Estimation of maternal effects on birth and weaning weight of Hereford cattle
by Rodolfo Juan Carlos Cantet

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Animal Science
Montana State University

Abstract:
Evidence has been found that maternal effects are important sources of variation in mammals. In beef cattle, evidence has been found to support the hypothesis that maternal effects can reduce the expected response to selection for growth traits, especially preweaning growth. It is not clear whether maternal effects in preweaning growth of beef cattle are genetic or environmental. Therefore, the present research was conducted to study the nature and. magnitude of maternal effects in birth and weaning weight of Hereford cattle. The data used were the records of 4,423 noncreep-fed beef calves raised at the Northern Agricultural Research Center, Havre, Mt from 1938 to 1983. Least-squares, fitting constants method (Henderson III) and Restricted Maximum Likelihood procedures were used to estimate eighteen covariances between different types of relatives. The basic models included the fixed effects of line-year, age of dam, sex of calf, age of dam by sex interaction and the regressions of birth weight on birthdate of calf and weaning weight on weaning age of calf. The source of variation depicting the relative relationship was considered a random effect. Multiple regression procedures were used to obtain the nine parameters: additive genetic, dominance genetic and environmental direct and maternal variances and the covariance between the direct and maternal source in each case.

All solutions showed a negative additive genetic correlation between additive direct effects and additive maternal effects (rG). The results were not clear regarding to the magnitude of rG for birth weight but the probable value for weaning weight was around -.60 to -.75. There was also evidence for a negative environmental correlation for maternal phenotype of the dam and daughter in the case of weaning weight. This path coefficient (fm) was calculated to be .08 for birth weight and -.10 for weaning weight. After correcting the expectations of the covariances between relatives for fm, rG was still present and negative for both weights. The solutions showed that dominance was also involved in determining maternal effects in preweaning growth of beef cattle but its effects may be confounded with epistasis.

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A thesis submitted in partial fulfillment
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APPROVAL

of a thesis submitted by

Rodolfo Juan Carlos Cantet

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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Date May 25, 1984

To my wife, to my mother and
to the memory of my father

VITA

Rodolfo Juan Carlos Cantet was born to Mr. and Mrs. Rodolfo Manuel Cantet in Buenos Aires, Argentina, on March 17, 1954.

He attended Liceo Militar General San Martin Highschool and was admitted to the Facultad de Agronomia, Universidad de Buenos Aires in 1972. He graduated as an Ingeniero Agronomo in 1978.

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In September 1982, he was admitted to Montana State University for his Master's degree in Animal Science (Animal Breeding).

He married Patricia Prandini in 1982.

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ABSTRACT

Evidence has been found that maternal effects are important sources of variation in mammals. In beef cattle, evidence has been found to support the hypothesis that maternal effects can reduce the expected response to selection for growth traits, especially preweaning growth. It is not clear whether maternal effects in preweaning growth of beef cattle are genetic or environmental. Therefore, the present research was conducted to study the nature and magnitude of maternal effects in birth and weaning weight of Hereford cattle. The data used were the records of 4,423 noncreep-fed beef calves raised at the Northern Agricultural Research Center, Havre, Mt from 1938 to 1983. Least-squares, fitting constants method (Henderson III) and Restricted Maximum Likelihood procedures were used to estimate eighteen covariances between different types of relatives. The basic models included the fixed effects of line-year, age of dam, sex of calf, age of dam by sex interaction and the regressions of birth weight on birthdate of calf and weaning weight on weaning age of calf. The source of variation depicting the relative relationship was considered a random effect. Multiple regression procedures were used to obtain the nine parameters: additive genetic, dominance genetic and environmental direct and maternal variances and the covariance between the direct and maternal source in each case.

All solutions showed a negative additive genetic correlation between additive direct effects and additive maternal effects (r_G). The results were not clear regarding to the magnitude of r_G for birth weight but the probable value for weaning weight was around -.60 to -.75. There was also evidence for a negative environmental correlation for maternal phenotype of the dam and daughter in the case of weaning weight. This path coefficient (fm) was calculated to be .08 for birth weight and -.10 for weaning weight. After correcting the expectations of the covariances between relatives for fm, r_G was still present and negative for both weights. The solutions showed that dominance was also involved in determining maternal effects in preweaning growth of beef cattle but its effects may be confounded with epistasis.

INTRODUCTION

The success of a breeding scheme to improve performance characteristics of farm animals depends on how genetic and environmental sources of variation are taken into account. Like other domestic mammals, beef cattle are subject to maternal environment from the early moments of gestation through weaning time. A maternal effect is an effect contributed to the phenotypic value of an individual by its dam (Willham, 1980). Although maternal effects are environmental so far as their influence on offspring is concerned, they are determined by genetic and environmental factors (Koch, 1972).

Birth weight is the result of gestational growth rate and gestation length. Weaning weight is the consequence of birth weight and growth during the suckling period. Both traits are measured as the phenotypic value of the calf, but they are composed of at least two components, offspring genetics for growth and a maternal effect contributed by the dam. This latter influence is produced by nutrients provided by the uterus (in the case of birth weight) and the mammary gland (in the case of weaning weight). As Robison (1981) comments, it has recently become apparent that other factors may be involved in this action, perhaps through circulating hormones, cytoplasm,etc.

The other contribution of the dam to the phenotypic value of the offspring is a sample half of her genes to the calf. Therefore, while the sire contributes to the phenotypic value of the offspring by passing a sample half of his genes to the offspring, the dam contributes in at least two ways. Willham (1980) points out that the confounding of the two contributions from the dam and the possibility of a negative genetic correlation between the direct and maternal effect constitute the bases for the paramount problems in estimating maternal effects. It is clear that heritabilities (h^2) can be biased because of the presence of maternal effects (Robison, 1981).

The modeling process to estimate maternal effects has been initiated by Dickerson (1947). Kempthorne (1955) was an important paper in solving the problem of the estimation of genetic and environmental variances based on covariances between relatives. The presentation included the basis of the actual theory for measuring maternal and direct variation. Koch and Clark (1955b) was the first paper to estimate the additive genetic covariance between direct and maternal effects (σAoAm) in beef cattle, by using path coefficients theory. Finally, Willham (1963) developed a linear model theory for estimating direct and maternal genetic covariances and variances by an extension of the procedures first developed by Kempthorne (1955).

The use of Willham's method applied to cattle records has been reported by Everett and Magee (1965), Hill (1965), Brown and Galvez (1969), Vesely and Robison (1971), Koch (1972), Philipsson (1976), Fisher and Williams (1978) and Burfening et al (1981) for birth weight. Hill et al (1965), Deese and Koger (1967), Hohenboken and Brinks (1967), Vesely and Robison (1971), Koch (1972), Beltran Bru (1978) and Kress et al (1979) dealt with weaning weight. The general conclusions from the reviewed literature were that heritability for additive genetic direct effects (h^2o) was larger for birth weight than the contributions of additive genetic maternal effects (hm^2). The converse was true for weaning weight. A negative genetic antagonism between additive genetic direct and additive genetic maternal effects (i.e., negative value of σAoAm) has been found for both traits. The magnitude of σAoAm is likely to be relatively greater for weaning weight than for birth weight. However, the exact value of AoAm has been the matter of some discussion (Koch, 1972; Baker, 1980). Van Vleck et al (1977) have shown that the value of σAoAm determines the long term response to selection for weaning weight.

Totusek (1968), Mangus and Brinks (1971), Kress and Burfening (1972), Martin et al (1981) and Ochoa et al (1981) have found that the environment in which the heifer calf is raised affects her future maternal phenotype that she provides for her calves. This complicates the matter of the relative magnitude of environmental and genetic sources of variation on the expression of maternal effects, as Koch (1972) and Hohenboken (1973) discuss.

The objectives of the present study were:

1) to estimate the amount of variation due to additive genetic direct and additive genetic maternal effects in birth weight and weaning weight of Hereford beef calves,

2) to clarify the problem of the relative importance of genotype and environment for the expression of maternal effects on both traits, and

3) to estimate the additive genetic covariance between direct and maternal effects for both birth weight and weaning weight of Hereford beef calves.

REVIEW OF LITERATURE

Estimation of direct and maternal sources of variation

As in most other animal breeding problems, maternal effects theory is strongly related to quadratic estimation. The models used to estimate variance components due to maternal effects started from the variance of the classic model:

$$\sigma^2 P = \sigma^2 G + \sigma^2 E \qquad (1)$$

where $\sigma^2 P$ is the total phenotypic variance, $\sigma^2 G$ is the variance due to genetic effects, and $\sigma^2 E$ is the environmental variance. During the entire modeling process, no attempt has been made to incorporate the genotype by environmental interaction source of variation ($\sigma^2 GE$) into maternal effects quadratic estimation.

A further partition of $\sigma^2 G$ can be made as follows:

$$\sigma^2 G = \sigma^2 A + \sigma^2 D + \sigma^2 I \qquad (2)$$

where $\sigma^2 A$ is the variance due to additive genetic effects, $\sigma^2 D$ is the variance due to dominance effects (i.e., intralocus interaction) and $\sigma^2 I$ is the variance due to epistasis (i.e., interlocus interaction).

Dickerson (1947) made the first partition of the variances in model (1) to incorporate maternal effects. He did not consider dominance or epistasis in his model as shown below:

$$\sigma^2 P = \sigma^2 Ao + \sigma^2 Am + \sigma Ao\ Am + \sigma^2 Em + \sigma^2 Eo \qquad (3)$$

The terms of model (3) are

$\sigma^2 Ao$ = variance due to additive direct effects,

$\sigma^2 Am$ = variance due to additive maternal effects,

$\sigma AoAm$ = covariance between additive maternal and additive direct effects,

$\sigma^2 Em$ = variance due to maternal environmental effects common to full-sibs and maternal half-sibs, and

$\sigma^2 Eo$ = variance due to random environment.

The model was used to estimate maternal and direct covariances in carcass data of swine. Dickerson (1947) developed the path coefficient diagram shown in Figure 1.

The phenotype of X (Px) is the result of its own genotype for direct effects (Gox) plus a commmon or maternal environment component among litter mates (Pmw), where w indicates the dam of X. Dickerson (1947) did not include the random environmental source of variation in the diagram but in the analysis. The transmissible genotype or additive genetic effects are split into two components: o (direct) and m (maternal). The Gmx component will be expressed only if individual X subsequently becomes a dam (Willham, 1963). The component Pmw is affected by the maternal genotype of W (i.e., Gmw). There was no intention to relate the maternal phenotype of w with the maternal phenotype of her dam, her maternal grand dam and so on.

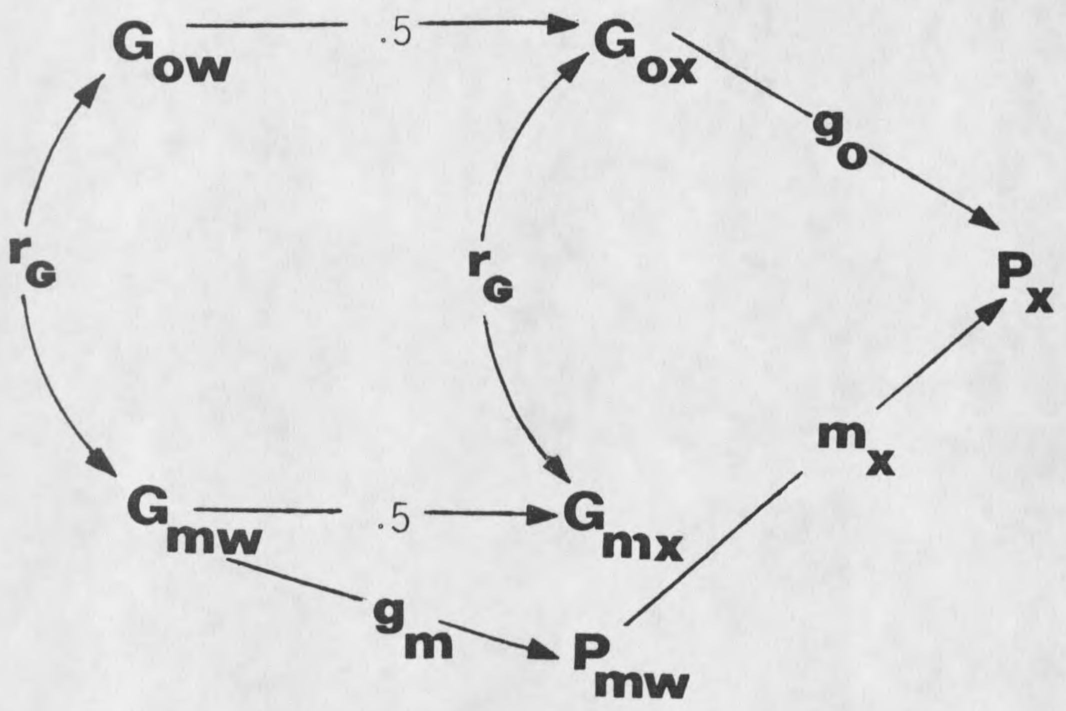


Figure 1. Path coefficient diagram of Dickerson's(1947) model.

In terms of the path coefficients of Figure 1, the heritability or regression of transmitted ability (Gox + Gmx) on individual performance (X) is

$$b(Go + Gmx)\ Px = go^2 + 3/2\ gogm\ r_{gogm} + 1/2\ gm^2 \qquad (4)$$

This expression is the numerator for what is called heritability for total effects where "total" stands for additive genetic direct plus additive genetic maternal effects.

The main contributions of Kempthorne (1955) to the theory of maternal effects was the inclusion of dominance in the model and the description of the basis for the coefficients of the direct and maternal covariances into the expectation of the covariance between relatives. His theory assumes that the genotypic value of an individual is additively determined by the joint effects of the genes possessed by the individual and its mother. The genetic variance of his model is

$$\sigma^2 G = \sigma^2 Ao + \sigma^2 Am + \sigma AoAm + \sigma^2 Do + \sigma^2 Dm + \sigma DoDm \qquad (5)$$

where $\sigma^2 Do$ and $\sigma^2 Dm$ are the variances due to dominance direct and dominance maternal deviations, respectively, and $\sigma DoDm$ is the covariance between the dominance effects.

Kempthorne (1955) did not consider the common or maternal source of environmental variation (i.e., $\sigma^2 Em$). The other expressions derived are the covariances between offspring and sire (cov(O,S)), offspring and dam (cov(O,D)) and among full-sibs (cov(FS)) as

$cov\ (0,S) = pq\ \sigma^2 Ao + 1/2\ pq\ \sigma AoAm,$

$cov\ (0,D) = pq\ \sigma^2 Ao + pq\ \sigma^2 Am + 5/4\ \sigma^2 AoAm + \sigma DoDm,$ and

$\mathrm{cov\ (FS)} = 1/2\ \sigma^2 Ao + \sigma^2 Am + 2\, pq\ \sigma AoAm + 1/4\ \sigma^2 Do + \sigma^2 Dm.$

p and q are the gene frequencies for genes A and a, respectively.

The most commonly used model for estimating maternal effects of birth weight and weaning weight in cattle was derived by Willham (1963). Basically, he generalized the work of Kempthorne (1955) adding epistasis to the model. However, this interlocus gene expression has always been assumed to be zero or negligible for both birth weight and weaning weight. Perhaps the most useful result of Willham's paper was the derivation of the coefficients for the additive and dominance covariances in the expected values of various kinds of relatives.

The coefficients that Kempthorne (1955) had expressed as functions of Wright's coefficient of relationship with no inbreeding or Malecot's "coefficient de parente" received concrete numerical values with the work of Willham.

Willham (1963) showed that the genotypic covariance between the phenotypes of individuals X and Y, with respective mothers W and Z, is equal to

$$\mathrm{cov}(Gx,\ Gy) = \mathrm{cov}(Gox,Goy) + \mathrm{cov}(Gox,Gmz) + \mathrm{cov}(Gmw,Goy) + \mathrm{cov}(Gmw,Gmz) \qquad (6)$$

where Gox and Goy are the genotypic values of X and Y for direct effects, and Gmw and Gmz are the genotypic values of the dams W and Z for maternal effects. Thus, the problem was reduced to calculating the four covariances in (6).

The first covariance between X and Y for component o was given by Kempthorne (1957) as

$$2pxy \ \sigma^2 Ao + u_{xy} \ \sigma^2 Do + \sum_{r,s} (2p_{xy})^r (u_{xy})^s \ \sigma^2(A^r D^s)_o$$

for $2 \leq r+s \leq N$

where

$\sigma^2(A^r D^s)_o$ is the epistatic component of genotypic variance for the direct component o. For this term, r and s refer to the number of loci involved in the interaction and N refers to the number of loci segregating for component o. The term p_{xy} is Wright's coefficient of relationship with no inbreeding or twice Malecot's "coeffiecient de parente". The coefficient u_{xy} is the probability that the two genes at a locus in individual x are identical by descent with the two genes at that locus in individual y. The value of u_{xy} is zero unless the two individuals are related by two lines of descent such as full sibs or double first cousins.

The second and third terms in (6) are the genotypic covariances between the individuals and their mothers for components o expressed in x or y and component m expressed in y or x, respectively. Since Mode and Robinson (1959) showed that the genotypic covariance between characters, or in this case components of a character can be partitioned in an analoguos manner to the genotypic variance, those terms are

$$2 \ p_{xz} \ \sigma AoAm + u_{xz} \ \sigma DoDm + \sum_{r,s} (2p_{xz})^r (u_{xz})^s \ \sigma(A^r D^s)_o \ (A^r D^s)_m$$

$2 \leq r+s \leq M$

and

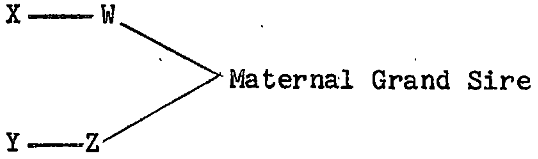
$$2\ p_{yw}\ \sigma AoAm + u_{yw}\ \sigma\ DoDm + \sum_{\substack{r,s \\ 2\le r+s\le M}} (2p_{yw})^r\ (u_{yw})^s\ \sigma\,(A^rD^s)_o\ (A^rD^s)_m$$

$\sigma(A^rD^s)_o\ (A^rD^s)_m$ is the epistatic covariance between o and m. M is the number of loci segregating that affect both o and m.

A general expression for the cov(Gx,Gy) assuming that epistasis is equal to zero is:

$$\mathrm{cov}(Gx,Gy) = 2\ p_{xy}\ \sigma^2 Ao + (2\ p_{xz} + 2\ p_{yw})\ \sigma AoAm + 2\ p_{wz}\ \sigma^2 Am + u_{xy}\ \sigma^2 Do + (u_{xz} + u_{yw})\ \sigma DoDm + u_{wz}\ \sigma^2 Dm \quad (7)$$

Table 1 shows the coefficients 2p and u for several relatives and is based on the relationships considered by Willham (1963) and Van Vleck and Hart (1966) for the genetic components of (7) with the more general expressions for the environmental components of variation as shown in Thompson (1976). Then, when x and y have the same maternal grand sire we have



$2\ p_{xy} = (1/2)^4 = 1/16$; $2\ p_{xz} = 1/8$; $2\ p_{yw} = 1/8$; $2\ p_{zw} = (1/2)^2 = 1/4$

Since x and y are not related by two lines of descent all u's are zero. Therefore, the expected value of σ^2_{MGS} is

$$E(\sigma^2_{MGS}) = 2\ p_{xy}\ \sigma^2 Ao + (2\ p_{xz} + 2\ p_{yw})\ \sigma\ AoAm + 2\ p_{wz}\ \sigma^2 Am$$

$$E(\sigma^2_{MGS}) = 1/16\ \sigma^2 Ao + 1/4\ \sigma AoAM + 1/4\ \sigma^2 Am$$

Any kind of relative relationship can be evaluated in the same way.

Covariances in Table 1 were divided into three groups. In the first group sire-type relationships are considered; hence, the

TABLE 1. COEFFICIENTS FOR THE DIRECT AND MATERNAL VARIANCES AND COVARIANCES IN THE EXPECTED VALUES OF THE COVARIANCES BETWEEN RELATIVES

Relatives	$\sigma^2 A_o$	$\sigma A_o A_m$	$\sigma^2 A_m$	$\sigma^2 D_o$	$\sigma D_o D_m$	$\sigma^2 D_m$	$\sigma^2 E_o$	$\sigma E_o E_m$	$\sigma^2 E_m$
Sire-type group									
Paternal Half-Sibs (PHS)	1/4	0	0	0	0	0	0	0	0
Paternal Grand Sire-Sibs (PGS)	1/16	0	0	0	0	0	0	0	0
Maternal Grand Sire-Sibs (MGS)	1/16	1/4	1/4	0	0	0	0	0	0
Maternal Great Grand Sire-Sibs (MGGS)	1/64	1/16	1/16	0	0	0	0	0	0
Maternal Grand Dam-Sibs (MGD)	1/16	1/4	1/4	0	0	0	0	0	0
Covariance group									
Offspring and Sire (COV(O,S))	1/2	1/4	0	0	0	0	0	0	0
Offspring and Dam (COV(O,D))	1/2	5/4	1/2	0	1	0	0	1	0
Offspring and Maternal Grand Dam (COV(O,MGD))	1/4	5/8	1/4	0	0	0	0	0	0
Maternal Grand Sire Progeny and Grand Offspring COV(S,MGS)	1/8	1/4	0	0	0	0	0	0	0
Maternal Full-Sib Aunt and Offspring (COV(MA,N))	1/4	3/4	1/2	0	1/4	0	0	0	0
Paternal Full-Sib Aunt and Offspring (COV(PA,N))	1/4	3/4	1/2	0	1/4	0	0	0	0
Relative relationships involving dominance									
Full-Sibs (FS)	1/2	1	1	1/4	0	1	0	0	1
Maternal Half-Sibs (MHS)	1/4	1	1	0	0	1	0	0	1
Single First Cousins (SFC)	1/8	1/2	1/2	0	0	1/4	0	0	0
PHS plus Dams MHS (PHS + MHSD)	5/16	1/4	1/4	1/16	0	0	0	0	0
PHS + SFC	3/8	1/2	1/2	1/8	0	1/4	0	0	0
FS plus PHS parents (FS + PHS)	5/8	5/4	1	25/64	0	1	0	0	1
PHS + PHS Dams (PHS + PHSD)	5/16	1/4	1/4	1/64	0	0	0	0	1

expectations only involves additive effects. The second group contains covariances between the offspring generation and a closely related individual of the parental generation. The last group is composed by the terms involving dominance. The error terms for models in which there is only one family component have not been extensively used. An unclear interpretation of the components involved in the expectation for those error terms is the possible reason.

So far it has been assumed there is no effect of the dam environment on the future maternal ability of the female offspring. This is likely to occur for weaning weight in beef cattle, as Koch (1972) pointed out. If this is true, maternal environment will be affected by grand maternal environment and the latter by maternal great grand dam environment and so on. In this sense, the maternal effect is viewed as partially affected by maternal environment from previous generations.

The first attempt to incorporate these effects into the model was made by Falconer (1965). The variance of his model is:

$$\sigma^2 P = \sigma^2 A + \sigma^2 M + 2\ \sigma AM + \sigma^2 D + \sigma^2 Em + \sigma^2 Eo \qquad (8)$$

where $\sigma^2 A$ is the variance of additive effects, $\sigma^2 M$ is the variance due to the maternal effects to which the individual is subject, $\sigma\ AM$ is the covariance between additive and maternal effects; $\sigma^2 D$ is the variance due to dominance deviations (Falconer included here also the epistatic deviations involving dominance), $\sigma^2 Em$ is the variance due to maternal or common environment, as before, and $\sigma^2 Eo$ is the variance due to random environment. The maternal effects (M) are defined as a linear function, fm, of the mother's phenotypic maternal value, P', measured as a deviation from the population mean, so that

$$M = fm\ P' \qquad (9)$$

Falconer (1965) admitted that the way M is defined is rather restricted because it excludes all maternal influences that are not correlated with the mother's phenotypic maternal value. But he also points out that if these other influences are present they will be included with the rest of the common or maternal environment (σ^2Em). The coefficient fm is defined to be "a partial regression coefficient relating daughters to mothers' phenotypic values in the absence of genetic variation among the mothers". Whether the relationship is really linear is, of course, open to question. Obviously, a linear relationship is easier to evaluate. It should also be noted that the D, Em and Eo terms in the model are uncorrelated with P'. Hence,all other covariances in (8) are zero but σAM. An interpretation of model (8) in terms of path coefficients is shown in Figure 2.

The prime in the graph indicates the previous generation. The arrow pointing at M' from the left indicates the carrying over of maternal effects from previous generations. Falconer (1965) derived the cov(O,D) in terms of fm as

$$\mathrm{cov}(O,D) = \sigma^2A\ (1/(2 - fm)) + fm\ \sigma^2Pm'$$

It is worth noting the derivation of σAM.

By definition $M = fm\ Pm' = fm\ (A' + M' + D' + Em' + Eo')$. Since D', Em' and Eo' are not correlated with A, they can be omitted while deriving σAM. Therefore, the relevant part of M can be written as

$$M = fm\ (A' + fm\ P'')$$

$$= fm\ (A' + fm\ (A'' + fm\ P'''))$$

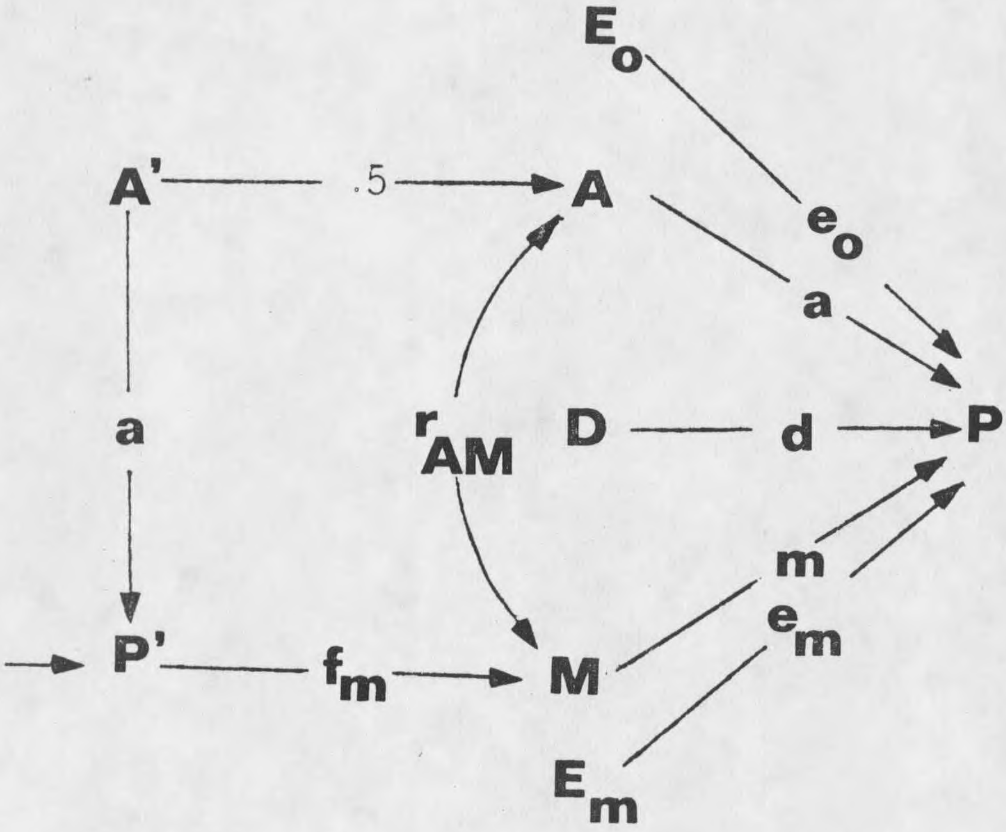


Figure 2. A path coefficient diagram describing Falconer's (1965) maternal effects model. P is the phenotype of the individual; A, his additive genotype; D, his dominance deviation; Em are the environmental factors common to full-sibs and maternal half-sibs that are not included in the maternal effect; M is the maternal effect; Eo are other environmental factors particular to the individual and r_{AM} is the correlation between additive genetic and maternal effects. Path coefficients (e_o, a, d, m, e_m, .5 and fm) are standard partial regression coefficients.

$$= fm\ (A' + fm\ (A'' + fm\ (A''' + \ldots\text{etc})$$

Therefore

$$\sigma AM = fm\ \ \sigma AA' + fm^2\ \ \sigma AA'' + fm^3\ \ \sigma AA''' + \ldots$$

$$\sigma AM = \ \sigma^2 A\ (1/2\ fm + 1/4\ fm^2 + 1/8\ fm^3 + \ldots$$

The expression in brackets is the geometric series with common ratio 1/2 fm. If $|fm| < 1$ the series converges with sum

$$\frac{(1/2)\ fm}{1 - fm/2} = \frac{fm}{2 - fm}$$

Hence

$$\sigma AM = \sigma^2 A \ \frac{fm}{2 - fm}$$

Thompson (1976) has derived the coefficients for fm in the expected values of some relative relationships.

Willham (1972) considered a model in which the effect of the maternal grand dam is present. The genotypic covariance between any two relatives is evaluated as in (6), but with nine covariances instead of four. An additive genetic term for the variation due to grand maternal effects (i.e. $\sigma^2 An$) is also defined. For genetic effects only the variance of this model is

$$\sigma^2 A = \ \sigma^2 Ao + \ \sigma AoAm + \ \sigma AoAn + \ \sigma^2 Am + \ \sigma AmAn + \sigma^2 An \qquad (9)$$

where $\sigma AoAn$ and $\sigma AmAn$ are the covariances between direct and grand maternal additive effects and maternal and grand maternal additive effects, respectively.

From a theoretical point of view, it is not clear whether to prefer the maternal-grand maternal additive model to the maternal additive model. Using the same reasoning, it is possible to include great grand maternal effects into the model and so on.

Additive genetic effects are carried by the dam side through several generations. However, the same theory of the covariance between relatives (Kempthorne, 1955) shows a high level of reliability in the evaluation of the additive genotype or breeding value by considering only one generation previous to the one considered. As a result of these ideas, Koch (1972) defined the most biologically meaningful model to evaluate maternal effects in beef cattle birth weight and weaning weight. The model combined Willham's (1963) additive and dominant components with Falconer's (1965) concept of transmitted maternal phenotype effects. The covariance between random environmental and maternal or common environmental effects (σ EoEm) was also added. The variance of Koch's (1972) model can be expressed as

$$\sigma^2 p = \sigma^2 Ao + \sigma AoAm + \sigma^2 Am + \sigma^2 Do + \sigma DoDm + \sigma^2 Dm + \\ + \sigma^2 Eo + \sigma EoEm + \sigma^2 Em \qquad (10)$$

The original expression in the paper does not differentiate between σ^2Do and σ^2Eo. It also does not split σ^2Dm and σ^2Em. These four variances appear in two terms: σ^2Do + σ^2Eo and σ^2Dm + σ^2Em. The classical genetic theory assumes no covariance between dominance and environmental deviations of any kind (Falconer, 1981). Koch (1972) justified his procedure by saying that the relationships usually available in beef cattle data do not provide critical contrasts for separating dominance and environmental deviations.

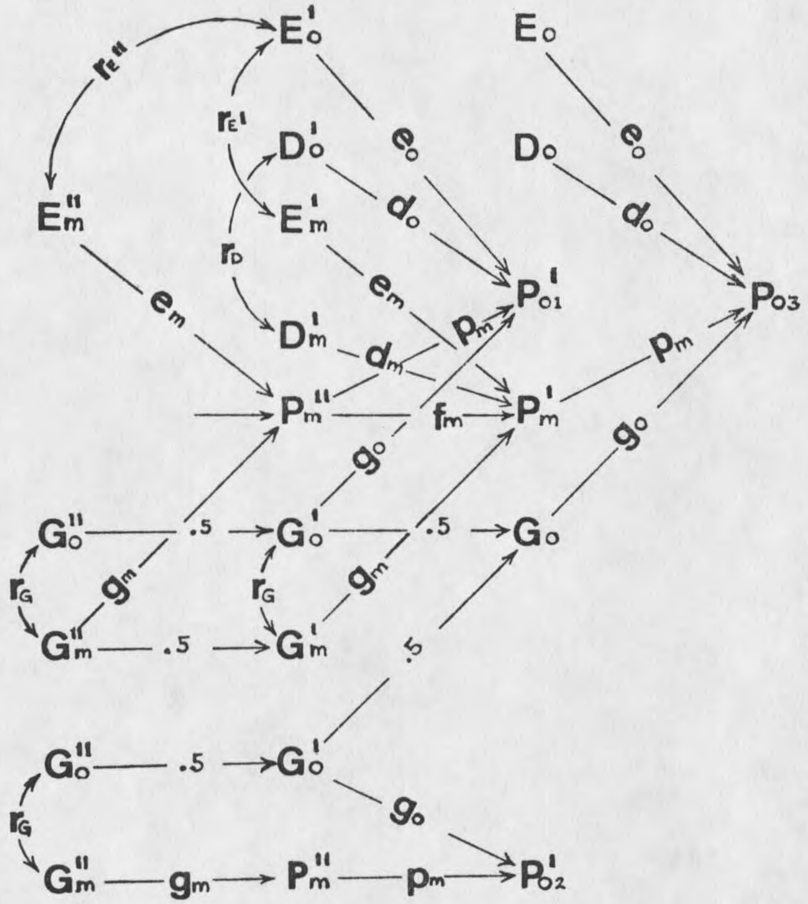


Figure 3. A path coefficient diagram describing Koch's (1972) model. Po is the phenotypic, Go is the additive genetic, Do is the dominance and Eo is the environmental value for birth weight or weaning weight expressed by individuals. Pm, Gm, Dm and Em are corresponding maternal effects. Primes on values represent parental values and double primes represent grandparent values. Path coefficients between symbols (.5, g, d, e, p, fm) are standard partial regression coefficients. Double arrows represent residual correlations between traits.

Figure 3 is the path diagram which summarizes the concepts of Koch (1972). In this diagram P_{o3}, P'_{o2} and P'_{o1} represent the phenotype for birth weight or weaning weight of the offspring, sire and dam, respectively. If all the possible paths exist, then

$$\mathrm{cov}(O,D) = 1/2\ \sigma^2 Ao + 5/4\ \sigma AoAm + 1/2\ \sigma^2 Am + \sigma DoDm + f^2 m + \\ + (1+fm)\ \sigma EoEm + fm/(2-fm)\ (1/2\ \sigma^2 Am + 5/4\ \sigma AoAm) \qquad (11)$$

Note that if $fm = 0$, this expression reduces to

$$\mathrm{cov}(O,D) = 1/2\ \sigma^2 Ao + 5/4\ \sigma AoAm + 1/2\ \sigma^2 Am + \sigma DoDm + \sigma EoEm \qquad (12)$$

as shown in Thompson (1976). The formulas (11) or (12) show that if genetic or environmental covariance terms are negative, the cov(O,D) can be lower than anticipated from direct genetic or maternal genetic effects (Koch,1972). This explains part of the disagreement between the estimates of h^2 by paternal half-sib analysis as compared to regression of offspring on dam ($h^2 b_{OD} = 2\ \mathrm{cov}(O,D)/\sigma^2 P$, Falconer, 1981).

The models for estimating direct and maternal variation of birth weight and weaning weight in beef cattle have been considered in order of complexity. Some difficulties arise in the application of the more complex models to beef cattle. That is the subject of the next section.

Problems in estimating direct and maternal genetic covariances

There are some problems in estimating maternal variation in any animal species. Also, there are specific problems in estimating maternal and direct covariances in beef cattle. The order in which the problems are presented implies no order of importance.

1. Standard error of the estimates and non independence of the coefficients in the expected values

This is a general problem. The large standard error of the estimates of maternal covariances is due to the generally small number of relatives involved (specially in beef cattle) and the multipliers used (i.e., 1/2, 1/4, 1/8, 1/16) (Koch, 1972; Willham,1980). As Koch (1972) points out, errors of estimates in one component tend to cause other components to differ in the opposite direction since the sum of components is forced to equal the whole.

In general, it is expected that increasing the number of relative relationships involved would decrease the standard errors of estimation.

Designed experiments that yield specific useful covariances that are uncorrelated have been suggested by Willham (1963) and Eisen (1967). Bondari et al (1978) used two designs suggested by Willham (1963) in *Tribolium castaneum* to investigate genetic maternal influences on pupa weight and family size. The designs were based on creating a system of matings between families of full-sibs and paternal half-sibs. Matings between different full-sib families are also involved. At least three generations are required in all the designs. The generation interval in *Tribolium* is 30 days (Bondari et al, 1978); while in beef cattle the generation interval is 4.3 years (Koch et al, 1982). The problem is aggravated by the fact that the fecundity rate in cattle is low and repeated matings to produce full-sib families should take place in different years. The result increases the generation interval. Therefore, the designs are better suited for laboratory animals than for beef cattle.

In case there are more covariances between relatives than direct and maternal covariances to evaluate, a method to solve simultaneously for the parameters should necessarily be used. Van Vleck and Hart (1966) have used least-squares, weighting the equations by the numbers of observations used in the estimate of the relative relationship. For the designs discussed in the previous paragraph, Eisen (1967) has suggested the use of the diagonal elements of $(X'X)^{-1}$ to weight the equations. He has also indicated that the procedure is not fully efficient if the variances of the estimates of the covariances between relatives are not homogeneous. This is likely to occur when different methods are used to estimate the variance components, and when the number of records used for the estimate are entirely different, as usually happens with beef cattle. To overcome this problem, Thompson (1976) has developed a modified maximun likelihood procedure. After assuming that the observations are normally distributed, the log of independent matrices of sum of squares is maximized. It is necessary to solve the equations iteratively. The case where parents are subject to culling was also considered by Thompson (1976). However, the fact that independent sum of squares is required precludes the use of the procedure when the data are not collected under a designed experiment. Another problem is that the method can not avoid the effects of the correlations between the coefficients even though the design is good (Thompson, 1976).

2. Small number of relatives involved in the estimation in beef cattle field data

This problem has partially been explained in the preceding section. Hohenboken (1973) said that it is difficult to locate enough types of families to equal the number of unknowns of interest, and it is difficult to account statistically for all environmental causes of likeness between relatives. Koch (1972) used seven relative relationships and the error of maternal half-sibs model. There is no other paper using more relative relationships than Koch(1972). The direct consequence is that some terms must be dropped from the model to solve for the rest. If the term dropped is not zero, the solution is biased and the other components are either underestimated or overestimated. The magnitude of the error depends on the correlation among the terms for that particular set of relatives and the size of the term dropped.

3. Maternal effects evaluation lenghtens the time to conduct the study

As Willham (1980) points out maternal effects are:

1) at least a generation behind the direct effects in their expression,

2) sex limited, and

3) occur late in the life of the female.

All these factors lengthen the evaluation time. If the records are taken over a long period of time, there is the possibility of introducing environmental correlations (Eisen, 1967); year by sire interaction is also possible to occur which in turn tends to inflate the sire variance component (Koch, 1972).

Estimates of direct and maternal genetic variances and covariances for birth weight and weaning weight in beef cattle

The estimates reviewed in this section are the results of applying the Willham (1963) and Koch (1972) procedures. The first approach to the problem was made by Koch and Clark (1955b).

1. Birth weight

Table 2 summarizes the estimates of published reports on birth weight. Three estimates of dairy cattle are also included.

In general, there is a trend for h^2o to be greater than h^2m. The means suggest that additive direct influences are two times the amount of additive maternal influences.

The correlation between additive direct and additive maternal effects (r_G) was negative in almost all the estimates. The few estimates and the big range of the values produce uncertainty about the real magnitude of r_G. A possible biological explanation given by Fisher and Williams (1978) is that the two opposing additive effects tend to prevent excesses in birth weight thereby protecting the survival of both calf and cow at parturition.

This hypothesis is supported by the fact that the estimates of r_G for dystocia, a trait strongly dependent on birth weight (Burfening et al, 1978), were -.19 for Philipsson (1976), -.54 for Burfening et al (1981) and -.38 (heifers) and -.25 (cows) for Thompson et al (1981).

The fifth column in Table 2 was included since Koch (1972) and Baker (1980) postulated that, when cov(O,D) is excluded from the analysis, the values of $\sigma A_o A_m$ and r_G are close to zero. The simple

TABLE 2. ESTIMATES OF DIRECT AND MATERNAL ADDITIVE GENETIC VARIANCES AND COVARIANCES ON BIRTH WEIGHT OF CATTLE

Heritabilities			Genetic correlation between additive direct and additive maternal effects (r_G)	Inclusion of COV (O,D) in the solution	Number of records used	Breed	Authors
Direct effects (h^2_o)	Maternal effects (h^2_m)	Total effects (h^2_t)					
.35	-	.42	>0	No	4,553	Hereford	Koch and Clark (1955c)
.22	.04	.00	-.93	No[a]	1,064	Holstein	Everett and Magee (1965)
.65	.15	.27	-.98	No[b]			
.56	.30	.36	-.58	Yes	789	Hereford	Brown and Galvez (1969)
.14	.25	.17	-.39	Yes	932	Angus	
.72	.48	-	-.55 to -.89	Yes	1,962	Hereford	Vesely and Robinson (1971)
.44 to .40	.05 to .12	-	-.17 to .27	Yes	4,060	Hereford	Koch (1972)
.44	.04 to .19	-	-.07 to .30	No			
.19	.08	-	-.53	No	6,724	Swedish-Friesian	Philipsson (1976)
.51	.26	.44	-.36	Yes	1,534	Holstein	Fisher and Williams (1978)
.21	.11	-	-.24	No	11,552	Simmental	Burfening et al. (1981)
.40	.17	.27	-.36				Averages

[a] Relatives included: σ^2PHS, σ^2MGS, COV(S,MGS)
[b] Relatives included: σ^2PGS, σ^2MGS, COV(S,MGS)

mean of the estimates without cov(O,D) is equal to −.35. This value does not seem to support that hypothesis.

The only two reports in which dominance and environmental maternal effects were included were Brown and Galvez (1969) and Koch (1972). However, both papers assumed σDoDm and σEoEm to be zero. The dominance direct effects accounted for 9 and 17 % of ^{2}P in Angus and Hereford, respectively (Brown and Galvez, 1969). The estimate of σ^2Dm was negative which is possibly suggesting that a negative source of variation was left out from the model. Koch (1972) presented a term for σ^2Dm + σ^2Em that accounted for 10 % of σ^2P. This author concluded that the environmental maternal ability of dams did not have a significant direct effect on maternal ability in the next generation.

2. <u>Weaning weight</u>

Estimates of direct and maternal additive genetic sources of variation on preweaning growth are shown in Table 3.

Contrary to birth weight, average daily gain or weaning weight have more variation for additive maternal effects than for additive direct effects. The mean of the estimates of r_G is highly negative. Koch (1972) emphasized the fact that the estimates of r_G when the cov (O,D) was excluded from the solution were smaller and suggested an overestimation of σAoAm. However, the last two estimates in Table 3 indicate that this is not necessarily the case. It should be noted that it is very difficult to compare estimates coming from different genetic models. The only study in which r_G was evaluated by a solution which only contains additive effects is the one of Kress et

TABLE 3. ESTIMATES OF DIRECT AND MATERNAL ADDITIVE GENETIC VARIANCES AND COVARIANCE OF CALF GROWTH THROUGH WEANING

Heritabilities			Genetic correlation between additive direct and additive maternal effects (r_G)	Inclusion of COV (O,D) in the solution	Number of records used	Breed	Authors
Direct effects (h^2_o)	Maternal effects (h^2_m)	Total effects (h^2_t)					
Average daily gain from birth to weaning							
.21	-	.12	-.65	No	4,553	Hereford	Koch and Clark (1955c)
.18	.15	.25	.0	Yes	725	Brahman	Deese and Koger (1967)
.40	.46	.17	-.73	Yes	466	Brahman x Shorthorn	
.20	.28	.32	-.05	No	4,060	Hereford	Koch (1972)
.26	.11	.12	-.40	Yes			
.26	.24	.17	-.45				Averages
Weaning Weight							
.32	.29	.34	-.31	Yes	717[a]	Hereford	Hill (1965)
.31	.50	.34	-.46	Yes	[b]		
.37	-	.17	-.73 to -1.07	Yes	1,692	Hereford	Vesely and Robison (1971)
.23	.54	.08	-.79	Yes	2,618	Hereford	Hohenboken and Brinks (1971a)
.23	.34	.28	-.28	No			
.14	.64	-	-1.14	Yes			
.14	.34	.32	-.07	No	228	Charolais	Baker (1980)
.20	.53	.09	-.90	Yes	3,765	Brahman	Beltran Bru (1978)
.20	.47	.02	-.75	No			
.12	.05	-	-.68	No	13,682	Simmental Crosses	Kress et al. (1979)
.22	.41	.20	-.65				Averages

[a] Relatives included: ^{2}PHS, ^{2}MGS, COV(S,MGS)
[b] Relatives included: ^{2}PGS, ^{2}MGS, COV(S,MGS)

al (1979). In the remaining ones, the solutions were obtained assuming that some of the direct and maternal covariances were zero. As discussed before, errors in the estimate of one covariance cause the other components to differ in the opposite direction, since the sum is forced to equal the total. When cov(O,D) was included in the solution, σDoDm and σEoEm were always assumed to be zero. If these terms are not null, then the inclusion of the cov(O,D) in the solution tends to overestimate the value of σAoAm and as a consequence, also of r_G.

The importance of determining the exact magnitude of σAoAm comes from the fact that response to selection for preweaning growth relies mostly on its value as shown by Van Vleck et al (1977). It is reasonable to suppose that σAoAm is negative since all its estimates have this sign (Table 3). This means that most of the progress made in one generation due to selection for growth rate is overcome by maternal effects in the next generation. After reviewing the literature of selection experiments in beef cattle, Koch et al (1982) concluded that the realized h^2 (the portion of the total or phenotypic change due to genetic progress) was .45 for birth weight, .24 for weaning weight, .35 for postweaning gain; .41 for final weight at the performance test and .33 for gain efficiency. Thus, selection would be less successful for weaning weight than for other growth and efficiency traits.

Important evidence for the presence of maternal effects on weaning weight are given by the comparison of maternal and paternal genetic parameters. Koch et al (1982) indicated that maternal half-sib correlations are larger than paternal half-sib correlations (.34 vs. .07). Hohenboken and Brinks (1971a) reported a disagreement between the cov(O,S) (48.7 kg^2) and the cov (O,D) (18.7 kg^2).

The averages of sire and dam contributions to genetic trends in weaning weightof commercial herds were 1.74 and .27 kg (Kennedy and Henderson, 1977) and 1.30 and .86 (Zollinger and Nielsen, 1984). If these estimates measured only transmitted or direct effects in a large closed herd over several years with consistent selection practices from year to year, sire and dam contributions would be expected to be equal. Therefore, if σAoAm (or σEoEm) is negative, the lower dam trend would be expected as compared to the trend estimate for sires (Zollinger and Nielsen, 1984). Hohenboken and Brinks (1971b) found negative genetic correlations between the maternal ability of beef heifers and growth traits of paternal half-sib brother steers. The reviewed values for the correlation between milk yield of dairy heifers with beef traits of paternal half-sibs brother is close to zero (White et al, 1981). Hill (1965) has found that r_G for weaning weights were -.16, -.31 and -.45, at 150, 180 and 210 d of age, respectively, which suggests that an important part of the negative association between direct and maternal effects is environmental and gives a partial explanation for such a small correlation in dairy cattle.

The above paragraph has introduced one of the most important problems in the association of direct and maternal effects for weaning weight. The problem is to determine how much of this negative correlation is genetic and how much is environmental.

Maternal ability of a beef cow is usually measured using her "most probable producing ability" (MPPA) (Lush, 1945). There is evidence that environmental sources of variation affect the relationship between early growth of a beef female and her subsequent maternal ability. For example, the phenotypic correlation between birth year means of the cow and MPPA was found to be -.52, -.20 and -.11 and the correlation between age of dam effects and MPPA for the two traits was -.70, -.68 and -.19, as reported by Ellicot et al (1970), Mangus and Brinks (1971) and Kress and Burfening (1972). These latter authors also reported a positive trend (b = .06 ± .03) for weaning weight on birth date and a negative trend (b = -.10 ± .02) for MPPA on birth date. Hence, the data indicated that at least part of the negative association between growth rate and subsequent maternal ability (or between direct and maternal effects) was caused by environmental sources of variation.

The basic calf food during the preweaning period is the milk produced by his mother. Cantet (1983) calculated an average correlation between cow milk production and calf weaning gain or weight of .58 from 26 studies. Therefore, a high average daily gain of the heifer calf is positively associated with her mother's milk production and negatively associated to her future maternal ability. Hence, the expected relationship between weaning weight of a cow and her subsequent milk production would be negative. Christian et al (1965) found negative correlations between dam weaning weight and milk and butter fat production. Totušek (1968) found that cows raised on low planes of nutrition previous to 240 d of age, weaned calves that weighed 8 and 10 kg more than calves weaned by cows raised on the medium and high planes of nutrition, respectively. Johnsson and Obst (1984) found that the rate of growth before weaning had more influence on subsequent maternal ability in the first three lactations than either growth between 8 to 14 mo of age or premating liveweight of Hereford heifers.

A major part of the development of the mammary gland takes place between birth and first calving (Sejrsen, 1978). Many studies reviewed by Koch (1972), Kress and Burfening (1972) and Sejrsen (1978) show that high levels of energy in the rearing period resulted in a decrease of subsequent milk yield of dairy heifers. The mechanism of this phenomenon is related to a decrease in growth hormone concentration in the blood and an increase in the amounts of fat in the udder, either at the same physiological or at the same chronological age, as the level of energy in the diet increases during the rearing period (Sejrsen, 1978). Martin et al (1981) and Ochoa et al (1981) reported that creep-feeding heifer calves resulted in a decreased lifetime productivity and MPPA for weaning weigth which is consistent with the earlier findings of inferior udder development.

From the studies reviewed above it is clear that the cows that had higher weaning weigths tended to produce calves with lower weaning weights. This result was partially due to a negative environmental association, i.e., negative value of $\sigma EoEm$. Koch (1972) speculates that the effects of maternal environment for preweaning growth of previous generations (the fm path in Figure 1) should have a value of -0.1 to -0.2 for the environmental covariance to satisfy observed correlations and regressions. Since the environmental covariance is also a function of σ^2Am and $\sigma AoAm$, as Koch (1972) showed, the only way to determine the relative contribution of $\sigma AoAm$ and $\sigma EoEm$ to the phenotypic variance of weaning weight is to solve simultaneously for all the covariances. This procedure has not been done yet.

Regarding dominance effects on weaning weight, Deese and Koger (1967) found a value of zero for σ^2Do while in Hohenboken and Brinks (1971a) study σ^2Do was 52.4 kg^2, corresponding to 10.3 % of the total variation. Their estimate of $\sigma DoDm$ (-76.7 kg^2, -17.8 % of the variance) is the only one found in the literature. However, since the authors assumed σ^2Dm to be zero in order to solve the equations, the estimate is possibly not very reliable since by the Cauchy-Schwarz inequality:

$$\sigma^2Do \,.\, \sigma^2Dm \geq \sigma DoDm.$$

MATERIAL AND METHODS

The data for this study were collected at the Northern Agricultural Research Center (NARC) located 13 km SW of Havre, Montana. The geographic coordinates of the station are: latitude 48° 30'N, longitude 109° 48'W.

The approximate altitude is 819 m above sea level. The area can be described as typical of the northern glaciated plains and is bordered on the south by the Bear Paw mountains. The Bear Paw mountains were the site of the Rocky Boy Indian Reservation lease located 48 km south of Havre and this lease was used as the summer grazing site from the lates 40's to the early 70's.

Weather

Weather statistics at NARC were taken by its own climatic station for the period 1951-1980 (USDC, 1982). Annual mean temperature was 6°C. Average temperature for the coldest month (January) and the hottest month (July) were -10.9°C and 20.7°C, respectively. The extreme temperatures registered were -49.4°C (January 1953) and 42.2°C (June 1900). Mean temperatures were approximately 4°C less at the Rocky Boy substation during the same period.

Annual mean precipitation was 297 mm at NARC and 438 mm at Rocky Boy. Most of the precipitation (80%) (Anderson, 1966) occurred between April and September. Anderson (1966) comments that the snow fall at the main station is light with a maximum height of the snow cover of 15 cm during most of the years. This is also related to the warming effects of the Chinook winds which tend to reduce the snow cover.

A large amount of evaporation in relationship to the precipitation occurs at NARC during the summer. The lower evaporation rate and greater precipitation at Rocky Boy produced better range conditions during the summer.

Soils

The NARC soils were classified as mixed aridic Argiborolls of the series Attewan, Telstad and Joplin (USDA-SCS,1982). Series Telstad and Joplin have fine-loamy texture. Whereas the Attewan texture is fine-loamy over sandy or sandy-skeletal.

Range Conditions

The pastures at NARC can be described as mixed praire grasslands. The species are native and introduced grasses like crested wheat (*Agropyron desertorum*), needle and thread (*Stipa comata*) and blue gramma (*Bouteloa gracilis*).

Anderson (1966) decribed the summer grazing species at Rocky Boy as basically grasses such as Timothy (*Phleum pratense*), June grass (*Koeleria cristata*), Idaho fescue (*Festuca idahoensis*), Rough fescue (*Festuca scabrella*) and Mountain brome (*Bromus spp.*).

Experimental Animals

Birth and weaning weights were taken on 4,423 calves from 1938 to 1983. Information on the same weights of the cows was also available since 1928. There were three different phases of data collection and breeding systems. The first one consists of the animals raised before 1946. These cattle were originated at Havre and were the stock graded to the oldest line developed at the Fort Keogh, Livestock and Range Research Station, Miles City, Montana in the second phase. This line was better known as line 4. The second phase is characterized by the creation and development of inbred lines and crosslines of Hereford cattle. The process was initiated in 1946 and was maintained through 1966. Inbred line 1 was initiated in 1946, line 2 in 1947 and line 3 in 1948. Line 4 acted as a control line. Crosslines calves were produced by mating cows from line 4 with bulls of lines 1, 2 and 3 to create lines 5, 6 and 7, respectively. The final phase started in 1975 and is continuing. The foundation of these line 4 cattle is from inbred stock purchased from Fort Keogh, Livestock and Range Station, Miles City in 1962 and 1963. These purebred cattle are selected by the index: I=365 d. adjusted weight-3.2 adjusted birth weight.

Further description of managemental and selection procedures has been given by Flower et al (1963) and Anderson (1966).

Management of the breeding herd

Heifers were bred to calve first as 3-year-olds in the earlier years of the project. After 1951, heifers were bred to calve as 2-year-olds. The breeding season lasted approximately 60 d beginning the first week of June. Natural service was used in single sire pastures at the summer grazing lease.

Heifers and cows were fed during the winter at NARC starting in December during most of the years. When native range pastures became an insufficient source of food supply, a ration consisting of almost equal parts of cereal straws and legume-grass hay ad-libitum was fed to the cows. In the later years, corn silage replaced the legume-grass hay. Corn silage was decreased prior to calving with hay being increased.

First calving heifers were wintered separately from the older cows and fed a different ration of grain and alfalfa hay. Since 1970, grain has not been fed and the roughage source was corn silage and alfalfa hay.

Nutrition after calving consisted of crested wheat grass pastures for all the females from the middle of April through May supplemented by decreased amounts of corn silage replaced by second cutting alfalfa hay. Then, the cows were trucked to the Rocky Boy substation to be alotted into their respective breeding herds in early June. After the breeding season, cows were combined into one herd which grazed the mountain pasture until approximately November. At that time, the herd was trailed back to NARC in order to pass the winter period. Since 1975, the purebred herd has been maintained at NARC during the summer primarily on irrigated pastures.

Selection and Breeding Procedures

The project initiated in 1946 was designed to measure general and specific combining ability of lines 1, 2 and 3. In order to fullfill this goal, a system of sequential selection on the male side was put into practice. Female selection accounted for a variable but smaller portion of the selection differentials of birth weight and weaning weight (Flower et al, 1964). A first culling of male calves took place at weaning time. Slow preweaning growth, conformation defects, or color pattern were the reasons for castrating approximately 17% of the bull calves. The remaining bull calves were put on a 168 d performance test with individual feeding. Therefore, mass selection was applied on the basis of growth rate through a year of age.

The recurrent phase of the selection scheme was produced by mating two high-gaining yearling bulls from each of the three purebred lines to cows of the grade tester line 4, using herds of 15 females per sire. This procedure was not always possible to achieve. At the conclusion of the progeny tests, the straightline bulls which performed best with respect to their crossline progeny weights and gains were selected to sire straightline calves unless current herd bulls had attained superior crossline progeny tests. Proven bulls were able to sire straightline calves as 3-year-olds. Selection pressure achieved by recurrent selection of bulls was negligible (Flower et al, 1964).

Approximately one-third of the tester line cows were bred to bulls of their own line to provide replacement heifers.

Some heifer culling was exerted at 18 mo based on weaning weight, 140-d gain test and 18-mo weight.

The ration for the bull feed test consisted of rolled barley, (35%), dried molasses beet pulp (35%), rolled oats (20%) and wheat bran (10%). Alfalfa hay ad-libitum was provided as a roughage source.

The heifers were group-fed in outside lots with good protection from the weather during 140 d. The ration was made of second cutting alfalfa hay plus .90 kg daily of rolled barley in latter years.

Kress and Burfening (1972) reported means and standard deviations of inbreeding percentage of cows of 12.6 ± 7.4%, 10.7 ± 6.5% and 11.4 ± 7.0% for lines 1, 2 and 3, respectively. A sample of years 1939, 1949 and 1959 had a value of 1.2 ± 2.6 for line 4 cows. Few cows had inbreeding percentages greater than 24 to 28 %.

Statistical procedures

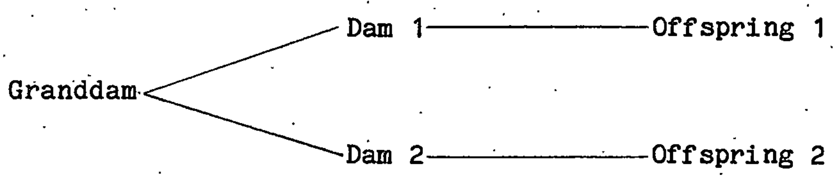
The original data set contained 5,173 observations. Editing procedures were based on deleting incomplete records (i.e., lack of one of the weights, unknown sire identification). There were 75 calves with either birth weight or weaning weight missing and 660 calves with an unknown sire, almost all coming from the earlier years. Abnormal values (i.e., weights below or above four standard deviations from the mean) were also deleted, though their number was comparatively small (15 calves) none of which were selecte as sires. The final data file for paternal half-sib analysis consisted on 4,423 observations.

The total number of sires that produced progeny was 202. All the sires raised at NARC (105) had records available on their own birth weight and weaning weight. The remaining bulls were raised at Miles City and, therefore, they were raised under different environmental conditions.

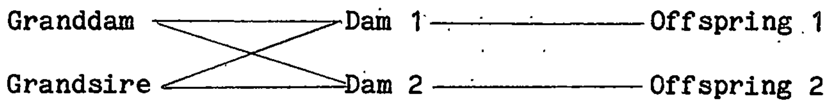
The great number of years of data allowed for a considerable number of repeated matings. Hence, families of at least two dams per sire and two or more calves per dam were selected and this resulted in 976 full-sib calves from 402 full-sib families.

Willham (1963) has suggested that the best set of relatives to use to estimate the importance of genetic maternal effects are sets of maternal cousins since their use reduces the environmental contribution to the maternal variance. Hence, the cousin patterns proposed by Van Vleck and Hart (1966) were evaluated. Also the covariance of full-sibs whose parents are paternal half-sibs and paternal half-sibs whose dams are paternal half-sibs were considered.

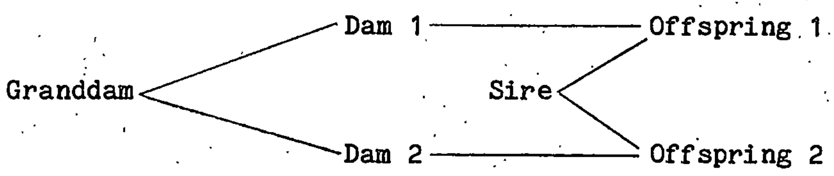
Maternal granddam-sibs (MGD)



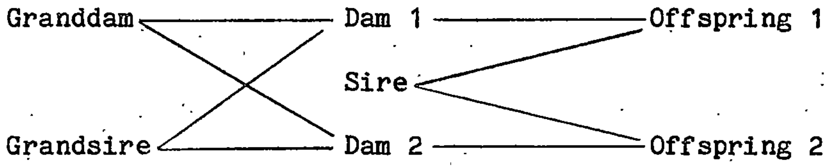
Single first cousins (SFC)



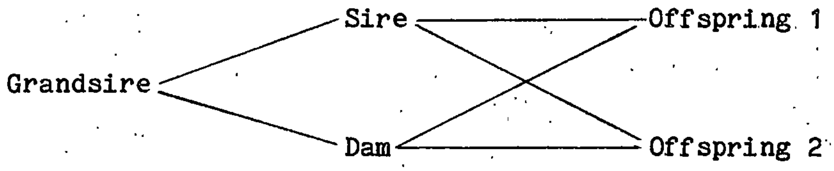
Paternal half-sibs plus maternal half-sib dams (PHS + MHSD)



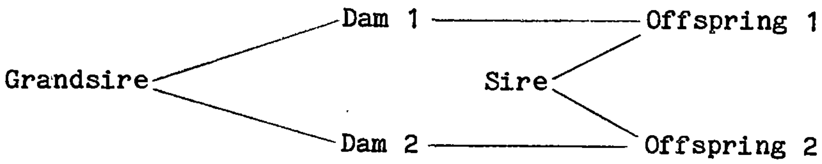
Paternal half-sibs plus single first cousins (PHS + SFC)



Full-sibs plus paternal half-sib parents (FS + PHSP)



Paternal half-sibs plus paternal half-sib dams (PHS + PHSD)



As expected, the closer the relative relationship is, the smaller the number of degrees of freedom for the analysis becomes. The reason for using these estimates was to increase the number of equations for estimating the nine direct and maternal variances and covariances and to provide more equations to estimate the dominance variances and the covariance between dominance direct and dominance maternal effects. Error terms were included since the number of degrees of freedom usually involved is high, which increases the accuracy of estimation. Expectations for the environmental components were obtained under the assumption that errors in the models including individuals related through sire-type relationships involved ^{2}Eo, $EoEm$ and ^{2}Em since almost one fourth of the records were full-sibs, which have maternal environment in their expectations.

Family relationships were analyzed by least squares procedures as outlined by Harvey (1977). The basic model used was

$$y_{ijklm} = u + l_i + a_j + s_k + (as)_{jk} + bX_{ijklm} + g_{il} + e_{ijklmn}$$

where

y_{ijklm} = observation on the m^{th} birth weight and weaning weight,

u = general mean common to all the observations,

l_i = effect of the i^{th} line-year, i = 4-38,...., 1-50, 2-50, 3-50, 4-50,.., 4-83,

a_j = effect of the j^{th} age of dam, j = 2,3,4,5,6-10,11 or more,

s_k = effect of the k^{th} sex, k = 1 (heifer), 2 (bull), 3 (steer),

$(as)_{jk}$ = effect of the interaction between the j^{th} age of dam and k^{th} sex,

bX_{ijklm}=regression of birth weight on birth date or weaning weight on age at weaning,

g_{il} =random family effect. This is a general term used for sire, maternal grandsire, paternal grand sire and maternal great grand sire nested within the i^{th} line-year, and

e_{ijklm} = random error.

The solution of the least-squares equations in the Harvey's package is obtained by imposing the restrictions

$$\sum_i l_i = \sum_j a_j = \sum_k s_k = \sum_j (as)_{jk} = \sum_k (as)_{jk} = 0$$

Table 4 shows the distribution of records per line and per year. Since during the earlier and later years line four calves are the only records available, data was classified by line-year subclasses instead of recording the two factors individually.

Due to the small number of observations per subclass, the records were corrected for line-year effects in some of the models using constants obtained from a fixed effects model. This model included the effects of age of dam, sex, line, year and the regressions of birth weight on birthdate and weaning weight on weaning age.

TABLE 4. DISTRIBUTION OF RECORDS BY LINES AND BY YEARS

Year	Lines						
	1	2	3	4	5	6	7
1938	-	-	-	78	-	-	-
1939	-	-	-	89	-	-	-
1940	-	-	-	42	-	-	-
1941	-	-	-	38	-	-	-
1942	-	-	-	44	-	-	-
1943	-	-	-	61	-	-	-
1944	-	-	-	69	-	-	-
1945	-	-	-	85	-	-	-
1946	-	-	-	95	-	-	-
1947	-	-	-	70	-	-	-
1948	6	-	-	108	7	-	-
1949	17	-	-	79	-	3	-
1950	14	15	5	60	1	1	1
1951	20	19	22	53	-	11	3
1952	20	18	22	25	16	18	14
1953	8	21	14	33	20	18	20
1954	12	25	19	21	22	21	20
1955	13	22	16	20	17	22	21
1956	10	16	13	21	19	23	22
1957	14	25	14	29	20	17	20
1958	13	19	14	20	18	22	17
1959	13	20	6	20	14	20	14
1960	14	27	10	16	18	14	16
1961	22	23	11	27	17	19	10
1962	19	18	14	22	18	11	3
1963	22	20	14	25	15	26	21
1964	17	21	12	21	22	17	18
1965	27	32	15	14	24	23	25
1966	27	28	21	11	21	27	30
1967	18	17	22	28	23	21	24
1968	7	6	4	36	18	18	20
1969	8	7	5	25	22	23	19
1970	5	4	5	33	15	32	21
1971	-	-	-	28	-	-	-
1972	-	-	-	38	-	-	-

(Continues on the next page)

TABLE 4. (Continued)

1973	-	-	-	44	-	-	-
1974	-	-	-	52	-	-	-
1975	-	-	-	55	-	-	-
1976	-	-	-	59	-	-	-
1977	-	-	-	61	-	-	-
1978	-	-	-	63	-	-	-
1979	-	-	-	70	-	-	-
1980	-	-	-	71	-	-	-
1981	-	-	-	79	-	-	-
1982	-	-	-	85	-	-	-
1983	-	-	-	133	-	-	-

The dam component was estimated from the full-sib model where dams were nested within sire and from a model in which dams were nested within maternal granddams.

The fitting constants method or Henderson's method III (Henderson, 1953) was used, as outlined by Harvey (1977), to estimate the variance components in all the analyses described above.

The covariances between offspring and dam (cov(O,D)), offspring and sire (cov(O,S)), offspring and maternal grand dam (cov(O,MGD)), aunt and niece (pattern D) (cov(A,N)) and aunt (full sib of the sire) and nephew or niece (cov(N,A)) were evaluated by simple linear regression procedures after adjusting both weights for all the fixed effects.

The covariance between maternal grand sire progeny and grand offspring (cov(S,MGS)) was obtained from a two-way random model without interaction with the data corrected for the fixed effects. The estimation procedure was Restricted Maximum Likelihood (Patterson and Thompson, 1971) as outlined by Jennrich and Sampson (1976) in the BMDP package. Since computer capabilities precluded the use of all the observations, the data used were the 1,774 calves of line 4.

The final solutions for the maternal genetic covariances were obtained through ordinary least-squares procedures. Basically, the estimates of the covariances between relatives for birth weight and weaning weight were regressed on the coefficients for the direct and maternal covariances in the expected values (Table 10). Therefore, the estimates of the direct and maternal covariances were the regression coefficents of a model with zero intercept. The nine terms were

$\sigma^2 Ao$ = variance due to additive direct effects,

$\sigma^2 Am$ = variance due to additive maternal effects,

$\sigma AoAm$ = covariance between additivedirect and additive maternal effects,

$\sigma^2 Do$ = variance due to dominance direct effects,

$\sigma^2 Dm$ = variance due to dominance maternal effects,

$\sigma DoDm$ = covariance between dominance direct and dominance maternal effects,

$\sigma^2 Eo$ = variance due to random environmental effects,

$\sigma^2 Em$ = variance due to maternal environmental effects, and

$\sigma EoEm$ = covariance between random and maternal environment effects.

The program used was the P1R of the BMDP package (Dixon et al, 1981) .

The value of fm (the effect of the dam maternal phenotype on the future daughter maternal phenotype as defined by Koch, 1972) was estimated by fitting Falconer's (1965) model. The procedure used to fit the model was ordinary-least squares. The estimates of the covariances between relatives were regressed on the cofficients for the terms in the model:

$$P = A + fm\,P' + D + C + E$$

where

P = phenotytpic value of an individual measured as a deviation from the population mean,

A = breeding value of the individual,

fm = partial regression coefficient relating daughters' to mothers' phenotypic values in the absence of genetic variation among the mothers,

P' = phenotypic value of the individual's mother,

D = dominance deviation of the individual,

C = environmental factors common to full-sibs that are not included in the maternal effect, and

E = environmental factor particular to the individual.

For convenience of analysis Thompson (1976) regrouped the components as it is shown in Table 12. The additive variance was split into a linear (2nd column from the right in Table 12) and a nonlinear term (3rd column from the right in Table 12). Estimates of $\sigma^2 P$, $\sigma^2 A$ and $\sigma^2 D$ were found for different values of fm: -1, -.5, 0, .5 and 1.0, since there were non-linear terms. Thompson (1976) proposed a modified maximum likelihood procedure based on designed experiments to estimate maternal variances and covariances. The estimates of the covariances between relatives in the present study were not independent. Therefore, the least-squares method was used instead. At each run a different value of fm (ranging from -1.0 to 1.0) was used and h^2 was calculated as the ratio $\sigma^2 A/ \sigma^2 P$. A priori it was decided to stop the iterative process when the estimated h^2 was equal to the estimate from the PHS method using all records since that estimate had the smallest standard error.

Heritability for additive direct effects (h^2o) was estimated as

$$h^2o = \frac{\sigma^2 Ao}{\sigma^2 P}$$

where $\sigma^2 P$ was defined in (10) (page 16).

Heritability for additive maternal effects (h^2m) was estimated as

$$h^2m = \frac{\sigma^2 Am}{\sigma^2 P}$$

Heritability for total additive effects was defined by Willham (1963) as

$$h^2_T = \frac{\sigma^2 Ao + 1.5 \ \sigma AoAm + .5 \ \sigma^2 Am}{\sigma^2 P}$$

It is the proportion of the phenotypic variance due to the contribution of all additive genetic sources of variation.

The genetic correlation between additive genetic effects and additive maternal effects (r_G) was estimated by

$$r_G = \frac{\sigma AoAm}{\sigma^2 Ao \quad \sigma^2 Am}$$

Finally, the environmental correlation between direct environmental and maternal environmental effects (r_E) was estimated by

$$r_E = \frac{\sigma EoEm}{\sigma^2 Eo \quad \sigma^2 Em}$$

RESULTS AND DISCUSSION

The analyses of variance for birth and weaning weight for those models in which the calves are related by sire-type relationships are presented in Table 5.

The models for the sire-type relatives accounted for 36 to 65 % and 56 to 72 % of the variation in birth weight and weaning weight, respectively. Line-year, age of dam, sex and the regressions of birth weight on birth date of calf and weaning weight on weaning age were significant ($P<.01$) sources of variation in all the models. The sire differences were significant in all the models except PGS for birth weight. The age of dam by sex interaction accounted for a small portion of the total variation in birth weight (.3 %) and weaning weight (.5 %) in the PHS model in which all available records (4,423) were used.

As the number of records decreased the age of dam by sex interaction became less important ($P>.05$) for both traits (Tables 5, 7 and 8). Least-squares means for age of dam by sex subclasses are shown in Table 6. The interaction was attributable to the higher difference between males (bulls and steers) and heifers growth rate out of older cows as compared to the same difference in younger cows. Similar results were found by Sellers et al (1970) and Schaeffer and Wilton (1974) in Hereford cattle.

The means for age of dam and sex (Table 6) agree with the values reviewed by Woldehawariat et al (1977) for Herefords. The regression of birth weight on birth date had the same value ($b = .02$) as the one

TABLE 5. ANALYSES OF VARIANCE FOR SIRE-TYPE RELATIVES

	Birth Weight									
	Sire		Maternal Grand Sire		Paternal Grand Sire		Maternal Great Grand Sire		PHS + PHSD[b]	
	df	MS	df	MS	df	MS	df	MS	df	MS
Line-Year (L-Y)	178	72.3**	174	52.7**	123	59.4**	164	43.8**	174	49.2**
Sire/L-Y[a]	202	22.2**	1263	13.1**	36	15.8	1323	12.9**	1261	14.4**
Age of Dam (A)	5	1322.7**	5	198.9**	5	1133.9**	5	496.3**	5	153.9**
Sex	2	1837.4**	2	461.5**	2	801.1**	2	238.3**	2	189.9**
A x Sex	10	30.1**	10	20.1	10	17.9	10	22.2	10	16.9
Regression on Birth Date	1	530.4**	1	432.7**	1	643.1**	1	524.1**	1	377.9**
Error	4024	12.4	2163	11.9	2166	12.9	1232	12.2	2162	11.8
R^2	.36		.52		.36		.65		.56	
	Weaning Weight									
	df	MS	df	MS	df	MS	df	MS	df	MS
Line-Year (L-Y)	178	3407**	174	2635**	123	2736**	164	2188**	174	2478**
Sire/L-Y	202	673**	1263	407**	36	546**	1323	400**	1261	458**
Age of Dam (A)	5	77029**	5	7259**	5	56517**	5	23863**	5	5088**
Sex	2	35455**	2	10189**	2	20389**	2	6816**	2	5387**
A x Sex	10	1766**	10	457	10	1343**	10	750*	10	638
Regression on Birth Date	1	718212**	1	331188**	1	357021**	1	169347**	1	201213**
Error	4024	376	2163	357	2166	371	1232	364	2162	355
R^2	.56		.63		.56		.72		.66	

*(P<.05) **(P<.01)

[a] stands for "genetic" source of variation in all analyses.

[b] PHS+PHSD is Paternal half-sibs plus dams PHS.

TABLE 6. LEAST-SQUARES MEANS FOR AGE OF DAM, SEX, AGE OF DAM BY SEX SUBCLASSES AND REGRESSIONS IN THE PHS MODEL

Item	n	Birth Weight (kg)	Weaning Weight (kg)
u	4423	35.5 ± .15	188.7 ± 1.02
Age of Dam			
2	485	32.3 ± .23	165.4 ± 1.43
3	751	35.1 ± .20	182.1 ± 1.25
4	704	36.3 ± .21	192.3 ± 1.29
5	572	37.2 ± .21	199.1 ± 1.33
6-10	1712	37.0 ± .17	201.0 ± 1.11
11 or +	199	35.1 ± .32	192.2 ± 1.86
Sex			
Heifer Calves	2409	33.9 ± .16	181.6 ± 1.08
Bull Calves	883	36.2 ± .21	194.2 ± 1.33
Steer Calves	1131	36.4 ± .20	190.3 ± 1.24
Age of Dam x Sex			
2-Heifers	257	31.0 ± .28	161.7 ± 1.65
2-Bulls	103	32.8 ± .41	166.3 ± 2.36
2-Steers	125	32.9 ± .38	168.2 ± 2.18
3-Heifers	394	33.6 ± .23	176.7 ± 1.41
3-Bulls	180	35.6 ± .32	184.8 ± 1.87
3-Steers	177	36.2 ± .31	184.6 ± 1.84
4-Heifers	404	35.1 ± .23	183.8 ± 1.41
4-Bulls	143	36.9 ± .35	186.6 ± 2.01
4-Steers	157	36.8 ± .33	194.4 ± 1.92
5-Heifers	305	35.3 ± .25	189.4 ± 1.50
5-Bulls	127	38.0 ± .36	209.0 ± 2.10
5-Steers	140	38.1 ± .34	198.9 ± 1.99
6 to 10 -Heifers	955	35.4 ± .18	191.9 ± 1.17
6 to 10 -Bulls	297	38.2 ± .27	210.6 ± 1.59
6 to 10 -Steers	460	37.4 ± .23	200.5 ± 1.41
11 or + -Heifers	94	32.9 ± .40	185.9 ± 2.32
11 or + -Bulls	33	35.7 ± .66	195.5 ± 3.66
11 or + -Steers	72	36.7 ± .46	195.1 ± 2.63
Regressions (kg/day)			
Birth Date (day of year)		.023 ± .003	-
Weaning Age		-	.881 ± .020

TABLE 7. ANALYSES OF VARIANCE FOR COUSINS FAMILIES

Birth Weight

Source of Variation	MGD		SFC		PHS + MHSD		SFC + PHS		FS + PHSP	
	df	MS	df	MS	df	MS	df	MS	df	MS
Relative	418	23.4**	79	19.3**	366	20.5**	95	15.8	42	17.3
Age of dam	5	1142.3**	5	220.2**	5	156.7**	5	59.9**	4	13.1
Sex	2	1002.6**	2	70.7**	2	113.7**	2	58.7**	2	5.5
Age of dam x sex	10	13.2	10	16.1	10	16.2	-	-	-	-
Regression on birth date	1	490.3**	1	161.6**	1	262.6**	1	91.1**	1	2.8
Error	2301	12.2	381	12.6	483	12.7	141	13.2	46	12.0
R^2	.39		.39		.59		.51		.59	

Weaning Weight

Source of Variation	MGD		SFC		PHS + MHSD		SFC + PHS		FS + PHSP	
	df	MS	df	MS	df	MS	df	MS	df	MS
Relative	418	1051**	79	877**	366	620**	95	584**	42	628*
Age of dam	5	41813**	5	8652**	5	6100**	5	1502**	4	491
Sex	2	22580**	2	2582**	2	2814**	2	3729**	2	749
Age of dam x sex	10	596	10	827**	10	592	-	-	-	-
Regression on birth date	1	334814**	1	37246**	1	41161**	1	11222**	1	4817**
Error	2301	342	381	331	483	359	141	274	46	297
R^2	.56		.56		.64		.67		.76	

*(P<.05) **(P<.01)

TABLE 8. ANALYSES OF VARIANCE FOR FULL-SIBS AND DAM-MATERNAL GRAND DAM MODELS

Birth Weight

Source of Variation	df	MS	Source of Variation	df	MS
Sires	50	49.1**	MGD	183	30.2**
Dams/S	402	16.7**	Dams/MGD	462	21.4**
Age of dam	5	53.4**	Age of dam	5	209.0**
Sex	2	102.1**	Sex	2	143.3**
Age of dam x sex	10	12.7	Age of dam x sex	10	27.0*
Regression on birth date	1	453.9**	Regression on weaning age	1	64.8**
Error	505	12.5	Error	650	11.7
R^2		.61			.57

Weaning Weight

Source of Variation	df	MS	Source of Variation	df	MS
Sires	50	1853**	MGD	183	1290**
Dams/S	402	658**	Dams/MGD	462	729**
Age of dam	5	949**	Age of dam	5	6153**
Sex	2	4761**	Sex	2	3903**
Age of dam x sex	10	600*	Age of dam x sex	10	717**
Regression on birth date	1	116431**	Regression on weaning age	1	61408**
Error	505	296	Error	650	283
R^2		.76			.71

*(P<.05) **(P<.01)

calculated by Kress and Burfening (1972) using part of the records of the present study. It indicates that late born calves had heavier birth weights. The most plausible explanation is that late calving cows had a better level of nutrition than early calving cows. The value of the regression of weaning weight on age at weaning ($b=.88$) is higher than the values reviewed by Cantet (1983) in Herefords (i. e., .64 to .75).

The models for cousins (Table 7), full-sibs and dam maternal grand dam (Table 8) showed trends similar to the sire models. Age of dam, sex, regressions and the between family components were significant sources of variation in almost all the models. As the number of records used became fewer, the interaction age of dam by sex was less important. Therefore, it was excluded in the PHS + SFC and FS + PHSP models to allow for more degrees of freedom in the error term. In the latter model only the between family component was significant for both traits and the regression of weaning weight on weaning age. The estimates of heritabilities and correlations are presented in Table 9. The estimates of the covariances between relatives are shown in Table 10. When maternal effects are present four times the sire variance component is an unbiased estimate for the additive genetic variance for direct effects (Table 1). Most of the estimates in Table 9 are comparable to the weighted averages in the review of Woldehawariat et al (1977). Of the three estimates of h^2 by the PHS method, the one obtained using all the records (PHS) is perhaps the most reliable. Unexpectedly, the estimate of h^2 for birth weight was similar to the estimate for weaning weight. The latter

TABLE 9. ESTIMATES OF HERITABILITIES AND CORRELATIONS FOR BIRTH WEIGHT AND WEANING WEIGHT

	Birth Weight		Weaning Weight	
Intraclass Correlations	Present Study	Literature Values	Present Study	Literature Values
PHS[a]	.07	.11[e]	.07	.06[e]
[b]	.10		.11	
[c]	.07		.10	
MHS[b]	.21	.27[e]	.32	.36[e]
[c]	.21		.30	
FS	.22	-	.44	.37[f]
Heritabilities				
PHS[a]	.28±.02	.44[e]	.28±.02	.26[e]
[b]	.41±.15		.47±.16	
[c]	.28		.42	
FS	.45±.08	-	.88±.08	.74[f]
MGS[d]	.54±.02	-	.23±.02	.21[g]
[c]	.06		.21	
2bod	.45±.02	.42[e]	.28±.02	.31[e]
2bos	.21±.04	.35[h]	.06±.02	.25[h]

Correlations Between Birth and Weaning Weight

Correlations	Present Study	Literature
Genetic	.56±.13	.54[e]
Phenotypic	.41	.38[e]
Environmental	.36	.24[i]

Standard errors for h^2 calculated as PHS correlations were estimated by formulae provided by Osborne and Patterson (1952). In the case of h^2 calculated as 2 b offspring-parent, standard errors were calculated as 2 times the standard error of bop. Finally, S.E. of the FS model were taken from the program (Harvey, 1977).

[a] Calculated from the PHS model.

[b] Calculated from the FS model.

[c] Calculated from the S-MGS model.

[d] Calculated from the MGS model.

[e] Review by Woldehawariat et al. (1977).

[f] Estimated by Hamman et al. (1963).

[g] Estimated by Crow and Howell (1982).

[h] Estimated by Koch and Clark (1955).

[i] Review by Preston and Willis (1970).

TABLE 10. COVARIANCES BETWEEN RELATIVES: ESTIMATES, DEGREES OF FREEDOM FOR ESTIMATION AND EXPECTED VALUES IN TERMS OF DIRECT AND MATERNAL COVARIANCES

Relatives	df	BW	WW	σ^2A_o	σA_oA_m	σ^2A_m	σ^2D_o	σD_oD_m	σ^2D_m	σ^2E_o	σE_oE_m	σ^2E_m
PHS[a]	202	.97	29.38	1/4	0	0	0	0	0	0	0	0
PHS[b]	50	1.69	62.65									
PHS[c]	96	1.02	44.62									
Within PHS[a]	4024	12.48	376.38	3/4	0	0	0	0	0	1	1	1
PGS	36	.26	16.04	1/16	0	0	0	0	0	0	0	0
Within PGS	2166	12.92	357.93	15/16	0	0	0	0	0	1	1	1
MGS[d]	1263	1.88	22.83	1/16	1/4	1/4	0	0	0	0	0	0
MGS[c]	96	.23	22.13									
Within MGS[d]	2163	11.88	371.55	15/16	3/4	3/4	0	0	0	1	1	1
MGGS	1323	0.44	19.99	1/64	1/16	1/16	0	0	0	0	0	0
Within MGGS	1232	12.18	364.93	63/64	15/16	15/16	0	0	0	1	1	1
MGD[e]	418	1.73	109.50	1/16	1/4	1/4	0	0	0	0	0	0
MGD[f]	183	1.38	93.38									
Within MGD[e]	2301	12.20	342.84	15/16	3/4	3/4	0	0	0	1	1	1
COV(O,S)	2344	1.73	11.53	1/2	1/4	0	0	0	0	0	0	0
COV(O,D)	3619	2.85	62.20	1/2	5/4	1/2	0	1	0	0	1	0
COV(O,MGD)	2573	1.25	48.64	1/4	5/8	1/4	0	0	0	0	0	0
COV(S,MGS)[c]	96	-.002	-5.32	1/8	1/4	0	0	0	0	0	0	0
Within S-MGS[c]	1582	12.37	357.65	9/16	1/2	3/4	0	0	0	1	1	1
COV(MA,N)	210	-.17	-45.33	1/4	3/4	1/2	0	1/4	0	0	0	0
Within MA,N	208	13.71	348.68	3/4	1/4	1/2	0	3/4	0	1	0	0
COV(PA,N)	104	-3.06	6.85	1/4	3/4	1/2	0	1/4	0	0	0	0
Within PA,N	102	14.51	509.39	3/4	1/4	1/2	0	3/4	0	1	0	0
FS[b]	402	3.67	234.09	1/2	1	1	1/4	0	1	0	0	1
Within FS[b]	523	12.55	296.27	1/2	0	0	3/4	0	0	1	0	0
MHS[b]	402	1.98	171.44	1/4	1	1	1/4	0	1	0	0	1
MHS[f]	462	3.55	164.26	1/4	1	1	0	0	1	0	0	1
SFC	479	1.17	95.94	1/8	1/2	1/2	0	0	1/4	0	0	0
Within SFC	381	12.62	331.01	7/8	1/2	1/2	0	0	3/4	1	0	0
PHS+MHSD	366	3.36	112.92	5/16	1/4	1/4	1/16	0	1	0	0	0
Within PHS+MHSD	483	12.72	359.29	11/16	3/4	3/4	15/16	0	0	1	0	0
PHS+SFC	95	1.03	126.86	3/8	1/2	1/2	1/8	0	1/4	0	0	0
Within PHS+SFC	141	13.27	274.75	5/8	1/2	1/2	7/8	0	3/4	1	0	0
FS+PHSP	30	2.63	259.69	5/8	5/4	1	25/64	0	1	0	0	1
Within FS+PHSP	46	12.03	297.99	3/8	-1/4	0	39/64	0	0	1	0	0
PHS+PHSD	901	1.19	45.77	5/16	1/4	1/4	1/64	0	0	0	0	0
Within PHS+ PHSD	1481	11.79	355.50	9/16	3/4	3/4	63/64	0	0	0	0	0

[a] Estimates from the PHS model; [b] Estimates from the FS model; [c] Estimates from the S-MGS model; [d] Estimates from the MGS model; [e] Estimates from the MGD model; [f] Estimates from the MGD-D/MGD model.

agreed closely with the literature mean estimate of Woldehawariat et al (1977).

The h^2 values by PHS estimated through the full-sib file were higher than the values estimated in the PHS file for both weights. Hamman et al (1963) also found a larger sire component using FS data than by using PHS data for weaning weight. Therefore, sampling error associated with a smaller number of records for estimation is a possible explanation for the larger sire component in the FS data set. Koch (1972) indicated that environmental correlations among sire progenies, sire-year interaction or a sizeable fraction of offspring being three-quarter sibs instead of half sibs in small herds are possible sources of biases in PHS estimates. When the records are taken over an extended period of time, changes in managemental procedures or environmental conditions could induce an overestimation of the sire component. This can come about because of a possible sire by line or sire by year interaction. Flower et al (1964) reported a negative environmental trend in birth and weaning weight in the herd under study possibly related to a decrease in rainfall during the grazing season (March to September) from 1952 to 1958. Sire by line-year interactions are a distinct possibility. It should be noted that due to restrictions in computer capabilities the sire component was estimated with the data corrected by line-years to allow for the dams to be nested within sires. In the PHS file, the sire component was evaluated in a within line-year basis. In this case the standard error of h^2 was almost ten times lower than the estimates obtained in the FS model (Table 9). Kennedy and Henderson (1975a) found that the sire by year interaction accounted for 1 to 4 % of the variation in weaning weight of Angus and Hereford calves whereas in the study of Dinkel and Busch (1973) this contribution was a 6.5 % in Hereford though it was not significant ($P>.05$).

The cow component (MHS) was estimated from the FS and dam-maternal grand dam models. There was an important difference in the MHS estimates for birth weight as compared to the values obtained for weaning weight (Table 10). When dams are nested within sires, the expectation also includes 1/4 σ^2Do. The estimates of repeatability were .13 ± .01 and .21 ± .03 in the case of birth weight and .36 ± .04 and .30 ± .03 for weaning weight. The estimates for birth weight were lower than the average of the studies reviewed by Woldehawariat et al (1977) and the one estimated by Kress and Burfening (1972) (.27 ± .02) who worked with the records from 1933 to 1966 of the present study. Since 1975 the herd has been selected by an index which discriminates against larger birth weight. It is known that selection reduces the additive variation (Bulmer, 1971; Robertson, 1977; Falconer, 1981). Thrift et al (1981) reported an important reduction in the sire variance component (PHS) and h^2 estimates of birth and weaning weight of three selected Hereford and Angus herds after 2, 1.25 and 1 generations of selection, respectively, as compared to the unselected control herds. The selection criterion was basically growth rate through one year of age. Unfortunately, no other reports dealing with selection in beef cattle in which a control line is included have reported h^2 for both herds (see the review of Koch et al,1982). Therefore, the evidence is not conclusive to support the hypothesis of a dramatic reduction of additive variation in birth weight in this data set.

Estimates of h^2 by FS in cattle are not common in the literature due to the fact that the cow is basically uniparous and bulls are commonly used for one or two years, decreasing the chance for having full-sib families. The full-sib estimate for birth weight (.45 ± .08) was close to the value reported by Legault and Touchberry (1962) (.51) by pooling data of different breeds of dairy cattle in a within-breed estimate with 432 calves. A value of .88 ± .08 was estimated for weaning weight through FS in the present study. Hamman et al (1963) found a h^2 of .74 using 332 Hereford calves. The expectations in Table 1 show that the estimation of h^2 by FS is biased when dominance and common or maternal environment are present. Therefore, since the estimates of h^2 through FS are different from the estimates using PHS (which, assuming presence of maternal effects, have a different genetic expectation), maternal effects could be involved in that difference for both traits.

The estimates of the cov(O,D) were larger in both traits than the estimates of cov(O,S) (Table 10). Heritabitilies using those covariances were .45 ± .02 and .21 ± .04 for birth weight and .28 ± 02 and .06 ± .004 for weaning weight by using cov(O,D) and cov(O,S), respectively. The values for cov(O,D) agreed with the averages of the estimates reviewed by Woldehawariat et al (1977). However, the values for cov(O,S) are lower than those reported by Koch and Clark (1955b) (.25), Hohenboken and Brinks (1971a) (.28), and Koch (1972) (.20) for the Hereford breed. The number of bulls used in the present study was higher than the number of bulls used in the other studies. Standard errors of those estimates are not reported. Thus, any further comparison is difficult.

The expectation of 4(cov(O,S) - 2 PHS) provides a gross estimate of σAoAm. This estimate is -.84 and -188.92 kg^2 for birth weight and weaning weight, respectively. The negative values indicate an antagonism between additive genetic direct and additive genetic maternal effects for preweaning growth. Using the estimates of Hohenboken and Brinks (1971), σAoAm was -38.8 kg^2 for weaning weight. In the case of Koch and Clark (1955a,b) σAoAm was of 1.84 and -26.72 kg^2 for birth and weaning weight, respectively. Buchanan et al (1982) found the cov(O,S) to be greater than cov(O,D) for birth weight and weaning weight as in the present study. However, the h^2 by 2 b_{OD} was negative for weaning weight (-.04). Under the maternal effects models previously discussed, the cov(O,D) (Table 1) has a rather complicated expectation. Since σ^2Ao and σ^2Am are involved, one or more of the covariances between direct and maternal effects should have a minus sign for the cov(O,D) to be negative. The covariances MGD and MGS have the same expected values in terms of direct and maternal variances, as Table 1 and 10 show. The estimates for birth weight were 1.73 and 1.38 kg^2, for MGD and 1.88 and .23 kg^2 for MGS. In the case of weaning weight the values were consistently larger for MGD (109.50 and 93.38 kg^2) as compared to the estimates for MGS (22.83 and 23.13 kg^2). If there exists an effect of the maternal phenotype of the dam on maternal phenotype of the daughter (fm path, figure 3), there is an extra difference in additive variation since a term fm (1/2 σ^2Am + 1/4

σAoAm) should be added to the MGD expectation (see appendix). This can cause the MGD and MGS estimates of covariance for weaning weight to be different. Crow and Howell (1982) calculated the maternal grandsire's contribution to their daughters' performance as mothers for weaning weight as

$$h^2_{MGS} = \frac{4\ \sigma^2_{MGS}}{\sigma^2_E + \sigma^2_{MGS}}$$

$$= \frac{1/4\ \sigma^2_{Ao} + \sigma_{AoAm} + \sigma^2_{Am}}{\sigma^2_{Ao} + \sigma_{AoAm} + \sigma^2_{Am} + \sigma^2_{Eo} + \sigma_{EoEm} + \sigma^2_{Em}}$$

For the Hereford breed these authors calculated h^2_{MGS} values of .20, .14, .25 and .23, for cows at their first, second, third and fourth or more parities, respectively. Therefore, the estimates found in the present study (.21 and .23) agree closely. By using the same procedure with the published values, it was calculated a h^2_{MGS} for birth weight of .01 in Holstein (Everett and Magee, 1965), .25 in Hereford and .26 in Angus (Brown and Galvez, 1969) and in Hereford .20 (Koch, 1972). The estimated values in the Havre Hereford herd were .54 and .06. The first estimate was obtained from over 3,619 calf records by using Henderson's method III. For weaning weight the values of the literature were .19 in Brahmans and .24 in crossbreds (Deese and Koger, 1967), .31 in Herefords (Hohenboken and Brinks, 1971a) and .32 in Herefords (Koch, 1972).

The cov(S,MGS) or covariance grand sire's progeny and grandoffspring (Koch, 1972) indicates the degree of association between the direct or transmitted effects of a sire for a given trait and the performance of his daughters as mothers for the same trait. In the present study the cov(S,MGS) was estimated from a two-way cross classified random model in which line 4 calves were coded by sire and maternal grand sire. Almost all bulls (95 out of 96) had progeny and grand progeny. Restricted Maximum Likelihood estimation of variance components, as outlined by Jennrich and Sampson (1976), was used with prior estimates being the ones obtained in the PHS and MGS models. The algorithm was convergent for both traits. The estimates of cov(S,MGS) were -.00023 and -5.32 kg^2 for birth and weaning weight, respectively (Table 11). The estimated correlations were -.00001 and -.01. Everett and Magee (1965) reported that cov(S,MGS) was .26 kg^2 for birth weight. The correlation obtained from their data is .0028. The covariance was obtained by using all possible combinations of maternal grandoffspring of a common grandsire. Koch (1972) reported a correlation of .05 for birth weight and .02 for average daily gain to weaning. The method used is not reported in the paper.

The cov(O,MGD) was 1.25 kg^2 for birth weight and 48.64 kg^2 for weaning weight. The correlations were .10 and .09. The corresponding estimates of Koch (1972) were .13 for both traits. He suggested the use of the difference (cov(O,D) - 2 cov(O,MGD)) to evaluate further evidence on environmental covariance through maternal ability. It provides an estimate of (1-2fm) (σDoDm + σEoEm (1+fm) + fm) if fm is different from zero, and of (σ DoDm +σEoEm), if fm is equals to zero. For birth weight the difference is .35 kg^2 suggesting a positive direct pathway, positive dominance covariance or both. In the case of

TABLE 11. ASYMPTOTIC VARIANCE - COVARIANCE MATRICES FOR THE SIRE-MATERNAL GRAND SIRE MODEL

	Birth Weight			Weaning Weight		
	Error	S	MGS	Error	S	MGS
Error	.1810	-.0057	-.0049	159.48	-9.05	-10.78
Sire	-.0057	.1032	-.0023	-9.05	113.15	-5.32
MGS	-.0049	-.0023	.0176	-10.78	-5.32	55.81

weaning weight the difference is -38.08 kg^2 suggesting negative direct effects (i.e., negative value of fm), negative σDoDm or both covariances. The results agree with those reported by Koch (1972).

Estimates of the covariances and variances from the other relative relationships have not been reported in the literature for birth and weaning weight in cattle. The path between maternal phenotypes of the dam and daughter (fm, figure 3) was estimated to be .08 and -.10 for birth and weaning weight, respectively (Table 12). The method of estimation was multiple regression least-squares in which the covariances between relatives for both weights were regressed on the coefficients derived by Thompson (1976) to fit Falconer's (1965) model, as explained in the review of literature. The h^2 from the PHS file was used as the convergence value since it was estimated using all available records. Koch (1972) speculated a value for fm of -.10 to -.20 for weaning weight. Furthermore, he pointed out that a path of that magnitude satisfies observed correlations and regressions. Thus, the value found in this study supports his hypothesis. No other estimates of fm were found for beef cattle. Falconer (1965) reported a negative value of fm for litter size in mice and Alsing et al (1981) a negative value for litter size in pigs.

The solutions for the direct and maternal variances and covariances are shown in Tables 13 and 14. The first approach to estimate the direct and maternal variances and covariances was to use solutions already tried by other researchers to compare results. The first estimates were the solutions utilized by Hohenboken and Brinks

TABLE 12. COEFFICIENTS OF COVARIANCES BETWEEN RELATIVES[a] AND SOLUTIONS FOR FALCONER'S (1965) MODEL

Relatives	BW	WW	σ^2P	σ^2A	$\frac{m}{2(2-m)}$ σ^2A	σ^2b
PHS	.97	29.38	0	1/4	0	0
PGS	.26	16.04	0	1/8	0	0
FS	3.67	234.09	m^2	1/2	4	1/4
Within FS	12.55	296.27	$1-m^2$	-1/2	-4	-1/4
COV (O,D)	2.85	62.20	m	1/2	1	0
COV (O,S)	1.73	11.53	0	1/2	1	0
COV (MA,N)	-.17	-45.33	m^3	(1+2m)/4	1+4m	m/4
COV (S,MGS)	-.0023	-5.32	0	(1+2m)/8	0	0
COV (PA,N)	-3.06	6.85	0	1/4	1	0
SFC + PHS	1.03	126.86	0	$(1+4(m+m^2))/16$	0	0

[a] As derived by Thompson (1976)

[b] $\sigma^2R = \sigma^2M + 2\sigma AM + \sigma^2D + \sigma^2EM + \sigma^2Eo$

Solution for Birth Weight

fm	σ^2P	σ^2A	σ^2R	h^2
-1.00	6.16	9.37	7.37	1.52
-.50	11.31	11.25	23.95	.99
-.25	14.67	10.31	28.99	.70
.00	16.22	6.16	46.52	.37
.05	16.35	5.06	49.53	.30
.08	17.40	5.02	49.09	.28
.05	13.77	.64	37.49	.04
1.00	9.01	-.76	9.47	-.08

fm (Birth Weight) = .08

Solution for Weaning Weight

fm	σ^2P	σ^2A	σ^2R	h^2
-1.00	218.66	260.33	-764.35	1.19
-.50	390.02	255.69	168.07	.65
-.37	444.14	232.33	483.48	.52
-.25	479.46	231.01	781.70	.48
-.12	515.84	153.20	1143.82	.29
-.10	546.52	157.30	1197.78	.28
.00	530.36	105.41	1413.62	.19
.50	417.22	-38.31	1403.95	-.09
1.00	250.18	-60.96	505.56	-.24

fm (Weaning Weight) = -.10

TABLE 13. SOLUTION FOR DIRECT AND MATERNAL COVARIANCES USED BY OTHER WORKERS

Hohenboken and Brinks'(1971) solutions

Solution	σ^2Ao	σAoAm	σ^2Am	σ^2Do	σDoDm	σ^2Eo	σ^2Eo	r_G	h^2o	h^2m	h^2_T
					Birth weight						
1 HB	3.88	-.84	7.39	.65	-1.73	9.64	-5.54	-.15	.28	.54	.46
2 HB	3.88	-3.15	9.70	-1.08	-	9.64	-5.54	-.51	.28	.72	.29
3 HB	3.88	-.84	7.39	-1.08	-	9.64	-5.54	-.15	.28	.54	.46
					Weaning weight						
1 HB	117.52	-188.92	250.86	-238.20	114.16	270.46	80.12	-1.10	.28	.61	-.09
2 HB	117.52	-36.70	98.64	-124.04	-	270.46	80.12	-.34	.28	.24	.27
3 HB	117.52	-188.92	250.86	- 61.71	-	208.13	80.12	-1.10	.28	.61	-.09

(Continues on the next page)

TABLE 13. (Continued)

Koch's (1972) solutions

Solution	σ^2_{Ao}	σ_{AoAm}	σ^2_{Am}	σ^2_{Dm+Em}	σ^2_{Do+Eo}	r_G	h^2_o	h^2_m	h^2_T
				Birth weight					
1 K	3.88	-.84	7.39	-5.54	9.64	-.15	.26	.50	.43
2 K	3.88	-1.94	8.49	-5.54	9.64	-.33	.26	.58	.35
3 K	4.61	-2.30	8.67	-5.54	9.09	-.36	.31	.59	.37
4 K	3.88	-.84	3.92	-2.07	9.64	-.21	.26	.27	.31
5 K	3.88	-1.94	6.67	-3.72	9.64	-.38	.26	.46	.29
6 K	5.42	-3.92	10.08	-5.54	8.48	-.53	.37	.69	.31
				Weaning weight					
1 K	117.52	-188.92	250.86	80.12	270.46	-1.10	.22	.47	-.07
2 K	117.52	-80.04	141.98	80.12	270.46	-.62	.22	.26	.13
3 K	44.93	-43.74	123.83	80.12	270.46	-.58	.08	.23	.20
4 K	117.52	-188.92	479.18	80.12	270.46	-.79	.22	.90	.14
5 K	117.52	-80.04	206.98	15.12	270.46	-.51	.22	.39	.19
6 K	16.04	14.03	73.27	80.12	346.57	.41	.03	.14	.14

(Continues on the next page)

TABLE 13. (Continued)

	Relatives used
1 HB	PHS, MHS, PHS + Error PHS, within FS, MGS, cov(0,S), cov(0,D)
2 HB	PHS, MHS, PHS + Error PHS, within FS, MGS, cov(0,D)
3 HB	PHS, MHS, PHS + Error PHS, within FS, MGS, cov(0,S)
1 K	PHS, cov(0,S), MGS, MHS
2 K	PHS, cov(S,MGS), MGS, MHS
3 K	cov(0,S), cov(S,MGS), MGS, MHS
4 K	PHS, cov(0,S), cov(0,D), MHS
5 K	PHS, cov(S,MGS), cov(0,D), MHS
6 K	cov(0,S), MGS, cov(0,D), MHS

Kress et al (1979)

	σ^2_{Ao}	σ_{AoAm}	σ^2_{Am}	r_G	h^2_o	h^2_m	h^2_T
Birth weight	4.08	-2.04	1.94	-.72	.30	.14	.14
Weaning weight	178.48	-110.52	158.42	-.65	.42	.37	.22

Relatives used: PHS, MGS, cov(S,MGS).

TABLE 14. SOLUTIONS FOR THE DIRECT AND MATERNAL VARIANCES^a, COVARIANCES^a AND HERITABILITIES

	Birth Weight			Weaning Weight				
	OLS^b	GLS^c	GLS^d	OLS^b	GLS^c	OLS^e and fm corrected	GLS^f and fm corrected	GLS^d
$\sigma^2 A_o$	3.76±1.3	3.66±1.0	4.51±.8	192.49±57.2	117.06±45.4	189.83±60.6	107.12±46.7	116.25±54.4
$\sigma A_o A_m$	-3.11±1.7	-.72±1.5	-2.51±1.1	-189.08±73.3	-54.41±66.2	-125.81±94.6	-19.32±99.4	-110.26±78.9
$\sigma^2 A_m$	2.41±1.8	.73±1.5	7.13±1.5	206.51±79.0	80.16±67.6	152.02±94.3	44.02±101.1	321.90±105.5
$\sigma^2 D_o$	1.11±.8	.35±.7	-	47.08±37.9	16.03±31.8	38.31±39.7	16.85±32.3	-
$\sigma D_o D_m$	2.27±.9	2.03±1.4	-	106.53±42.5	71.59±62.5	87.26±44.0	16.85±46.1	-
$\sigma^2 D_m$	2.10±.7	1.72±.9	-	29.38±33.3	49.88±41.3	29.81±34.0	72.18±34.6	-
$\sigma^2 E_o$	8.98±1.2	9.63±1.0	-	137.92±51.2	216.70±46.5	152.47±51.2	217.04±46.5	-
$\sigma E_o E_m$	.61±1.0	-.54±1.2	-	-32.92±46.1	-40.48±55.9	-32.33±35.9	-5.13±36.8	-
$\sigma^2 E_m$	-.23±.9	.02±1.0	-	72.07±40.3	72.03±48.3	59.53±30.9	46.51±35.9	-
$\sigma^2 P$	17.90	16.88	g	569.98	528.56	551.19	496.12	g
$h^2 o$	.21	.21	.26	.33	.22	.34	.21	.22
$h^2 m$	.13	.04	.42	.36	.15	.27	.08	.61
h^2_T	.01	.17	.25	.02	.14	.14	.20	.21
r_G	-1.03	-.44	-.44	-.94	-.56	-.74	-.28	-.57
r_E	-	-1.23	-	-.33	-.32	-.33	-.05	-

[a] In kg^2

[b] OLS = Ordinary Least-Squares

[c] GLS = Generalized Least-Squares. Weighted by the number of records of estimation in the covariances between relatives.

[d] GLS = For covariances with additives components only

[e] OLS = After correcting by fm

[f] GLS = After correcting by fm

[g] Heritabilities calculated by using σ^2P of GLS^3.

(1971a) (HB, Table 13). The second group of solutions consists of those suggested by Koch (1972) (K, Table 13). Almost all (18 out of 19) the estimates for r_G in both traits were negative. Solutions HB1, HB2 and HB3 produced r_G estimates of -.15, -.51 and -.15 for birth weight and -1.10, -.34 and -1.10 for weaning weight. The trend was opposite to the results of Hohenboken and Brinks (1971a) for weaning weight who found values of -.28, -.79 and -.28, for solutions 1, 2 and 3, respectively. Solution HB2 includes the cov(O,D) but not the cov(O,S) and does not use the cov(O,S). Solution HB1 includes both covariances. The cov(O,D) was smaller than the cov(O,S) for weaning weight in Hohenboken and Brinks (1971a) study while the cov(O,D) was larger than the cov(O,S) for both traits in the present study.

All the solutions in Table 13 are based on solving a consistent system of equations of size no greater than 7 by 7. The estimates of the variances and covariances for direct and maternal effects are the unknowns to solve for. Since the number of covariances between relatives estimated in the studies of Hohenboken and Brinks (1971a) and Koch (1972) was less than nine, some of the unknowns were assumed to be zero in order for the solution to be consistent. A dependency is then created by which one direct or maternal variance and/or covariance depends mostly on the estimates of one or more covariances between relatives. For example σ^2Ao depends on the estimate of PHS whose expectation involves one non zero term (1/4 σ^2Ao) and the rest are all zeroes. This is due to the fact that by using elementary row operations into the system of equations the matrix of the coefficients is reduced to a lower triangular matrix (Johnson and Riess, 1981).

The equation for PHS is then multiplied by 4 to obtain a 1 in the first row-first column position. The rest of the elements in the first column are reduced to zeroes. The next equation must have a non zero term in the second row-second column position. All the remaining elements in the second column are then reduced to zero. Therefore, if the second unknown is $\sigma AoAm$, its estimate will depend on a covariance between relatives whose expectation involves a non zero term in the second row-second column position and a non zero term in the second row-first column ($\sigma^2 Ao$ is involved in all the equations, Table 1 and 10). The rest of the terms will be zero. Hence, σ AoAm will depend on the estimates of cov(O,S) or cov(S,MGS) and, of course, PHS. The next unknown ($\sigma^2 Am$) will depend on cov(O,MGS) or MGS, etc, and so on.

In conclusion, the first unknown depends on only one estimate of covariances between relatives, the second on two, and so on. Therefore, the information available is not evenly used in the estimation process and errors in one estimate of direct and maternal variances and covariances can cause the other to differ in the opposite direction since the sum of components is forced to equal the whole (Koch, 1972). The problem is even more serious when it is erroneously assumed that a component is zero. This seems to be the explanation for the negative value for $\sigma^2 Do$, $\sigma^2 Dm$ and $\sigma^2 Em$ in various solutions of the present study and in the one of Hohenboken and Brinks (1971a) when $\sigma EoEm$ is assumed to be zero in the expectation of the cov(O,D). In the first section evidence has been reviewed (Totusek, 1968; Ellicot et al, 1970; Mangus and Brinks, 1971; Kress and Burfening, 1972) that there exists a negative environmental association between preweaning growth of the heifer calf and her future maternal ability. In a previous paragraph this relationship was quantified. The expectations in Tables 1 and 10 also show that EoEmis the only possibility since the other two covariances have already been considered in these solutions.

The simple means of the three heritabilities in Table 13 are h^2o = .28 and .20, h^2m= .54 and .42 and h^2_T= .36 and .09 for birth and weaning weight, respectively. They are suggesting that maternal additive genetic variation is larger than direct additive genetic variation for both traits. For birth weight, this result disagrees with the results of Everett and Magee (1965), Koch (1972), Fisher and Williams (1978) and the solution for Herefords of Brown and Galvez (1969). In the case of weaning weight the results are similar to those of Deese and Koger (1967) (crossbred herd), Hohenboken and Brinks (1971a) and Koch (1972). The results of Deese and Koger (1967) (Brahman herd), Hill et al (1965) and Vesely and Robison (1971) showed a h^2o slighty greater than h^2m for weaning weight or average daily gain to weaning.

The last solution in Table 13 is based on the independent estimates of PHS, MGS and cov(S,MGS) from the sire-maternal grandsire model by REML procedures. It only involves additive components in its expectation. It is the solution to the following system of equations:

	σ^2Ao	$\sigma AoAm$	σ^2Am
PHS	1/4	0	0
cov(S,MGS)	1/8	1/4	0
MGS	1/16	1/4	1/4

The standard error of the estimates of PHS and MGS are the square root of the second and third diagonal elements of the matrix in Table 11. No standard error for the estimates of the more complicated models using Henderson's method III of estimation of variance components were available. They presumably involve extensive matrix manipulation (Searle, 1971; p. 451). The estimated values for h^2o, h^2m and h^2_T from the last solution in Table 13 were .30, .14 and .14 for birth weight and .42, .37 and .22 for weaning weight. Using the same solution but with nonindependent components, Kress et al (1979) found a value for h^2o of .12 and for h^2m of .05 and r_G of -.68, for weaning weight. In the present study, the values of r_G were -.72 for birth weight and -.65 for weaning weight. The results of this solution show a totally different picture for birth weight as compared to the results obtained in the first and second set of solutions regarding to the relative importance of additive direct effects and additive maternal effects. The value of r_G for birth weight is higher in this final solution. However, r_G for weaning weight (-.68) is close to the simple mean of the HB and K solutions (-.72).

Hohenboken and Brinks (1971a) pointed out that the greatest weakness of the technique of simultaneously equating observed covariances to their theoretical expectations is the inability of the expectation to account for all causes of environmental covariance among relatives. In order to overcome this problem several covariances between relatives were evaluated so that the number of equations used was several times greater than all previous research on the subject. Solutions in Table 14 are the result of using ordinary least-squares estimators (OLS) and weighted or generalized least squares estimators (GLS) on the design matrix of Table 10. The basic procedure is a multiple regression method of regressing the estimates of the covariances between relatives on the coefficients of their respective expectations. The intercept was set equal to the origin and the regression coefficients were the estimates of the direct and maternal variances and covariances. The weights used in the GLS-solutions were the numbers of records in the file for estimating the particular covariance between relatives, as suggested by Van Vleck and Hart (1966). These authors indicated the method should be very similar to weighting according to the inverse of the variances of the covariances between relatives. Standard errors of the regression coefficients are included to compare the accuracy of the different estimates. The first two columns of birth and weaning weight are the OLS and GLS solutions using all 37 equations. The next two columns in the case of weaning weight are the OLS and GLS solution after correcting all the expectations by fm. This correction consisted of introducing the proportionality of environmental correlation into the coefficients for $\sigma AoAm$, $\sigma^2 Am$ and $\sigma EoEm$ as suggested by Koch (1972). Finally, the last solution in both traits is GLS using the 11 equations (Table 10) with only additives components in their expectations.

In general, the weighting procedure increased the coefficient of variation and reduced the value for σ^2P; this was defined as the simple sum of the nine variances and covariances. The estimates for r_G were all negative. The estimates for h^2o were greater than the values for h^2m except in the solution based on the additives components for both traits and the OLS solution for weaning weight. The standard deviations for the GLS solution were the lowest of all the estimates of additive components in Table 14. A value of fm for weaning weight as the one estimated in the present study (-.10) negatively modifies terms like the cov(S,MGS) and the coefficient for $\sigma AoAm$ is reduced from .250 (1/4, Tables 1 and 10) to .225. The expected value of the cov(O,MGD) contains fm as the coefficient for DoDm (Koch, 1972). Therefore, in order to take these factors into account, a GLS solution for additives components after correcting the cov(S,MGS), cov(O,MGD) and MGD by fm, was obtained for weaning weight. The values were σ^2Ao: 127.18 ± 55.2, $\sigma AoAm$: -136.44 ± 80.4 and σ^2Am: 341.15 ± 106.31. The corresponding genetic parameters were h^2o= .24, h^2m= .65, h^2_T=.17 and r_G= -.65.

Eisen (1967) indicated that the deletion of any independent variable will lead to biased estimates of the causal components of variance (partial regression coefficients) if there is a significant correlation between the deleted variable and any of the remaining independent variables. The matrix of the simple correlation coefficients for the system of equations used, as given by the program, is shown in Table 15. These correlations coefficients measure the degree of association between the coefficients of the nine

TABLE 15. SIMPLE CORRELATION COEFFICIENTS AMONG THE COEFFICIENTS OF DIRECT AND MATERNAL VARIANCES AND COVARIANCES

	$\sigma^2 A_o$	$\sigma A_o A_m$	$\sigma^2 A_m$	$\sigma^2 D_o$	$\sigma D_o D_m$	$\sigma^2 D_m$	$\sigma^2 E_o$	$\sigma E_o E_m$	$\sigma^2 E_m$
$\sigma^2 A_o$	1.00								
$\sigma A_o A_m$	.27	1.00							
$\sigma^2 A_m$	.38	.88	1.00						
$\sigma^2 D_o$	.22	.15	.19	1.00					
$\sigma D_o D_m$	.17	.20	.09	-.17	1.00				
$\sigma^2 D_m$	.03	.46	.52	.16	-.18	1.00			
$\sigma^2 E_o$	.81	-.07	.16	.41	.08	-.17	1.00		
$\sigma E_o E_m$	.63	.23	.22	-.03	.09	-.27	.53	1.00	
$\sigma^2 E_m$	.53	.47	.60	.06	-.22	.31	.34	.66	1.00
BW	.83	-.03	.21	.41	.13	-.05	.97	.51	.37
WW	.84	.13	.41	.38	.12	.09	.89	.50	.54

parameters in pairs, for the particular equations involved in that solution. For example, a high value for the correlation between σ^2Ao and σ^2Eo means that if the coefficient for σ^2Ao is large, the coefficient for σ^2Eo would also be large for that equation. The greatest correlations in Table 14 are the ones between σ^2Ao and σ^2Eo and between σ^2Am and σAoAm. The same thing was observed in the designs of Eisen (1967). In general, the correlations in the present study are lower than the ones in Eisen's designs. The high correlation between σ^2Am and σAoAm (.88) suggests that if one is overestimated, then the other will be too. This can be the cause for σ^2Am to be high in the solution for additive components.

In deciding which solution is the most reliable several considerations should be made. First, Seber (1977) analysed the effects of underfitting or overfitting a linear model. He has clearly shown that underfitting results in biased estimates of the vector of parameters, the direct and maternal variances and covariances in the present case. Instead, overfitting results in no biased estimates of the parameters but leads to inflated expressions for the variances of the parameters (Seber, 1977, page 143). Therefore, as Eisen (1967) previously discussed, the first two sets of solutions in Table 13 are biased and the OLS and GLS solutions have larger standard errors than the true ones. Second, the solutions for the 9 parameters in Table 14 are based on the assumption that the error terms for the sire-type relative relationships contain σEoEm and σ^2Em. This assumption is based on the fact that those files contained 25 % of full-sibs. More than 2/3 of the cows in the present study had two or more calves. If

EoEm and ^{2}Em are not involved in those expectations, the only covariance in which EoEm is present is cov(O,D). This produces (X'X) to be ill-conditioned (Seber, 1977, p. 319-322). In other words, a small change in the data provokes a big change in the solutions. The third point resides in the observation of Thompson (1976) with respect to weighting the equations by the number of records. He suggested that this procedure proposed by Van Vleck and Hart (1966) is not fully efficient if the variances and covariances of the covariances between relatives are not homogeneous. The GLS-solutions tended to produce values far below the average of the literature reviewed, especially for weaning weight. The fourth and last consideration is related to the fact that there was clear evidence for the existence of a path between maternal phenotype of the dam and daughter (fm) in this study. Thus, the expectations should reflect that effect. The OLS and GLS solutions that were corrected for fm for weaning weight take that into account.

Putting it all together, it seems that the OLS-fm corrected solution for weaning weight is perhaps the most reliable in the study. It is not clear which solution is the counterpart for birth weight. However, the solutions in Table 14 seems to be more reliable than those solutions in Table 13. In summary, maternal effects affected birth and weaning weight of beef calves in this Hereford herd. Maternal effects in weaning weight of beef cattle have a genetic and environmental origin. In birth weight it seemed that the basis for maternal effects is mostly genetic. It is clear that genetic effects were not only additive in this study. Dominance was also involved.

However, the large value of $\sigma DoDm$ as compared to $\sigma^2 Do$ and $\sigma^2 Dm$ suggested that some epistasis would be involved. Willham's (1963) original model contained terms for epistasis. However, the coefficients in the expected values of the covariance between relatives of the dominance components are highly correlated to those of epistasis. In statistical terms this implies to reparameterize a regression model with 9 parameters to a model with 12 parameters highly correlated among themselves. Then, these 12 parameters have to be estimated with 37 equations at most.

A direct path between the maternal phenotype of the dam and the maternal phenotype of the daughter as suggested by Koch (1972) was also found for both traits. Even though the value for birth weight (.08) was close in absolute value to the estimate for weaning weight (-.10), its biological meaning is not clear. Additive maternal effects seems to be less important for birth than for weaning weight. The latter seems to be of the same magnitude or perhaps even larger than additive direct effects (see h^2o and h^2m in Table 14). The sign of the covariance between additive genetic direct and additive maternal effects was clearly negative for both weights in this study. The nature of the data used and the restrictions of the analyses make it difficult to suggest a highly accurate value, especially for birth weight. However, the value for r_G of weaning weight seems to be smaller than -.50, possibly between -.65 and -.75. A practical implication of this value is the reduction in the expected response to selection for weaning weight theoretically shown by Van Vleck et al

(1977) and observed in those selection experiments in beef cattle reviewed by Koch et al (1982).

A final suggestion for future research on the subject is related to the experimental design to study maternal effects in beef cattle. Willham (1980) indicated that rather than using field data to estimate the direct and maternal variances and covariances, designed projects that yield specific useful covariances that are uncorrelated should be attempted. Considerations commented in the literature review also indicate that this is a difficult task with beef cattle. However, covariances like cov(S,MGS) in a design in which bulls are tested as sires and maternal grand sires are appealing. The condition is that only those years in which there are progeny and grand progeny should be included. This is only an example. In the future, the general applicability of techniques like embryo transfer, can help the animal breeding researcher to have a more comprehensive understanding of this intriguing problem of maternal effects in beef cattle.

SUMMARY

Birth and weaning weights of 4,423 noncreep-fed Hereford calves raised at the Northern Agricultural Research Center, Havre, Mt from 1938 to 1983 were used to study maternal effects over both traits. Calves were produced out of 202 bulls and 1,271 cows. The herd was kept in range conditions during the summer and supplemented only during the winter.

The basic models included fixed effects of line-year, age of dam, sex, age of dam by sex interaction and the regression of birth weight on birth date of calf and weaning weight on weaning age of calf. The relative relationships were the random effects. The covariances between relatives were estimated by the fitting constants method (Henderson, 1953) and were paternal half-sibs, maternal grand sire sibs, paternal grand sire sibs, maternal great grand sire sibs, maternal grand dam sibs, full-sibs, maternal half-sibs, single first cousins, paternal half-sibs plus full- sib dams, paternal half-sibs plus paternal half-sibs dams and full-sibs plus paternal half-sib parents. The sire (paternal half-sibs) and maternal grand sire (maternal grand sire sibs) components were also estimated by Restricted Maximum Likelihood as outlined by Jennrich and Sampson (1976) in a two-way cross classified random model with 1,774 calves out of line 4. The covariance between the two random effects served as an estimate of the covariance sire-maternal grand sire. Falconer's (1965) model was also fitted to obtain an estimate of the correlation between maternal phenotype of the daughter and dam for birth and

weaning weight (fm path, Koch, 1972). The procedure used was least-squares multiple regression of the coefficients (for the phenotypic variance, a linear and a non linear term for the additive variance, and a term including dominance and environmental deviations) on the estimates of the covariances between relatives for both weights, as suggested by Thompson (1976). The equations were solved for different values of fm (-1.0, -.5, 0, .5 and 1.0) and iterations were made to a convergence value of the estimated heritability (h^2) by paternal-half sibs for birth and weaning weight. The direct and maternal sources of variation to be estimated were: σ^2Ao, additive genetic direct variance; σ^2Am, additive genetic maternal variance; $\sigma AoAm$, covariance between additives genetic direct and maternal effects; σ^2Do, direct dominance variance; σ^2Dm, maternal dominance variance; $\sigma DoDm$, covariance between direct and maternal dominance effects; σ^2Eo, random environment over the direct phenotype; σ^2Em, maternal environmental variance or variation common to maternal half-sibs and full-sibs and $\sigma EoEm$, environmental covariance between direct and maternal effects. These nine parameters were estimated by ordinary and weighted least-squares multiple regression techniques where the estimates of the covariances between relatives were regressed on the expected coefficients for the direct and maternal variances and covariances. The weights used were the number of records of estimation for the particular covariance between relatives considered.

Heritability estimates were .28 for both weights through paternal half-sibs and .45 and .88 through full-sibs for birth and weaning weight, respectively. Repeatability estimates were .21 for birth weight and .32 for weaning weight. Heritabilities through regression of offspring on dam and offspring on sire were .45 and .21 for birth weight and .28 and .06 for weaning weight. Genetic, phenotypic and environmental correlations were estimated to be .56, .41 and .36 for birth weight and .54, .38 and .41 for weaning weight, respectively.

All solutions showed a negative correlation between additive direct and additive maternal effects (r_G). Estimates of r_G ranged from -.36 to -1.03 for birth weight and from -.28 to -.94 for weaning weight. The estimates of heritability for direct effects (h^2o), heritability for maternal effects (h^2m) and heritability for total additive genetic effects ($h^2{}_T$) were .21 to .26, .02 to .42 and .01 to .25 for birth weight and .21 to .34, .08 to .61 and .02 to .21 for weaning weight. Dominance also affected both direct and maternal effects on birth and weaning weight. Larger values of $\sigma DoDm$ with respect to the product of $\sigma^2 Do$ and $\sigma^2 Dm$ suggest that epistasis may be also involved. The environmental covariance ($\sigma EoEm$) was clearly negative for weaning weight (-5.13 to -40.48 kg^2). This result was supported by a negative estimate of fm (-.10) for weaning weight. This effect involving maternal phenotypes of dam and daughter was less clear for birth weight where fm was positive (.08) but the two estimates of $\sigma EoEm$ were not in close agreement (.61 and -.56 kg^2).

The results obtained in this study indicated that $\sigma AoAm$ is largely negative for both traits causing genetic improvement to be more difficult (Van Vleck et al, 1977). Results also indicated that environmental covariance between maternal phenotype of the dam and daughter was negative for weaning weight.

REFERENCES CITED

Alsing, I., J. Krippl and F. Pirchner. 1980. Maternal effects on heritability of litter traits in pigs. Z. Tierz. Zuchtungsbiol. 97:241.

Anderson, D. C. 1966. Some factors affecting performance in three closed lines of Hereford cattle. M.S. thesis. Montana State University, Bozeman, Mt.

Baker, R. L. 1980. The role of maternal effects on the efficiency of selection in beef cattle - A Review. Proc. NZ. Soc. Anim. Prod. 40:285.

Beltran Bru, J. J. 1978. Evaluation of direct and maternal effects on weaning traits in Brahman cattle. Diss. Abstr. Int(B). 5669.

Bondari, K., R. L. Willham and A. E. Freeman. 1978. Estimates of direct and maternal genetic correlations for pupa weight and family size of Tribolium. J. Anim. Sci. 47: 358.

Brown, C. J. and V. Galvez. 1969. Maternal and other effects on birth weight of beef calves. J. Anim. Sci. 28:162.

Buchanan, D. S., M. K. Nielsen, R. M. Koch and L. V. Cundiff. 1982. Selection for growth and muscling score in beef cattle. II. Genetic parameters and predicted response. J. Anim. Sci. 55:526.

Bulmer, M. G. 1971. The effect of selection on genetic variability. American Naturalist. 105:201.

Bulmer, M. G. 1976. Regressions between relatives. Genet. Res. 28:199.

Burfening, P. J., D. D. Kress, R. L. Friedrich and D. D. Vaniman. 1978. Phenotypic and genetic relationship between calving ease, gestation length birth weight and preweaning growth. J. Anim. Sci. 47:595.

Burfening, P. J., D. D. Kress and R. L. Friedrich. 1981. Calving ease and growth rate of Simmental-sired calves. III. Direct and maternal effects. J. Anim. Sci. 53:1210.

Cantet, R. J. C. 1983. El crecimiento del ternero. Hemisferio Sur. Buenos Aires, Argentina (1ra. Ed.).

Christian, L.L., E. R. Hauser and A. B. Chapman. 1965. Association of preweaning and postweaning traits with weaning weight in cattle. J. Anim. Sci. 24:652.

Crow, H. G. and W. E. Howell. 1982. Genetic parameters of the maternal grandsire contribution to beef cattle weaning weights. Can. J. Anim. Sci. 62:1057.

Deese, R. E. and M. Koger. 1967. Maternal effects on preweaning growth rate in cattle. J. Anim. Sci. 26:250.

Dickerson, G. E. 1947. Composition of hog carcasses as influenced by heritable differences in rate and economy of gain. Iowa Agric. Exp. Sta. Res. Bull. No. 354.

Dinkel, C. A. and D. A. Busch. 1973. Genetic parameters among production carcass composition and carcass quality traits of beef cattle. J. Anim. Sci. 36:832.

Dixon, W. J., M. B. Brown, L. Engelman, J. W. Frane, M. A. Hill, R. I. Jennrich and J. D. Toporek. 1981. BMDP statistical software 1981. University of California Press, Los Angeles, Ca.

Eisen, E. J. 1967. Mating designs for estimating direct and maternal genetic variances and direct-maternal genetic covariances. Can. J. Genet. Cytol. 9:13.

Ellicott, G. H., L. A. Holland and A. L. Neumann. 1970. Most probable producing ability of Hereford cows. Proc. West. Sec. Amer. Soc. Anim. Sci. 21:363.

Everett, R. W. and W. T. Magee. 1965. Maternal ability and genetic ability of birth weight and gestation length. J. Dairy Sci. 48:957.

Falconer, D. S. 1965. Maternal effects and selection response. Genetics Today. Proc. XI Int. Congress of Genetics. The Hague, The Netherlands. September 1963. Vol. 3, p. 763.

Falconer, D. S. 1981. Introduction to quantitative genetics. Longman, NY. (2nd. Ed.).

Fisher, L. J. and C. J. Williams. 1978. Effect of environmental factors and fetal and maternal genotype on gestation length and birth weight of Holstein calves. J. Dairy Sci. 61:1462.

Flower, A. E., J. S. Brinks, J. J. Urick and F. S. Willson. 1963. Comparisons of inbred lines and linecrosses for performance traits in Hereford range cattle. J. Anim. Sci. 22:914.

Flower, A. E., J. S. Brinks, J. J. Urick and F. S. Willson. 1964. Selection intensities and time trends for performance traits in range Hereford cattle under mass and recurrent selecion. J. Anim. Sci. 23:189.

Hamann, H. K., S. Wearden and W. H. Smith. 1963. Estimation of genetic and environmental factors affecting weaning weights of creep-fed cattle. J. Anim. Sci. 22:316.

Harvey, W. R. 1977. User's guide to LSML 76 mixed model least-squares and maximum-likelihood computer program. Ohio State Univ. Columbus (Mimeo.).

Henderson, C. R. 1953. Estimation of variance and covariance components. Biometrics 9:226.

Hill, J. R., Jr. 1965. The inheritance of maternal effects in beef cattle. Unpublished Ph. D. Thesis, North Carolina State University, Raleigh, NC. Cited by Robison (1981).

Hill, J. R. Jr., J. E. Legates and E. U. Dillard. 1965. Inheritance of maternal effects in beef cattle. J. Anim. Sci. 25:264 (Abstr.).

Hohenboken, W. D. 1973. Relationship between direct and maternal effects on weaning weight in cattle. In: Ralph Bogart (Ed.). Genetic Lectures. Vol. 3, p. 149. Oregon State University Press, Covallis.

Hohenboken, W. D. and J. S. Brinks. 1971a. Relationships between direct and maternal effects on growth in Herefords: II. Partitioning of covariance between relatives. J. Anim. Sci. 32:26.

Hohenboken, W. D. and J. S. Brinks. 1971b. Relationships between direct and maternal growth in Herefords. III. Covariance of paternal half-brother and sister performance. J. Anim. Sci. 32:35.

Jennrich, R. I. and P. I. Sampson. 1976. Newton-Raphson and related algorithms for maximum likelihood variance component estimation. Technometrics. 18:11.

Jonhson, I. D. and J. M. Obst. 1984. The effects of level of nutrition before and after 8 months of age on subsequent milk and calf production of beef heifers over three lactations. Anim. Prod. 38:57.

Johnson, L. W. and R. D. Riess. 1981. Introduction to linear algebra. Addison Wesley, Ca. (1st. Ed.).

Kempthorne, O. 1955. The correlation between relatives in random mating populations. Cold Spring Harbor Symp. on Quant. Biol. 22:60.

Kennedy, B. W. and C. R. Henderson. 1975. Components of variance of growth traits among Hereford and Aberdeen Angus calves. Can. J. Anim. Sci. 55:493.

Kennedy, B. W. and C. R. Henderson. 1977. Genetic trends among sires and dams in record of performance tested herds. Can. J. Anim. Sci. 57:339.

Koch, R. M. 1972. The role of maternal effects in animal breeding: VI. Maternal effects in beef cattle. J. Anim. Sci. 35:1316.

Koch, R. M. and R. T. Clark. 1955a. Genetic and Environmental relationships among economic characters in beef cattle. I. Correlation among paternal and maternal half-sib. J. Anim. Sci. 14:775.

Koch, R. M. and R. T. Clark. 1955b. Genetic and environmental relationships among economic characters in beef cattle. II. Correlations between offspring and dam and offspring and sire. J. Anim. Sci. 14:786.

Koch, R. M. and R. T. Clark. 1955c. Genetic and environmental relationships among economic characters in beef cattle. III. Evaluating maternal environment. J. Anim. Sci. 14:979.

Koch, R. M., K. E. Gregory and L. V. Cundiff. 1982. Critical analysis of selection methods and experiments in beef cattle and consequences upon selection programs applied. Proc. 2nd. World Congress on Genetics Applied to Livestock Prod. Madrid Spain, Oct. 4-8.

Kress, D. D. and P. J. Burfening. 1972. Weaning weight related to subsequent most probable producing ability in Hereford cows. J. Anim. Sci. 35:327.

Kress, D. D., P. J. Burfening and R. L. Friedrich. 1979. Direct genetic and maternal genetic effects on weaning weight in Simmental-sired calves. J. Anim. Sci. 49 (Suppl. 1):162 (Abstr.).

Legault, C. R. and R. W. Touchberry. 1962. Heritability of birth weight and its relationship with production in dairy cattle. J. Dairy Sci. 45:1226.

Lush, J. L. 1945. Animal breeding plans. Iowa State College Press, Ames, Ia. (3rd. ed.)

Mangus, W. L. and J. S. Brinks. 1971. Relationships between direct and maternal effects on growth in Herefords: I. Environmental factors during preweaning growth. J. Anim. Sci. 32:17.

Martin, T. G., R. P. Lemenager, G. Srinivassan and R. Alenda. 1981. Creep feed as a factor influencing performance of cows and calves. J. Anim. Sci. 53:33.

Mode, C. J. and H. F. Robison. 1959. Pleiotropism and the genetic variance and covariance. Biometrics. 15:518.

Ochoa, P. G., W. L. Mangus, J. S. Brinks and A. H. Denhan. 1981. Effect of creep feeding bull calves on dam most probable producing ability values. J. Anim. Sci. 53:567.

Osborne, R and W. S. B. Paterson. 1952. On the sampling variance of heritability estimates derived from variance analyses. Proc. Royal Soc. Edinb., B. 64:456.

Patterson, H. D. and R. Thompson. 1971. Recovery of inter-block information when blocks sizes are unequal. Biometrika. 58:545.

Philipsson, J. 1976. Studies on calving difficulty, stillbirth and associated factors in Swedish cattle breeds. III. Genetic Parameters. Acta Agr Scand. 26:211.

Preston, T. R. and M. B. Willis. 1970. Intensive beef Production. Pergamon Press, NY. (1st. Ed.).

Robertson, A. 1977. The effect of selection on the estimation of genetic parameters. Z. Tierz. Zuchtungsbiol. 94:131.

Robison, O. W. 1981. The influence of maternal effects on the efficiency of selection; a review. Livest. Prod. Sci. 8: 121.

Schaeffer, L. R. and J. W. Wilton. 1974. Age of dam, sex, and enviromental interactions affecting preweaning average daily gains of beef cattle. Can. J. Anim. Sci. 54:183.

Searle, S. R. 1971. Linear models. John Wiley and Sons Ltd., NY. (1st. Ed.).

Seber, G. A. F. 1977. Linear regression analysis. John Wiley and Sons, NY. (1st Ed.).

Sejrsen, K. 1978. Mammary development and milk yield in relation to growth rate in dairy and dual-purpose heifers. Acta Agr. Scand. 28:41.

Sellers, H. I., R. L. Willham and R. C. DeBaca. 1970. Effects of certain factors on weaning weight of beef calves. J. Anim. Sci. 31:5.

Thompson, J. R., A. E. Freeman and P. J. Berger. 1981. Age of Dam and maternal effects for dystocia in Holsteins. J. Dairy Sci. 64:1603.

Thompson, R. 1976. The estimation of maternal genetic variances. Biometrics. 32:903.

Thrift, F. A., E. U. Dillard, R. R. Shrode and W. T. Butts. 1981. Genetic parameter estimates based on selected and control beef cattle populations. J. Anim. Sci. 53:57.

Totusek, Robert. 1968. Early weaning vs. normal weaning vs. creep feeding of heifer calves. Okla. Agr. Exp. Sta. Misc. Pub. MP No. 80:72.

United States Department of Agriculture. Soil Conservation Service. 1982. Soils of Montana. Bull. No. 744. Bozeman, Mt.

United State Department of Commerce. 1982. Monthly normals of temperature, precipitation and, heating and cooling degree days 1951-1980. Montana Climatography of the United States. No. 81 (by State).

Van Vleck L. D. and C. L. Hart. 1966. Covariances among first-lactation milk records of cousins. J. Dairy Sci. 49:41.

Van Vleck, L. D., D. St. Louis and J. I. Miller. 1977. Expected phenotypic response in weaning weight of beef calves from selection for direct and maternal genetic effects. J. Anim. Sci. 44:360.

Vesely, J. A. and O. W. Robison. 1971. Genetic and maternal effects on preweaning growth and type score in beef calves. J. Anim. Sci. 32:825.

White, J. M., W. E. Vinson and R. E. Pearson. 1981. Dairy cattle improvement and genetics. J. Dairy Sci. 64:1305.

Willham, R. L. 1963. The covariance between relatives for characters composed of components contributed by related individuals. Biometrics. 19:18.

Willham, R. L. 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. J. Anim. Sci. 35:1288.

Willham, R. L. 1980. Problems in estimating maternal effects. Livest. Prod. Sci. 7:405.

Woldehawariat, G., M. A. Talamantes, R. R. Petty and T. C. Cartwright. 1977. A summary of genetic and environmental statistics for growth and conformation characters of beef cattle. Texas Agr. Exp. Sta. Tech. Rep. No. 103.

Zollinger, W. A. and M. K. Nielsen. 1984. An evaluation of bias in estimated breeding values for weaning weight in Angus beef cattle field records. I. Estimates of within herd genetic trend. J. Anim. Sci. 58:545.

APPENDIX

Derivation of the expectations for the maternal grand dam (MGD) and maternal grand sire (MGS) components by using path coefficients

Figure 4 describes the phenotype of two grandoffspring under the maternal effect model (Koch, 1972). The abbreviations are defined by Koch (1972). Po is the phenotypic, Go is the additive genetic, Do is the dominance and Eo is the environmental value for birth weight or weaning weight expressed by individuals. Pm, Gm, Dm and Em are corresponding maternal effects. Primes on values represent parental values and double primes represent grandparent values. Path coefficient between symbols (.5, g, d, e, p, fm) are standard partial regression coefficients. Double arrows represent residual correlations between traits.

P_{o1} and P_{o2} are either maternal granddam sibs or maternal grandsire sibs. G'_1 and G'_2 are the genotypes of the daughters of G'' (genotype of maternal grand dam or a maternal grand sire). The correlation between P_{o1} and P_{o2} is

$$r(P_{o1}, P_{o2}) = 1/16\ g_o^2 + 1/4\ r_G\ g_o\ g_m + 1/4\ g_m^2\ pm^2 \qquad (1)$$

but $g_o^2 = \sigma^2 Ao / \sigma^2 P$, $r_G\ g_o\ g_m = (\sigma AoAm\ \ \sigma Ao\ \ \sigma Am)/(\sigma Ao\ \ \sigma Am\ \ \sigma^2 P)$ and $g_m^2\ pm^2 = \sigma^2 Am / \sigma^2 P$, (Koch, 1972). Therefore, on dividing both sides of (1) by $\sigma^2 P$, the covariance between P_{o1} is

$$cov(P_{o1}, P_{o2}) = 1/16\ \sigma^2 Ao + 1/4\ \sigma AoAm + 1/4\ \sigma^2 Am$$

This term is common for MGD and MGS. If the path (fm) between maternal phenotypes of the grand dam (P"m) and of the daughter (P'm) exists then

$$r(P_{o1},P_{o2}) = 1/16\ go^2 + 1/4\ r_G\ go\ gm\ pm + 1/4\ gm^2 + pm^2\ fm^2 +$$

$$+ 1/2\ pm^2\ fm\ gm^2 + 1/4\ pm\ fm\ g_o\ r_G\ g_m$$

$$= 1/16\ {}^2Ao + 1/4\ \sigma AoAm + 1/4\ \sigma^2 Am + pm^2\ fm^2 +$$

$$+ 1/2\ pm^2\ fm\ \sigma^2 Am + 1/4\ pm\ fm\ \sigma AoAm$$

and

$$cov(P_{o1},P_{o2}) = 1/16\ \sigma^2 Ao + 1/4\ \sigma AoAm + 1/4\ \sigma^2 Am + pm^2\ fm^2\ \sigma^2 P +$$

$$+ 1/2\ \sigma^2 Am\ fm + 1/4\ fm\ \sigma AoAm$$

$$= 1/16\ \sigma^2 Ao + (1/4 + 1/4\ fm)\ \sigma AoAm +$$

$$+ (1/2 + 1/2\ fm)\ \sigma^2 Am$$

If $fm = -.1$, as it was estimated in the present study, $fm^2 = .01$. The term pm^2 is the variance of maternal phenotypes in "absence of additive genetic effects among the dams", as defined by Falconer (1965). Because of the way this variance (pm^2) is defined, it is not expected to be large. Therefore, this term is negligible and the approximate difference between MGD and MGS is

$$= 1/4\ fm\ \sigma AoAm + 1/2\ fm\ \sigma^2 Am$$

$$= fm\ (1/4\ \sigma AoAm + 1/2\ \sigma^2 Am).$$

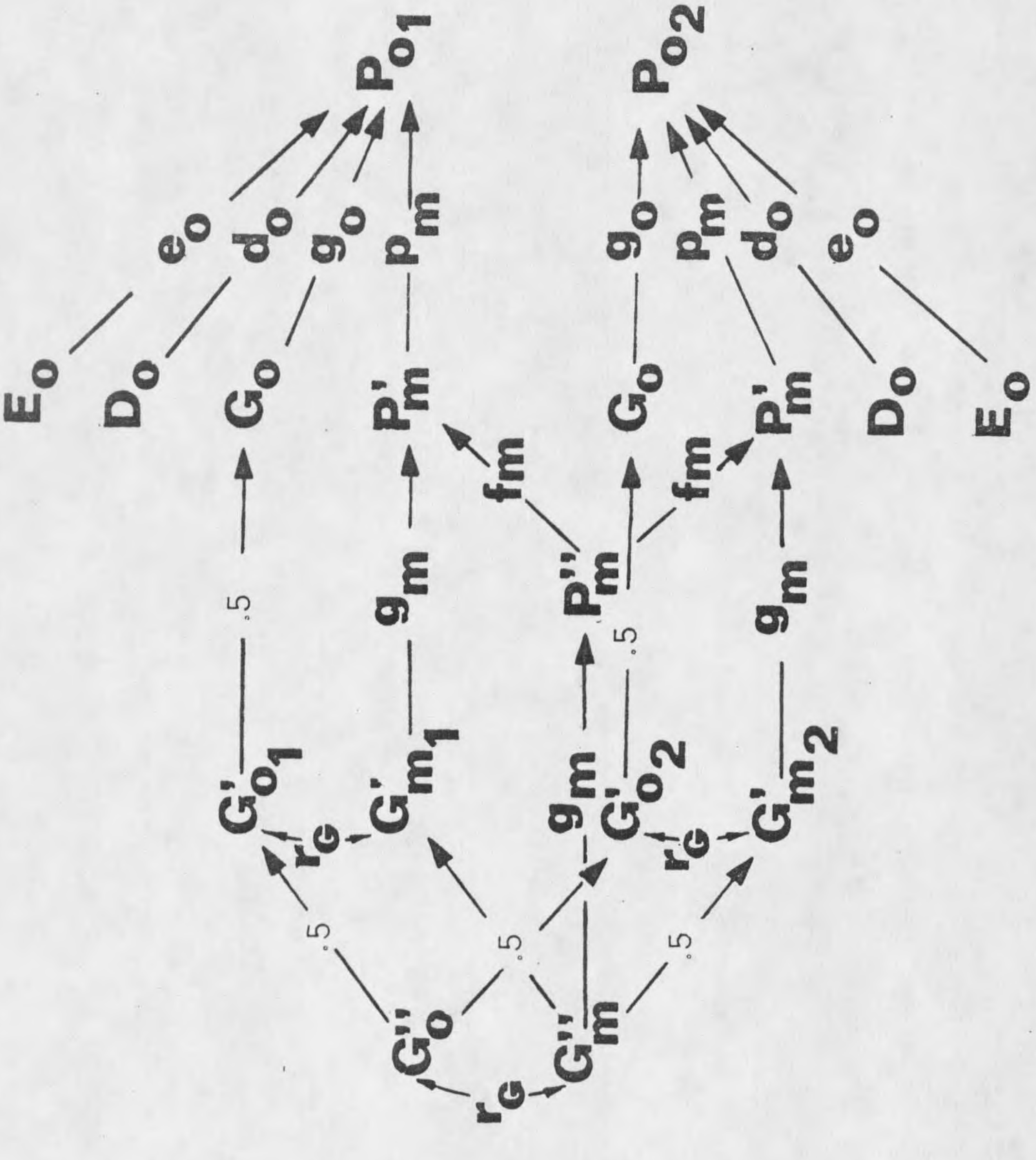


Figure 4. A path coefficient diagram describing the covariance between maternal grand progeny.

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