
<th>PREWEANING DAILY GAIN MS</th>
<th>205-DAY WEANING WEIGHT MS</th>
<th>WEANING SCORE MS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>8</td>
<td>165.8**</td>
<td>.03**</td>
<td>1263.**</td>
<td>255.5**</td>
</tr>
<tr>
<td>g_{11}</td>
<td>1</td>
<td>14.9</td>
<td>.12**</td>
<td>5439.**</td>
<td>1.8</td>
</tr>
<tr>
<td>g_{41}</td>
<td>1</td>
<td>90.9*</td>
<td>.01</td>
<td>189.</td>
<td>3.2</td>
</tr>
<tr>
<td>g_{61}</td>
<td>1</td>
<td>240.3**</td>
<td>.12**</td>
<td>7412.**</td>
<td>.89</td>
</tr>
<tr>
<td>g_{101}</td>
<td>1</td>
<td>.5</td>
<td>.00</td>
<td>136.</td>
<td>.12</td>
</tr>
<tr>
<td>g_{2M}</td>
<td>1</td>
<td>50.1^+</td>
<td>.08**</td>
<td>4245.**</td>
<td>31.8</td>
</tr>
<tr>
<td>g_{4M}</td>
<td>1</td>
<td>1.8</td>
<td>.02</td>
<td>743.</td>
<td>1.9</td>
</tr>
<tr>
<td>g_{6M}</td>
<td>1</td>
<td>209.0**</td>
<td>.04^+</td>
<td>603.</td>
<td>25.1</td>
</tr>
<tr>
<td>g_{10M}</td>
<td>1</td>
<td>3.8</td>
<td>.02</td>
<td>685.</td>
<td>14.1</td>
</tr>
<tr>
<td>FC</td>
<td>1</td>
<td>69.2*</td>
<td>.13**</td>
<td>7132.**</td>
<td>57.6*</td>
</tr>
<tr>
<td>FD</td>
<td>1</td>
<td>8.5</td>
<td>.00</td>
<td>196.</td>
<td>53.5*</td>
</tr>
<tr>
<td>Residual</td>
<td>990</td>
<td>15.1</td>
<td>.01</td>
<td>429.</td>
<td>11.4</td>
</tr>
</tbody>
</table>

*(P < .05)

**(P < .01)

^+(P < .01)
TABLE 4. DIRECT GENETIC EFFECTS \((g^I)\) AND MATERNAL GENETIC EFFECTS \((g^M)\) AND THEIR CORRELATIONS \((r_{g^I g^M})\) IN PHASE II.

<table>
<thead>
<tr>
<th>LINE</th>
<th>BIRTH WEIGHT (kg)</th>
<th>PREWEANING DAILY GAIN (kg)</th>
<th>205-DAY WEANING WEIGHT (kg)</th>
<th>WEANING SCORE (pt)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(g^I) (g^M)</td>
<td>(g^I) (g^M)</td>
<td>(g^I) (g^M)</td>
<td>(g^I) (g^M)</td>
</tr>
<tr>
<td>1</td>
<td>-.23 1.23</td>
<td>.08 -.02</td>
<td>15.90 -3.30</td>
<td>.91 -.66</td>
</tr>
<tr>
<td>4</td>
<td>2.68 -.91</td>
<td>.06 -.05</td>
<td>13.23 -11.23</td>
<td>2.30 -1.20</td>
</tr>
<tr>
<td>6</td>
<td>-.09 -2.41</td>
<td>-.09 .11</td>
<td>-17.80 19.04</td>
<td>-.31 2.60</td>
</tr>
<tr>
<td>9</td>
<td>-3.23 .82</td>
<td>-.07 .003</td>
<td>-15.75 .82</td>
<td>-3.60 1.10</td>
</tr>
<tr>
<td>10</td>
<td>.86 1.27</td>
<td>.02 -.04</td>
<td>4.43 -5.34</td>
<td>0.68 -1.80</td>
</tr>
<tr>
<td>(r_{g^I g^M}^a)</td>
<td>-.29 -.79</td>
<td>(r_{g^I g^M}^b) = -.10 -.90</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(r_{g^I g^M}^a\) Including line 9
\(r_{g^I g^M}^b\) Excluding line 9
TABLE 5. DIRECT GENETIC EFFECTS (g\textsuperscript{I}) AND MATERNAL GENETIC EFFECTS (g\textsuperscript{M}) AND THEIR CORRELATIONS (r\textsubscript{g\textsuperscript{I}g\textsuperscript{M}}) IN PHASE III.

<table>
<thead>
<tr>
<th>LINE</th>
<th>BIRTH WEIGHT (kg)</th>
<th>PREWEANING DAILY GAIN (kg)</th>
<th>205-DAY WEANING WEIGHT (kg)</th>
<th>WEANING SCORE (pt)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>g\textsuperscript{I}</td>
<td>g\textsuperscript{M}</td>
<td>g\textsuperscript{I}</td>
<td>g\textsuperscript{M}</td>
</tr>
<tr>
<td>1</td>
<td>0.59</td>
<td>1.10</td>
<td>0.05</td>
<td>0.04</td>
</tr>
<tr>
<td>4</td>
<td>1.36</td>
<td>0.19</td>
<td>-0.01</td>
<td>-0.02</td>
</tr>
<tr>
<td>6</td>
<td>-2.10</td>
<td>-1.95</td>
<td>-0.05</td>
<td>0.03</td>
</tr>
<tr>
<td>10</td>
<td>0.18</td>
<td>0.68</td>
<td>0.01</td>
<td>-0.05</td>
</tr>
</tbody>
</table>

r\textsubscript{g\textsuperscript{I}g\textsuperscript{M}} = 0.85
TABLE 6. CORRELATIONS BETWEEN $g^I$ IN PHASE II AND $g^I$ IN PHASE III AND BETWEEN $g^M$ IN PHASE II AND $g^M$ IN PHASE III.

<table>
<thead>
<tr>
<th>Correlation</th>
<th>TRAITS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>BWT</td>
</tr>
<tr>
<td>$r_{g_2g_3}^I$</td>
<td>.64</td>
</tr>
<tr>
<td>$r_{g_2g_3}^M$</td>
<td>.93</td>
</tr>
</tbody>
</table>
Figure 1. Distribution of line $g_I$ and $g_M$ effects (converted to percent of and deviations from appropriate least-squares means) on birth weight.
Figure 2. Distribution of line $g^I$ and $g^M$ effects (converted to percentage of and deviations from appropriate least-squares means) on weaning weight.
LITERATURE CITED


Harvey, W.R. 1975. Users guide for least-squares and maximum likelihood computer program. Ohio State University, Columbus, Ohio.


## APPENDIX TABLE 1. LEAST-SQUARES ANALYSES OF VARIANCE FOR GROWTH AND MATERNAL TRAITS

<table>
<thead>
<tr>
<th>Source of Variance</th>
<th>D.F.</th>
<th>ABWT-MPPA</th>
<th>AWNS-MPPA</th>
<th>APDG-MPPA</th>
<th>AGOSWT-MPPA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>BWT</td>
<td>POG</td>
<td>BWT</td>
<td>POG</td>
</tr>
<tr>
<td>Line of Sire (LS)</td>
<td>4</td>
<td>120.3</td>
<td>95.3</td>
<td>38.2*</td>
<td>5691.0</td>
</tr>
<tr>
<td>Sire/LS&lt;sup&gt;3&lt;/sup&gt;</td>
<td>15</td>
<td>166.4&lt;sup&gt;*&lt;/sup&gt;</td>
<td>90.4&lt;sup&gt;*&lt;/sup&gt;</td>
<td>7.3&lt;sup&gt;**&lt;/sup&gt;</td>
<td>4227.5&lt;sup&gt;**&lt;/sup&gt;</td>
</tr>
<tr>
<td>Sex</td>
<td>1</td>
<td>0.97</td>
<td>1.7</td>
<td>-0.00</td>
<td>287.2</td>
</tr>
<tr>
<td>LS x Sex</td>
<td>4</td>
<td>162.2</td>
<td>118.0</td>
<td>28.7</td>
<td>5488.0</td>
</tr>
<tr>
<td>Sire/LS x Sex&lt;sup&gt;3&lt;/sup&gt;</td>
<td>15</td>
<td>86.2&lt;sup&gt;**&lt;/sup&gt;</td>
<td>68.8&lt;sup&gt;**&lt;/sup&gt;</td>
<td>3.3&lt;sup&gt;**&lt;/sup&gt;</td>
<td>2917.5&lt;sup&gt;**&lt;/sup&gt;</td>
</tr>
<tr>
<td>Line of Dam (LD)</td>
<td>4</td>
<td>523.4</td>
<td>27.0</td>
<td>19.7</td>
<td>1333.0</td>
</tr>
<tr>
<td>LS x LD</td>
<td>16</td>
<td>64.2</td>
<td>35.2</td>
<td>3.6</td>
<td>2077.7</td>
</tr>
<tr>
<td>LD x Sex</td>
<td>4</td>
<td>329.0</td>
<td>123.4</td>
<td>18.2</td>
<td>1429.3</td>
</tr>
<tr>
<td>Residual</td>
<td>356</td>
<td>38.9</td>
<td>60.6</td>
<td>3.3</td>
<td>2940.2</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Source of Variance</th>
<th>D.F.</th>
<th>ABWT-MPPA</th>
<th>AWNS-MPPA</th>
<th>APDG-MPPA</th>
<th>AGOSWT-MPPA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>BWT</td>
<td>POG</td>
<td>BWT</td>
<td>POG</td>
</tr>
<tr>
<td>Line of Sire (LS)</td>
<td>4</td>
<td>277.0</td>
<td>68.1</td>
<td>0.14</td>
<td>5178.6</td>
</tr>
<tr>
<td>Sire/LS&lt;sup&gt;3&lt;/sup&gt;</td>
<td>15</td>
<td>138.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>76.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.09&lt;sup&gt;a&lt;/sup&gt;</td>
<td>4087.2&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Sex</td>
<td>1</td>
<td>0.69</td>
<td>6.4</td>
<td>0.03</td>
<td>292.3</td>
</tr>
<tr>
<td>LS x Sex</td>
<td>4</td>
<td>231.8</td>
<td>52.4</td>
<td>0.20</td>
<td>5812.8</td>
</tr>
<tr>
<td>Sire/LS x Sex&lt;sup&gt;3&lt;/sup&gt;</td>
<td>15</td>
<td>95.7&lt;sup&gt;a&lt;/sup&gt;</td>
<td>64.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.05&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3042.4&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>LO</td>
<td>4</td>
<td>379.7</td>
<td>40.9</td>
<td>0.03</td>
<td>1186.3</td>
</tr>
<tr>
<td>LS x LD</td>
<td>16</td>
<td>67.2</td>
<td>40.6</td>
<td>0.11</td>
<td>2084.1</td>
</tr>
<tr>
<td>LD x Sex</td>
<td>4</td>
<td>421.1</td>
<td>64.7</td>
<td>0.05</td>
<td>1480.7</td>
</tr>
<tr>
<td>Residual</td>
<td>356</td>
<td>82.9</td>
<td>56.3</td>
<td>0.06</td>
<td>2812.0&lt;sup&gt;**&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Source of Variance</th>
<th>D.F.</th>
<th>ABWT-MPPA</th>
<th>AWNS-MPPA</th>
<th>APDG-MPPA</th>
<th>AGOSWT-MPPA</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>BWT</td>
<td>POG</td>
<td>BWT</td>
<td>POG</td>
</tr>
<tr>
<td>Line of Sire (LS)</td>
<td>4</td>
<td>1026.5</td>
<td>711.8</td>
<td>591.2</td>
<td>5823.9</td>
</tr>
<tr>
<td>Sire/LS&lt;sup&gt;3&lt;/sup&gt;</td>
<td>15</td>
<td>495.1&lt;sup&gt;**&lt;/sup&gt;</td>
<td>359.4&lt;sup&gt;**&lt;/sup&gt;</td>
<td>258.9&lt;sup&gt;**&lt;/sup&gt;</td>
<td>4619.0&lt;sup&gt;**&lt;/sup&gt;</td>
</tr>
<tr>
<td>Sex</td>
<td>1</td>
<td>37.1</td>
<td>99.4</td>
<td>30.1</td>
<td>576.9</td>
</tr>
<tr>
<td>LS x Sex</td>
<td>4</td>
<td>707.4</td>
<td>603.1</td>
<td>594.5</td>
<td>6363.7</td>
</tr>
<tr>
<td>Sire/LS x Sex&lt;sup&gt;3&lt;/sup&gt;</td>
<td>15</td>
<td>328.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>379.7&lt;sup&gt;a&lt;/sup&gt;</td>
<td>327.9&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2592.9&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>LO</td>
<td>4</td>
<td>433.3</td>
<td>28.4</td>
<td>33.2</td>
<td>1474.5</td>
</tr>
<tr>
<td>LS x LD</td>
<td>16</td>
<td>134.4</td>
<td>148.6</td>
<td>202.2</td>
<td>2271.0</td>
</tr>
<tr>
<td>LD x Sex</td>
<td>4</td>
<td>604.7</td>
<td>263.7</td>
<td>34.0</td>
<td>1477.1</td>
</tr>
<tr>
<td>Residual</td>
<td>356</td>
<td>212.2</td>
<td>156.2</td>
<td>125.4</td>
<td>2971.2</td>
</tr>
</tbody>
</table>

*p < 0.05, **p < 0.01*  
*For K<sub>1</sub> and K<sub>2</sub> as coefficients of /LS x Sex and /LS were 9.01 and 19.62, respectively*
## APPENDIX TABLE 2. AGE OF DAM ADJUSTMENT FACTORS FOR PHASES II AND III RECORDS

<table>
<thead>
<tr>
<th>Age in Years</th>
<th>Birth Weight</th>
<th>Weaning Score</th>
<th>Avg. daily Gain</th>
<th>205-Weaning Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>1.07</td>
<td>1.07</td>
<td>1.29</td>
<td>1.26</td>
</tr>
<tr>
<td>3</td>
<td>1.05</td>
<td>1.04</td>
<td>1.12</td>
<td>1.13</td>
</tr>
<tr>
<td>4</td>
<td>1.00</td>
<td>1.02</td>
<td>1.06</td>
<td>1.04</td>
</tr>
<tr>
<td>5</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.01</td>
</tr>
<tr>
<td>6</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>7</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.01</td>
</tr>
<tr>
<td>8</td>
<td>1.00</td>
<td>1.01</td>
<td>1.02</td>
<td>1.02</td>
</tr>
<tr>
<td>9</td>
<td>1.00</td>
<td>1.03</td>
<td>1.04</td>
<td>1.03</td>
</tr>
<tr>
<td>&gt;10</td>
<td>1.03</td>
<td>1.06</td>
<td>1.07</td>
<td>1.06</td>
</tr>
</tbody>
</table>

Urich et al. (1981)
## APPENDIX TABLE 3. AGE OF DAM ADJUSTMENT FACTORS FOR PHASE I RECORDS

<table>
<thead>
<tr>
<th>Age in Years</th>
<th>Birth Weight</th>
<th>Weaning Score</th>
<th>Avg. daily Gain</th>
<th>205-Weaning Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>1.05</td>
<td>1.09</td>
<td>1.13</td>
<td>1.12</td>
</tr>
<tr>
<td>4</td>
<td>1.03</td>
<td>1.04</td>
<td>1.05</td>
<td>1.05</td>
</tr>
<tr>
<td>5</td>
<td>1.00</td>
<td>1.03</td>
<td>1.02</td>
<td>1.02</td>
</tr>
<tr>
<td>6</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>7</td>
<td>1.00</td>
<td>1.00</td>
<td>1.01</td>
<td>1.01</td>
</tr>
<tr>
<td>8</td>
<td>1.00</td>
<td>1.01</td>
<td>1.02</td>
<td>1.02</td>
</tr>
<tr>
<td>9</td>
<td>1.00</td>
<td>1.03</td>
<td>1.02</td>
<td>1.03</td>
</tr>
<tr>
<td>10</td>
<td>1.03</td>
<td>1.06</td>
<td>1.07</td>
<td>1.06</td>
</tr>
</tbody>
</table>

Koch and Clark (1955)
APPENDIX TABLE 4. PARTIAL REGRESSION COEFFICIENTS FOR INBREEDING OF CALF AND DAM AND SEX ADJUSTMENT FACTORS

<table>
<thead>
<tr>
<th>Source of Inbreeding and sex</th>
<th>TRAITS</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Birth Weight</td>
<td>Weaning Score</td>
<td>Preweaning Daily Gain</td>
<td>205-day Weaning Weight</td>
</tr>
<tr>
<td>Inbreeding of Calf (Male)</td>
<td>-.09(^a)</td>
<td>(.09(^b))</td>
<td>-.27(^a)</td>
<td>-.64(^l)</td>
</tr>
<tr>
<td>Inbreeding of Calf (Female)</td>
<td>-.37(^b)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inbreeding of Dam</td>
<td>-.02(^l)</td>
<td>.32(^b)</td>
<td>-.49</td>
<td>-.88</td>
</tr>
<tr>
<td>Bulls</td>
<td>.93(^c)</td>
<td>1.00(^c)</td>
<td>.95(^c)</td>
<td>.95(^c)</td>
</tr>
</tbody>
</table>

\(^a\) Brinks and Knapp (1975)

\(^b\) Brinks et al. (1965)

\(^c\) Urick et al. (1981)