DISSERTATION

GENETIC RELATIONSHIPS BETWEEN SEX-SPECIFIC TRAITS IN A CROSSBRED BEEF CATTLE POPULATION

Submitted by

Nevil C. Speer

Department of Animal Science

In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer, 1993

COLORADO STATE UNIVERSITY

April 14, 1993

WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY NEVIL CRAFT SPEER ENTITLED "GENETIC RELATIONSHIPS BETWEEN SEX-SPECIFIC TRAITS IN A CROSSBRED BEEF CATLLE POPULATION" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

Adviser

Department Head

ABSTRACT OF DISSERTATION

GENETIC RELATIONSHIPS BETWEEN
SEX-SPECIFIC TRAITS
IN A CROSSBRED BEEF CATTLE POPULATION

Data used were obtained from the Fort Keogh Livestock and Range Research Laboratory (LARRL), Miles City, Montana. Data were from a crossbreeding experiment involving Hereford, Angus and Charolais cattle collected from 1962 to 1977. Traits studied and considered separate with respect to sex, included male and female birth weight (BWM and BWF), weaning weight (WWM and WWF), and postweaning average daily gain (ADGM and ADGF). Other traits studied were average adjusted mature weight (MW) of cows and fat thickness (FT), ribeye area (REA), yield grade (YG), quality grade (QG) and days on feed (DOF) of bulls and steers slaughtered at a weight constant endpoint of 1000 - 1050 lb.

Multi-trait sire-maternal grandsire REML analyses were performed on straightbred and crossbred Hereford, Angus, and Charolais cattle. Observations on 2888 animals contributed to development of the A-inverse which represented relationships among 138 sires and maternal grandsires. Models for BWM, BWF, WWM, WWF, ADGM, ADGF, and MW analyses models included birth year, age of dam (2,

3, 4, 5+) and linear regression on weaning age. The DOF analysis model included birth year, age of dam, sex of calf (bull vs steer), age of dam-sex of calf interaction and linear regression on weaning age. Carcass trait (FT, REA, YG, QG) models included birth year, age of dam, sex of calf, age of dam-sex of calf interaction and linear regression on carcass weight. Linear regressions on individual breed percentage, combined reciprocal cross percentage (individual heterosis), dam breed percentage and dam combined reciprocal cross percentage (maternal heterosis) were also included in all models for analyses of all traits of interest.

Correlations between direct components of birth weight, weaning weight, and postweaning average daily gain considered seperately between male and female calves were .93, .90 and .74 respectively. The correlation between direct components of MW and DOF was -.66. Correlations between direct components of MW and carcass traits were -.54, -.18, -.18, and .41 for FT, REA, YG and QG, respectively.

Correlations between maternal components of birth weight, weaning weight, and postweaning average daily gain considered seperately between male and female calves were .86, .98 and .42, respectively. The correlation between maternal components of MW and DOF was -.71. Correlations between maternal components of MW and carcass traits were .40, .10, .08, and -.06 for FT, REA, YG and QG, respectively. Correlations between mat-dir and dir-mat of the same traits studied were moderate and ranged from -.44 to .47.

Predictions of correlated responses in mature weight per standard deviation of direct response in male carcass traits were -32 lb, -13 lb, -10 lb, and 31 lb respectively for FT, REA, YG and QG. Correlated response predictions indicate selection for improved carcass cutability on a weight constant basis (increased leanness and decreased yield grades) would increase mature weight while selection for increased ribeye area and decreased quality grade scores (favorable) on a weight constant basis would result in decreased mature weights of females. Strong selection pressure for leanness may be antagonisitic to commercial beef producers since results suggest sires selected on the basis of reducing fat in steer progeny also produce females that are larger at maturity when cattle are slaughtered at a constant weight endpoint. It should be noted, however, relationships between carcass traits and mature weight may differ when cattle are slaughtered at a constant age endpoint.

Nevil Craft Speer
Department of Animal Sciences
Colorado State University
Fort Collins, CO 80523
Summer, 1993

ACKNOWLEDGEMENTS

I am very fortunate to have been provided the opportunity to work with Dr. Brinks. It is difficult to envision working with anyone else and my appreciation for his abilities increases with each day. Dr. Brinks is an extremely gifted person. He is among the elite of animal breeders, an effective communicator to cattlemen and an enjoyable person who cares about others. Dr. Brinks managed to not only teach, educate, and advise, but also allowed me freedom to be involved with other activities and opportunities. His guidance through graduate school will always be valued.

Special appreciation needs also be expressed to my other committee members. Drs. Field, Richardson, and Tatum have all been a pleasure to work with. Each of these committee members possess the ability to balance research with application. Their input and insight has been extremely meaningful.

My thanks to Dr. Mike MacNeil, Fort Keogh Livestock and Range Research Laboratory, Miles City, Montana. Dr. MacNeil has enabled this project to be possible. I am hopeful this is only the beginning of future joint projects.

The time I have spent in graduate school also represents the development of some very special

friendships. My opportunities to work with the young people on the livestock judging team will always be treasured. These students have contributed so much to my life and I will be forever indebted to them for all they have done for me. They are my confidence in the future of the livestock industry.

Brad Gillmore has managed to keep things in perspective for me. Brad has always been there to listen regardless of my concerns or complaints and offer useful advice. I am certain that I would have taken many things far too seriously without him. There are few people like Brad. And as a result, there are few friendships like he provides.

Clint Rusk represents many things to me. He has been an employer, a teacher and most importantly a friend. Clint has given and contributed so much during my time in graduate school. I will always value his thoughts, beliefs, concerns, and loyalty. It is difficult to imagine how different things might have been without him.

Finally, and most importantly, my wife Sandra has always freely offered her loving support. Thank you, for without you and your love this would not have been possible.

TABLE OF CONTENTS

TABLE OF CONTENTS CONTINUED

LIST OF TABLES

LIST OF TABLES CONTINUED

CHAPTER I

INTRODUCTION

In recent years, considerable discussion, money, and time has been devoted to economic considerations involved in the production of the beef industry's "end product". This is a result of demands by the U.S. consumer which have changed more in the last dozen years than at anytime in history (Smith, 1989). The beef industry has also simultaneously realized that greater efficiency in production must be obtained in order to remain competitive with other meat products.

Assessment of consumer demands intensified in 1986 when the National Cattlemen's Association (NCA) sponsored the National Consumer Household Beef Study (NCHBS) and the National Consumer Retail Beef Study (NCRBS). The major conclusion of both studies was that excess fat must be removed from beef in order to improve its image and increase sales (Smith, 1990). Beef Industry Council (BIC), NCA and the USDA cooperated on a follow-up study, The National Beef Market Basket Study (NBMBS), which indicated that the industry had responded to production of excess fat through retail trimming of outside fat.

The National Cattlemen's Association responded to to these studies by creating the Value-Based Marketing Task Force founded on the premise that "...the marketing systems that tolerate and even encourage excess waste fat production have not changed" (NCA, 1990) indicating that merely trimming fat was not a suitable long-term solution. The Task Force outlined eight seperate recommendations

(NCA, 1990) for decreasing fat production and increasing profitability. The Task Force executive summary stated, "The Task Force unanimously endorses the belief that excess fat production is a detriment to the industry, in terms of production costs and in meeting contemporary consumer demand" and that costs due to excess fat production are four billion dollars per year. These developments have led to discussion concerning value-based marketing especially in light of the highly segmented nature of the beef industry; "The more clearly an industry is integrated, the less it needs a value-based marketing system..." (Smith, 1991).

The U.S. beef industry has also recognized the need to define, characterize, and rethink the logic of what has normally been defined as "quality" (Smith, 1991) of its end product. The issue of excess fat production has been coupled with concerns relative to safety, consistency, and efficiency. These concerns resulted in NCA sponsoring the National Beef Quality Audit - 1991. The goal of the quality audit was "to conduct a quality audit of slaughter steers/heifers (their carcasses, cuts and dress-off/offal items) for the U.S. beef industry in 1991, establishing baselines for present quality shortfalls and identifying targets for desired quality levels by the year 2001" (NCA, 1991).

These trends have resulted in breed associations focusing attention on carcass characteristics of their respective breeds in order to favorably position their product for the future. The American Angus Association now publishes carcass EPDs as a part of their semi-annual sire summaries. The American Hereford Association recently devoted nearly $85,000 (American Hereford Journal, November, 1991) for the CSU/Monfort Project to study feedlot and carcass characteristics of Hereford cattle. The American Charolais Association is currently pursuing the development of carcass EPDs.

During the past three decades, the beef industry has been primarily concerned with investigation of production of beef cattle. There was very little concern within the industry regarding consumers and their demands, except for a small amount of endpoint research published in the mid- to late-1960s. As a result, a large majority of work concerning beef cattle has been focused upon "production traits". It is the production traits that largely dictated profitability for producers. The beef industry has become very efficient in terms of production; the industry has nearly eliminated Bang's disease, has increased growth, developed efficient crossbreeding systems, and created reliable genetic predictors (EPDs) for growth traits.

The industry's focus on its end product has also occured with the recognition for the need to reexamine the goals of current production systems. A renewed emphasis on profitability in production systems is occurring. The "quest for size" (Knop, 1992) in the past decade has ended. No longer is maximum growth the ultimate goal. This has caused Integrated Resource Management programs to enjoy large amounts of study and popularity across the country.

Geneticists are also now beginning to study questions concerning across-breed EPDs. An attempt is being made to equate differences between breeds for the respective traits for which EPDs are available. This has created the need for investigation of crossbred populations to fairly evaluate and report rankings between the large number of beef cattle breeds available to the commercial producer. Across-breed EPDs have exposed the need for refinement of analytical techniques of crossbred populations in order to attain accurate and appropriate results. The literature review is largely devoted to previous analytical techniques of crossbred cattle populations.

Current marketing schemes solely reward efficiency of production before cattle become the packer's possession. However, if the industry wants to remain competitive it will increasingly pressure producers for cattle that meet current market demands. "If beef products are to be competitive in the 1990s and beyond, a reward system must be devised that will encourage production of exemplary cattle, carcasses and cuts" (Smith, 1990). It is likely that if value-based marketing begins there will be large adjustments from all facets of the beef production sector

(Cornett, 1990). There will be a need for producers to obtain seedstock whose progeny will produce palatable beef carcasses with desired amounts of muscling and fatness (Allender, 1990). However, seedstock producers will need to become increasingly efficient in order to remain profitable. Progeny will also still need to excel in growth, breed early, wean heavy calves, rebreed each year, etc...

The objective of this study is to examine relationships in a crossbred beef cattle population between economically important sex related traits using REML procedures. It is designed to investigate genetic relationships between important production characteristics with a special emphasis on mature size and carcass measures and to answer questions concerning: 1) appropriate analytical techniques of crossbred beef cattle populations and 2) the feasability of producing cattle that excel in terms of efficiency both for the producer and the packer.

CHAPTER II

REVIEW OF LITERATURE

INTRODUCTION

This study and the author's preceding master's project utilized data which consisted of purebred and crossbred cattle. Data of this type present several complexities and considerations in analyses that properly account for significant sources of genetic variation (Golden, 1991).

Traditional approaches to analyses of crossbred populations may have several inherent problems. Multibreed analyses require consideration of three additional factors not normally considered in analyses of purebred populations. These factors include: 1) foundation subpopulations may possess different means, 2) foundation subpopulations may possess different variances, and 3) heterosis may be present (Golden, 1991).

These considerations result in this review to focus primarily upon analytical techniques and strategies for crossbred data. Limited previous studies have been reported concerning proper methods of analysis of crossbred data. Robison (1981) explains this situation:

> "Although considerable research has evaluated crossbreeding in farm animals, the analyses and reporting of the results have often been inadequate. Generally, the breed group means and heterosis values have been presented. However, little attention has been paid to evaluation of the genetic components - e.g., average breed effects, average heterosis, specific heterosis, etc. - or to the development of parameters that allow prediction of the performance of crosses that have not actually been tested."

The review of literature contains several sections dealing with crossbreeding and analyses of crossbred populations which include:

1. summary of master's review of literature,
2. review of crossbreeding,
3. evolution of crossbred population analytical methods,
4. grouping strategies for crossbred populations,
5. summary.

SUMMARY OF MASTER'S REVIEW OF LITERATURE

The primary objective of this study is to investigate genetic relationships which exist among growth, carcass, and female productivity traits. The master's thesis (Speer, 1991) preceding this study included a review of literature focused on previous work concerning the relationships of interest. The literature review included discussions of carcass, growth, and maternal traits, as well as the relationships among them. In addition, the review also included parameter estimates concerning these traits and relationships.

In summary, breeds that excel in growth also tend to be characterized by females who are slightly more fertile, have greater maternal ability (milk plus one-half direct effects) and are larger at maturity. However, breeds that excel solely in carcass leanness, that is not a result of increased growth, are characterized by females who tend to be older at puberty, possess lower levels of fertility, and are larger at maturity (MacNeil, 1988). The highest levels of female fertility and maternal ability are observed in breeds which produce carcasses of intermediate composition and tend to be only slightly above average for postweaning growth rate (MacNeil, 1988).

Female lines selected for maternal ability tend to easily lose growth and carcass efficiency if these traits are ignored (Smith, 1964). Smith also reported that maternal traits can be appropriately ignored in terminal sire lines as replacement females will not be retained. As a result, the use of generalized or "complete" breeds, those that are above average in all traits, are effective if the relationships between direct, carcass, and maternal effects are independent or favorable. If the relationships between beef (carcass and growth) and maternal traits is antagonistic, the use of breeds in specialized roles will likely become far more prominent within the beef industry.

REVIEW OF CROSSBREEDING

The objective of well-designed crossbreeding systems is to advantageously combine additive breed effects, breed complementarity, and heterosis effects simultaneously (MacNeil et al., 1988; Gregory and Cundiff, 1980; Willham, 1970; Cundiff, 1970). There are large differences among the various breeds in terms of gene frequencies, and therefore additive breed effects (Willham, 1970), resulting in large differences in reproduction efficiency, growth rate, and caracass composition (MacNeil et al., 1988). It has been well documented that heterosis enables additional opportunities (beyond usage of additive breed effects and breed complementarity) to increase efficiency and profitability of commercial beef operations. MacNeil (1987) showed that for each commercial operation there exists a unique breed composition which fully takes advantage of gene complementarity and heterosis thereby enhancing profit. Stated another way, the deleterious effects of inbreeding on vigor has also been well documented and these effects can be reversed through crossing inbred lines (crossbreeding) which may result in increased profit (Parekh and Tourchberry, 1974).

The advantages of utilizing a well-planned, systematic crossbreeding program for increasing efficiency of commercial beef production is well documented (Gregory and Cundiff, 1980) and much literature concerning this topic is readily available.

EVOLUTION OF CROSSBRED POPULATION ANALYTICAL METHODS

Analysis of crossbred data in comparison to straightbred data creates some unique problems in dealing with epistatic and heterotic effects. These effects are further complicated when considering their interaction with maternal influences. There is a large amount of literature reporting the performance of crossbred populations. As mentioned previously, a limited amount of literature compares specific analytical models and their appropriateness for use in studying crossbred data.

Damon et al. (1961) performed some of the first analyses concerning crossbred beef cattle. Damon's least-squares analyses involved six different breeds (Hereford, Angus, Brangus, Brahman, Charolais, and Shorthorn). The analytical model attempted to account for general combining ability and specific combining ability. In addition, the model also accounted for specific direct and heterotic effects. The model included breed-cross designations for the purpose of analyzing general combining ability, specific combining ability, and additive breed effects. The model also included designations for purebred versus crossbred individuals (all calves were either purebred or F_1's). Finally, analyses also included maternal additive breed effects (all cows were purebreds) by designation of breed of cow. The model appeared to be adequate in accounting for significant sources of variation. Damon et al. (1961) concluded: "...large differences were demonstrated among breeds and cross of breeds in different types of gene action".

Gardner and Eberhart (1966) proposed the first analytical models to identify and quantify specific sources of genetic variation in crossbred populations. The proposed analytical model was developed to investigate crossbred populations of plants. These models attempted to account for additive, dominance, additive by additive epistatic, and heterotic gene effects. The effects included in the analytical model allowed Gardner and Eberhart to "characterize" means for the different varieties and variety crosses. It also enabled accounting for major genetic sources of variation with "minimum confounding".

Eberhart and Gardner (1966), a short time later, applied the above mentioned model to six lines of maize and diallel combinations of these lines to test the usefulness of the previously proposed analytical model. The analytical techniques appeared to appropriately account for the genetic sources of variation and adequately avoid confounding among these sources of variation. Eberhart and Gardner reported realistic constants for lines, average heterosis, line heterosis, specific heterosis, and epistatic effects.

The data used for this study was a result of the crossbreeding experiment conducted at the Fort Keogh Livestock and Range Research Laboratory, Miles City, MT, (LARRL) involving Hereford, Angus, Charolais, and Brown Swiss cattle. There have been several reports in the literature concerning the the results of this experiment. The first published literature from this crossbreeding experiment was reported by Pahnish et al. (1969). This study investigated calf performance from birth to weaning. Analysis was performed on a population resulting from phase I of the experiment which included straightbred calves and first generation two-way cross calves (F_1's). The least-squares model accounted for additive and heterotic effects through inclusion of breed of sire of calf, breed of dam of calf, and interaction of breed of sire - breed of dam.

Knapp et al. (1980) reported on maternal preweaning and weaning heterosis utilizing data produced from phases I and II of the crossbreeding experiment at LARRL. The model included breed of sire of cow and breed of dam of cow in order to account for additive gene effects. The model also included breed of sire of cow * breed of dam of cow interactions in order to account for heterotic effects.

Several other reports, previous to Urick et al. (1986) have been published as a result of this Hereford, Angus, Charolais, and Brown Swiss crossbreeding study. Pahnish et al. (1971) investigated postweaning performance of heifers. Urick et al. (1974) reported results of carcass quality and quantity traits. Reynolds et al. (1986) analyzed performance for pregnancy rate, calf survival, weaning age, and weaning rate. All three of these studies utilized identical analytical methods described by Pahnish et al. (1969) to account for additive and heterotic effects.

Urick et al. (1986) compared and summarized results for birth and preweaning traits resulting from all phases (I, II, and III) of the crossbreeding experiment performed at LARRL. This report included results of least-squares analyses of purebred, 2-way cross calves, 3-way cross calves, and composite cattle of varying breed percentages and levels of heterozygosity. Urick's analytical model differed from Pahnish et al. (1969) and Knapp et al. (1980). Urick et al. (1986) accounted for breed and heterotic effects by including: mating systems (straightbred, 2-way cross, 3-way cross, or composite), breeds nested within the straightbred mating system, specific breed crosses nested within the 2-way cross system, and breed crosses nested within the 3-way cross system. Each specific breed cross was uniquely identified and nested within the particular mating system. This particular methodology is a strategy to account for additive and heterotic effects.

The master's project (Speer, 1991) preceding this study utilized mixed model, least-squares analysis methods for the purpose of parameter estimation. Analytical models included calf breed-year contemporary group designations and sire nested within calf breed-year contemporary group. Calf breed designations were specific to breed of sire-breed of dam crosses thereby accounting for differences in breed composition, heterozygosity levels between specific crosses, and specific combining ability. This approach was utilized to minimize confounding between sires and years and account for genetic differences mentioned above.

Donald et al. (1977) attempted to account for all major genetic sources of variation similar to Gardner and Eberharts' work. However, they utilized an approach that differed from Gardner and Eberhart (1966) to investigate major sources of genetic variation in a crossbred dairy cattle population. Each line or specific cross was accounted for in the model as a group. The experimental population was comprised of British Friesian, Jersey, and Ayrshire breeds. The primary objective of the project was to investigate differences in milk yield as a result of crossbreeding. A secondary objective was to characterize the means of the specific crosses and purebreds. Least-squares means were attained for each specific cross after adjustment for age at calving, year at first calving, and month of calving. They accounted for the sources of genetic variation (additive, nonadditive, and epistatic effects) through the utilization of groups. This approach has an advantage in requiring fewer degrees of freedom but constants for specific heterotic effects are unattainable.

Gregory et al. (1978; I, II, III, IV) reported results concerning preweaning traits (I), growth rate and puberty in females (II), growth traits in steers (III), and carcass traits in steers (IV). Their experimentation involved a crossbred population consisting of Hereford, Angus, Red Poll, and Brown Swiss cattle raised at the Meat Animal Research Center, Clay Center, NE. All four investigations utilized least-squares analytical models that accounted for genetic sources of variation identical to the method described by Pahnish et al. (1969). Long and Gregory (1974) reported on preweaning traits in Hereford, Angus, and Hereford-Angus (F_1) cross calves also employing the least-squares methodology described by Pahnish et al. (1969) to account for sources of genetic variation.

Dillard et al. (1980) and Robison et al. (1981) performed the first experimentation that applied analytical principles of crossbred populations set forth by Gardner and Eberhart (1966). Dillard et al. (1980) studied differences in additive and nonadditive direct and maternal genetic effects in crossbred cattle involving Angus, Charolais, and Hereford cattle. Dillard et al. (1980) performed analyses with a multiple regression approach in order to "estimate the contributions of breed additive genetic, direct heterosis (intra-locus interaction), breed maternal and average maternal heterosis effects to differences in the traits. Coefficients used for the independent variables were expressed as fractions based on the expected proportion of genes contributed by each breed for additive genetic, heterozygous loci and maternal effects. Herd, year, sex and age of dam were also included in the model and regarded as fixed effects.

Dillard et al. (1980) performed analyses on four preweaning traits with the following model:

$$Y_{ijklm} = u + H_i + T_j + S_k + D_l + (HT)_{ij} + b_1A_1 + b_2A_2 + b_3A_3 + b_4H_{12} + b_5H_{13} + b_6H_{23} + b_7M_1 + b_8M_2 + b_9M_3 + b_{10}H_m + b_{11}G + e_{ijklm}$$

where

Y_{ijklm} = observation of the nth calf of the mth breed group for the lth age of dam for the kth sex in the jth year of the ith herd.
u = mean,
H_i = effect due to the ith herd (i=1,2),
T_j = effect due to the jth year (j=63,64,65,...76),
S_k = effect due to the kth sex of calf (k=1,2),
D_l = effect due to the lth age of dam at birth

$(l=2,3,...10)$,

$(HT)_{ij}$ = effect due to the interaction of herd and year,

b_{11} = partial regression coefficient of Y_{ijklm} on G

G = age of calf in days at weaning,

b_1, b_2, b_3 = breed additive effects for breeds 1,2 and 3 respectively,

A_1, A_2, A_3 = percentage of genes contributed by breeds 1, 2 and 3,

b_4, b_5, b_6 = heterosis effect due to interaction of two alleles at the same locus, with the alleles being from breeds 1 and 2, 1 and 3, and 2 and 3, respectively,

H_{12}, H_{13}, H_{23} = percentage of loci occupied by genes from breeds 1 and 2, 1 and 3, and 2 and 3, respectively,

b_7, b_8, b_9 = breed maternal effects for breeds 1, 2 and 3, respectively,

M_1, M_2, M_3 = percentage of genes in dam from breeds 1, 2 and 3 respectively,

b_{10} = average maternal heterosis due to the interaction of two alleles at the same locus, with alleles being from different breeds,

H_m = percentage of loci in dam with one gene from one breed and the other gene from a different breed, and

e_{ijklm} = random error

The model utilized by Dillard et al. (1980) results in a singular matrix. They imposed restrictions such that breed additive and breed maternal effects for Angus and Charolais were computed as deviations from Hereford.

Robison et al. (1981) performed the first experimentation that was a direct application of Gardner and Eberharts' model to cattle populations. The purpose of the experiment was "to extend the work of Gardner and Eberhart to animal breeding data". Extension of Gardner and Eberharts' work to animal breeding data would allow for estimation of genetic effects resulting from a crossbred dairy population.

The notation used by Gardner & Eberhart and reported by Robison et al.:

$u + a_j + d_j + h_{ij}$ where

u is the mean of random inbred lines from all breeds

$u + a_j$ is the mean of random inbred lines from the jth breed and

$u + a_j + d_j$ is the mean of the jth breed

a_j and d_j represent contribuions of homozygous and heterozygous loci respectively and are titled the additive effects.

h_{ij} are heterosis parameters that are due to differences in gene frequencies in breeds i and j and to dominance expressed when i and j are crossed.

These factors were expanded to include maternal additive and heterotic effects.

Robison et al. (1981) assumed the following model in their experimentation:

$$C_{i,j(j=1...n)} = u + Ek_i a_i + Ek_j a_j + Ek_{ij} h_{ij} + Ek'_j m_j + e$$

where

k_i = percentage of genes contributed by breed i through the sire

k_j = percentage of genes contributed by breed j through the dam

a_i = average breed effect for the ith breed

a_j = average breed effect for the jth breed

k_{ij} = percentage of loci in individuals with one gene from the ith breed and the other gene from the jth breed

h_{ij} = heterosis expressed for the ijth combination

k'_j = percentage of genes in the dam from the jth breed and

m_j = average breed maternal effect for the jth breed as a female.

This model, very similar to the model used by Dillard et al. (1980), also results in a singular matrix because the breed percentages in each individual will always sum to one. It is, therefore, necessary to impose restrictions on the model. One breed must be restricted (eliminated) from the analysis. Resulting breed constants are computed as deviations from the restricted breed means.

The model used by Robison et al. (1981) was applied to data from a crossbreeding project that was comprised of straightbred dairy cattle and all possible two- and three-way crosses. It was reported that this procedure provided "results identical to those obtained by estimating each breed group constant, equating it to its genetic expectation, weighting each constant by the number of observations and solving the system of equations. Further, a simulated data set with known values for a, m, and h was analyzed. The appropriate values were recovered."

Crossbreeding experiments had commonly been analyzed by least-squares, fixed-model procedures previous to MacNeil et al. (1982). They utilized Robison's strategy through incorporation of the same analytical techniques in mixed-model methodology. Robison et al. (1981) used the model in an analysis that included only fixed effects. MacNeil et al. (1982) included random effects in analysis of weaning weight records on 47,652 calves in 371 contemporary groups obtained from the South Dakota Beef Cattle Improvement Association and used to estimate breed individual and maternal additive effects and heterotic effects on 205-d weight. The experiment resulted in reasonable estimates (constants) for major sources of genetic variation. The data were comprised of individuals of varying breed percentages, breed combinations, and heterozygosity levels.

MacNeil et al. reported:

> "Methodology used to arrive at these estimates differed from that used in most previous studies. The usual procedure has been to estimate parameters of interest through specific linear constrasts. However, specific linear contrasts may not utilize all the information available, particularly that from survey type data bases. The procedures employed in this study made use of all the data and were particularly useful for data not obtained from planned crossbreeding experiments."

Komender and Hoeschele (1989) compared a fixed model and four mixed models (sire model ignoring relationships, sire model with relationships, sire-dam model ignoring relationships and an animal model accouting for all additive genetic relationships). They performed comparisons using data from a diallel crossbreeding experiment with pigs. Komender and Hoeschele concluded that in a balanced design a fixed model "can probably provide reasonable estimates of the crossbreeding parameters". They indicated the most appropriate method of analyses is utilization of an animal model and the importance of the animal model increases when analyzing unbalanced experiments and field data.

Summary

Analytical models for crossbred populations have become increasingly more sophisticated. This is largely due to an ever-increasing level of computer technology and the need to accurately reflect differences due to breed composition and heterozygosity levels. Analytical models have evolved from least-squares analyses which included specific breed cross designations and breed of dam (Damon et al., 1961) to mixed model methodolgy including random effects of sire and dam and linear regression on individual breed percentage, dam breed percentage, individual heterozygosity, and dam heterozygosity (MacNeil et al., 1982). Analytical models which are increasingly complex require more computational resources but should allow for more accurate solutions relative to the specific sources of variation (i.e. breed composition and heterozygosity).

GROUPING STRATEGIES FOR CROSSBRED POPULATIONS

Analyses of crossbred populations results in animals which can be classified on the basis of breed effects (Donald et al., 1977). Animals then correspond to breed (group) proportions estimated by pedigrees or relationships (Robinson, 1986). The result is that two animals with identical breed compositions would have an equal proportion of group solutions contributing to their individual estimation of genetic merit. Methods have been described to properly utilize groups within analyses (Westell et al., 1988; Robinson, 1986). Westell's (1988) and Robinson's

(1986) methods, though, do not account for heterozygosity within a group or properly handle more than two breeds within a given population (Golden, 1991).

Grouping strategy can account for differences in means and variances of foundation populations in crossbred populations. Group designations can be arbitrary, but if properly designated and included in analysis, these techniques can account for different genetic means and variances from foundation subpopulations (VanVleck, 1990). Also, the use of a genetic relationship matrix diminishes the need for grouping. Furthermore, the criteria of proper grouping is complicated when genetic relationships are utilized (Quass et al., 1981). Finally, usage of group subclasses is inconvenient when having to deal with an ever-increasing number of groups over time (Elzo and Famula, 1985).

SUMMARY

Analysis of crossbred data poses problems because foundation populations (foundation breeds) possess differing means and variances. Furthermore, analysis of crossbred data also includes heterotic effects and the interaction among heterosis and foundation populations. These special considerations, specifically foundation populations possessing differing means and variances, are certainly valid concerning the data used for this project. The data results from three very different breeds. All

CHAPTER III

MATERIALS AND METHODS

DESCRIPTION OF DATA SOURCE

Data used for this study were obtained from the Fort Keogh Livestock and Range Research Laboratory (LARRL), Miles City, Montana. The data were a result of the crossbreeding and composite experiment involving Hereford, Angus, Charolais and Brown Swiss cattle. The data were selected due to several factors: 1.) growth and carcass measurements were recorded on a sufficient number of animals for a reasonably conclusive study, 2.) crossbred cattle were produced and thus were typical of most commercial cow-calf operations in the United States, and 3.) the environment and management scheme at the station is also very representative of many commercial beef operations.

The crossbreeding study was implemented in three distinct phases. Phase I (1962-1965) utilized only purebred sires and dams designed to measure heterotic effects between purebred and all two breed combination offspring. Phase II (1965-1967) utilized only crossbred sires bred to both pure- and crossbred dams resulting from phase I to produce three-breed cross offspring. The purpose of phase II was to measure maternal heterosis. Phase III (1967-1977) examined alternative systems of maintaining heterosis over time among respective crossbreeding systems. This third and final phase compared 2-way, 3-way, and composite crossbreeding systems.

Purebred dams and sires of Angus and Charolais breeds were purchased in 1961 and utilized for the 1962 calving season. Hereford females were derived from a "grade" herd maintained at the station. Brown Swiss females were also purchased and utilized for beef X beef and beef X dairy comparisons and development of a four-breed composite (Charolais, Angus, Hereford, and Brown Swiss) in phase III. Management of the cattle was similar among all three phases. Calving occured primarily from Mid-March to late May. Females were then seperated into single sire breeding pastures during June and July. During the remainder of the year breeding age females were maintained in a single herd. Male calves were castrated at the end of the calving season (branding) and all calves were managed identically until weaning in mid-October. Castration practices were the only thing that was not similar among the three phases. Two male calves of each breed cross were randomly selected and remained intact for future use during Phase I and Phase II. However, a random half of the calves were castrated during Phase III.

New sires were used each year of the study. Females remained in the herd as long as it was believed she was able to wean a calf each year. Females were randomly assigned to sires each year within development of breed crosses and composites. Breeding combinations occurred over time such that continuous distribution of breed and heterozyogisty percentages in the population was attained.

A more specific description of the experiment is described by Pahnish et. al. (1969), Knapp et. al. (1980) and Urick et. al. (1986). Detailed mating plans for each phase are described by Speer (1991).

DESCRIPTION OF DATA SET

Data used for the study included 2888 calves born from 1962 to 1977. The data included straightbred and crossbred individuals that possessed only beef cattle breeding (Hereford, Angus, Charolais). All calves were used in analyses for creation of a relationship matrix. However, some individuals had missing observations for the respective traits of interest. Description of actual observations for the trait of interest is described in table 1.

TABLE 1. TOTAL OBSERVATIONS USED IN ANALYSES

		Number
Total observations used for A^{-1}		2888
Bulls		634
Steers		795
Heifers		1459
Total sires included in A^{-1}		138
Actual observations for:		
Birth weight		2886
Bulls	634	
Steers	794	
Heifers	1458	
Weaning weight		2745
Bulls	572	
Steers	776	
Heifers	1397	
Average daily gain		2462
Bulls	466	
Steers	659	
Heifers	1337	
Days on Feed		1109
Bulls	462	
Steers	647	
Mature weight		690
Fat thickness		875
Bulls	402	
Steers	473	
Ribeye area		875
Bulls	402	
Steers	473	
Yield grade		875
Bulls	402	
Steers	473	
Quality grade		875
Bulls	402	
Steers	473	

Age of dam groupings for analyses purposes were grouped according to B.I.F. recommendations (2, 3, 4, 5-10, and 11 & older).

Steer weaning weight was adjusted to a bull basis (steer weaning weight plus 7 pounds). The adjustment factor resulted from the Master's study least-squares estimates (Speer, 1991). The adjustment allowed for covariance estimation between bull-basis male weaning weight and female weaning weight.

Postweaning average daily gain for steers was adjusted to a bull basis (steer average daily gain plus .52 lb/day). The adjustment factor resulted from the Master's study least-squares estimates (Speer, 1991) and was performed for the same purposes as described in the weaning weight section above.

Mature weights were adjusted to a mature (6-9 years old), wet lactation status, equal year basis. Mature weight was adjusted for year of measurement, age of cow, and lactation status at fall weaning. Adjusted mature weights were averaged for each female and the average adjusted mature weight was used for analysis. Analysis and adjustment is described by Speer (1991).

Yield grades were calculated according to the U.S.D.A. yield grade equation utilizing ribeye area, fat thickness, k.p.h. fat and carcass weight. The yield grade equation is given below:

YG = 2.50 + (2.5 * fat thickness in inches) + (.2 * k.p.h.

%) + (.0038 * hot carcass weight in pounds) - (.32 * ribeye area in square inches.)

Quality grade scores were assigned as follow:

2 = Prime$^+$	4 = Prime^o	6 = Prime$^-$
8 = Choice$^+$	10 = Choice^o	12 = Choice$^-$
14 = Select$^+$	16 = Select^o	18 = Select$^-$
20 = Standard$^+$	22 = Standard^o	24 = Standard$^-$

A more specific discussion of obtaining carcass data is given by Urick et. al. (1974)

Reciprocal breed cross percentages were combined for analytical purposes. For example, a calf could be out of a crossbred sire and a crossbred dam. As a result, the percentage of outcrossing due to percentage Hereford in the sire crossed with percentage Angus in the dam was combined with percentage Angus in the sire crossed with percentage Hereford in the dam. This was done for all six possible reciprocal crosses (Hereford X Angus + Angus X Hereford, Hereford X Charolais + Charolais X Hereford, Angus X Charolais + and Charolais X Hereford) to attain three separate values: Hereford-Angus outcrossing percentage, Hereford-Charolais outcrossing percentage, and Angus-Charolais outcrossing percentage. A calf sired by a Charolais-Hereford bull and out of a Angus-Hereford cow would have values of .25, .25, and .25 for Hereford-Angus outcrossing, Hereford-Charolais outcrossing, and Angus-Charolais outcrossing percentages respectively. These reciprocal outcrossing percentages were combined for both calves and dams. Combining reciprocal outcrossing percentages was performed in order to avoid confounding between breed composition of dam and specific crossing percentage. It should be noted that the sum of the three combined crossing percentages equals heterozygosity of the individual.

All carcass traits were analyzed to a weight constant endpoint consistent with the original design of the crossbreeding experiment. Furthermore, the master's study (Speer, 1991) showed that analyses on a weight constant basis were more appropriate for this population as compared to analyses on an age constant basis.

ANALYSES

Multi-trait iterative REML techniques were used to derive variance and covariance estimates among traits of interest. Starting variance values for respective REML analyses were derived through utilization of mixed-model, least-squares analysis methods as described by Harvey (1975). A complete description of models and analysis techniques for derivation of starting values can be found in the master's project preceding this study (Speer, 1991).

Multi-trait techniques were used with one trait being specific to male calves and the other trait being specific to female calves. Therefore, each trait of interest was specific and unique to sex of animal. Analyses were performed to estimate the given variance and covariance components:

V_{dm} : direct variance component - male trait
V_{mm} : total maternal variance component - male trait
COV_{dmmm} : direct-maternal covariance - male trait
V_e : error variance component - male trait

V_{df} : direct variance component - female trait
V_{mf} : total maternal variance component - female trait
COV_{dfmf} : direct-maternal covariance - female trait
V_e : error variance component - female trait

COV_{dmdf} : direct component/male trait - direct component/female trait covariance
COV_{mmdf} : maternal component/male trait - direct component/female trait covariance
COV_{dmmf} : direct component/male trait - maternal component/female trait covariance
COV_{mmmf} : maternal component/male trait - maternal component/female trait covariance

Multi-trait analyses were performed with each analysis including a trait specific to males and a trait specific to females. Specific analyses are listed in table 2.

TABLE 2. MULT-TRAIT REML ANALYSES

	Male trait	Female trait
1.	Birth weight	Birth weight
2.	Weaning weight	Weaning weight
3.	Postweaning ADG	Postweaning ADG
4.	Days on feed	Mature weight
5.	Fat thickness	Mature weight
6.	Ribeye area	Mature weight
7.	Yield grade	Mature weight
8.	Quality grade	Mature weight

MODELS

As mentioned previously, multi-trait REML techniques were utilized to estimate variance and covariance components of interest. Schaeffer and Wilton (1978) described REML procedures in this way: "...the simplest explanation of the method is to say that one first solves Henderson's (1973) mixed model equations, and then equates quadratic forms of these solutions to their expectation." Each analysis was performed with the use of a sire-maternal grandsire relationship matrix, A^{-1}, where A^{-1} is defined as the inverse of relationships among sires. The general model utilized in analyses expressed in mixed-model matrix notation is given below:

$$Y = XB + Z_1S_1 + Z_2MGS_2 + e$$

where Y = matrix of observations
X = incidence matrix relating to fixed effects
B = vector of solutions relating to fixed effects
Z_1 = incidence matrix relating to sire
S_1 = vector of solutions relating to sire
Z_2 = incidence matrix relating to maternal grandsire
MGS_2 = vector of solutions relating to maternal grandsire
e = error

The *abtk* (animal breeders toolkit) softward (Golden et al., 1992) was used to assemble and solve the mixed model equations in all analyses. Variances and covariance estimates were calculated by solving the following mixed model:

Analytical models accounting for the following fixed effects are listed below:

Model 1

Mu
Year of birth
Age of dam
Linear regression on weaning age
Linear regression on calf percent Hereford
Linear regression on calf percent Angus
Linear regression on calf percent Charolais
Linear regression on calf percent Hereford-Angus crossing
Linear regression on calf percent Hereford-Charolais crossing
Linear regression on calf percent Angus-Charolais crossing
Linear regression on dam percent Hereford
Linear regression on dam percent Angus
Linear regression on dam percent Charolais
Linear regression on dam percent Hereford-Angus crossing
Linear regression on dam percent Hereford-Charolais crossing
Linear regression on dam percent Angus-Charolais crossing

Model 2

Mu
Year of birth
Sex of calf
Age of dam
Sex of calf - Age of dam interaction
Linear regression on weaning age
Linear regression on days on feed
Linear regression on calf percent Hereford
Linear regression on calf percent Angus
Linear regression on calf percent Charolais
Linear regression on calf percent Hereford-Angus crossing
Linear regression on calf percent Hereford-Charolais crossing
Linear regression on calf percent Angus-Charolais crossing
Linear regression on dam percent Hereford
Linear regression on dam percent Angus
Linear regression on dam percent Charolais
Linear regression on dam percent Hereford-Angus crossing
Linear regression on dam percent Hereford-Charolais crossing
Linear regression on dam percent Angus-Charolais crossing

Model 3

Mu
Year of birth
Sex of calf
Age of dam
Sex of calf - Age of dam interaction
Linear regression on carcass weight
Linear regression on calf percent Hereford
Linear regression on calf percent Angus
Linear regression on calf percent Charolais
Linear regression on calf percent Hereford-Angus crossing
Linear regression on calf percent Hereford-Charolais crossing
Linear regression on calf percent Angus-Charolais crossing
Linear regression on dam percent Hereford
Linear regression on dam percent Angus
Linear regression on dam percent Charolais
Linear regression on dam percent Hereford-Angus crossing
Linear regression on dam percent Hereford-Charolais crossing
Linear regression on dam percent Angus-Charolais crossing

Table 3 lists appropriate models used for analysis of respective traits.

TABLE 3. ANALYTICAL MODELS

Trait[a]	Model
BWM	1
BWF	1
WWM	1
WWF	1
ADGM	1
ADGF	1
MW	1
DOF	2
FT	3
REA	3
YG	3
QG	3

[a] BWM = birth weight - males, BWF = birth weight - females, WWM = weaning weight - males, WWF = weaning weight - females, ADGM = postweaning average daily gain males, ADGF = postweaning average daily gain females, MW = female mature weight, DOF = days on feed, FT = fat thickness, REA = ribeye area, YG = yield grade, QG = quality grade.

VARIANCE AND COVARIANCE ESTIMATION

REML procedures were used to estimate observational variance and covariance components with the following generalized equation:

$$V_i = u'A^{-1}u + (tr(A^{-1}C^{ii})) / n$$

where: V_i = variance or covariance estimate
u = vector of breeding value solutions
A^{-1} = relationship matrix
C^{ii} = submatrix of augmented coefficient matrix (submatrix of inverse of $Z_i'Z_i + g^{ii}A^{-1}$)
n = number of solutions in vector u

Error variance components were calculated as:

$$V_e = (Y'Y - B'X'Y - u_1'Z_1'Y - u_2'Z_2'Y) / df$$

where: V_e = error variance estimate
Y = vector of observations
B = vector of fixed effect solutions
X = incidence matrix relating to fixed effects
u_1 = vector of breeding value solutions relating to sire
Z_1 = incidence matrix relating to sire effects
u_2 = vector of breeding value solutions relating to maternal grandsire
Z_2 = incidence matrix relating to maternal grandsire effects
df = degrees of freedom equivalent to total number of observations minus rank of X

Observational variance component estimates were converted to causal variance component estimates with the following matrix multiplication:

$$\begin{bmatrix} 1/4 & 0 & 0 & 0 \\ 1/16 & 1/4 & 1/4 & 0 \\ 1/8 & 0 & 1/4 & 0 \\ 11/16 & 3/4 & 3/4 & 1 \end{bmatrix}^{-1} * \begin{bmatrix} \text{Vsire} \\ \text{Vmgs} \\ \text{COVs-mgs} \\ \text{Vresid} \end{bmatrix} = \begin{bmatrix} \text{Va} \\ \text{Vm} \\ \text{COVdm} \\ \text{Ve} \end{bmatrix}$$

where: Vsire = observational variance component related to sires
Vmgs = observational variance component related to maternal grand sires

COVs-mgs = observational covariance component related to covariance between sires and maternal grandsires
Vresid = residual variance
Va = causal additive variance component
Vm = causal maternal variance component
COVdm = causal additive-maternal covariance component
Ve = error variance

Observational covariance component estimates were converted to causal covariance component estimates with the following matrix multiplication:

$$\begin{bmatrix} 1/4 & 0 & 0 & 0 \\ 1/8 & 1/4 & 0 & 0 \\ 1/8 & 0 & 1/4 & 0 \\ 1/16 & 1/8 & 1/8 & 1/4 \end{bmatrix}^{-1} * \begin{bmatrix} \text{COVsm/sf} \\ \text{COVsm/mgsf} \\ \text{COVmgsm/sf} \\ \text{COVmgsm/mgsf} \end{bmatrix} = \begin{bmatrix} \text{COVdmdf} \\ \text{COVdmmf} \\ \text{COVmmdf} \\ \text{COVmmmf} \end{bmatrix}$$

where: COVsm/sf = observational covariance component related to sires of male trait and sires of female trait
COVsm/mgsf = observational covariance component related to sires of male trait and maternal grandsires of female trait
COVmgsm/sf = observational covariance component related to maternal grandsires of female trait and sires of male trait
COVmgsm/mgsf = observational covariance component related to maternal grandsires of male trait and maternal grandsires of female trait
COVdmdf = causal additive-additive covariance component
COVdmmf = causal additive-maternal covariance component
COVmmdf = causal maternal-additive covariance component
COVmmmf = causal maternal-maternal covariance component

CHAPTER IV

RESULTS AND DISCUSSION

FIXED EFFECT SOLUTIONS

Fixed effect solutions for birth weight, weaning weight, and postweaning average daily gain are listed in table 4. Fixed effect solutions for days on feed, mature weight and carcass traits are listed in tables 5, 6, and 7 respectively. Solutions are presented for relative comparison among the various fixed effects. Solutions include intercept, year, sex of calf, age of dam, and linear regression on weaning age, days on feed, & carcass weight.

Birth weight, weaning weight, and postweaning average daily gain

Table 4 lists fixed effect solutions for birth weight, weaning weight and postweaning average daily gain analyzed as separate traits of males and females.

Birth weight

Age of dam solutions follow typical patterns, where older dams generally produced heavier calves at birth. Two-year-old dams produced the lightest birth weights both in male and female calves (-7.8 and -5.7 lb respectively). Male calves from 4-year-old dams were heaviest at birth (+.68) whereas female calves were heaviest when born out of mature dams.

The linear regression on weaning age for birth weight was .002 lb/d in male calves and -.002 lb/d in female calves. Weaning age regressions for birth weight were very small and differences in birth weight due to day of birth within the calving season is negligible.

Weaning weight

Calves out of younger cows had progressively lighter weaning weights than calves with relatively older dams. Effects for all four age of dam levels (2, 3, 4, 5-10) were larger in males (-80 lb, -44 lb, -13 lb, and 0 respectively) than females (-65 lb, -29 lb, -9 lb and 0 respectively). Male calves possess inherently more growth potential as compared to female calves. As a result, weaning weights of male calves were more adversely affected by young dams than weaning weights of female calves. This is appropriately reflected in the age of dam solutions.

Linear regressions on weaning age for male and female weaning weight were very similar (1.868 lb/d and 1.854 lb/d, respectively).

Postweaning average daily gain

A large difference existed between intercepts for male and female postweaning average daily gain (3.23 lb/d and 1.58 lb/d respectively). This represents different management and nutritional schemes where males were fed a higher-energy ration resulting in larger gains relative to female calves.

Postweaning average daily gain was higher for calves of both sexes out of younger cows as compared to calves from mature cows except for male calves from 3-year-old dams (-.02 lb/d). Calves from younger dams possessed relatively lighter weaning weights. Higher postweaning gains in calves from younger cows likely reflects an advantage due to compensatory gain.

Linear regression on weaning age was very small and identical for both sexes (-.003 lb/d/d).

TABLE 4. FIXED EFFECT SOLUTIONS

BIRTH WEIGHT, WEANING WEIGHT AND POSTWEANING AVERAGE DAILY GAIN[a]

	Males			Females		
EFFECT	BW (lb)	WW (lb)	ADG (lb/d)	BW (lb)	WW (lb)	ADG (lb/d)
INTERCEPT	82.2	87	3.23	75.6	52	1.58
YEAR						
62	-.9	13	-.11	1.1	27	-.48
63	-3.3	-6	-.50	.4	7	-.31
64	.8	-3	-.62	1.7	19	-.36
65	-2.1	-26	-.06	1.1	-21	-.23
66	-7.3	-56	-.14	-3.9	-50	-.32
67	.5	-25	.07	2.2	-17	-.37
68	-.3	-5	.10	2.7	4	-.40
69	-5.2	-9	.17	-.5	-9	-.34
70	-1.5	-21	.18	.03	-20	-.27
71	-1.7	-14	.03	-2.4	-14	-.36
72	3.7	-17	-.04	5.1	-14	-.04
73	-1.5	-47	.12	1.1	-41	.29
74	3.0	-18	-.23	3.0	0	.06
75	3.3	1	-.09	3.9	9	.05
76	-3.2	-32	.06	-.7	-26	.21
77	0	0	0	0	0	0
AGE OF DAM						
2	-7.8	-80	.02	-5.7	-65	.11
3	-3.8	-44	-.02	-2.4	-29	.06
4	.7	-13	.04	-.4	-9	.01
5+	0	0	0	0	0	0
LINEAR REGRESSION ON WEANING AGE (lb/d)						
	.002	1.868	-.003	-.002	1.854	-.003

[a] BW = birth weight, WW = weaning weight, ADG = postweaning average daily gain.

Days on feed

Table 5 lists fixed effect solutions for days on feed for male calves. Year solutions for 1963, 1964, and 1970 are especially large (52 d, 52 d, and 100 d respectively) representing more time on feed to reach the specified slaughter endpoint (1000 - 1050 lb). Year effects for postweaning average daily gain (table 3) in 1963 and 1964 indicated the poorest gains (-.50 lb/d and -.62 lb/d respectively) and may explain the extra time on feed to reach the specified slaughter weight. The year 1970 was favorable for postweaning average daily gain (+.18 lb/d) and unfavorable for weaning weight (-21 lb). Cattle born in 1970 were unable to compensate for lighter weaning weights through increased gains and required an especially long amount of time on feed.

Bulls required 36 less days compared to steers to reach specified slaughter weight. Male calves with heavier weaning weights due to either having dams which were older or being older at weaning required less time on feed. Cattle out of 2-year-old dams required 17 more days on feed as compared to cattle out of mature cows. Cattle out of 3- and 4-year-old dams required an additional 9 d and 3 d respectively compared to cattle out of mature cows. The linear regression on weaning age (-.385 d/d) indicated that older calves at weaning required less time on feed.

TABLE 5. FIXED EFFECT SOLUTIONS

DAYS ON FEED[a]

EFFECT	DOF (d)
INTERCEPT	311
YEAR	
62	9
63	52
64	52
65	28
66	20
67	0
68	-2
69	-5
70	100
71	-2
72	13
73	4
74	25
75	8
76	6
77	0
SEX	
BULLS	-36
STEERS	0
AGE OF DAM	
2	17
3	9
4	3
5+	0
LINEAR REGRESSION ON WEANING AGE	-.385

[a] DOF = days on feed.

Mature weight

Table 6 lists fixed effect solutions for mature weight. Solutions are presented from multi-trait analyses of mature weight and five other traits. Solutions for mature weight from four multi-trait analyses (fat thickness, ribeye area, yield grade, and quality grade) were all very similar. Multi-trait analyses with carcass weight or any trait that is highly correlated to carcass weight yields similar estimates when being slaughtered at a constant weight because carcass weight is a significant source of variation for most carcass measurements (Dinkel and Busch, 1973).

Intercepts for mature weight-carcass trait analyses were similar ranging from 1073 lb to 1077 lb. The intercept for mature weight-days on feed analysis was larger (1094 lb) compared to other analyses.

Trends for all fixed effects among the five analyses are similar. All year solutions were negative relative to 1975 and the general trend of year solutions increased through the duration of the experiment. This general trend may be attributable to several factors. The trend may reflect actual permanent environmental effects on mature weight due to year. The trend may also reflect some genetic trend if the relationship matrix was not adequate in eliminating confounding between sire and year. This general trend for year solutions occurred with mature weight as it was the only trait studied which year had a permanent environmental effect; it was not largely influenced by maternal factors, nor was it a result of constant slaughter weights over all years.

Age of dam constants indicate that females out of 3-year-old dams were slightly heavier at maturity than females out of older cows while females out of 2-year-old and 4-year-old dams were lighter at maturity. Linear regression on weaning age ranged from .89 lb/d to .91 lb/d indicating that older cattle at weaning are heavier at maturity. Ferjani (1976) reported linear regressions on weaning age of .29 lb/d, .75 lb/d, 1.21 lb/d and .66 lb/d for 6, 7, 8, and 9 year old cows respectively; the average linear regression is .73 lb/d.

TABLE 6. FIXED EFFECT SOLUTIONS

MATURE WEIGHT (lb)

MULTI-TRAIT ANALYSIS[ab]

EFFECT	FT	REA	YG	QG	DOF
INTERCEPT	1077	1074	1074	1074	1094
YEAR					
62	-139	-136	-137	-136	-142
63	-170	-167	-169	-168	-169
64	-165	-157	-160	-157	-158
65	-177	-177	-177	-176	-186
66	-108	-108	-105	-103	-126
67	-124	-123	-125	-121	-115
68	-85	-82	-84	-83	-95
69	-96	-97	-97	-98	-99
70	-75	-69	-71	-69	-76
71	-46	-45	-45	-44	-49
72	-20	-20	-22	-21	-30
73	-40	-34	-36	-30	-33
74	-12	-9	-10	-12	-13
75	0	0	0	0	0
AGE OF DAM					
2	-41	-41	-41	-41	-43
3	4	3	3	3	2
4	-6	-6	-6	-6	-4
5+	0	0	0	0	0
LINEAR REGRESSION ON WEANING AGE					
	.90	.91	.91	.91	.89

[a] Fixed effect solutions listed are derived from each multi-trait analysis of mature weight and trait listed.

[b] FT = fat thickness, REA = ribeye area, YG = yield grade, QG = quality grade, DOF = days on feed.

Carcass traits

Table 7 lists fixed effect solutions for carcass traits of interest (fat thickness, ribeye area, yield grade, and quality grade score).

Year solutions for all traits fall within a very small range. Cattle were slaughtered at the same weight constant endpoint (1000 - 1050 lb) during all years which reduced variation due to yearly influences.

Bulls were leaner (-.21 in), possessed larger ribeye areas (+1.73 in^2), had lower yield grades (-1.28), and less favorable quality grade scores (+4.32) compared to steers.

Magnitude of age of dam solutions were very small for all traits. Age of dam solutions for fat thickness and yield grade indicate that males out of younger dams were leaner and subsequently had lower yield grades. Males with 4-year-old dams had a slight disadvantage in quality grade scores (+.10) and ribeye area (-.03 in^2) whereas cattle from 2-year-old and 3-year-old dams possessed more favorable quality grade scores (-.16 and -.01 respectively) and slightly larger ribeye areas (+.30 in^2 and +.21 in^2).

Linear regression on carcass weight reflects that heavier cattle were fatter (.0002 in/lb), had larger ribeye areas (.011 in^2/lb), higher yield grades (.0009/lb) and more favorable quality grade scores (-.0001/lb).

TABLE 7. FIXED EFFECT SOLUTIONS

CARCASS TRAITS[a]

EFFECT	FT (in)	REA (in^2)	YG	QG
INTERCEPT	.48	4.65	2.72	13.08
YEAR				
66	-.09	.37	-.43	-.17
67	-.15	-.32	-.28	.49
68	-.14	-.82	.03	1.32
69	-.08	-.89	.23	.06
70	-.11	-.93	.22	-.13
71	-.09	-.33	.03	1.78
72	-.08	-.60	.12	1.00
73	-.10	-.74	.11	-.31
74	-.13	-.11	-.24	.48
75	-.05	-.34	.03	-.69
76	-.07	.09	-.24	-.73
77	0	0	0	0
SEX				
BULLS	-.21	1.73	-1.28	4.32
STEERS	0	0	0	0
AGE OF DAM				
2	-.04	.30	-.19	-.16
3	-.02	.21	-.12	-.01
4	-.01	-.03	-.02	.10
5+	0	0	0	0
LINEAR REGRESSION ON CARCASS WEIGHT	.0002	.011	.0009	-.001

[a] FT = fat thickness, REA = ribeye area, YG = yield grade, QG = quality grade

BREED AND RECIPROCAL BREED CROSS SOLUTIONS

Breed and reciprocal breed cross solutions for birth weight, weaning weight, and postweaning average daily gain are listed in table 8. Breed and reciprocal breed cross solutions for days on feed, mature weight and carcass traits are listed in tables 9, 10, and 11, respectively.

Solutions are listed for individual breed (direct), individual reciprocal breed cross (individual heterosis), dam breed (maternal + 1/2 direct), dam maternal breed, and dam reciprocal cross (maternal heterosis) effects. Straightbred Hereford individuals and straightbred Hereford dams were equations restricted in analyses; thus breed solutions are deviations from Herefords. Solutions result from linear regression on breed composition of individuals and dams. Breed solutions reflect differences in purebred individuals and purebred dams. Reciprocal breed cross solutions reflect differences in F_1 cattle (100% heterozygosity) of specific cross.

Birth weight, weaning weight, and postweaning average daily gain

Table 8 lists breed and reciprocal breed cross solutions for birth weight, weaning weight, and postweaning average daily gain in males and females.

Birth weight

Charolais direct breed effect resulted in the the heaviest birth weights for males and females (+18.3 lb and +15.4 lb for male and female calves, respectively). Angus direct breed effect resulted in the lightest birth weights with males being 5.8 lb lighter and females being 5.7 lb lighter than Hereford calves. Dillard et al. (1980) reported identical breed rankings with respect to birth weight.

Crossbred calves resulted in heavier birth weights compared to straightbred calves in all cases except for Angus-Charolais reciprocal cross female calves (-.57 lb). Differences among reciprocal breed cross effects were very small relative to individual breed effects on birth weight.

Charolais direct breed effect results in heavier calves at birth yet Charolais maternal effect results in lighter calves at birth (-16.0 lb and -11.2 lb for male and female calves respectively). Angus total maternal effect was -1.2 lb and -1.0 lb for male and female calves but maternal effect was +1.4 and +1.0 lb respectively. Dillard et al. (1980) and Long and Gregory (1974) reported maternal breed effects on birth weight in the opposite direction of those found in this study. Dillard et al. (1980) reported that Charolais deviations were postive for birth weight and both Dillard et al. (1980) & Long and Gregory (1974) reported that Angus maternal deviations were negative relative to Hereford maternal effect. Hereford total maternal effect resulted in heavier calves at birth relative to both the Angus and Charolais total maternal effect.

Crossbred dams produced heavier calves compared to straightbred dams except for Hereford-Angus reciprocal cross dams giving birth to female calves (-.37 lb). Differences in birth weight due to maternal heterosis were small.

Weaning weight

Direct breed effect of Charolais resulted in males and females that were the heaviest at weaning (+51 lb and +54 lb respectively). The Charolais maternal breed effect also resulted in heavier calves for both sexes (+11 lb and +3 lb respectively). Dillard et al. (1980), Gregory et al. (1965), Brown and Galvez (1969), Turner (1969), Koch (1972), Ellis et al. (1979) and Gaines et al. (1978) all reported Charolais maternal ability exceeded that of both Hereford and Angus for weaning weight. Angus direct breed effect showed that male calves were heavier than Hereford male calves at weaning (+11 lb). MacNeil et al. (1982) reported these same breed rankings among Angus, Hereford, and Charolais cattle for weaning weight. Female calves, however, deviated slightly from males and the results of MacNeil et al. (1982) as Angus females were slightly lighter than Hereford female calves at weaning (-2 lb) as a result of the direct breed effect.

Angus females possessed a maternal effect which resulted in weaning heavier calves for both males and females (+6 lb and +21 lb respectively) compared to the Hereford maternal effect. Long and Gregory (1974) reported that calves nursing Angus dams gained faster from birth to weaning and exhibited heavier weaning weights.

Crossbred males were heavier at weaning than straightbred males for all reciprocal crosses. Hereford-Angus and Hereford-Charolais reciprocal cross female calves were heavier (+13 and +17 lb). Angus-Charolais reciprocal cross female calves were slightly lighter (-2 lb) than straightbred female calves.

Angus-Charolais reciprocal cross dams had no advantage in terms of weaning heavier male calves. Hereford-Angus and Hereford-Charolais reciprocal cross dams weaned heavier male calves compared to straightbred dams (+27 lb and +12 lb). All reciprocal cross dams maintained an advantage for female weaning weight. Ranking among respective crosses for individuals and dams were identical in both male and female weaning weight.

<u>Postweaning average daily gain</u>

Direct Angus and Charolais breed effect resulted in larger postweaning average daily gains compared to the Hereford direct breed effect. Male calves from Angus and Charolais dams were heavier at weaning but apparently experienced less compensatory gain and resultingly gained less compared to calves from Hereford dams (-.05 lb/d and -.43 lb/d respectively) due to maternal effects. Female calves from Angus dams gained more (+.02 lb/d) due to maternal effects. Charolais maternal effect yielded solutions for female calves that gained less than calves with Hereford dams (-.07 lb/d).

Hereford-Angus (+.13 lb/d) and Hereford-Charolais (+.05 lb/d) calves had an advantage in gain postweaning while Angus-Charolais calves gained less than straightbred calves (-.03 lb/d). All crossbred female calves had an advantage over straightbred calves in gain after weaning. Male calves from Hereford-Angus cross dams gained less (-.05 lb/d) while male calves from Hereford-Charolais or Angus-Charolais dams had an advantage in postweaning average daily gain. Crossbred dams produced female calves that either had no advantage or gained less than calves from straightbred dams. This is likely a result of crossbred dams weaning heavier female calves resulting in decreased gain because of less compensatory gain and greater maintenance requirements under a relatively limited postweaning environment.

TABLE 8. BREED[a] AND RECIPROCAL BREED CROSS[b] SOLUTIONS

BIRTH WEIGHT, WEANING WEIGHT, AND POSTWEANING AVERAGE DAILY GAIN[c]

	Males			Females		
BREED CROSS	BW (lb)	WW (lb)	ADG (lb/d)	BW (lb)	WW (lb)	ADG (lb/d)
INDIVIDUAL BREED EFFECT						
H	0	0	0	0	0	0
A	-5.2	11	.05	-5.7	-2	.11
C	18.1	51	.47	15.4	54	.25
INDIVIDUAL RECIPROCAL BREED CROSS EFFECT						
HA-AH	2.8	17	.13	1.2	13	.06
HC-CH	3.2	20	.05	2.1	17	.04
AC-CA	2.2	14	-.03	-.6	-2	.01
DAM TOTAL MATERNAL (MATERNAL + 1/2 DIRECT) BREED EFFECT						
H	0	0	0	0	0	0
A	-1.2	11	-.03	-1.0	20	.02
C	-6.9	37	-.19	-3.5	30	-.07
DAM MATERNAL BREED EFFECT						
H	0	0	0	0	0	0
A	1.4	6	-.05	1.8	21	-.03
C	-16.0	11	-.43	-11.2	3	-.19
DAM RECIPROCAL BREED CROSS EFFECT						
HA-AH	1.0	27	-.05	-.4	22	-.02
HC-CH	1.1	12	.07	.2	18	0
AC-CA	2.3	0	.01	1.7	7	-.01

[a] H = Hereford, A = Angus, C = Charolais.

[b] HA-AH = Hereford-Angus reciprocal cross, HC-CH = Hereford-Charolais reciprocal cross, AC-CA = Angus-Charolais reciprocal cross.

[c] BW = birth weight, WW = weaning weight, ADG = postweaning average daily gain.

Days on feed

Breed and reciprocal breed cross solutions for days on feed are listed in table 9.

Charolais cattle possessed the largest advantage in terms of both weaning weight and postweaning average daily gain. As a result, Charolais cattle required the fewest days on feed to reach the specified slaughter weight endpoint (-58 d) due to the direct breed effect. Angus cattle also maintained an advantage in weaning weight and postweaning average daily gain and required 11 fewer days compared to purebred Hereford individuals.

Angus and Charolais dams weaned heavier calves which gained less postweaning resulting in a maternal effect that requires more days on feed (+9 d and +38 d respectively) to reach a constant weight endpoint compared to Hereford dams. This is likely a reflection of compensatory gain advantage where calves out of Hereford dams had the lightest weaning weights, but compensate for it postweaning with relatively higher gains.

All reciprocal crosses in individuals required fewer days on feed with Hereford-Charolais cross cattle having the largest advantage (-16 d) and Angus-Charolais cross individuals possessing the smallest advantage (-4 d). Crossbred males likely are able to withstand environmental stresses more adequately thereby maintaining more consistent gains throughout the feeding period. Reciprocal cross solutions for dams were all very similar.

TABLE 9. BREED[a] AND RECIPROCAL BREED CROSS[b] SOLUTIONS

DAYS ON FEED[c]

Males

BREED CROSS	DOF
INDIVIDUAL BREED EFFECT	
H	0
A	-11
C	-58
INDIVIDUAL RECIPROCAL BREED CROSS EFFECT	
HA-AH	-14
HC-CH	-16
AC-CA	-4
DAM TOTAL MATERNAL (MATERNAL + 1/2 DIRECT) BREED EFFECT	
H	0
A	3
C	9
DAM MATERNAL BREED EFFECT	
H	0
A	9
C	38
DAM RECIPROCAL BREED CROSS EFFECT	
HA-AH	-7
HC-CH	-6
AC-CA	-5

[a] H = Hereford, A = Angus, C = Charolais.

[b] HA-AH = Hereford-Angus reciprocal cross, HC-CH = Hereford-Charolais reciprocal cross, AC-CA = Angus-Charolais reciprocal cross.

[c] DOF = days on feed.

Mature weight

Table 10 lists breed and reciprocal breed cross solutions for mature weight from five multi-trait analyses.

Charolais direct breed effect resulted in the heaviest mature weights ranging from +70 lb (mature weight-days on feed analysis) to +90 lb (mature weight-ribeye area analysis). The direct breed effects for weaning weight resulted in the largest advantage for Charolais cattle and it appears they maintain this advantage through maturity. Angus females were the lightest at maturity ranging from -65 lb (mature weight-fat thickness analysis) to -90 lb (mature weight-days on feed analysis). The Angus direct breed effect for weaning weight was -2 lb relative to Herefords. However, it appears that the differences between the Angus and Herefords widens as females mature. Mature weights were not adjusted for condition score and this difference between Angus and Hereford mature weights may be a reflection of body condition at the fall weight. Angus females maintained a 21 lb maternal advantage over Herefords in weaning weight and are possibly lighter in the fall as a result.

Crossbred individuals were heavier at maturity compared to straightbred females in all analyses. The Hereford-Angus, Hereford-Charolais, and Angus-Charolais reciprocal breed crosses averaged 24, 20, and 35 lb heavier at maturity compared to straightbred females. This possibly reflects Itulya et al.'s (1987) argument that growth performance in a limited environment is largely a resistance to stress rather than actual growth potential and cattle with increased heterozygosity are more resistant to environmental stresses.

Angus maternal effects resulted in heavier weaning weights for female calves and mature weights of their daughters while Charolais maternal effects resulted in lighter mature weights. Crossbred dams produced calves that were heavier at maturity. Angus-Charolais reciprocal cross dams produced the heaviest females at maturity. Hereford-Charolais reciprocal cross dams produced the lightest females at maturity relative to the maternal heterosis effect.

TABLE 10. BREED[a] AND RECIPROCAL BREED CROSS[b] SOLUTIONS

MATURE WEIGHT[c]

	Females				
	MULTI-TRAIT ANALYSIS[d]				
	FT	REA	YG	QG	DOF
BREED CROSS	MW (lb)	MW (lb)	MW (lb)	MW (lb)	MW (lb)
INDIVIDUAL BREED EFFECT					
H	0	0	0	0	0
A	-65	-70	-68	-71	-90
C	88	90	87	88	70
INDIVIDUAL RECIPROCAL BREED CROSS EFFECT					
HA-AH	24	24	24	24	24
HC-CH	20	20	20	20	20
AC-CA	35	35	34	35	34
DAM TOTAL MATERNAL (MATERNAL + 1/2 DIRECT) BREED EFFECT					
H	0	0	0	0	0
A	10	12	11	13	16
C	13	11	13	12	15
DAM MATERNAL EFFECT					
H	0	0	0	0	0
A	42	47	45	48	60
C	-31	-35	-30	-32	-20
DAM RECIPROCAL BREED CROSS EFFECT					
HA-AH	17	17	17	17	20
HC-CH	5	4	5	6	3
AC-CA	25	25	25	25	21

[a] H = Hereford, A = Angus, C = Charolais.

[b] HA-AH = Hereford-Angus reciprocal cross, HC-CH = Hereford-Charolais reciprocal cross, AC-CA = Angus-Charolais reciprocal cross.

[c] MW = mature weight. Solutions listed are derived from each multi-trait analysis listed above.

[d] FT = fat thickness, REA = ribeye area, YG = yield grade, QG = quality grade, DOF = days on feed.

Carcass traits

Carcass trait breed and reciprocal breed cross solutions are listed in table 11. Solutions are listed for carcass weight, fat thickness, ribeye area, yield grade, and quality grade.

Charolais cattle were the leanest (-.28 in), possessed the largest ribeye areas (+1.86 in^2), the lowest yield grades (-1.33) and the poorest quality grade scores (3.35). Angus cattle were slightly fatter (+.12 in) and had higher yield grades (+.46) but also had the most favorable quality grade scores (-2.22). Crossbred males had more desireable quality grade scores compared to straightbred steers and bulls. However, heterosis effects were small relative to breed effects. Kincaid (1962) reported that there was little evidence of the effect of heterosis on carcass traits.

Total maternal and maternal effects on carcass traits were small. Angus maternal and total maternal effects resulted in calves with increased ribeye areas (+.38 and +.37 in^2 for maternal and total maternal effects) and lower yield grades (-.43 and -.19 respectively). Charolais maternal and total maternal breed effects resulted in calves with decreased ribeye areas (-.94 and -.011 in^2) and higher yield grades (+.86 and +.19).

Angus total maternal effect resulted in more desirable quality grades (-.15) while the strictly maternal effect of Angus dams resulted in less desireable quality grades (+.96). The advantage Angus cattle have in terms of quality grade scores is a result of the direct component and reflected in the total maternal effect. Charolais have an advantage in quality grade scores through the maternal component, though the difference is only one-third of a quality grade. Charolais maternal and total maternal breed effects resulted in more desireable quality grades (-1.68 and -.008 respectively for maternal and total maternal effects). Crossbred dams produced cattle that had larger ribeye areas, lower yield grades, but also less desireable quality grade scores.

TABLE 11. BREED[a] AND RECIPROCAL BREED CROSS[b] SOLUTIONS

CARCASS TRAITS[c]

EFFECT	FT (in)	REA (in^2)	YG	QG
INDIVIDUAL BREED EFFECT				
H	0	0	0	0
A	.12	-.01	.46	-2.22
C	-.28	1.86	-1.33	3.35
INDIVIDUAL RECRIPROCAL BREED CROSS EFFECT				
HA-AH	.035	-.33	.21	-1.03
HC-CH	-.003	.01	.01	-.97
AC-CA	-.009	-.60	.20	-1.30
DAM TOTAL MATERNAL (MATERNAL + 1/2 DIRECT) BREED EFFECT				
H	0	0	0	0
A	-.001	.37	-.19	-.15
C	.070	-.01	.19	-.01
DAM MATERNAL BREED EFFECT				
H	0	0	0	0
A	-.060	.38	-.43	.96
C	.209	-.94	.86	-1.68
DAM RECIPROCAL BREED CROSS EFFECT				
HA-AH	.037	.34	-.01	.88
HC-CH	-.009	.18	-.14	.30
AC-CA	.003	.11	-.04	.82

[a] H = Hereford, A = Angus, C = Charolais.

[b] HA-AH = Hereford-Angus reciprocal cross, HC-CH = Hereford-Charolais reciprocal cross, AC-CA = Angus-Charolais reciprocal cross.

[c] FT = fat thickness, REA = ribeye area, YG = yield grade, QG = quality grade.

BREED GROUP PREDICTIONS

Breed group predictions for birth weight, weaning weight, and postweaning average daily gain are listed in table 12. Breed group predictions for days on feed, mature weight, and carcass traits are listed in tables 12, 13 and 14 respectively. Predictions were calculated to compare differences among breed and breed crosses and among prediction means and actual population means.

Solutions represent the appropriate sums of direct breed effects, individual heterosis, maternal breed effects, and maternal heterosis. Solutions are based upon an average of year effects, average weaning age of 191 days, average days on feed of 222 days, and average carcass weight of 607 lb. Predictions listed are for individuals on a mature dam basis. Actual population means listed for each trait are arithmetic averages and incorporation of age of dam predictions would likely increase correspondence between predicted and actual population means.

Birth weight, weaning weight, and postweaning average daily gain

Birth weight

Male calves from Charolais sires crossed with Hereford dams were predicted to have the heaviest birth weights (93.8 lb) (table 12). Female calves from Charolais sires crossed with Hereford dams were also predicted to be the heaviest at birth (86.0 lb). Charolais male and female calves were estimated to be the heaviest straightbred calves at birth with respect to straightbred Angus and Hereford calves. Angus calves (male and female) were predicted to be the lightest straightbred calves at birth. Dillard et al. (1980) reported the same rankings among Hereford, Angus, and Charolais straightbred breed group predictions for birth weight.

Weaning weight

Straightbred male and female Hereford calves possessed the lightest weaning weight predictions (427 lb and 397 lb respectively). Charolais calves were predicted to be the heaviest at weaning, and Angus were intermediate with respect to straightbred breed groups. Dillard et al. (1980) reported weaning weight straightbred group prediction rankings identical to those in this study. Charolais sired calves out of Angus-Hereford reciprocal cross dams were predicted to be the heaviest males at weaning (503 lb). Charolais sired female calves out of Hereford-Charolais reciprocal cross dams were predicted to be the heaviest female calves at weaning (466 lb).

Postweaning average daily gain

Charolais sired male and female calves from Hereford dams resulted in the highest postweaning average daily gain predictions (2.96 lb/d and 1.01 lb/d respectively). As mentioned previously, this breed group also possessed the heaviest birth weight predictions for both sexes. This may be an indication of pleiotropic effects where genes that influence birth weight also influence postweaning average daily gain. Charolais sired calves from Hereford females may also experience a high level of compensatory gain due to the Hereford maternal effect on weaning weight. Angus sired calves from Charolais dams had the lowest postweaning average daily gains (2.48 lb/d) among male estimates. Hereford sired female calves out of Hereford-Charolais reciprocal cross dams had the poorest postweaning average daily gain prediction (.82 lb/d).

Means for male calf predictions were 83.5 lb, 471 lb, 2.73 lb/d for birth weight, weaning weight, and postweaning average daily gain respectively while actual means were 83.3 lb, 454 lb, and 2.84 lb/d. Means for female calf predictions were 77.1 lb, 437 lb, and .90 lb/d for birth weight weaning weight, and postweaning average daily gain. Actual means for female calves were 77.2 lb, 427 lb, and .99 lb/d respectively.

TABLE 12. REML PREDICTIONS SPECIFIC BREED GROUPS[a]

BIRTH WEIGHT, WEANING WEIGHT, AND POSTWEANING AVERAGE DAILY GAIN[b]

	Males			Females		
BREED CROSS	BW (lb)	WW (lb)	ADG (lb/d)	BW (lb)	WW (lb)	ADG (lb/d)
H	81.6	427	2.68	76.2	397	.84
A	77.7	444	2.68	72.3	416	.91
C	83.7	490	2.72	80.4	454	.90
H-A	83.1	455	2.78	76.4	431	.92
A-H	81.7	449	2.83	74.5	410	.96
H-C	77.8	483	2.53	74.8	445	.81
C-H	93.8	472	2.96	86.0	442	1.01
A-C	74.2	483	2.48	69.2	424	.83
C-A	91.6	478	2.85	82.3	442	.99
H-AH	83.3	469	2.67	75.9	436	.87
A-AH	80.7	474	2.70	73.0	435	.92
C-AH	93.7	503	2.85	83.8	464	.98
H-HC	80.8	468	2.67	75.7	439	.82
A-HC	79.1	479	2.72	72.1	435	.89
C-HC	89.8	493	2.91	83.4	466	.95
H-AC	82.8	469	2.67	77.3	444	.85
A-AC	78.3	463	2.59	72.5	427	.86
C-AC	90.0	484	2.80	83.0	555	.93
PREDICTION MEAN	83.5	471	2.73	77.1	437	.90
ACTUAL POPULATION MEAN	83.3	454	2.84	77.2	427	.99

[a] H = Hereford, A = Angus, C = Charolais.

[b] Estimates based upon average of all year effects, weaning age of 191 days, and calves from mature dams

Days on feed

Table 13 lists predictions for specific breeds and crosses for days on feed for steer and bull calves respectively. Charolais sired calves out of straightbred Hereford dams were predicted to require the fewest days on feed. This breed group also possessed the highest postweaning gain predictions (table 12) resulting in fewer days on feed required to reach the specified slaughter weight endpoint. Straightbred Hereford had the largest estimate for time on feed. Straightbred Charolais calves possessed the smallest prediction for required days on feed relative to other straightbred cattle.

Prediction means were 239 d and 203 d for steers and bulls. Actual means were 235 d and 202 d for steers and bulls respectively.

TABLE 13. REML PREDICTIONS FOR SPECIFIC BREED GROUPS[a]

DAYS ON FEED[b]

BREED CROSS	STEERS (d)	BULLS (d)
H	257	221
A	255	219
C	237	201
H-A	246	210
A-H	237	202
H-C	250	214
C-H	213	177
A-C	256	221
C-A	227	192
H-AH	245	209
A-AH	239	204
C-AH	213	177
H-HC	247	211
A-HC	240	205
C-HC	218	183
H-AC	243	207
A-AC	251	215
C-AC	227	192
PREDICTION MEAN	239	203
ACTUAL POPULATION MEAN	235	202

[a] H = Hereford, A = Angus, C = Charolais

[b] Estimates based upon average of all year effects, weaning age of 191 days, and calves from mature dams.

Mature weight

Mature weight predictions for specific crosses are listed in table 14. Ranking of predictions for straightbred cattle resulted in Charolais being the heaviest at maturity, Herefords intermediate, and Angus females being the lightest at maturity. Straightbred Angus cattle were estimated to have the lightest mature weights of all breed group predictions. Charolais sired females out of Angus-Charolais reciprocal cross dams were predicted to be the heaviest at maturity in four of the five analyses. Charolais sired females out of Angus-Hereford reciprocal cross dams had the heaviest mature weight prediction in the days on feed analysis.

Prediction means for average adjusted mature weight ranged from 1195 lb to 1202 lb. The actual mean for mature weight in the entire population was 1189 lb.

TABLE 14. REML PREDICTIONS FOR SPECIFIC BREED GROUPS[a]

MATURE WEIGHT[bc]

	MULTI-TRAIT ANALYSIS[d]				
BREED CROSS	FT (lb)	REA (lb)	YG (lb)	QG (lb)	DOF (lb)
H	1159	1159	1159	1160	1171
A	1136	1136	1137	1137	1142
C	1215	1215	1216	1215	1220
H-A	1192	1195	1195	1196	1210
A-H	1150	1148	1150	1148	1149
H-C	1192	1190	1193	1292	1205
C-H	1223	1225	1223	1224	1226
A-C	1174	1170	1173	1171	1175
C-A	1247	1251	1248	1251	1256
H-AH	1193	1194	1194	1195	1210
A-AH	1160	1159	1161	1159	1165
C-AH	1252	1255	1253	1255	1261
H-HC	1181	1179	1181	1181	1192
A-HC	1167	1163	1166	1165	1166
C-HC	1224	1224	1224	1225	1226
H-AC	1217	1217	1218	1219	1228
A-AC	1180	1178	1179	1179	1179
C-AC	1256	1258	1257	1259	1259
PREDICTION MEAN	1195	1195	1196	1196	1202
ACTUAL POPULATION MEAN	1189	1189	1189	1189	1189

[a] H = Hereford, A = Angus, C = Charolais

[b] Fixed effect solutions listed are derived from each multi-trait analysis listed above.

[c] Estimates based upon average of all year effects, weaning age of 191 days, and calves from mature dams.

[d] CWT = carcass weight, FT = fat thickness, REA = ribeye area, YG = yield grade, QG = quality grade, DOF = days on feed.

Carcass traits

Predictions for specific breed crosses derived from REML analyses for fat thickness, and ribeye area are listed in table 15. Breed and breed cross predictions for yield grade and quality grade are listed in table 16.

Straightbred Charolais calves were the leanest among straightbred breed groups and possessed the largest ribeye areas relative to all breed groups. Angus were the fattest and intermediate for ribeye area while Hereford cattle were predicted to have the smallest ribeye areas relative to straightbred cattle.

The advantage in increased ribeye area and decreased fat thickness levels resulted in Charolais cattle also having the most desirable yield grade predictions relative to straightbred cattle. Charolais steers and bulls out of Hereford-Charolais reciprocal cross dams possessed the lowest yield grade predictions relative to all breed groups. Angus sired cattle from Hereford dams had the highest yield grade prediction. However, Angus straightbred cattle also had the most desirable quality grade prediction compared to Charolais and Hereford straightbred steers and bulls. Angus sired cattle out of Charolais dams possessed the most favorable quality grade estimates in comparison to all breed groups.

Rankings among straightbred Hereford, Hereford X Angus, Angus X Hereford, Charolais X Hereford and Hereford X Charolais steers are similar to those reported by

Huffhines et al. (1993). Results of this study show Hereford-Angus reciprocal cross steers to be the fattest, have the smallest ribeye areas, highest yield grades, and the most desirable quality grade scores. This study's results also indicate Hereford-Charolais reciprocal cross steers to be the leanest, possess the largest ribeye areas, lowest yield grades and the poorest quality grade scores. Hereford steers were intermediate in all categories in this study. Huffhines et al. (1993) reported similar rank orders between straightbred Hereford, Hereford X British and Hereford X Continental European steers with the exception of Hereford X British steers possessing larger ribeye areas than straightbred Hereford steers.

Prediction means for steer calves were .52 in, 11.23 in^2, 3.18, and 12.25 (high-select to low-choice) for fat thickness, ribeye area, yield grade, and quality grade, respectively. Actual steer calf means for the same traits were .48 in, 11.58 in^2, 2.97, and 12.75 respectively. Prediction means for bull calves were .32 in, 12.95 in^2, 1.91, and 16.57 while actual means were .30 in, 13.36 in^2, 1.79, and 17.18 for carcass weight, fat thickness, ribeye area, yield grade and quality grade.

TABLE 15. REML PREDICTIONS FOR SPECIFIC BREED GROUPS[a]

CARCASS TRAITS[bc]

	FT		REA	
BREED CROSS	STEERS (in)	BULLS (in)	STEERS (in^2)	BULLS (in^2)
H	.52	.31	10.90	12.63
A	.57	.37	11.26	12.99
C	.45	.24	12.81	13.54
H-A	.55	.35	10.94	12.67
A-H	.61	.40	10.56	12.29
H-C	.58	.38	10.90	12.62
C-H	.37	.17	11.84	13.56
A-C	.64	.43	10.28	12.01
C-A	.37	.16	11.60	13.33
H-AH	.57	.36	11.26	12.99
A-AH	.63	.42	11.26	12.98
C-AH	.41	.20	12.06	13.79
H-HC	.54	.33	11.07	12.80
A-HC	.61	.41	10.60	12.33
C-HC	.40	.19	12.00	13.73
H-AC	.57	.36	11.03	12.75
A-AC	.61	.40	10.88	12.60
C-AC	.41	.20	11.81	13.54
PREDICTION MEAN	.52	.32	11.23	12.95
ACTUAL POPULATION MEAN	.48	.30	11.58	13.36

[a] H = Hereford, A = Angus, C = Charolais
[b] FT = fat thickness, REA = ribeye area
[c] Estimates based upon average of all year effects, 607 lb carcass weight, and calves from mature dams

TABLE 16. REML PREDICTIONS FOR SPECIFIC BREED GROUPS[a]

CARCASS TRAITS[bc]

BREED CROSS	YG STEERS	YG BULLS	QG[d] STEERS	QG[d] BULLS
H	3.27	1.99	12.52	16.84
A	3.31	2.03	11.26	15.58
C	2.79	1.52	14.19	18.51
H-A	3.28	2.01	11.34	15.66
A-H	3.71	2.43	10.38	14.70
H-C	3.47	2.20	11.54	15.86
C-H	2.62	1.34	13.23	17.55
A-C	3.89	2.61	10.10	14.42
C-A	2.61	1.33	12.74	17.07
H-AH	3.27	1.99	12.81	17.13
A-AH	3.50	2.23	11.69	16.02
C-AH	2.60	1.33	13.86	18.18
H-HC	3.23	1.95	12.33	16.65
A-HC	3.66	2.38	10.54	14.86
C-HC	2.56	1.29	14.01	18.33
H-AC	3.34	2.06	12.26	16.58
A-AC	3.56	2.28	11.50	15.82
C-AC	2.66	1.39	14.28	18.60
PREDICTION MEAN	3.18	1.91	12.25	16.57
ACTUAL POPULATION MEAN	2.97	1.79	12.75	17.18

[a] H = Hereford, A = Angus, C = Charolais

[b] CWT = carcass weight, FT = fat thickness, REA = ribeye area, YG = yield grade, QG = quality grade

[c] Estimates based upon average of all year effects, 607 lb carcass weight, and calves from mature dams

[d] 10=Choice^{o}, 12=Choice^{-}, 14=Select^{+}, 16=Select^{o}

WEANING WEIGHT COMPARISONS

Tables 17 and 18 list comparisons of REML breed group predictions for weaning weight and 205-d weaning weight predictions reported previously by the Fort Keogh Livestock Range and Research Laboratory (LARRL). Results have been published by LARRL concerning weaning weight from all three phases of the crossbreeding study. Phase I and III results are directly comparable to this study's results as these phases dealt with weaning weight as a trait of the individual calf. Phase II dealt strictly with weaning weight as a trait of the dam. It should be noted that REML analyses were based upon weaning weights for males adjusted to a bull basis (steer weaning weight plus 7 lb).

In most cases, REML predictions for male calves were larger than those previously estimated by LARRL. REML predictions are based upon bull calves while LARRL estimates are based upon steer calves. Ranking of specific breed crosses are very similar between the two seperate set of estimates. Weaning weight predictions for heifer calves are very similar between REML analyses and those previously reported by LARRL.

The prediction mean for bull calves in phase I was 502 lb while the actual mean for bull calves weaned during this phase was 534 lb. LARRL predicted mean for steer calves in phase I was 497 lb and the actual mean for steer calves in phase I was 503 lb. Predicted means for heifer calves were 472 lb and 476 lb from REML and LARRL, respectively. The actual phase I mean for heifer weaning weight was 482 lb.

The REML prediction mean for bull calves weaned in phase III was 497 lb with the actual mean being 487 lb. The LARRL predicted mean for steer calves in phase III was 469 lb and the actual steer weaning weight mean was 477 lb. Predictions for heifer calves were 462 lb and 448 lb respectively from REML and LARRL. The actual heifer weaning weight mean in phase III was 455 lb. Previous LARRL analyses restricted class effects to sum to zero whereas current analyses for a particular class to zero and differences among comparison may be partially attributable to differences in restrictions.

TABLE 17. COMPARISON OF REML PREDICTIONS AND LARRL REPORTED PREDICTIONS FOR SPECIFIC BREED GROUPS[a]

WEANING WEIGHT - PHASE I (1962 - 1965)

	Male		Female	
	REML Estimate	LARRL Estimate	REML Estimate	LARRL Estimate
BREED CROSS	WWM[b] (lb)	WWM[c] (lb)	WWF[d] (lb)	WWF[e] (lb)
H	465	438	440	436
A	481	458	459	446
C	527	557	497	528
H-A	493	481	473	448
A-H	487	473	453	458
H-C	521	524	488	488
C-H	510	507	485	487
A-C	521	538	467	495
C-A	516	495	485	495
PREDICTION MEAN	502	497	472	476
ACTUAL POPULATION MEAN	534	503	482	482

[a] H = Hereford, A = Angus, C = Charolais.

[b] WWM = weaning weight males, REML estimates adjusted to 205-day, mature cow, bull calf basis. Estimate includes average year effect from 1962 to 1965.

[c] WWM = weaning weight males, LARRL estimates adjusted to 205-day, mature cow, steer calf basis

[d] WWF = weaning weight females, REML estimates adjusted to 205-day, mature cow basis. Estimates includes average year affect from 1962 to 1965.

[e] WWF = weaning weight females, LARRL estimates adjusted to 205-day, mature cow basis.

TABLE 18. COMPARISON OF REML PREDICTIONS AND LARRL REPORTED PREDICTIONS FOR SPECIFIC BREED GROUPS CONT[a]

WEANING WEIGHT - PHASE III (1967 - 1977)

	Male		Female	
	REML Estimate	LARRL Estimate	REML Estimate	LARRL Estimate
BREED CROSS	WWM[b] (lb)	WWM[c] (lb)	WWF[d] (lb)	WWF[e] (lb)
H	453	398	421	378
A	470	450	440	430
C	515	517	478	496
H-AH	494	466	459	445
A-AH	500	438	459	417
C-AH	528	n/a	487	n/a
H-HC	493	498	462	477
A-HC	504	n/a	458	n/a
C-HC	519	478	489	457
H-AC	495	n/a	468	n/a
A-AC	489	479	450	458
C-AC	509	493	478	472
PREDICTION MEAN	497	469	462	448
ACTUAL POPULATION MEAN	487	477	455	455

[a] H = Hereford, A = Angus, C = Charolais

[b] WWM = weaning weight males, REML estimates adjusted to 205-day, mature cow, bull calf basis. Estimate includes average year effect from 1967 to 1977.

[c] WWM = weaning weight males, LARRL estimates adjusted to 205-day, mature cow, steer calf basis

[d] WWF = weaning weight females, REML estimates adjusted to 205-day, mature cow basis. Estimates includes average year effect from 1967 to 1977.

[e] WWF = weaning weight females, LARRL estimates adjusted to 205-day, mature cow basis.

VARIANCE AND COVARIANCE COMPONENT ESTIMATION

Estimated variance and covariance components are listed in table 19. The components are categorized according to direct variance component estimates, maternal variance component estimates, direct-maternal covariance estimates, and error variance component estimates.

Covariance estimates between direct and maternal components for male and female traits are listed in table 20. The components are categorized according to separate analyses.

TABLE 19. VARIANCE AND COVARIANCE ESTIMATES (lb^2)

Trait[a]	Direct	Maternal	D-M Covariance[b]	Residual
BWM(lb^2)	42.22	43.75	.32	32.39
BWF(lb^2)	49.34	25.86	-3.21	18.17
WWM(lb^2)	263.98	2319.51	27.79	-46.26
WWF(lb^2)	469.95	1473.24	219.86	-196.80
ADGM(lb/d^2)	.031	.017	-.013	.067
ADGF(lb/d^2)	.015	.003	.0002	.018
DOF(d^2)	448.88	448.10	-146.03	146.45
MW(dof)(lb^2)	6685.36	842.54	1971.56	-756.20
MW(ft)(lb^2)	6705.00	838.93	1524.38	-410.17
MW(rea)(lb^2)	6511.32	605.07	1649.98	-155.71
MW(yg)(lb^2)	6701.00	623.89	1712.46	-377.12
MW(qg)(lb^2)	6502.88	576.17	1707.12	-162.18
FT(in^2)	.004	.0005	.0007	.014
REA(sq in^2)	.433	.072	-.081	.851
YG($units^2$)	.075	.044	-.001	.252
QG($units^2$)	3.062	1.498	-1.643	4.342

[a] BWM = birth weight - males , BWF = birth weight - females, WWM = weaning weight - males adjusted to bull basis, WWF = weaning weight - females, ADGM = postweaning average daily gain adjust to bull basis, ADGF = postweaning average daily gain - females, DOF = male days on feed, MW = average adjusted female mature weight listed for five multi-trait analyses, FT = fat thickness, REA = ribeye area, YG = yield grade, QG = quality grade.

[b] D-M = direct - maternal

TABLE 20. COVARIANCE COMPONENTS[a] AMONG SEX SPECIFIC TRAITS[b]

Traits[c]	COV DM-DF	COV DM-MF	COV MM-DF	COV MM-MF
BWM-BWF	42.60	-12.43	12.97	28.99
WWM-WWF	316.87	-1.50	351.30	1809.52
ADGM-ADGF	.016	-.0008	-.007	.003
DOF-MW	-1135.48	-186.44	-700.53	-438.24
FT-MW	-2.82	.19	-.31	.26
REA-MW	-9.69	-.71	10.22	2.36
YG-MW	-4.12	-.33	-4.41	.40
QG-MW	58.21	16.20	.51	-1.73

[a] DM = direct component - male trait
DF = direct component - female trait
MM = maternal component - male trait
MF = maternal component - female trait

[b] BWM = birth weight - males , BWF = birth weight - females, WWM = weaning weight - males adjusted to bull basis, WWF = weaning weight - females, ADGM = postweaning average daily gain adjusted to bull basis, ADGF = postweaning average daily gain - females, DOF = days on feed, MW = average adjusted mature weight listed for five multi-trait analyses, FT = fat thickness, REA = ribeye area, YG = yield grade, QG = quality grade.

[c] Male trait listed first, female trait second.

HERITABILITY AND DIRECT-MATERNAL CORRELATION ESTIMATES

Heritability estimates and direct-maternal correlation estimates are listed in table 21. All breeds were combined in the analyses and breed was included in the analytical model resulting in pooled, within-breed estimates.

Direct effects on female birth weight accounted for a larger portion of total variance compared to male birth weight. Maternal effects on birth weight between the sexes were similar but male birth weight was slightly more affected by the maternal environment. Direct heritability estimates for male and female birth weight were .36 and .53, respectively. Maternal heritability estimates were .37 and .28. Woldehawariat et al. (1977) reported an average heritability estimate for the direct effect on birth weight of .39. Itulya (1987) reported birth weight heritability estimates of .53 and .52 for males and females, respectively. Direct-maternal correlations estimates for birth weight were very low in both sexes (.01 and -.09 for male and female calves, respectively) indicating selection concerning birth weight is relatively free of direct-maternal antagonisms.

Direct heritability estimates for weaning weight were .10 and .24 in male and female calves, respectively. Female calves were able to express a larger portion of their growth potential as they receive more milk per unit of body weight (Robison et al., 1978; Rutledge et al., 1971; Melton et al., 1967) thus direct additive genetic resulting in a higher heritability estimate for heifer calves. Denise and Torabi (1989) reported that genetic parameters change in response to the level of environmental stress and sexes respond differently to these conditions.

Variance due to maternal effects accounted for a major portion of total variance in both sexes and resulted in very high maternal heritability estimates. Maternal heritability estimates were .90 and .76 in males and females respectively. This may reflect the relatively limited environment at LARRL where calves possess inherently high growth potential and differences in weaning weight are largely due to differences in milk production. Itulya (1987) reported that age of dam and the interaction between age of dam and year significantly affect weaning weight.

In this study, sires and subsequent maternal grand sires are totally confounded with year, and as a result are also confounded with age of dam and the interaction between them. If the relationship matrix utilized in the analysis does not adequately eliminate confounding, a large portion of weaning weight variability will be absorbed by the maternal component due to the factors discussed. Direct-maternal correlations for male and female weaning weight were both positive but relatively low (.04 and .26 respectively). Correlation estimates indicate this population allows selection for increased growth without antagonisms towards increased maternal ability.

Heritability estimates of direct effects upon postweaning average daily gain were .27 for males and .41 for females. Maternal heritability estimates for postweaning average daily gain were low for both sexes; .14 and .09 for males and females respectively. Maternal influences appear to have a slightly larger influence on male postweaning average daily gain compared to females. The direct-maternal correlation in postweaning gain for males was -.58 and .03 in females. Males are more dependent upon the maternal environment to weaning. Furthermore, males were fed a higher level of nutrition postweaning. As a result, maternal heritability and the direct-maternal correlation for postweaning gain was higher in males reflecting a larger interaction between preweaning and postweaning environment. Heritability estimates for the direct and maternal components of days on feed were .41 and .43 respectively.

Heritability estimates for the direct component of mature weight were high and ranged from .89 to .92. These estimates are somewhat higher than other previously reported heritability estimates concerning mature weight (h^2=.54, MacNeil et al., 1984; h^2=.55, Brinks et al., 1964; h^2=.74, Brinks et al., 1962). Maternal heritability estimates for mature weight were small and ranged from .08 to .11. All residual estimates concerning mature weight were negative. The high heritability estimates concerning the direct component of mature weight are likely an indication of confounding among sires and years. Mature weight can be highly affected by year of birth and may result in abnormally high heritability estimates. As mentioned previously the sire - maternal grandsire model may not eliminate confounding between sire and year in this particular data set. As a result, both year and sire influences are reflected in the direct component of variance resulting in high heritability estimates. It should also be noted that year effect estimates were progressively larger from 1962 to 1975 (table 6). As mentioned previously, these possibly reflect not only actual year effects but also genetic trend. Nonetheless, the analyses resulted in the direct component absorbing a large proportion of the variance while the maternal component accounted for the remainder of total variance.

The direct-maternal correlation estimates for mature weight were highly positive ranging from .64 to .88 indicating that direct selection for mature weight results in selection for maternal environments affecting mature weight in the same direction. McMorris and Wilton (1986) reported that milk yield appears to be positively affected by cow size with larger cows producing more milk, thus weaning heavier calves. It appears that female calves who are heavier at weaning due to being older or having mature dams maintain their advantage at maturity (table 6).

Therefore, larger cows who may be able to wean heavier calves because of increased milk production (McMorris and Wilton, 1986) produce females who are heavier at maturity causing the high direct-maternal correlation of mature weight.

Direct heritability estimates were .21, .32, .20, and .34 for fat thickness, ribeye area, yield grade, and quality grade respectively. Speer (1991) reported average carcass trait heritability estimates from Koch et al. (1982), Wilson (1987), and Benyshek (1988) of .43, .40, and .41 for fat thickness, ribeye area, and quality grade. Yield grade heritability estimates average .36 within the literature (Speer, 1991). Heritability estimates concerning carcass traits are somewhat lower than previously reported literature estimates and may be a result of very small variation in carcass weight. Dinkel and Busch (1973) and Brackelsburg et al. (1971) indicated that carcass weight is a significant source of variation concerning amounts and components of carcass yield. Cundiff et al. (1969) also reported that heritability estimates are lower for carcass traits considered on a weight adjusted basis versus an age adjusted basis. Maternal heritability estimates were low; .03, .06, .12, and .17 for fat thickness, ribeye area, yield grade and quality grade, respectively.

Direct-maternal correlation estimates for fat thickness, ribeye area, yield grade, and quality grade were

.49, -.46, -.02, and -.77, respectively. The correlation estimate for fat thickness indicates that direct selection for leanness results in females who also produce leaner calves. However, the selection for leanness may also result in "poorer keeping" females that inherently have lower fat levels. This relationship may result in decreased milk levels and poorer reproductive performance.

The direct-maternal correlation estimate for ribeye area is unfavorable as it indicates that direct selection for increased ribeye area results in dams who produce calves who are relatively less muscular. The large direct-maternal correlation estimate for quality grade is also antagonistic. It indicates that selection for improved quality grade scores (lower scores) in males, results in selection for females who produce calves with poorer quality grade scores (higher scores). The unfavorable direct-maternal correlations among ribeye area and quality grade may reflect that direct selection for these traits may result in decreased maternal ability. As a result, dams will produce calves which are relatively less mature at slaughter and therefore have smaller ribeye areas and poorer quality grade scores. Maternal effects on both traits, though, were relatively small as indicated by relatively low maternal heritability estimates.

It appears the sire - maternal grandsire model does a good job of yielding variance components if the trait is not largely influenced by environmental factors associated with year effects (i.e. carcass traits). All cattle throughout the study were slaughtered at a weight constant basis. As a result, no large year influences tend to be confounded with sire or maternal grandsire concerning carcass traits.

TABLE 21. HERITABILITY ESTIMATES AND CORRELATIONS AMONG DIRECT AND MATERNAL COMPONENT

Trait[a]	h^2 direct	h^2 maternal	r^{D-M}[b]
BWM	.36	.37	.01
BWF	.53	.28	-.09
WWM	.10	.90	.04
WWF	.24	.76	.26
ADGM	.27	.14	-.58
ADGF	.41	.09	.03
DOF	.41	.43	-.33
MW(dof)	.89	.11	.83
MW(ft)	.89	.11	.64
MW(rea)	.92	.08	.83
MW(yg)	.91	.09	.84
MW(qg)	.92	.08	.88
FT	.21	.03	.49
REA	.32	.06	-.46
YG	.20	.12	-.02
QG	.34	.17	-.77

[a] BWM = birth weight - males , BWF = birth weight - females, WWM = weaning weight - males adjusted to bull basis, WWF = weaning weight - females, ADGM = postweaning average daily gain adjust to bull basis, ADGF = postweaning average daily gain - females, DOF = days on feed, MW = average adjusted mature weight listed for six multi-trait analyses, FT = fat thickness, REA = ribeye area, YG = yield grade, QG = quality grade.

[b] rD-M = correlation between direct and maternal component

CORRELATIONS BETWEEN SEX SPECIFIC TRAITS

Table 22 lists the correlations between the specific sex related traits.

Direct component-male trait/direct component-female trait

Direct components for the same trait measured in separate sexes were strongly positively related. Correlations were .74 (average daily gain analysis), .90 (weaning weight analysis), and .93 (birth weight analysis). It is apparent that a large proportion of the same genes are responsible for performance of one trait analyzed seperately between sexes. Selection pressure in either sex for the trait of interest results in selection pressure in the same direction in the other sex for birth weight, weaning weight, and average daily gain.

Correlations between mature weight and fat thickness was highly negative (-.54). Increased mature weight in females results in leaner carcasses in male sibs on a weight adjusted basis. MacNeil et al. (1984) reported a genetic correlation between fat trim weight on an age constant basis and mature weight of -.09. They reported that females from sires selected for reduced fat trim of steer progeny are larger at maturity. On a weight constant basis, as selection pressure on growth increases, the correlated response is equivalent to selection for leanness (Cundiff et al., 1969).

The correlations between female mature weight and male ribeye area & male yield grade were both -.18. Selection for decreased yield grades results in increased mature size while selection for increased ribeye area results in decreased mature size when male progeny are being slaughtered at a constant weight endpoint. Slaughtering at a constant weight endpoint largely reflects maturity at a specific endpoint. Cattle that have inherently more growth potential will also be physiologically less mature when slaughtered on a constant weight basis. As a result, as mature weight (growth potential) increases in females, maturity and ribeye area in male sibs decreases.

The correlation between mature weight and quality grade (.41) indicates that increased mature size in females is related to less favorable quality grade scores (higher scores). Relationships between growth, maturity, and slaughter endpoint that affect ribeye area may also affect quality grade scores. Fat and marbling are positively correlated with earlier maturing cattle (Koch et al., 1982).

The correlation between mature weight and days on feed was also highly negative (-.66). Sires which produce females that are larger at maturity also produce cattle which require less time on feed; and are leaner, have smaller ribeye areas, lower yield grades, and less desirable quality grade scores on a weight constant basis.

Direct component-male trait/maternal component-female trait

The correlations between the direct component for male birth weight, weaning weight, and average daily gain and the maternal component for the same traits measured in females were -.38, 0, and -.08 respectively. There appears to be no relationship between weaning weight direct for males and weaning weight maternal for females. Selection for increased average daily gain in male calves yields selection for less desirable maternal environments for average daily gain in females. As mentioned previously, females which are heavier at weaning experienced less postweaning gain due to higher maintenance requirements and less compensatory growth.

The correlations of mature weight and the male carcass trait of interest ranged from -.05 to .39. The correlation between mature weight and days on feed was -.30. Sires which produce male calves who require less time on feed also sire dams which produce progeny which are larger at maturity. Correlations between mature weight and fat thickness (.10), ribeye area (-.04), & yield grade (-.05) were small and there was little relationship between the direct component of carcass traits and the maternal component for mature weight. The correlation between quality grade and mature weight was .39. Selection for decreased quality grade scores (more desirable) at a constant weight endpoint results in selection for a maternal environment for decreased mature size.

Sires that produce dams that have females that are larger at maturity also produce male calves which require less time on feed, have slightly increased fat thickness levels, smaller ribeye areas, lower yield grades, and less desireable quality grade scores.

<u>Maternal component-male trait/direct component-female trait</u>

Correlations for male and female birth weight (.28), weaning weight (.34), and postweaning average daily gain (-.44) were moderate. There is a positive relationship in weaning weight (.34) between the maternal component in male calves and the direct component in female calves in contrast to an apparent lack of relationship between the maternal component in female calves and the direct component in male calves. Selection for sires that produce female calves that are heavier at weaning appears to be favorably related to the maternal component for male weaning weight. The relationship among postweaning average daily gain between the sexes is the same direction and much stronger concerning the male maternal component/female direct component than the female maternal component/male direct component. Male postweaning average daily gain is more largely affected by the maternal component (maternal h^2=.14) and female postweaning average daily gain is more largely affected by the direct component (h^2=.41) resulting in a stronger correlation between these components.

Mature weight and days on feed were negatively correlated (-.40). Mature weight and fat thickness & yield grade were also negatively related (-.17 and -.26 respectively). Selection for females that produce male calves who are leaner and have lower yield grades results in selection for increased mature size. Ribeye area and mature weight were moderately and positively related (.47) concerning the respective components. Selection for increased mature weight would result in maternal environments that increase ribeye area. This relationship may also be a function of the relationships reported by McMorris and Wilton (1986) discussed previously. Increased mature size resulting in increased milk production may also result in increased relative maturity and subsequent ribeye area of males because of a favorable maternal environment prior to slaughter.

Maternal component-male trait/maternal component-female trait

The correlation between the maternal components for mature weight and days on feed was -.71. Selection for maternal environments which result in increased mature size would result in decreased days on feed in male calves to a constant weight endpoint. Maternal environments which increase growth prior to weaning likely result in fewer days on feed required to reach a constant weight slaughter endpoint and a preweaning advantage for females that may also be apparent at maturity.

Carcass weight, fat thickness, ribeye area, and yield grade were positively associated with mature weight. Dams which produce larger female progeny at maturity also produce male progeny which have increased fat thickness levels, larger ribeye areas and higher yield grades. Quality grade and mature weight were negatively correlated (-.06). Dams which produce larger females calves at maturity also produce male calves which have lower quality grade scores (favorable relationship).

Correlations among birth weight, weaning weight, and average daily gain were .86, .98, and .42 respectively. Birth weight and weaning weight between the sexes were strongly correlated concerning the maternal environment. Maternal environments which result in increased birth weights and weaning weights in male calves also result in increased weights in female calves.

TABLE 22. CORRELATIONS AMONG SEX RELATED TRAITS[ab]

$r^{DM - DF}$

Male Trait	Female Trait MW	BWF	WWF	ADGF
DOF	-.66			
FT	-.54			
REA	-.18			
YG	-.18			
QG	.41			
BWM		.93		
WWM			.90	
ADGM				.74

$r^{DM - MF}$

Male Trait	Female Trait MW	BWF	WWF	ADGF
DOF	-.30			
FT	.10			
REA	-.04			
YG	-.05			
QG	.39			
BWM		-.38		
WWM			0	
ADGM				-.08

TABLE 22. CORRELATIONS AMONG SEX RELATED TRAITS[ab]
CONT...

r^{MM} - DF

Male Trait	Female Trait MW	BWF	WWF	ADGF
DOF	-.40			
FT	-.17			
REA	.47			
YG	-.26			
QG	.01			
BWM		.28		
WWM			.34	
ADGM				-.44

r^{MM} - MF

Male Trait	Female Trait MW	BWF	WWF	ADGF
DOF	-.71			
FT	.40			
REA	.10			
YG	.08			
QG	-.06			
BWM		.86		
WWM			.98	
ADGM				.42

[a] BWM = birth weight - males , BWF = birth weight - females, WWM = weaning weight - males adjusted to bull basis, WWF = weaning weight - females, ADGM = postweaning average daily gain adjusted to bull basis, ADGF = postweaning average daily gain - females, DOF = days on feed, MW = average adjusted mature weight listed for six multi-trait analyses, FT = fat thickness, REA = ribeye area, YG = yield grade, QG = quality grade.

[b] DM = direct component - male trait, MM = maternal component - male trait, DF = direct component - female trait, MF = maternal component - female trait

CORRELATED RESPONSE TO SELECTION

The primary purpose of this study is to investigate genetic relationships among important production characteristics with a special emphasis on mature size and carcass characterisitics. These relationships can be utilized to calculate response of a correlated trait if the genetic correlation and the heritabilities of the two traits of interest are known (Falconer, 1981). Tables 23 and 24 list predicted correlated responses in female and male traits per standard deviation of direct response in male and female traits respectively.

Birth weight, weaning weight and postweaning average daily gain in both sexes respond in similar directions (table 23). As a result, one should be able to make selection decisions based upon a trait in one sex and expect favorable response in the other sex. Selection for decreased birth weight, increased weaning weight, and increased postweaning average daily gain results in response of the same direction for the same trait in the opposite sex.

The response in male birth weight is larger per selection in females than response in female birth weight per selection in males due to more genetic variability in male birth weight. The response in weaning weight between the sexes (9 lb and 10 lb in females and males, respectively) is very similar when selection occurs for weaning weight in the opposite sex. Selection for increased male postweaning average daily gain results in increased female postweaning average daily gain but the correlated response is larger in males than in females.

Selection pressure on increased leanness and decreased yield grades on a constant weight basis is antagonistic with mature weight (table 23). At the same time, selection pressure to decrease mature size of females results in males who will be fatter and subsequently have higher yield grades when slaughtered on a weight constant basis (table 24). Woodward et al. (1954) reported that increased inherent growth potential (increased mature size) is negatively correlated with deposition of external fat. Fat thickness levels at a constant weight are largely a function of the growth curve and maturity levels at that given weight (Brackelsburg et al., 1971).

Ribeye area and quality grade when being considered on a weight adjusted basis are favorably related with mature weight. Selection for increased ribeye area on a weight constant basis results in response of related females for decreased mature size. As growth potential is decreased, relative maturity and subsequent muscularity (ribeye area) is increased at a constant weight endpoint. Furthermore, earlier maturing cattle also have an advantage in the fact that they are able to fatten more quickly, reach a "market readiness" composition earlier and thus have higher quality grade scores (Speer, 1991).

Selection for decreased days on feed to a weight constant basis in order to increase efficiency in the feedlot is related to increased mature size of related females (table 23). Cattle with inherently more growth potential tend to gain more quickly thereby reaching a specific weight endpoint sooner but also are larger at maturity.

TABLE 23. PREDICTED CORRELATED RESPONSES IN FEMALE TRAITS PER STANDARD DEVIATION OF DIRECT RESPONSE IN MALE TRAITS

	Male Trait[b] and (standard deviation)							
Female trait[a] (mean)	BW[c] (9.1)	WW[c] (44)	ADG[d] (.26)	FT[d] (.12)	REA[d] (.92)	YG[d] (.50)	QG[d] (2.1)	DOF[d] (12.1)
BW (77)	5.6							
WW (427)		9						
ADG (.99)			.05					
MW (1189)				-32	-13	-10	31	-54

[a] BW = birth weight (lb), WW = weaning weight (lb), ADG = postweaning average daily gain (lb/d), MW = mature weight (lb).

[b] BW = birth weight (lb), WW = weaning weight (lb), ADG = postweaning average daily gain (lb/d), FT = fat thickness (in), REA = ribeye area (in^2), YG = yield grade, QG = quality grade, DOF = days on feed (d)

[c] Standard deviations result from least-squares analyses

[d] Standard deviations result from REML analyses

TABLE 24. PREDICTED CORRELATED RESPONSES IN MALE TRAITS PER STANDARD DEVIATION OF DIRECT RESPONSE IN FEMALE TRAITS

	Female Trait[b] and (standard deviation)			
Male trait[a] (mean)	BW[c] (8.7)	WW[c] (40)	ADG[d] (.13)	MW[c] (84)
BW (83)	4.0			
WW (452)		10		
ADG (2.87)			.10	
FT (.40)				-.05
REA (12.40)				-.14
YG (2.43)				-.06
QG (14.79)				.75
DOF (222)				-7.8

[a] BW = birth weight (lb), WW = weaning weight (lb), ADG = postweaning average daily gain (lb/d), FT = fat thickness (in), REA = ribeye area (in^2), YG = yield grade, QG = quality grade, DOF = days on feed (d)

[b] BW = birth weight (lb), WW = weaning weight (lb), ADG = postweaning average daily gain (lb/d), MW = mature weight (lb).

[c] Standard deviations result from least-squares analyses

[d] Standard deviations result from REML analyses

CHAPTER V

APPLICATION

The magnitude and accuracy of EPDs are influenced by parameter estimates (heritabilities and genetic correlations), regardless of how accurately adjustments are made, how well contemporary groups are formed or how sophisticated analyses become (Speer et al, 1991; DeNise and Torabi, 1989). It is conclusive from this study that parameter estimates and the resulting proportions of direct and maternal effects responsible for expression of traits measured in both sexes vary depending upon sex of calf. Furthermore, it has been shown that these differences may also interact with the given environment (Itulya et al., 1987). Parameter estimates which vary between sexes and are not static in varying environments may affect genetic response to selection decisions (Speer et al., 1991). Weaning weight and postweaning average daily gain are traits measured in both sexes and are important selection criteria to many beef producers. However, these traits are influenced very differently between sexes and seedstock producers who use similar selection criteria between sexes may not be realizing efficient response to selection.

The current trend within the beef industry forces cattlemen to produce cattle that excel not only in terms of maternal traits but also in terms of growth and carcass merit. These trends are summarized well by Brinks (1990): "Several trends in consumer demand, cattle production and marketing are becoming evident. Consumers are asking for leaner beef while maintaining quality and tenderness. Feedlot operations emphasize growth and efficiency. Thus, leaner, fast growing and perhaps more heavily muscled cattle will be in demand. Crossbreeding in various forms will be the major breeding system to take advantage of breed complementarity and heterosis. At the producer level, increased emphasis needs to be placed on matching cow size, milk level and overall biological type to available resources."

Carcass performance is becoming more important in response to the beef industry's current focus on consumer demands. As a result, there is increasing pressure to increase leanness and muscularity of slaughter cattle. However, large amounts of selection pressure regarding leanness may be antagonistic to commercial beef producers. Results of this study indicate that sires which are selected on the basis of reducing fat trim in steer progeny may also produce females which are larger at maturity when cattle are being slaughtered on a weight constant basis. Inception of value based marketing systems are likely to reward producers with uniform lots of cattle in terms of size and weight. This occurence may result in the need to find seedstock which are able to counteract the antagonisms between increasing leanness and mature size. However, breeds that excel solely in carcass leanness that is not a result of increased growth are characterized by females who tend to be older at puberty and possess lower levels of fertility (MacNeil, 1988).

Across-breed EPDs are receiving an increasing amount of attention by industry geneticists. Questions remain concerning the current limited basis for comparison between breeds. This study utilized an analytical model which accounted for direct breed and heterotic differences within a crossbred population. Results from analyses and breed group predictions are consistent with previous literature reports. Several problems may still exist, though, with analytical techniques of crossbred populations. These problems primarily concern the interaction of additive and heterotic effects with maternal influences. Maternal reciprocal crosses were combined within these analyses. Differences may exist between specific crosses and breed maternal deviations may be affected by these analytical techniques.

Numerous challenges currently face the U.S. beef industry. Several of these challenges have been discussed within this section. These challenges include the need to accurately and efficiently estimate population parameters especially in light of continuously increasing amounts of data. Industry geneticists will need to refine analytical techniques applied to crossbred data and use these techniques on large amounts of data if they are to provide meaningful across-breed EPDs. Most importantly, though, cattlemen will need to be more conscious of carcass composition when making selection decisions. It appears that selection for increased leanness may result in antagonisms towards productivity and in order to remain profitable beef producers may have to learn to compromise between these antagonisms. Increasing knowledge of relationships concerning traits of economic importance is critical and should allow to more efficiently reach selection goals in terms of both carcass merit and female productivity.

LITERATURE CITED

Allender, Steve. 1990. Request for proposals on genetic evaluation for beef carcass merit. NCA correspondence.

American Hereford Journal. November, 1991. Consolidataed Balance Sheets. p 38-40.

Benyshek, L.L. 1988. Personal communication through J.S. Brinks, Department of Animal Science, Colorado State University, Fort Collins, CO.

Brackelsberg, P.O., E.A. Kline, R.L. Willham, and L.N. Hazel. 1971. Genetic parameters for selected beef carcass traits. J. Anim. Sci. 33:13.

Brinks, J.S., R.T. Clark, N.M. Kieffer and J.R. Quesenberry. 1962. Mature weight in Hereford range cows - heritability, repeatability, and relationship to calf performance. J. Anim. Sci. 21:501.

Brinks, J.S., R.T. Clark, N.M. Kieffer and J.J. Urick. 1964. Estimates of genetic, environmental and phenotypic parameters in range Hereford females. J. Anim. Sci. 23:711.

Brinks, J.S. 1990. Expected progeny differences. Definitions, Calculations, Interpretations, and Uses.

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

Cornett, Steve. 1990. War on fat: at last a plan. Drovers Journal. Sept, 1990. p. 14.

Cundiff, L.V., K.E. Gregory, R.M. Koch, and G.E. Dickerson. 1969. Genetic variation in total and differential growth of carcass components in beef cattle. J. Anim. Sci. 29:233.

Cundiff, L.V. 1970. Experimental results on crossbreeding cattle for beef production. J. Anim. Sci. 30:694.

Damon, R.A. Jr., W.R. Harvey, C.B. Singletary, S.E. McCraine and R.M. Crown. 1961. Genetic analysis of crossbreeding beef cattle. J. Anim. Sci. 20:849.

DeNise, S.K. and M. Torabi. 1989. Genetic parameter estimates for postweaning traits of beef cattle in a stressful environment. J. Anim. Sci. 67:2619.

Dillard, E.U., Oswaldo Rodriguez and O.W. Robsion. 1980. Estimation of additive and nonadditive direct and maternal genetic effects from crossbreeding beef cattle. J. Anim. Sci. 50:653.

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.

Donald, H.P., D. Gibson and W.S. Russell. 1977. Estimations of heterosis in crossbred dairy cattle. Anim. Prod. 25:193.

Eberhart, S.A. and C.O. Gardner. 1966. A general model for genetic effects. Biometrics 22:864.

Ellis, W.W., M.R. Ellersieck, L. Langford, B. Sibbit and J.F. Lasley. 1979. Effects of mating systems on weaning traits in beef cattle. J. Anim. Sci. 48:7.

Elzo, M.A. and T.R. Famula. 1985. Multibreed sire evaluation procedures within a country. J. Anim. Sci. 60:942.

Falconer, D.S. Introduction to Quantitative Genetics. John Wiley and Sons. New York. p. 280.

Ferjani, Youssef. 1976. Heterosis in weights of Hereford females. M.S. Thesis. Colorado State Univ., Fort Collins, CO.

Gaines, J.A., C. Hill, W.H. McClure, R.C. Carter and W.T. butts. 1978. Heterosis from crosses among British breeds of cattle. I. Straightbred versus crossbred cows. J. Anim. Sci. 47:1246.

Gardner, C.O. and S.A. Eberhart. 1966. Analysis and interpretation of the variety cross diallel and related populations. Biometrics 22:439.

Golden, B.L. 1991. A new model for the analysis of multibreed data. Personal reference.

Golden, B.L., W.M. Snelling and C.H. Mallinckrodt. 1992. Animal breeder's toolkit: Users guide and reference manual. Colo. St. Univ. Agric. Exp. Sta. Tech. Bull. LTB92-2.

Gregory, K.E., L.A. Swiger, R.M. Koch, L.J. Sumption, W.W. Rowden and J.E. Ingalls. 1965. Heterosis in preweaning traits of beef cattle. J. Anim. Sci. 24:21.

Gregory, K.E., L.V. Cundiff, R.M. Koch, D.B. Lasater, and G.M. Smith. 1978. Heterosis and breed maternal and transmitted effects in beef cattle. I. Preweaning traits. J. Anim. Sci 47:1031.

Gregory, K.E., D.B. Laster, L.V. Cundiff, R.M. Koch and G.M. Smith. 1978. Heterosis and breed maternal and transmitted effects in beef cattle. II. Growth rate and puberty in females. J. Anim. Sci 47:1042.

Gregory, K.E., R.M. Koch, D.B. Laster, L.V. Cundiff and G.M. Smith. 1978. Heterosis and breed maternal and transmitted effects in beef cattle. III. Growth traits of steers. J. Anim. Sci 47:1054.

Gregory, K.E., J.D. Crouse, R.M. Koch, D.B. Laster, L.V. Cundiff and G.M. Smith. 1978. Heterosis and breed maternal and transmitted effects in beef cattle. IV. Carcass traits of steers. J. Anim. Sci 47:1063.

Gregory, K.E., and L.V. Cundiff. 1980. Crossbreeding in beef cattle: Evaluation of systems. J. Anim. Sci. 51:1224.

Henderson, C.R. 1953. Estimation of variance and covariance components. Biometrics 9:320.

Huffhines, C.P., G.C. Ledall, J.E. Cannon, J.D. Tatum, T.G. Field, M.A. Head, J.B. Morgan and G.C. Smith. 1993. Carcass characteristics and cooked-steak palatability of straightbred Hereford steers and heifers and Hereford crossbred steers. Colorado State Univ. Beef Program Report. p. 145.

Itulya, S.B., D.E. Ray, C.B. Roubicek and C.R. Benson. 1987. Genetic parameters, maternal ability and related selection criteria for unsupplemented Hereford range cows. J. Anim. Sci. 64:1630.

Kincaid, C.M. 1962. Breed crosses with beef cattle in the south. A report of cooperative research under Southern Regional Project S-10. Southern Cooperative Series Bull. 81.

Knapp, B.W., O.F. Pahnish, J.J. Urick, J.S. Brinks and G.V. Richardson. 1980. Preweaning and weaning heterosis for maternal effects of beef x beef and beef x dairy crosses. J. Anim. Sci. 50:800.

Knop, Fred. 1992. New mindset need for optimal genetics. Drovers Journal, July. p. 31.

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., L.V. Cundiff, and K.E. Gregory. 1982. Heritabilities and genetic, environmental and phenotypic correlations of carcass traits in a population of diverse biological types and their implications in selection programs. J. Anim. Sci. 55:1319.

Komender, P. and I. Hoeschele. 1989. Use of mixed-model methodology to improve estimation of crossbreeding parameters. Livestock Production Science. 21:101.

Long, C.R., and K.E. Gregory. 1974. Heterosis and breed effects in preweaning traits of Angus, Hereford, and reciprocal cross calves. J. Anim. Sci. 39:11.

MacNeil, M.D., C.A. Dinkel and L.D. VanVleck. 1982. Individual and maternal additive and heterotic effects on 205-day weight in beef cattle. J. Anim. Sci. 54:951.

MacNeil, M.D., L.V. Cundiff, C.A. Dinkel and R.M. Koch. 1984. Genetic correlations among sex-limited traits in beef cattle. J. Anim. Sci 58:1171.

MacNeil, M.D. 1987. Formation of optimal composite populations. Theor. Appl. Genet. 74:837.

MacNeil, M.D., L.V. Cundiff, and K.E. Gregory. 1988. Crossbreeding systems for beef production. App. Ag. Rsrch. 3:44.

MacNeil, M.D. 1988. Consequences of selection for growth and tissue development on maternal qualities. Proceedings of 3rd World Congress on Sheep and Beef Cattle Breeding.

McMorris, M.R., and J.W. Wilton. 1986. Breeding system, cow weight and milk yield effects on various biological variables in beef production. J. Anim. Sci. 63:1361.

Melton, A.A., J.K. Riggs, L.A. Nelson, and T.C. Cartwright. 1967. Milk production, composition, and calf gains of Angus, Charolais, and Hereford cows. J. Anim. Sci. 26:804.

National Cattlemens' Association. 1990. The war on fat. A report from the Value Based Marketing Task Force.

National Cattlemens' Association. 1991. Executive summary. National Beef Quality Audit - 1991.

Pahnish, O.F., J.S. Brinks, J.J. Urick, B.W. Knapp and T.M. Riley. 1969. Results from crossing beef x beef and beef x dairy breeds: calf performance to weaning. J. Anim. Sci. 28:291.

Pahnish, O.F., B.W. Knapp, J.J. Urick, J.S. Brinks and F.S. Willson. 1971. Results from crossing beef x beef and beef x dairy breeds: postweaning performance of heifers. J. Anim. Sci. 33:736.

Parekh, H.K.B. and R.W. Tourchberry. 1974. Comparative performance of purebreds and crossbreds in respect to reproductive traits: 1st parity records of four generations crossbreeding experiment. Proceedings 1st World Congress on Genetics Applied to Livestock Production. 3:601.

Reynolds, W.L., R.A. Bellows, J.J. Urick and B.W. Knapp. 1986. Crossing beef x beef and beef x Brown Swiss: pregnancy rate, calf survival, weaning age and rate. J. Anim. Sci. 63:8.

Robinson, G.K. 1986. Group effects and computing strategies for models for estimating breeding values. J. Dairy Sci. 69:3106.

Robison, O.W., M.K.M. Yusuff, and E.U. Dillard. 1978. Milk production in Hereford cows. I. Means and correlations. J. Anim. Sci. 47:131.

Robison, O.W., B.T. McDaniel and E.J. Rincon. 1981. Estimation of direct and maternal additive and heterotic effects from crossbreeding experiments in animals. J. Anim. Sci. 52:44.

Rutledge, J.J., O.W. Robison, W.T. Ahlschwede, and J.E. Legates. 1972. Estimating milk yield of beef cows. J. Anim. Sci. 34:9.

Schaefer, L.R. and J.W. Wilton. 1978. Simultaneous estimation of variance and covariance components from multitrait mixed model equations. Biometrics 34:199.

Smith, Charles. 1964. The use of specialized sire and dam lines in selection for meat production. Animal Production 6:337.

Smith, G.C. 1989. Report card on beef. Personal correspondence.

Smith, G.C. 1990. Value based beef marketing. AMI/FMI Meat Marketing Conference - Presentation. Cincinnati, Ohio.

Smith, G.C. 1991. Trends in production and marketing. FMI/AMI Meat Marketing Conference - Presentation. San Antonio, Texas.

Smith, G.C. 1991. What is beef quality. The Future for Beef Conference - Presentation. Brisbane, Australia.

Speer, N.C. 1991. Parameter estimation and genetic relationships within a crossbred beef cattle populations. Master's thesis. Colorado State Univ.

Speer, N.C., J.S. Brinks, G.V. Richardson and M.D. MacNeil. 1991. Genetic parameters for growth traits of crossbred bulls and steers. Colorado State Univ. Beef Program Report. p. 165.

Turner, J.W. 1969. Preweaning production differences among reciprocal crossbred beef cows. J. Anim. Sci. 29:857.

Urick, J.J., B.W. Knapp, R.L. Hiner, O.F. Pahnish, J.S. Brinks and R.L. Blackwell. 1974. Results from crossing beef x beef and beef x Brown Swiss: carcass quantity and quality traits. J. Anim. Sci. 39:292.

Urick, J.J., O.F. Pahnish, W.L. Reynolds and B.W. Knapp. 1986. Comparison of two- and three-way rotational crossing, beef x beef and beef x Brown Swiss composite breed production. J. Anim. Sci 62:344.

VanVleck, L.D. 1990. Breeding value prediction with maternal genetic groups. J. Anim. Sci. 68:3998.

Westell, R.A., R.L. Quaas, and L.D. Van Vleck. 1988. Genetic groups in an animal model. J. Dairy Sci. 71:1310.

Wiggans, G.R., I. Misztal, and L.D. VanVleck. 1988. Animal model evaluation of Ayrshire milk yield with all lactations, herd-sire interaction, and groups based on unknown parents. J. Dairy Sci. 71:1319.

Willham, R.L. 1970. Genetic consequences of crossbreeding. J. Anim. Sci. 30:690.

Wilson, D.E. 1987. Personal communication through J.S. Brinks, Department of Animal Science, Colorado State University, Fort Collins, CO.

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

Woodward, R.R., J.R. Quesenberry, R.T. Clark, C.E. shelby, and O.G. Hankins. 1954. Relationships between preslaughter and postslaughter evaluations of beef cattle. U.S.D.A. Circular #945, May 1954.

APPENDIX

TABLE 25. SIRE (DIRECT) AND MATERNAL GRANDSIRE (TOTAL MATERNAL) EPD MINIMUM, MAXIMUM AND MEAN VALUES

EPDs INDEPENDENT OF ADDITIVE BREED EFFECTS

	Sire			Maternal Grandsire		
Trait[a]	Minimum	Maximum	Mean	Minimum	Maximum	Mean
BWM	- 7.39	+ 7.95	.08	- 9.36	+ 6.61	0
BWF	- 7.23	+ 7.99	.07	- 7.19	+ 4.73	-.02
WWM	-11.01	+16.66	.20	-65.17	+52.37	.19
WWF	-19.09	+20.95	.29	-56.56	+44.77	.17
ADGM	- .10	+ .19	0	- .09	+ .04	0
ADGF	- .09	+ .13	0	- .06	+ .08	0
DOF	-22.27	+18.57	.07	-16.27	+24.95	-.08
MW(dof)	-88.98	+82.29	.11	-77.69	+61.55	.18
MW(ft)	-67.60	+67.29	1.23	-51.60	+52.56	.99
MW(rea)	-64.81	+67.47	1.08	-50.80	+52.19	.80
MW(yg)	-69.54	+65.17	1.00	-52.37	+51.47	.89
MW(qg)	-68.55	+68.17	.99	-53.35	+52.39	.80
FT	- .04	+ .06	0	- .03	+ .04	0
REA	- .51	+ .66	-.01	- .21	+ .28	0
YG	- .25	+ .15	0	- .14	+ .19	0
QG	- 1.71	+ 1.97	.02	- .58	+ .49	0

[a] BWM = birth weight - males, BWF = birth weight - females, WWM = weaning weight - males adjusted to bull basis, WWF = weaning weight - females, ADGM = postweaning average daily gain - males adjusted to bull basis, ADGF = postweaning average daily gain - females, DOF = days on feed, MW = average adjusted mature weight listed for five multi-trait analyses with DOF,FT,REA,YG,QG respectively, FT = fat thickness, REA = ribeye area, YG = yield grade, QG = quality grade.

TABLE 26. SIRE (DIRECT) AND MATERNAL GRANDSIRE (TOTAL MATERNAL) EPD MINIMUM, MAXIMUM AND MEAN VALUES

EPDs WITH ADDITIVE BREED EFFECTS

	Sire			Maternal Grandsire		
Trait[a]	Minimum	Maximum	Mean	Minimum	Maximum	Mean
BWM	- 7.10	+15.65	2.24	- 9.36	+ 5.21	-1.35
BWF	- 9.36	+14.75	1.70	- 7.19	+ 3.93	- .76
WWM	- 9.85	+34.97	10.52	-65.17	+61.62	8.17
WWF	-19.96	+42.12	8.96	-56.56	+52.27	8.47
ADGM	- .09	+ .36	.09	- .14	+ .04	-.04
ADGF	- .08	+ .22	.06	- .08	+ .08	-.01
DOF	-42.42	+15.92	-11.42	-12.56	+24.95	1.91
MW(dof)	-88.98	+86.23	-3.07	-77.69	+69.30	5.32
MW(ft)	-88.36	+106.58	5.17	-51.60	+57.56	4.80
MW(rea)	-81.04	+108.05	4.54	-50.80	+58.19	4.61
MW(yg)	-83.39	+106.33	4.28	-52.37	+56.97	4.87
MW(qg)	-82.97	+97.52	3.95	-53.35	+58.89	4.95
FT	- .18	+ .11	-.03	- .03	+ .06	.01
REA	- .49	+ 1.51	.30	- .16	+ .39	.06
YG	- .81	+ .38	-.14	- .21	+ .20	0
QG	- 2.33	+ 2.85	.21	- .58	+ .41	-.03

[a] BWM = birth weight - males, BWF = birth weight - females, WWM = weaning weight - males adjusted to bull basis, WWF = weaning weight - females, ADGM = postweaning average daily gain - males adjusted to bull basis, ADGF = postweaning average daily gain - females, DOF = days on feed, MW = average adjusted mature weight listed for five multi-trait analyses with DOF,FT,REA,YG,QG respectively, FT = fat thickness, REA = ribeye area, YG = yield grade, QG = quality grade.