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DISSERTATION

GENETIC PREDICTION OF MATURE WEIGHT AND MATURE COW MAINTENANCE ENERGY REQUIREMENTS IN RED ANGUS CATTLE

Submitted by

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In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Spring 2001

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY JOHN LAWRENCE EVANS ENTITLED GENETIC PREDICTION OF MATURE WEIGHT AND MATURE COW MAINTENANCE ENERGY REQUIREMENTS IN RED ANGUS CATTLE 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 PREDICTION OF MATURE WEIGHT AND MATURE COW MAINTENANCE ENERGY REQUIREMENTS IN RED ANGUS CATTLE

The objectives of the multivariate mature weight analysis were 1) to determine if mature weight was a heritable trait in Red Angus cattle, 2) to determine if the assumptions of a repeated measures model were valid for prediction of mature weight, and 3) to evaluate the feasibility of developing a mature weight prediction using random regression models.

I obtained cow weight data on animals 2 years of age and older from the Red Angus Association of America, Denton, TX. The data included 111,460 weight observations. After editing the data for incomplete fixed effects and missing contemporary group information, the reduced data set included 74,124 observations. A subset of 29,380 records representing four Red Angus herds was used in the multivariate analysis.

Results of the first analysis showed that weight in Red Angus cattle 2 to 10 yr of age is a heritable trait with estimates of .50 to .78. Genetic correlations between different ages remained high with a range of .86 to .98; residual correlations ranged from -.04 to .50 and were inconsistent in magnitude; and, phenotypic correlations were .42 to .71. The estimates of genetic, residual, and phenotypic correlations satisfied some of the assumptions for a repeated measures model, but the genetic, residual, and phenotypic

covariances exhibited a scaling pattern with increasing variation as age increased. According to this study, the assumptions of a repeated measures model are not appropriate for analysis of mature cow weight.

Modifications were made to existing Method R variance components software to estimate variance components using random regression models. Validation of the techniques showed that it was feasible to obtain variance components using random regression models. Simulated data results showed that three to four records per animal were needed to obtain reliable variance components estimates.

Mature weight predictions were obtained using random regression models and BLUP procedures. The variance components for this analysis included those from the repeated measures model analysis, which were adapted for use with random regression models. Previous attempts to estimate variance components using a random regression model resulted in inflated variance component estimates. Predictions from the random regression analysis were compared with the repeated measures model results. There was an improved fit with the random regression model compared to the repeated measures model (R^2 = .940 vs. .804). The correlations between estimated breeding values from different models were .95 to .98, for ages 2 to 6 yr.

The objectives of the weaning weight and postweaning gain with mature weight analysis were 1) to determine if there was a genetic relationship between mature weight and weaning weight or postweaning gain in Red Angus cattle; and 2) to determine if the genetic relationship changed across cow weight age classes. Genetic correlation estimates between weaning weight (direct) and weight at 2, 3, and 4 to 9 yr of age were .61, .53, and .81, respectively. Genetic correlation estimates between postweaning gain

and weight at 2, 4, 6, 8, and 2 to 9 yr of age were .65, .60, .67, .64, and .68, respectively. An additive genetic relationship was present between mature weight and weaning weight, and postweaning gain. Including immature growth traits in a multivariate analysis with mature weight may serve to increase accuracy of mature weight genetic predictions.

I analyzed Red Angus cow weight with stayability using a multivariate continuous and categorical model. The objective was to evaluate the additive genetic relationship between traits. For the RAAA, stayability is defined as the probability of daughters staying in the herd to six years of age. Genetic correlation estimates between 2, 3, and 5 yr old weight with stayability were .28, .03, and .04, respectively. Results of the multivariate analysis showed a genetic relationship between weight at 2 yr of age with stayability, but this went to zero at older ages. These results were inconclusive and further study with different analytical procedures was needed.

Using additive genetic groups models, I analyzed stayability with cow weight genetic groups. Results showed there was a nonlinear genetic relationship between traits. Additional genetic groups models were fit to assist the interpretation, because results of the first analysis were inconclusive. Using alternative grouping strategies, results showed that there was still a nonlinear relationship between traits. The results showed that animals with different EBV for yearling growth were present in the same mature weight group.

A mature cow maintenance energy EPD was developed using genetic predictions for mature cow weight and maternal weaning weight. The mean, SD, and range of EPD were 22.37, 102.14, and –427.95 to 581.88 Mcal / yr. The genetic trend for years 1970 to

present was increasing and followed the same pattern as the genetic trend for mature weight.

Using the results of the mature cow maintenance energy study, it is feasible to develop a genetic prediction for a new economically relevant trait. Further work is needed to determine the best model for prediction of mature cow maintenance energy requirements.

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DEDICATION

This dissertation is dedicated to my fiancée Julie Dechant. Her support, love, and friendship made this dissertation possible and I look forward to spending my life with her.

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CHAPTER I

INTRODUCTION AND OBJECTIVES

Introduction

A primary focus of the commercial cow-calf enterprise is production of biologically and economically efficient cattle. For the commercial producer, selection decisions are made to match a suitable biological type to a specific production environment. In order for a commercial producer to select an appropriate biological type, estimated breeding values for economically important trait categories, such as milk, growth, and reproduction, should be at his disposal (Brinks et al., 1997).

Categorizing mature animals into biological types for maintenance energy requirements is necessary for selecting a match with a production environment, especially when average maintenance requirements for a mature cow represent 70% to 75% of feed input expenses (Ferrell, 1988). In a commercial cow-calf setting, emphasis is on genetic selection for low input yet productive cattle. Having genetic predictions for maintenance energy requirements, such as feed intake at maintenance, may provide a commercial producer an additional selection tool to manage their economic risk.

Previous research reports that feed intake at maintenance, metabolizable energy at maintenance, and fasting heat production are heritable traits in cattle (Hotovy et al., 1991; Fan et al., 1996). However, the collection and recording of large volumes of individual feed intake data is prohibitively expensive. Therefore, past research suggests using

mature cow weight as an indicator of maintenance intake efficiency. Mature cow weight is a moderate to highly heritable trait (Northcutt et al., 1993; Meyer et al., 1995) and genetically correlated with feed intake (Koots et al., 1994b). A limitation to using mature cow weight observations is the time required before a sufficient number of observations from a sire's daughters are collected.

The maintenance intake requirement for mature dams is the economic trait of interest; however, collection of individual maintenance data can be impractical and expensive. In place of actual maintenance data, an index of aggregate additive genetic merit for maintenance requirements may be a good alternative. The aggregate index for maintenance would be a function of independent breeding values for indicator traits.

Objectives

The objectives of this study are separated into multiple sections including:

Mature weight analysis

1. To determine if mature weight observations in Red Angus cattle can be analyzed using a repeated measures model.
2. To evaluate if mature weight is a heritable trait in the Red Angus breed.
3. To determine if an additive genetic relationship is present between weaning weight or postweaning gain and mature weight
4. To evaluate the feasibility of using Random Regression techniques with Method R variance components procedures to generate predictions for mature weight.

Mature weight and stayability analysis

1. To determine if there is an additive genetic relationship between mature weight and stayability in Red Angus cattle.
2. To evaluate the additive genetic relationship between immature growth traits and stayability in Red Angus cattle.

Mature cow maintenance energy intake analysis

1. To determine the feasibility of developing a mature cow maintenance energy prediction.
2. To propose future research and the direction for development of a new genetic prediction for mature cow maintenance energy requirements.

CHAPTER II

REVIEW OF LITERATURE

Mature Cow Weight

Beef cattle are managed in multiple environments making it difficult to determine the optimum biological type of mature animal. For cattle, no one biological type maximizes profitability across all environments. Multiple biological types of cattle, at least for mature size, are going to rank differently for profitability across production and marketing environments. Therefore, a profitable animal in one environment may yield a financial loss in another environment. Selection for a suitable match between animal and both production and market environments should be made to increase profitability (Morris et al., 1976; Johnson et al., 1990).

Definition of Mature Size

Mature weight in cattle represents the later stages of an animal's growth curve. It is the growth phase where an individual reaches its asymptote of weight gain and size does not change (Field, 1990). Fitzhugh and Taylor (1971) described mature weight as the mean weight over many years after positive growth of skeletal and muscular tissue has become insignificant. However, the definition of mature weight can change with time depending on the hypothesis being tested and how the data are being analyzed (Fitzhugh et al., 1971).

Growth Physiology

Growth is a product of changes to both tissue quantity and structure. Tissues are composed of fat, protein, and mineral components that are formed into bone, muscle, fat, connective tissue, and nervous tissue. Interestingly, each type of tissue has its own growth curve that peaks at a different time during the animal's growth period (Pearson et al., 1991). In the post-natal animal, body tissues are deposited in the order of skeleton, muscle, and lastly fat. However, a large proportion of vital organ growth occurs in the pre-natal individual. Obviously, a mature compared to a younger animal has a slower rate of skeletal and protein accretion but a faster rate of fat deposition. The result of tissue accretion is weight gain of the individual (Forbes et al., 1993).

There are two main cellular-level processes associated with growth. These processes include hyperplasia, an increase in cell numbers, and hypertrophy, which is an increase in cell size. Hypertrophy typically occurs in adipose (fat) cells when they increase in size. Cellular hyperplasia is more active during the acceleration phase of growth. The decelerating phase of a growth curve is dominated by a higher percentage of tissue hypertrophy. A higher hypertrophy level indicates that an animal is in the decelerating phase of their growth curve and approaching physiological maturity. However, previous research reports cattle exhibit both hyperplasia and hypertrophy processes during muscle tissue accretion and at later stages of postnatal growth. The evidence of this process is an increase in both muscle DNA and muscle protein (Pearson et al., 1991).

Growth Curves

Growth curves are useful for describing the sigmoid shape of an animal's weight pattern over time. Fitzhugh (1976) stated that "growth curves reflect the lifetime interrelationships between an individual's inherent impulse to grow and mature in all body parts and the environment in which these impulses are expressed." Algebraically, these functions explain the self-accelerating phase and self-inhibiting phase of growth (Field, 1990; Brody, 1945).

Animals reared in an environment with ad libitum access to feed and having weights measured at different ages will exhibit this characteristic sigmoid-shaped growth curve. In fact, this sigmoid-shaped curve is commonly observed across species (Forbes et al., 1993; Lawrence et al., 1997). The curve can be separated into an accelerating phase, a linear phase, and decelerating phase. But, many biologists argue that the sigmoid curve is highly oversimplified for describing growth rate and level of maturity (Lawrence et al., 1997).

Several scientists have developed methods, such as growth curve functions, to model this sigmoid-shaped growth pattern (Brody, 1945) (Johnson et al., 1990). Brody (1945) described an animal's growth curve as increasing at an accelerating rate until a point of inflection is reached, and then the curve increases at decelerating until maturity. Growth curves work well for longitudinal data that follow a non-linear pattern.

The trajectory of growth observations both before and after reaching mature weight are termed longitudinal data. Longitudinal data are repeated observations taken on an animal over time. Using longitudinal data instead of a single observation reduces prediction errors caused by variation in temporary environment (Johnson et al., 1990).

An animals' mature size may differ across ages because of variation in age, year, and season.

Summarizing multiple observations on a trait can be difficult, but growth curve functions work well for this situation. These functions consolidate information and generate informative model parameters with biological interpretation (Johnson et al., 1990). It is easier to analyze one observation per animal, but a single observation is subject to larger temporary environmental effects.

The common growth curve functions are Von Bertalanffy, Gompertz, logistic, Brody's, and Richards' models (Johnson et al., 1990). All models except the Richards' four-parameter model are three parameter functions. Functions with fixed inflection points are Von Bertalanffy, Gompertz, and Logistic. Those with a variable inflection point include the Richards and generalized logistic (Table 2.1) (DeNise, 1982).

Table 2.1. Growth curve models, asymptotic weight, maturing rate, and point of inflection*

Model	Equation	Asymptotic Weight	Maturing Rate	Inflection Point
Von Bertalanffy	$A(1-Be^{-Kt})^3$	A	K	_
Brody	$A(1-Be^{-Kt})$	A	K	_
Gompertz	$Ae^{-be(-Kt)}$	A	K	_
Logistic	$A/(1-Be^{-Kt})$	A	K	_
Richards	$A(1-Be^{-Kt})^M$	A	K	M

*Brown et al. (1976)

Growth Curve Parameters. There are several growth models available for analysis of weight-age data. The most appropriate functions for analysis of cattle growth data are a Brody's and Richards' models. Other models have been implemented but they

are known to mis-estimate both immature and mature weights. These models include: Logistic, Gompertz, and Von Bertalanffy (Brown et al., 1976; Johnson et al., 1990). An advantage of using a Brody's growth curve model is its computational tractability. It is a widely used growth model in the literature, especially for animals at or past six months of age. According to Johnson et al. (1990), a Richards' growth curve function is more appropriate for cattle weight data than a Brody's growth curve function. However, there is a higher computational requirement because four parameters are estimated instead of three parameters.

Table 2.1 is a list of several commonly used growth curve functions and their biological parameters. For Brody's (1945),

$$W_t = A(1-Be^{-kt})$$

where

W_t= weight of the animal at age t, A= asymptotic weight, B = constant of integration or a time-scale parameter, k= rate of maturing, rate of growth, or rate of change for a logarithmic function of weight change per unit of time, and t= age in days (Brown et al., 1976; Johnson et al., 1990). A Richards' function differs from a Brody's function because of an additional shape parameter, m, which is used to change the inflection point. In beef cattle, A is an estimate of mature weight, while k estimates growth rate and earliness of maturity. For example, individuals with a predisposition for early maturity have larger k values then those with later maturity.

Several studies have modeled growth of beef cattle using the above mentioned functions (Brown et al., 1976; DeNise, 1982; Johnson et al., 1990; Kaps et al., 1999). In most studies the authors applied more than one growth curve function and reported heritabilities and genetic correlations for model parameters.

Using inbred Hereford lines and a Red Angus line of cattle, (DeNise-Kersey et al., 1985) compared the Brody's and Richards' functions and obtained estimates of genetic parameters for A (asymptotic weight) and k (maturing rate). Heritability estimates for A, asymptotic weight, on both functions was .44 ± .27 and estimates for k on the Brody's and Richards function were .20 ± .26 and .32 ± .27, respectively. The authors obtained a .82 estimate of the genetic correlation between b and k for the Brody's (1945) curve, and genetic correlation estimates between A and k were −1.16 ± 1.7 for the Brody's and -.84 ± 1.1 for the Richards' model. Cows with lighter mature weights and smaller birth weights were associated with earlier maturity. They did obtain a -.97 ± 1.78 estimate of the genetic correlation between b and k for the Richards' function. This estimate was opposite to the .82 ± 1.05 estimate of the genetic correlation for a Brody's function. The Richard's function estimates were difficult to interpret because of high estimated standard errors and the b parameter has a different interpretation in the Richards' function. According to Denise et al. (1985), the b-parameter can not be used to describe birth weight.

In a different study, Brown (1970) reported heritability estimates for Brody's growth curve parameters A and k of .34 and .33, respectively. For Angus, heritability estimates were .21 for A and .75 for k. The genetic correlation estimates between A and

k for Hereford and Angus were -.95 and -.29, respectively. Results of their study showed that Hereford cattle were later maturing and larger than Angus cattle.

Kaps et al. (1999) estimated genetic and environmental parameters for asymptotic mature weight with a modified Brody's model. To obtain reliable predictions of the asymptote, the authors limited the records to individuals over 4.5 years of age and up to 6.5 years. They did not estimate heritabilities for growth curve parameters; rather they used the Brody function to obtain asymptotic mature weight and used it as a single observation of mature weight. They compared the estimates from the previous study to heritability estimates using a repeated measures model. Heritability estimates for asymptotic mature weight and mature weight using a repeated measures model were .52 and .53, respectively. To remove the effects of culling bias, the authors obtained estimates using weaning weight as the second trait in a multivariate animal model.

Breed Differences

There are dissimilarities among and within breeds for mature size and growth rate. These differences are a source of variation for selection decisions to change mature weight. Using data from the USDA Meat Animal Research Center in Clay Center, Nebraska, Jenkins et al. (1991) analyzed mature weight on several breeds from birth to seven years of age using a Brody's (1945) growth curve model. Heritability estimates for asymptotic weight for between and within breeds were .91 ± .27 and .61 ± .11, respectively. Their results showed that the mature size of future progeny could be changed with selection among breeds; however, within breed selection was reported to be more effective at changing rate of maturity and altering the shape of the growth curve.

These results indicated that it was feasible to modify mature size and growth rate in cattle. However, the target for mature size cannot clearly be defined across environments because of differences in production practices, resources, and markets (Johnson et al., 1990). Likely, a target for mature size would be dictated by the firm level profit generated by the cattle enterprise.

Heterosis

Heterosis levels for weight are lower, on average, in an older group of cattle than the levels of heterosis of younger animals. Previously reported heterosis levels for size range from 4% (Morris et al., 1976) to 6% (Nelsen et al., 1982). These decreased levels of heterosis can be partially explained by higher estimated heritabilities for the trait (Morris et al., 1976). However, Cundiff (1970) reported an estimated 40% increase in the mature weight of a two-way cross of British breeds over the purebreds. This increase was attributed to a higher level of fatness and there was a lower level of heterosis for metabolic body size.

Using Angus, Brahman, Hereford, Jersey, Holstein, and all subsequent breed crosses, (Nelsen et al., 1982) estimated levels of heterosis for both weight and height in cattle 9 through 66 months of age. Results showed higher degrees of heterosis for weight over height, where weight increased 6.2% and height increased 2.0%. Heterosis levels decreased with age, 9 mo animals had heterosis levels of 10.9% and this declined to 7.1% for 60 mo animals. However, Brahman crosses achieved significantly higher heterosis levels compared to all *Bos taurus* crosses. Progeny with Brahman influence outperformed parents up to 15% at 48 mo of age.

A study by Ferjani (1976) estimated increases in performance due to heterosis by comparing the performance of linecross and inbred Herefords from birth to ten years of age. The average heterosis for weight was 6.63% on weights taken from 24 to 120 mo. Nelsen et al. (1982) also reported a decline in heterosis levels from pre-weaning through later stages of maturity. After 12 mo of age, post-weaning heterosis levels would decline and remain constant until 120 mo of age (Cundiff, 1970; Nelsen et al., 1982).

Body Condition Score

Klosterman et al. (1968) emphasized the importance of assessing body condition in determining maintenance energy requirements. They reported a significant correlation between condition score and weight-height ratio. Cows with a higher weight to height ratio gained more weight than cows with a lower ratio. The authors also observed a weight gain for animals with a higher degree of finish. Using these results, they proposed that the mature cow nutrient intake be adjusted using degree of body condition.

Body condition differences are reported to contribute a significant proportion of the variation in mature weight and an influence maintenance, growth, and reproduction (Northcutt et al., 1992). Body condition scoring is a subjective measure of percent body fat of an animal scored from 1 (emaciated) to 9 (obese). Body condition data are easy to collect and it is an indicator of available energy reserves (NRC, 1996). Furthermore, body condition is a highly repeatable trait relative to other subjectively scored traits (Benyshek et al., 1973).

Previous scientific studies with mature weight disagree on whether to adjust for body condition score. Certain studies pre-adjusted mature weight data to a constant

condition score prior to heritability estimation (Northcutt et al., 1993; Marlowe et al., 1985). For example, Marlowe et al. (1985) analyzed mature cow weights with two different models; the first model included body condition as a covariate and the second model excluded body condition. The authors observed an increase in both among and within sire variance after they fit the model without a covariate of body condition score. Heritability estimates for the body condition adjusted and unadjusted mature weight models were .38 and .29, respectively.

Heritability estimates for body condition score are reported to be low to moderate. Marlowe et al. (1985), Andersen et al. (1988), and Meyer (1995) reported body condition score heritability estimates of .31, .42, .15, respectively. In addition to being moderately heritable, body condition is genetically correlated with mature weight. Marlowe et al. (1985) estimated a .32 genetic correlation in Angus cattle and Meyer (1995) estimated genetic correlations in Herefords and Wokalups of .78 and .64, respectively.

Using American Angus Association mature cow weight and body condition data, (Northcutt et al., 1993) reported heritability estimates of .48 and .45 for mature weights that were unadjusted and adjusted for body condition score. Unadjusted and adjusted mature weight heritability estimates were similar, but Northcutt et al. (1993) emphasized that these heritability estimates may represent different traits. In fact, they reported rank correlation of .94 between mature weight EPDs on data unadjusted and adjusted for body condition.

An additive genetic relationship exists between body condition and mature weight in beef cattle. Some mature weight studies have pre-adjusted mature weight for body condition. Historically, one problem with adjusting mature weight for body condition has

been the limited amounts of body condition data. A few studies involving mature weight cited that either body condition data were unavailable or they thought that adjusting for body condition would result in adjusting out genetic differences for mature cow weight (Marlowe et al., 1985; Kaps et al., 1999). A study by Bullock et al. (1993) estimated variance components for Hereford mature weight without a covariate for body condition score. They argued against an adjustment for body condition because it could bias the mature weight predictions.

Genetic Parameter Estimates

Mature weight is classified as moderate to highly heritable in beef cattle (Table 2.2). Previous research shows several different methods for analysis of longitudinal data, however some methods are more appropriate than others for modeling growth data. Previous methods included analysis of single mature weight observations with a univariate model, analysis of repeated mature weight observations using a simple repeated measures model, growth curve functions, and multivariate statistical models. Ultimately, the goal is to apply a biological interpretation to a large number of weights at different ages (Johnson et al., 1990). Ideally, the model used should have the least number of traits to model the data adequately and not be computationally prohibitive (Meyer et al.; 1997).

Table 2.2. Literature heritability (h^2) estimates for mature cow weight in beef cattle

Study	Model (Trait(s))	$h^2 \pm$ SE
Benyshek et al. (1973)	Sire	.52 ± .16 to 1.00 ± .16
Brinks et al. (1964)	Paternal Half-sib/ Univariate	
	Spring Mature Weight	.52
	Fall Mature Weight	.57
Bullock et al. (1993)	Sire/Multivariate	.52
DeNise-Kersey et al. (1985)	Paternal Half-sib/Univariate (Asymptotic weight)	.44 ± .27
Field (1990)	Sire/Average mature weight 33-66 mo and 6 to 9 years of age	.45, .54
Kaps et al. (1999)	Animal / Univariate	.44[1]
Kaps et al. (1999)	Animal / Multivariate (Weaning weight and Asymptotic mature weight)	.52
Kaps et al. (1999)	Animal / Multivariate (Weaning weight and repeated mature weight)	.53
Koots et al. (1994)	Multiple types (Review paper)	.50 ± .15
Marlowe et al. (1985)	Paternal Half-sib/Single Trait	
	(I. Adjusted for BCS)	.38 ± .11
	(II. Unadjusted for BCS)	.29 ± .11
Meyer et al. (1995)	Animal/Univariate (Herefords)	.30 to .40
	Animal/Univariate (Wokalups)	.50 to .60
Northcutt et al. (1993)	Sire/Multivariate	.48 ± .10
Northcutt et al. (1993)	Sire/Multivariate[2]	.45 ± .10

[1]Standard errors (SE) were not available for all h^2 estimates.
[2]Data were preadjusted for body condition score.

Brinks et al. (1962) obtained heritability estimates with a paternal half-sib analysis using both a single observation and average of mature weight observations on animals three to ten years of age. Estimates differed because the h^2 estimates were .75 for average spring mature weight and .57 for the single observation method. The lower heritability estimate for the single observation method was caused by larger within cow variation and environmental variation. Using similar procedures with average mature weights, Field (1990) obtained heritability estimates for ages two to five and six to nine years of .45 and .54, respectively.

Using Hereford and Wokalup groups of cattle, Meyer (1995) applied both a Gompertz curve model and a univariate model with repeat observations to mature weight data. Asymptotic heritability estimates for Hereford and Wokalups were .47 and .73, respectively. Heritability estimates for repeatedly measured mature weight were .29 and .54, respectively. Using a univariate model with a Gompertz function, heritability estimates for asymptotic weight were higher than repeated measures model estimates. The authors concluded that the Gompertz growth model was accounting for environmental variation better than the univariate repeated measures model. But, to achieve this better fit using a Gompertz function required more than one observation and weights taken at or past four years.

Repeated Measures. Longitudinal data can be treated as a repeated measure of the same trait. However, this assumes that the covariance structure between traits is consistent (Mrode, 1996). If observations on a particular trait are collected at different ages (yr), assumptions of the repeatability model may be violated. The group of genes controlling growth at two years of age is probably different than the set of genes at age

five (Meyer et al., 1997). In fact, cattle are capable of gaining weight through age eight, but the rate and type of tissue deposition changes with maturity. As an animal gets older, there is a transition from depositing higher percentages of bone and muscle tissue to a higher proportion of adipose tissue (Lawrence et al., 1997).

Univariate models for repeated measures data are used to analyze longitudinal data, which should result in estimated breeding values with higher accuracy. Higher accuracy values are observed because of a reduction in variance due to temporary environment. However, variance components estimates and subsequent estimated breeding values could have a higher incidence of being biased because the model assumptions for repeated measures are violated. If the genetic correlations between ages changes noticeably as the distance between ages increases than the repeatability model assumptions are invalid. The repeated measures model assumes the genetic correlation between traits is one.

Growth Curves. Growth curve functions are used to model longitudinal data because they concentrate weight-age data into biologically interpretable parameters (Brown et al., 1976; Johnson et al., 1990). Several studies have reported fitting different growth curve functions to growth data and estimating genetic variance components for growth curve parameters (Johnson et al., 1990). The specific parameters of interest are asymptotic weight, A, and k for maturing rate. Asymptotic weight is synonymous with mature weight and k is an estimate of growth rate. As previously discussed, the most commonly used growth curve functions are Brody's and Richards' models (DeNise-Kersey et al., 1985; Johnson et al., 1990; Jenkins et al., 1991). However, Meyer (1995)

has applied a Gompertz function to mature weight data and estimated growth curve parameters for two Australian cattle populations.

According to Johnson et al. (1990), growth curve functions provide a mathematical interpretation of growth. But estimating growth curve parameters for longitudinal data does have its disadvantages. First, the fit of a model is very dependent on the number of observations at different ages. Second, the predictions using a fitted curve should not go beyond the data space. DeNise-Kersey et al. (1985) emphasized that certain growth models will fit better than others; however, the most appropriate function must be applied to the data.

In a previous section on growth curves, Brody's and Richards functions were considered to be the most appropriate for describing the growth of beef cattle. The Brody's function may not be as robust as a Richards' model, but the parameters are easier to interpret. Brown et al. (1976) stated that a Brody's function was equivalent to a Richards' function for animals past six mo of age, but the growth parameters were not perfectly correlated. The Brody's function does not have a point of inflection, which can be informative for determining environmental effects on growth. Other growth curve functions, such as the Gompertz, Logistic, and Von Bertalanffy have been used in analyzing growth data in beef cattle, but these functions are known to over- or under-estimate weights at different ages. In beef cattle data sets, Gompertz and Von Bertalanffy functions will overestimate weights at early ages and the logistic will mis-estimate asymptotic weight.

A polynomial funictions is an alternative to using a growth curve function to analyze longitudinal data. There are fewer cited studies available in the literature, but it

is feasible to fit polynomial functions to growth data and predict asymptotic weight. In a Hereford study, Bullock et al. (1993) fit a quadratic function with a plateau value with growth and mature size data. The authors applied a quadratic function because individual growth curves, including a Brody's function (Brody, 1945), resembled a quadratic function.

Genetic Correlations Between Growth Traits

When selection decisions are made to change a trait, the outcome of those decisions is not independent of other traits. It is possible that correlated trait will change because of pleiotropic effects (Bourdon, 1997). Many traits including birth weight and weaning weight have genes in common. Those common gene effects among multiple traits can be quantified using a genetic correlation. A genetic correlation statistically determines the strength of the additive genetic relationship between two traits. It is "a measure of the strength of the relationship between breeding values for one trait and breeding values for another trait" (Bourdon, 1997).

Genetic correlations between immature weights and mature weights are reported to be high and positive (Brinks et al., 1964; Brown et al., 1972b). Because both mature and immature weights reflect skeletal growth, immature weights should be good indicators of the performance for mature weight (Schafer, 1991; Fitzhugh, 1976). Table 2.3 is a summary of genetic correlation literature estimates between mature weight and several immature weights. Selection for early growth weights should influence changes in mature size, especially for the traits recorded near maturity.

The change of a trait because of selection on a correlated trait is important information for making selection decisions. However, there are larger implications for a genetic correlation between traits. For example, a breed association may want to develop a genetic predictor for mature cow weight, but their mature weight data are limited. However, many cattle breed associations routinely collect large quantities of weaning weight data. Using a multivariate analysis combined with knowledge of the genetic relationship between traits, the breed association can incorporate weaning weight data into the analysis. The weaning weight data can serve as an added source of accuracy for mature weight genetic predictions.

In field data, it is unlikely that producers collect and report data on several traits unless their breed association makes it policy. The incomplete reporting of data contributes to bias of genetic predictions, especially for weights taken later in an animal's life. Yearling weight is a good example of a trait with selection bias. However, this bias can be reduced using a multivariate animal model between a completely reported trait, such as weaning weight, and the trait of interest.

Mature cows that are selected to be in a herd reflect a highly selected group and their predictions are good candidates for selection bias. To reduce this bias, a multivariate analysis should be conducted between mature weight and a completely reported immature weight, such as weaning weight. For breed associations like the Red Angus Association of America, weaning weight is less influenced by selective reporting because the association requires submission of weaning weights to register (Northcutt et al., 1993; Kaps et al., 1999). Having information on a previous trait that was completely

reported removes bias due to prior selection, particularly when all previous selection was done with the completely reported trait.

Table 2.3. Literature estimates of genetic and phenotypic correlations between immature weights and mature weight in beef cattle

Trait	Study	Correlation	
		Genetic	Phenotypic
Birth Weight	Brinks et al. (1964)	.61, .68	.35
	Bullock et al. (1993)	.64	.33
	Northcutt et al. (1993)	.57	.19
Weaning Weight	Brinks et al. (1964)	.59, .51	.45
	Bullock et al. (1993)	.80	.32
	Northcutt et al. (1993)	.62	.37
Yearling Weight	Brinks et al. (1964)	.66, .62	.57
	Brown et al. (1972)	.73 ± .40	.12 ± .16
		.05 ± .64	.21 ± .17
	Bullock et al. (1993)	.89	.46
	Northcutt et al. (1993)	.45	.41
18 mo. Weight	Brinks et al. (1964)	.84, .74*	.67
24 mo. Weight	Brown et al. (1972)	.65 ± .32**	.33 ± .15
		.32 ± .60***	.56 ± .12
36 mo. Weight	Brown et al. (1972)	.75 ± .23	.59 ± .11
		.69 ± .39	.84 ± .05

Hereford estimates * Angus estimates

Analytical Procedures for Longitudinal Data

For variance component estimation, the most appropriate model to describe the data should be used while simultaneously avoiding high computational demands (Meyer et al., 1997). For many traits, a univariate model is appropriate for estimation of variance components because the trait is observed only once in an animal's lifetime. However, different analytical procedures are needed for analysis of longitudinal data. Because longitudinal data are measured on the same individual over time, it is computationally easier to analyze it with a univariate model and treat the data as repeated records of the same trait (Kuehn, 2000). The assumption with using this type of model is all observations are treated as the same trait. Adjacent observations could be highly correlated to each other, but estimates of the genetic correlations may decrease as the distance between ages increases (Laird et al., 1982; Meyer et al., 1997; Meyer, 1999). Therefore, a model that accounts for the covariance structure of a repeatedly measured trait should be fit.

Using a single observation to analyze a longitudinally observed trait limits our ability to draw inference about the trait with respect to time. Examples of different forms of longitudinal data are body weight, growth data, milk production, feed intake, fat deposition, and egg production (Schaeffer, 1999). A single trait 'repeatability' model is one method of analyzing repeated records. If a repeated measures model is applied, there are assumptions of constant variance across traits with genetic correlations between traits equal to unity (Meyer, 1999). It is an easier model to implement and computationally more tractable (Van der Werf et al., 1997); however, the model assumptions are violated when estimates of variance components change with time.

A multivariate model is an alternative to using a univariate model for repeated measures. Fitting a multivariate model with the number of traits equal to the number of observation categories is feasible, but the model becomes highly overparameterized (Meyer et al., 1997). In a multivariate analysis, the number of parameters to estimate is equal to $t(t+1)/2$, where t = the maximum number of observations. Analyzing all traits at the same time creates a large computational demand and requires more observations per trait to obtain reliable variance component estimates. Furthermore, a multivariate model does not account for the trajectory and the structure of the observations with respect to time.

Random Regression models are an alternative method for analysis of longitudinal data. It can be used to estimate the covariance structure of a trait and it also overcomes previously stated problems of multivariate analysis. Many dairy test day record and growth data sets have been analyzed using random regression models. Previously, some of the growth data and lactation data were analyzed with either repeatability models or multivariate models (Meyer et al., 1997; Schaeffer, 1999).

In dairy cattle lactation studies, random regression models are more complex to model compared to analyses with just fixed lactation curve functions (Ptak et al., 1993; Jamrozik et al., 1997b). In fitting a random regression model, fixed regression coefficients are applied to individuals from the same subclass groups, which is equivalent to the average lactation function. Then the predictions for random regression coefficients are represented by deviations from the fixed regression function. Using a random regression function, covariances are estimable between regression coeffecients that

indicate how additive genetic, permanent environmental, and residual variances and covariances change with the trajectory of observations on age (Jamrozik et al., 1997a).

The following is a general description of a random regression model for breeding value prediction (Schaeffer, 1999; Gengler et al., 1999; Kuehn, 2000):

$$y = Xb + Z_1u + Z_2p + e$$

$$\text{var}\begin{bmatrix} u \\ p \\ e \end{bmatrix} = \begin{bmatrix} A \otimes G & 0 & 0 \\ 0 & I \otimes P & 0 \\ 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

where

y = a vector of longitudinal data on animal, X = a known coefficient matrix including the incidence of observations in y related to fixed effects in b and fixed regression coefficients, b = vector of fixed effects and fixed regression coefficients, Z_1 = known coefficient matrix of covariates relating observations in y to additive genetic random regression coefficients, u = vector of random additive direct genetic effects of animals (regression coefficients), Z_2 = a known coefficient matrix of covariates relating observations in y to permanent environmental random regression coefficients, p = vector of random regression coefficients for each animal representing permanent environmental effects, e = vector of residual errors, A = Wright's numerator relationship matrix between all animals, $\otimes$ = Kronecker product, G = additive direct genetic covariance matrix for the random regression coefficients, I = identity matrix with the order equal to the number of

observations, P = covariance matrix for the permanent environmental random regression coefficients, and σ^2_e = residual error variance.

A random regression model can be fit with homogeneous or heterogeneous residual variance. For random regression models on dairy lactation curves, some studies allowed residual variance to change through the age range of the data (Schaeffer, 1997). A heterogeneous residual covariance matrix would have the following structure:

$$\text{Var}[e] = \text{diag}\left[\sigma^2_{e_k}\right],$$

where

k = the number of residual variance terms in the model. The number of residual variances can be as high as the number of measurement periods. However, many random regression analyses using random regression for test-day yield, consolidate residual terms into different age ranges. Then the residual variance structure is based on the number of measurement periods (Kuehn, 2000).

Random regression models and covariance functions have been used in other disciplines to model longitudinal data. In human medicine, random regression models are routinely used to analyze blood pressure, cholesterol levels, lung volume, glucose levels, and results of pharmaceutical trials (Laird et al., 1982). Animal breeders have recently discovered random regression to be a useful alternative analytical approach for several categories of longitudinal traits. A sample list of these traits includes mature weight, feed intake, milk production, and fat deposition. The majority of research with livestock has been with dairy cattle lactation (Meyer, 1999; Schaeffer, 1999).

Applications of Random Regression

In beef cattle, random regression models have been applied to postweaning growth and mature weight data to estimate covariance functions (Meyer et al., 1995; Meyer et al., 1997). The random regression studies with mature weight have been limited to those reported by Meyer (1999). Other species, such as swine, have started to use random regression models to analyze growth data but results have been sparse relative to dairy studies (Andersen et al., 1995).

Meyer (1999) has applied growth curve models, such as a Gompertz function, to mature weight data. However, current studies fit a random regression model to estimate covariance functions for repeatedly observed mature weight. Covariance functions estimated from random regression coefficients were shown to be equivalent to an infinite dimensional covariance matrix. (Kirkpatrick et al., 1994) labeled this an "infinite dimensional" analysis because the covariance structure of an infinite number of traits can be described over a range of ages.

Meyer (1999) analyzed mature weight in two research herds using a random regression model for January mature cow weights for ages 19 to 119 mo. The data included two herds, one was Polled Hereford and the other was a Wokalup herd. Both herds were part of the Wokalup Research station in southwest Australia. The Wokalup is a synthetic breed composed of Charolais, Brahman, Friesian, Angus, and Hereford. In this analysis, mature weight was regressed on orthogonal ages and covariance functions were estimated from covariances between random regression coefficients. In each of Meyer's (1999) random regression studies, REML procedures were used to estimate covariance functions from random regression models (Meyer et al., 1997).

The results of Meyer's (1999) mature weight study showed that weights at different ages were different traits and it was incorrect to assume a constant variance structure across age groups. The author reported lower genetic correlations between two year-old cows and older age cows compared to genetic correlations between three year-old cows and older age cows. There were differences between herds, but Meyer (1999) attributed this to data structure and an artifact of modeling later ages. Estimates of additive direct genetic and permanent environmental variance exhibited erratic changes at 100 mo of age. These erratic changes in variances may be a result of a limited number of observations to obtain estimates.

Meyer (1999) fit several random regression models each with a different order of fit and tested the fit with a likelihood ratio test. The order of different polynomials ranged from a 2nd order (linear) to a 7th order polynomial. Results of Meyer's study (1999) showed a cubic function to work well for modeling both herds, but the order of fit could be reduced to a quadratic without a large change in the likelihood. Heritability estimates obtained for the random regression functions were comparable with average estimates of .47 using a Gompertz function. For the Wokalup herd, Meyer (1999) obtained heritability estimates for 19 mo to 119 mo of .42 to .49. Heritability estimates in the Herefords for 19 to 119 mo were .57 to .37. Estimates of the genetic correlations between older animals were near one, but the magnitude of the genetic correlations estimates decreased as the distance between ages increased. Additive genetic relationships between two or three year-old dams and older age groups indicated that genes controlling mature weight observations at younger ages are less likely to be the same set of genes for older mature weight observations.

Lactation. Other forms of longitudinal data have been analyzed using random regression models to estimate covariance functions and predict subsequent breeding values. Numerous studies have estimated variance components on test day yields in dairy cattle (Jamrozik et al., 1997a; Van Der Werf et al., 1998; Pool et al., 1999). These studies reported variance component estimates for different test day yields and generated predictions for different random regression coefficients. Instead of generating predictions for one measurement of milk production, several milk records are used over time. Van der Werf et al. (1998) emphasized many advantages to using random regression models and multiple observations over a single observation method. The advantages were a direct correction for environmental effects on the test day, an improved ability to account for variation in number of tests recorded, and a better method to predict lactation persistency.

Jamrozik et al. (1997a) has used random regression models to estimate covariance functions for milk, fat, and protein using multivariate variance component procedures. This required a large number of variance component estimates because they analyzed the data in two trait pairs with a random regression model. Therefore, one objective was to determine if alternative models could be used to estimate covariances with a reduced number of parameters. They reported estimating 27 additive genetic parameters and 71 environmental parameters using a reduced model. For a full model, estimates on 1,176 genetic parameters and 312 environmental parameters were required. Results of Veerkamp et al. (1998) reported the genetic correlations between milk and fat, milk and protein, and fat and protein were .38, .83, and .59, respectively. Jamrozik et al.

(1997) reported heritability estimates for protein, fat, and milk were .28, .28, and .32, respectively.

In cattle, random regression models have also been applied to body condition score data. Jones et al. (1999) analyzed first-calf heifer condition score data to determine if there were differences between sires for condition score. They used a cubic polynomial to estimate breeding values and heritabilities for twelve stages of lactation. Their results showed that the rankings of sire EBV changed at each stage of lactation. Additionally, the range of heritability estimates was .20 to .28. The authors emphasized that condition score EBV could be used to select for dairy cattle that can maintain high levels of milk production during peak production and not deplete energy reserves (Jones et al., 1999). Koenen et al. (1998) conducted a similar study to evaluate body condition in Holsteins. They reported heritability estimates for condition score at different lactation stages of .21 to .45.

Mature Weight and Reproduction

Estimates of maintenance energy requirements in a mature beef herd are 65% to 75% of total energy intake (Jenkins et al., 1984). The failure to meet these nutritional requirements may reduce reproductive performance (Jenkins et al., 1984; Martin et al., 1992). Mature weight is one indicator of maintenance energy requirements and larger animals require a higher caloric intake compared to smaller sized individuals. Therefore, selection decisions to change mature size should be made with simultaneous consideration of change in other trait categories such as reproduction. Ignoring these

additive genetic relationships between traits may be detrimental to production and profitability.

A study by Buttram et al. (1989) looked at the effects of size and management on the reproductive performance of cattle from synthetic lines. These synthetic lines included breed percentages of Jersey, Angus, and Simmental. They wanted to determine the correlated response of reproductive performance based on selection for size. They claimed that smaller cattle were more reproductively efficient than larger cattle. In their study third parity dams of small, medium, and large biological types had calving rates of 80%, 66%, and 69%, respectively. Furthermore, the different genotypes re-ranked for reproductive performance across environments.

Past research suggests that direct measures of fertility are lowly heritable (Koots et al., 1994a), and indicator traits would be more effective for increasing heifer fertility (Smith et al., 1989; Evans et al., 1999). However, this notion has changed with the development of sustained fertility traits such as stayability in beef cattle. Using more appropriate analytical procedures for categorically observed data, heritability estimates for stayability were reported higher than other reproductive measures. Snelling et al. (1995) estimated the heritability of stayability for five year-old Angus and Red Angus cattle at .12 and .14, respectively.

There are very few studies on the genetic relationship between mature cow reproduction and mature size. Koots et al. (1994b) reported an estimate of -.02 for the genetic correlation between mature cow weight and conception rate. This indicated no linear relationship between reproduction and mature size, but the estimate was derived from one study and the additive genetic relationship may be nonlinear (Evans et al.,

1999). To assist producers in making more informed and profitable selection decisions, additional research is needed to determine the additive genetic relationships between mature size and reproductive traits.

Maintenance energy requirements

Definition. According to Young (1991), the definition for maintenance energy is the maintenance energy requirement of metabolizable energy (MEm), where MEm is the point of zero energy balance for net energy gain or loss. Previously, the concept of maintenance energy has been poorly used and has been a candidate for misinterpretation.

It is more profitable to select for biologically and economically efficient cattle that match their production environment. On average, mature cow maintenance energy requirements account for 70% of total metabolizable energy requirements (NRC, 1996). A growing animal's maintenance energy expenditures are approximately 35% of the total energy expenditure (Ferrell, 1988). For the whole herd, maintenance energy requirements account for 65% of total energy expenditures. In order to enhance selection for more energy efficient cattle and lower production costs, it is important to identify sources of variation for maintenance energy requirements. There are several sources of variation for maintenance requirements, including breed of animal, age, sex, and physiological status (i.e. lactation).

Breed Differences. Breeds of cattle are developed in different production environments. In these production environments, breeds of animals are selected for different production characteristics such as meat, milk, or draft. Because populations are selected in various environments, differences exist for adaptation to an environment and

corresponding metabolic maintenance requirements. Therefore, maintenance requirements will be different for breeds raised under different nutritional environments (Ferrell et al., 1985). Specific environments may cause more nutritional stress for certain genotypes than others and subsequent differences in maintenance requirements. For example, Charolais cattle are not selected to produce milk like a Holstein. Because of the differences in physiological status and the Holsteins' emphasis on milk production, the average metabolic rate for a Charolais population will be lower than many higher milking breeds. In the Holstein breed, cattle are predisposed to higher maintenance energy requirements because of the high physiological demand of lactation.

Table 2.4 lists average maintenance requirements for several breeds and breed crosses (Ferrell and Jenkins, 1985). There were differences among breeds for various physiological states including lactation and pregnancy status. An Angus, non-lactating, non-pregnant female had a metabolizable energy at maintenance requirement of 118 kcal/($kg^{.75}$ •d) versus a Simmental cow of similar age and production status at 134 kcal/ ($kg^{.75}$ •d). If breed of animal was equivalent to genotype then differences in maintenance requirement were present for the reported genotypes because of predisposition toward different levels of milk and potential for growth.

Table 2.4. Estimates of metabolizable energy required for maintenance (MEm) of various breeds or breed crosses (Ferrell and Jenkins, 1985).

Breed or breed cross	Physiological state	MEm, kcal/($kg^{.75}$ •d)
Angus-Hereford[1]	Nonpregnant, nonlactating, 9-10yr	130
Charolais X	" " "	129
Jersey X	" " "	145
Simmental X	" " "	160
Angus	Non-pregnant, lactating, 5-6yr	149
Hereford	" " "	141
Simmental	" " "	166
Charolais	" " "	165
Angus	Non-pregnant, non-lactating, 5-6yr	118
Hereford	" " "	120
Simmental	" " "	134
Hereford	Growing-finishing, 9-15mo.	106
Simmental	" " "	126
Angus-Hereford[1]	Pregnant, lactating, 8-9yr	151
Red Poll X	" " "	157
Brown Swiss X	" " "	156
Gelbvieh X	" " "	158
Maine Anjou X	" " "	146
Chianina X	" " "	174

[1]Crossbred cows produced by mating Angus, Hereford, Charolais, Jersey, Simmental, Red Poll, Brown Swiss, Gelbvieh, Maine Anjou or Chianina bulls to Angus or Hereford cows.
[2]The Diet ME used to establish maintenance ME values was reported at 2.53 Mcal/kg (Ferrell and Jenkins, 1984).

Within Breed Variation. If sufficient genetic variation in metabolizable energy at maintenance (MEm) is present within a breed, it is feasible to select individuals to change maintenance energy requirements. Using mature, nonpregnant and nonlactating Angus cattle, DiCostanzo et al. (1990) reported a standard deviation for daily MEm of 18.4 kcal/kg $BW^{.75}$. This estimate represented 35% of within herd variation and was comparable to estimates from studies with multiple breeds and breed crosses. The level of variation implied that there were sufficient differences within a breed and among genotypes. For example, dams with different genotypes for milk production were likely to express differences for maintenance energy requirements.

Between Breed Variation. As discussed earlier, MEm requirements can be a function of selection pressure for production performance of certain traits. Therefore, differences in MEm are expected to exist between breeds. Jenkins et al. (1991) compared the energy requirements of Simmental and Hereford cattle at different levels of production. Simmental cattle had higher daily levels of heat production but lower rates of increased heat production over different physiological states and dry matter intakes (DMI). At a level of .0193 kg of DMI/kg of liveweight, they reported that Herefords were more efficient because they had lower fasting heat production. But, Simmentals exhibited greater energy efficiency at higher DMI compared to Herefords of equal weight. However, Simmentals were more efficient with DMI compared to Hereford cattle for different combinations of pregnancy and lactation status.

Montano-Bermudez et al. (1990) reported a significant difference for estimates of maintenance energy requirements between high or medium and low milking groups. The groups included Hereford × Angus (low), Red Poll × Angus (medium), and milking

Shorthorn × Angus (high). The 205 d estimated milk production for the high group was higher than the low and medium groups by 561 and 186 kg, respectively. Using weigh-suckle-weigh procedures, feeding trial data, and two different analytical techniques, the authors estimated maintenance requirements. The procedures included either (1) estimating maintenance using daily weight gain/loss in addition to partitioning lactation requirements or (2) using known intake data and an assumed 1.06 Mcal/kg of the diet toward lactation. Their results showed that the higher milk groups required a 12% increase in MEm compared to the lower milk groups.

An interesting result occurred with comparison of steer progeny from low versus moderate and high genotypes for milk. Low milk potential steer progeny had more external fat than the higher milk potential groups, which had higher internal fat contents. The lower milk group cattle had an advantage for lower MEm requirements because their increased external insulation lowered heat loss (Montano-Bermudez et al., 1990).

There are cases when MEm differences between breeds are too small to be of importance. Wurgler and Bickel (1985) reported no differences for MEm between breeds of Angus × Braunvieh, Swiss Braunvieh, and Friesian steers. Braunvieh cattle had a tendency toward lower MEm values, but the differences were deemed biologically unimportant. The authors speculated that there was an energy sparing effect present at restricted feeding levels.

A recent study reported on energy utilization of several breeds using slaughter balance procedures for three groups of animals; an initial slaughter group, a limit-fed group, and ad libitum fed group (Ferrell et al., 1998a; Ferrell et al., 1998b). Both papers reported estimates of nonlinear regressions between heat energy (HE) and metabolizable

energy intake (MEI). The first study using Angus, Belgian Blue, Hereford, and Piedmontese sires had nonlinear relationships between MEI and HE. The authors emphasized that a nonlinear relationship between heat production and MEI would cause the efficiency of energy use for maintenance to shift with changes in MEI. Furthermore, they reported an asymptotic relationship between energy gain and MEI, which indicated a loss in efficiency at higher intake levels. They concluded that there was a decrease in gains with higher levels of intake and maximum efficiency would probably occur at a level less than maximum intake.

The divergent development of *Bos indicus* and *Bos taurus* breeds has resulted in maintenance energy requirements differences. The NRC (1996) states *Bos indicus* cattle are expected to have lower average maintenance energy requirements compared to *Bos taurus* breeds. In previous scientific Literature, lower maintenance requirements values of 10% and 5% have been reported for *Bos indicus* and *Bos indicus* × *Bos taurus* compared to pure *Bos taurus* breeds. However, current research by the U.S. Meat Animal Research Center scientists contradicted prior estimates of lower maintenance energy requirements for *Bos indicus* breeds (Ferrell et al., 1998a). They reported sire breed differences for maintenance requirements for Angus and Brahman cattle of 94 and 119 kcal/($kg^{.75}$ • d), respectively. Their results showed that *Bos indicus* cattle did not have an advantage over *Bos taurus* breeds for maintenance energy requirements. The authors argued that the increased maintenance requirements of the Brahman cattle were attributed to interactions between feed level and temperature, compensatory gain for the limit-fed group, and exposure to extreme winter conditions.

Heritability. Many sources of variation contribute to phenotypic variation for maintenance energy requirements. However, the focus until now has been on breed differences for maintenance energy requirements. In the following paragraphs, two studies will be presented on identical twin data. In each study, the authors estimated broad-sense heritabilities for MEm and traits associated with MEm.

Using twin monozygotic beef calves from Angus × Hereford and Barzona × Hereford lines, Carstens et al. (1989) reported broad-sense heritability estimates for MEm on animals 9 and 20 months of age of .71 and .49, respectively. In a similar study, Hotovy et al. (1991) estimated broad sense heritabilities for MEm and fasting heat production of .52 ± .22 and .75± .13, respectively. These heritability estimates are evidence that genetic variation exists for maintenance energy requirements and it might be feasible to change MEm requirements through selection.

Selection for Maintenance Energy Requirements. The information previously presented supports MEm has additive genetic variation; breeds exhibit variation for MEm requirements, and it is a heritable trait. So, it is possible to make genetic change for MEm. In previously reported research, selection studies for maintenance energy requirements and indicators of MEm have been conducted with mice (Nielsen et al., 1997a). Jones et al. (1992) used the liver as an indicator for maintenance energy in mice and estimated a genetic correlation between liver mass and liver mass/body mass of .75. An increase in liver mass without a change in body mass should result in an increase in the maintenance requirements. Heritability estimates for liver mass, body mass and liver mass/body mass were moderate at .53, .54, and .36, respectively. A selection index with estimated coefficients was used to keep liver mass constant and allowed body mass to

change. The expected response to the index was 40% as effective as just selecting on body mass. Understand that the goal for this selection line was to keep liver mass constant.

In a different study, (Nielsen et al., 1997b) used divergent selection to modify heat loss in a population of 9 to 11 week old male mice. The authors used fifteen generations of divergent selection to obtain realized heritabilities for high lines and low lines of heat loss of .31 and .26, respectively. Using data from a different phase of their project, they reported genetic correlation estimates between heat loss and feed intake of .27 to .40. They showed that selection decisions to modify feed intake had a favorable and correlated effect on maintenance energy requirements. However, the authors also reported an unfavorable genetic relationship between feed intake and litter size. In mice, selection decisions for feed efficiency caused a decrease in fertility. According to Nielsen et al. (1997b), this impact on fertility could have a greater economic impact on non-litter species compared to litter bearing species. Therefore, selection for an increased or decreased feed intake needs to account for changes in fertility.

Visceral Organ Mass. We have previously discussed the differences for both between and within breed MEm requirements. Many of these differences in MEm can be accounted for at the organ and tissue level. Distinctions between groups of animals for average maintenance energy requirements are possible because the visceral organs (e.g., liver, heart, and intestinal tract) are large consumers of total metabolizable energy. If we compare the average MEm requirements of a group of dairy animals to the average requirements for a group of beef animals, we would expect the energy demand for dairy animals to be higher than the beef group. Previous research shows that breeds selected

for higher milk production have, on average, a larger visceral organ mass because a greater quantity of energy is needed to support lactation (Ferrell and Jenkins, 1985).

There are differences among breeds for visceral organ mass because of specialized functions within breed, such as lactation, which places a higher physiological demand on energy requirements. This same argument would apply to differences among genotypes for MEm within a breed. Therefore, differences in visceral organ mass should be correlated with differences in levels of milk production. If all factors except visceral organ mass are equal, dams with genes for higher milk production are more likely to have a larger visceral organ mass compared to individuals with genes for lower levels of lactation. The variation among genotypes for milk potential will also manifest as differences in visceral organ mass (Solis et al., 1988).

The physiological demand of lactation is higher than other physiological functions such as gestation and pregnancy. Animals with genotypes for higher milk production will often have increased maintenance requirements and larger visceral organs. In fact, Montano-Bermudez et al. (1990) estimated that milk production was responsible for 23% of the variation for maintenance energy requirements. This increased energy requirement is also present in dairy animals (i.e., steers) that are incapable of lactation. Both their visceral organ mass and MEm requirements will be higher compared to most beef breeds.

A review article by Ferrell and Jenkins (1985) summarized and distinguished energy expenditures at maintenance for lactating compared to non-lactating cattle. They compared Angus-Hereford, Charolais, and Jersey-cross animals. Their results showed that the Jersey-cross animals had higher energy expenditures on a per metabolic body weight scale than other breeds. Because Jerseys are known for higher levels of milk

production than the majority of beef breeds, they are predisposed to greater maintenance energy requirements (Table 2.4).

The differences in maintenance energy requirements for the whole animal can also be assessed by tissue type. At the tissue level, energy can be diverted to protein synthesis, ion transport, nervous system functions, fat and muscle tissue repair, and active transport during absorption (Baldwin, 1995). For example, the estimates of energy use by liver, heart, and kidney or brain tissues in the non-lactating Holstein cow were 1.55, 2.41, 4.1 MJ/kg, respectively. In contrast, the energy usage of visceral fat and skin was .06 and .07 MJ/kg, respectively. The following paragraphs briefly describe a few of the energy sinks for MEm requirements. These examples are only a small proportion of the tissue level MEm requirements.

Protein synthesis is reported to use approximately 20% of an animal's total energy intake (Lobley, 1991). This allotment of energy is used for functions such as reformation of polypeptides and subsequent protein structures. Protein turnover in liver tissue uses large amounts of MEm because it has a higher rate of change relative to the average rate of tissue renewal for the whole-body. Using oxidation rate of tissues as an indicator, the liver oxidizes 3.5 kJ of ME/g/day compared to the whole body average of 0.1 kJ of ME/g/day (Johnson et al., 1990).

Other processes that consume large quantities of energy intake include ion transport, urea synthesis, and gluconeogenesis. Sodium and K^+ ion transport paths and Na^+/K^+ ATPase function accounts for 35, 20, and 24% of the energy expenditures in the liver, GI tract, and muscle tissue, respectively (Lobley, 1991). Ion-transport and gluconeogenesis make up a large portion of the maintenance energy needs in the liver and

visceral organs (Baldwin, 1995). The large caloric demand of visceral organs make the liver, heart, GI tract, and other vital organs potential indicators of maintenance energy requirements.

CHAPTER III

MATERIALS AND METHODS

Data Description

I received the data for this study from the Red Angus Association of America (RAAA) located in Denton, Texas. The RAAA supplied performance and pedigree field data on 111,460 cow weight observations, 1,703 hip height observations, and 7,731 body condition score observations representing data for years 1968 to 1998. Each individual record included: registration number, herd prefix, date of birth, sex of animal, cow registration number, weaning date, cow's weight, height and body condition score at weaning, weaning contemporary group code for the calf, weaning weight feed code, weaning weight irregular code, and weaning weight work group. Any supplementary information to complete the mature weight database was obtained from the archive of the 1998 RAAA sire summary. The additional data extracted from the RAAA 1998 archive included: herd prefix, birth date, percentage Red Angus, owner and breeder codes, sire and dam registration numbers, actual and adjusted birth weight, RAAA birth weight contemporary group, adjusted and actual weaning weight, weaning date, RAAA weaning weight contemporary group, actual and adjusted yearling weight, yearling date, and yearling weight contemporary group. The added information was used to generate values for age of the calf's dam, age at weaning and yearling, and age of the cow's dam for mature weight (BIF, 1996).

A preliminary evaluation of data showed that there was insufficient data to warrant including hip height and body condition score in a variance components analysis. These data were reported over several years with a high level of incomplete reporting; any variance component estimates obtained for these traits would be biased and uninformative. Therefore, I analyzed only cow weight observations and excluded all body condition score and hip height data.

The data set represented 111,460 weight observations on 45,241 cows prior to data removal for incomplete records. These data are reported from 1,557 registered RAAA breeder codes where the mean and SD for number of observations was 70 and 428, respectively. Of the 1,557 breeders, 33 of them submitted greater than 500 cow weight records and approximately 10 breeders have submitted more than 1,000 observations.

The early years of data collection, 1968 to 1972, had a limited number of cow weight observations. The range of weight observations for years 1968 to 1998 was 1 to 7,385. The average, SD, and range of observations per animal were 2.40, 1.90, and 1 to 15, respectively. The mean and SD of cow weight were 495 kg and 90.50 kg, respectively.

Mature Weight Multivariate Analysis

Data. Performance data included cow weight observations, subsequent fixed effects information, and pedigree records on four Red Angus herds. In this analysis, I defined an observation of mature weight as a weight record taken at weaning on a female at least two years of age. I recognize that a cow does not reach her full mature weight

until 4 to 5 years of age. In order to avoid confusion, I will label cow weight observations of animals at younger ages (i.e. 2, 3, and 4 yr of age) as being mature weights. The RAAA records the cow's weight concurrently with the calf's weaning weight record. Prior to analysis of the mature weight data, I removed weight observations on animals outside a weight range of 272.1 kg to 907.0 kg (210 records). This weight range was more conservative than what is currently used for sifting yearling weight in the annual RAAA (1998) genetic evaluation. Currently, there is not a universal standard for classifying mature weight observations. The weight range was determined from previous research and differences in the plot of observations. In previous studies of mature weight, data removal criteria differed among analyses. The range I used to remove data was comparable with previous research studies (Johnson et al., 1990; Meyer, 1999). In addition to reviewing the literature, I plotted the mature weight observations and most weights were between 320 kg and 820 kg. Any records outside the designated weight range were either unrealistic mature weights (i.e. 2000 kg) or weights that can be classified as outliers. Further data editing resulted in removal of individuals with missing birth date information (1 record), individuals outside an age range of 1.75 yr to 20 yr (2,460 individuals less than 1.75 yr and 5,118 animals >20 yrs), missing weights (132 records), animals less than 50% Red Angus breeding (4,757 records), and missing contemporary group information (24,215 records). This reduced the number of complete weight records to 82,278.

The age range of 1.75 yr to 20 yr represented a preliminary removal of animals too young or too old for the analysis. Using descriptive statistics, I reduced the age range to animals between 2 and 10 yr of age, which is consistent with results from prior studies

(Bullock et al., 1993; Meyer, 1999). Preliminary analysis of the data showed a distinct break in the number of observations per age group at age 9 to 10 yr. Likely animals greater than 10 yr of age are highly selected and represent a small proportion of the data. In many production environments, animals at that age are likely to be culled for age or production status. Furthermore, those animal at later ages (greater than 10 yr of age) would represent a highly selected group of individuals and including these animals in an analysis would only serve to add bias to their genetic predictions (B. L. Golden and R. M. Bourdon, personal communication).

Contemporary Group. The literature reports multiple definitions for mature weight contemporary group. In a preliminary analysis, I determined an appropriate definition for mature weight contemporary group to meet the minimum standards found in the literature and to determine if there was any advantage to appending on additional information to the definition. I conducted the evaluation of contemporary group as a fixed effect using animals 2 to 10 yr of age by year.

I evaluated the importance of two different contemporary group definitions to determine the statistical significance of one definition versus a different definition. The definitions that I analyzed included only weaning contemporary group of the cow's calf and both weaning contemporary group of the current calf of the cow and the weaning contemporary group of the cow. I selected weaning contemporary group of the cow's calf because it included information on individuals managed in similar environments and subdivided those groups if their calves received special treatment. Also, weaning contemporary group was easy to implement and currently was part of the annual genetic evaluation analysis for RAAA.

To determine the appropriate contemporary group definition, I used an earlier data set than the one described in previous paragraphs. The previously constructed data set was a subset of the larger data set (41,155 records) and after removal for missing contemporary group information, missing weights, and no age of dam information reduced it to 26,679 records. This data set structure was not reflective of those that were used in future analyses because these data determined the formation of mature weight contemporary group. Table 3.1 represents those animals that had a reported weaning contemporary group of a cow's calf and cow and a valid cow weight observation. After the contemporary group was determined, the final edits of data were completed.

Table 3.1. Data structure for mature weight (kg) by contemporary group in Red Angus cattle prior to data removal

Age (yr)	N[1]	Phenotypic mean/SD of Mwt (kg)		No. of weaning contemporary groups		Avg contemporary group size	
		Mean	SD	Calf	Cow	Calf	Cow
2	6,674	413.70	61.22	647	795	10.3	8.4
3	4,783	463.05	65.82	757	732	6.3	6.5
4	3,650	501.63	70.24	797	718	4.6	5.1
5	2,984	522.65	69.08	717	643	4.2	4.6
6	2,321	536.16	67.75	636	569	3.7	4.1
7	1,901	542.92	66.74	548	1353	3.5	3.8
8	1,429	549.11	65.59	463	449	3.2	3.3
9	1,146	543.03	63.97	412	390	2.8	2.9
10	769	536.61	61.34	312	316	2.5	2.4

[1]N = Number of observations

I defined weaning weight contemporary group according to what is used by the RAAA. The definition for weaning weight contemporary group included: weaning workgroup, weigh date, calf sex, breeder management code, and birth contemporary

group. Birth contemporary group consisted of birth workgroup, calf sex, breeder management code, and percentage Red Angus. For birth contemporary group, animals greater than 87.5% Red Angus were placed in one contemporary group and those 50% to 87.5% Red Angus were assigned to a different contemporary group.

Fixed Effects Test. I tested different models fixed effects using procedures described by Boik et al. (1993). This procedure tests different model fits using a likelihood ratio test, F-test. According to the authors, this method of testing fixed effects is a more powerful test for fixed effects than alternative methods because it makes a distinction between fixed effects and random additive genetic effects in addition to including relationships among animals.

Boik et al. (1993) developed three computational procedures for testing fixed effects that include: inverse of the covariance matrix, generalized inverse of the mixed model equations, and solutions to the mixed-model equations. The following list describes the equations needed to compute tests of fixed effects using the solutions to both fixed and random effects:

$$F = \frac{\left(\frac{SS1}{r - r_1}\right)}{\left(\frac{SSE}{N - r}\right)}$$

$$SSE = y'R^{-1}y - y'R^{-1}X\hat{b} - y'R^{-1}Z\hat{u}$$

$$SS_1 = y'R^{-1}(X\hat{b} - X_r\hat{b}_r) + y'R^{-1}Z(\hat{u} - \hat{u}_r)$$

where

y= vector of observations on the trait, X and X_r = known full and reduced incidence matrices relating fixed effects in b to observations in y, Z = known incidence matrix relating observations in y to random additive direct genetic effects, $b_{F(R)}$ = vector of fixed effects for the full and reduced models, $u_{F(R)}$ = vector of random additive direct genetic effects of animals (i.e. breeding values), R = known matrix of residual variance p-values, N = number of total degrees of freedom, SS_1 = difference in sums of squares error between the reduced and full models, SSE = sums of squares error, r = rank of the full animal model, r_1 = rank of the reduced animal model.

The likelihood ratio test is a suitable method for determining what effects to include in a statistical model. However, these results can be distorted when there are a large number of observations available to test effects in the model. In fact, a particular fixed effect may be significant, but the actual variation attributed to the effect could be very small. In data sets where there are thousands of degrees of freedom to test an effect, any small difference between models due to an effect will be deemed significant.

Using a likelihood ratio test (Boik et al., 1993), I evaluated the statistical importance of models that included both weaning contemporary group of the cow's calf and the cow compared to using just weaning contemporary group of the cow's calf as fixed effects. Solutions to both random and fixed effects were obtained using BLUP (Henderson, 1984) with a full and reduced animal model where the reduced model represented weaning contemporary group of a cow's calf as the only fixed effect. The solutions were generated using a performance programmed BLUP program, 'tkblup' (Golden, unpublished). The Animal Breeder's Tool Kit (Golden et al., 1992) was used to assemble incidence matrices and vectors of solutions and observations for use in

testing fixed effects. The full model included fixed effects of weaning contemporary group of cow and the cow's calf. Random effects included a random additive direct effect of animal and residual. Including contemporary group of cow in the mature weight contemporary group represented the only difference between the full and reduced animal models for each analysis by year. Because I had not estimated variance components, I assumed a h^2 of .50 based on literature values (Table 2.2).

Results of statistical tests can be misleading, so alternative methods should be used to evaluate the inclusion of effects in the model. One method is to evaluate the magnitude of fixed effect solutions and the corresponding standard errors of the estimates to determine importance of the effects. A different approach is to simply evaluate changes in the mean square error or the coefficient of determination of one model versus another model when components are added. In addition, the mean square error can be used to calculate a coefficient of determination.

Using the results of the preliminary analysis on contemporary group, I completed the mature weight data preparation. Mature weight contemporary group included weaning contemporary group of the cow's calf when the mature weight was recorded and percentage Red Angus of the animal. The removal of individuals with invalid contemporary groups codes animals greater than 10 yr of age, and contemporary groups with no variation reduced the data to 74,124 observations.

Data Reduction. Multivariate analyses are known to be computationally intensive and attempting to estimate variance components from all 74,124 mature weight records creates an intractable problem. Instead of analyzing all the data, I sampled four well-reported herds from the larger data set. I used breeder codes of the four herds and

corresponded them with breeder codes for both the calf and cow in the mature weight data set. I created a subset of data using the breeder codes and then extracted additional animals that were part of the same contemporary groups. The breeder codes came from four herds including Beckton Red Angus, Sheridan, Wyoming; Buffalo Creek Red Angus, Leiter, Wyoming; Leachman Cattle Company, Billings, Montana; and Schuler Red Angus, Bridgeport, Nebraska. They represented mature weight data collected for years 1970 to 1998. Three of the herds mentioned have routinely been used in variance component analyses for other growth traits (birth weight, weaning weight, and postweaning gain) because of their exceptional performance recording programs. This reduced data set represented approximately 29,380 animals and I used it to test additional fixed effects and estimate variance components. I reported the data structure by year, by age group (years), by pedigree structure, a summary of contemporary group information (Tables 3.2 to 3.5), and a plot of records by year (Figure 3.1).

Table 3.2. Descriptive statistics for Red Angus mature wt (kg) data by year of observation

Year	No. of Observations	Mean, kg	SD, kg	Range, kg	
				Minimum	Maximum
1970	44	487.55	53.87	402.72	585.49
1971	66	479.06	50.81	367.35	590.93
1972	288	481.67	54.96	355.10	622.68
1973	550	480.75	57.24	339.68	624.49
1974	574	466.88	61.83	325.17	631.75
1975	651	470.84	61.92	317.46	657.60
1976	714	464.30	65.99	308.84	721.09
1977	719	452.44	67.69	294.78	709.75
1978	690	474.81	71.00	307.94	714.29
1979	700	471.63	65.70	310.66	714.29
1980	860	460.56	67.26	307.03	684.81
1981	869	457.04	66.42	311.11	660.77
1982	953	460.54	67.68	299.32	704.31
1983	553	465.77	67.75	317.46	696.15
1984	877	462.57	61.97	292.06	665.31
1985	959	423.30	68.05	273.47	634.92
1986	774	460.09	77.24	274.83	766.44
1987	1,042	454.49	71.22	276.64	684.81
1988	1,290	477.11	74.51	272.11	716.55
1989	1,094	465.59	80.93	290.25	900.23
1990	2,179	500.72	78.14	292.52	750.57
1991	2,069	493.62	78.45	299.32	727.89
1992	1,400	494.55	85.59	272.11	735.15
1993	1,784	501.80	83.15	294.78	783.22
1994	1,700	510.49	96.22	285.71	800.91
1995	2,395	522.33	88.35	276.64	779.14
1996	1,776	511.11	91.34	319.73	861.68
1997	1,810	524.82	94.97	303.85	827.66

Table 3.3. Descriptive statistics of mature weight by age of cow subclasses for Red Angus cattle

Age (yr)	No. of Observations	Mean, kg	SD, kg	CV, %	Range, kg	
					Minimum	Maximum
2	7,419	412.39	60.95	14.8	272.11	727.89
3	5,384	461.73	65.78	14.2	280.27	761.91
4	4,064	501.15	69.81	13.9	297.95	900.23
5	3,370	521.70	68.75	13.2	335.60	861.68
6	2,690	535.63	67.12	12.5	337.87	827.66
7	2,239	541.24	65.54	12.1	376.42	800.91
8	1,785	546.44	65.17	11.9	378.69	818.59
9	1,453	542.25	63.55	11.7	385.49	761.91
10	976	534.14	60.22	11.3	385.49	772.79

Table 3.4. Pedigree structure for different ages of mature weight in Red Angus cattle including number of animals, known sires, known dams, and foundation animals

Age (yr)	No. of Animals	No. of Sires	No. of Dams	No. of Foundation Animals[1]
2	13,104	1,176	7,365	3,482
3	10,928	1,128	6,363	2,923
4	9,237	1,069	5,474	2,535
5	8,023	978	4,832	2,295
6	6,962	886	4,277	2,081
7	6,120	823	3,719	1,806
8	5,316	769	3,203	1,689
9	4,557	704	2,737	1,448
10	3,316	600	1,973	1,117
All Years	17,418	1,418	9,467	4,310

[1]An individual was considered a foundation animal if one or both parents were unknown.

Table 3.5. Description of contemporary group size across ages of animals with mature weight observations in Red Angus cattle

Age (yr)	No. of Contemporary groups	Avg. CG size	SD of CG size
2	629	11.7	15.4
3	841	6.3	8.3
4	817	4.8	6.0
5	771	4.3	5.0
6	703	3.7	4.5
7	616	3.5	4.1
8	559	3.2	3.3
9	507	2.8	3.1
10	406	2.4	2.1
All years	2,105	13.8	20.9

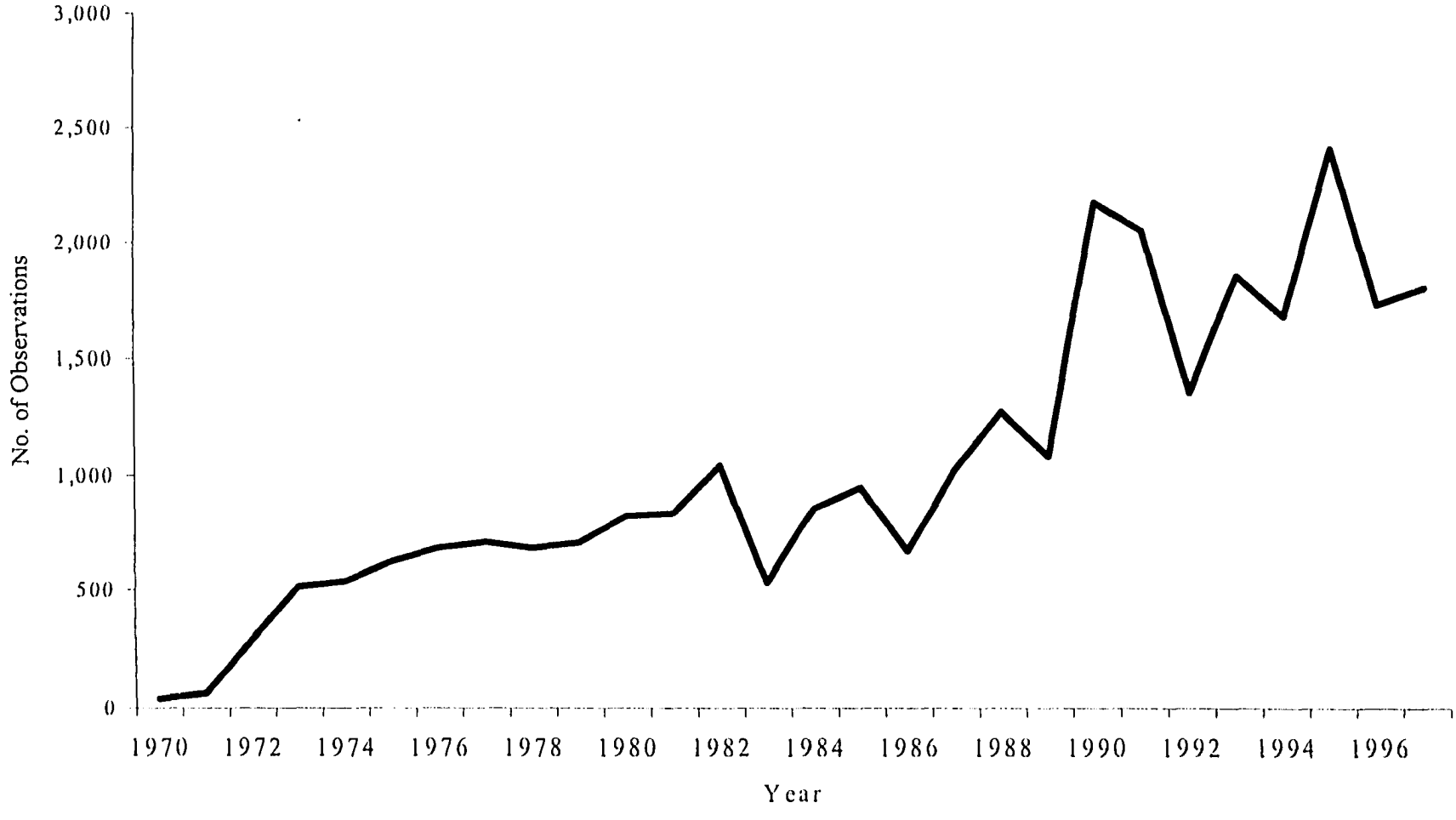

Figure 3.1. Number of mature weight observations by year for the Red Angus Breed.

Statistical Procedures. I estimated variance components using Method R procedures (Reverter et al., 1994) with a multivariate single component animal model (1984). This analysis was done with a performance C-programmed beta-version Method R software package named 'ds6' (Golden, unpublished). From the data, I used random 50% sub samples and compared those subsamples to all the data to generate approximately 20 sets of variance component estimates. A converged estimate was obtained after 500 rounds of iteration on the R statistic or when the average change between rounds of variance component iteration was less than 1×10^{-6}.

For the multiple trait and single component model, this version of the Method R software is programmed to ignore any genetic and residual variance starting values. In the beginning, the software iterates on each trait and solves it as a single trait model until converged estimates are obtained on the diagonal elements of the covariance matrix. Then it will begin estimating covariance components by releasing the off-diagonal elements that were previously constrained to zero (Golden, unpublished). Empirical evidence in previous research shows this approach improves computational efficiency (Golden, personal communication).

Fixed Effects. I evaluated the importance of fixed effects for the cow's age of dam and weaning weight of her calf in a mature weight analysis. I fit these effects in the model based on previous research or indications that they may have some impact on mature weight. I analyzed the fixed effects by age categories 2 to 10 yr by building data sets by year of age and analyzing both the cow's dam age and weaning weight of the cow's calf.

The effects were tested using previously described procedures to determine contemporary group (Boik et al., 1993). The method of evaluation included a likelihood ratio test, mean square error, and evaluation of the magnitude of fixed effects. The single trait animal model used to generate solutions included fixed effects of mature weight contemporary group, age of the cow's dam, and weaning weight of cow's calf. The random effects included random additive genetic effects of animal and residual error.

Multivariate Analysis

For the multivariate analysis, I analyzed mature weight data from animals 2 to 10 yr of age using an animal model in two trait pairs (Henderson and Quaas, 1976; Henderson, 1984). The following multivariate animal model is a generalized version of the models used for mature weight at one age (MW_1) (i.e., 2 yr of age) with mature weight at a different age (MW_2) (i.e., 3 yr of age):

$$\begin{bmatrix} \mathbf{y}_{MW_1} \\ \mathbf{y}_{MW_2} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{MW_1} & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_{MW_2} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{MW_1} \\ \mathbf{b}_{MW_2} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{MW_1} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_{MW_2} \end{bmatrix} \begin{bmatrix} \mathbf{u}_{MW_1} \\ \mathbf{u}_{MW_2} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{MW_1} \\ \mathbf{e}_{MW_2} \end{bmatrix},$$

where

$y_{MW_1(MW_2)}$ = vector of phenotypic observations on $MW_1(MW_2)$, $X_{MW_1(MW_2)}$ = known incidence matrix of observations related to fixed effects in $b_{MW_1(MW_2)}$, $b_{MW_1(MW_2)}$ = vector of fixed effects related to $MW_1(MW_2)$, $Z_{MW_1(MW_2)}$= incidence matrix relating random additive direct genetic effects to $Y_{MW_1(MW_2)}$, $u_{MW_1(MW_2)}$= vector of random additive direct genetic effects for $MW_1(MW_2)$, $e_{MW_1(MW_2)}$= vector of random residual errors for $MW_1(MW_2)$.

The model distributed random effects as follows:

$$\text{var}\begin{bmatrix} \mathbf{u}_{MW_1} \\ \mathbf{u}_{MW_2} \\ \mathbf{e}_{MW_1} \\ \mathbf{e}_{MW_2} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma^2_{MW_1} & \mathbf{A}\sigma_{MW_1 \cdot MW_2} & \mathbf{0} & \mathbf{0} \\ \mathbf{A}\sigma_{MW_2 \cdot MW_1} & \mathbf{A}\sigma^2_{MW_2} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma^2_{e_{MW_1}} & \mathbf{I}\sigma_{e_{MW_1} \cdot e_{MW_2}} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_{e_{MW_2} \cdot e_{MW_1}} & \mathbf{I}\sigma^2_{e_{MW_2}} \end{bmatrix}$$

and

$$\mathbf{E}\left[\mathbf{y}_{MW_1(MW_2)}\right] = \mathbf{Xb}$$

where

A = Wright's numerator relationship matrix, I = identity matrix, $\sigma^2_{MW_1(MW_2)}$= additive genetic variance for direct effects of $MW_1(MW_2)$, $\sigma_{MW_1 \cdot MW_2}$= additive genetic covariance for direct effects between MW_1 and MW_2, $\sigma^2_{e(MW_1(MW_2))}$= residual error variance for $MW_1(MW_2)$, $\sigma_{e(MW_1 \cdot MW_2)}$ = residual error covariance between MW_1 and MW_2.

The two-trait animal models included Beef Improvement Federation (BIF, 1996) age of dam classes 2, 3, 4, 5 to 9, 10, 11, 12, and 13+ yr of age, mature weight contemporary group defined as weaning contemporary group of the individual's calf and percentage Red Angus as fixed effects. Random effects included random additive direct genetic effect of animal and residual error.

A different pedigree was compiled for each multivariate analysis. For each multivariate analysis between traits (i.e., 2yr MW with 3yr MW), I included pedigree data on all animals with at least one trait observed for either of the two traits plus their parents and grandparents. The result was the formation of a three generation pedigree,

which was used to form a unique list of individuals and Wright's inverse numerator relationship matrix. The number of unique animals in each pedigree ranged from 15,150 to 5,185. I used the Animal Breeders Tool Kit software (ABTK) to assemble and solve all components of the pedigree and inverse numerator relationship matrix (Golden et al., 1992).

I summarized the results of the multivariate analysis and reported the number of method R subsamples, the median, 95% CI for both the variance components and heritability estimates. The median of estimates was used rather than the mean estimate because recent research determined that Method R is an unbiased median estimator (Mahabir and Chapman, 1999). Therefore, I reported median estimates and 95% confidence intervals of heritabilities, genetic and residual correlations. Furthermore, I used a non-parametric confidence interval procedure for medians, which was different from those reported in most texts for means (SAS, 1990; Hahn et al., 1991).

Univariate Analysis

In addition to the multivariate analysis, I estimated variance components with single trait animal models on individuals 2 to 10 yr of age. However, I obtained variance component ratios instead of variance component estimates using Method R variance components procedures (Reverter et al., 1994). Unlike the multivariate Method R procedures, the single trait-single component procedure uses a binary iteration strategy to solve the variance ratios (Reverter et al., 1998). For each single trait analysis, I estimated variances ratios and calculated subsequent heritabilities from Method R subsamples of the data. Approximately 30 Method R estimates per dam age group were used to

determine the average heritability. Previously, Reverter et al. (1998) determined that reliable confidence regions are obtainable with a limited number of Method R estimates. Therefore, it was not necessary to estimate large numbers of variance component ratios unless the standard errors of the mean was high.

The univariate animal models for cow weight at different ages had the same fixed and random effects as previously reported in the multivariate models. I used the following univariate animal model for analysis of cow weight at different ages (yr):

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_a\mathbf{u}_a + \mathbf{e},$$

where

$$\text{var}\begin{bmatrix}\mathbf{u}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{A}\sigma_a^2 & 0\\ 0 & \mathbf{I}\sigma_e^2\end{bmatrix}$$

and

$$\mathbf{E}[\mathbf{y}] = \mathbf{Xb}$$

y = vector of phenotypic observations on mature weight, X = known incidence matrix of observations related to fixed effects in b, b = vector of fixed effects related to the trait, Z_a= incidence matrix relating random additive direct genetic effects to y, u= vector of random additive direct genetic effects for the trait, e = vector of random residual error, I = identity matrix, σ_a^2 = additive direct genetic variance, and σ_e^2 = residual error variance.

Repeated Measures Model

I estimated variance components using Method R (Reverter et al., 1994) variance component procedures and a univariate multiple component animal model for repeated measures. I used the following model for analysis of mature weight:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_a\mathbf{u}_a + \mathbf{Z}_p\mathbf{c}_p + \mathbf{e},$$

where

$$\text{var}\begin{bmatrix}\mathbf{u}\\ \mathbf{c}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{A}\sigma_a^2 & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{I}\sigma_p^2 & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_e^2\end{bmatrix}$$

$$\mathbf{E}[\mathbf{y}] = \mathbf{Xb}$$

y = vector of repeated phenotypic observations on mature weight, X = known incidence matrix of observations related to fixed effects in b, b = vector of fixed effects related to the trait, Z_a= incidence matrix relating random additive direct genetic effects to y, u_a= vector of random additive direct genetic effects for the trait, Z_p = incidence matrix relating random permanent environmental effects to y, c_p = vector of random permanent environmental effects, e = vector of random residual error, I = identity matrix, σ_a^2 = additive direct genetic variance, σ_p^2 = permanent environmental variance , σ_e^2 = residual error variance.

Fixed effects for the repeated measures animal model for mature weight included mature weight contemporary group and an interaction of age of cow (yr) and age of the cow's dam. I fitted an interaction between age of the cow's dam and age of cow to simultaneously account for the main effects of cow age, age of dam, and the interaction between them. A preliminary analysis of fixed effects showed the existence of a possible interaction. Random effects included random additive direct genetic effects for animal, random permanent environmental effects of animal, and residual error.

Random Regression Analysis

Software Development. Reverter et al. (1994) developed the Method R variance components procedure based on the principle that regression of more accurate on less accurate predictions should be equal to an expected value of one. If the regression coefficient deviated from one then a biased estimate of the heritability was being used. The Method R variance components procedures have not been widely applied to problems requiring random regression models. The next section describes the modifications made to the current version of Method R that is performance programmed in C (B. L. Golden, unpublished).

The current version of the Method R variance components software (B. L. Golden, unpublished) is capable of analyzing data with single trait and multivariate animal models of various that have single or multiple components. However, this version is not capable of estimating variance components for random regression models.

I used the current beta version of the Method R variance component software and changed the necessary functions for analysis of models with random regression

properties. I made these modifications according to previously published notes and random regression methodology in the scientific literature (Schaeffer, 1997; Schaeffer, 1999). The modifications I made to the existing Method R variance components software are located in Appendix A.

Using the following example and data (Table 3.6) I will demonstrate how I modified the functions in the current beta version of the Method R software (version ds6, B. L. Golden, unpublished) to estimate variance components with random regression models (Schaeffer et al., 1997).

$$\mathbf{y} = \mathbf{Xb} + \begin{bmatrix} \mathbf{Z}_{b0} & \mathbf{Z}_{b1} & \mathbf{Z}_{b2} \end{bmatrix} \begin{bmatrix} \mathbf{u}_{b0} \\ \mathbf{u}_{b1} \\ \mathbf{u}_{b2} \end{bmatrix} + \mathbf{e}$$

where

y = vector of mature weights on females; b = vector of fixed effects including fixed regression coefficients; u_{b0}, u_{b1}, and u_{b2} = vectors of random additive direct genetic effects for the random regression coefficients (intercept, linear and quadratic terms); X = a matrix of relating mature weight observations to fixed effects and fixed random regressions for the intercept, linear, and quadratic terms (covariates); Z_{b0}, Z_{b1}, and Z_{b2} = a matrices relating observations to additive genetic random regression coefficients for the intercept; linear, and quadratic terms (matrix of covariates); e = vector of temporary residual effects for each observation.

Table 3.6. Example mature weight data including identification, age, and weight for analyzing random regression models using Method R

Identification	Age (yr)	Age^2, yr^2	Weight, kg
1	2	4	450
2	3	9	460
3	4	16	500
1	3	9	470
2	4	16	480
3	5	25	510

$$\mathbf{X} = \begin{bmatrix} 1 & 2 & 4 \\ 1 & 3 & 9 \\ 1 & 4 & 16 \\ 1 & 3 & 9 \\ 1 & 4 & 16 \\ 1 & 5 & 25 \end{bmatrix} \quad \text{and} \quad \mathbf{Z} = \begin{bmatrix} 1 & 4 & 16 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 3 & 9 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 4 & 16 \\ 1 & 3 & 9 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 4 & 16 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 5 & 25 \end{bmatrix}$$

The matrices X and Z pictured above illustrate what could be used to construct the mixed model equations for random regression functions. The Z matrix is constructed from the coefficient matrices of random effects for the intercept, linear, and quadratic regression coefficients. For the random regression case, incidence values are replaced with the covariates corresponding to a specific animal at a particular age.

Before making the software modifications to different functions in the Method R variance components software, two small studies that involved the parameterization of random regression models were completed using tools from the ABTK (Golden et al., 1992) to construct random regression animal models (Evans and Golden, 1996; Kuehn,

2000). However, a new tool, 'random_r', was developed using a modified version of gen_z (Appendix B). The gen_z program was used to form an incidence matrix for random effects using the unique list of identifications from the pedigree, a list of animals from the data, and a vector of animals with observations. The changes outlined above were made so that covariates could be incorporated into the mixed model equation random effects. These modifications were then used as a model for the variance components package.

Software Capabilities. This alpha version of Method R (Appendix A), dsreg, can be used for variance component estimation of random regression models. The modifications should allow someone to fit models with different order polynomials (i.e., linear, quadratic, cubic, etc). Because no modifications were made to the augmentation function, this version is able to yield estimates for different augmentations including genetic and permanent environmental effects. However, this version uses a homogeneous residual error variance for a univariate models. The assumption of homogeneous error was consistent with previous versions of the software. This assumption may present problems for longitudinally observed traits that are expressed over extended periods (e.g., years). Those traits observed over time might have scaling of variation due to heterogeneous measurement error variation. At a later stage of the methods, I describe the procedures used to adjust for heterogeneous residual variance.

Software Modifications. I used the description of random regression models provided by (Schaeffer, 1999) to modify functions within the C-code for the Method R variance components procedures (B. L. Golden and L. A. Kuehn, personal communication)(Appendix A). The changes I made to the C-code involved the functions

for building the effects list file and reading the necessary model components, the allocation of memory and data storage routines, and routines that involved making contributions to the right hand side or the coefficient matrix. I did not change any functions responsible for the augmentation file or dependent variable file (B. L. Golden, unpublished).

I first modified the effects list function to recognize the effect code of '6' for the random regression case. Other effects codes include: fixed effect = 1, random effect = 2, covariate = 3, and mean = 4. The C-code for random effects provided the base idea and I modified the code to place the covariate of interest instead of a 1 or 0 for incidence. The software was modified to use the constraint field to designate where the covariate could be obtained as the mixed model equations were being constructed. This correctly pulled the right covariate or fixed regression and assigned it to the correct location in the coefficient matrix and right handside. This was a critical change because both the coefficient matrix and right hand side are directly built. I used several example data sets to prove that the covariates were being correctly placed in the coefficient and right hand side of the mixed model equations.

Additional functions that I modified included 'load.c'. This part of the program allocates memory and loads the data into memory for the mixed model equations. Modifications were made to allocate memory for the random regression case.
I also made changes to functions in the mme.c and do_cont.c code, which builds the mixed model equations. These changes reflected those that allowed the independent variable (covariate) to be correctly added to the linear system of equations. These changes also included routines for the input of coefficients to both diagonal and off-

diagonal elements (e.g., do_coef_contrib(), do_diag_contrib()). Furthermore, the getCov() function was adjusted for incorporation of the random regression case. The modifications to dsreg.c were to the fillEffects() function which opens files to be read and reports information about the different effects in the model. Other functions from def.c that assign memory and define structures of matrices were also modified to account for the random regression case. Using the existing code, I added on C-code to read in a random regression effect. All the functions and changes to the Method R variance components software are located in Appendix A.

Software Validation. After I made the necessary modifications to the Method R variance components software, dsreg, I ran the software with small data sets (10 to 15 records) to determine if covariates for the random regression were correctly added to both the coefficient and right hand side matrices.

In a random regression analysis, Kuehn (2000) used simulated data to estimate variance components with this version of the Method R software. This was done for two reasons, 1) to determine the number of observations to parameterize a random regression model and 2) to estimate variance components, but also to determine how well the variance components were being estimated using random regression models. The study by Kuehn (2000) showed that the variance components software validated the estimation procedures using random regression models.

Repeated Measures Model. In a separate study by Kuehn (2000), Variance components were estimated for both a simple repeated measures model and a random regression model that included both additive genetic and permanent environmental effects. This study was done simply to further validate Kuehn's results and test both the

outcome of a applying a simple repeated measures model and a random regression model with permanent environmental effects.

I simulated data for a simple repeated measures model using procedures outlined by Kuehn (2000), which I modified to include an effect of permanent environment. The multiple trait simulator required: Cholesky decompositions of the genetic, permanent environment, and residual variance structures; Cholesky decomposition of the numerator relationship matrix. Prior to the analysis a simulated pedigree was built using a C-programmed tool 'datagen' (B. L. Golden, unpublished).

The data for the repeated measures model was simulated for a 10,000 animal pedigree that contained 10 foundation sires and 100 foundation dams. The foundation sires and dams made up approximately .10% and 1.0% of the pedigree, which created a high level of inbreeding. This pedigree structure had a higher level of inbreeding compared to what was previously done by Kuehn (2000). I simulated 8 observations per animal to represent mature weight observations for ages 2 to 9 yr using the following model:

$$\mathbf{y}_{ij} = \mathbf{b}_{A0_i} + \mathbf{b}_{P0_i} + \mathbf{e}_{ij}$$

and

$$\text{var}\begin{bmatrix} \mathbf{b}_{A0} \\ \mathbf{b}_{A0} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{I}\sigma_p^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

where

y_{ij}= phenotype of animal i at record j, b_{A0i} = random additive direct genetic effect of animal i, b_{P0i} = random permanent environmental effect of animal i, e_{ij}= random residual error for animal i's phenotypic observation at record j, A = Wright's numerator relationship matrix, I_1= identity matrix with an order equal to the number of individuals in the pedigree, I_2 = identity matrix with an order equal to the number of observations, σ^2_a = additive direct genetic variance, σ^2_p = permanent environmental variance, σ^2_e = residual error variance (Kuehn, 2000). The input values for the additive genetic variance, the permanent environmental variance, and the residual error variance were 1,234.05 kg^2, 617.00 kg^2, and 514.20 kg^2 , respectively.

I estimated variance components with several subsets of the 8 record data repeated measures data. Using the simulated data set of 8 records per individual, I removed records to build different data sets with 1, 2, 3, and 5 records per individual. Then each data set was analyzed using Method R procedures to estimate variance components; however, I treated the inputs into the software as if it was for a random regression model. The coefficient values were loaded as coefficients and not just incidence values of 1's and 0's. I used the repeated measures model to obtain variance component estimates:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_A\mathbf{u}_A + \mathbf{Z}_P\mathbf{u}_P + \mathbf{e}$$

$$\text{var}\begin{bmatrix}\mathbf{u}_A \\ \mathbf{p}_P \\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{A}\sigma^2_a & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{I}_1\sigma^2_p & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}_2\sigma^2_e\end{bmatrix}$$

where

y = vector of mature weight observations, X = incidence matrix of observations related to fixed effect in b, Z_A = coefficient matrix relating random additive direct genetic effects for mature weight to y, Z_p = coefficient matrix relating random permanent environmental effects for mature weight to y, e = vector of residual error, u_A = vector of random additive direct genetic effects for each animal, and u_P = vector of permanent environmental effects for each animal.

For each data set, I obtained estimates of variance components using Method R procedures (Reverter et al., 1994) random 50% subsamples of the data. I generated approximately 15 sets of variance component estimates for each data set. The convergence criteria for the Gauss Seidel rounds was set to 1×10^{-6}.

I used the previous variance component estimates to calculate the median, SD, and 95% CI. I compared the true values for the simulated data to the median value for that variance component to evaluate how well the Method R variance component procedure could estimate the true values for a random regression model. Furthermore, I wanted to determine the number of records to obtain reasonable estimates of variance components for different models.

The data for the linear random regression model was simulated for a 10,000 animal pedigree that had the same foundation and pedigree structure as the repeated measures model. Furthermore, I simulated the same number of traits using the model below:

$$\mathbf{y}_{ij} = \mathbf{b}_{A0_i} + \mathbf{b}_{A1_i}\mathbf{x}_{ij} + \mathbf{b}_{P0_i} + \mathbf{b}_{P1_i}\mathbf{x}_{ij} + \mathbf{e}_{ij}$$

and

$$\text{var}\begin{bmatrix} b_{A0} \\ b_{A1} \\ b_{P0} \\ b_{P1} \\ e \end{bmatrix} = \begin{bmatrix} A\sigma^2_{b0_A} & A\sigma_{b0_A,b1_A} & 0 & 0 & 0 \\ A\sigma_{b0_A,b1_A} & A\sigma^2_{b1_A} & 0 & 0 & 0 \\ 0 & 0 & I_1\sigma^2_{b0_P} & I_1\sigma_{b0_P,b1_P} & 0 \\ 0 & 0 & I_1\sigma_{b0_P,b1_P} & I_1\sigma^2_{b1_P} & 0 \\ 0 & 0 & 0 & 0 & I_2\sigma^2_e \end{bmatrix}$$

where

y_{ij}= phenotype of animal i at record j, b_{A0i} = random additive direct genetic effect of animal i, b_{A1i} = random additive direct genetic effect of animal i's regression coefficient, b_{P0i} = random permanent environmental effect of animal i, b_{P1i} = random permanent environmental effect of animal i's regression coefficient, x_{ij} = age for animal i when record j was observed, e_{ij}= random residual error for animal i's phenotypic observation at record j, σ^2_{b0A}= additive genetic variance of the intercept term, σ^2_{b1A}= additive genetic variance of the linear regression coefficient, $\sigma_{b0A, b1A}$ = additive genetic covariance of the intercept and linear regression coefficient, σ^2_{b0P}= permanent environmental variance of the intercept term, σ^2_{b1P}= permanent environmental variance of the linear regression coefficient, $\sigma_{b0P, b1P}$ = permanent environmental covariance of the intercept and linear regression coefficient, σ^2_e = residul error variance (Kuehn, 2000).

I estimated variance components with several subsets of the 8 record data repeated measures data. Using the simulated data set of 8 records per individual, I removed records to build different data sets with 2, 3, and 5 records per individual. Then

each data set was analyzed using Method R procedures to estimate variance components; however, I treated the inputs into the software as if it was for a random regression model. The coefficient values were loaded as coefficients and not just incidence values of 1's and 0's. I used the repeated measures model to obtain variance component estimates:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_{b0_A}\mathbf{u}_{b0_A} + \mathbf{Z}_{b1_A}\mathbf{u}_{b1_A} + \mathbf{Z}_{b0_P}\mathbf{u}_{b0_P} + \mathbf{Z}_{b1_P}\mathbf{u}_{b1_P} + \mathbf{e}$$

$$\text{var}\begin{bmatrix} \mathbf{u}_{b0_A} \\ \mathbf{u}_{b1_A} \\ \mathbf{u}_{b0_P} \\ \mathbf{u}_{b0_P} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma^2_{b0_A} & \mathbf{A}\sigma_{b0_A,b1_A} & 0 & 0 & 0 \\ \mathbf{A}\sigma_{b0_A,b1_A} & \mathbf{A}\sigma^2_{b1_A} & 0 & 0 & 0 \\ 0 & 0 & \mathbf{I}\sigma^2_{b0_P} & \mathbf{I}\sigma_{b0_P,b1_P} & 0 \\ 0 & 0 & \mathbf{I}\sigma_{b0_P,b1_P} & \mathbf{I}\sigma^2_{b1_P} & 0 \\ 0 & 0 & 0 & 0 & \mathbf{I}\sigma^2_e \end{bmatrix}$$

where

y = vector of mature weight observations, X = incidence matrix of observations related to fixed effect in b, Z_{b0A} = incidence matrix relating random additive direct genetic intercepts to y, Z_{b1A} = matrix of covariates relating random additive direct genetic linear regression coefficient to y, Z_{b0p} = incidence matrix relating random permanent environmental effects for mature weight to y, Z_{b1p} = matrix of covariates relating random permanent environmental linear regression coefficients to y, e = vector of residual error, u_{b0A} = vector of random additive direct genetic effects for each animal, u_{b1A} = vector of random additive direct genetic linear regression coefficients for each animal, u_{b0p} = vector of random additive direct genetic effects for each animal, u_{b1p} = vector of random additive direct genetic linear regression coefficients for each animal.

I listed the following genetic, permanent environment and residual (co)variances used to generate the multivariate data for a random regression model.

$$G = \begin{bmatrix} \sigma^2_{b0_A} & \sigma_{b0_A,b1_A} \\ \sigma_{b0_A,b1_A} & \sigma^2_{b1_A} \end{bmatrix} = \begin{bmatrix} 1429.44 & -35.58 \\ -35.58 & 22.21 \end{bmatrix}$$

$$P = \begin{bmatrix} I\sigma^2_{b0_P} & I\sigma_{b0_P,b1_P} \\ I\sigma_{b0_P,b1_P} & I\sigma^2_{b1_P} \end{bmatrix} = \begin{bmatrix} 514.19 & -12.95 \\ -12.95 & 8.03 \end{bmatrix}$$

$$E = 1645.40$$

For each data set, I obtained estimates of variance components using Method R procedures (Reverter et al., 1994) random 50% subsamples of the data. I generated approximately 15 sets of variance component estimates for each data set. The convergence criteria for the Gauss Seidel rounds was set to 1×10^{-6}.

I used the two previous groups variance component estimates to calculate the median, SD, and 95% CI. I compared the true values for the simulated data to the median value for that variance component to evaluate how well the Method R variance component procedure could estimate the true values for a random regression model. Furthermore, I wanted to determine the number of records to obtain reasonable estimates of variance components for different models.

Mature Weight Random Regression Analysis

Variance components procedures and random regression were applied to Red Angus mature weight data (RAAA, 1998). This analysis was done to determine the

feasibility of estimating variance components from a mature weight field data set and to develop an improved mature weight genetic prediction. In addition, I wanted to compare predictions and subsequent accuracy of the random regression model to those values from a simple repeated measures model.

The first random regression analysis used data from the previous multivariate analyses with mature weight (Table 3.7). However, I reduced the number of herds used to three herds to make the problem more tractable. Among the herds there were 26,709 mature weight observations. After removal for missing contemporary group information, observations, observations from animals greater than 9 yrs of age, empty fixed effects classes, and single animal contemporary groups and contemporary groups with no variation, the data set was reduced to 24,704 weight observations on 10,207 cows. The mean, SD, and range of weights were 474.51 kg, 78.40 kg, and 272.1 to 900.2kg, respectively. The mean and SD of the number of mature weight observations were 2.4 and 1.7, respectively. There was an average 13.2 individuals per contemporary group and 1,874 contemporary groups.

Table 3.7. Age of mature wt, mean weight, SD, and no of obs by age groups for mature weight in Red Angus cattle

Age (yr)	N	Mean (kg)	SD (kg)
2	6,772	406.154	56.879
3	4,816	453.830	60.733
4	3,490	492.304	64.286
5	2,951	514.161	63.941
6	2,256	527.697	61.725
7	1,840	531.875	59.844
8	1,418	537.253	59.726
9	1,161	533.886	58.091

I built a three-generation pedigree for this data that contained 14,775 unique individuals, 1,178 unique sires, and 7,227 unique dams. The pedigree included all animals with an observation plus their parents and grandparents. I assembled all the components for the pedigree and corresponding inverse numerator relationship matrix using the Animal Breeders Tool Kit software (Golden et al., 1992).

Random Regression Models

Random Regression Model 1. I estimated variance components using modified Method R variance components procedures (Reverter et al., 1994) with a univariate random regression model. There were multiple random regression models fit to determine which model provided the best fit.

For the first random regression variance components analysis, I fitted a univariate random regression model with multiple components (Schaeffer, 1999; Kuehn, 2000). This animal model included the following:

$$\mathbf{y} = \mathbf{Xb} + \begin{bmatrix} \mathbf{Z}_{b0} & \mathbf{Z}_{b1} & \mathbf{Z}_{b2} \end{bmatrix} \begin{bmatrix} \mathbf{u}_{b0} \\ \mathbf{u}_{b1} \\ \mathbf{u}_{b2} \end{bmatrix} + \begin{bmatrix} \mathbf{W}_{b0} & \mathbf{W}_{b1} & \mathbf{W}_{b2} \end{bmatrix} \begin{bmatrix} \mathbf{p}_{b0} \\ \mathbf{p}_{b1} \\ \mathbf{p}_{b2} \end{bmatrix} + \mathbf{e}$$

where

y = vector of weight observations for ages 2 to 9 yr. , X = a known coefficient matrix including the incidence of observations in y related to fixed effects in b and covariates of animal age (yr), b = vector of fixed effects including fixed regression for

age (yr), Z_{b0} = incidence matrix 0's and 1's relating random additive direct genetic intercept random regression coefficients to y, Z_{b1} = matrix of covariates relating random additive direct genetic linear random regression coefficients to y, Z_{b2} = matrix of covariates relating random additive direct genetic quadratic random regression coefficients to y, u_{b0} = vector of random additive direct genetic effects for the intercept regression coefficients, u_{b1} = vector of random additive direct genetic effects for linear regression coefficients, u_{b2} = vector of random additive direct genetic effects for quadratic regression coefficients, W_{b0} = incidence matrix of 0's and 1's relating random permanent environmental intercept random regression coefficients to y, W_{b1} = matrix of covariates relating random permanent environmental linear random regression coefficients to y, W_{b2} = matrix of covariates relating random permanent environmental quadratic random regression coefficients to y, p_{b0} = vector of random permanent environmental effects for the intercept regression coefficients, p_{b1} = vector of random permanent environmental effects for the linear regression coefficients, p_{b2} = vector of random permanent environmental effects for the quadratic regression coefficients, e = vector of random residual errors. The model random effects were distributed as follows:

$$\text{var}\begin{bmatrix} u_{b0} \\ u_{b1} \\ u_{b2} \\ p_{b0} \\ p_{b1} \\ p_{b2} \\ e \end{bmatrix} = \begin{bmatrix} A\sigma^2_{b0} & A\sigma_{b0,b1} & A\sigma_{b0,b2} & 0 & 0 & 0 & 0 \\ A\sigma_{b0,b1} & A\sigma^2_{b1} & A\sigma_{b1,b2} & 0 & 0 & 0 & 0 \\ A\sigma_{b0,b2} & A\sigma_{b1,b2} & A\sigma^2_{b2} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & I_1\sigma^2_{b0} & I_1\sigma_{b0,b1} & I_1\sigma_{b0,b2} & 0 \\ 0 & 0 & 0 & I_1\sigma_{b0,b1} & I_1\sigma^2_{b1} & I_1\sigma_{b1,b2} & 0 \\ 0 & 0 & 0 & I_1\sigma_{b0,b2} & I_1\sigma_{b1,b2} & I_1\sigma^2_{b2} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & I_2\sigma^2_e \end{bmatrix}$$

I_1 = identity matrix with the order equal to the number of unique animals with observations, I_2 = identity matrix of the order equal to the number of observations, σ^2_{b0}= additive direct genetic variance of the intercept random regression coefficients, σ^2_{b1}= additive direct genetic variance of the linear random regression coefficients, σ^2_{b2}= additive direct genetic variance of the quadratic random regression coefficients, $\sigma_{b0,b1}$= the additive direct genetic covariance between the intercept random regression coefficients and the linear regression coefficients, $\sigma_{b0,b2}$= the additive direct genetic covariance between the intercept random regression coefficients and the quadratic regression coefficients, $\sigma_{b1,b2}$= the additive direct genetic covariance between the linear random regression coefficients and the quadratic regression coefficients, σ^2_{b0}= permanent environmental variance of the intercept random regression coefficients, σ^2_{b1}= permanent environmental variance of the linear random regression coefficients, σ^2_{b2}= permanent environmental variance of the quadratic random regression coefficients, $\sigma_{b0,b1}$= the permanent environmental covariance between the intercept random regression coefficients and the linear regression coefficients, $\sigma_{b0,b2}$= the permanent environmental covariance between the intercept random regression coefficients and the quadratic regression coefficients, $\sigma_{b1,b2}$= the permanent environmental covariance between the linear random regression coefficients and the quadratic regression coefficients, and σ^2_e = residual error variance (Schaeffer, 1999; Kuehn, 2000).

The random regression model included fixed effects of mature weight contemporary group, fixed linear and quadratic age covariates, and an interaction between the cow's age of dam (AOD = 2, 3, 4, 5 to 9, 10, 11, 12, 13+ yr of age)(BIF, 1996) and age of cow (yr). Random effects included additive direct genetic effects of

animal for the intercept, linear, and quadratic random regression coefficients (2nd order polynomial), permanent environmental effects for the intercept, linear, and quadratic random regression coefficients and residual error.

In a second analysis, I reduced the model order for both the additive genetic and permanent environment components to intercept and linear terms. This reduction in parameters was done because of the estimates from the previous model would not remain in the parameter space. This reduced order fit should improve the computationally feasibility and overcome problems with estimation of variance components. The model was as follows:

$$\mathbf{y} = \mathbf{Xb} + \begin{bmatrix} \mathbf{Z}_{b0} & \mathbf{Z}_{b1} \end{bmatrix} \begin{bmatrix} \mathbf{u}_{b0} \\ \mathbf{u}_{b1} \end{bmatrix} + \begin{bmatrix} \mathbf{W}_{b0} & \mathbf{W}_{b1} \end{bmatrix} \begin{bmatrix} \mathbf{p}_{b0} \\ \mathbf{p}_{b1} \end{bmatrix} + \mathbf{e}$$

where

$$\text{var}\begin{bmatrix} \mathbf{u}_{b0} \\ \mathbf{u}_{b1} \\ \mathbf{p}_{b0} \\ \mathbf{p}_{b1} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma^2_{b0} & \mathbf{A}\sigma_{b0,b1} & 0 & 0 & 0 \\ \mathbf{A}\sigma_{b0,b1} & \mathbf{A}\sigma^2_{b0} & 0 & 0 & 0 \\ 0 & 0 & \mathbf{I}_1\sigma^2_{b0} & \mathbf{I}\sigma_{b0,b1} & 0 \\ 0 & 0 & \mathbf{I}\sigma_{b0,b1} & \mathbf{I}_1\sigma^2_{b1} & 0 \\ 0 & 0 & 0 & 0 & \mathbf{I}_2\sigma^2_e \end{bmatrix}$$

The reduced order random regression model included the same fixed effects as the previous model with the fixed age regression reduced to a linear function. The random additive direct genetic and permanent environmental effects were reduced to intercept and linear terms.

In the first random regression analysis, results indicated that the data structure was insufficient to model polynomials higher than a linear function for both genetic and

permanent environmental effects. The number of individuals with 1, 2, 3, 4, 5, 6, 7, and 8 observations were 4197 (41.1%), 2459 (24.1%), 1284 (12.8%), 855(8.3%), 600(5.9%), 463 (4.5%), 253 (2.5%), 96 (.94%). So, I compiled a data set with more observations per animal to overcome previous problems with overfitting the model (B.L. Golden, personal communication).

The first random regression data set had approximately 2.4 observations per animal prior to data removal. Because the number of observations were limited, it was necessary to increase the number of observations per animal to fit higher order polynomials. This meant changing the data structure to increase the average number of observations per animal without introducing additional bias or reducing the size of the pedigree.

Before I removed any data, I grouped together mature weight observations of animals that were 7 yr of age and older. This decision was made using previous research (Johnson et al., 1990) and estimates of the fixed effects for cow age. I estimated fixed effect solutions for age of cow with a simple repeated measure model as described in previous analyses. Then I generated fixed effects solutions for age of cow and evaluated the magnitude of the solutions. Animals that were 7 years of age and older were grouped into the age 7 category. A problem was created from grouping the animals because some individuals had observations past 7 yr of age. Therefore, I only kept observations closest to 7 yr of age and removed all others from the analysis. This prevented an animal from having more than one observation at 7 yr of age. The removal of redundant records past 7 yr of age reduced the number of mature weight observations per animal to an average of 2.23 observations per individual.

Several methods were used to increase the number of observations per animal. These included: removing animals in contemporary groups with a small number of observations, eliminating animals with less than two observations per animal, and the removal of small contemporary groups. The removal of contemporary groups containing animals with low numbers of observations appeared to be the best method for increasing the average number of observations per animal. This modification reduced the data set size to 18,134 records.

Using the reduced data set, I selected the Beckton Stock farms and Schuler herds, based upon the average number of observations per animal and knowledge of their performance recording programs. The average observations per animal for the Beckton and Schuler herds were 2.53 and 2.81, respectively. The two herds represented 15,095 observations from contemporary groups with variation. The observations were taken on 5,871 dams with 2.54 observations per animal. For the reduced data set, the pedigree included 8,446 animals, 757 known sires, and 4,591 known dams.

The same group of random regression models previously applied to the larger mature weight data set was used to estimate variance components. The new variance component estimates should reflect the changes made to the data and the consolidation of animals of age 7, 8, and 9 yr.

Random Regression Model 2. In a second set of analyses, I analyzed Red Angus mature weight with a different random regression model. After the first analysis, I decided to change the model effects to overcome problems with fitting higher order polynomials. For this set of analyses, I began with the linear model because variance

components estimates were obtainable. If I was successful then higher order polynomial functions would be attempted.

The first model I fitted had fixed effects contemporary group, cow's age of dam (BIF, 1996), and age as a linear covariate. Because age of cow as a class effect did not work with the assumptions that weight changed linearly with age, I removed it from the model fixed effects. Random effects included additive direct genetic effects of animal for both the intercept and linear regression coefficients, permanent environmental effects of the same order as the genetic, and residual error.

Prior to the random regression variance components analysis, I performed some preliminary fixed effects tests. Specifically, I tested a subclass regression of cow age with age of the cow's dam to see if important effects were present.

For this analysis, fixed effects included mature weight contemporary group, age of the cow's dam, and cow age as a covariate. Age as a covariate replaced the class effect of age of cow (Meyer, 1999). The covariate of age and the interaction between the age (covariate) and age of cow's dam were tested before estimation of variance components. Instead of analyzing fixed effects with a random regression model, I applied a repeated measures animal model to test age as a covariate and the subclass regression of age within age of dam. Additionally, the likelihood ratio test used included random effects and required estimates of fixed effects. Therefore, I used a simple repeated measures model because I already had realistic variance component estimates available from previous analyses.

The procedures for testing fixed effects (Boik et al., 1993) required both fixed and random effect solutions from both a full and reduced model. I fitted a full model that

included fixed effects of mature weight contemporary group, age as a covariate, age of the cow's dam, and a subclass regression of age within age of the cow's dam. Random effects included additive direct effect of animal, a permanent environmental effect of animal, and residual error. I used variance component estimates that were equivalent to a median heritability of .53 and the proportion of variance due to permanent environment equaled .25. I obtained these variance components from an earlier repeated measures analysis. Using the procedure for reduction sums of squares, I tested both the interaction between age (covariate) and age of cow's dam and age as a covariate for statistical importance.

The importance of fixed effects was evaluated using procedures described by Boik et al. (1993), changes in MSE, and estimates of fixed effects solutions and corresponding SE. I did not use an F-test to determine importance of model fixed effects because previous experience showed that the test would consider an effect with a small impact to be significant.

I fitted a second random regression model because parameter estimates would not remain in the parameter space for the previous model that included linear polynomials for both genetic and permanent environment effects. The only modification I made to the model was to reduce the order of fit for the permanent environmental effects. Variance components were estimated with this modified random regression model.

Orthogonalization. Orthogonal polynomials can be used in place of ordinary polynomials in models to uncorrelate regression coefficients. I applied Legendre polynomials to this analysis to transform ordinary age polynomials to orthogonal polynomials. Legendre polynomials were selected because of previous application in

other studies (Kirkpatrick et al., 1990; Meyer et al., 1997). The Legendre polynomial transformation accepts standard age values on a scale of −1 to +1, so ages in years were transformed to a −1 to +1 scale. I standardized ages for both the larger data set and reduced data sets; however, the larger data set included ages from 2 to 9 yr of age while the smaller data set age range was 2 to 7 yr of age. The following formula was applied to standardize age in years to a scale of −1 to +1 (Kirkpatrick et al., 1990; Schaeffer, 1999):

$$st_i = -1 + 2\left[\frac{t_i - t_{min}}{t_{max} - t_{min}}\right]$$

where

st_i = standardized time numbers between −1 to +1, t_i = standardized variable, t_{min} = minimum time value observed in the data, and t_{max} = maximum time value in the data. Standardized ages were transformed to orthogonal polynomials using the following equations (Schaeffer, 1999):

$$P_0(x) = 1$$
$$P_1(x) = x$$
$$P_{n+1}(x) = \frac{1}{n+1}\left((2n+1)xP_n(x) - nP_{n-1}(x)\right)$$

After I calculated the Legendre polynomials, I normalized each term using the following formula:

$$\varphi_n(x) = \left(\frac{2n+1}{2}\right)^{.5} P_n(x)$$

For this analysis, I applied the following equations to determine the first three Legendre polynomial functions:

$\varphi_0(x) = .7071$ (Intercept), $\varphi_1(x) = 1.2247x$ (Linear), $\varphi_2(x) = -.7906 + 2.3717x^2$ (Quadratic)

I used the following equations to confirm that a pair of functions were orthogonal to each other (Kirkpatrick et al., 1990)

$$\int_u^v \phi_i(x)\phi_j(x)dx = 0 \text{ and } \int_u^v \phi_i^2(x)dx = 1$$

where the interval [u,v] = -1 to +1. If the correlation between orthogonal coefficients was zero then the polynomials were orthogonal.

The previously described procedures were applied to ages for mature weight to transform polynomials with ordinary age to orthogonal polynomials. However, I obtained negative residual error variance component estimates and results of the analysis would not stay in the parameter space. I attempted to resolve the problem by fitting standardized ages in the analysis and the result was similar. Because I was only fitting a linear regression, I decided to use ordinary age. However, this analytical problem should be resolved for future analyses to overcome problems with highly correlated polynomial terms.

Repeated Measures Model

I estimated variance components using Method R procedures (Reverter et al., 1994) with a repeated measures model and the current cow weight data with ages 2 to 7 yr. There were multiple models fit with the difference being how the fixed effects were modeled. The estimates of variance components were used to predict breeding values from the reduced data set. The general model for all variance component estimates was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_a\mathbf{u}_a + \mathbf{Z}_p\mathbf{c}_p + \mathbf{e},$$

where

$$E[\mathbf{y}] = \mathbf{Xb}$$

$$\text{var}\begin{bmatrix}\mathbf{u}\\ \mathbf{c}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{A}\sigma_a^2 & 0 & 0\\ 0 & \mathbf{I}\sigma_p^2 & 0\\ 0 & 0 & \mathbf{I}\sigma_e^2\end{bmatrix}$$

y = vector of repeated phenotypic observations on cow weight, X = known incidence matrix of observations related to fixed effects in b, b = vector of fixed effects related to the trait, Z_a= incidence matrix relating random additive direct genetic effects to y, u_a= vector of random additive direct genetic effects for the trait, Z_p= incidence matrix relating random permanent environmental effects to y, c_p= vector of random permanent environmental effects, e = vector of random residual error, A = Wright's numerator relationship matrix, I = identity matrix, σ_a^2 = additive direct genetic variance, σ_p^2 = permanent environmental error variance , σ_e^2 = residual error variance.

The repeated measures animal model for mature weight included fixed effects of mature weight contemporary group, age of the cow's dam, and age of cow (yr). Age of the animal was fit either in classes (ages 2 to 7 yr of age), or as a fixed regression (covariate). In a previous analysis, I fitted an interaction between age of the cow's dam and age of cow to account for both the main effects and any subsequent interactions. However, additional evaluation and testing showed that the interaction was not necessary; therefore, I only included the main effects of age and cow's dam age in the final model.

Random effects included random additive direct genetic effects for animal, random permanent environmental effect of animal, and residual error.

For the random regression and repeated measures analyses, I reported medians, 95% CI, and SEM for both variance component and heritability estimates. I used the median instead of the mean to report estimates because current research has shown that Method R estimates are unbiased when the median is used (Mahabir, 1999).

Heterogeneous Variation

Past literature and results of the multivariate analysis report that variances for mature weight will scale with age as animals mature. Because scaling residual variance was present in Red Angus mature weight, I implemented a multiplicative mixed model to correct for it. But, the current version of the Method R variance component software assumes residual variances are homogeneous within trait. I circumvented this problem by using a method that would adjust for heterogeneous variance after I obtained variance component estimates.

For the both the repeated measures and random regression analyses, I adjusted for heterogeneous variance using a multiplicative mixed model to account for the across age heterogeneous variation (Kachman et al., 1993; Reverter et al., 1997). This procedure appeared to be appropriate for this problem and has been implemented previously in large field data sets for dairy and beef cattle.

Reverter et al. (1997) developed a C-programmed tool, 'hetero', to implement the multiplicative mixed model procedures (Kachman et al., 1993). This program included functions for a Gauss-Seidel iteration, updating of the fixed and random effects solutions,

and updating of the vector of age effects and scaling factors. It required constructing both the coefficient and right hand side of the mixed model equations in addition to providing the residual variance, a vector of phenotypes, plus a vector and unique list of age effects. The data vector of ages held the different levels of heterogeneity and the list contained the unique levels. It was not required to have the data vector represented as a fixed effect in the model (A. Reverter, personal communication).

Using the procedures described previously, I modeled age effects with a multiplicative mixed model for repeated measures (Kachman and Everett, 1993). I modeled records for age i as:

$$\mathbf{y}_i = (\mathbf{X}_i\mathbf{b} + \mathbf{Z}_i\mathbf{u} + \mathbf{W}_i\mathbf{c} + \mathbf{e}_i)\boldsymbol{\lambda}_i$$

where

X = incidence matrix of observations in y_i related to fixed effects in b, b = vector of fixed effects, Z_i = incidence matrix relating observations in y_i to random additive genetic effects in u, u = vector of random additive genetic effects, W_i = incidence matrix relating random permanent environmental effects to y_i, c= vector of random permanent environmental effects, e_i = vector of random residual error, λ_i = scaling factor for age **i**.

I used procedures described by Reverter et al. (1997) to calculate and update multiplicative adjustment factors between rounds. Multiplicative adjustment factors were calculated for the m^{th} iteration using

$$\boldsymbol{\lambda}^{[m]} = \exp\left(\frac{\boldsymbol{\beta}^{[m]}}{2}\right),$$

where

β= vector of unknown age effects. Then a Fisher scoring algorithm was used:

$$\mathbf{W}^m\boldsymbol{\beta}^{m+1} = \mathbf{W}^m\boldsymbol{\beta}^m + \mathbf{z}^m,$$

for the (m+1) iteration. The z_i elements are updated during the iterations as

$$z^m{}_i = \frac{1}{2}\left(\frac{y_i^{m'} y_i^m - y_i^{m'} \hat{y}_i^m}{\sigma_e^2} - n_i \right) \text{ and } \mathbf{W}^m = \mathbf{diag}(\mathbf{Var}(z_i^m))$$

where

$$\mathbf{Var}(z_i^m) = \frac{1}{4}\left(\frac{\hat{y}_i^{m'} \hat{y}_i^m}{\sigma_e^2}\right) + \frac{1}{2} n_i \quad ,$$

and n_i = the number of records in the age category i. Initially, the values of predictions for y_i were obtained from solving the following mixed model equations:

$$\begin{bmatrix} X'X & X'Z & X'W \\ Z'X & Z'Z + \frac{\sigma_e^2}{\sigma_u^2} A^{-1} & Z'W \\ W'X & W'Z & W'W + \frac{\sigma_e^2}{\sigma_c^2} A^{-1} \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{u} \\ \hat{c} \end{bmatrix} = \begin{bmatrix} X'y_s \\ Z'y_s \\ W'y_s \end{bmatrix}$$

where

y_s = vector of scaled observations calculated as $y_s = y/\lambda_i$ for each age and A^{-1} = Wright's inverse numerator relationship matrix. I used the same procedures described by Reverter et al. (1997) to do the following: obtain median estimates of variance components for

mature weight using repeated measures model; solve the estimated breeding values (EBV) using BLUP and the estimates of variance components; and submit this information to the 'hetero' tool to calculate scaled observations and scaling factors for each age class. According to Reverter et al. (1997), the procedures called for doing one round of Gauss Seidel iteration to update the solutions vector, then updating both β and λ from equations represented above, and testing the convergence of λ. If lambda converged within the specified criteria of $1x\ 10^{-6}$, then the software would output scaled observations and scaling factors. I used the scaled data with the previous fixed and random effects and original variance components to generate EBV that were adjusted for heterogeneous residual variance. If the convergence criterion was not met, then iteration continued until convergence was met or the procedure generated 10,000 rounds of iteration.

After the EBV were adjusted for heterogeneous variation, I performed several tests to confirm that heterogeneous variation was removed. First, I evaluated the change in scaling factors and lambda values that were generated both before and after adjusting the data. Second, I applied Levene's test for homeogeniety of variance (Snedecor and Cochran, 1989) to both scaled and unscaled mature weight data after pre-adjusting for fixed effects. I used the Levene's test because it was considered a more robust test and less sensitive to deviations from normality compared to Bartlett's or Hartley's test for homogeneous variance (Reverter et al., 1997).

The scaled data for mature weight were used to re-estimate variance components with a repeated measures model. These new estimates should have reflected the changes due to adjustments for heterogeneous residual variance and the changes in accuracy of

prediction. According to A. Reverter (personal communication), it is not necessary to re-estimate variance components and recalculate the scaling factors. However, it provides an indicator of the expected gain in accuracy due to correction for scaling measurement error variance.

Several comparisons were made between analyses that included and did not include the multiplicative scaling techniques to determine its effectiveness. This was done for both the repeated and random regression analyses. The comparisons included correlations between breeding values both before and after data were scaled, a coefficient of determination (R^2), and evaluation of the magnitude of both the scaling factors and change in mature weight observations.

In a preliminary analysis, I wanted to compare the importance of using random regression models relative to the repeated measures model with data that were unscaled for heterogeneous variation. The comparisons included calculation of eigenvalues for both the genetic and permanent environmental variance matrices, calculation of R^2, determination of the change in mean square error between models, and calculation of the correlations between breeding values at different ages.

Random Regression and Repeated Measures Models

I compared the repeated measures model to the proposed model for random regression to evaluate the differences in accuracy and correlations between breeding values from each model. The comparison I made here differed from what I had previously done because I generated predictions for all the data in the Red Angus breed. I obtained all the mature weight data before any records were eliminated for different

criteria. The data were prepared with similar criteria to previous analyses, but I grouped together animals that were 7 years and older and did not remove animals by contemporary group based upon their average number of observations.

Using all data, I obtained 82,278 mature weight records of all the data from the previous multivariate mature weight analyses prior to sampling the data by breeder. I removed an additional 2,521 cows that were 10 yr of age and older, and 2,115 with missing age of dam codes, which reduced the number of observations to 71,127. Because data were consolidated for individuals over 7 yr of age, observations were removed on animals with more than one age 7 yr observation and kept the observation closest to age 7yr (4,495 observations). After data removal for no variation and single animal contemporary groups (2,080 observations), I reduced the total to 64,102 weight observations. This set of data contained 2, 3, 4, 5, 6, 7 and older animals that accounted for 23.7%, 19.7%, 16.9%, 13.7%, 11.1%, and 13.3%, respectively. Animals 2, 3, and 4 yr. of age represented 60% of all the data. There were 33,378 animals with observations and an average of 1.92 observations per animal (Table 3.8).

Table 3.8. Descriptive statistics of all usable mature weight data in the Red Angus breed by age of the animal (yr)

Age, yr	N	Mean, kg	SD, kg	Min/Max, kg
All individuals	64,102	492.62	84.52	272.11 to 900.23
Age Groups				
2	15,483	432.76	67.31	272.11 to 759.64
3	12,820	474.82	73.11	274.28 to 759.64
4	10,982	507.15	77.44	281.63 to 900.23
5	8,932	525.26	78.76	297.05 to 893.42
6	7,228	535.02	77.38	301.59 to 863.95
7	8,657	538.55	77.59	292.06 to 860.77

Pedigree. For the analysis using all the data, I generated a new three-generation pedigree. The number of individuals, unique sires, and unique dams consisted of 56,582 individual animals, 5,912 unique sires, and 31,131 unique dams. From this pedigree, I calculated inbreeding coefficients and Wright's inverse numerator relationship matrix.

I generated breeding values using BLUP (Henderson, 1984) procedures and a random regression animal model. The model included fixed effects of mature weight contemporary group, age of the cow's dam, and age of cow in years as a covariate. Random effects included random additive genetic effects of animal for the intercept and linear coefficients of age, permanent environment effects for the intercept and linear coefficient of age, and residual error. The variance components used to generate predictions for mature weight were obtained using estimates from the repeated measures analysis. Because previous mature weight variance components estimates were inflated, I decided to use previously estimated variance component estimates from the repeated measures model and partition them according to estimates in the literature (Meyer, 1999).

$$\mathbf{y} = \mathbf{Xb} + \begin{bmatrix}\mathbf{Z}_{b0}\mathbf{Z}_{b1}\end{bmatrix}\begin{bmatrix}\mathbf{u}_{b0}\\ \mathbf{u}_{b1}\end{bmatrix} + \begin{bmatrix}\mathbf{W}_{b0}\mathbf{W}_{b1}\end{bmatrix}\begin{bmatrix}\mathbf{p}_{b0}\\ \mathbf{p}_{b1}\end{bmatrix} + \mathbf{e}$$

and

$$\text{var}\begin{bmatrix}\mathbf{u}_{b0}\\ \mathbf{u}_{b1}\\ \mathbf{p}_{b0}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma^2_{b0} & \mathbf{A}\sigma_{b0,b1} & 0 & 0 & 0\\ \mathbf{A}\sigma_{b0,b1} & \mathbf{A}\sigma^2_{b0} & 0 & 0 & 0\\ 0 & 0 & \mathbf{I}_1\sigma^2_{b0} & \mathbf{I}_1\sigma_{b0,b1} & 0\\ 0 & 0 & \mathbf{I}_1\sigma_{b0,b1} & \mathbf{I}_1\sigma^2_{b1} & 0\\ 0 & 0 & 0 & 0 & \mathbf{I}_2\sigma^2_e \end{bmatrix}$$

Expected Progeny Differences. Estimated breeding values were produced for both the intercept and linear coefficients of the random regression model on all animals and were divided in half to convert them to expected progeny differences (EPD). Because random regression creates a function with respect to age, I summed the random regression intercept breeding value with the linear coefficient breeding value and expressed the mature weight EPD at 5 yr of age.

Genetic and Environmental Trends. I plotted genetic trends for mature weight by taking the average EBV by birth year for all animals. For the environmental trend, I calculated the average contemporary group solution for the year that the contemporary group represented. I used year the contemporary group was represented because animals of different ages were in the same contemporary group. This meant that the environmental trend for animals was shifted forward relative to the genetic trend.

Accuracy Values. Both the BIF (1996) and regular accuracy values from the simple repeated measures model and those from the random regression model were deterimed. The prediction error variances and covariances for calculating accuracy values were obtained for the intercept and linear terms from respective diagonal elements of the inverse coefficient matrix. I obtained the inverse and the diagonal elements using an ABTK (Golden et al., 1992) tool named 'tinv' that takes a direct inverse of the coefficient matrix.

I calculated BIF (1996) and regular accuracy after I obtained prediction error variances, inbreeding coefficients, and necessary variance components estimates of animals at 5 yr of age. The equations for calculating accuracy values are listed below.

Accuracy:

$$\mathbf{Acc}_i = \left(1 - \frac{\mathbf{PEV}_i}{\sigma_a^2(1+F_i)}\right)^{.5}$$

BIF Accuracy:

$$\mathbf{Acc\_BIF}_i = 1 - \left(\frac{\mathbf{PEV}_i}{\sigma_a^2(1+F_i)}\right)^{.5}$$

where

Acc_i = animal I's accuracy of prediction, Acc_BIF_i = animal I's BIF accuracy of prediction, PEV_i = prediction error variance for animal i, σ^2_a = the additive genetic variance of the trait, F_i = coefficient of inbreeding for animal i.

The functions listed below were used to calculate accuracy at a specific age (5 yr). Both equations were modified to account for age of prediction of animal using a linear random regression function.

Regular Accuracy:

$$\mathbf{Acc}_i(a_j) = \left(1 - \frac{\mathbf{PEV}_i(a_j)}{\sigma_a^2(a_j)(1+F_i)}\right)^{.5}$$

BIF (1996) Accuracy:

$$\mathbf{Acc\_BIF_i(a_j) = 1 - \left(\frac{PEV_i(a_j)}{\sigma^2_a(a_j)(1+F_i)} \right)^{.5}}$$

where

$Acc_i(a_j)$ = accuracy of animal i's prediction at age a_j, $Acc\_BIF_i(a_j)$ = accuracy of animal i's prediction at age a_j, $PEV_i(a_j)$ = prediction error variance for animal i's mature weight prediction at age a_j , $\sigma^2_a(a_j)$ = additive genetic variance at age a_j for mature weight, F_i = animal i's inbreeding coefficient. I calculated the prediction error variance at age a_j (e.g., age 5 yr) using:

$$\mathbf{PEV_i(a_j) = PEV_i(b_{0_i}) + a_j^2 PEV(b_{1_i}) + 2a_j PECOV_i(b_{0_i}, b_{1_i})}$$

where

$PEV_i(bo_i)$= prediction error variance of the intercept for animal i, $PEV(b_{1i})$= animal i's prediction error variance of the linear regression coefficient, $PECOV_i(bo_i, b_{1i})$= prediction error covariance between the intercept and linear regression coefficient for animal i.

In addition to calculating the prediction error variance, I calculated the genetic variance at 5 yr of age to used in determining accuracy values. This next equation was used to obtain genetic variation for animals at age a_j.

$$\mathbf{\sigma^2_a(a_j) = \sigma^2_{b0_a} + a_j^2 \sigma^2_{b1_a} + 2a_j \sigma_{b1_a, b0_a}}$$

where

$\sigma^2_a(a_j)$ = the additive genetic variance at age a_j, a_j = age of mature weight observation, σ^2_{b0a} = additive genetic variance of the intercept, σ^2_{b1a} = additive genetic variance of the

linear coefficient, $\sigma_{b1_a, b0_a}$ = additive genetic covariance between the intercept and linear regression coefficient (Schaeffer 1999; Kuehn, 2000).

The size of the linear system combined with computer resources and software made it impossible to obtain prediction error variances and calculate accuracy values. Taking a direct inverse of the coefficient matrix was not possible because of the size of the linear system and computer memory required for the job. The matrix dimensions were 155,147 rows, 155,147 columns, and 2,393,055 non-zero elements with all the data. There was not enough memory available for the needs of the task; therefore, I reduced the number of equations by including just contemporary group as a fixed effect. This had no effect on my ability to obtain prediction error variances.

Data Reduction. Given the size of the linear system for the random regression, it was not feasible to invert the coefficient matrix. This problem was still present after the size of the data set was reduced by 50%. The goal was to compare two models, the random regression and repeated measures, for predicting mature weight. I decided that a small sample of mature weight data would make this comparison between models (B. L. Golden, personal communication). A sample of the data made the comparisons between models tractable and accuracy values could be obtained with a direct inverse of the coefficient matrix to obtain prediction error variances.

I constructed a smaller set of data to compare predictions from the random regression model and simple repeated measures model. I selected three herds from the larger set of data to make this comparison, which represented Beckton Stock Farms, Buffalo Creek Red Angus, and Schuler Red Angus. This set of data was similar to the one used for the analysis of mature weight and post-weaning gain. The reduced data set

included 22,792 mature weight observations on 10,191 unique cows with an average of 2.24 mature weight observations per cow. The average, SD, and range of weights across all ages 2 to 7 years were 469.75 kg, 78.03 kg, and 272.11kg to 900.23 kg, respectively. The reduced data set pedigree included 14,458 unique individuals, 1,176 unique sires, and 7,843 dams.

Breeding values and accuracy values were generated in the same format as described earlier, only these values were generated with a reduced data set. Therefore, the same models and variance components were implemented to obtain EBV and corresponding accuracy values. For calculating accuracies, I included only contemporary group as a fixed effect to remove any potential problems with taking a direct inverse of the coefficient matrix.

I compared both the random regression and repeated measures model using accuracy values, I calculated the average overall accuracy, accuracy of sires, and accuracy of low accuracy animals from both the repeated measures model and random regression model. Additionally, I correlated the mature weight breeding values at ages 2 to 7 yr using the random regression model intercept and linear term breeding values with breeding values from the repeated measures model.

Multivariate Analysis with Weaning Weight and Post Weaning Gain

Mature weight data were merged with immature weight data to estimate the additive genetic relationship between weaning weight and postweaning gain. However, I did not analyze all ages of cow weight with either weaning weight or postweaning gain

because of the high additive genetic relationship present between traits reported in the multivariate analyses.

Data Description. The RAAA submitted 546,780 weaning weight and 215,132 yearling weight records for the analysis of weaning weight and postweaning gain with mature weight. I standardized actual weaning weights to 205 d of age and adjusted for age of dam and a sex by age of dam interaction (Golden et al., 1994). To form postweaning gain observations, I calculated the difference between yearling weight and weaning weight observations and then standardized each weight observation to 160 d (BIF, 1996). Editing of adjusted weaning weight data removed records involving multiple births, foster dams, ages outside the range of 160 to 250 d, less than 50% Red Angus breeding, or with missing weaning weight contemporary group information. I removed postweaning gain records of individuals that were missing contemporary group information, had invalid weaning weight contemporary groups, or were outside an age range of 320 to 410 d (BIF, 1996). Data editing reduced the number of weaning weight and postweaning gain observations to 385,597, and 173,466, respectively. There was no additional data preparation for mature weight because I used a previously prepared set of mature weight data.

Using information supplied by the RAAA (RAAA, 1998), I formed contemporary groups for weaning weight and postweaning gain. Weaning contemporary group included weaning workgroup, weigh date, calf sex, breeder management code, and birth contemporary group. Birth contemporary group consisted of birth workgroup, calf sex, breeder management code, and percentage Red Angus. I assigned animals greater than 87.5% Red Angus to one contemporary group and I grouped those with 50% to 87.5%

Red Angus breeding into another contemporary group. I formed postweaning gain contemporary groups using yearling workgroup, yearling weigh date, calf sex, breeder management code, and weaning contemporary group.

For variance components analyses, I selected three highly reported herds located in Nebraska and Wyoming. The herds had multiple years of mature weight data, a large number of mature weight records, and reputable data recording systems. In addition, I limited the weaning weight and postweaning gain data to years 1984 to 1998 to make the variance components analysis more tractable (Tables 3.9 to 3.11).

Table 3.9. Descriptive statistics of phenotypic performance and contemporary group (CG) information for the traits of weaning weight (WW) and mature weight (MW) at 2, 3, and 4 to 9 yr of age in Red Angus cattle

		MW		
	WW	2 yr	3 yr	4-9yrs
N[1]	22,651	6,874	4,634	13,295
Mean (kg)	233.58	406.33	454.00	517.67
SD (kg)	30.23	56.66	60.82	64.32
Range (kg)	102.49 to 348.30	272.11 to 673.47	280.27 to 730.16	299.54 to 902.27
No. of CG	1,021	580	550	1,108
Mean CG size	22.2	11.9	8.4	12.0
SD of CG size	28.4	15.7	9.1	16.6

[1]N = number of observations

Table 3.10. Number of animals per analysis with both mature weight (MW) and weaning weight (WW) observations and pedigree structure for multivariate analyses of 2yr (2-WW), 3yr (3-WW), 4 to 9 yr old (4-9.WW) MW with WW

	2-WW	3-WW	4 to 9-WW
No. of individuals with WW and MW observations	3,756	2,389	2,099
No. of Individuals	22,651	31,070	31,930
No. of Sires	1,260	1,304	1,367
No. of dams	11,712	2,389	12,312

Table 3.11. Descriptive statistics of the phenotypic performance and contemporary group information on post weaning gain (PW) and cow weight (MW) at 2, 4, 6, and 8 yr of age among data analyzed in Red Angus cattle

		MW				
	PW	2 yr	4 yr	6 yr	8 yr	2 to 9 yr
N[1]	19,180	6,874	3,295	2,022	1,264	24,704
Mean (kg)	149.95	406.33	492.78	529.31	537.85	474.51
SD (kg)	63.73	56.66	64.08	61.98	59.76	78.40
Range (kg)	1.81 to 396.83	272.10 to 900.23	298.87 to 900.23	337.87 to 783.22	378.68 to 764.17	272.10 to 900.20
No. of contemporary groups (CG)	1,016	580	484	373	296	1,874
Avg. CG size	18.88	11.85	6.81	5.42	4.30	13.25
SD of CG size	27.70	15.78	6.30	4.20	2.98	18.85

[1]N = number of observations

Table 3.12. Number of observations per analysis and pedigree structure per analysis for multivariate analyses of 2yr (2-PW), 4yr (4-PW), 6yr, 8yr, 2 to 9 yr old (2 to 9-PW) weight (MW) with post weaning gain (PW) in Red Angus cattle

	2-PW	4-PW	6-PW	8-PW	2 to 9-PW
No. of individuals with PW and MW observations	3,467	1,331	603	218	4,441
No. of Individuals	27,861	27,233	26,913	26,607	29,804
No. of Sires	1,163	1,190	1,156	1,141	1,318
No. of dams	10,707	10,579	10,447	10,240	11,772

Statistical Procedures. I estimated variance components using Method R procedures (Reverter et al., 1994) and multivariate animal models (Henderson et al., 1976; 1984). Estimates from each analysis were obtained from 20 to 35 random 50% subsamples of the data. I initially estimated (co)variance components between weaning weight and cow weight at 2 yr (MW_2) and 3 yr (MW_3) of age using the following multivariate animal model:

$$\begin{bmatrix} \mathbf{y}_{MW_2(MW_3)} \\ \mathbf{y}_{WW} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{MW_2(MW_3)} & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_{WW} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{MW_2(MW_3)} \\ \mathbf{b}_{WW} \end{bmatrix} +$$

$$\begin{bmatrix} \mathbf{Z}_{MW_2(MW_3)} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_{WWd} & \mathbf{Z}_{WWm} \end{bmatrix} \begin{bmatrix} \mathbf{u}_{MW_2(MW_3)} \\ \mathbf{u}_{WWd} \\ \mathbf{u}_{WWm} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{MW_2(MW_3)} \\ \mathbf{e}_{WW} \end{bmatrix}$$

where

$$\mathrm{Var}\begin{bmatrix} u_{MW_2(MW_3)} \\ u_{WWd} \\ u_{WWm} \end{bmatrix} = \begin{bmatrix} A\sigma^2_{MW_2(MW_3)} & A\sigma_{MW_2(MW_3)\cdot WWd} & A\sigma_{MW_2(MW_3)\cdot WWm} \\ A\sigma_{MW_2(MW_3)\cdot WWd} & A\sigma^2_{WWd} & A\sigma_{WWd\cdot WWm} \\ A\sigma_{MW_2(MW_3)\cdot WWm} & A\sigma_{WWd\cdot WWm} & A\sigma^2_{WWm} \end{bmatrix}$$

$$\mathrm{Var}\begin{bmatrix} e_{MW_2(MW_3)} \\ e_{WW} \end{bmatrix} = \begin{bmatrix} I\sigma^2_{e_{MW_2(MW_3)}} & I\sigma_{e_{MW_2(MW_3)}\cdot e_{WW}} \\ I\sigma_{e_{MW_2(MW_3)}\cdot e_{WW}} & I\sigma^2_{e_{WW}} \end{bmatrix}$$

$y_{MW2(MW3)}$ = vector of phenotypic observations on $MW_2(MW_3)$, y_{WW} = vector of phenotypic observations on weaning weight, $X_{MW2(MW3)}$ = known incidence matrix of observations on $MW_2(MW_3)$ related to fixed effects in $b_{MW2(MW3)}$, X_{WW} = known incidence matrix of weaning weight observations related to fixed effects in b_{WW}, $b_{MW2(MW3)}$ = vector of fixed effects related to $MW_2(MW_3)$, b_{WW} = vector of fixed effects on weaning weight, $Z_{MW2(MW3)}$ = incidence matrix of 0's and 1's relating random additive direct genetic effects of $MW_2(MW_3)$ to $y_{MW2(MW3)}$, Z_{WWd} = incidence matrix of 0's and 1's relating random additive direct genetic effects on weaning weight to y_{ww}, Z_{WWm} = incidence matrix of 0's and 1's relating random additive maternal effects of weaning weight to y_{WW}, $u_{MW2(MW3)}$= vector of random additive direct genetic effects for $MW_2(MW_3)$, u_{WWd} = vector of random additive direct genetic effects for weaning weight, u_{WWm} = vector of random additive maternal genetic effects for weaning weight, $e_{MW2(MW3)}$ = vector of random residual errors for $MW_2(MW_3)$, and e_{WW} = vector of random residual errors for weaning weight. A = Wright's numerator relationship matrix, I = identity matrix, $\sigma^2_{MW2(MW3)}$ = additive direct genetic variance for $MW_2(MW_3)$, σ^2_{WWd} = additive direct genetic variance for weaning weight, σ^2_{WWm} = additive maternal genetic variance for weaning weight, $\sigma_{MW2(MW3)\cdot WWd}$ = covariance between additive direct genetic

$MW_2(MW_3)$ and additive direct genetic weaning weight effects, $\sigma_{MW2(MW3)\text{-}WWm}$ = covariance between additive direct genetic $MW_2(MW_3)$ and additive maternal genetic weaning weight, $\sigma_{WWd\text{-}WWm}$ = covariance between additive direct genetic weaning weight and additive maternal genetic weaning weight effects, $\sigma^2_{eMW2(MW3)}$ = residual error variance for $MW_2(MW_3)$, σ^2_{eWW} = residual error variance for weaning weight, and $\sigma_{eMW2(MW3)\text{-}WW}$ = residual error covariance between $MW_2(MW_3)$ and weaning weight.

The animal model for MW_2 and MW_3 included fixed effects of contemporary group and age of the cow's dam plus random effects included additive direct genetic effects of animal and residual. Fixed effects for weaning weight were weaning contemporary group, sex by age of dam interaction, and a covariate of weaning age. Random effects included random additive direct and maternal genetic effects of animal, and residual error. I excluded the weaning weight random permanent environmental effect of the dam because variance component estimates for WW-MW_3 were consistently outside the parameter space.

In a separate analysis, I estimated (co)variance components between weaning weight and cow weight for ages 4 to 9 yr ($MW_{4\text{-}9}$) using a repeated measures analysis. For this analysis, I grouped ages 4 to 9 yr and analyzed the WW-$MW_{4\text{-}9}$ data using the following multivariate animal model (Mrode, 1996):

$$\begin{bmatrix} y_{MW_{4-9}} \\ y_{WW} \end{bmatrix} = \begin{bmatrix} X_{MW_{4-9}} & 0 \\ 0 & X_{WW} \end{bmatrix} \begin{bmatrix} b_{MW_{4-9}} \\ b_{WW} \end{bmatrix} +$$

$$\begin{bmatrix} Z_{MW_{4-9}} & Z_c & 0 & 0 \\ 0 & 0 & Z_{WWd} & Z_{WWm} \end{bmatrix} \begin{bmatrix} u_{MW_{4-9}} \\ u_{c_{4-9}} \\ u_{WWd} \\ u_{WWm} \end{bmatrix} + \begin{bmatrix} e_{MW_{4-9}} \\ e_{WW} \end{bmatrix}$$

where

$$\mathbf{Var}\begin{bmatrix} u_{MW_{4-9}} \\ u_{c_{4-9}} \\ u_{WWd} \\ u_{WWm} \end{bmatrix} = \begin{bmatrix} A\sigma^2_{MW_{4-9}} & 0 & A\sigma_{MW_{4-9}\cdot WWd} & A\sigma_{MW_{4-9}\cdot WWm} \\ 0 & I\sigma^2_{c_{4-9}} & 0 & 0 \\ A\sigma_{MW_{4-9}\cdot WWd} & 0 & A\sigma^2_{WWd} & A\sigma_{WWd\cdot WWm} \\ A\sigma_{MW_{4-9}\cdot WWm} & 0 & A\sigma_{WWd\cdot WWm} & A\sigma^2_{WWm} \end{bmatrix}$$

$$\mathbf{Var}\begin{bmatrix} e_{MW_{4-9}} \\ e_{WW} \end{bmatrix} = \begin{bmatrix} I\sigma^2_{e_{MW_{4-9}}} & I\sigma_{e_{MW_{4-9}}\cdot e_{WW}} \\ I\sigma_{e_{MW_{4-9}}\cdot e_{WW}} & I\sigma^2_{e_{WW}} \end{bmatrix}$$

$y_{MW4\text{-}9}$ = vector of phenotypic observations on $MW_{4\text{-}9}$, y_{WW} = vector of phenotypic observations on weaning weight, $X_{MW4\text{-}9(WW)}$ = known incidence matrix of observations on $MW_{4\text{-}9}$(weaning weight) related to fixed effects in $b_{MW4\text{-}9(WW)}$, $b_{MW4\text{-}9(WW)}$ = vector of fixed effects related to $MW_{4\text{-}9}$(weaning weight), $Z_{MW4\text{-}9(WWd)}$ = incidence matrix of 0's and 1's relating random additive direct genetic effects on $MW_{4\text{-}9}$(WW) to $y_{MW4\text{-}9(WW)}$, Z_c = incidence matrix of 0's and 1's relating random permanent environmental effects on $MW_{4\text{-}9}$ to $y_{MW4\text{-}9}$, Z_{WWm} = incidence matrix of 0's and 1's relating random additive maternal genetic effects of weaning weight to y_{WW}, $u_{MW4\text{-}9(WWd)}$ = vector of random

additive direct genetic effects for MW_{4-9}(weaning weight), u_{WWm} = vector of random additive maternal genetic effects for weaning weight, u_{c4-9} = vector of random permanent environmental effects for MW_{4-9}, $e_{MW4-9(WW)}$ = vector of random residual errors for MW_{4-9}(weaning weight). A = Wright's numerator relationship matrix, I = identity matrix, $\sigma^2_{MW4-9(WWd)}$= additive genetic variance for direct effects of MW_{4-9}(weaning weight), σ^2_{WWm} = additive maternal genetic variance of weaning weight, σ^2_e= permanent environmental variance for MW_{4-9}, $\sigma_{MW4-9\cdot WWd}$ = covariance between additive direct genetic MW_{4-9} and additive direct genetic weaning weight effects, $\sigma_{MW4-9\cdot WWm}$ = covariance between additive direct genetic MW_{4-9} and additive maternal genetic WW, $\sigma_{WWd\cdot WWm}$ = covariance between additive direct genetic weaning weight and additive maternal genetic weaning weight effects, $\sigma^2_{eMW4-9(WW)}$= residual error variance for MW_{4-9}(weaning weight), and $\sigma_{e(MW4-9\cdot WW)}$ = residual error covariance between MW_{4-9} and weaning weight.

In the weaning weight with MW_{4-9} analysis, fixed effects for MW_{4-9} included contemporary group and an age of the cow's dam by age of cow interaction. Random effects included random additive direct genetic effects of animal, a random permanent environmental effect, and residual error. Fixed and random effects for weaning weight were the same as those fit in the WW-$MW_{2(3)}$ analyses.

Postweaning Gain and Mature Weight

An analysis between postweaning gain and mature weight was done with 2, 4, 6, 8, and 2 to 9 yr of age (Tables 3.11 and 3.12). Additionally, I also used a repeated measures analysis for mature weight to analyze postweaning gain and mature weight at

ages 2 through 9 yr ($MW_{2\text{-}9}$). The animal model for the multivariate single component analyses between 2, 4, 6, 8 yr of age and mature weight was:

$$\begin{bmatrix} y_{MW_{age}} \\ y_{PW} \end{bmatrix} = \begin{bmatrix} X_{MW_{age}} & 0 \\ 0 & X_{PW} \end{bmatrix} \begin{bmatrix} b_{MW_{age}} \\ b_{PW} \end{bmatrix} + \begin{bmatrix} Z_{MW_{age}} & 0 \\ 0 & Z_{PW} \end{bmatrix} \begin{bmatrix} u_{MW_{age}} \\ u_{PW} \end{bmatrix} + \begin{bmatrix} e_{MW_{age}} \\ e_{PW} \end{bmatrix}$$

where

$$Var\begin{bmatrix} u_{MW_{age}} \\ u_{PW} \end{bmatrix} = \begin{bmatrix} A\sigma^2_{MW_{age}} & A\sigma_{MW_{age}\cdot PW} \\ A\sigma_{MW_{age}\cdot PW} & A\sigma^2_{PW} \end{bmatrix}$$

$$Var\begin{bmatrix} e_{MW_{age}} \\ e_{PW} \end{bmatrix} = \begin{bmatrix} I\sigma^2_{e_{MW_{age}}} & I\sigma_{e_{MW_{age}}\cdot e_{PW}} \\ I\sigma_{e_{MW_{age}}\cdot e_{PW}} & I\sigma^2_{e_{PW}} \end{bmatrix}$$

y_{MWage} = vector of phenotypic observations on mature weight at ages 2, 4, 6, and 8 yr of age, $X_{Mwage\,(PW)}$ = known incidence matrix of observations on MW_{age}(postweaning gain) related to fixed effects in $b_{MWage(PW)}$, $b_{MWage(PW)}$ = vector of fixed effects related to MW_{age}(postweaning gain), $Z_{MWage(PW)}$ = incidence matrix of 0's and 1's relating random additive direct genetic effects of MW_{age}(postweaning gain) to $Y_{MWage(PW)}$, $u_{MWage(PW)}$ = vector of random additive direct genetic effects for MW_{age}(postweaning gain), $e_{MWage(PW)}$ = vector of random residual errors for MW_{age}(postweaning gain). A = Wright's numerator relationship matrix, I = identity matrix, $\sigma^2_{MWage(PW)}$= additive genetic variance for direct effects of MW_{age}(postweaning gain), σ^2_{cage} = permanent environmental variance for MW_{age}, $\sigma_{MWage\cdot PW}$= covariance between additive direct genetic MW_{age} and additive direct genetic postweaning gain effects, $\sigma^2_{eMWage(PW)}$= residual error variance for

MW_{age}(postweaning gain), and $\sigma_{e(MWage\text{-}PW)}$ = residual error covariance between MW_{age} and postweaning gain.

For mature weight ages 2 to 9 yrs, the animal model for the repeated measures analysis was:

$$\begin{bmatrix} y_{MW_{2-9}} \\ y_{PW} \end{bmatrix} = \begin{bmatrix} X_{MW_{2-9}} & 0 \\ 0 & X_{PW} \end{bmatrix} \begin{bmatrix} b_{MW_{2-9}} \\ b_{PW} \end{bmatrix} + \begin{bmatrix} Z_{MW_{2-9}} & Z_c & 0 \\ 0 & 0 & Z_{PW} \end{bmatrix} \begin{bmatrix} u_{MW_{2-9}} \\ u_{c_{2-9}} \\ u_{PW} \end{bmatrix} + \begin{bmatrix} e_{MW_{2-9}} \\ e_{PW} \end{bmatrix}$$

where

$$\mathbf{Var}\begin{bmatrix} u_{MW_{2-9}} \\ u_{c_{2-9}} \\ u_{PW} \end{bmatrix} = \begin{bmatrix} A\sigma^2_{MW_{2-9}} & 0 & A\sigma_{MW_{2-9}\cdot PW} \\ 0 & I\sigma^2_{c_{2-9}} & 0 \\ A\sigma_{MW_{2-9}\cdot PW} & 0 & A\sigma^2_{PW} \end{bmatrix}$$

$$\mathbf{Var}\begin{bmatrix} e_{MW_{2-9}} \\ e_{PW} \end{bmatrix} = \begin{bmatrix} I\sigma^2_{e_{MW_{2-9}}} & I\sigma_{e_{MW_{2-9}}\cdot e_{PW}} \\ I\sigma_{e_{MW_{2-9}}\cdot e_{PW}} & I\sigma^2_{e_{PW}} \end{bmatrix}$$

$y_{MW2\text{-}9}$ = vector of phenotypic observations on $MW_{2\text{-}9}$, $X_{MW2\text{-}9(PW)}$ = known incidence matrix of observations on $MW_{2\text{-}9}$(postweaning gain) related to fixed effects in $b_{MW2\text{-}9(PW)}$, $b_{MW2\text{-}9(PW)}$ = vector of fixed effects related to $MW_{2\text{-}9}$(postweaning gain), $Z_{MW2\text{-}9(PW)}$ = incidence matrix of 0's and 1's relating random additive direct genetic effects of $MW_{2\text{-}9}$(postweaning gain) to $y_{MW2\text{-}9(PW)}$, Z_c = incidence matrix of 0's and 1's relating random permanent environmental effects of $MW_{2\text{-}9}$ to $y_{MW2\text{-}9}$, $u_{MW2\text{-}9(PW)}$ = vector of random additive direct genetic effects for $MW_{2\text{-}9}$(postweaning gain), $u_{c2\text{-}9}$ = vector of random permanent environmental effects for $MW_{2\text{-}9}$, $e_{MW2\text{-}9(PW)}$ = vector of random residual errors for $MW_{2\text{-}9}$(postweaning gain). A = Wright's numerator relationship matrix, I = identity

matrix, $\sigma^2_{MW2\text{-}9(PW)}$= additive genetic variance for direct effects of $MW_{2\text{-}9}$(PW), $\sigma^2_{c2\text{-}9}$ = permanent environmental variance for $MW_{2\text{-}9}$, $\sigma_{MW2\text{-}9\text{-}PW}$= covariance between additive direct genetic $MW_{2\text{-}9}$ and additive direct genetic postweaning gain effects, $\sigma^2_{eMW2\text{-}9(PW)}$= residual error variance for $MW_{2\text{-}9}$(postweaning gain), and $\sigma_{e(MW2\text{-}9\text{-}PW)}$ = residual error covariance between $MW_{2\text{-}9}$ and postweaning gain.

The fixed effects for $MW_{2\text{-}9}$ were identical to those effects fit in the analysis of WW with $MW_{4\text{-}9}$. Fixed effects for postweaning gain included contemporary group and a sex by age of dam interaction.

For WW-MW_2, WW-MW_3, WW-$MW_{4\text{-}9}$, PW-$MW_{2,4,6,8}$, and PW-$MW_{2\text{-}9}$ analyses, I used the RAAA supplied data and pedigree to construct three-generation pedigrees. Pedigrees consisted of the individuals with a valid MW or immature weight observation (WW or PW), their parents, and their grandparents.

Using the variance component estimates from all analyses of mature weight with weaning weight and postweaning gain, I calculated the median and 95% CI for heritability estimates, genetic correlations and residual correlations for each multivariate analysis (Hahn and Meeker, 1991).

Multivariate Analysis of Mature Weight and Stayability

Data Description. The RAAA supplied me with 121,147 stayability records for the year 1998 and I merged these data with the mature weight data from the previous multivariate analyses between mature weight and weaning weight analyses on animals 2 to 9 yr of age. In the RAAA database, stayability is defined as the probability of daughters staying in the herd to six years of age (RAAA, 1999). A valid observation for

stayability required usable birth information on both the calf and dam of the calf for animals that were six years of age. The mature weight data were edited previously; therefore, I did not remove any additional data. For stayability I eliminated records on animals with missing contemporary group information and recorded as embryo transfers reducing the data to 81,431 records. All contemporary groups with no variation were removed and this reduced the number of observations to 80,875 complete stayability records. There were 7,133 contemporary groups prior to removal for no variation and 7,039 contemporary groups after removal of records for no variation in contemporary group.

Contemporary groups for mature weight and stayability were formed using information supplied by the RAAA (1998). The definition for mature weight contemporary group remained the same as in previous analyses; therefore, I did not make any modifications to the definition. The contemporary group definition for stayability included the birth year of the dam, the breeder of the dam, and the breeder of that dam's calves through six years of age (Snelling, 1995; Hyde et al., 1996). According to Snelling (1994), this definition for stayability accounts for animals that were moved or sold from one herd to another during their lifetime and does not remove dams that failed to calve each year or if the breeder failed to report a calf.

I used mature weight and stayability data from three herds. These were the same herds used for previous variance component analyses of weaning weight and postweaning gain with mature weight. Table 3.13 has descriptive statistics for the analyses of stayability and cow weight at 2, 3 and 5yr of age. Stayability data for these three herds contained 9,808 complete records. The complete records had 4,532 favorable

and 5,276 unfavorable observations. There were 274 contemporary groups with an average of 35 animals per contemporary group.

Table 3.13. Descriptive statistics for phenotypic performance and contemporary group information of cow weight (MW) at ages 2 yr (MW_2), 3 yr (MW_3), and 5 yr (MW_5) among data analyzed in Red Angus cattle

	MW_2	MW_3	MW_5
N[1]	6,874	4,634	2,736
Mean (kg)	406.33	454.00	514.79
SD (kg)	56.66	60.82	63.92
Range (kg)	272.11 to 673.47	280.27 to 730.16	335.60 to 800.45
No. of CG	1,021	580	452
AVG CG size	22.2	11.9	6.1
SD of CG size	28.4	15.7	5.2

[1]N = number of mature weight observations.

Pedigree. I used the joined data sets to construct several multi-generation pedigrees. I assembled a three generation pedigrees using all animals with either a stayability or mature weight observation. The pedigrees included animals with a unique identification and observation plus their parents and grandparents. Table 3.14 reports the data structure for the pedigrees in analyses of 2yr old, 3yr old, and 5yr old cow weight with stayability.

Table 3.14. Number of individuals, sires, dams, and foundation animals for each multivariate analysis of 2yr, 3yr, and 5yr cow weight (MW) with stayability (ST)

	MW2-ST	MW3-ST	MW5-ST
No. of Individuals	14,500	13,948	12,880
No. of Sires	1,016	1,019	922
No. of dams	7,263	6,985	6,444
No. of foundation individuals[1]	4,149	4,193	4,066

[1]A foundation animal was an individual with either or both parents designated as unknown.

Statistical Procedures. I estimated (co)variance components for weight at ages 2, 3, and 5 yr of age with stayability using Method R procedures and a continuous and categorical model (Reverter et al., 1994; Kaiser, 1996). The following describes the multivariate model used for analysis of mature weight at ages 2, 3, or 5 yr of age ($\mathbf{y}_1$) and stayability ($\mathbf{y}_2$). For mature weight (Trait 1), the model was:

$$\mathbf{y}_1 = \mathbf{X}_1\mathbf{b}_1 + \mathbf{Z}_1\mathbf{u}_1 + \mathbf{e}_1$$

and for stayability (Trait 2),

$$\mathbf{y}_2 = \mathbf{X}_2\mathbf{b}_2 + \mathbf{Z}_2\mathbf{u}_2 + \mathbf{e}_2$$

$$\mathbf{y}_2 = \mathbf{X}_2\mathbf{b}_2 + \mathbf{Z}_2\mathbf{u}_2 + \mathbf{E}(\mathbf{e}_2 \mid \mathbf{e}_1) + \mathbf{e}_2^*$$

$$\mathbf{y}_2 = \mathbf{X}_2\mathbf{b}_2 + \mathbf{Z}_2\mathbf{u}_2 + \mathbf{b}^*(\mathbf{y}_1 - \mathbf{X}_1\mathbf{b}_1 - \mathbf{Z}_1\mathbf{u}_1) + \mathbf{e}_2^*,$$

where

y_2 = observations of stayability on the liability scale, $X_{1(2)}$ = known coefficient matrix including the incidence matrix relating fixed effects to observations on Trait 1(2) and age as covariates, $Z_{1(2)}$ = incidence matrix relating random animal additive direct genetic effects to observations on Trait 1(2), $b_{1(2)}$ = vector of fixed effects related to Trait 1(2), $u_{1(2)}$ = vector of random additive direct genetic effects for Trait 1(2), e_1 = vector of random errors associated with Trait 1, $E(e_2|e_1)$ = expectation of errors associated with Trait 2 given the observed errors for trait 1, e^*_2 = vector of random errors associated with Trait 2 independent of the random errors for Trait 1, and b^* = partial regression coefficient for e_2 on e_1 (Kaiser, 1996).

The model distributed random additive direct genetic effects as follows:

$$\begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \\ \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} \sim N\left\{ \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{g} \otimes \mathbf{A} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{I}_1 \sigma^2_{e1} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{I}_2 \sigma^2_{e2} \end{bmatrix} \right\}$$

where

g = 2 by 2 additive direct genetic (co)variance matrix, A = Wright's numerator relationship matrix, $\otimes$ = Kronecker product, $I_{1(2)}$ = identity matrix of the same order as $e_{1(2)}$, σ^2_{e1} = variance of the mature weight residual error, and σ^2_{e2} = the variance of the stayability residual error. By default, the residual error variance for stayability was constrained to one and the matrix corresponding to the continuous-threshold residual covariance was pre-set to zero (Kaiser, 1996).

Models. I fitted the same multivariate animal models for analyses of stayability with cow weight at 2, 3, and 5 yr of age. Model fixed effects included mature weight contemporary group and age of the cow's dam. Random effects included additive direct genetic effects of animal and residual error. The model for stayability had contemporary groups as its only fixed effect. Random effects included random additive genetic effects due to animal and residual error (Snelling et al., 1995).

The preliminary results of the multivariate analysis between mature weight and stayability were not consistent and yielded genetic correlation estimates that were low to near zero. In previous analyses by Evans et al. (1999), this result occurred because of a nonlinear relationship between genetic effects of a continuous and categorical trait. The same phenomenon might be present between stayability and mature weight; therefore, I decided to fit an animal model with additive genetic groups to identify the presence of a nonlinear genetic relationship between traits.

Additive Genetic Groups Analysis

The advantages to using additive genetic groups in an analysis are that it uses previous information from other BLUP (Henderson, 1984) analyses of mature weight and stayability, it is a faster and more tractable procedure than multivariate models, there is a minimal increase on the size of the linear system, and it provides a method to determine the presence of a nonlinear relationship between two traits (Kaiser, 1996; Evans et al., 1999).

Data Description. Using the data and pedigree information from the previous multivariate analysis between mature weight and weaning weight, I applied an additive genetic groups model to explain the potential non-linear relationship between mature weight and stayability. I generated breeding value predictions for mature weight using a performance programmed turnkey BLUP procedure, "tkblup" (B. L. Golden, unpublished), previous multivariate heritability estimates for weight at 2, 3, and 5 yr of age, and a three generation multivariate pedigree for mature weight and stayability. For mature weight, I formed genetic groups using breeding value predictions from foundation animals. A foundation animal was an individual with at least one parent unknown (Table 3.14). Using mature weight breeding value predictions, I grouped foundation animals from low to high into four equal-sized groups. In previous studies, four genetic groups appeared to be a good intermediate to illustrate potential nonlinear relationships between traits. Using a larger number of genetic groups made it difficult to analyze with reasonable SE of genetic group estimate (Golden et al., 1994; Evans et al., 1999).

After I formed the genetic groups, I used foundation animal information and procedures outlined by Westell et al. (1988) to build genetic group equations. A

transformation described by Quaas and Pollak (1981) was used to disperse the groups throughout the pedigree and rebuild the inverse numerator relationship matrix with a C-programmed ABTK (Golden et al., 1992) tool called "grps". Then the stayability breeding value predictions were generated on the underlying scale with a categorical model (Kaiser, 1996). Fixed effects for the genetic groups model were identical to what was previously described for forming the genetic groups; however, mature weight genetic groups were included in the model as fixed effects. Random effects included a random additive direct genetic effect of animal and residual error. Because the genetic groups solutions were expressed on a standardized underlying scale, I transformed them from the underlying liability scale to the percentage probability scale. Then I calculated standard errors from the prediction error variances that I obtained from the diagonal elements of the inverse coefficient matrix. Furthermore, the genetic groups solutions were expressed as deviations from the lowest group, because I constrained the first mature weight genetic group.

An additive genetic groups model was used to generate breeding values for stayability with mature weight (MW) groups. I used previously described additive genetic groups procedures and the following animal model to obtain predictions for stayability on the underlying scale (Mrode, 1996).

$$\mathbf{y}_{ST} = \mathbf{X}_{ST}\mathbf{b}_{ST} + \mathbf{Z}_{ST}\mathbf{u}_{ST} + \mathbf{Z}_{ST}\mathbf{Q}\mathbf{g}_{ST} + \mathbf{e}_{ST}$$

where

$$\mathrm{Var}\begin{bmatrix}\mathbf{u}_{ST}\\ \mathbf{e}_{ST}\end{bmatrix} = \begin{bmatrix}\mathbf{A}\sigma^2_{aST} & \mathbf{0}\\ \mathbf{0} & \mathbf{I}\sigma^2_{eST}\end{bmatrix}$$

y_{ST} = a vector of sub-class "pseudo-observations" on Stayability, X_{ST} = known incidence matrix of observations on ST related to fixed effects in b_{ST}, b_{ST} = vector of fixed effects related to ST, Z_{ST} = an incidence matrix of 0's and 1's relating random additive direct genetic effects of ST to y_{ST}, u_{ST} = vector of random additive direct genetic effects of animal plus additive genetic group effects for ST, Q = a matrix of independent covariates relating fractional fixed additive genetic group effects to y_{ST}, g_{ST} = vector of fixed additive genetic group effects for ST, e_{ST} = vector of random residual errors, A = Wright's numerator relationship matrix between all animals, σ^2_a = the additive genetic variance for stayability, and σ^2_e = the residual error variance for stayability (Golden et al., 1994). When the categorical model is used to calculate stayability predictions, the error variance is fixed to one.

It can be informative to fit genetic groups models that are the reciprocals of each other of the initial analysis (Evans et al., 1999). I fitted animal models to predict cow weight at 2, 3, and 5 yr of age with stayability genetic groups. The preliminary results of the study were inconclusive and not meaningful; therefore, I only fitted models to predict stayability with mature weight genetic groups.

Alternative Genetic Groups Strategies. Initial results of the additive genetic groups analysis for stayability using mature weight groups were not consistent and were inconclusive. Due to these results, I decided to change my strategies for assigning foundation animals to genetic groups (R. M. Bourdon and B. L. Golden, personal communication). I applied multiple methods to determine if the assignment of animals to different groups would improve the interpretation of the genetic relationship between traits.

For the first method I grouped animals based upon the distance of their EBV from the mean EBV for that analysis. Before I assigned animals to groups I followed the same procedures in previously reported analyses for generating mature weight breeding values to use in a stayability analysis. Instead of placing animals into equal sized groups I calculated the mean EBV and standard deviation of foundation animals EBV and grouped them into 5 groups of unequal size. The genetic groups ranged from 1 to 5 with 1 being the lowest EBV group and 5 the highest. The lowest group was –1.5 SD below the mean, group 2 was –1.49 to –.5 SD below the mean, the middle group, group 3 was -.49 to +.5 Std around the mean, group 4 was .5 to 1.49 SD from the mean, and group 5 was all animals greater than 1.5 SD away from the mean.

Using the different method I divided the range of EBV for foundation animals into equal strides prior to making group assignments. I calculated the range of EBV for mature weight related to the foundation animals and separated the range of EBV into four groups of equal length. Then I assigned animals to their respective groups based on the correspondence between their EBV and the ranges of the genetic groups.

Another strategy I used to determine if there were growth differences among animals in the same mature genetic group. I placed animals into four equal-sized genetic groups using mature weight EBV and divided these groups by low and high yearling weight EBV. I obtained the yearling weight EBV from the 1998 RAAA summer genetic analysis. So, the low mature weight group was separated into two groups where the first group had foundation animals with low yearling weight EBV and the second, animals with high yearling weight EBV. I did fit models with a greater number of yearling weight genetic groups, but I observed that two yearling weight groups per mature weight group were informative. Fitting additional groups only served to increase the SE of the genetic groups solutions and distort the magnitude of the solutions.

Mature Weight and Immature Weights. I used the same genetic groups models described above to improve my interpretation of the genetic relationship between immature weights and stayability. Genetic groups were built with genetic predictions from birth weight, weaning weight (direct), weaning weight (maternal), and yearling weight. I fitted different models for each analysis and the only difference between models was the trait grouped. I formed the genetic groups for immature weights using EBV for birth, weaning, and yearling weight EBV that originated from the 1998 summer RAAA genetic evaluation.

For the stayability with birth weight analysis, I identified the foundation animals using a three generation pedigree and obtained their unformatted birth weight EBV from the 1998 RAAA genetic evaluation (RAAA, 1998). I then grouped the animals into four equal-sized groups from low to high based upon their EBV for birth weight and applied the previously described genetic groups procedures for groups of equal size. After

analyzing stayability with genetic groups for birth weight, I generated group effects solutions.

Additional models were fit that included additive genetic groups for weaning weight (direct), weaning weight (maternal), and yearling weight. I obtained the EBV for each trait from the 1998 summer RAAA genetic evaluation, the same source as birth weight. This was recommended over using genetic predictions from specific herds because of increased accuracy of the predictions and ease of implementation.

Maintenance Energy Analysis

In this section I describe procedures to develop a prototype genetic prediction of mature beef cow maintenance energy requirement in cattle. The equations were derived from consultations with nutritionists (D. E. Johnson and M. J. Jarosz, personal communication) and animal breeders (B. L. Golden and R. M. Bourdon, personal communication), the Nutritional Requirements of Beef Cattle (NRC, 1996), and current genetic prediction research (MacNeil et al., 2000).

Data Source. The data and genetic predictions for calculating mature cow maintenance energy requirements were obtained from previously described data sources (Table 3.8) and BLUP analyses of both mature weight (Mature weight EBV) and maternal weaning weight (Milk EBV). The genetic predictions for mature weight were generated from all mature weight data and BLUP analyses in this study (Table 3.8). The predictions used for this analysis were obtained from the EPD analysis of all mature weight data (Table 3.8). This implemented the animal model used to generate EPD for previous genetic and environmental trends. The animal model was a linear random

regression model with both additive and permanent environmental effects. I previously describe the model in the analysis used to generate EPD for all animals in the RAAA (N=56,582). However, the predictions for maternal weaning weight (Milk) were obtained from the RAAA summer national cattle evaluation (RAAA, 1998). The predictions for maternal weaning weight were those predictions prior to a base adjustment for a specific year and had not undergone any form of rounding.

Analytical Procedures. MacNeil and Mott (2000) changed the NRC (1996) algebraic equations to calculate mature cow maintenance energy requirements (MEm) using mature weight genetic predictions instead of phenotypic mature weight observations. I made additional changes to these equations used to calculate energy requirements to make them more appropriate for mature animals, account for the additional maintenance energy due to production status, and separated energy needs at maintenance from those for production (milk, growth, and gestation). But, before I describe my modifications, I will briefly describe the methods used by the NRC (1996) and (MacNeil et al., 2000) to generate predictions for energy requirements of beef cattle.

The NRC (1996) equations used to calculate net energy requirements at maintenance levels (NE_m) account for a base requirement and then adjust this maintenance energy requirement for breed, lactation status, sex of the animal, activity level, heat loss, and their previous level of feeding. I will only present the base equation and the first set of adjustments for breed effect, lactation status, sex of animal, and composition. Because of the limited amounts of information the adjustments presented were set to default values in the NRC (1996). Furthermore, the equations predicted will be used to generate predictions for metabolizable energy for maintenance (MEm) in place

of NEm. Metabolizable energy at maintenance is equivalent to NE_m/k_m. For the purpose of this analysis, I used a k_m = to .60. I selected this value using the calculated k_m values for a typical mature cow diet (NRC, 1996). The base equation for the prediction of ME_m is

$$ME_m = \frac{a1 * SBW.75}{k_m} = \frac{NE_m}{k_m}$$

with adjustments for breed, lactation, sex, and composition it is

$$ME_m = (a1 * SBW^{.75} (BE) (L) (SEX) (COMP)) + a_2$$

where

ME_m = metabolizable energy required for maintenance (Mcal/d); $k_m = NE_m / ME_m$, the partial efficiency for maintenance energy; a1 = .077, the thermal neutral maintenance requirement (Mcal/d/$sbw^{.75}$); SBW = shrunk body weight (kg); BE = breed effect on ME_m; L = lactation status and its effect on ME_m; SEX = sex effect on ME_m; COMP = effect of previous plane of nutrition as a function of condition score; and a2 = adjustment of ME_m for previous ambient temperature.

MacNeil and Mott (2000) replaced SBW with values equal to a genetic prediction for an animal's mature weight plus the population mean. This value was submitted to the NRC (1996) Table Generator program to obtain NE_m. This provided the authors with a method to generate genetic predictions for maintenance energy requirements using existing genetic and nutritional prediction equations.

MacNeil and Mott (2000) had EBV for both maternal weaning weight and gain from birth to weaning, which they used to determine energy requirements due to lactation (ME_l). They adapted a Wood's lactation function (Wood, 1979) to determine peak milk

yield production and time of peak yield production. Their modifications allowed for genetic predictions, such as weaning weight maternal (Milk), to be used to predict the lactation values necessary for the NRC equations. I will explain the foundation Wood's function and the changes made to it for incorporation of genetic predictions such as weaning weight maternal EBV and dam's age at lactation.

This represents a standard Wood's function for lactation:

$$Y = AT^{B} e^{(-CT)}$$

where

Y = milk yield at week T, A, B, C = constants that describe the lactation function, T = time in weeks, e = base of natural logarithims.

MacNeil and Mott (2000) modified the Wood's function to incorporate both the age of the dam and maternal breeding values for weaning weight gain from birth to weaning. The new equation for lactation changed to the following:

$$Y = A'T^{B'} e^{(-CT)}$$

where

$$A' = A(1+a_1 m + a_2 aod),$$

$$B' = B(1+b_1 m).$$

The authors modified the equation to express A as a function of maternal breeding value (m) and age of dam (AOD). The a_1 and a_2 parameters coefficients that account for the changes in the A parameter associated with changes in age of dam and maternal

breeding value, while b_1 = change in the B parameter associated with changes in maternal breeding value for calf gain.

The modified Wood's equation can be used to determine both peak milk yield and time of peak yield from EBV for maternal weaning weight gain or maternal weaning weight. According to Wood (1969) the time of peak milk yield is equal to B/C. The modified equations proposed by MacNeil and Mott (2000) calculated time of peak milk yield (T) as B'/C which is equal to $B(1+b_1m) / C$. Then peak milk yield = $A'(B'/C)^{B'}e^{(-B')}$. The values for peak milk yield and time of peak milk yield can be used in the NRC (1996) to calculate total milk yield with this group of equations:

$k = 1/T$,

T = Time of peak lactation or milk yield (wk)

$a = 1/(Yke)$,

Y = Peak milk yield, kg/d

Milk yield (kg) at time n, $Y_n = n/ae^{kn}$

Total Yield (kg) for lactation in n weeks = $(-7/ak)*[ne^{-kn} + (1/k)e^{-kn} - (1/k)]$.

The equations above are used to derive values for a, k, and Total Milk Yield. The value for Total Milk Yield is then determined by taking the integral of the function for the length of time 1 to n of the lactation equation for milk yield on a particular week. Using the value for total milk production and known values for energy per kg of milk, I determined the total energy required for lactation. The equations listed below outline how to determine energy for lactation from Total Lactation Yield. The total energy for milk was calculated as follows:

Total Energy for Lactation per day (Mcal/d), $\text{TotalE} = \left(\frac{E * \text{TotalY}}{197\ d}\right)$

$$E = .092*MF + .049*SNF - .0569$$

where

TotalE = total energy for lactation (Mcal), E = energy content of milk (Mcal/kg), MF = milk fact percentage, SNF = milk solids not fat composition of the milk percentage. Because these animals were not sampled for MF and SNF, I assumed values of 4.0% for MF and 8.3% for SNF equating to .72 Mcal/kg of milk as the energy content (NRC, 1996). From these equations, a value for energy to lactate can be calculated.

Modified Equations. I used these equations and methods proposed by MacNeil and Mott (2000), the NRC (1996), and nutrition literature to derive a different set of functions for prediction of mature cow maintenance energy requirement. These modifications were based on both research on maintenance energy requirements (CSIRO, 1990; NRC, 1996) and consultation with a nutritionist (D. E. Johnson, personal communication). The following section shows the modifications that I made to calculate the predictions for mature cow maintenance energy requirements (MEm_i):

$$MEm_i \text{ (Mcal/d)} = MEm(MW_i) \pm .10*MEp_i$$

$$MEm(MW_i) = a_{l*}*(MW_i)^{.75} - a_{l*}*(MW_{avg})^{.75}$$

$$MEp_i = \left(\frac{(TotalEi - TotalEavg)}{k_l} \right)$$

$$a_{l*} = \frac{a_l}{k_m} = \frac{.077}{.60} = .128$$

$$k_l = .60$$

where

a_i = thermal neutral maintenance energy requirement (Mcal/d/$MW^{.75}$), MEm(MW_i) = Estimated breeding value (EBV) for metabolizable energy requirement at maintenance (Mcal / d), MEp_i = Energy required for lactation ME_l (Net energy for lactation) per day on animal i, MW_i = Mature weight EBV + population mean for mature weight, MW_{avg} = population mean for mature weight (MW EBV = 0), k_l = partial efficiency of milk production, $TotalE_i$ = Total energy of lactation (Mcal/d) for animal i, $TotalE_{avg}$ = average Total Energy (Mcal/ d) based on animals with a zero weaning weight maternal EBV. I derived the value for the population mean from the expectation of contemporary group. The value for ME_p assumes that the individual lactates for 28 weeks with their peak yield occurring at 30.7 d (MacNeil et al., 2000) and it is expressed as a deviation from an average milking animal. An average milking animal would be one with a zero EBV for maternal weaning weight.

The equation I listed excludes adjustments for previous plane of nutrition because of the limited body condition score data. Furthermore, I removed the adjustments for acclimatization, lactation status, and breed effect because the information was not available or the adjustment would have no affect on the outcome of the equations. To account for individuals with higher levels of production due to potential milk production, I changed maintenance energy requirements by a coefficient of .10*MEp. This was a method to account for an animal's higher maintenance energy requirements because of higher milk production or potential for higher milk production (CSIRO, 1990).

The value for MEp is calculated using the NRC (1996) equations, modified equations that I have described above, and Wood's lactation function parameters derived by MacNeil and Mott (2000). I expressed MEp as a deviation from an "average" animal

and that value was used in the previously described equations. The average animal represented the MEp for an individual with a zero maternal weaning weight EBV. The constant k_l, the partial efficiency for lactation, is used to adjust up the energy needed for the physiological process of lactation.

The parameters for the Wood's lactation function represent Hereford cattle, but they should be sufficient to develop a prototype (D. E. Johnson, personal communication). These parameters included the a_1 and a_2 for both maternal EBV on weaning weight and age of dam at time of lactation. Because I used maternal weaning weight EBV in place of the EBV for weaning gain, the value for B remained constant. The parameter estimates for A, a1, a2, B and C were 2.82, .017, .06, .25, and .0081, respectively. These parameters were obtained from studies with Line 1 Hereford cattle at the Fort Keogh Livestock and Range Research Laboratory, Miles City, MT. Because weaning weight maternal EBV were used the time of peak milk yield remained constant at B/C = 30.7 days (4.38 wk). The length of lactation was standardized to 197 d, which I determined from the average age at weaning in the Red Angus breed (MacNeil and Mott, 2000). I obtained weaning weight EBV for maternal weaning weight using the 1998 summer RAAA sire summary.

Estimated breeding values for metabolizable energy for maintenance, MEm_i, were calculated and expressed on a Mcal per day basis. I wanted to express this on a year scale and output predictions with units of Mcal per year. Therefore, I multiplied the existing predictions by 365 d and then divided them in half to be expected progeny differences. Results of the analysis were expressed using descriptive statistics of the EPD and the genetic trend by birth year plot.

CHAPTER IV

RESULTS AND DISCUSSION

Mature Weight Fixed Effects

Contemporary Group. In a preliminary analysis, I evaluated different mature weight contemporary group definitions because previous studies were variable. The simplest definition included herd, year, and season of measurement (Northcutt et al., 1993) and detailed definitions combined both the cow's and the cow's calf weaning contemporary group codes (Bullock et al., 1993).

I tested two contemporary group definitions based on the literature. The simple definition for contemporary group included weaning contemporary group of cow's calf when the cow's mature weight was recorded. The second and more complex definition included both the weaning contemporary group of the cow's calf and weaning contemporary group of the cow.

Using likelihood ratio tests for each age, there appeared to be no benefit to including cow's weaning contemporary group in the mature weight definition (Table 4.1). The results of the F-test and evaluation of changes in mean square error showed a small reduction in error when weaning contemporary group of cow was added to the model. According to the likelihood ratio test, weaning contemporary group of the cow's calf was sufficient and in agreement with previous work. Because mature weight is measured over an individual's lifetime, contemporary groups can change when animals are sold or moved to different locations. Including weaning contemporary group of cow

Table 4.1. Fixed effects tests for contemporary group formation including age, model d.f., error d.f., sums of squares (SS) and sums of squares error(SSE), mean square error (MSE), F-value, and probability level (p) for different definitions of contemporary group (CG)

Age (yr)	Model	Degrees of freedom		SS	SSE	MSE	F value	Pr>F
		Model	Error					
2	CG1[a]	647	6,027	620,723.54	2,113.17	.351		
	CG2[b]	1,441	5,233	621,009.43	1,827.34	.349	1.032	.274
3	CG1	757	4,026	481,377.55	1,591.93	.395		
	CG2	731	3,295	481,614.24	1,355.24	.411	.788	.999
4	CG1	797	2,853	378,302.28	1,291.51	.453		
	CG2	1,514	2,136	378,566.37	1,027.42	.481	.766	.999
5	CG1	717	2,267	346,512.18	1,046.67	.462		
	CG2	1,359	1,625	346,733.27	825.58	.508	.678	.999
6	CG1	636	1,685	294,538.47	786.68	.467		
	CG2	1,204	1,117	294,738.91	586.25	.525	.672	.999
7	CG1	548	1,353	254,696.86	667.88	.494		
	CG2	1,045	856	254,872.68	492.06	.575	.615	.999
8	CG1	463	1,029	211,600.31	517.84	.503		
	CG2	911	581	211,764.95	353.20	.608	.604	.999
9	CG1	412	734	167,032.44	414.54	.565	.	
	CG2	801	345	167,186.41	260.57	.755	.524	.999
10	CG1	312	457	118,993.22	252.21	.552		
	CG2	627	142	119,099.30	146.15	1.030	.327	.999

[a]CG1 = contemporary group of the cow's calf.

[b]CG2 = contemporary group of the cow's calf and contemporary group of the cow.

Table 4.2. Fixed effects tests for cow's age of dam(AOD) and adjusted weaning weight of the cow's calf (WW) including age of animal model and error d.f., sums of squares(SS) and sums of squared error(SSE), mean square error (MSE), F-value, and probability level (p) in Red Angus cattle(Ages 2 to 5 yr)

Age (yr)	Model Fixed effects	Degrees of freedom		SS	SSE	MSE	F value[a]	Pr>F
		Model	Error					
2	MU,CG	766	6,653	691,806.98	2,394.60	.360	-	-
	MU,CG, AOD	773	6,646	691,882.37	2,319.21	.349	30.871	.0000
	MU,CG, AOD, WW	774	6,645	691,887.49	2,314.09	.348	14.713	.0001
3	MU,CG	938	4,446	539,579.04	1,801.62	.405	-	-
	MU,CG, AOD	945	4,439	539,620.66	1,759.99	.396	15.010	.0000
	MU,CG, AOD, WW	946	4,438	539,621.77	1,758.89	.396	2.803	.0943
4	MU,CG	937	3,127	425,567.21	1,461.10	.467	-	-
	MU,CG, AOD	944	3,120	425,596.28	1,432.04	.459	9.051	.0000
	MU,CG, AOD, WW	945	3,119	425,599.94	1,428.37	.458	7.991	.0047
5	MU,CG	859	2,511	393,613.21	1,188.26	.473	-	-
	MU,CG, AOD	866	2,504	393,631.73	1,169.75	.467	5.665	.0000
	MU,CG, AOD, WW	867	2,503	393,632.39	1,169.09	.467	1.413	.2368

[a]This is the F-value for the reduction in error sums of squares. I did not report anything for contemporary group.
[b]The difference between models was negative. P-value couldn't be calculated.

Table 4.3. Fixed effects tests for the cow's age of dam(AOD) and adjusted weaning weight of the cow's calf (WW) including age of animal model and error d.f., sums of squares(SS) and sums of squared error(SSE), mean square error (MSE), F-value, and probability level (p) in Red Angus cattle (Ages 6 to 10 yr)

Age (yr)	Model Fixed effects	Degrees of freedom		SS	SSE	MSE	F value[a]	Pr>F
		Model	Error					
6	MU,CG	789	1,901	347,043.10	947.17	.498	-	-
	MU,CG, AOD	796	1,894	347,057.38	932.89	.493	4.14	.0002
	MU,CG, AOD, WW	797	1,893	347,057.87	932.40	.493	.99	.3198
7	MU,CG	687	1,552	309,094.88	797.19	.514	-	-
	MU,CG, AOD	692	1,547	309,107.91	784.15	.507	3.671	.0007
	MU,CG, AOD, WW	693	1,546	309,115.30	776.76	.502	14.721	.0002
8	MU,CG	612	1,173	253,926.00	606.97	.517	-	-
	MU,CG, AOD	619	1,166	253,931.60	601.40	.516	1.547	.1474
	MU,CG, AOD, WW	620	1,165	253,930.63	602.38	.517	-1.876	1.000[b]
9	MU,CG	555	898	213,957.23	510.22	.568	-	-
	MU,CG, AOD	562	891	213,963.27	504.18	.566	1.524	.1550
	MU,CG, AOD, WW	563	890	213,965.97	501.48	.563	4.796	.0304
10	MU,CG	448	528	155,231.44	311.01	.589	-	-
	MU,CG, AOD	455	521	155,237.77	304.68	.585	1.535	.1532
	MU,CG, AOD, WW	456	520	155,243.00	299.45	.576	1.297	.2552

[a]This is the F-value for the reduction in error sums of squares. I did not report anything for contemporary group.

[b]The difference between models was negative. P-value couldn't be calculated.

would only increase data losses by generating a higher percentage of single animal contemporary groups.

Fixed Effects. The results from fixed effects tests of the cow's age of dam and the cow's calf weaning weight are reported in Table 4.2. In addition to tests of fixed effects, I computed fixed effects estimates and corresponding standard errors (Appendix C). Results showed that there was a significant age of dam effect on mature weight of the cow and fixed effect estimates were higher and more important for weight observations where the cow's dam was younger. Several mature weight age categories showed weaning weight of the cow's calf was statistically important; however, this trend was not consistent. A more important comparison of the fixed effect solutions showed that weaning weight had a small impact on mature weight despite being significant for some mature weight age groups (Appendix C, Tables C.1 to C.3).

Past research with mature weight did not include many fixed effects beyond contemporary group or cow age. Northcutt et al. (1993) included fixed effects of contemporary group (herd-year-month) and pre-adjusted mature weight data for body condition score. Both Kaps et al. (1999) and Bullock et al. (1993) fitted similar fixed effects in their analyses. However, Schafer (1991) and Field (1990) reported a significant effect for age of cow and this was supported by the magnitude of the fixed effects estimates.

I fitted age of dam of the cow and weaning weight of the cow's calf as fixed effects because of the potential impact they would have on weight observations at younger ages (i.e. 2 and 3 yr. of age). It seemed that mature weight research ignored the potential impact of these fixed effects on the prediction of mature weight in beef cattle.

Future studies should determine the impact of other fixed effects on mature weight, including sex of the cow's calf, lactation status of the cow, and the cow's body condition score.

Previous research does not agree on whether to adjust mature weight observations for body condition score (Bullock et al., 1993; Northcutt et al., 1993; Choy et al., 1998). I did not confirm or refute the claims of previous research because body condition score observations were limited in this data set and selectively reported to the RAAA. Furthermore, including body condition as a covariate may only be removing variation for mature weight and consequently reduce genetic variation. A better alternative to adjusting mature weight for body condition is to include it as a separate trait in a multivariate analysis.

Multivariate Analysis

Estimates of heritability, genetic correlations, and residual correlations are reported in Table 4.5 and phenotypic correlations are listed in Table 4.6. I obtained these estimates from multivariate analyses (two-trait) for weight at 2 to 10 yr of age. Table 4.4 lists the number of converged subsamples for each multivariate analysis and those analyses I was unable to obtain variance component estimates. It was not feasible to estimate variance components for every two-trait combination. For some two-trait analyses, a high percentage of estimates would not remain in the parameter space or returned variance components that were not converged. Most of the problems I described were from data sets with a limited number of observations on either or both traits. To

obtain good variance component estimates requires a minimum of 5,000 records and preferably an equal number of observations reported on each trait.

Heritability. Heritability estimates for weight at ages 2 to 10 yr are presented in Table 4.5. In the Red Angus population, mature weight appears to be highly heritable and should respond well to selection. These heritability estimates represent the average of the median estimates from each two trait analysis. I did not analyze more than two traits because there were limited amounts of data in older age groups and simultaneously analyzing all traits (ages 2 to 10 yr) with a multivariate model may be computationally prohibitive.

Estimates from this study at ages 2, 3, and 4 yr agreed with estimates from Brinks et al. (1964) of .57 on fall season mature weight and Kaps et al., (1999) .52 and .53 heritability estimates for asymptotic and repeated measures mature weight. Heritability estimates of heritability were slightly higher for ages 5 to 7 yr of age; however, the differences between estimates are small. At ages 9 and 10 yr of age, I obtained estimates of the heritability of .64 and .78, respectively. Estimates for older ages were higher than most previously reported in the literature. Schafer (1991) reported a heritability estimate of .63 after analyzing average mature weight in Red Angus cattle, but the estimate obtained from Schafer's study had a standard error of .13. A study by Brinks et al. (1962) yielded estimates for fall and spring Hereford mature weight of .73 and .75, respectively.

Heritability estimates from this study were increasing with increasing ages of weight. Table 4.5 shows that at 5 to 10 yr of age there appears to be a higher heritability for cow weight than at younger ages. One could argue that our estimate of heritability at

younger ages, 2 yr, is a result of analyzing younger animals that are still immature. Furthermore, the younger animals are still growing and changing and the heritability estimates may reflect the increased proportion of residual variation. Despite the possible explanations why the estimates at 9 and 10 yr of age are noticeably higher, they were obtained from limited sets of data on highly selected individuals. Furthermore, these estimates may not be different from those reported previously if the standard error is high enough.

I did not report standard errors of the heritability estimates because I obtained estimates from multiple data sets on the same population of animals and with a different number of subsamples per analysis. I attempted to keep the number of subsamples even across each two-trait analysis. It was difficult to do this for data sets with limited data and a higher percentage of estimates outside the parameter space (Table 4.4).

To calculate standard errors for median heritability estimates, I proposed using methods described by Koots et al. (1994) to pool median heritability estimates and report the corresponding standard errors. Because estimates were obtained from the same set of data and in two-trait pairs, the application of this method was not straightforward. In their study, they pooled heritability estimates by adjusting each heritability estimate by the standard error for that analysis. Using these procedures assumes that the analyses came from uncorrelated and independent data sets (H Iyer, personal communication). To correctly implement this procedure requires adjusting for the correlation between estimates.

The heritability estimates reported were the average of median estimates from multiple two-trait analyses. I did not use a more sophisticated procedure to pool median

estimates because of challenges discussed in the previous paragraph. I decided that taking the simple average of median heritability estimates would be sufficient. These estimates were mainly generated to determine more appropriate analytical models for generating mature weight predictions and test the repeated measures model assumptions; therefore, it was not important to have a pooled heritability estimate for each age category. For this study, only the average of median estimates was reported with no subsequent confidence intervals and standard errors.

Table 4.4. Number of usable repeated random 50% subsamples using multivariate Method R variance component procedures with the percentage of estimates that were outside the parameter space in parentheses

Age (yr)	3	4	5	6	7	8	9	10
2	24 (4%)	28 (7%)	24 (0%)	23 (32%)	24 (4%)	23 (34%)	NE	NE
3		22 (0%)	23 (4%)	24 (0%)	23 (15%)	25 (3%)	20 (24%)	3 (72%)
4			25 (0%)	19 (5%)	17 (35%)	19 (3%)	18 (18%)	NE
5				23 (18%)	21 (0%)	19 (24%)	17 (32%)	NE
6					10 (60%)	24 (23%)	23 (8%)	4 (67%)
7						13 (59%)	19 (44%)	NE
8							11 (69%)	4 (78%)
9								NE

[1]NE = A median estimate was not obtained because variance component estimates did not remain in the parameter space. At least 10 method R subsamples were taken to determine feasibility of obtaining an estimate.

Table 4.5. Median heritability, genetic correlation, and residual correlation estimates for weight in Red Angus cattle between ages 2 to 10 yr of age

Age (yr)	2	3	4	5	6	7	8	9	10
2	**.56**[1]	.95 (.93 to .96)	.96 (.94 to .97)	.95 (.94 to .97)	.95 (.90 to .96)	.92 (.90 to .94)	.90 (.86 to .93)	-	-
3	.01 (-.48 to .25)	**.55**	.96 (.94 to .97)	.97 (.97 to .99)	.94 (.92 to .95)	.93 (.91 to .96)	.90 (.88 to .93)	.88 (.82 to .92)	.86 (.56 to .90)
4	.33 (.25 to .40)	-.04 (-.52 to .10)	**.55**	.96 (.95 to .98)	.95 (.92 to .98)	.98 (.95 to .99)	.96 (.92 to .99)	.95 (.90 to .97)	-
5	.17 (.11 to .33)	.19 (.06 to .22)	.03 (-.14 to .15)	**.59**	.98 (.96 to .98)	.98 (.97 to 1.00)	.97 (.94 to .98)	.96 (.93 to .98)	-
6	.40 (.23 to .53)	-.04 (-.16 to .03)	.18 (.01 to .36)	.34 (.22 to .40)	**.60**	.97 (.93 to 1.00)	.96 (.93 to .99)	.94 (.90 to .98)	.89 (.73 to .97)
7	.13 (-.02 to .28)	.03 (-.07 to .07)	.13 (-.06 to .27)	.17 (.10 to .37)	.26 (-.02 to .63)	**.58**	.96 (.94 to .99)	.97 (.94 to .99)	-
8	.14 (-.03 to .37)	.24 (.13 to .34)	.20 (.06 to .26)	.39 (.25 to .46)	.05 (-.08 to .29)	.50 (.25 to .57)	**.50**	.95 (.88 to .98)	.92 (.77 to .99)
9	-	.09 (-.04 to .19)	.08 (.01 to .19)	.21 (.08 to .34)	.11 (.03 to .22)	.33 (.14 to .43)	.44 (-.83 to .51)	**.64**	-
10	-	.07 (-.50 to .49)	-	-	.16 (-.05 to .31)	-	.11 (-.10 to .45)	-	**.78**

[1]The average median heritability estimates are located along the diagonal, the median genetic correlation estimates are above the diagonal and residual correlation estimates are below the diagonal, and 95% CI in parentheses.

Table 4.6. Median phenotypic correlations and 95% CI in parentheses for weight in Red Angus cattle ages 2 to 10 yr

Age (yr)	3	4	5	6	7	8	9	10
2	.61 (.54 to .68)	.68 (.65 to .70)	.68 (.66 to .70)	.69 (.63 to .75)	.62 (.57 to .66)	.62 (.58 to .66)	-	-
3		.65 (.63 to .67)	.69 (.66 to .72)	.54 (.50 to .59)	.59 (.56 to .61)	.61 (.60 to .62)	.58 (.52 to .60)	.52 (.21 to .68)
4			.69 (.67 to .72)	.60 (.54 to .63)	.62 (.54 to .65)	.57 (.54 to .61)	.52 (.49 to .56)	-
5				.71 (.67 to .76)	.69 (.56 to .73)	.63 (.60 to .70)	.57 (.55 to .65)	-
6					.61 (.52 to .73)	.56 (.31 to .59)	.56 (.49 to .66)	.49 (.31 to .68)
7						.65 (.56 to .74)	.67 (.61 to .75)	-
8							.56 (.35 to .68)	.48 (.42 to .54)
9								-
10								-

Correlations. The estimates of the genetic correlations for ages 2 to 10 yr of age were in the range of .86 to .98 (Table 4.5). Interestingly, these estimates were high, greater than .95, for those estimates closest to the diagonal but remained above .90 even as the distance between ages increased. The decrease in correlation estimates was less than I expected to report.

Few estimates are available on the genetic correlation between ages on the same trait over multiple years. In earlier studies, Brinks et al. (1962, 1964) reported estimates of .81 and .93 for the genetic correlation between spring and fall weights on Hereford cows. In the Brinks et al. (1964) study, they also reported genetic correlations between other traits such as 18-mo weight with fall and spring mature weights of .84 and .74, respectively. Field (1990) reported correlation estimates between ages of 18 mo, 30 mo, 42 mo, and 54 mo that were slightly lower than estimates reported in this study; however, there were some estimates that were lower. For example, genetic correlation estimates between 18 mo and 30 mo; 30 mo. and 42 mo; and 42 mo. and 54 mo were .92; .93; and .96, respectively. No standard errors of the estimates were reported for these genetic correlation estimates. A study by Koenen et al. (1998) evaluated live weight in dairy cattle and observed similar results where the genetic correlation estimates between traits averaged .88 to 1.00; however, these estimates were obtained from weights taken at regular intervals during a one lactation.

I do not think it is unusual to estimate high genetic correlations between different weights at different ages, especially, when there are likely numerous genes in common for weight at different ages. In fact, I would expect that the genetic correlation estimate for adjacent traits to be relatively high. The important result is how high the genetic

correlations remain beyond the adjacent ages to those ages of mature weight with more distance (Table 4.5).

Residual correlation estimates are listed in Table 4.5. The residual correlations were less informative because of an erratic pattern. Estimates ranged form -.04 to .50 with large 95% CI. Previously, Brinks et al. (1964) reported residual correlations estimates between 18 mo weight with spring and fall mature weights of .50 and .59, respectively. Field (1990) reported residual correlations ranging from .36 to .94. These estimates were from two trait analyses and analyses between mature weight and average mature weight for ages 2 to 5 yr and 2 to 6 yr.

I presented phenotypic correlation estimates in Table 4.6. These estimates followed a similar pattern to those estimates reported for the genetic correlation (Table 4.5). The phenotypic correlations are moderate to high and remain high even as ages between weights increases. Compared to estimates by Field (1990), these estimates were in close agreement. He reported phenotypic correlations between ages 18 mo to 54 mo of .56 to .78. The traits for their study were recorded at different times and are not directly comparable; however, this pattern of correlations across ages was similar to what appeared in Table 4.6. In comparison to this study, (Brown et al., 1972a) reported phenotypic correlations between asymptotic weight and weights taken at 20 mo, 24 mo, and 36 mo. at .43, .56, and .84, respectively. Brinks et al. (1964) reported a .67 correlation between mature weight and 18 mo. weight and a .87 phenotypic correlation between spring and fall mature weights.

Variance Components. Genetic, residual, and phenotypic variance component estimates are provided in Tables 4.7 and 4.8 (Appendix C, Tables C.5 to C.8) for

individuals 2 to 10 yr of age. Figure 4.1 is a plot of the median diagonal elements of the genetic, residual, and phenotypic variances. I reported estimates of the variances along the diagonal as the average of median estimates at that age using results from two trait analyses. Using the average of median heritability estimates seemed acceptable given the scope of the objective (B. L. Golden, personal communication). The off diagonal covariance estimates were reported as the median values for each two trait analysis. Alternative methods for summarizing the median estimates were investigated, however, it was not necessary to evaluate the results with respect to the objective of testing the repeated measures assumption.

The pattern of genetic, residual and phenotypic variance estimates exhibited an increasing trend as animals aged (Figure 4.1). In response to increases in age and distance between ages, genetic covariance estimates appeared to be increasing in two directions. Brown et al. (1972) observed a similar pattern where genetic and phenotypic variances increased for ages 4 to 36 mo and at maturity for both Hereford and Angus cattle. In different studies with mature weight, researchers reported similar finding and observed increasing genetic and phenotypic variances as animals increased both in age and size (Meyer et al., 1997; Meyer, 1999).

Residual variances (Table 4.8) increased as an animal grew older in size. This is suitable given the other traits scale up with age the magnitude of the residual variance would also scale with age and the rate of change may fluctuate given ages 4 to 7 yr appeared to level off or decrease in magnitude. In general these was an increasing trend between ages 2 and 10 yr of age. Meyer and Hill (1997) observed similar results for ages

2 to 6 yr where the residual variance increased in the beginning and decreased in the later ages.

Repeatability Model Assumptions. A main objective of doing this multivariate analysis was to determine if the application and assumptions of the simple repeated measures model as it applied to mature weight in beef cattle. The assumptions of a repeated measures model include: observations are recorded on the same trait over time, the genetic correlations between observations taken at different ages are unity, environmental correlations between traits are consistent, the covariances between ages is constant as the distance increases between ages, and the magnitude of the variances remains constant or at least consistent over time (Mrode, 1996).

If I based my comparison of the results (Table 4.5) to what was assumed in the model, the repeated measures model would be acceptable for generating genetic predictions for mature weight in beef cattle. For ages 2 to 7 yr, the heritability estimates remain consistent and change from .55 to .60. The more informative results include the genetic and phenotypic correlation estimates. The magnitude and pattern of the genetic correlations across ages remained high and did not decrease rapidly as expected when the distance increased between ages of mature weight. According to Tables 4.5 and 4.6 the simple repeated measures model assumptions were met. There were some discrepancies between the assumptions and results of this analysis, especially at older ages, but these differences may be a function of limited data on older animals.

The summary of estimates for variances and covariances provided a different perspective on how well the repeated measures model assumptions held with mature weight. According to Tables 4.7 and 4.8, scaling variation was present for ages 2 to 10 yr

and it increased as both age and mean weights increased (Figure 4.1). The large changes in variation occurred at the early and later stages of an animal's life, specifically from 2 to 3 yr of age. Meyer (1999) and Arango et al. (2000) reported similar results about the application of a repeated measures model to mature weight data. Each stated that using the repeated measures model did not provide the best fit for mature weight data. Using a random regression approach, Arango et al. (2000) stated that a linear genetic and quartic permanent environmental model provided a superior fit to both the repeatability model and other lower order random regression models.

Using the results of my study combined with previous research, the simple repeated measures model was not the best model for producing mature weight predictions and a better model fit can be achieved with higher order random regression models (Meyer, 1999). In addition the results showed that cow weight at different ages might not be the same trait. The genes controlling weight at 2 and 3 yr of age are expected to be different than the genes for weight at 10 yr of age. Younger ages are still growing and partitioning energy to growth and lactation. In older animals, the differences observed are influenced more by changes in body condition, milking ability, and sometimes age of the animal. It is unlikely the older animals will be expressing any large differences for growth. Therefore, the genes for weight at 2 yr of age should be different than those reported for older age groups.

Table 4.7. Median and 95% confidence limits of genetic (g) and residual (r) covariances for weight in Red Angus Cattle 2 to 10 yr of age (multivariate analyses)

Age (yr)	2 (kg^2)	3	4	5	6	7	8	9	10
2	**893.39 (g)**[1] **684.69 (r)**	1,214.05[1]	1,378.13	1,477.27	1,519.13	1,582.56	1,685.35	-	-
3	10.15	**1,252.36 (g) 984.57 (r)**	1,887.69	1,721.73	1,530.86	1,641.74	1,785.09	2,252.98	4,816.74
4	370.45	-32.28	**1,842.67 (g) 1,461.74 (r)**	2,109.57	1,682.85	1,759.92	2,129.19	2,153.75	-
5	134.68	188.15	20.93	**2,165.19(g) 1,360.75(r)**	2,479.52	1,817.54	2,150.21	2,438.43	-
6	497.63	-50.61	268.54	464.18	**2,668.44(g) 1,786.16(r)**	1,923.14	2,121.31	2,722.19	3,780.43
7	146.09	28.56	170.45	172.11	428.64	**2,804.13(g) 1,520.87(r)**	2,201.67	3,146.88	-
8	141.94	337.60	296.62	674.25	60.77	791.44	**2,794.51(g) 2,206.20(r)**	2,388.22	4,114.67
9	-	139.12	201.51	407.62	182.56	629.66	1,290.49	**4,764.54(g) 2,609.61(r)**	-
10	-	139.97	-	-	720.45	-	1,368.36	-	**17,485.70(g) 10,361.16(r)**

[1]Genetic covariances are above the diagonal and residual covariances below the diagonal. Genetic and residual variances along the diagonal.

Table 4.8. Median phenotypic (co) variance component estimates for weight age classes 2 to 10 yr of age in Red Angus Cattle

Age (yr)	2 (kg^2)	3	4	5	6	7	8	9	10
2	**1,579.17**[1]	1,412.35	1,877.44	1,611.04	2,091.45	1,837.92	1,882.31	-	-
3		**2,287.29**	1873.29	18401.11	1,433.53	1,602.07	2,103.44	2,374.53	4,039.86
4			**3,482.27**	2,356.14	2,206.43	2,073.37	2,320.84	2,513.07	-
5				**3,531.27**	2,785.05	2,169.67	2,620.10	2,971.33	-
6					**4,549.57**	2,959.14	2,366.34	2,955.64	4,077.72
7						**4,079.29**	2,776.42	3,364.11	-
8							**8,686.86**	3,986.20	5,380.84
9								**8,044.49**	-
10									**27,618.31**

[1]Variances on the diagonal are in bold and represent pooled median estimates from bivariate analyses of mature wt. for that age class

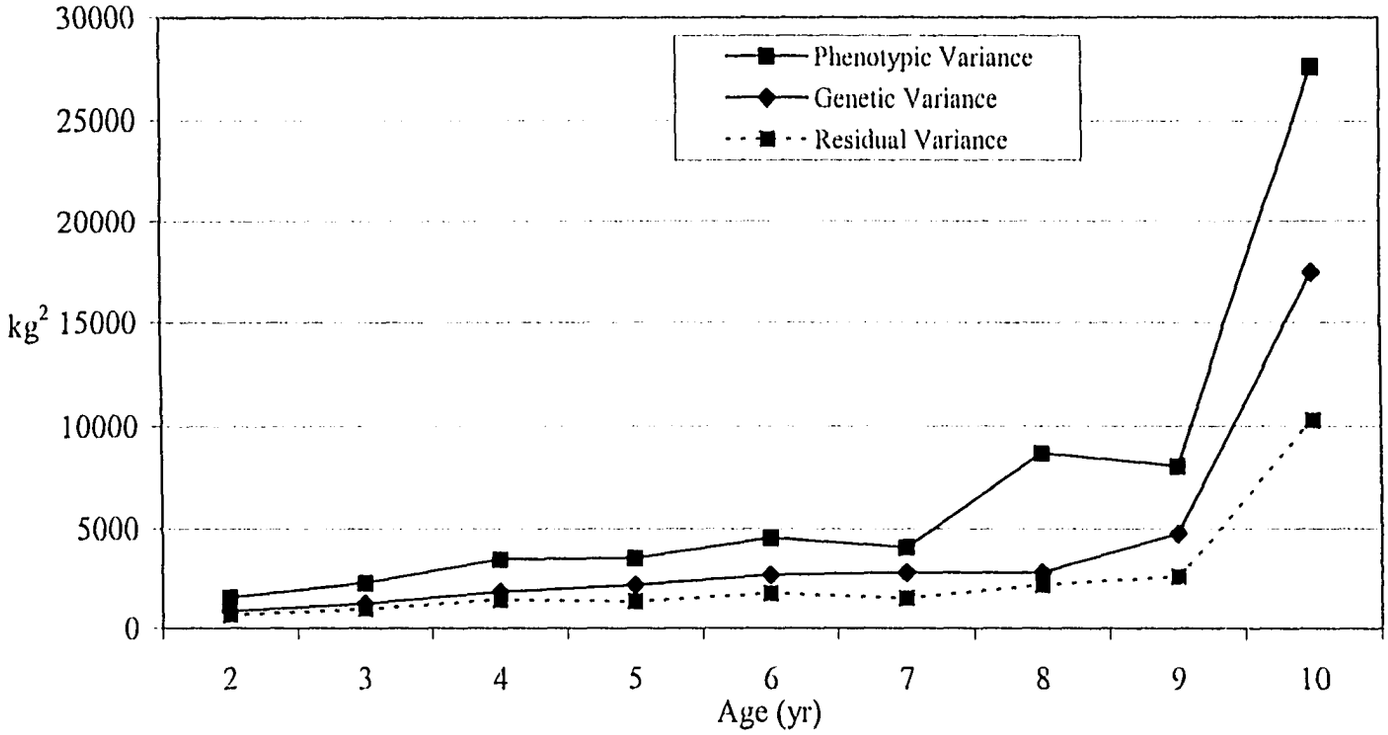

Figure 4.1. Average of median phenotypic, genetic, and residual variances from multivariate (two-trait) analyses of Red Angus mature weight for ages 2 to 10 yr

Univariate Analysis. The results of the univariate variance components analysis for weight at ages 2 to 10 yr are reported in Table 4.9. These estimates were generated from fitting a single trait animal model for each age. I obtained the median and 95% CI of heritability (h^2) estimates from 20 random subsamples of the data..

Previous studies reported mature weight heritability estimates that were in agreement with the range of estimates from my analysis. In prior studies, Northcutt et al. (1993); Koots et al. (1994); Meyer et al. (1995); and Brinks et al. (1964) reported heritability estimates of .48 and .45; .50, .30 to .40; and .52; respectively.

In studies that evaluated mature weight with Angus cattle, Schafer (1991), Northcutt et al. (1993), and Kaps et al. (1999) reported mature weight h^2 estimates of .44; .48; and .51 to .63, respectively. Estimates from the univariate analysis are in agreement with these reported literature estimates. Heritability estimates of Schafer (1991) were estimated from the Beckton Stock Farm herd and represented the best comparisons. The previous estimates from this Red Angus cattle population are in agreement with estimates most h^2 in my study if you consider the magnitude of the estimates.

At older ages, 7 yr of age and older, the heritability estimates declined and the width of 95% CI increased in size. These estimates are lower than what is reported for the multivariate analyses of mature weight. Likely, these lower single trait estimates are the result of using highly selected and limited data for parameter estimation. Heritability estimates from the multivariate analysis are in agreement with the single trait estimates; however, estimates for ages 8 to 10 yr of age are higher in the multivariate analyses (Table 4.9). The higher heritability estimates at older ages might be the result of

correction for culling bias because previously reported mature weights were used (Kaps et al., 1999).

Table 4.9. Number of of 50% random subsamples, median heritability estimates (h^2), standard error of mean (SE), and 95% CI for univariate analyses of weight in Red Angus cattle 2 to 10 yr of age

Age (yr)	[1]N	Median h^2 (SE)	95% CI
2	20	.57 (.008)	.54 to .59
3	20	.54 (.009)	.51 to .56
4	20	.44 (.011)	.41 to .48
5	20	.47 (.017)	.43 to .52
6	20	.52 (.019)	.47 to .56
7	20	.49 (.022)	.40 to .54
8	20	.31 (.032)	.27 to .43
9	20	.42 (.017)	.36 to .48
10	20	.30 (.030)	.22 to .36

[1]N = Number of random 50% subsamples

Repeated Measures Analysis. Variance component estimates and heritability estimates for weights from 2 to 10 yr of age are reported in Tables 4.10 and 4.11. The heritability estimate reported for this study was different from those reported in either the multivariate or univariate analyses. Estimates from the multivariate analyses were higher; however, those differences may not be appreciable because the differences between median estimates were small. Estimates from this study agreed with estimates from univariate analyses of ages 3 and 6 yr. At older ages, the univariate heritability estimates were lower than the repeated measures estimate.

Previously, Schafer (1991) reported a .51 ± .05 heritability estimate for Red Angus mature weight using paternal half-sib analyses with a repeated measures model. A study by Kaps et al. (1999) reported a heritability estimate of .53 from a multivariate

analysis where mature weight in Angus cattle was analyzed with a repeated measures model. Other studies that reported mature weight heritability estimates were Brinks et al. (1964) and Bullock et al. (1993) of .52 to .57 and .52, respectively. According to estimates of previous work, the repeated measures model estimate is acceptable.

Estimates of the proportion of variation attributed to permanent environment were higher than estimates reported by Schafer (1991) because they reported a repeatability of .58. The estimate of repeatability for this study was .78 and in agreement with previous estimates of .75 from Field (1987) and a .77 estimate reported using Angus cattle from the Colorado State University Beef Improvement Center, Saratoga Wyoming (Choy et al., 1998).

Results of this analysis using a repeated measures model on animals 2 to 9 yr of age are favorable compared to estimates reported in the literature. Differences are present compared to previous univariate analyses but it is because the multiple observations per animal and reduction in error of the estimates because multiple traits are being used per animal.

Table 4.10. Estimates of genetic, permanent environment, and residual variance components for weight in Red Angus cattle ages 2 to 9 yr of age using a simple repeated measures model ($N^1 = 40$)

Parameter Estimate	Median (kg^2)	95% CI (kg^2)	SEM (kg^2)
Genetic Variance	1,110.22	1,100.24 to 1,316.41	30.70
Permanent Environmental Variance	581.41	548.71 to 609.58	15.40
Residual Variance	477.66	461.83 to 526.90	12.26

[1]The number of repeated random 50% subsamples for Method R.

Table 4.11. Median heritability (h^2) estimates, 95% CI, and standard error of the mean (SEM) using a simple repeated measures model in Red Angus cattle ages 2 to 9 yr (N^1=40)

Estimate	Median	95% CI	SEM
h^2	.530	.523 to .540	.0046
c^2	.254	.247 to .260	.0037

[1]The number of repeated random 50% subsamples for Method R.

Random Regression Analysis

Validation of Software. I estimated variance components with simulated data sets to validate modifications I made to the Method R Variance components software (B. L. Golden, unpublished) to estimate variance components using random regression models. I used two simulated data sets to validate the procedures for a simple repeated measures model and a random regression model with both a linear additive and linear permanent environmental effect. Results are reported in Figures 4.2 to 4.3. (Appendix C, Tables C.9 to C.15).

Previously, Kuehn (2000) conducted a parameterization study using a linear additive direct genetic random regression model to test the software changes. The results of my study reflect further validation that the software would yield estimates for a permanent environmental effect using the random regression case. Kuehn (2000) showed that variance components could be estimated with Method R procedures and random regression models. I used similar procedures as Kuehn (2000) to do this study and evaluated the impact of including a permanent environmental effect and estimation from a simulated herd.

Repeated Measures Model. I estimated variance components using simulated data for a simple repeated measures model to determine if any differences existed in the

estimates generated using the previous version (ds6; B. L. Golden, unpublished) of the software and my version (dsreg; J. L. Evans, L. A. Kuehn, and B. L. Golden, unpublished). The previous version of the Method R variance components procedures was capable of estimating variance components with a simple repeated measures model. I only generated estimates from five method R subsamples, which was sufficient to determine if both the current and past version of Method R software was returning the same values. I obtained identical estimates from either Method R software package. These results proved that the simple repeated measures model was working properly in the newer, random regression version of the software.

In a separate analysis, I estimated variance components for an intercept random regression model (repeated measures model) with both additive genetic and permanent environmental effects. I reported medians and standard errors of the mean for an eight record data set in Tables 4.12. The results showed variance component estimates for a simple random regression model could be obtained near to the true values. I generated 21 random repeated subsamples for calculation of the medians and standard errors of the mean. Results in Table 4.12 were reasonably close to the true values, but variance component estimates were consistently below the true value. These differences were not important between the true and predicted values. Additionally, there was no strong indication of bias given the true values are captured within the 95% CI. The additive genetic variance and residual variance were reported to be more than one SEM from the true value; however, these differences were small and might be an artifact of the data I simulated data for this analysis.

Table 4.12. Median, 95% CI, and standard error of the mean (SEM) for estimates of additive genetic (G), permanent environmental (PE), and residual variance (E) components from simulated weight data (2 to 9 yr of age) using a repeated measures model (N^1=21)

Parameter Estimate	Median, (kg^2)	95% CI, (kg^2)	SEM, (kg^2)	True Value (kg^2)
G	1,198.46	1,140.06 to 1,357.22	33.021	1,234.05
PE	607.97	582.37 to 639.35	14.640	617.03
E	512.13	509.46 to 516.03	1.019	514.19

[1]N= number of estimates from repeated random 50% subsamples of the data.

Random Regression Model. I summarized the estimates from the linear random regression model variance component analysis with simulated data in Figures 4.2 to 4.8 and Tables (Appendix C, Tables C.9 to C.15). Using a format similar to Kuehn (2000), I reported variance component estimates on the additive genetic and permanent environment intercept term, linear term, and covariance between the intercept and linear terms. To assess how well the true value was being estimated, I included the true values for each variance component on the figures for comparison.

It was possible to obtain variance components with a linear random regression model for both genetic and permanent environment; however, the results indicated that sufficient data were needed to get accurate estimates. Figures 4.2 to 4.8 showed that animals with two or three records would not be sufficient to obtain accurate variance component estimates for the random regression case with both genetic permanent environmental effects. For animals with only two records each, I was unable to obtain any variance component estimates. I did obtain variance component estimates for individuals with 3 records each, but the percentage of converged estimates was less than

50%. Only for those data sets with more than three records per individual was I able to obtain all variance component estimates. It is likely that more data will be required as more components are added to the model and higher order polynomials are fit (K. Meyer, personal communication).

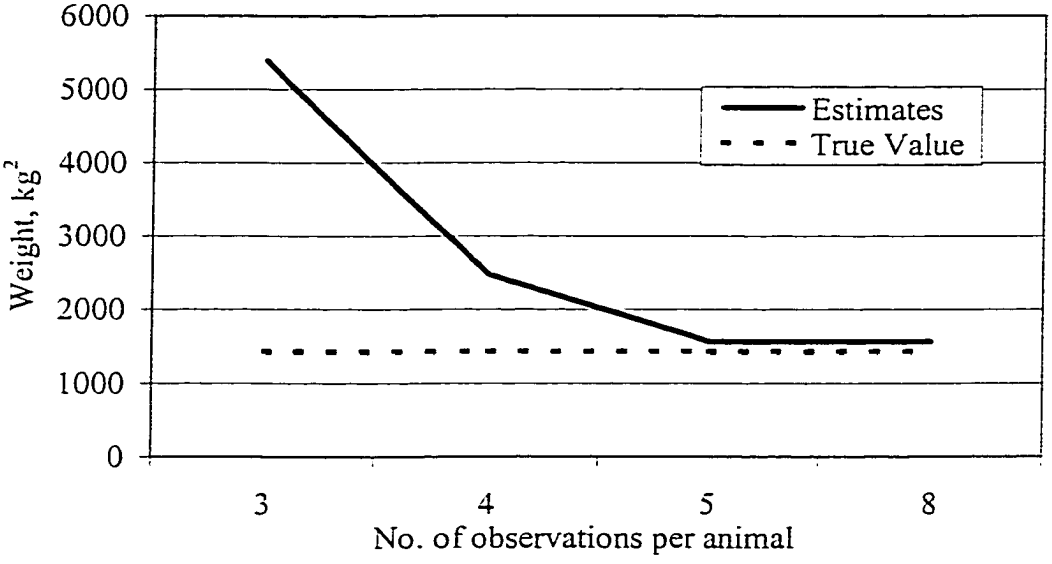

Figure 4.2. Median additive genetic variance component estimates for the intercept term using simulated weight data with 3 to 8 records per animal

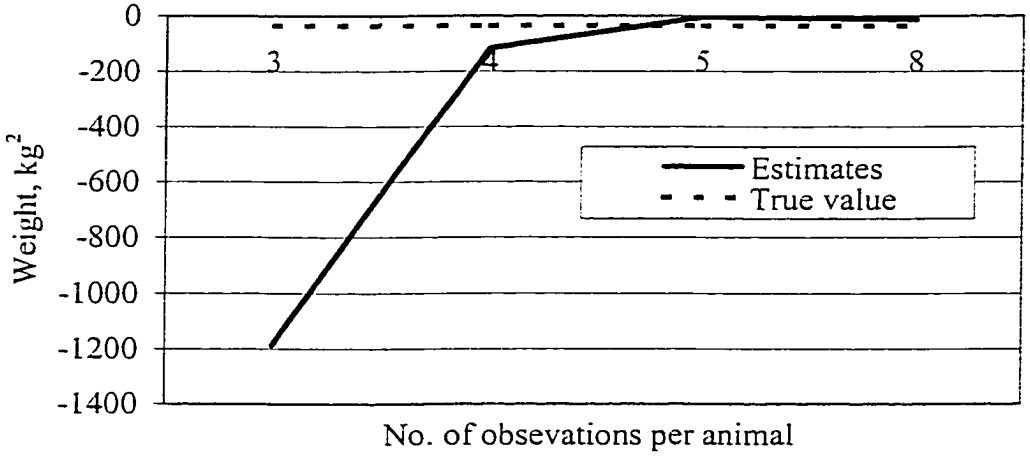

Figure 4.3. Median additive genetic variance component estimtes for the covariance between intercept and linear terms using simulated weight data with 3 to 8 records per animal

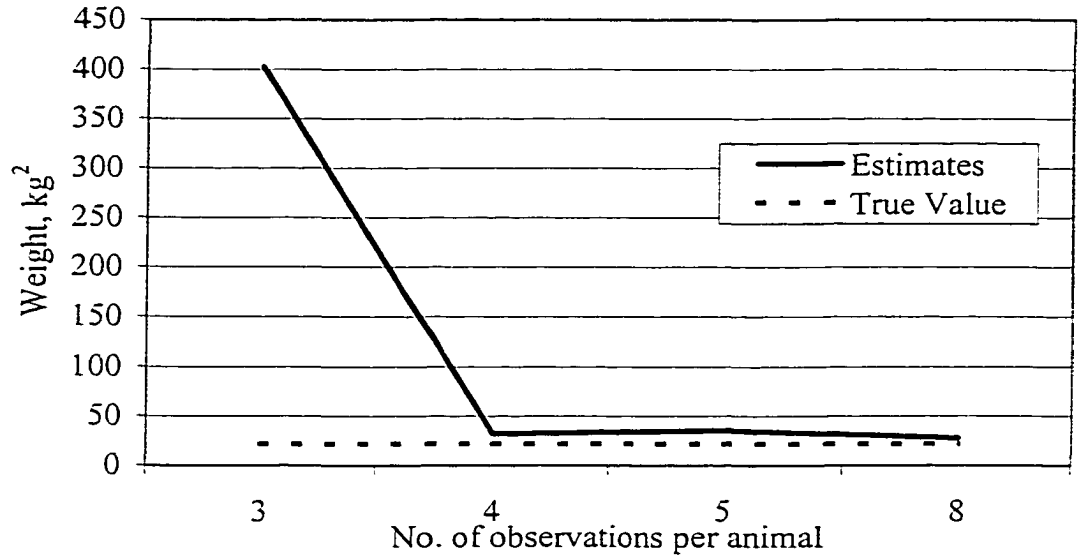

Figure 4.4. Median additive genetic variance component estimates for the linear term using simulated weight data with 3 to 8 records per animal

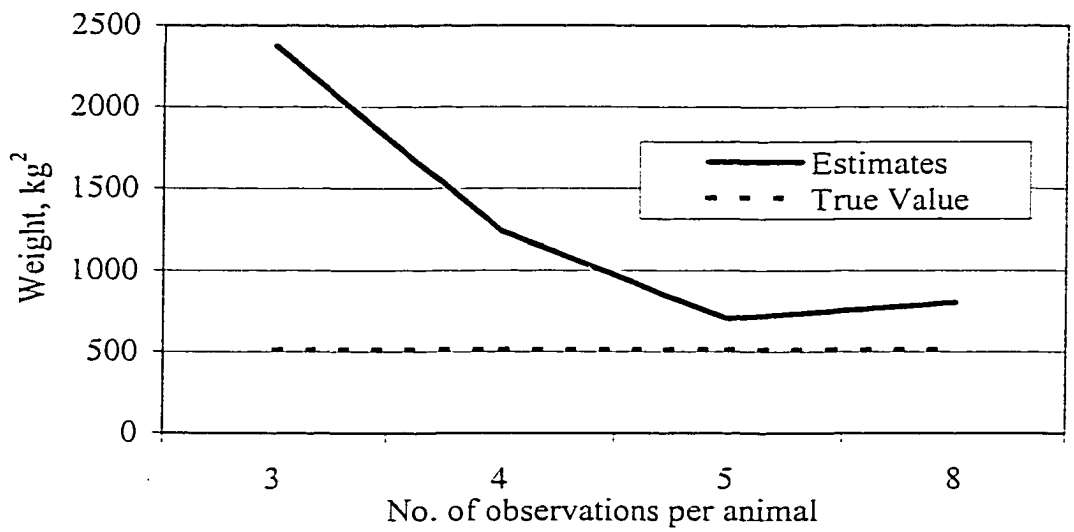

Figure 4.5. Median permanent environmental variance component estimates for the intercept term using simulated weight data with 3 to 8 records per animal

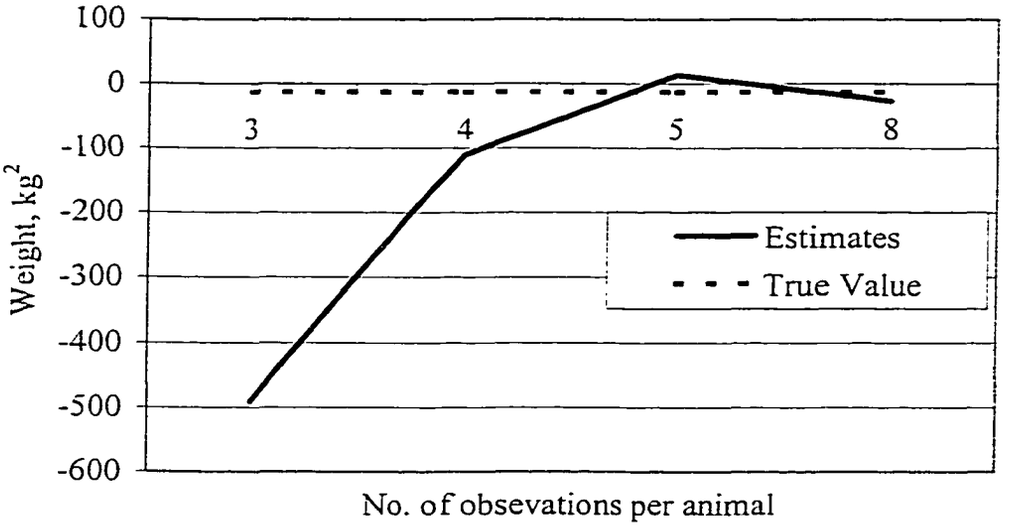

Figure 4.6 . Median permanent environmental variance component estimates for the covariance between the intercept and linear term using simulated weight data with 3 to 8 records per animal

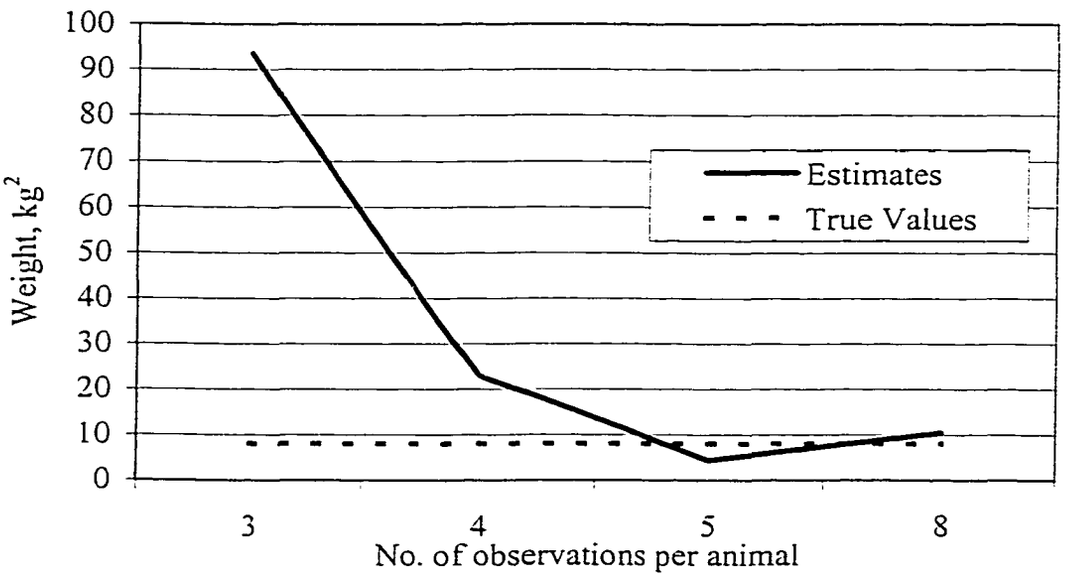

Figure 4.7. Median permanent environmental variance component estimates for the linear term using simulated weight data with 3 to 8 records per animal

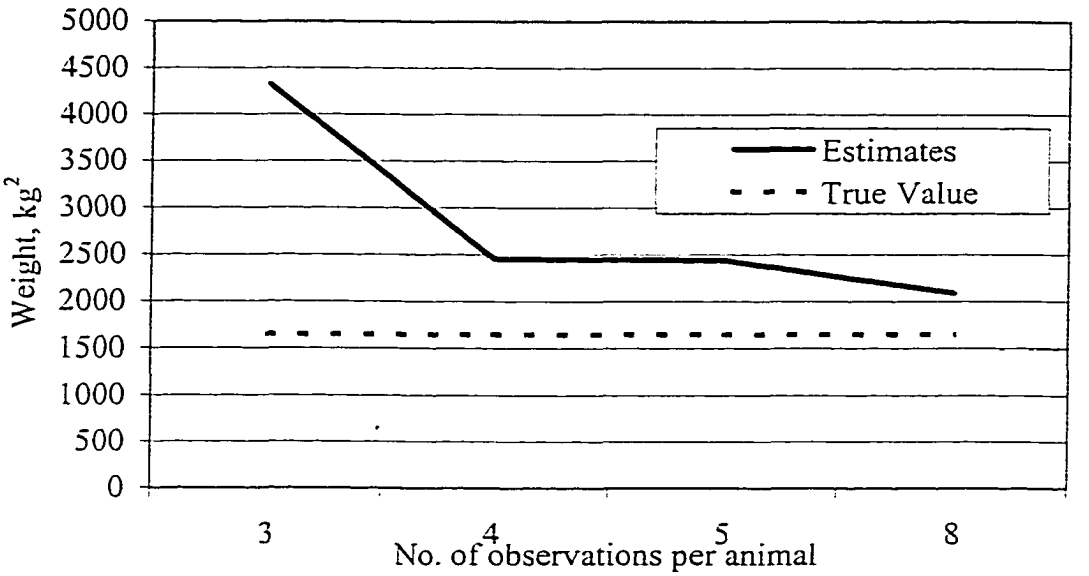

Figure 4.8. Median residual variance component estimates using simulated weight data with 3 to 8 records per animal

The results of the variance components analysis using simulated data were similar to what Kuehn (2000) reported using only a linear random regression model. For each analysis, I obtained median estimates of each variance component from 15 random 50% subsamples. Each figure represents results for each variance component including genetic intercept and linear terms, the permanent environmental intercept and linear terms, the covariances between genetic and permanent environmental terms, and residual error.

Results showed that it was feasible to obtain reliable variance component estimates for a linear random regression model using Method R procedures. At least three weight observations per animal were necessary to estimate variance components for the proposed model and four records per animal were needed to obtain reliable variance component estimates. Kuehn (2000) reported similar findings using only a linear

additive genetic model where 2.5 records were required to obtain estimates. In addition, Kuehn (2000) observed that as more records were added the closer one came to the true value; however, the previous study and results of this study showed a positive bias for each of the variance component estimates.

Additional research is needed to identify the cause of the positive bias being observed in this analysis and Kuehn (2000). Further research is needed to document fitting higher order random regression models using method R variance component procedures.

Variance Component Analysis

Results of the variance components analyses using random regression models for weight at 2 to 9 yr of age are reported in Tables 4.13 to 4.21. For each analysis, I reported the median of estimates for each variance component, the calculated genetic, permanent environmental, and phenotypic variances for ages 2, 4, and 6 yr; and the estimates of heritability and the proportion of variation due to permanent environmental effects (c^2). Two sets of results are reported here using two different models (model 1 and model 2) and two sets of cow weight data.

Random Regression Model 1. The results of the linear random regression model (model 1) for animals 2 to 9 yr of age is reported in Tables 4.13, 4.14, and 4.15. For this random regression model, I included both linear functions for additive genetic and permanent environment. I obtained these estimates from 11 random repeated subsamples. Because of the size of the data and compute feasibility only 11 estimates were generated to calculate the median values.

From the previously described variance component estimates (Table 4.14), I calculated additive genetic, permanent environmental, and phenotypic variances for ages 2, 4, and 6 yr. As I expected, the genetic, permanent environment, and phenotypic variances increased with age of animal, however, there was a small deviation from what I expected for permanent environment variance at 4yr. The median variance at 4 yr of age was lower than previously reported 2 yr permanent environmental variance, but these estimates are not different because of overlapping 95% confidence intervals (95% CI).

Estimates of heritability and the proportion of variation due to permanent environment (c^2) ranged from .543 to .605 and .240 to .234, respectively. Heritability estimates for ages 2, 4, and 6 yr are in agreement with previously reported estimates from the multivariate analyses (Table 4.5). There are small differences between estimates from the multivariate analysis and those from the random regression analysis, but they are not important differences. Using a random regression model for mature weight, Meyer (1999) reported heritability estimates of .42 to .49 for ages 19 mo to 119 mo in Wokalup cattle and .37 to .57 for Hereford cattle. Estimates in this study for 2 and 4 yr animals were in the range of estimates reported and closer to those for Hereford cattle.

Estimates of c^2 ranged from .223 to .240 for ages 2 to 6 yr and these seemed to agree with estimates from the previously reported repeated measures models. In the previously reported repeated measures model, I listed an estimate for c^2 of .254 with a 95% CI of .247 to .260 for animals at ages 2 to 9 yr (Tables 4.10 and 4.11). Meyer (1999) reported estimates of c^2 ranging from approximately .18 to .38.

Estimates of variances and heritability (Tables 4.13 and 4.16) show that weight in Red Angus cattle 2 to 9 yr of age is a heritable trait and these previous heritability

estimates are in agreement with reported estimates from past multivariate analyses. The results also indicate that weight at different ages is not the same trait and variance components scale with age of the animal (Table 4.14). It is incorrect to assume that a repeated measures model is appropriate to predict mature weight over several ages. These results and previous research (Meyer, 1999) are evidence of why random regression models are more appropriate because repeated measures model assumptions are violated.

Other random regression studies with beef cattle (Meyer, 1999; Arango et al., 2000) estimated variance components using higher order functions for mature weight. In some analyses the fit was as high as 4^{th} and 5^{th} order polynomials; however, these estimates were obtained from research beef herds with multiple mature weight observations per year on animals kept in the herd for multiple years. In this analysis, I used Red Angus field data that had a limited number of observations per animal and incomplete data recording. I fitted models of higher orders than the linear reported here but did not successfully obtain variance component estimates in the parameter space.

Beef cattle grow and mature in a nonlinear fashion and it would be ideal to fit a random regression function that is also nonlinear. As described in the previous random regression analysis, I was unable to estimate variance components for more than a linear model and attempts to fit higher order functions failed to yield variance component estimates. In this next study, I applied the same random regression model to a modified mature weight data set to determine if I could fit higher order polynomials. I modified the existing mature weight data to improve the number of observations from 2.23 to 2.54 per animal. I attempted to increase the average to 3.00 records per animal, but this

limited the number of usable observations and reduced the number of individuals in the pedigree.

Using an improved data structure for weights at ages 2 to 7 yr of age, I analyzed the weight data with the same random regression model proposed in the previous analysis. Tables 4.16, 4.17, and 4.18 list estimates of variances and heritabilities obtained for the model components and weight at different ages. I obtained these estimates from 26 repeated random 50% subsamples of the data using a linear random regression model. I fitted higher order functions (e.g., quadratic) for both genetic and permanent environmental effects and did not obtain variance component estimates. A high percentage of the estimates would not stay within the parameters space fitting higher order polynomials terms.

I reported variance component estimates that were, on average, lower in magnitude than reported in the previous study. This translated to the genetic, permanent environmental and phenotypic variances, which were lower in magnitude than results in Table 4.14 for the 2 to 9 yr old data set. Furthermore, heritability estimates in Table 4.18 were higher than those reported in the 2 to 9 yr old data set, which might be a function of analyzing a subset of the larger data set and modifications to data structure. I also observed a decrease in the estimates of permanent environmental variance compared to those estimates reported in Table 4.14.

Random Regression Model 2. In a second group of analyses, I modified the order of fit for the random regression model and removed the age of cow class effect. I decided to make this modification after comparing the models I had fitted to those reported in the literature. I changed the fit of the model to eliminate age as class effect and only fitted as

a covariate. This was intended to model the fixed effects appropriately with the assumptions of the model because weight of the animal was now changing with time. Additionally, I removed the interaction between age of dam and age of cow because the effect was non-significant.

The results of the random regression analysis of weight at ages 2 to 9 yr using modified models from the previous analysis that excluded age of cow are reported in Tables 4.19, 4.20, and 4.21. I obtained these estimates from 10 Method R estimates using 50% subsamples of all the data. Using a modified data set I also obtained estimates of variance components for cow weight at ages 2 to 7 yr of age. The only differences between this analysis and first random regression analyses are the model.

The results of the analysis with modifications to fixed effects did not improve model fit. In fact, I was able to fit linear regression for additive genetic only and an intercept coefficient for permanent environment. Attempts were made to fit higher order polynomials, including using the modified data sets with more records per animal. These analyses, like the previous set of random regression analyses, would not yield reliable variance component estimates. In addition to being unable to fit higher order functions, the results of both analyses yielded extremely high additive genetic, permanent environmental, and residual variance component estimates. These values were several orders of magnitude higher than what had been reported previously in the multivariate or repeated measures analyses (Tables 4.7, 4.8, and 4.10).

Inflated Variances. The results of the second random regression analysis indicated that there was a problem with the magnitude of the variance components estimates. The estimates I obtained from this random regression analysis were extremely

high and not the same magnitude as those reported both in the previous multivariate analysis (Table 4.8). The estimates of variances for weight at different ages compared to Table 4.7 of the multivariate analysis revealed that the random regression results were not realistic despite yielding reasonable heritability estimates for ages 2, 4, and 6 yr of age (Table 4.21).

The inflated variances from the second group of random regression analyses (Tables 4.19) prompted me to evaluate estimates for the first group of analyses. In the first group of random regression analyses, I observed lower increase in the variances when compared to the multivariate analyses; however, the increases were not acceptable compared to multivariate analyses variance component estimates.

The increases in variation I reported for the random regression analysis was uniform; therefore, the estimates of heritability or proportion due to permanent environment appeared reasonable. I fitted additional models that differed in fixed and random effects for permanent environment. These random regression models had fixed effects or permanent environmental effects that were over parameterized and not always the same order (D. Van Vleck, personal communication; Arango et al., 2000). The outcome of the variance components did not change enough to warrant a re-analysis. I also changed the fit of the random regression function for permanent environment. Some recent work suggests that assuming all effects in the model change the same way as an animal ages may be incorrect (D. Van Vleck, personal communication). In past studies, Meyer (1999) consistently assumed that polynomials for permanent environment and additive genetic effects were of the same order. Therefore, I attempted to fit models with different order polynomials with little success.

Table 4.13. Median, 95% CI, and standard error of the mean (SEM) for genetic and permanent environmental variance component estimates for the intercept term (b0), linear term (b1), and covariance between them using a linear random regression model with Red Angus cattle 2 to 9 yr of age (Model 1)($N^1 = 11$)

Parameter Estimate	Median (kg^2)	95% CI (kg^2)	SEM (kg^2)
Genetic			
Var(b0)	6,740.85	6,092.69 to 7,331.72	268.53
Var(b1)	89.05	77.33 to 123.41	7.43
Cov(b1,b0)	5.18	-197.86 to 185.31	58.88
Permanent Environment			
Var(b0)	3,719.64	2,636.10 to 4,030.17	215.92
Var(b1)	58.23	38.26 to 88.23	6.35
Cov(b1,b0)	-124.43	-232.02 to –9.05	34.96
Var(residual)	2,729.73	2,602.89 to 3043.79	64.38

[1]N=number of variance component estimates from random repeated 50% subsamples of the data

Table 4.14. Median, 95% CI, and standard error of the mean (SEM) for genetic, permanent environmental, and phenotypic variance component estimates using a random regression model (linear) at ages 2, 4, and 6yr in Red Angus cattle (Model 1)

Parameter Estimate	Median ,kg^2	95% CI , kg^2	SEM, kg^2
2yrs			
Var(genetic)	7,006.13	6,262.21 to 7800.25	206.18
Var(permanent Env)	3,181.39	2,791.02 to 3,514.99	121.97
Var(phenotypic)	12,744.57	12,045.39 to 14,359.24	294.73
4yrs			
Var(genetic)	8,081.41	6,987.52 to 9,103.41	369.85
Var(permanent Env)	3,148.67	2,950.54 to 3,746.99	110.20
Var(phenotypic)	14,050.54	12,818.94 to 15,529.76	430.14
6yrs			
Var(genetic)	10,179.46	7,744.37 to 11,851.99	617.07
Var(permanent Env)	3,800.47	3,522.48 to 4,528.57	152.66
Var(phenotypic)	16,630.48	14,535.36 to 19,334.74	665.89

Table 4.15. Median h^2 and c^2 (proportion of variance due to permanent environment) estimates with 95% CI and standard error of the mean (SEM) from a linear random regression model using Red Angus cattle 2 to 9 yr of age (Model 1)($N^1 = 11$)

Parameter Estimates	Median	95% CI	SEM
2yrs			
h^2	.543	.521 to .573	.0084
c^2	.240	.224 to .259	.0078
4yrs			
h^2	.570	.548 to .604	.0110
c^2	.223	.215 to .258	.0097
6yrs			
h^2	.605	.540 to .640	.0161
c^2	.234	.198 to .287	.0130
Genetic Corr(b0, b1)	.005	-.263 to .272	.0697

[1]N=number of variance component estimates from random repeated 50% subsamples of the data

Table 4.16. Median, 95% CI, and standard error of the mean (SEM) for genetic and permanenet environmental variance component estimates for the intercept term (b0), linear term (b1), and covariance between them using a linear random regression model with Red Angus cattle 2 to 7 yr of age (Model 1)($N^1 = 26$)

Parameter Estimate	Median (kg^2)	95% CI (kg^2)	SEM (kg^2)
Genetic			
Var(b0)	4,777.70	4,527.13 to 5,064.52	127.511
Var(b1)	92.56	71.57 to 103.66	4.330
Cov(b1,b0)	-137.20	-175.35 to –43.22	21.690
Permanent Environment			
Var(b0)	1,707.46	1,578.94 to 1,807.27	74.500
Var(b1)	38.77	27.04 to 45.04	3.270
Cov(b1,b0)	-73.22	-107.16 to –53.68	11.210
Var(residual)	1,559.84	1,444.60 to 1652.68	45.200

[1]N=number of variance component estimates from random repeated 50% subsamples of the data

Table 4.17. Median, 95% CI, and standard error of the mean (SEM) for genetic, permanent environmental (Env), and phenotypic variance component estimates using a random regression model (linear) at ages 2, 4, and 6yr in Red Angus cattle (Model 1)

Parameter Estimate	Median ,kg^2	95% CI , kg^2	SEM, kg^2
2yrs			
Var(genetic)	4,711.25	4,426.59 to 5,103.47	145.59
Var(permanent Env)	1,566.91	1,463.38 to 1,634.99	51.63
Var(phenotypic)	7,965.50	7,554.26 to 8,283.15	174.00
4yrs			
Var(genetic)	5,383.35	4,936.26 to 5,994.05	218.00
Var(permanent Env)	1,626.45	1,512.13 to 1,822.52	64.55
Var(phenotypic)	8,555.49	8,117.36 to 9,366.84	254.43
6yrs			
Var(genetic)	6,778.78	5,795.16 to 7,815.51	322.51
Var(permanent Env)	2,022.99	1,836.89 to 2,444.00	107.38
Var(phenotypic)	10,729.25	9,306.66 to 11,554.18	376.18

Table 4.18. Median h^2 and c^2 (proportion of variance due to permanent environment) estimates with 95% CI and standard error of the mean (SEM) from a linear random regression model using Red Angus cattle 2 to 7 yr of age (Model 1)(N = 26)

Parameter Estimate	Median	95% CI	SEM
2yrs			
h^2	.600	.585 to .624	.0083
c^2	.203	.177 to .224	.0072
4yrs			
h^2	.615	.596 to .647	.0099
c^2	.193	.169 to .224	.0087
6yrs			
h^2	.638	.623 to .694	.0119
c^2	.206	.166 to .243	.0108
Genetic Corr(bo, b1)	-.198	-.256 to -.056	.0358

[1]N=number of variance component estimates from random repeated 50% subsamples of the data

Table 4.19. Median, 95% CI, and standard error of the mean (SEM) for genetic variance component estimates for the intercept term (b0), linear term (b1), and covariance between them and permanent environmental variance of the intercept (b0) using a linear random regression model with Red Angus cattle 2 to 9 yr of age (Model 2)(N^1 = 10)

Parameter Estimate	Median (kg^2)	95% CI (kg^2)	SEM (kg^2)
Genetic			
Var(b0)	40,545.246	36,074.475 to 49,842.401	2,675.059
Var(b1)	2,743.363	2,464.179 to 3,070.552	88.982
Cov(b1,b0)	-3,159.630	-4,161.538 to –1,915.473	318.695
Permanent Environment			
Var(b0)	22,368.972	20,579.902 to 24,660.712	598.720
Var(residual)	23,421.825	23,235.792 to 23,773.839	83.861

[1]N=number of variance component estimates from random repeated 50% subsamples of the data

Table 4.20. Median, 95% CI, and standard error of the mean (SEM) for genetic and phenotypic variance component estimates using a random regression model (linear) at ages 2, 4, and 6yr in Red Angus cattle 2 to 9 yr of age (Model 2)(N = 10)

Parameter Estimate	Median ,kg^2	95% CI , kg^2	SEM, kg^2
2yrs			
Var(genetic)	38,848.011	38,344.106 to 45,652.583	1,679.7912
Var(phenotypic)	86,440.732	81,030.434 to 90,700.068	1,636.181
4yrs			
Var(genetic)	59,847.080	55,182.357 to 65,417.392	1,586.119
Var(phenotypic)	105,566.302	100,047.614 to 111,655.123	1,605.866
6yrs			
Var(genetic)	99,108.91	94,313.172 to 114,878.266	2970.631
Var(phenotypic)	145,082.142	139,132.357 to 162,671.315	3076.161
Var(permenent env)[1]	22,368.972	20,579.902 to 24,660.712	598.7200

[1]N=number of variance component estimates from random repeated 50% subsamples of the data

Table 4.21. Median h^2 and c^2 (proportion of variance due to permanent environment) estimates with 95% CI and standard error of the mean (SEM) from a linear random regression model using Red Angus cattle 2 to 9 yr of age (Model 2)(N = 10)

Parameter Estimate	Median	95% CI	SEM
2yrs			
h^2	.465	.444 to .503	.0126
c^2	.258	.235 to .285	.0088
4yrs			
h^2	.574	.536 to .592	.0078
c^2	.207	.193 to .240	.0063
6yrs			
h^2	.693	.667 to .708	.0065
c^2	.148	.137 to .168	.0048
Genetic Corr(bo, b1)	-.285	-.372 to -.206	.0212

[1]N=number of variance component estimates from random repeated 50% subsamples of the data

Orthogonalization. In previous studies that estimate variance components using random regression models, the independent variable (i.e., age) is orthogonalized before analysis. Orthogonalization uncorrelates the regression terms, improves compute feasibility, makes it easier to fit higher order polynomials, and makes it feasible to translate the results of the random regression analysis to a covariance function (Van der Werf and Schaeffer, 1997).

In the analysis of mature weight, I standardized and orthogonalized ages of cow prior to estimation of variance components. I was unable to obtain variance components for any random regression model fit. I encountered problems keeping the analysis in the parameter space where I had previously obtained estimates using ordinary age. Using orthogonal ages, I consistently observed negative residual variances. This problem

persisted despite my attempts to change the fixed and random effect in the model. I was not able to overcome the problem of negative error variances. Because I could only fit a linear random regression model I decided to ignore using orthogonal polynomials and continue using ordinary age (B. L. Golden, personal communication).

Repeated Measures Analysis. Variance component estimates and heritabilities from the simple repeated measures model for animals previously analyzed age 2 to 7 yr are provided in Tables 4.22 to 4.24. These estimates were generated to make comparisons between random regression and repeated measures analyses. I obtained estimates of variance components from 10 repeated random 50% subsamples of the data.

Heritability estimates and permanent environmental estimates are reasonable compared to previously reported estimates using a repeated measures model on ages 2 to 9 yr. of age. In a previous analysis with additional data heritabilities were lower and permanent environmental effects c^2 higher but these estimates were obtained using more age categories and additional data from other herds (Table 4.10). Using Angus cattle, Kaps et al. (1999) reported heritability and permanent environmental estimates using a repeated measures model at .53 and .12, respectively.

Table 4.22. Median, 95% CI, and standard error of the mean (SEM) for genetic and environmental variance components from a simple repeated measures model in Red Angus cattle (N = 10)

Parameter Estimate	Median (kg^2)	95% CI (kg^2)	SEM (kg^2)
Genetic Variance			
b0(Intercept)	1,264.07	1,105.82 to 1,357.84	52.46
Permanent Environment Variance			
b0(Intercept)	429.26	329.44 to 480.20	22.94
Residual variance	427.02	362.97 to 504.97	23.28

[1]Repeated measures model includes an intercept term for both the additive genetic and permanent environmental effects of animal.
[1]N=number of variance component estimates from random repeated 50% subsamples of the data

Table 4.23. Median, 95% CI, and standard error of the mean (SEM) for genetic and environmental variance components from a simple repeated measures model and adjusted for heterogeneous variation in Red Angus cattle (N = 10)

Parameter Estimate	Median (kg^2)	95% CI (kg^2)	SEM (kg^2)
Genetic			
Var(b0)	1,486.85	1,302.08 to 1,724.53	68.68
Permanent Environment			
Var(b0)	484.18	400.04 to 528.32	26.75
Var(residual)	519.30	423.65 to 535.26	21.65

[1]N=number of variance component estimates from random repeated 50% subsamples of the data

Table 4.24. Median heritability (h^2) estimates, 95% CI, and standard error of the mean(SEM) using a simple repeated measures model and weight data unscaled and scaled for heterogeneous variance in Red Angus cattle

Parameter Estimate	Median	95% CI	SEM
Unscaled data (N=10)			
h^2	.583	.555 to .621	.0096
c^2	.201	.168 to .227	.0076
Scaled data (N=10)			
h^2	.599	.56 to .652	.0118
c^2	.202	.151 to .219	.0092

[1]N=number of variance component estimates from random repeated 50% subsamples of the data

Table 4.25. Variance component estimates for analysis of random regression models and development of genetic predictions for mature wt. in Red Angus cattle

	Genetic Variance, kg^2		Permanent Environmental Variance, kg^2		Eigenvalue, %*
	Intercept, b0	Linear, b1	Intercept, b0	Linear, b1	
Intercept, b0	1,238.58	.00	.00	.00	98.00
Linear, b1	.00	25.29	.00	.00	2.00
Intercept, b0	.00	.00	424.93	.00	99.00
Linear, b1	.00	.00	.00	4.32	1.00
Residual	426.98				

*Variance component estimates were derived from the eigenvalues of previous studies using random regression models and the variance components of repeated measures model analysis (Meyer and Hill, 1997; Meyer, 1999)

Random Regression Variance Components. Due to the variance components from the random regression analysis being inflated, I had to use alternative methods to generate a new set of random regression variance components. Using the repeated measures variance components from the previous analysis and past literature values to

determine proportions of variation, I calculated random regression variance components for a linear model (Table 4.25).

Heterogeneous Variation. The results of the mature weight multivariate analysis showed that it might be necessary to incorporate heterogeneous error variance when applying random regression models to mature weight. The results listed in Table 4.7 showed scaling of both genetic and residual variation. The current version of Method R variance components software does not estimate heterogeneous residual variation for the single trait case (B. L. Golden, unpublished). Therefore, I researched methods that would be both tractable and available to use for correction of heterogeneous residual variation.

Many animal breeders have estimated variance components for longitudinal data using random regression models (Meyer et al., 1997; Meyer, 1999; Schaeffer, 1999). However, there are differences in the residual variance structures used by various research groups. One difference between studies was the use of a homogeneous or heterogeneous residual error structure. A homogeneous variance structure can be used if covariances remain reasonably constant over time. But, Meyer (1999) reported that heritability estimates do deviate from the expected when there is heterogeneous variation.

In my research with mature weight, I used techniques described by Reverter et al. (1997) to adjust for heterogeneous variation. This analysis was conducted with a subset of the larger mature weight data set to evaluate the importance of adjusting for heterogeneous error variance. First, I applied the multiplicative scaling technique to adjust for variation by age using a simple repeated measures model (Table 4.26). This illustrated that the technique for heterogeneous variation worked and this provided a comparison for the random regression scenario.

The results showed that it is possible to adjust for heterogeneous measurement error variation using multiplicative mixed model equations (Table 4.26). The difference in variation among age categories ranged from 34.76 to 44.8 before scaling mature weight with scaling factors of .76 to .98; however, the range of SD went to 44.3 to 45.9 kg with scaling factors of 1.00 for scaled data. It is obvious that the differences among SD decreased when I applied the multiplicative scaling technique.

I applied a Levene's test for homogeneity of variances to test mature weight age categories both before and after scaling data and determine if the multiplicative procedure reduced variation across ages (Snedecor and Cochran, 1989). Before I adjusted for heterogeneous variation, there was a significant difference in mature weight by age group ($P < .0001$). After the application of multiplicative mixed model equations and adjustment for fixed effects solutions, the differences were non significant ($p = .336$) difference by ages.

It is not necessary to re-estimate variance components after adjustment for heterogeneous error variation, but this can be implemented to project increases in accuracy. In a second analysis with repeated measures model, I estimated variance component and calculated subsequent heritabilities using adjusted mature weight data to determine the impact on both variance components and heritability estimates after scaling. Tables 4.26 and 4.27 report the means, variances and scaling factors by age category, and Table 4.24 reports the estimates of heritability both before and after scaling mature weight data. Results showed no differences in heritability differences from scaling for error variation and scaling factors showed no important differences across

ages; however, I observed an increase in the magnitude of variance component estimates compared to previous estimates with unscaled mature weight data.

Table 4.26. Adjusted Red Angus weight (2 to 7 yr of age) phenotypic means, variances, and scaling factors both before and after correcting for heterogeneous residual variation using a repeated measures model

		Before			After		
Age (yr.)	N	Mean, kg	SD, kg	Scaling factor	Mean, kg	SD, kg	Scaling Factor
2	3,687	-.797	34.763	.7664	-.793	44.321	1.0000
3	3,340	2.081	40.672	.8998	2.946	45.443	1.0000
4	2,537	3.629	44.342	.9753	4.459	45.701	.9999
5	2,178	2.992	44.027	.9700	3.754	45.639	1.0000
6	1,621	3.015	43.284	.9494	3.761	45.811	1.0000
7	1,732	2.147	44.809	.9840	2.747	45.905	1.0000

Table 4.27. Adjusted Red Angus weight (2 to 7 yr of age) phenotypic means, variances, and scaling factors following correction for heterogeneous residual variation and variance component re-estimation using a repeated measures model after re-estimation with scaled data

Age (yr.)	N	Mean, kg	SD, kg^2	Scaling factor
2	3,687	-.699	44.270	.9148
3	3,340	2.987	45.395	.9150
4	2,537	4.482	45.652	.9142
5	2,178	3.779	45.589	.9136
6	1,621	3.779	45.765	.9132
7	1,732	2.764	45.873	.9135

After evaluation of the multiplicative scaling results with the repeated measures model, I applied it the random regression models. Use of the multiplicative equations to adjust for measurement error variation seemed promising for use with Random regression models. Using these techniques, I evaluated and tested the effects of heterogeneous variation both before and after mature weight observations were scaled.

The results of adjusting for heterogeneous variation using a random regression model are reported in Table 4.29. There was no noticeable improvement in the amount of variation present within and across age categories. After scaling the data for heterogeneous variation and doing the adjustment for fixed effects, the scaling factors went to 1.000 but there was an increase in the SD of mature weight by age. Both before and after correction for heterogeneous variation, I calculated significant differences in variances due to age group ($p<.0001$).

The adjustment factors and results of correction for heterogeneous error variance with random regression models deviated from what was expected based upon results of the repeated measures analysis. I expected that the outcome would be similar to what I observed for the simple repeated measures model and this method seemed appropriate for adjusting heterogeneous variation. Prior studies used univariate single component models (Reverter et al., 1997) and Meuwissen et al. (1996) commented that fitting more complex models would be straightforward.

An additional analysis was done to determine if an adjustment for heterogeneous variation was needed and, if so, what contribution does correction for heterogeneous error variance make. Table 4.28 provided information for the correlations between fixed and random effects solutions from analyses with adjusted and unadjusted mature weight data. For the random regression case, fixed effects solutions and estimated breeding values were highly correlated (>.99); but the correlation between breeding values for the linear coefficient term was .96 (Table 4.28). Reverter et al. (1997) reported correlations between estimated breeding values with and without correction for heterogeneous variation of .97 or higher for all traits.

In a second analysis, I calculated sums of squares regression, error and mean square error, and a coefficient of determination to evaluate model fit for the repeated measures model, random regression model without correction for heterogeneous variation, and random regression with correction for heterogeneous variation (Table 4.30). According to the results of the model comparison, the random regression models had a better model fit based upon the mean square error and calculated R^2 for the repeated measures and random regression models for data not adjusted for heterogeneous variation. There was only a 2.7% change in R^2 when I accounted for heterogeneous variation.

Tables 4.28 and 4.30 showed that the impact of adjusting for heterogeneous error variance and the change in breeding values for the different terms in the random regression model was small. Furthermore, the scaling factors are large in magnitude given that the expectation should be one if data require no scaling for heterogeneous variation. Because of the large scaling effect for weight at different ages, the small contribution of improving model fit, and significant Levene's test for heterogeneous variation (Snedecor and Cochran, 1989), I recommend that the data not be adjusted for heterogeneous variation. The technique is valid for application to the random regression case; however, it is difficult to diagnose why these problems occur when working with a field data set; therefore, I recommend doing additional research with simulated data and a research cattle herd to validate the procedure for the random regression model scenario.

Residual Variance Structure. Many random regression papers discuss using heterogeneous error variance structures. For some, the authors applied heterogeneous residual variance except when it was not feasible. For variance component estimation,

several authors estimated covariance matrices for additive direct genetic and permanent environmental regression coefficients, and then estimated a diagonal matrix of residual variances for each observation category. Using lactation records as an example, they estimated residual variances for each test day record in the analysis (i.e. 7 days, 14 days, etc.). Several studies reported fitting homogeneous error variance. The main reason was computational limitations, but in some cases estimates were from earlier work (Strabel et al., 1999).

Random regression studies by Van der Werf et al., (1998) and Strabel and Misztal, (1999) estimated variance components using random regression models with homogeneous error variance. Both groups observed deviations of heritability estimates from the expected at both early and late stages of lactation. The authors used previous multivariate results to make the comparisons.

Both Van der Werf et al. (1998) and Strabel and Misztal (1999) believed that the random regression models did a poor job of modeling the variances at the edges of the polynomial functions. Van der Werf (1998) stated that the polynomial functions were doing a poor job of estimating variance components at the periphery of a function and there were significant deviations from the results of a previous bivariate analysis. At early stages of lactation, Strabel and Misztal (1999) thought the fluctuations were an artifact of single trait random regression models. For the later lactation stages, they attributed changes in heritability estimates to limited data. These results led both groups to recommend using heterogeneous error structures to correct for potential biases.

Using lactation data, Olori et al. (1999) compared variance component estimates from models with either a homogeneous or heterogeneous error structure. Residual

variance estimates were higher in early lactation compared to late lactation, which biased heritability estimates. The authors observed no change in the estimates of additive direct or permanent environmental variance components using heterogeneous over homogeneous residual variance. However, the log-likelihoods increased as the number of error terms per age category increased. Meyer (1999) reported similar results in a study where homogeneous and heterogeneous error variances were used to model mature weight data. The consensus of both studies was that heterogeneous error structures should be used when analyzing longitudinal data with a random regression model.

Transformations. One alternative to using a heterogeneous error structure is to apply a transformation to the data (H. Iyer, personal communication). If an appropriate transformation is used then scaling effects should be minimized. This would allow for application of a random regression model fit with a homogenous error structure. Transformations that might be suitable for the Red Angus mature weight data are a log, cube root, or use of Box-Cox procedures to identify a transformation (1997).

There are challenges with using transformations. An immediate problem with using a transformation is how to interpret the final results. It is possible to overcome this problem by using reverse transformation on the output. Another challenge with transformations is whether all the scaling effects are removed from the data. In an analysis of Simmental weaning weight, Garrick et al. (1989) commented that a transformation does not always remove all the heterogeneity. In animal breeding, the observed heterogeneous variation may be the result of additive and/or multiplicative effects.

Table 4.28. Simple correlations between fixed effects estimates and estimated breeding values generated from a repeated measures or linear random regression model using unscaled and scaled mature wt data

	Correlations	
	Repeated Measures Model	Random Regression Models
Fixed and Random effects Solutions	.9999	.9998
Fixed effects only	.9962	.9961
Genetic (b0), intercept	.9977	.9917
Genetic (b1), linear term	_	.9570
Permanent Environment (b0), intercept	.9957	.9900
Permanent Environment (b1), linear term	_	.9906

Table 4.29. Adjusted Red Angus weight (2 to 7 yr of age) phenotypic means, variances, and scaling factors both before and after correcting for heterogeneous residual variation using a linear random regression model

		Before			After		
Age (yr.)	N	Mean, kg	SD, kg	Scaling factor	Mean, kg	SD, kg^2	Scaling Factor
2	3687	-.099	33.523	.6907	.545	48.398	.9999
3	3340	3.647	39.358	.7141	5.935	55.219	1.000
4	2537	10.295	44.028	.7251	9.132	60.952	1.000
5	2178	5.873	45.773	.6640	9.803	67.896	1.000
6	1621	6.783	46.394	.6055	11.573	73.512	1.000
7	1732	6.004	49.604	.5654	11.102	82.585	1.000

Table 4.30. Model sums of squares (SS), sums of squares error (SSE), mean square error (MSE), and coefficient of determination (R^2) for mature wt. in Red Angus cattle using simple repeated measures model or random regression linear models (Adjusted or unadjusted for scaling variation)

Model	d.f. (Model)	d.f. (Error)	SS	SSE	MSE	R^2
Repeated[a]	1,166	13,929	66,023.00	15,134.14	1.087	.804
Random Regression[b]	1,166	13,929	167,671	10,852.36	.779	.940
Random Regression[c]	1,166	13,929	723,800	24,270	1.742	.967

[a]Model effects included: contemporary group, age of dam, age of cow (class effect), animal, and permanent environment.
[b]Model effects included: contemporary group, age of dam, age of cow (class effect), animal intercept, animal-linear, and permanent environment (intercept and linear terms) and not adjusted for scaling variation.
[c]Model effects included: contemporary group, age of dam, age of cow (class effect), animal intercept, animal-linear, and permanent environment (intercept and linear terms) and adjusted for scaling variation

Model Comparisons

Genetic Predictions. Table 4.31 summarizes the genetic predictions for mature weight using all the Red Angus data available. Using variance components derived from repeated measures analyses, I generated predictions for a random regression model on mature weight. The predictions were generated before I made any comparison with the repeated measures model. Table 4.31 listed the mean, SD, and range of EPD for the intercept, linear coefficient term, and prediction of weight at age 5 yr. Past literature and research (Johnson et al., 1990; Northcutt et al., 1993), estimates of heritability from this study for weight at 5 yr of age, and estimates of fixed effects were used to determine an appropriate age for mature weight. Five years appeared to be an acceptable age to consider weight of an animal mature.

Table 4.31 summarizes the EPD available for the intercept terms, linear coefficient terms, and predictions at 5 yr of age with a random regression function. This was done using all data (N = 56,682) to calculate individual trajectories. A review of Table 4.31 shows that the intercept term has the greatest range of EPD and a higher variation among predictions compared to the range of predictions for the linear term. This was expected because of the proportion of variation set using literature eigenvalues for mature weight. There seems to be sufficient variation for the genetic predictions at 5 yr of age to make change in mature weight through selection.

Table 4.31. Mean, SD, and range of mature weight (MW) expected progeny differences (EPD) for the intercept term (b0), linear term (b1), and linear random regression function (5yr of age, MW-5yr) in Red Angus Cattle (N = 56,682)

	EPD		
	Mean, kg	SD, kg	Range, kg
B0, intercept term	.718	9.977	-42.93 to 57.72
B1, linear term	.449	1.234	-5.54 to 8.56
MW-5yr	2.965	13.589	-54.56 to 79.17

[1]N= Number of unique identification number used to construct the pedigree and numerator relationship matrix (A).

Genetic and Environmental Trends. The genetic and environmental trends for mature weight are represented in Figures 4.9 and 4.10, respectively. For the genetic trend, I reported average estimated breeding values by year of birth for 5 yr old predictions and predictions of both the intercept and linear coefficient terms. Predictions were generated for years 1945 to 1995 even though animals were recorded in 1997 and 1998. The data space for the analysis was from 1970 to 1995 with observations recorded at time of weaning. The slope of the 5 yr mature weight EBV trend was .498 over all years with predictions and .966 for year 1970 to 1995. For the years 1945 to 1965 the genetic trend decreases until about 1970 where there is a change in slope to increasing

mature weight genetic trends. The absolute change in average EBV between years 1965 to 1994 was 25 kg.

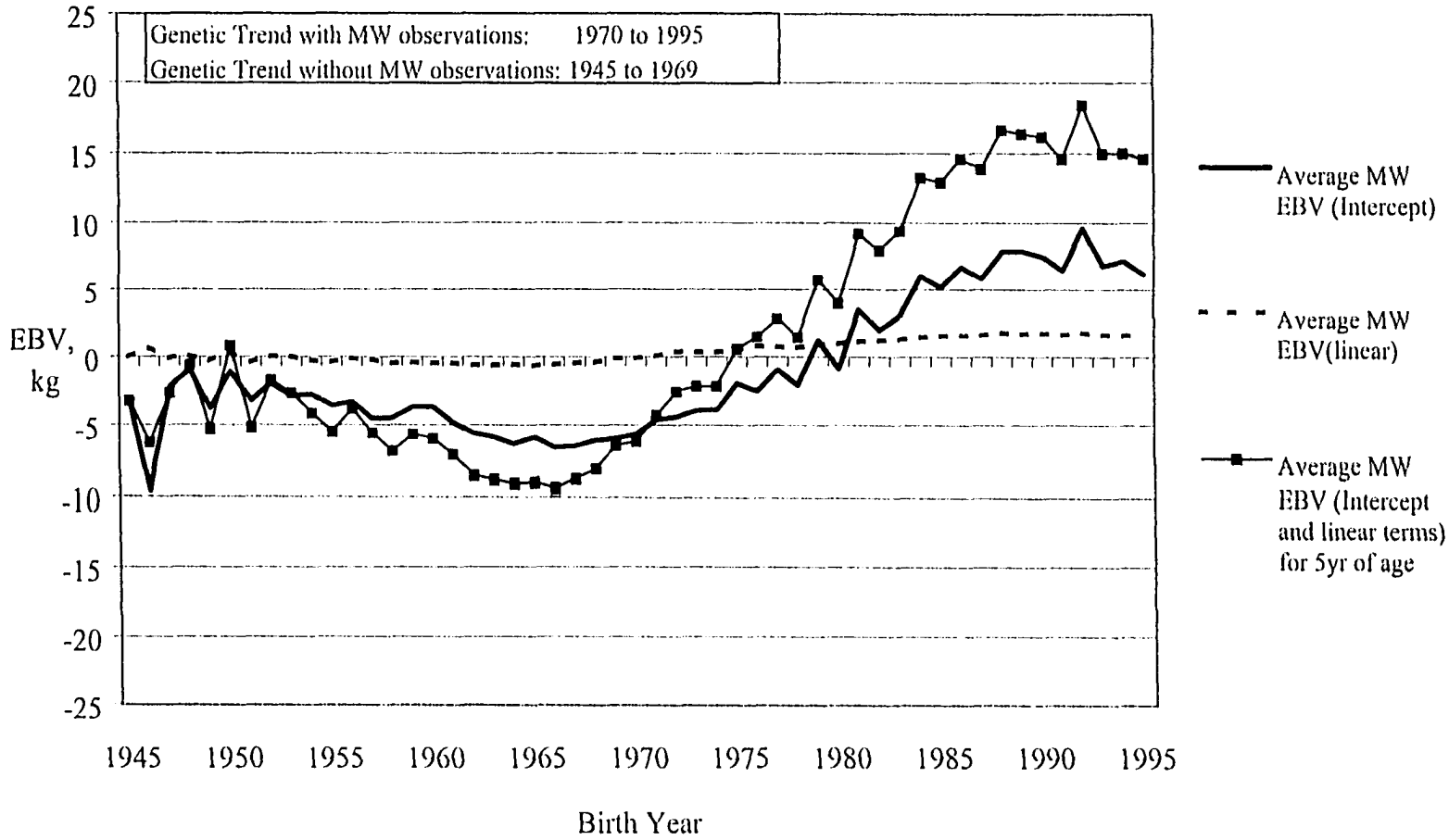

Figure 4.9. Average mature wt. EBV(kg) of the intercept term, linear term at 5 yr of age, and the linear random regression function at 5 yr of age by birth yr. in Red Angus cattle

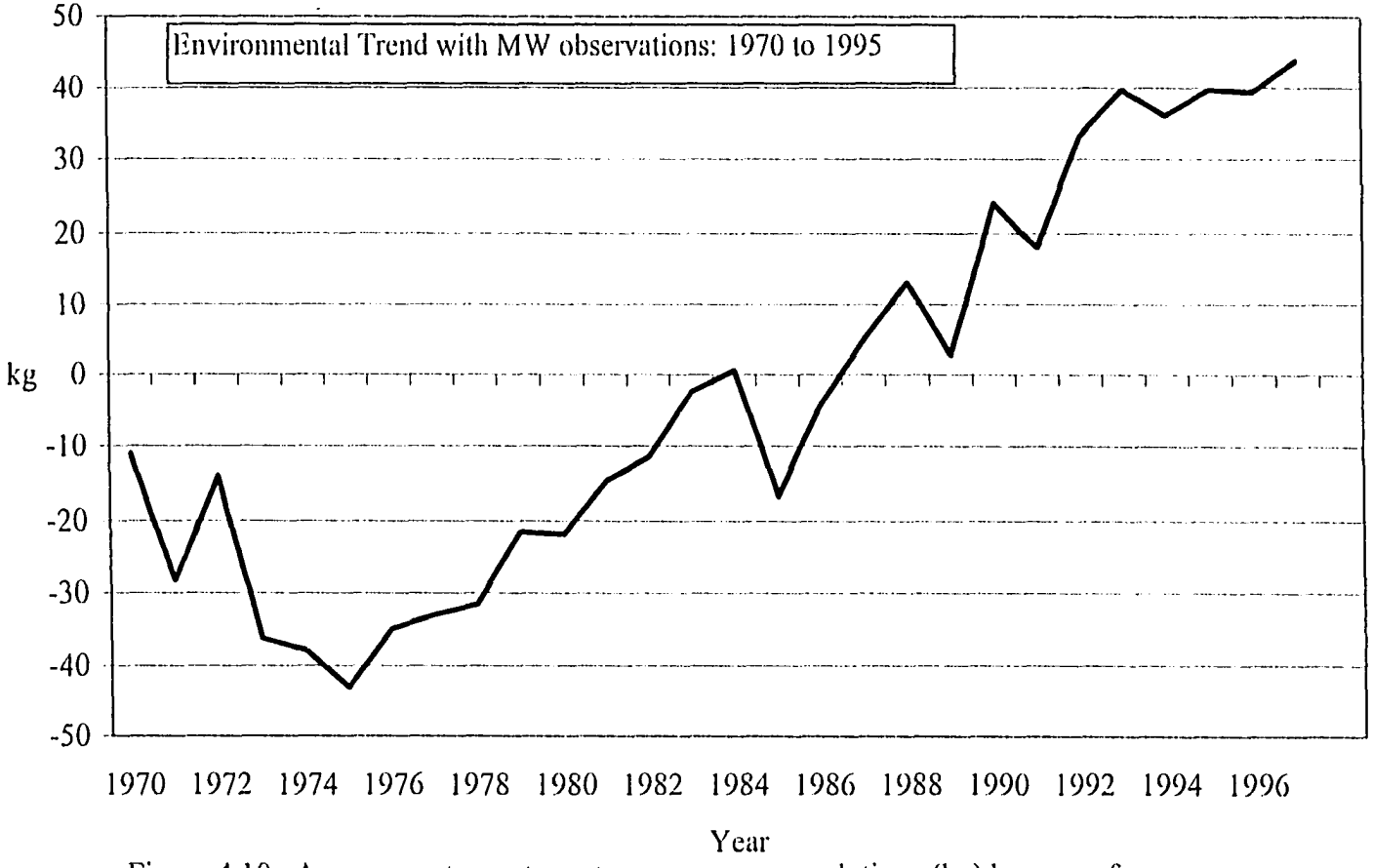

Figure 4.10. Average mature wt. contemporary group solutions (kg) by year of observation for years 1970 to 1997 in Red Angus cattle.

In a previous study with Red Angus data, Schafer (1991) reported an increasing trend using with a slope of .816 kg per year for years 1967 to 1987. However, this genetic trend reflected only one herd and up to 1987. Genetic trends from the 1999 national cattle evaluation for the Red Angus breed show similar patterns of change for other immature growth traits (weaning weight and yearling weight) for the years 1955 to 1999. The difference is that the magnitude of the change over the years is different but illustrates the additive genetic relationship between traits. The trends in immature growth traits reflect an increase and because a prediction has not been available for mature weight in the Red Angus breed mature weight has increased in a similar way.

The environmental trend for mature weight was increasing for years 1970 to 1997 at a rate of .123 kg / yr. For this trend, I reported the average contemporary groups solution by year of observation. In past studies, researchers report trends by birth year. This was not possible for my analysis of mature weight because a contemporary group could have multiple animals of different ages. Instead I used year of the observation to designate it. I thought this would work well because animals of different ages could be part of them and birth year would be difficult to classify a group with multiple individuals. These results contradicted conclusions by Schafer (1991) who reported a decreasing environmental trend of –7 kg / yr. Schafer (1991) attributed the decreasing environmental trend to restricted feed conditions. Furthermore, the author claimed that the expected slope for the genetic trend should be higher; however, the strong downward environmental trend may have tempered it.

Model Comparison. In previous research, random regression models are shown to be superior over the repeated measures model because they overcome the assumptions

of the simple repeat measures model (Meyer, 1999; Arango et al., 2000). As part of the analysis, I compared the outcome of the random regression model with the outcome from the repeated measures model (Tables 4.32 to 4.34).

I attempted to compare models using all the data and concurrently obtain accuracy values and other measures for comparison. I was unable to generate prediction error variances by taking a direct inverse of the coefficient matrix because the problem was intractable with the available computer memory. The size of the linear system for these random regression models made it difficult to take an inverse. Because prediction error variances were not attainable using this method, I could not generate accuracy values by direct methods. In future analyses, accuracy values will be determined from approximations of the breeding values because of the large number of equations and corresponding traits on each animal (Schaeffer et al., 2000). I suggested using a reduced animal model to obtain accuracy values, but did not pursue this method because it had not been validated for the random regression case (B. L. Golden, personal communication).

The first attempt was unsuccessful at generating prediction error variances to calculate accuracy values; therefore, I reduced the size of the data set to make the problem more tractable given the available hardware and memory capabilities. The data used to make comparisons between models was equivalent to what I used to estimate variance components for mature weight and postweaning gain.

The results of the model comparison are reported in Tables 4.32, 4.33, and 4.34. The comparisons included differences by model among sires (N = 1,176) and all animals (N = 14,458)

Using a reduced data set with fewer animals and herds made the problem tractable for comparing the two models. I compared all animals' genetic predictions (EPD) from the repeated measures model to those reported in at 5 yr of age in the random regression (Tables 4.32 to 4.34). The results showed there was a 1 kg difference between the means, but the SD were equivalent, and the range of EPD was less for the repeated measures model compared to the random regression at 5 yr of age. I obtained similar genetic predictions using the random regression model and repeated measures model; however, the random regression model yielded a wider range of EPD. A comparison of sires showed that the repeated measures model and random regression were closer. The average, SD, and range of EPD were all very similar to each other and probably not different from one another (Table 4.32 and 4.33).

In addition to comparing EBV, I also evaluated differences in accuracy values, BIF (1996) accuracy values, and prediction error variances. There were no important differences between accuracy values using regular or BIF (1996) between the repeated measures model and random regression; furthermore, I did not see any important differences among accuracy values for sires. This shows that predictions from the random regression model will achieve equivalent accuracy levels to those from a repeated measures model. Kuehn (2000) observed that predictions from random regression models yielded accuracy values equivalent to those from a single component repeated measures model.

Correlations. In a second comparison, I calculated both the simple and Spearman rank correlations between the EBV from the repeated measures model and random regression model. I provided the results of this analysis in Table 4.34. Comparison of

the repeated measures model with the random regression at ages 2 to 6 yr ranged from .95 to .98 for the simple correlation between estimated breeding values and .944 to .978 for the Spearman rank correlations.

The correlations between breeding values were higher than I expected prior to doing the analysis. It seems that the correlations between solutions from the repeated measures and random regression decreases with age of the prediction; however, this decrease for years 2 to 6 is approximately 3 % (Table 4.34). This change in correlations is most likely a result of genetic predictions being generated as a function in the random regression case. Simple correlations between models for low and high accuracy animal showed no differences between accuracy value groups, but there was a .08 difference with the Spearman rank correlation. It is possible to use the repeated measures model to generate genetic predictions for mature cow weight; however, it is likely that there will be some re-ranking of sires.

In previous studies, comparisons using a likelihood ratio test have been done and shown that random regression models give a better fit to mature weight data (Meyer et al., 1997; Arango et al., 2000). Model fit has been evaluated using log likelihood ratio tests. The results of this study support those conclusions that the fit of a random regression model is superior to the repeated measures model. I would recommend that future mature weight analyses generate genetic predictions with a random regression models to avoid problems with violating assumptions of the simple repeated measures model, predictions can be tailored to a specific age, and it is better for assessing how different animals grow and mature.

Research is needed to determine what model should be fit for a mature weight analysis using field data. Variance components should be estimated from a group of animals with more observations per year because this analysis and those from Kuehn (2000) showed that several observations per animal are needed to obtain reliable variance component estimates for mature weight. Once reliable estimates are obtained for analysis, then predictions can be developed from field data sets with low numbers of observations per animal. Method for determination of accuracy values is also needed or at least a study to determine if good approximations can be developed to determine accuracy levels for genetic predictions from random regression models.

Table 4.32. Mean, standard deviation (SD), and range of expected progeny differences (EPD), prediction error variances (PEV), inbreeding percentage, accuracy, and Beef Improvement Federation accuracy (BIF) from using a repeated measures model on Red Angus mature weight

	Mean	SD	Range
All Animals (N^1 = 14,458)			
EPD, kg	1.852	12.159	-39.739 to 57.492
PEV, kg^2	540.602	294.871	46.262 to 1263.880
Inbreeding, %	.023	.034	.000 to .333
Accuracy	.731	.209	.000 to .982
Accuracy, (BIF)	.373	.166	.000 to .809
Sires (N^1 = 1,176)			
EPD, kg	2.196	11.130	-32.045 to 50.499
PEV, kg^2	696.517	370.388	46.262 to 1257.090
Inbreeding, %	.020	.030	.000 to .289
Accuracy	.619	.269	.073 to .982
Accuracy (BIF)	.295	.218	.003 to .809

[1]N= Number of unique identification numbers used to construct the pedigree and numerator relationship matrix (A).

Table 4.33. Mean, standard deviation (SD), and range of expected progeny differences (EPD), prediction error variances (PEV), inbreeding percentage, accuracy, and Beef Improvement Federation accuracy (BIF) using a random regression model on Red Angus mature weight

	Mean	SD	Range
All Animals (N=14,458)			
EPD (Intercept Term), kg	.073	10.245	-44.417 to 51.661
EPD (Linear Term), kg	.558	1.324	-6.743 to 8.188
EPD (5 yr), kg	2.864	12.910	-50.531 to 67.940
PEV, kg^2	794.317	969.775	144.461 to 4,125.619
Inbreeding, %	.023	.034	.00 to .333
Accuracy	.734	.209	.001 to .982
Accuracy (BIF)	.376	.169	.000 to .813
Sires ([1]N=1,176)			
EPD (Intercept Term), kg	.404	9.179	-30.007 to 39.206
EPD (Linear Term), kg	.528	1.248	-3.763 to 6.390
EPD (5yr), kg	3.04	11.090	-32.346 to 49.268
PEV, kg^2	1,029.406	542.146	144.462 to 4,099.587
Inbreeding, %	.020	.030	.000 to .289
Accuracy	.621	.266	.079 to .982
Accuracy (BIF)	.294	.214	.00316 to .813

[1]N= Number of unique identification numbers used to construct the pedigree and numerator relationship matrix (A).

Table 4.34. Simple and Spearman Rank correlations between estimated breeding values from a simple repeated measures model and random regression at ages 2, 4, 5, 6 yr of age, high and low accuracy animals, and sires in Red Angus cattle

	Linear Correlation	Spearman Rank Correlation
All Animals (N = 14,458)		
2 yr	.981	.978
4 yr	.979	.977
5 yr	.958	.963
6yr	.950	.944
Low Accuracy (<.50)	.967	.962
High Accuracy (>.49)	.971	.970
Sires (N = 1,176)		
5 yr	.958	.957

[1]N= Number of unique identification numbers used to construct the pedigree and numerator relationship matrix (A).

Mature Weight and Weaning Weight

Results of the variance component analyses between weaning weight (WW) and cow weight at 2, 3, and 4 to 9 yr (WW-MW_2, WW-MW_3, and WW-MW_{4-9}) are reported in Tables 4.35 through 4.37. Heritability estimates for MW_2, MW_3, and MW_{4-9}, were .52, .43, and .61, respectively. In previous studies, Brinks et al. (1964), Bullock et al. (1993), and Kaps et al. (1999) reported h^2 estimates for mature weight of .52 and .57, .52, and .50, respectively. Heritability estimates of my study are in agreement with published literature values and show that mature weight is a heritable trait in Red Angus cattle.

Estimates for the proportion of phenotypic variance due to permanent environment for MW_{4-9} was .22 (Tables 4.37). Kaps et al. (1999) previously reported an estimate of .12 in Angus cattle and Schafer (1991) reported an estimate of .07 in Red Angus cattle.

Estimates for h^2 of additive direct genetic weaning weight (WWd) from analyses with MW_2 and MW_3 (Tables 4.35 and 4.36) were similar to prior literature estimates. Koots et al. (1994a) reported a weighted h^2 estimate of .24 for WWd and the RAAA currently uses a h^2 estimate of .23 (RAAA, 1998). In a separate analysis between weaning weight and MW_{4-9}, I obtained a higher h^2 estimate for WWd (Table 4.37).

Heritability estimates for additive genetic maternal weaning weight (WWm) were .35 to .36 (Tables 4.35 to 4.37). Koots et al. (1994a) and Kaps et al. (1999) reported h^2 estimates for WWm of .20 and .17, respectively. Heritability estimates of WWm from this study were higher than previously reported literature estimates (Koots et al., 1994a). The estimates may be inflated because I excluded a random permanent environment effect due to the dam in the model. This was done because estimates between MW_3 and

$MW_{4\ to\ 9}$ mature weight with weaning weight analyses would not remain within the parameter space. I attempted to correct the problem by removing the fixed covariate of age with no success.

Correlations. Genetic correlation estimates for analyses of WWd with MW_2, MW_3, MW_{4-9} were .61, .53, and .81, respectively. Brinks et al. (1964), Northcutt et al. (1993), and Kaps et al. (1999) obtained genetic correlation estimates between mature weight and WW of .59, .62, and .63, respectively. Estimates of the genetic correlations for WWd with $MW_{2(3)}$ agreed with previously reported estimates. However, I estimated a genetic correlation of .81 between WWd and MW_{4-9} (Table 4.37). This estimate agreed with a .85 genetic correlation estimate previously reported by Kaps et al. (1999). They estimated variance components for mature weight and weaning weight using a multivariate animal model and treated mature weight as a repeatedly observed trait. The authors attributed the higher genetic correlation estimate to an increase in the additive direct genetic covariance between mature weight and WWd and a lower temporary environmental covariance due to repeated mature weight observations.

Genetic correlation estimates were near zero for analyses combining WWm with MW_2 and WWm with MW_3 (Table 4.35 and 4.36). However, the genetic correlation estimate for WWm with MW_{4-9} was -.24 (Table 4.37). Kaps et al. (1999) estimated a -.34 and -.45 genetic correlation between WWm and mature weight. There may be a negative additive genetic relationship between WWm and mature weight at different ages. However, estimates from this study and the literature show that the genetic correlation between WWm and cow weight at different ages is not consistently negative.

Further research is needed to confirm the magnitude and direction of the genetic relationship between WWm and cow weight across all ages.

Table 4.35. Median heritability, genetic correlation, and residual correlation estimates from the multivariate analysis between weight at 2 yr of age (MW_2) and weaning weight (WW) in Red Angus Cattle (N=25)

Trait[2]	MW_2	WWd	WWm
MW_2	.52[1]	.61	-.04[1]
	(.49 to .53)	(.59 to .68)	(-.06 to -.02)
WWd		.22	-.12
		(.20 to .24)	(-.15 to -.10)
WWd			.35
			(.34 to .36)
r_e	.61		
	(.58 to .64)		

[1]Heritability estimates are located along the diagonal, genetic correlations above the diagonal, and 95% CI in parentheses.
[2]d = additive direct and m = additive maternal

Table 4.36. Median heritability, genetic correlation, and residual correlation estimates from the multivariate analysis between weight at 3yr of age (MW_3) and weaning weight (WW) in Red Angus Cattle (N=20)

Trait[2]	MW_3	WWd	WWm
MW_3	.43[1]	.53	.01[2]
	(.40 to .47)	(.35 to .56)	(-.11 to .09)
WWd		.20	-.09
		(.17 to .21)	(-.11 to -.04)
WWm			.35
			(.33 to .36)
r_e	.67		
	(.65 to .69)		

[1]Heritability estimates are located along the diagonal, genetic correlations above the diagonal, and 95% CI in parentheses.
[2]d = additive direct and m = additive maternal

Table 4.37. Median heritability, proportion of phenotypic variance due to permanent environment, genetic correlations, and residual correlations (r_e) estimates from the multivariate analysis between weight at 4 to 9 yr. of age (MW_{4-9}) and weaning (WW) in Red Angus Cattle (N=28)

Trait[2]	MW_{4-9}	MW_{pe}	WWd	WWm
MW_{4-9}	.61[1]	–	.81	-.24
	(.58 to .63)		(.78 to .84)	(-.25 to -.20)
MW_{pe}		.22	–	–
		(.20 to .24)		
WWd			.32	-.23
			(.26 to .37)	(-.28 to -.19)
WWm				.36
				(.35 to .38)
r_e	.31			
	(.29 to .34)			

[1]Heritability estimates are located along the diagonal, genetic correlations above the diagonal, and 95% CI in parentheses.
[2]d = additive direct, m = additive maternal, and pe = permanent environment

Mature Weight and Postweaning Gain

Results of variance component analyses of mature weight and postweaning gain are listed in tables 4.38 through 4.42. The heritability estimates of weight at 2, 4, 6, 8, and 2 to 9 yr of age were .57, .46, .62, .54, and .55, respectively. The estimates were in agreement with the literature and previous estimates from the multivariate analysis between weaning weight and mature weight. The estimate for 2 yr of age was higher in this analysis but the differences were small and most likely a function of the number of method R subsamples

The h^2 estimates for postweaning gain with weight at ages 2, 4, 6, 8 and 2 to 9 yr of age were .28, .28, .29, .30, and .31, respectively (Tables 4.38 to 4.42). In previous

studies, Bullock et al. (1993), Golden et al. (1994), and Koots et al. (1994a) reported h^2 estimates of .23, .36, and .29, respectively. However, this postweaning gain h^2 estimate was higher than the .22 currently used by RAAA (RAAA, 1998). The differences we observed in the h^2 estimates for post weaning gain could be due to estimating variance components using an updated data set and cattle from a restricted set of Red Angus breeders. The data used in the analysis were from different breeders previously used to obtain the .22 h^2 estimate.

Correlations. In the multivariate analysis between postweaning gain and mature weight, I estimated genetic correlations at ages 2, 4, 6, 8, and 2 to 9 yr of age of .65, .60, .67, .64, and .68, respectively (Table 4.38 to 4.42). The estimates from this study were lower compared to a previously reported estimate of .76 (Bullock et al., 1993). Koots et al. (1994b) reported a .17 genetic correlation estimate for postweaning gain with mature weight and a .40 genetic correlation estimate for yearling gain with mature weight. The estimates of the genetic correlation between postweaning gain and mature weight remained consistent across analyses.

The results of both the weaning weight and post weaning gain analyses indicate a moderate to strong additive genetic relationship between cow weight at different ages and immature growth traits. If either or both of these immature growth traits is included an analysis with mature weight, the potential exists to increase accuracy of mature weight genetic predictions. A more important benefit to including a completely reported trait like weaning weight is the reduction in selection bias.

It is common for most beef producers to practice some form of selection in their herd. On the female side of the herd their selection includes culling dams for

reproduction, performance of her and her calves, disease, and herd reduction. Because mature weight is recorded only on mature females, it is a highly selected trait especially as animals increase in age. Cows that are 9 yr of age are going to represent a very select group relative to those that are 2 yr of age. This selection introduces bias for the mature weight genetic predictions and a lower level of accuracy relative to some other traits such as weaning weight. Additionally, some breed associations, such as the American Angus Association (Northcutt et al., 1993), will not include cow weights less than 4.5 yr of age. This reduces the amount of information a sire has on daughters and creates a lag effect with gains in accuracy levels.

Mature weight predictions could be improved by including immature growth traits (i.e. weaning weight) into a multiple trait analysis. The RAAA (1999) requires complete reporting of weaning weight; therefore, weaning weight is used as an "anchor trait" in many multiple trait analyses. Because mature weight predictions have limited amounts of data per animal, weaning weight is a good candidate to increase accuracy of prediction for mature weight. This would be a benefit to younger and lower accuracy sires because their daughters are not in production. Besides the advantage of added information, including WW would reduce culling bias and provide information on male siblings.

Table 4.38. Median heritability, proportion of phenotypic variation due to permanent environment, genetic correlations, and residual correlations from the multivariate analysis between postweaning gain (PW) and weight for 2 to 9 yr. of age (MW_{2-9}) in Red Angus Cattle (N = 35)

Trait[2]	MW_{2-9}	MW_{pe}	PW
MW_{2-9}	.55[1]	–	.68
	(.53 to .57)		(.67 to .70)
MW_{pe}	–	.23	–
		(.22 to .25)	
PW	.13	–	.31
	(.12 to .14)		(.29 to .32)

[1]Heritability estimates are located along the diagonal, genetic correlations above the diagonal, residual correlations below the diagonal, and 95% CI in parentheses.
[2]pe = permanent environment.

Table 4.39. Median heritability, genetic correlations, and residual correlations from the multivariate analysis between postweaning gain (PW) and weight at 2 yr of age (MW_2) in Red Angus Cattle (N= 25)

Trait[2]	MW_2	PW
MW_2	.57 (.56 to .60)	.65 (.63 to .69)
PW	.14 (.13 to .18)	.28 (.27 to .30)

[1]Heritability estimates are located along the diagonal, genetic correlations above the diagonal, residual correlations below the diagonal, and 95% CI in parentheses.

Table 4.40. Median heritability, genetic correlations, and residual correlations from the multivariate analysis between postweaning gain (PW) and weight at 4 yr of age (MW_4) in Red Angus Cattle (N= 25)

Trait[2]	MW_4	PW
MW_4	.46 (.41 to .48)	.60 (.50 to .71)
PW	.09(.06 to .11)	.28 (.27 to .30)

[1]Heritability estimates are located along the diagonal, genetic correlations above the diagonal, residual correlations below the diagonal, and 95% CI in parentheses.

Table 4.41. Median heritability, genetic correlations, and residual correlations from the multivariate analysis between postweaning gain (PW) and weight at 6 yr of age (MW_6) in Red Angus Cattle (N=27)

Trait[2]	MW_6	PW
MW_6	.62 (.52 to .67)	.67 (.59 to .73)
PW	.05 (.03 to .07)	.29 (.26 to .31)

[1]Heritability estimates are located along the diagonal, genetic correlations above the diagonal, residual correlations below the diagonal, and 95% CI in parentheses.

Table 4.42. Median heritability, genetic correlations, and residual correlations from the multivariate analysis between postweaning gain (PW) and weight for 8 yr of age (MW) in Red Angus cattle (N = 25)

Trait[2]	MW_8	PW
MW_8	.54 (.51 to .68)	.64 (.47 to .73)
PW	.02 (.00 to .04)	.30 (.27 to .30)

[1]Heritability estimates are located along the diagonal, genetic correlations above the diagonal, residual correlations below the diagonal, and 95% CI in parentheses.

Future Applications. The potential exists to use immature growth traits in a multivariate analysis with cow weight to increase accuracy of mature weight genetic predictions. There is a different and related opportunity to include birth weight, weaning weight, and yearling weight into a random regression analysis with cow weight to model animal growth curves from birth until maturity. Besides modeling growth curves, adding traits to the analysis, such as yearling weight should improve our ability to fit higher order regression functions.

Mature Weight and Stayability

Results of the multivariate analysis between stayability and cow weight for ages 2, 3, and 5 yr of age are reported in Tables 4.43, 4.44, and 4.45, respectively. I obtained these estimates from 45 random repeated 50% subsamples of the data. Using variance component estimates, I reported heritabilities for cow weight at ages 2, 3, and 5 yr of age and stayability as defined by the RAAA (1998); estimates of the genetic correlation between traits and not the residual correlation estimates. The current version of the Method R variance component software using continuous-categorical models has the residual covariance set to zero. In previous studies, researchers have had difficulties with residual variance components going out of the parameter space (Kaiser, 1996).

Heritabilities. Heritability estimates for weight at 2 yr and 3 yr of age (Tables 4.43 and 4.44) were in agreement with previously reported single trait estimates (Table 4.9), except estimates for 5 yr old weight, which were higher than the reported .47 estimate. However, estimates for animals 3 and 5 yr of age from the multivariate analyses were higher at .55 and .59, respectively. In multivariate analyses between different ages of cow weight and stayability (Tables 4.43 to 4.45), I reported 95% CI that captured the multivariate heritability estimate. The differences I observed between heritabilities from this analysis and previous multivariate analyses would have very little impact on genetic predictions.

Estimates of heritability for stayability ranged from .16 to .18 when analyzed with cow weight at different ages (Tables 4.43 to 4.45). These estimates for stayability were higher than previously reported for Red Angus cattle of .123 ± .028, but less than an estimate of .23 for Angus cattle (Snelling, 1994; Snelling et al., 1995). I attributed the

differences in heritability estimates between Snelling et al. (1995) and this study to heritability estimates being derived from different populations.

Correlations. Estimates of the genetic correlation between stayability and 2, 3, and 5 yr old weight were .28, .03, and .04, respectively (Tables 4.43 to 4.45). The estimate between weight at 2 yr of age and stayability shows the presence of a linear genetic relationship between traits. Selection for either stayability or 2 yr weight would result in an increase in breeding value for the other trait. In subsequent analyses between stayability and weight at 3 and 5 yr of age the genetic correlations were near zero meaning that changes in one trait are not linear compared to changes in the second trait.

There is a limited amount of research on the genetic relationship between mature weight and reproduction in mature animals. Koots et al. (1994b) reported a -.02 genetic correlation between mature cow weight and conception rate. The low number of studies on mature weight and sustained fertility is partially a function of stayability being a new trait in beef cattle and belief that reproductive traits are lowly heritable (Snelling et al., 1995; Evans et al., 1999).

According to the results of the stayability with 2 yr old weight analysis, there is a linear genetic association between traits; however, this changes with increases in age at which mature weight is observed. I could argue that the traits of cow weight at 3 and 5 yr of age are different traits; therefore, the additive genetic relationship between them and stayability are different compared to individuals at age two. The traits might be different, but previous work shows that the genetic relationship between traits is high (>.90) and that many of the genes for weight at 2 yr of age are very similar to those for 3 yr of age. For the stayability analysis with 3 and 5 yr old weight, I expected that the genetic

correlation between stayability and weight at 3 and 5 yr of age would be positive and different from zero. My expectation was based on the previous analysis with 2 yr old weight and the high additive genetic relationship between traits at different ages (Table 4.43).

Table 4.43. Estimates of heritability and the genetic correlation from the multivariate analysis between weight at 2 yr of age (MW_2) and staybility (ST) in Red Angus cattle ($N^2 = 45$)

	MW_2	ST
MW_2	.58 (.56 to .60)	.28 (.18 to .31)
ST	-	.18 (.15 to .19)

[1]Heritability estimates are located along the diagonal, genetic correlations above the diagonal, and 95% CI in parentheses. The residual correlation was not estimable
[2]N = Number of random 50% subsamples.

Table 4.44. Estimates of heritability and the genetic correlation from the multivariate analysis between weight at 3 yr of age (MW_3) and staybility (ST) in Red Angus cattle ($N^2 = 45$)

	MW_3	ST
MW_3	.52 (.51 to .53)	.03 (-.02 to .09)
ST	-	.16 (.15 to .18)

[1]Heritability estimates are located along the diagonal, genetic correlations above the diagonal, and 95% CI in parentheses. A residual correlation was not estimable
[2]N = Number of random 50% subsamples.

Table 4.45. Estimates of heritability and the genetic correlation from the multivariate analysis between weight at 5 yr of age (MW_5) and staybility (ST) in Red Angus cattle ($N^2 = 45$)

	MW_5	ST
MW_5	.54 (.51 to .57)	.04 (-.02 to .10)
ST	-	.16 (.15 to .18)

[1]Heritability estimates are located along the diagonal, genetic correlations above the diagonal, and 95% CI in parentheses. A residual correlation was not estimable
[2]N = Number of random 50% subsamples.

Additive Genetic Groups. The previous multivariate analysis was evidence for a non-linear relationship between traits. If this nonlinear relationship was present between

weight at ages 3 and 5 yr of age than linear analytical procedures were not effective in reveling this genetic relationship. The following lists the results of analyses of additive genetic groups analyses to determine if a nonlinear genetic relationship was present between traits.

In the first set of additive genetic groups analyses, foundation animals were assigned to groups based on their estimated breeding values (EBV) to form four equal-sized genetic groups. The results of the analysis confirmed the presence of a nonlinear additive genetic relationship between stayability and mature weight (Figures 4.11, 4.12, and 4.13). For each of the figures, there appeared to be an initial decrease in stayability from group 1 to group 2 and then an increasing trend in stayability for mature weight groups 2 to 4. This is evidence for a near zero genetic correlation between stayability and mature weight at ages 3 and 5 years; however, I interpreted these results with caution because of a high SD on some additive genetic groups (Appendix C, Tables C.16, C.20, and C.24).

This preliminary additive genetic groups analysis (Figures 4.11 and 4.13) confirmed why the genetic correlation estimates between stayability and weight at 3 and 5 yr were near zero. The results were evidence for a nonlinear relationship between traits; however, the pattern of this nonlinear relationship did not follow my prior expectations. Prior to the analysis, I expected to see the additive genetic groups solutions favor the small and moderate body weight animals for stayability, instead I observed a large decrease in the second weight genetic group and the largest weight group had higher stayability than the other genetic groups. It was possible that individuals with very different profiles for other growth traits (i.e. yearling weight EPD) were present in

the same weight genetic groups. If this were true, this may have affected the outcome for stayability genetic groups and made them difficult to interpret.

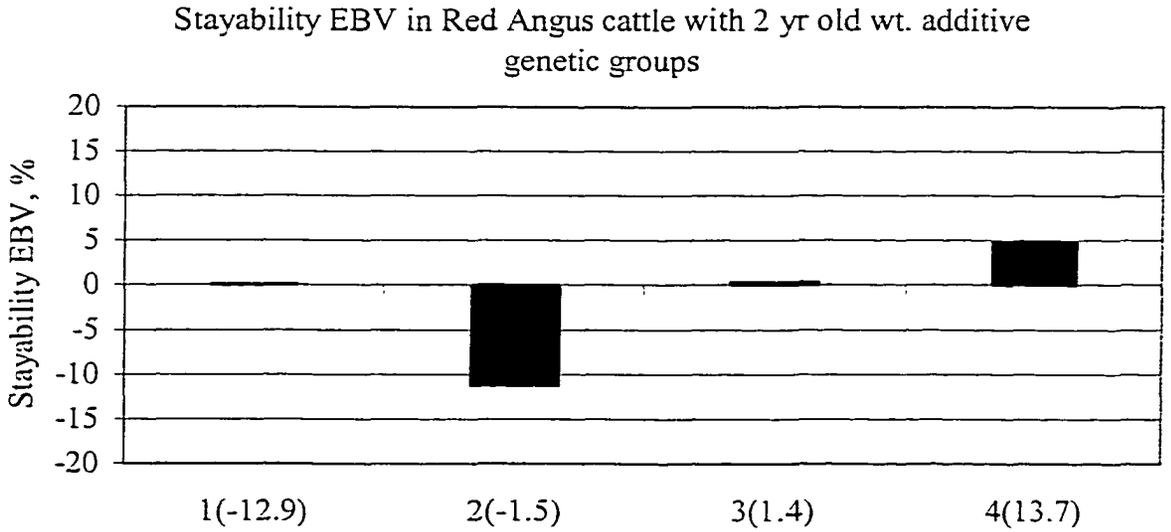

Figure 4.11 . Group solutions of low (1), low-middle (2), high-middle(3), and high(4) 2 yr wt on stayability expressed as a deviation from the low 2 yr old wt group with the average weight EBV (kg) grouped by observations in parentheses.

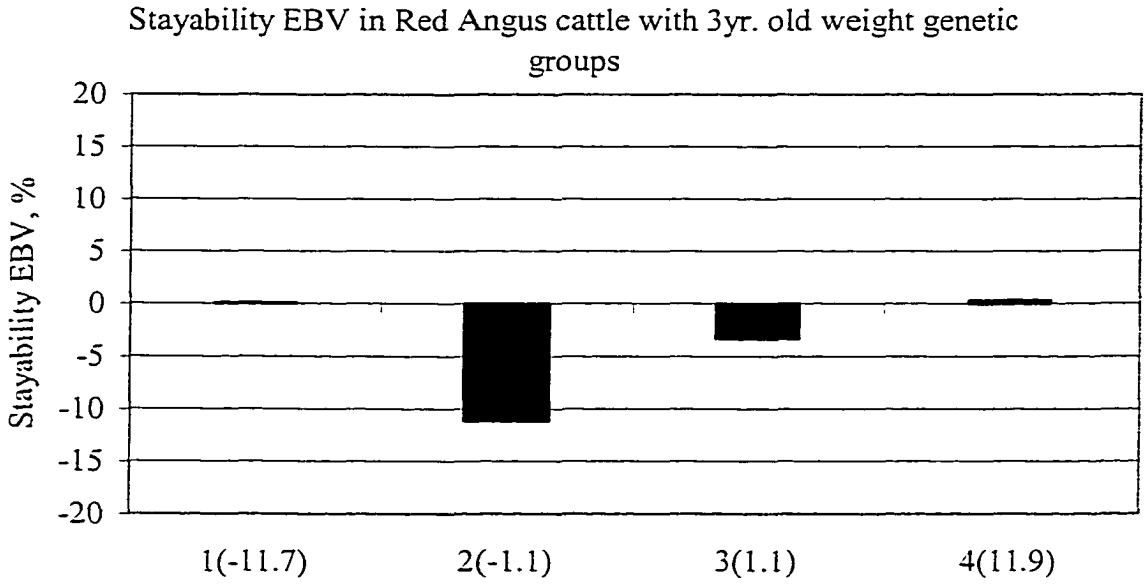

Figure 4.12. Group solutions of low (1), low-middle (2), high-middle(3), and high(4) 3 yr old weight on stayability expressed as a deviation from the low weight group with the average weight (kg) EBV grouped by observations in parentheses.

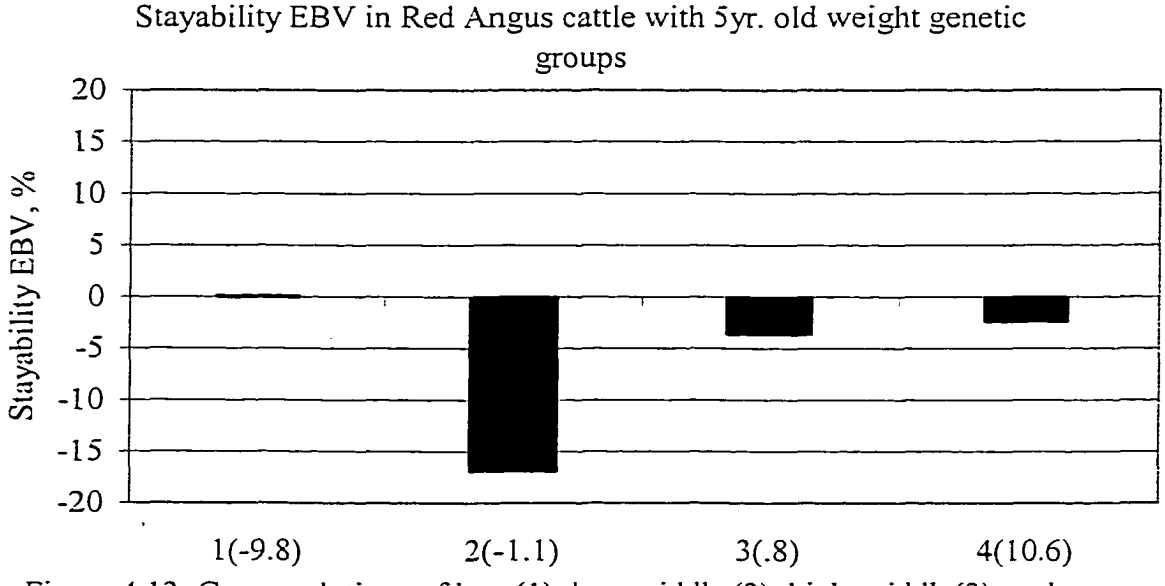

Figure 4.13. Group solutions of low (1), low-middle (2), high-middle(3), and high(4) 5yr old weight on stayability expressed as a deviation from the low weight group with the average mature wt EBV grouped by observations in parentheses.

In a second analysis, B. L. Golden and R. M. Bourdon (personal communication) recommended modifying the way I assigned foundation animals to additive genetic groups to improve our understanding of the group of results. Groups were formed using standard deviations from the mean, equal distances of breeding values, and subdividing the mature weight groups with equal observations into low and high yearling weight groups.

The analysis between 2 yr old weight with stayability revealed that a nonlinear relationship might be present between traits (Figure 4.14 to 4.16). In Figure 4.15 there was a increasing trend for stayability across mature weight with individuals grouped by equal lengths of EBVs. This pattern is not linear, but evidence for the .20 genetic correlation I estimated between 2 yr old weight and stayability. Figures 4.14 and 4.16 both showed nonlinear patterns between traits and differences for yearling weight within a weight group were observed in Figure 4.16. When I grouped animals into low and high yearling weight categories within an adult weight group, I saw important differences for adult weight groups (Figure 4.16).

In the lowest adult weight group, there was a 12.3 kg difference between the yearling weight subgroups. This difference was one explanation why the genetic groups for the lowest mature weight group was different than a high yearling weight group within the same adult weight group. This problem seems to be corrected for in the high-middle adult weight group but on the high mature weight group there was separation between the low and high yearling weight subgroups. Animals with very different yearling weight breeding values in either the high or low adult weight groups can distort the results for stayability. Using the yearling weight subgroups helped to reveal some of

the unusual things being observed in the early genetic groups analyses. Each figure is evidence of a nonlinear association between traits and Figure 4.15 gives some explains why I am observing the results on the extreme groups that originally seemed counterintuitive.

Figures 4.17, 4.18, and 4.19 (Appendix C, Tables C.20 to C.23) represent alternative genetic groups strategies for animals of the 3 yr old weight group. There were similarities in this analysis to the results of the 2 yr old weight with stayability analysis. Figure 4.17 had group solutions for weight that were scaled lower than the two year old equivalents and Figure 4.18 was less informative because of the high SD for each of the group solutions (Appendix C, Table C.23). The analysis with mature weight groups subdivided by yearling weight exhibited similar pattern to the two yr old analysis but there were differences in the magnitude of the solutions. The group solutions of the middle mature weight genetic groups were not different from zero because of high SD for the group solutions. It is difficult to interpret differences among groups solutions given the solutions are not different from zero.

I observed no important differences in the reported results of the 5 yr old weight with stayability analysis (Figures 4.20, 4.21, and 4.22). The results of this analysis do not appear different than previously reported 3 yr old weight with stayability analyses. The only differences I observed were changes in magnitude of the solutions.

The alternative genetic grouping strategies helped to differentiate and explain results from previous groups analyses. Animals that are part of the same mature weight genetic group may be different for other traits such as milk, growth, and fertility. If the

differences are drastic within a mature weight genetic group, results can be misleading and hard to interpret.

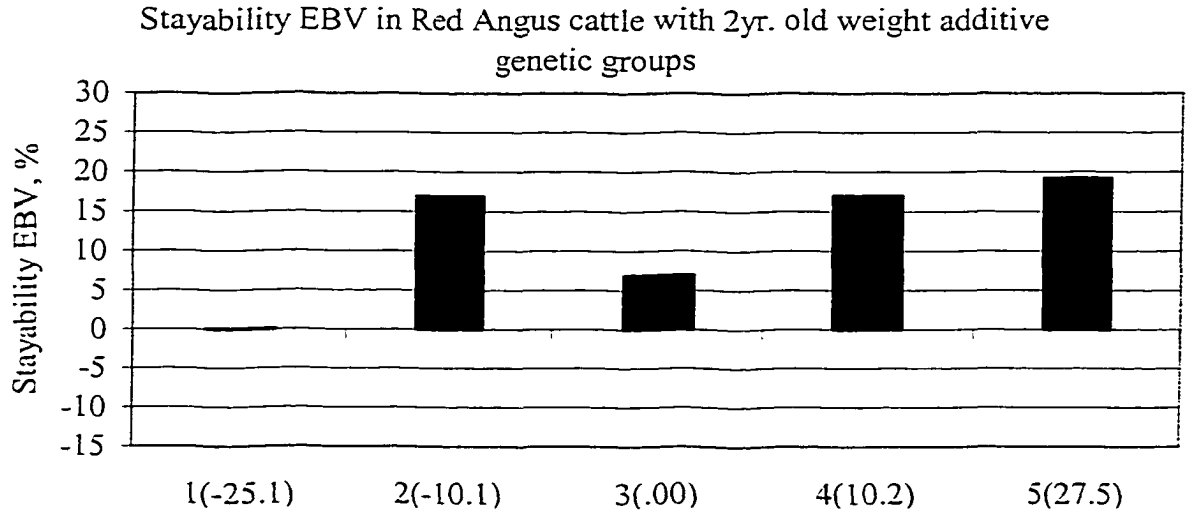

Figure 4.14. Group solutions of low (1), low-middle (2), middle (3), high-middle(4), and high(5) 2yr weight on stayability expressed as a deviation from the low weight group with the average weight EBV (kg) grouped by standard deviation from the mean in parentheses.

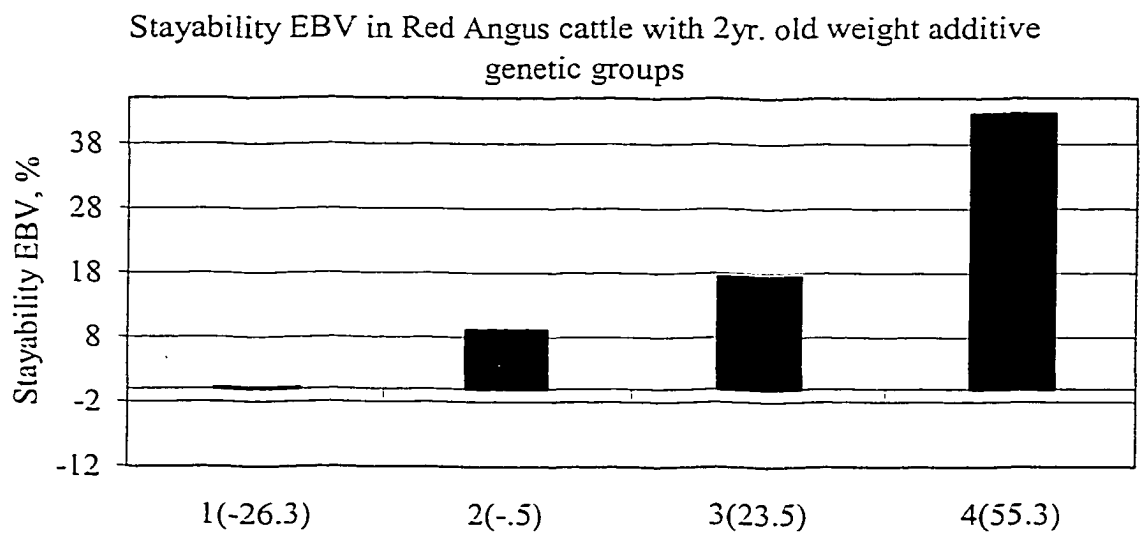

Figure 4.15. Group solutions of low (1), low-middle (2), high-middle(3), and high(4) 2yr old weight on stayability expressed as a deviation from the low weight group with the average weight EBV(kg) grouped by equal strides of breeding values parentheses.

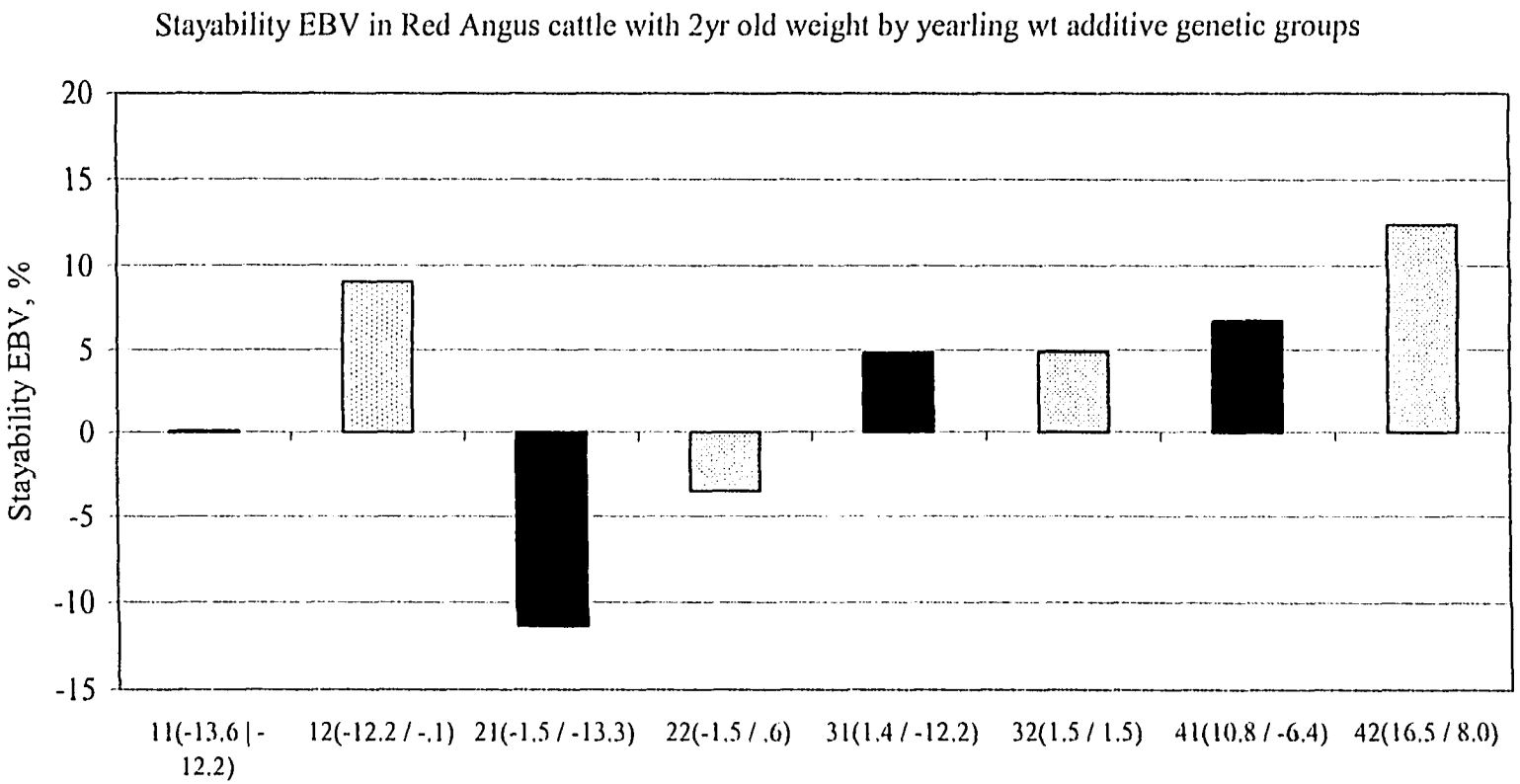

Figure 4.16. Group solutions of low (11,12) low-middle(21,22), high-middle(31, 32), and high (41,42) 2yr old weight(MW)-- yearling wt(YW) on stayability expressed as a deviation from the low MW--low YW group. The average MW and YW EBV, (kg) are in parentheses.

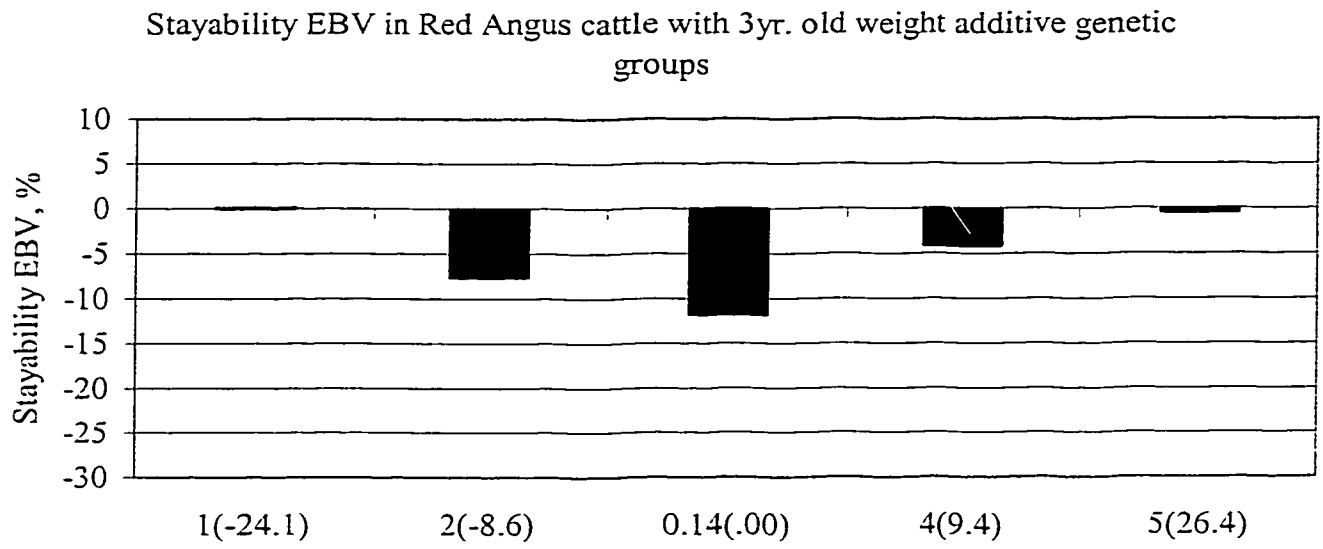

Figure 4.17. Group solutions of low (1), low-middle (2), middle (3), high-middle(4), and high(5) 3 yr old weight on stayability expressed as a deviation from the low weight group with the average weight EBV (kg) grouped by standard deviation from the mean in parentheses.

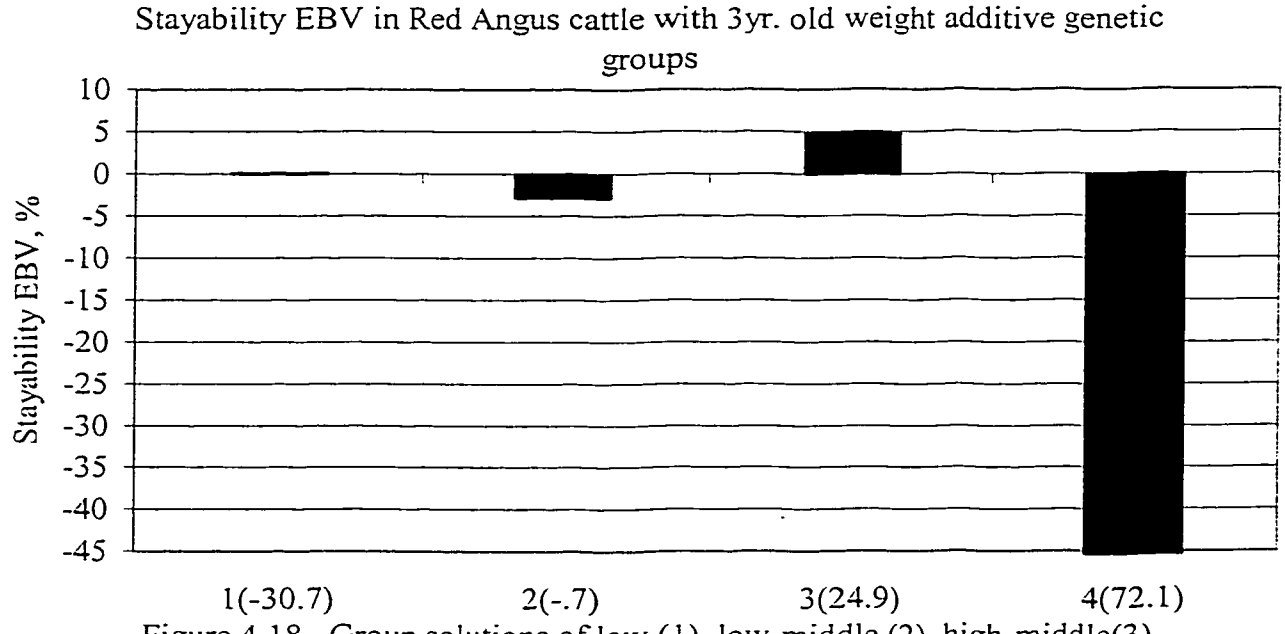

Figure 4.18. Group solutions of low (1), low-middle (2), high-middle(3), and high(4) 3 yr old weight on stayability expressed as a deviation from the low weight group with the average weight EBV(kg) grouped by equal strides of breeding values parentheses.

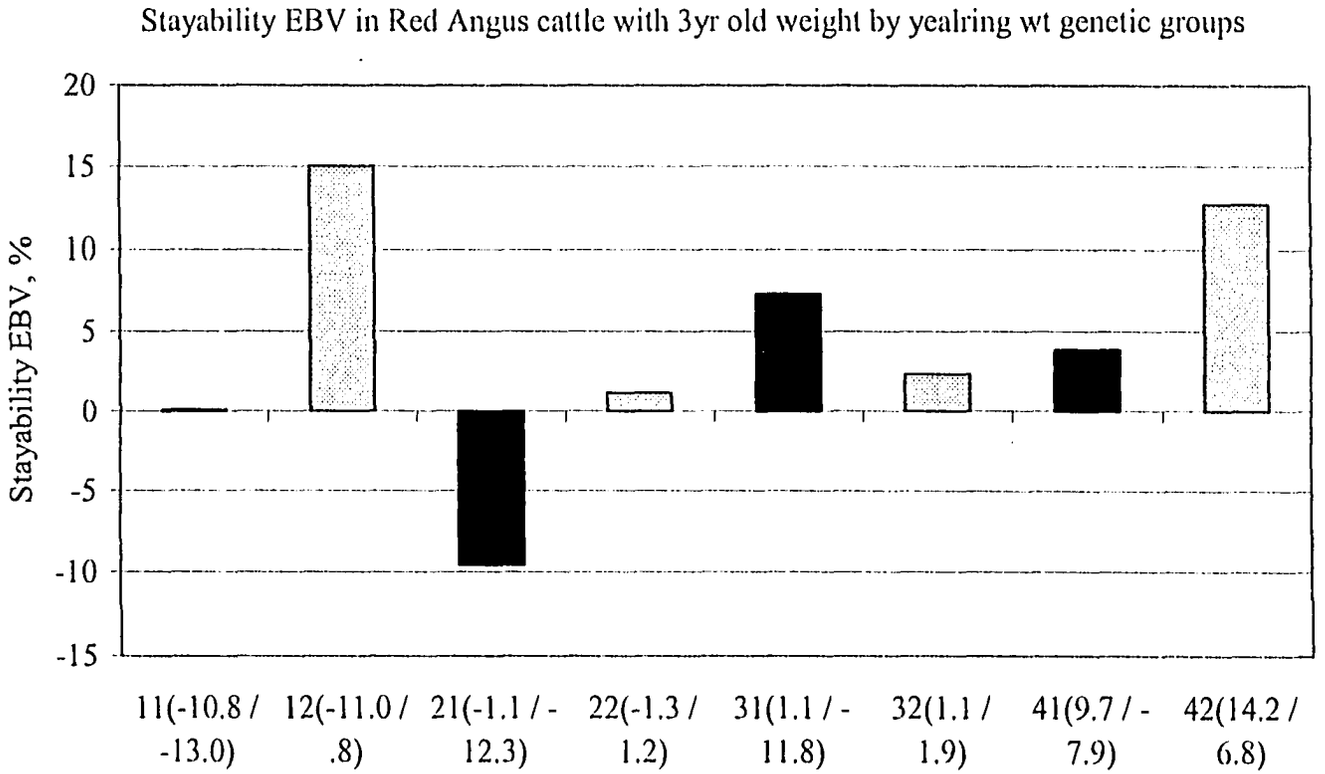

Figure 4.19. Mature weight (MW) by yearling wt.(YW) groups. The first number represents the mature weight category 1(low to 4(high) and the second identifies the yearling weight genetic group of 1(low) and 2(high). The average EBV (kg) are in parentheses.

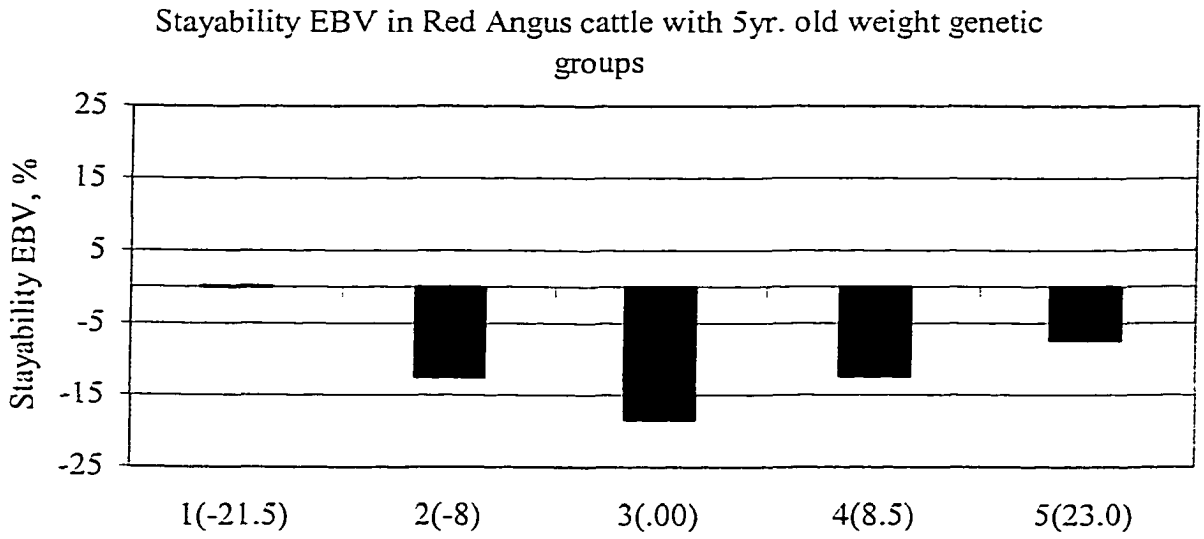

Figure 4.20. Group solutions of low (1), low-middle (2), middle (3), high-middle(4), and high(5) 5 yr old weight on stayability expressed as a deviation from the low weight group with the average weight EBV (kg) grouped by standard deviation from the mean in parentheses.

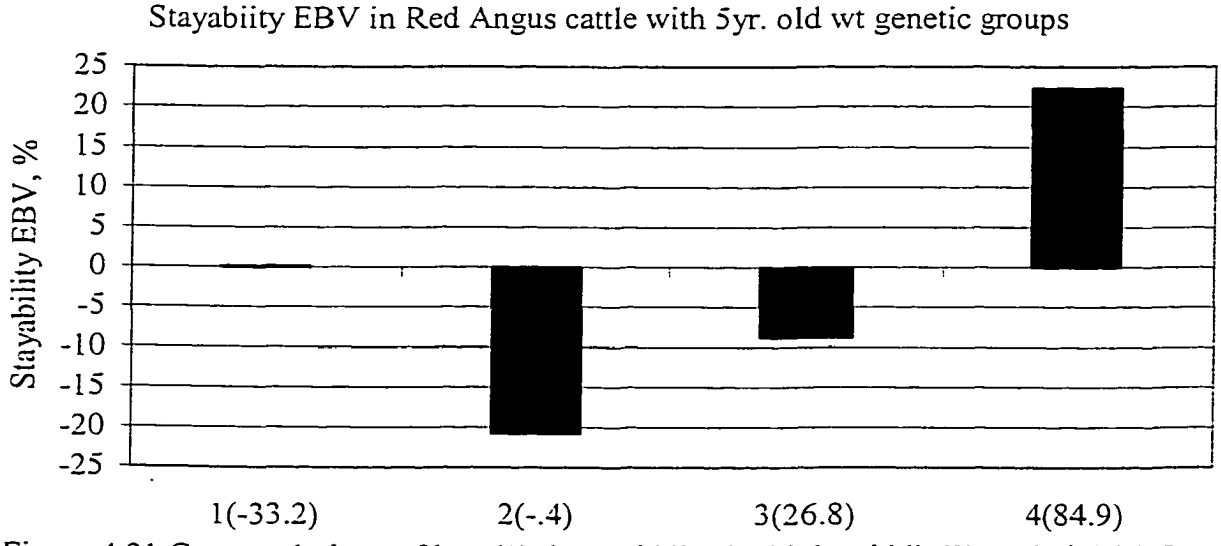

Figure 4.21 Group solutions of low (1), low-middle (2), high-middle(3), and high(4) 5 yr old wt on stayability expressed as a deviation from the low mature wt group with the average weight EBV(kg) grouped by equal strides of breeding values in parentheses.

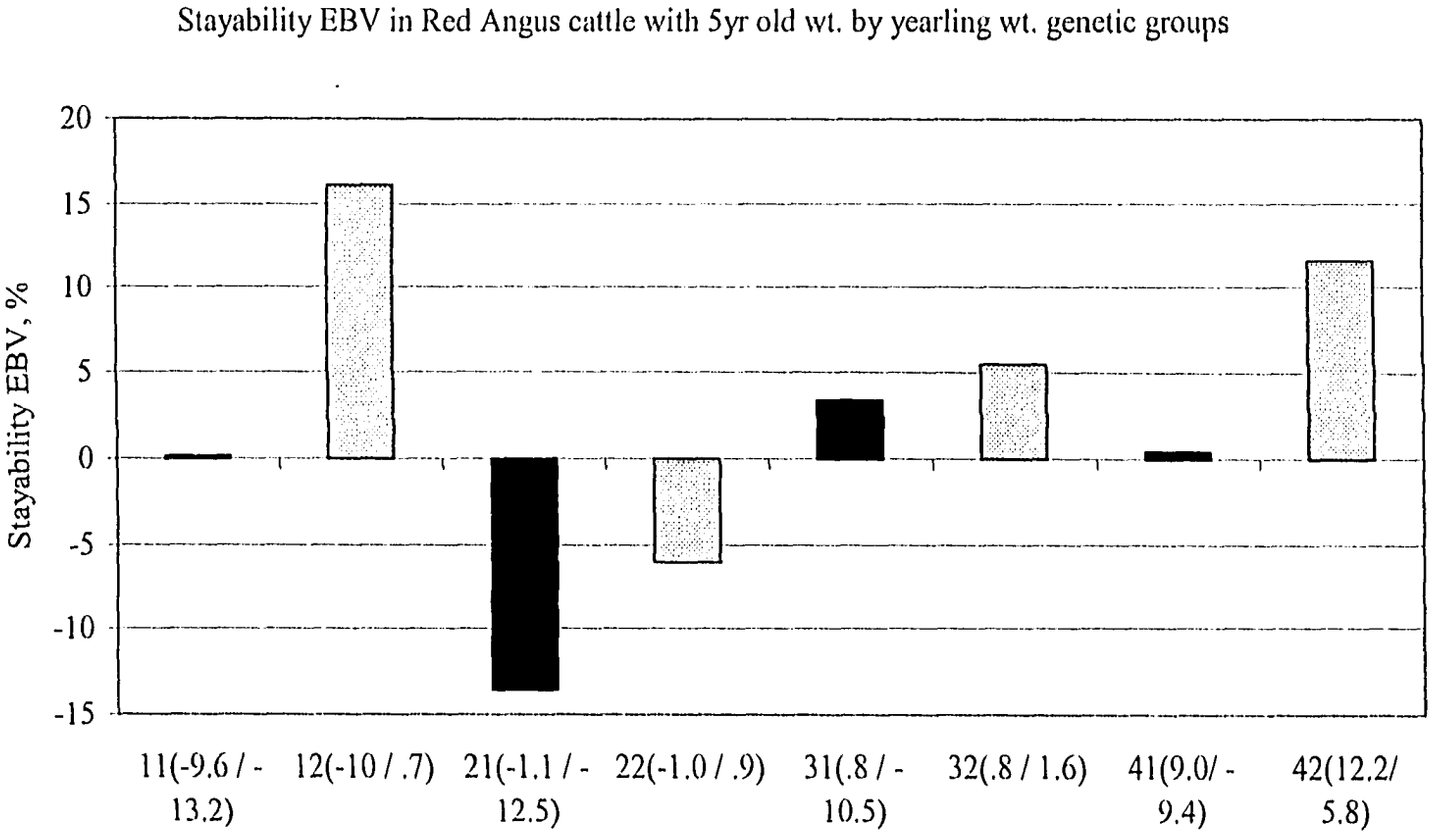

Figure 4.22. Group solutions of low (11,12) low-middle(21,22), high-middle(31, 32), and high (41,42) 5 yr old wt(MW)-- yearling wt(YW) on stayability expressed as a deviation from the low MW--low YW group. The average MW and YW EBV (kg) are in parentheses.

Stayability and Immature Growth Traits. I analyzed stayability with birth weight, weaning weight, milk, and yearling weight because these traits are less influenced by selection and physiological status. Analyzing immature weights with stayability using additive genetic could provide a clearer separation of results seen in previous analyses (Figures 4.23 to 4.26; Appendix C, C.31 to C.34).

The results of the immature weights with stayability analyses showed that as the average breeding values for growth and milk increased there was a corresponding increase in stayability. Plots of weaning weight direct (growth) and weaning weight maternal (milk) showed increases in stayability with increased EBV for those traits (Figures 4.24 and 4.25). Weaning weight maternal showed large differences in the last group suggesting that higher milking animals are favored to remain in the herd.

I was unsuccessful in finding literature directly related to this analysis, except the work done by Snelling (1994), who evaluated the correlations between predictions for immature traits and stayability. Snelling (1994) reported correlations between genetic predictions for immature traits of birth weight, weaning weight direct, weaning weight maternal (milk), and yearling weight with stayability defined as having a calf at age 6 given she had one at age 5 yr and were .249, .414, .428, and .462, respectively. These were not genetic correlations but they are one way to determine the direction and magnitude of the additive genetic relationships between traits. Additionally, Snelling (1994) evaluated additive genetic groups solutions for stayability based upon additive genetic groups for birth weight, weaning weight, and post weaning gain where these were generated from the Red Angus, America Angus analysis. The high SD on the genetic group solutions made it difficult to interpret group solutions.

Analyses between stayability and immature growth traits were closer to being linear than what I reported for mature weight genetic groups. Figures 4.23 to 4.26 clearly showed that increases in average EBV for birth weight, weaning weight (direct), weaning weight (maternal), and yearling weight were associated with increased stayability EBV. Therefore, selection to increase immature growth traits should result in an increase for stayability.

The results of this study show an additive genetic nonlinear relationship is present between stayability and adult cow weight. Because of the nonlinear relationship, traditional BLUP procedures will not work.

Mature cow weight by itself is not an economic trait, but it is an indicator of mature cow maintenance energy requirements, which has a direct effect on cost of production. Estimation of the genetic relationship between mature weight and stayability provides a way to tie together the genetic relationships between traits of economic importance. Stayability has economic importance relative to other traits available for national cattle evaluation because of the influence it has on profitability (Charteris et al., 1999). This influence on profit makes it necessary to determine what the additive genetic relationship is with other traits, especially those traits that directly impact profitability.

Future research should evaluate the genetic relationships between stayability and various economically relevant traits. Additional research is needed between stayability in beef cattle and both immature and mature growth traits to explain some of results from my analysis. Development of a simulation study could be helpful in explaining some of the earlier results.

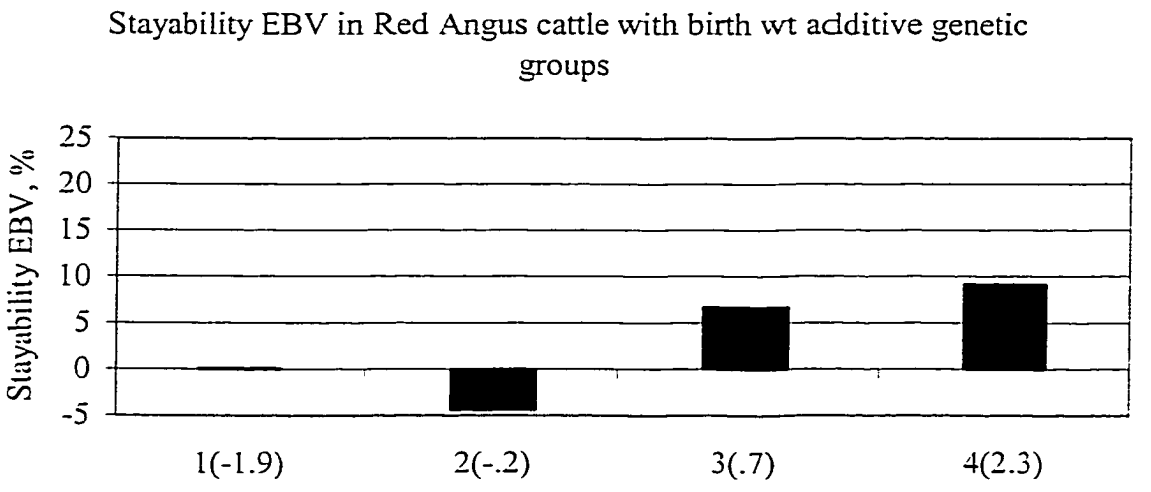

Figure 4.23. Additive genetic group solutions of low (1), low-middle (2), high-middle(3), and high(4) birth wt (kg) on stayability expressed as a deviation from the low birth wt group with the average birth wt EBV (kg) grouped by observations in parentheses.

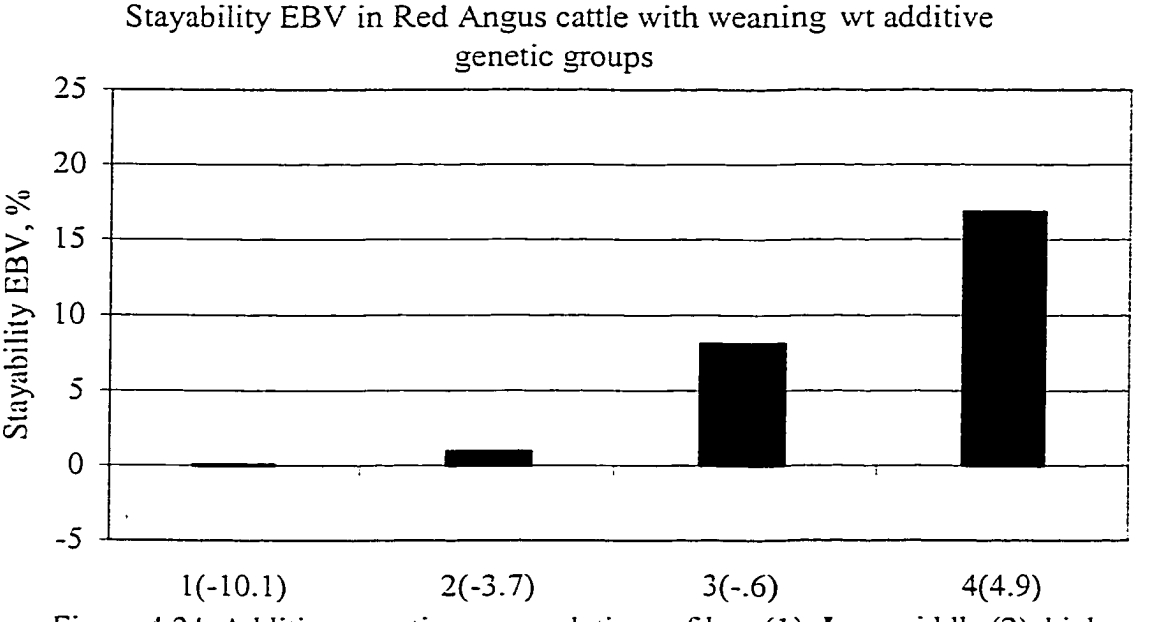

Figure 4.24. Additive genetic group solutions of low (1), low-middle (2), high-middle(3), and high(4) weaning wt(direct) on stayability expressed as a deviation from the low weaning wt group with the average weaning wt EBV(kg) grouped by observations in parentheses.

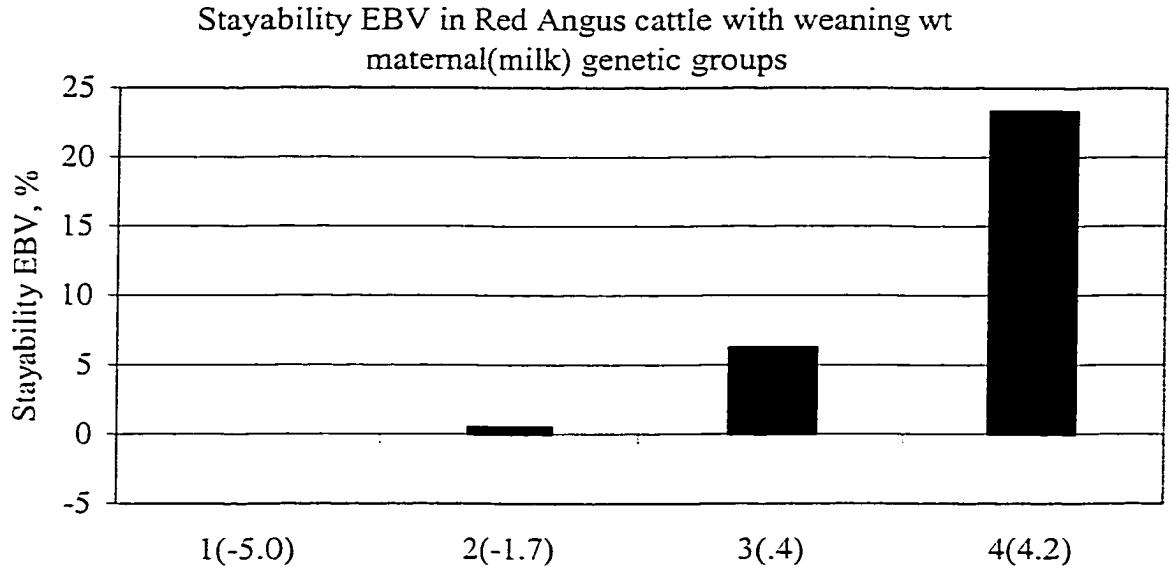

Figure 4.25. Additive genetic group solutions of low (1), low-middle (2), high-middle(3), and high(4) weaning wt(maternal) on stayability expressed as a deviation from the low weaning wt (maternal) group with the average weaning wt (maternal) EBV grouped by observations in parentheses.

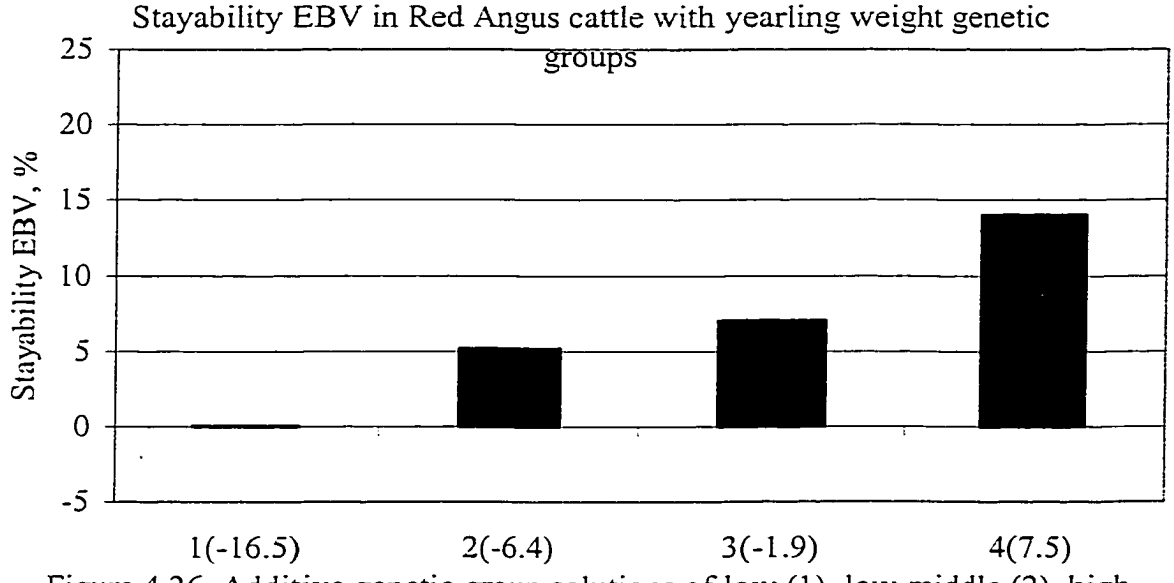

Figure 4.26. Additive genetic group solutions of low (1), low-middle (2), high-middle(3), and high(4) yearling wt on stayability expressed as a deviation from the low yearling wt group with the average yearling wt EBV(kg) grouped by observations in parentheses.

Mature Cow Maintenance Energy

For the last objective of the dissertation, I proposed and developed a prototype genetic prediction for mature cow maintenance energy in beef cattle. It is a new economically relevant trait for beef cattle producers because it has a direct impact on profitability. According to Bourdon and Golden (1999), the definition of an economically relevant trait is any trait that directly affects profitability by being associated with a specific cost of production or an income stream from the sale of a product.

The idea for a mature cow maintenance energy prediction originated from my committee meeting and the discussion about the production of an expected progeny difference for Red Angus mature cow weight. In beef cattle, mature weight is used as an indicator for maintenance energy requirements because it is affiliated with an animal's ability to maintain its tissue, such as body condition, and milking ability. As our discussion continued, Dr. Bruce Golden questioned the use of a mature cow weight expected progeny difference when making selection decisions and he argued for a prediction on mature cow maintenance energy requirements. Mature cow maintenance energy requirement represents the economically important trait and mature weight is an indicator of it (B. L. Golden, personal communication).

Maintenance Energy Prediction. Collection of mature cow maintenance energy data is cost prohibitive, therefore, mature cow maintenance energy data are limited in comparison to traits like weaning weight. This led me to explore alternative methods and indicator traits for maintenance energy in beef cattle. Dr. Bruce Golden (personal

communication) suggested using established formulas for prediction of nutrient requirements in beef cattle as a place to start (1996).

The mature cow maintenance energy requirements prediction equations in this study were developed from nutrition research (CSIRO, 1990; NRC, 1996) and consultation with D. E. Johnson (personal communication). I implemented previous NRC (1996) prediction equations and modified equations of MacNeil and Mott (2000) to predict mature cow maintenance requirements in beef cattle. First, I predicted maintenance requirements for cow weight at 5 yr of age using estimated breeding values from a previous random regression analysis. Using the same maintenance energy equation published by the NRC (1996), I calculated maintenance requirements with mature weight predictions; however, I adapted these predictions so they would work with the NRC (1996) equations (MacNeil and Mott, 2000).

There is evidence that using an exponent of .90 instead of .75 is more appropriate for predicting intraspecies mature animal maintenance requirements (D. E. Johnson, personal communication; Blaxter, 1972); therefore, I researched the use of .90 over .75 in prediction of mature cow maintenance requirements. I decided not to use a .90 exponent because I did not find strong evidence to support this claim for cattle. Furthermore, Van Es (1972) reported an error rate of 5% using .75 vs .60 or .90 for the weight range of 350 kg to 650 kg. In a preliminary analysis, I calculated a .999 correlation between breeding values using an exponent of .75 compared to those using .90. This proved that the difference was minimal between methods.

In a recent study by MacNeil and Mott (2000), no additional changes were made to NRC (1996) equations for prediction of nutritional requirements. The inputs they used

to obtain information on energy requirements were generated from information on mature weight, weaning weight-maternal or gain, birth weight, age of dam, and milk yield. All other inputs were set to default values. Their methods accounted for maintenance energy of production at maintenance levels and when the animals were in lactation, but the predictions do not increase annual maintenance requirements for high or low lactating animals. However, the NRC (1996) uses a 1.2 adjustment of maintenance energy requirements for the months the animal is lactating. To account for differences in ability to milk, I imposed an adjustment factor and appended it to the maintenance energy requirement determined from mature weight. This adjusted the maintenance energy requirements for animals known to differ for milking ability despite being the same mature weight.

Differences in maintenance energy requirements for high and low milking animals are present while animals are in production and remain after lactation (Ferrell and Jenkins, 1985). Solis et al. (1988) reported that there were differences in the maintenance energy of animals with various milk production potentials and these differences were present during non-lactation periods. The authors explained that these differences were a function of differences in visceral organ mass. Individuals with greater potential to milk will, on average, have a larger visceral organ mass relative to lower lactation animals. A few examples of visceral organs that are large consumers of maintenance energy and have high cellular turnover are the liver, heart, and intestines (Baldwin, 1995).

The prediction equations used by MacNeil and Mott (2000) do not account for the differences in maintenance energy costs at production levels. For this prediction of

maintenance energy, I added an adjustment for metabolizable energy for production (MEp) to adjust maintenance requirements for high and low producing animals (CSIRO, 1990). I used MEp to change the maintenance energy requirements of animals based upon their estimated breeding value for maternal weaning weight (Milk) because it was the closest predictor and equations to incorporate the genetic predictions were developed. Using the milk estimated breeding values and a Wood's lactation function, I calculated an energy value for milk. Because parameters for the Wood's lactation function were not available for Red Angus cattle, I used parameter estimates from Line 1 Hereford cattle at the Fort Keogh research station in Miles City, MT. (MacNeil and Mott, 2000). Ideally, these parameters should be estimated for the Red Angus breed; however, the parameters I obtained from the Hereford study were the only ones available. I expressed the energy value for milk as a deviation from a designated average animal. I considered the average animal to have a milk EBV of zero. Because this value is not representative of the energy necessary to produce milk, I adjusted it further with the partial efficiency (k_l) of milk production to account for the efficiency level to convert feed to milk (CSIRO, 1990).

The value I calculated for MEp was multiplied by a coefficient of .10 and added onto the previously calculated MEm requirement for mature weight. This additional 10% was used to account for increased MEm requirements due to being at production levels. I adapted this adjustment factor from prediction equations developed for the Australian livestock industry (CSIRO, 1990) and recommendations of D. E. Johnson (personal communication). So, each animal had a prediction generated with mature weight and milk estimated breeding value that represented the daily MEm requirement. The current value is generated on a per day basis and I converted it to a year value by multiplying by

365 d and expressed it as an expected progeny difference (EPD). This additional source of information, such as maternal weaning weight, should help explain a higher percentage of variation for mature cow maintenance energy requirements.

Expected Progeny Differences. Using Red Angus mature weight EBV and maternal weaning weight EBV from the National Genetic Evaluation, I generated a prototype genetic prediction for mature cow maintenance energy requirements. The mean, SD, and range of EPD available for the Red Angus breed are summarized in Table 4.46. There appears to be available variation among genetic predictions for maintenance energy requirements to make selection decisions. In a study by MacNeil and Mott (2000), they conducted a genetic evaluation for mature cow maintenance energy requirements, but they did not provide descriptive statistics for the genetic prediction using Line1 Herefords. Furthermore, the authors reported their outcome as total predicted net energy requirements, which included all requirements for maintenance, lactation, and gestation. It was not possible to compare analyses, however, I calculated a simple phenotypic example to provide a comparison. A 453 kg nonlactating, nonpregnant, and 5 yr old Angus female can require 11.6 Mcal per day or 4,234 Mcal per year (Ferrell et al., 1985).

Genetic Trend. The genetic trend for mature cow maintenance energy requirements is illustrated in Figure 4.27. This trend represents the average of EBV by birth year over the years 1945 to 1995. For all years, 1945 to 1995, I calculated a slope of 3.92 Mcal per year and for years 1970 to 1995 the slope was 7.66 Mcal per year. The genetic trend for mature cow maintenance requirement (Figure 4.27) follows a similar pattern to what I previously reported for mature weight (Figure 4.9). According to this

trend, there was about a 143 Mcal per year change in annual MEm requirements from 1945 to 1995 years.

Table 4.46. Descriptive statistics for mature cow maintenance energy EPD (Mcal / yr) for Red Angus cattle

	All Animals (N = 56,582)	Sires (N = 5,912)
	EPD, Mcal / yr	EPD, Mcal / yr
Mean	22.36	23.80
SD	102.14	94.79
Minimum	-427.95	-381.91
Maximum	581.88	433.95

Table 4.47. Descriptive statistics for lactation including peak milk yield (kg), total lactation yield (kg), lactation energy (Mcal/d) using maternal weaning weight EBV (Milk) from Red Angus cattle (N = 56,582)

	Peak Lactation Yield, kg	Total Lactation Yield, kg	Milk Energy Content (Mcal/d)
Mean	6.80	560.89	2.05
SD	.47	38.95	.14
Minimum	4.11	338.48	1.24
Maximum	9.19	757.24	2.77

Trait Expression. An important aspect for the development of a new genetic prediction is trait expression or the units of measure used for the trait. For example, growth traits are expressed in pounds or kilograms, heifer pregnancy and stayability are on a percentages probability scale, and then there are other units associated with traits for carcass merit. Ideally, several groups in the beef cattle industry and literature should be consulted during the development of a new trait. These groups would include scientists in your field of interest, scientists in other but related fields, the groups using the trait, and anyone using the new prediction as a tool to make selection decisions.

There are multiple units to express units of energy. A few of the units include: animal unit monthly (AUM), megacalories (Mcal), total digestible nutrients (TDN), kilocalories (kcal), and megajoules (MJ). Some of these units are unique to an application and others are functions of other units (i.e. Mcal = 1000 kcal). For my analysis, I wanted to select a unit of measure that satisfied the rigor of the scientific community and met the needs of your average cattle producer. Using the literature and the Animal Genetics Discussion Group (AGDG), which is a worldwide contingent of animal breeders, I decided to use a megacalories (Mcal) scale. It is the standard unit of measure in the NRC (1996); Nutrient Requirements for beef cattle; it is accepted by nutritionists in beef cattle nutrition; it is easy to calculate and a standard unit of measure; cattle producers should have an understanding of a calorie unit; and it can be transformed into other units of energy.

The informal survey I conducted on the AGDG was used to probe the Animal Breeding group for their input on this area. The responses came from several sources and are not cited here. Multiple responses favored using Mcal as the unit of measure and emphasized that other measures including MJ or Kcal are simply functions of each other. Other responses emphasized that units should be set based on what the farmers and ranchers can comprehend. A few responses stated that expressing the trait in units of dry matter per day (DM/d) of a standard feed. One response suggested using a proportional scale and setting the average cow to 100 and then deviate other around it (AGDG, 2000).

I think using a standard unit of measure, such as Mcal, would be an effective way to express mature cow maintenance energy requirements. The use of Mcal as a measurement unit will be more informative when coupled with information for a set of

standard diets. Furthermore, the Mcal unit conforms to standards developed by National Research Council for the nutrient requirements of beef cattle (NRC, 1996), is interpretable and easy to convert to units around the world, and interpretable by the producer. Examples of standard diets will provide a frame of reference for producers to interpret and compare animals for maintenance energy requirements. These diets could include a standard pasture grass, feedlot, or hay diet. Let us assume that alfalfa hay is our choice of feed and it contains approximately 2.31 Mcal of metabolizable energy per kg of feed. Using this prior value, I would assume that the average Angus cow requires 11 Mcal / d or 4,015 Mcal/yr. The feed needed to sustain this animal would be 4.7 kg / d (10.5 lbs/d) or 1,738.1 kg/yr of alfalfa hay (3,832 lbs/yr).

Future Equation Modifications. The mature cow maintenance energy equation I proposed is a prototype and additional enhancements are needed to incorporate additional sources of information and further enhance the predictions. In a previous analysis, MacNeil and Mott (2000) used weaning weight gain predictions instead of weaning weight maternal EPD. In this analysis, I used milk instead of weaning weight gain because predictions were available. According to D. E. Johnson (personal communication), I could improve the present prediction equation by accounting for individual animal growth. These are suggestions for future analyses of mature cow maintenance energy requirements and the development of better predictions.

Lactation Prediction. A benefit to adjusting maintenance energy requirements for milk production is an additional predictor for total lactation energy (ME_l) is produced in the process. It represents the energy needed for lactation and I determined this based upon maternal weaning weight estimated breeding values (Milk EBV) and used it as part

of the calculation for MEm. This prediction could be adapted to construct a new predictor for lactation energy and coupled with energy requirements for growth, pregnancy, and other physiological processes.

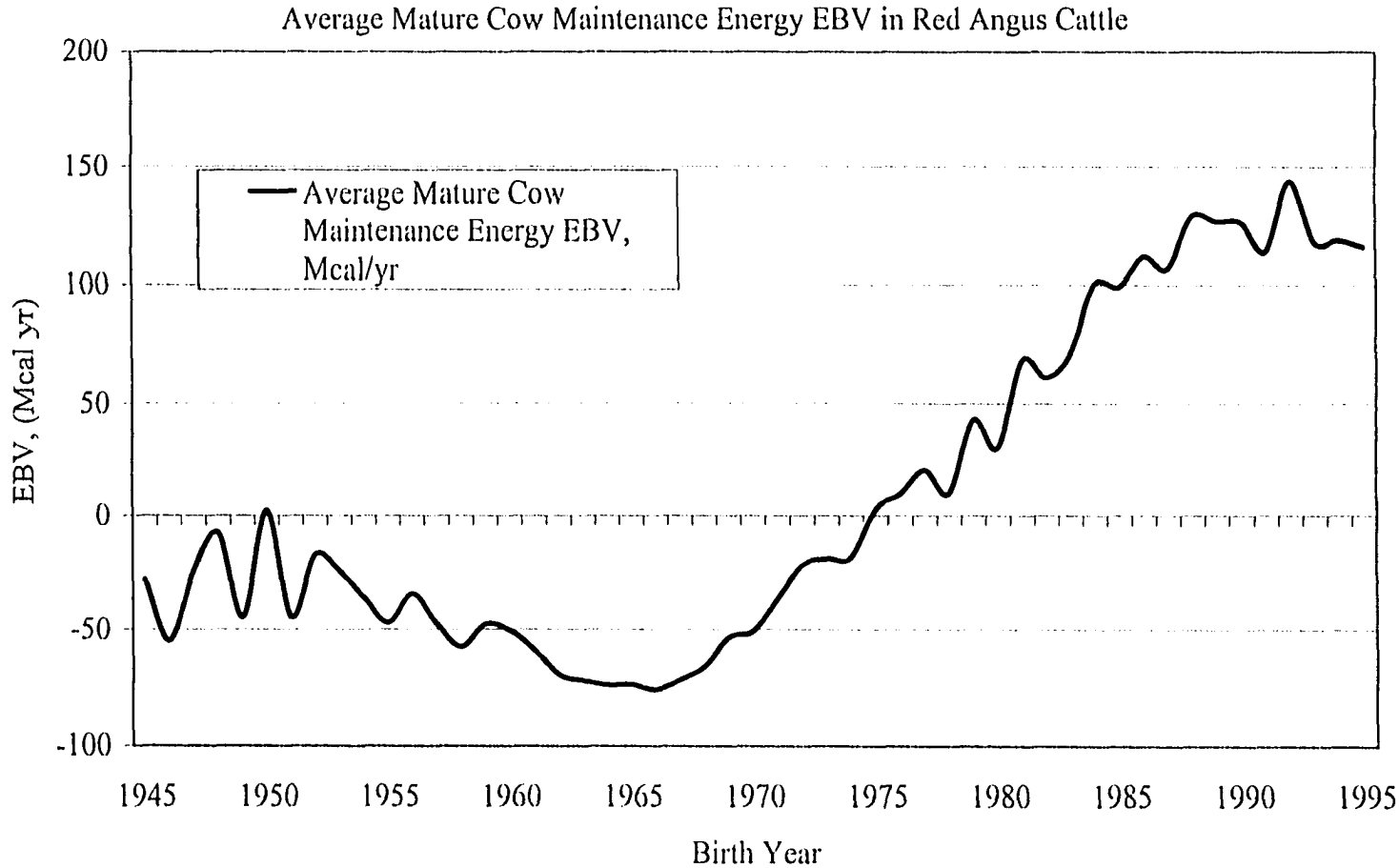

Figure 4.27. Average EBV (Mcal / yr) for mature cow maintenance energy requirements by birth year in Red Angus cattle.

Indicators of Maintenance Energy (MEm). The main reason for developing indicator traits for mature cow maintenance energy requirements is the expense incurred with collection of maintenance energy data. The most commonly used methods for collection of maintenance energy requirements are calorimetry and slaughter balance. These methods are time consuming and costly and should be used when necessary. A calorimetry trial to evaluate a diet or feedstuff can cost up to $5,000 to $6,000 per animal (M. Jarosz, personal communication). Obviously, this is not cost-effective method to measure maintenance energy requirements on hundreds of animals, which would be needed for generating genetic prediction with respectable levels of accuracy.

For this analysis, the sources of data for a mature cow maintenance energy requirement prediction are estimated breeding values for mature weight and milk (maternal weaning weight). The genetic predictions for these indicators are available making it easy to incorporate them in the development of a prediction for maintenance energy requirements. Alternative indicators or direct measures of maintenance energy needs should be investigated and what contributions they can make to improvement of the predictions through increased accuracy.

Visceral organs are indicators of mature cow maintenance energy requirements and they may be an important source of information for increased accuracy of prediction. The visceral organs include liver, heart, both small and large intestines, kidneys, stomach, and lungs. Several studies have been conducted and report that, on average, the visceral organs consume large quantities of metabolizable energy compared to other tissue in the body (Ferrell, 1988). Furthermore, breed differences exist for different organs, such as gastrointestinal tract, heart, lung, liver, and spleen (Ferrell and Jenkins, 1998a). A good

way to emphasize the energy use is to compare different tissues. For example, Johnson et al (1990) reported that fat and skin have energy requirements of .06 and .07 MJ/kg while the energy needs of the liver, heart and kidney were 1.55, 2.41, and 4.1 MJ/kg, respectively. In fact, the liver consumes approximately 22.5% of the energy expenditure as a function of fasting heat production but only represents 1.6% of the body weight (Ferrell, 1988).

Of the visceral organs available, the liver has been proposed as an indicator trait candidate to include in a mature cow maintenance energy requirements prediction. The liver uses a large quantity of maintenance energy and one of the most metabolically active visceral organs. The liver oxidation rate is 3.5 KJ of ME/(g•d) compared to a whole body average of .1 kJ of ME/(g•d) (Johnson et al., 1990).

One of the challenges with visceral organs and specifically the liver is how to collect data without harvesting the mature animal and removing that animal from production status. This challenge led me to review the literature for alternative methods. A study using ultrasound technology to determine liver size reported favorable results for taking linear measures to predict liver size (Braun, 1990; Braun and Gerber, 1994). According to the authors, the best predictors of liver weight were the liver thickness over the portal vein and the caudal vena cava. Based on the information provided, it seemed plausible to measure liver size without having to harvest the animal for the needed information, but a study was needed to confirm or refute these findings.

A study related to work done by Braun (1990) was conducted at Colorado State University to investigate the application of ultrasound technology for assessing liver size in beef cattle (R. Ruppert, personal communication). For this study, researchers

measured the liver thickness using both portal vein and caudal vena cava and correlated those values with actual liver weight. The results showed that it was feasible to collect these measures using ultrasound technology, but the correlation between liver weight and distance to portal vein or caudal vena cava was near zero (R. Ruppert, unpublished data). According to these results, ultrasound technology does not seem to be useful for measuring liver size in beef cattle.

The results of the previous study make it difficult to incorporate liver size into the prediction for mature cow maintenance energy because data would need to come from harvested animals. Alternative methods of collecting liver size may need to be developed so liver size can be an indicator of the economically relevant trait for mature cow maintenance requirements. If data are collected from harvested animals then a high percentage of it will originate from castrated animals and heifers. The collection of slaughter data may be difficult, especially for collection of visceral organ tissue; however, current work with individual animal identification could overcome this challenge.

If inexpensive and practical methods are developed to measure liver size in beef cattle, then analytical methods will be needed to incorporate liver observations into a prediction for mature cow maintenance energy requirements. I have described a few methods that could be used to incorporate liver observations and other new indicator traits for prediction of mature cow maintenance energy requirements in beef cattle.

Using a multivariate animal model and BLUP (Henderson, 1984) would be one method to generate predictions for mature cow maintenance requirements with correlated traits (e.g., mature weight). Using multivariate procedures, several traits could be

included in the model, preferably those traits that explain most of the variation for maintenance energy requirements (e.g. liver size, mature weight, and milk). Estimated breeding values would be generated for all traits; however, I would only publish the economically relevant trait. Publishing both groups of traits when the indicator traits are already used in the multivariate analysis to predict mature cow maintenance energy requirements lowers the accuracy of the selection decision (Golden et al., 1999). If an economically relevant trait is generated with a multivariate analysis, then all the information has been included from the indicator and economically relevant traits. Including both the indicator trait and economically relevant trait as part of the selection lowers the accuracy of the selection because the information of the indicator trait is counted twice, thus increasing the prediction error variance of the selection decision.

This approach would require estimation of genetic parameters for across and between all combinations of traits and a preliminary analysis of important fixed effects. Some of these additive genetic relationships may already be estimated, but not all (i.e., liver size). Because a large amount of data would be needed to estimate the genetic parameters, alternatives should be considered. This may require estimation of parameters in two-trait pairs, however, it is feasible to generate predictions for maintenance energy and calculate prediction error variances for determination of accuracy values. Another point to consider is including completely reported traits, such as weaning weight, in the analysis to reduce selection bias.

A different method to include liver size into a prediction would use existing NRC (1996) prediction equations (D. E. Johnson, personal communication). In the NRC (1996), $.077*(MW)^{.75}$ is used to predict NEm and the general equation is $y = a(MW)^{b}$. It

was suggested that scaling the a-value using liver size would be a way to incorporate liver size into the previouisly described prediction for maintenance energy requirements. Essentially, the maintenance energy requirement would be scaled for liver size, so if there were two groups of animals of equal weight, those with larger livers would have higher MEm requirements and the opposite would be true for individuals with smaller livers. Before this option is considered viable, research is needed to determine if the a-value is correlated to liver size. Using this approach would vary liver size around some average function for MEm.

Future Research. The proposed trait for mature cow maintenance energy requirements is a prototype. Additional research is needed to improve it and find better analytical methods and sources of data to improve the predictions for it. This will require a large effort on the part of the Animal Breeding researchers and research groups in other disciplines. The following is a list of areas that I envision needing research.

First, we need to estimate covariances for the genetic relationships between economically relevant traits and their indicators. Estimates of heritabilities and correlations need to be obtained from existing literature or estimated from current populations. Unfortunately some of the new traits posed as indicators might require initial data collection. This effort should be coordinated among different animal breeding groups to prevent duplication of efforts. A preliminary investigation of existing data sources should be conducted to estimate parameters between indicator traits and economically relevant traits. If these sources are available, financial resources could be diverted to other projects. For example, it may be possible to estimate genetic parameters for mature weight and liver size using the USDA Meat Animal Research Data base.

The estimation of genetic parameters for indicators of maintenance energy requirements should include new trait development. Using liver size as an example, there is additional research needed to determine if other traits are valuable to increasing accuracy of prediction for mature cow maintenance energy requirements. These data sources include but are not limited to body condition score, feed intake, visceral organ mass, and cellular-level assays.

The advances in medical diagnostic equipment may make it feasible for us to measure mitochondria activity and directly determine cellular metabolic rate. Ramsey (1995) reported that proton leak across the inner mitochondria membrane could be used as an indicator of metabolic rate and cellular heat production. Karlson et al., (1998) used a microcalorimetry technique with Ouabain, an inhibitor of Na^{+}-K^{+}-ATPase, to measure heat production of renal epithelial tissue. Additionally, there may be effective and cheap methods to measure cellular activity of the liver, requiring us to take a liver biopsy to measure an animal's metabolism. There is an opportunity to use advanced technologies such as magnetic resonance imaging (MRI) to measure multiple visceral organs and predict maintenance energy requirements (Gallagher et al., 1998). Other technologies in use by the Japanese and military are near-infrared lasers to measure cerebral oxygen consumption and energy expenditure in sheep and humans (Takahashi et al., 1997; Kobayashi et al., 2000). These technologies may be available for use to predict maintenance energy requirements, but the information they provide will be weighed against the cost in collection of data.

Simulation modeling is a different but related area of research that could be used to explore different genetic relationships between mature cow maintenance energy

requirements and other production traits. Multiple research groups have simulation models specific to growth, lactation, and liver metabolism (Baldwin et al., 1987; Freetly et al., 1993). For example, Baldwin (1995) discussed the development of a mechanistic model for liver metabolism. This model and other models for different physiological functions could be incorporated into existing animal breeding simulation modeling efforts.

Economic values for the economically relevant traits will need to be derived for traits determined to have a direct effect on profit. This will require coordination of both the animal breeding research groups and agricultural economics to determine those values. Likely, these economic values will need to be derived for multiple scenarios involving several ranching enterprises and various marketing schemes. For mature cow maintenance energy requirements, the economic values will need to be determined (Golden et al., 1999). There are research efforts in progress to derive economic values for other groups of traits (Charteris et al., 1999; Charteris et al., 2000).

CHAPTER V

CONCLUSIONS AND IMPLICATIONS

The results of both the multivariate and univariate analyses indicate that mature weight in Red Angus cattle is a moderate to highly heritable trait. It is feasible to develop genetic predictions for mature weight using existing cow weight data.

The results of this study showed that mature weight does not meet the necessary criteria to be analyzed using a simple repeated measures model. The heritability estimates for cow weight over several ages remained consistent through multiple age levels but increased in magnitude at older ages. Genetic correlations between different ages remained high even as distance increased between ages, and the phenotypic correlations remained consistent and moderate to high. The pattern of heritability estimates and genetic correlations were strong indicators that a repeated measures model would be appropriate for modeling mature weight data; however, this did not account for the scaling genetic, phenotypic, and residual variation as age of animal increased. A simple repeated measures model assumption is that variances remain constant as age increases. Random regression models were applied instead to overcome problems with assumptions of the simple repeated measures models.

Using Method R variance components procedures and a random regression model, it was feasible to obtain variance component estimates variance using a random regression model. Multiple random regression models were fit that differed in fixed and random effects and the results showed that a linear polynomial was the highest order

function allowed for both the additive genetic and permanent environmental effects. The estimates of variance components I obtained from the random regression study were not usable because the estimates were several orders of magnitude higher than previously reported in the multivariate (two-trait) analyses. These results suggest that the current Red Angus cow weight data are not appropriate for estimation of variance components using random regression functions. Further research is needed to estimate better variance components from a research herd with multiple observations per year. Once a high quality set of usable variance components are obtained, then the transition is easy to development of genetic predictions using random regression models.

I developed genetic predictions for mature weight using linear random regression models and adapted variance components for the repeated measures models. Genetic predictions for weight at 5 yr. of age were generated using a linear random regression polynomial. There appeared to be a better fit of the model to the data with the random regression over the repeated measures model. Using the random regression model was more appropriate than a repeated measures model because model assumptions were more appropriate for the data.

The results of the immature weight and mature weight analysis indicated a moderate to strong additive genetic relationship between weaning weight and mature weight. There was a difference in the magnitude of the additive genetic relationship between weaning weight and mature weight for different age categories. In the postweaning gain and mature weight analysis, the results confirmed a genetic relationship between traits. The use of immature weights, such as weaning weight or postweaning gain, in a multivariate analysis has the potential to increase accuracy of mature weight

genetic predictions. More importantly, including completely reported traits like weaning weight should reduce selection bias.

The analysis of mature weight with stayability suggested there was a linear additive genetic relationship between 2 yr old weight and stayability; however, there was a near zero genetic correlation between weight at 3 and 5 yr of age with stayability. Further analysis with additive genetic groups analyses suggested the presence of a nonlinear genetic relationship between traits. Weight at 3 and 5 yr of age appeared to change nonlinearly with mature weight genetic groups. This non-systematic change of stayability across contemporary groups did not correspond with prior beliefs. Using alternative additive genetic grouping strategies revealed that differences observed were nonlinear and at both the lowest and highest mature weight genetic groups contained animals with different profiles for growth.

Immature traits of birth weight through yearling weight were analyzed with stayability and showed a nonlinear and positive additive genetic relationship between traits. Because immature growth traits are associated with earlier stages of life, they are more likely to be associated with growth and not confounded by other effects (e.g., milk production and body condition). The pattern showed that selection for increased growth at early stages of life would be associated with favorable increases in stayability.

A prototype mature cow maintenance energy prediction was developed, as one of several economically relevant traits because of the potential impact selection for it will have on profitability of commercial cow-calf enterprise. Using modified equations for determining maintenance energy requirements, it was feasible to develop a new genetic predictor. The traits used included weaning weight maternal (Milk) and mature weight

EBV. Variation in mature cow maintenance energy requirements was present to make selection decisions. Based on these results it was feasible to develop a new genetic prediction for mature cow maintenance energy requirements.

The new economically relevant trait will require additional development and validation to improve the prediction and increase levels of accuracy. Future technologies should be considered, especially those that will be more direct indicators of maintenance energy needs of the animal. Some of these areas include gene markers, liver mass or visceral organ mass, and body condition score. Besides the development of new indicator traits, additional research is needed to determine the best units of measures to make the new prediction easy to interpret and apply in making selection decisions to reduce costs and subsequently increase profit. A predictor for mature cow maintenance energy requirements will provide both commercial and seedstock producers selection tools with a direct impact on cost of production.

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APPENDIX A

Modifications to DSREG Software

Description

Modified version of Beta-version of ds6 Method R variance components software.

Usage: dsreg –e (effects spec) –r (Right hand side spec) –C (output coefficient matrix) –R (output right hand side) –n (number of subsamples) –a (augmentation specs) –c (convergence criteria) –B (output MME solutions) –b (restart beta) –w (data file) –s (long integer seed number) [-g (genetic variance) –E (residual variance)] [-f (floor no. of MME iterations]

Def.c

```
/*****************************************************************************
        Purpose:
                to define some setup stuff
*****************************************************************************/
void defineWholeMme( mme )
struct MME *mme;
{
        extern unsigned num_input_fields, bflg;
        extern char *ARGV0, cname[], rname[], bname[];
        extern double *rankX;
        unsigned i;
        FILE *fpb;

            /* allocate the memory for the struct matrix */
         if( (mme->mp = (struct matrix *) malloc( sizeof( struct matrix ) ))
                                        == (struct matrix *)NULL ){
         fprintf( stderr, "%s: Cannot allocate space for the matrix pointer for the %s\n", ARGV0,
                mme->name );
         exit( -1 );
    }

        if( (mme->rhs = (struct matrix *) malloc( sizeof( struct matrix ) ))
                                        == (struct matrix *)NULL ){
         fprintf( stderr, "%s: Cannot allocate space for the matrix pointer for the %s\n", ARGV0,
                mme->name );
         exit( -1 );
    }

            /* Setup the storage mode details of the MME */
                    /* set dimensions */
        mme->mp->row_dim = mme->mp->col_dim = mme->rhs->row_dim =
                    (mme->efflist+mme->neffects-1)->mme_eq_no - 1
                    + (mme->efflist+mme->neffects-1)->nlevels;
        mme->rhs->col_dim = 1;
        mme->mp->num_elem = mme->rhs->num_elem = 0;
        strcpy( mme->mp->name, cname );
        strcpy( mme->rhs->name, rname );


    define_fork_matrix( mme->mp );
        mme->mp->put_elem = add_fork_value;     /* replace the replacer function */


            /* Setup the storage mode details for the RHS matrix */
        define_fork_matrix( mme->rhs );
        mme->rhs->put_elem = add_fork_value;            /* replace the replacer function */

                    /* setup the record read routine */

        mme->readRoutine = readWholeRecord;

        if( (mme->diagonal = malloc( sizeof( double ) * mme->mp->row_dim )) == NULL ){
                fprintf( stderr, "%s: Cannot allocate memory for %d diagonal elements\n",
                    ARGV0, mme->mp->row_dim );
```

```
                exit( -1 );
        }

        if( (mme->beta = malloc( sizeof( double ) * mme->mp->row_dim )) == NULL ){
                fprintf( stderr, "%s: Cannot allocate memory for %d beta elements\n",
                        ARGV0, mme->mp->row_dim );
                exit( -1 );
        }

        if( bflg ){
                if( (fpb = fopen( bname, "r" )) == NULL ) {
                        fprintf( stderr, "%s: Cannot open restart beta %s\n", ARGV0, bname );
                        exit( -1 );
                }
                fprintf( STATUS, "reseeding beta %d\n", mme->mp->row_dim );
                for( i=0; i< mme->mp->row_dim; i++){
                        fscanf( fpb, "%lg", (mme->beta+i) );
                        *(mme->diagonal+i) = 0;
                }
                fclose( fpb );
        } else
        for( i=0; i< mme->mp->row_dim; i++)
                *(mme->beta+i) = *(mme->diagonal+i) = 0.;

                                                /* sloppy setup for rank of X */

        for( i=0; i<mme->ndependants; i++ )
                (mme->obslist+i)->rankX = 0.;

        for( i=0; i<mme->neffects; i++ )
                if( (mme->efflist+i)->type != RANDOM && (mme->efflist+i)->type != RANDREG ){

                /* je/lk modification for RandReg case, 9/7/99 */
                        (mme->obslist+(mme->efflist+i)->trait-1)->rankX += (double)(mme->efflist+i)-
>nlevels
                                                                - (double)(mme->efflist+i)->constrain;

                }
        fprintf( STATUS, "Rank of X: " );
        for( i=0; i<mme->ndependants; i++ )
                fprintf( STATUS, "%g ", (mme->obslist+i)->rankX );
        fprintf( STATUS, "\n" );
        return;

}
```

do_cont.c

```
/*************************************************************
        Purpose:
                compute the contribution to the i, j location
*************************************************************/
void do_coef_contrib( mme, i, j, observed, equation_i )
struct MME *mme;
unsigned i, j, observed, equation_i;
{
        unsigned trait_i, trait_j, equation_j;

        double get_value(), v;

                        /* shorten the notation */
        trait_i = (mme->efflist+i)->trait;
        trait_j = (mme->efflist+j)->trait;

                        /* get the indices in the MME */
        equation_j = get_equation( mme->efflist+j );

        v = get_value( mot+observed, trait_i, trait_j );


        if( (mme->efflist+i)->type == COVARIATE )
                v *= getCov( mme->efflist+i );


        if( (mme->efflist+j)->type == COVARIATE )
                v *= getCov( mme->efflist+j );

                                                        /* je/lk modification , start */

        if( (mme->efflist+i)->type == RANDREG )
         v *= getCov( mme->efflist+i );

        if( (mme->efflist+j)->type == RANDREG )
         v *= getCov( mme->efflist+j );

                                                        /* je/lk modification, end */
        add_fork_value( mme->mp, equation_i, equation_j, v );

        add_fork_value( mme->mp, equation_j, equation_i, v );

        return;
}



/*****************************************************************/
double getCov( eff )
struct effect *eff;
{
        extern unsigned current_record;

        if( eff->type == RANDREG )
```

```
                                        /*  modification je/lk - 9/14/99 */
                return( (((struct RRDATASTORE *)eff->data + current_record - 1)->value) );
                /*  return( ( ((struct RRDATASTORE *)(eff->data)->value) + current_record - 1) );    */
        else
                return( *( ((double *)eff->data) + current_record - 1) );
}
```

dsreg.c

```
/*************************************************************
        Fill the specifications of the effects.  Not
        error checking at all.  This is a prototype for
        testing of other routines. - 1/9/95 - blg.
*************************************************************/
void fillEffects( mme, file )
struct MME *mme;
char *file;
{
        FILE *efp, *lfp;
        unsigned firsteq=1, i, j;
        int comp_level();

        if( (efp = fopen( file, "r" )) == NULL ){
                fprintf( stderr, "%s: Cannot open effects specification file %s for input\n",
                        ARGV0, file );
                exit( -1 );
        }

        fscanf( efp, "%d", &(mme->neffects) );
        fprintf( STATUS, "Number of effects in the model: %d\n", mme->neffects );

        if( (mme->efflist = malloc( sizeof( struct effect ) * mme->neffects )) == NULL ){
                fprintf( stderr, "%s: Cannot allocate memory for the effects specifications\n", ARGV0 );
                exit( 0 );
        }

        for( i=0; i < mme->neffects; i++ ){

                fprintf( STATUS, "\tEFFECT LEVEL %d SPECIFICATIONS\n", i );

                fscanf( efp, "%s %d %d %d %d",
                                (mme->efflist+i)->name,
                                &((mme->efflist+i)->type),
                                &((mme->efflist+i)->data_col),
                                &((mme->efflist+i)->trait),
                                &((mme->efflist+i)->constrain) );

                if( (mme->efflist+i)->type == MU )
                        ismu++;


                (mme->efflist+i)->mme_eq_no = firsteq;


                if( !isDupDataCol( mme->efflist, i ) )
                        num_input_fields++;

        /* je/lk: modification, start */

                if( (mme->efflist+i)->type == FIXED || (mme->efflist+i)->type == RANDOM || (mme-
                >efflist+i)->type == RANDREG ){
                        if( (lfp = fopen( (mme->efflist+i)->name, "r" )) == NULL ){
                                fprintf( stderr, "%s: Cannot open %s to read levels of effect\n",
```

```
/* je/lk: modification, end */
                        ARGV0, (mme->efflist+i)->name );
                exit( -1 );
        }

        (mme->efflist+i)->nlevels = nrecs( lfp );
        if( ((mme->efflist+i)->levels = malloc( sizeof( struct level )
                                        * (mme->efflist+i)->nlevels )) == NULL ){
                fprintf( stderr, "%s: Cannot allocate space for levels of this effect\n",
                        ARGV0 );
                exit( -1 );
        }


fprintf( STATUS, "\t\tName:\t\t%s\n", (mme->efflist+i)->name );
fprintf( STATUS, "\t\tType:\t\t%d\n", (mme->efflist+i)->type );
fprintf( STATUS, "\t\tNumber levels:\t%d\n",  (mme->efflist+i)->nlevels );
fprintf( STATUS, "\t\tIndex of Data Col:\t%d\n", (mme->efflist+i)->data_col );
fprintf( STATUS, "\t\tIndex of trait:\t%d\n", (mme->efflist+i)->trait );
fprintf( STATUS, "\t\tIndex of 1st eq:\t%d\n", (mme->efflist+i)->mme_eq_no );
        fprintf( STATUS, "\t\tConstrain?:\t\t%d\n", (mme->efflist+i)->constrain );

 firsteq += (mme->efflist+i)->nlevels;


        for( j=0; j < (mme->efflist+i)->nlevels; j++ ){
                fscanf( lfp, "%s", ((mme->efflist+i)->levels+j)->id );
                ((mme->efflist+i)->levels+j)->index = j;
        }

        fclose( lfp );

        fprintf( STATUS, "First 3 levels before sort: %s %s %s...\n",
                ((mme->efflist+i)->levels+0)->id,
                ((mme->efflist+i)->levels+1)->id,
                ((mme->efflist+i)->levels+2)->id );

        fprintf( STATUS, "Last 3 levels before sort: " );
                for( j = (mme->efflist+i)->nlevels-3; j<(mme->efflist+i)->nlevels; j++ )
                        fprintf( STATUS, "%s ", ((mme->efflist+i)->levels+j)->id );
                fprintf( STATUS, "...\n" );

        qsort( (mme->efflist+i)->levels, (mme->efflist+i)->nlevels,
                sizeof( struct level ), comp_level );

        fprintf( STATUS, "First 3 levels after sort: %s %s %s...\n",
                ((mme->efflist+i)->levels+0)->id,
                ((mme->efflist+i)->levels+1)->id,
                ((mme->efflist+i)->levels+2)->id );

        fprintf( STATUS, "Last 3 levels after sort: " );
                for( j = (mme->efflist+i)->nlevels-3; j<(mme->efflist+i)->nlevels; j++ )
                        fprintf( STATUS, "%s ", ((mme->efflist+i)->levels+j)->id );
                fprintf( STATUS, "...\n" );
```

```
        } else  if( (mme->efflist+i)->type == COVARIATE ){

                (mme->efflist+i)->mme_eq_no = firsteq++;
                (mme->efflist+i)->nlevels = 1;

            fprintf( STATUS, "\t\tName:\t\t%s\n", (mme->efflist+i)->name );
            fprintf( STATUS, "\t\tType:\t\t%d\n", (mme->efflist+i)->type );
            fprintf( STATUS, "\t\tNumber levels:\t%d\n",  (mme->efflist+i)->nlevels );
            fprintf( STATUS, "\t\tIndex of Data Col:\t%d\n", (mme->efflist+i)->data_col );
            fprintf( STATUS, "\t\tIndex of trait:\t%d\n", (mme->efflist+i)->trait );
            fprintf( STATUS, "\t\tIndex of 1st eq:\t%d\n", (mme->efflist+i)->mme_eq_no );

              /* je/lk modification, start */
              } else if( (mme->efflist+i)->type == RANDREG ){        /* Je/lk  modifications  */

            (mme->efflist+i)->mme_eq_no = firsteq++;
            (mme->efflist+i)->nlevels = 1;

            fprintf( STATUS, "\t\tName:\t\t%s\n", (mme->efflist+i)->name );
            fprintf( STATUS, "\t\tType:\t\t%d\n", (mme->efflist+i)->type );
            fprintf( STATUS, "\t\tNumber levels:\t%d\n",  (mme->efflist+i)->nlevels );
            fprintf( STATUS, "\t\tIndex of Data Col:\t%d\n", (mme->efflist+i)->data_col );
            fprintf( STATUS, "\t\tIndex of trait:\t%d\n", (mme->efflist+i)->trait );
            fprintf( STATUS, "\t\tIndex of 1st eq:\t%d\n", (mme->efflist+i)->mme_eq_no );
                    fprintf( STATUS, "\t\tConstrain?:\t\t%d\n", (mme->efflist+i)->constrain );
        }

            fprintf( STATUS, "\n" );


    }

    fclose( efp );
    return;
}
```

load.c

```
/*****************************************/
void loadData( mme )
struct MME *mme;
{
        extern unsigned ndatarecs;
        unsigned i, j;
        extern char *ARGV0;
/**/    double lars, john;                                  /* added to test for core dump lak
9/7/99 */
/**/    FILE *LARS, *JOHN;

        ndatarecs = nrecs( mme->dfp );

/**/    JOHN = fopen( "check1", "w" );
/**/  LARS = fopen( "check2", "w" );

        for( i=0; i < mme->neffects; i++ )
                /* je/lk modification, start */

                if( (mme->efflist+i)->type == COVARIATE ){
                        if( ((mme->efflist+i)->data = (double *) malloc( sizeof( double ) * (ndatarecs +
1) ))
                                == NULL ){
        /* je/lk modification , end */
                                        fprintf( stderr, "%s: Cannot allocate storage for data\n", ARGV0 );
                                        exit( -1 );
                                }
                } else if ( (mme->efflist+i)->type == RANDREG ) {
                        if( ((struct RRDATASTORE *)((mme->efflist+i)->data) = (struct
                                RRDATASTORE *) malloc( sizeof( struct RRDATASTORE ) *
                                (ndatarecs + 1) ))
                    == NULL ){

 /* je/lk modification , end */
                        fprintf( stderr, "%s: Cannot allocate storage for data\n", ARGV0 );
                        exit( -1 );
                }
                   } else {
                if( ((mme->efflist+i)->data = (double *) malloc( sizeof( unsigned ) * (ndatarecs + 1) ))
                  == NULL ){
                        fprintf( stderr, "%s: Cannot allocate storage for data\n", ARGV0 );
                        exit( -1 );
                }
                   }

        for( i=0; i < mme->ndependants; i++ ){
        if( ((mme->obslist+i)->data = (double *) malloc( sizeof( double ) * (ndatarecs+1) ))
             == NULL ){
               fprintf( stderr, "%s: Cannot allocate storage for dependant data\n", ARGV0 );
               exit( -1 );
         }
        if( ((mme->obslist+i)->usabledata = (int *) malloc( sizeof( int ) * (ndatarecs+1) ))
             == NULL ){
               fprintf( stderr, "%s: Cannot allocate storage for usable logical\n", ARGV0 );
```

```
                exit( -1 );
                  }
        }

        for( j=0; j < ndatarecs; j++ ){

                if( read_record( mme ) == EOF ){
                        fprintf( stderr, "%s: Premature EOF on data file\n", ARGV0 );
                        exit( -1 );
                }

                        for( i=0; i < mme->neffects; i++ ) {
                        if( usable( mme, i ) ) {


                                if( (mme->efflist+i)->type == COVARIATE ){
                         /* je/lk modification start */


                        /* je/lk check 9/7/99 error checking */
                        /*              john = atof( (mme->efflist+i)->curr_val );
                                                fprintf( JOHN, "%lg \n", john );
                                                *(((double *)((mme->efflist+i)->data))+j) = john;
*/
                                *(((double *)((mme->efflist+i)->data))+j) = atof( (mme->efflist+i)->curr_val );

                                        }

                                        if( (mme->efflist+i)->type == RANDREG ){
/* je/lk check 9/7/99 */ /*              lars = atof( (mme->efflist+i)->curr_val_rr );
                                                fprintf( LARS, "%lg \n", lars );

                                        *(((double *)((mme->efflist+i)->data))+j) = lars;
*/

                                            ((((struct RRDATASTORE *)(mme->efflist+i)->data))+j)->value
                                            = atof( (mme->efflist+i)->curr_val_rr );
                                        ((((struct RRDATASTORE *)(mme->efflist+i)->data))+j)->index =
                                                find_equation( mme->efflist+i, j );

                                        } else {
                                /* je/lk modification, end */

                                                *(((unsigned *)((mme->efflist+i)->data))+j) =
                                                        find_equation( mme->efflist+i, j );
                                        }

                                }

                        }

                for( i=0; i < mme->ndependants; i++ )
                        if( (mme->obslist+i)->usable ){
                                *((mme->obslist+i)->data+j) = atof( (mme->obslist+i)->curr_val);

                                *((mme->obslist+i)->usabledata+j) = TRUE;
```

```
                        } else
                                *((mme->obslist+i)->usabledata+j) = FALSE;
        }

        return;
}
```

mme.c

```
/*****************************************************************************
        Purpose:
                Determine the contribution to the C and RHS
*****************************************************************************/
void do_contribution( mme, observed )
struct MME *mme;
unsigned observed;
{
        extern unsigned current_record;
        unsigned i, j, this_equation;
        double v, get_value();

        for( i=0; i < mme->neffects; i++ ){

                        /* don't do anything if the record has something missing for this effect */
                if( usable( mme, i ) ) {

                        /* figure the diagonals */

                        this_equation = get_equation( mme->efflist+i );

                        doDiagContrib( mme, mme->efflist+i, this_equation, observed );
                /* figure the contributions for other effects */
                for( j=i+1; j <  mme->neffects; j++ )
                        if( usable( mme, j ) )
                                do_coef_contrib( mme, i, j, observed, this_equation );

                        /* do the RHS */

                v = 0;
                for( j=0; j < mme->ndependants; j++ )

                        if( (mme->obslist+j)->usable ) {
                                v += get_value( mot+observed,
                                                (mme->efflist+i)->trait,
                                                (mme->obslist+j)->trait )
                                        * getObs( mme->obslist+j );
                        }

                if( (mme->efflist+i)->type == COVARIATE )
                        v *= getCov( mme->efflist+i );

                                        /* je/lk modification, start */

                if( (mme->efflist+i)->type == RANDREG )
                  v *= getCov( mme->efflist+i );

                                        /* je/lk modification end */

/* printf( "LOC 1 this_equation = %d v=%f\n", this_equation, v ); */

                add_fork_value( mme->rhs, this_equation, 1, v );
```

```
                }
        }


        return;
}
/*****************************************************************************
 Purpose:
    Read a data record into record buffer.
*****************************************************************************/
int read_record( mme )
struct MME *mme;
{
  unsigned nfields, i;
  extern unsigned recno, num_input_fields;
  extern char **field_pointer;

        /* Read the records into the read buffer for parsing */
  if( fgets( read_buffer, REC_BUF_LEN, mme->dfp ) != NULL ){

                /* get ride of nl character */
                if( read_buffer[ strlen( read_buffer ) - 1 ] == '\n' )
                        read_buffer[ strlen( read_buffer ) - 1 ] = '\0';

        recno++;

                        /* do a little error checking */

        if( (nfields = parse_record( read_buffer, field_pointer )) == 0 ) {

          fprintf( stderr, "Record length of zero in input data file at line %d\n", recno );
          exit( -1 );

        } /* else  if ( nfields < num_input_fields ){

          fprintf( stderr, "The number of fields in the record is less then the number of fields\n\t on the
                        INPUT statement. Record number: %d\n", recno );
           exit( -1 );
        } */

                        /* set the pointers in the effects to the locations in the read buffer */

        for( i=0; i < mme->neffects; i++ ){

        if( ( mme->efflist+i )->type == RANDREG )
        /* je/lk modification, 9/6/99, start */
          (mme->efflist+i)->curr_val_rr = *(field_pointer + (mme->efflist+i)->constrain-1);

                                                        /* curr_val_rr is used to pull the independent
                variable from the contraint field of the effects field */

          (mme->efflist+i)->curr_val = *(field_pointer + (mme->efflist+i)->data_col-1);

        /* je/lk modification, 9/6/99, end */
        }
```

```
            for( i=0; i < mme->ndependants; i++ )
               (mme->obslist+i)->curr_val = *(field_pointer + (mme->obslist+i)->data_col-1);

                        /* determine what is and isn't usable */
            set_usable( mme );

            return( NULL );
      }

      return( EOF );

   }
   /*****************************************************************************
     Purpose:
        set the usable value for each effect.
   *****************************************************************************/
   void set_usable( mme )
   struct MME *mme;
   {
         unsigned i, j;
            for( i=0; i < mme->ndependants; i++ ){

                  (mme->obslist+i)->usable = TRUE;

                     /* Is the RHS observed? */
                      if( strcmp( (mme->obslist+i)->curr_val, UNKNOWN ) == NULL )
                        (mme->obslist+i)->usable = FALSE;

                           /* Are any of the effects levels unknown (accept random effects) */
                      for( j=0; j < mme->neffects; j++ ){

            /* je/lk modification, 9/7/99, start */
            /*                    if( (mme->efflist+j)->type == RANDREG ){


                                 if( (mme->efflist+j)->trait == (mme->obslist+i)->trait &&
                                    strcmp( (mme->efflist+j)->curr_val_rr, UNKNOWN ) == NULL )
                                          (mme->obslist+i)->usable_rr = FALSE;
                                  } */
            /* je/lk modification, 9/7/99, end */


                                 if( (mme->efflist+j)->trait == (mme->obslist+i)->trait &&
                                    strcmp( (mme->efflist+j)->curr_val, UNKNOWN ) == NULL )

                                          (mme->obslist+i)->usable = FALSE;
                        }

            }

            return;
   }

   /*****************************************************************************/
   void doDiagContrib( mme, eff, this_eq, observed )
   struct MME *mme;
```

```
struct effect *eff;
unsigned this_eq, observed;
{
        double v, r,  get_value();

        switch( eff->type ){


                case RANDOM:
                case FIXED:
                case MU:

                *(mme->diagonal+this_eq-1) += get_value( rmot+observed,
                                        eff->trait,
                                eff->trait );

                        break;

                                                        /* je/lk modification, start, 9/6/99 */

                case RANDREG:
                case COVARIATE:

                        v = getCov( eff );
              *(mme->diagonal+this_eq-1) += get_value( rmot+observed,
                                eff->trait,
                                eff->trait )
                                                                * v * v;


              break;
        }

        return;
}


/*******************************************************/
unsigned get_equation( eff )
struct effect *eff;
{
        extern unsigned current_record;


/**/     if( eff->type == COVARIATE || eff->type == MU )

                return( eff->mme_eq_no );

/*  modification je/lk- 9/14/99, start */
        else if( eff->type == RANDREG )

                return( (((struct RRDATASTORE *)eff->data)+ current_record - 1)->index );

        /* modification je/lk -9/14/99, end */

        else
```

```
        return( *((unsigned*)eff->data + current_record - 1) );
}
```

include/methodr.h

```
/* methodr.h

        Purpose:
                stuff for coef matrix builder engine.

        Revision Record:
                9/1/94 - blg: Initial codeing.
                9/6/99 - je/lk: added definitions to effect object for random regression
                9/14/99 - je/lk:  added on the RRDATASTORE object

*/

#include <limits.h>
#include <matrix.h>

#define         MAXNAME 20


/* definition of the RRDATASTORE object   modification for Random regression case- je/lk 9/14/99  */
struct RRDATASTORE {
        double          value;
        unsigned        index;
};

/* definition of the effect object */
struct effect {

        char            name[MAXNAME];      /* Name of effect in data file */
        unsigned        type;               /* Fixed, random, coef */

        struct level    *levels;  /* Pointer to the list of levels names */
        unsigned        nlevels;  /* Number of levels in the factor */

        unsigned        data_col;       /* index number of the data column */
        unsigned        trait;          /* index of the model statement, ie 1st, 2nd, etc */

        unsigned        mme_eq_no;      /* The equation number of 1st level */

        char            *curr_val;      /* value from most recent rec read */
        char            *curr_val_rr;   /* The actual value from most recent record read for the
random regression case.  It is assigned in the constrain field of the effects(eff) file  je/lk 9/6/99  */


        double          *data;          /* Data stored in core, indexes or covariate */
        unsigned        constrain;      /* logical TRUE = don't solve last equation */
                                        /* Also, TRUE = location of independent variable in the data
set */
        };

/* Definition of RHS structure */
struct OBS {

        unsigned        trait;          /* which model */
        unsigned        data_col;       /* index in record buffer */
```

```
        char            *curr_val;              /* pointer into record_buffer */
        char            *curr_val_rr;   /* value from most recent record read , random regression
        case  je/lk 9/6/99  */

        unsigned        usable;         /* Logical for missing value in current rec/trait */
                                        /* i.e., Can the current rec be used for this trait */
        double          *data;          /* data stored in core */
        int             *usabledata;    /* logical for if usable */

        double          rankX;          /* rank of the fixed effects matrix */
        double          top;            /* top of the binary iteration */
        double          bot;            /* bottom of the binary iteration */
        unsigned        usable_rr;  /* missing independent variable for randreg case */

        };

/* def of augmentation specifications */
struct AUG {
        struct matrix *amp;
        struct effect *eff;
        };


/* Definition of the coefficient matrix object */
struct MME {

        char name[ PATH_MAX ];

        struct matrix   *mp;    /* pointer to the coef matrix */
        struct effect   *efflist;  /* pointer to the effect list */
        unsigned        neffects; /* number of factors in efflist */
        double          *diagonal;      /* pointer to the diagonal elements */

        struct matrix   *rhs;   /* store the RHS */
        struct  OBS     *obslist; /* pointer to dependants list */
        unsigned        ndependants;    /* number of dependant variables */

        struct AUG      *auglist; /* list of augmentation specs */
        unsigned        naugments;      /* number of augmentations to do */

        double          *beta;          /* solutions */

        FILE            *dfp;           /* pointer to the data file */

        int             (*readRoutine)(); /* routine to read the record */

        };
```

include/methrproto.h

```
/* methrproto.h

        Purpose:
                define prototypes for functions in the Method R
```

```
                software.

        Revision Record:
                10/7/94 - blg: Initial codeing.
                7/3/99 - je/lk:  Added definition "6"  for randreg

*/

#define         REC_BUF_LEN 2024

#define         FIXED       1
#define         RANDOM      2
#define         COVARIATE   3
#define         MU          4
#define         RANDREG     6
```

APPENDIX B

Random_r

Description

Modified version of gen_z for generating a coefficient matrix.
Added a covariate vector to place the covariate instead of incidence in a random effects matrix

Usage: random_r -d (datalist) -e (effect_list) -r (right hand side) -c (vector of covariates) -o (matrix of covariates).

```
/* random_r.c
        Purpose:
                Create a coefficient matrix for the random regression case  (Modified gen_z)

        Usage:
                random_r -d datalist -e effect_list -r  rhs -c vector of covariates -o incidence matrix.

        Revision Record:
                4/14/90 - blg: Initial codeing
                11/1/90 - blg: Added error msg supress flag feature.
                11/28/90 - blg: Modified from fef.
                12/12/90 - blg: modified to use bsearch() instead of tsearch.
                 1/6/96 - je/bw/blg: modified gen_z for random regression case.


*/

#include        <stdio.h>
#include         <stdlib.h>
#include        "matrix.h"

#define                 SCRATCH ".scrgenz"

struct level d, *dx, *effectp = NULL;

FILE *fpr, *fpp, *fp, *fpo, *fpc, *fopen();

short supress_flag = FALSE;

main( argc, argv )
int argc;
char *argv[];
{
        char rhs_value[FIELD_WIDTH], id[FIELD_WIDTH], dummy[FIELD_WIDTH];
        unsigned i = 0, nelem = 0, col = 0, row = 0;
        unsigned peff = 0, neff = 0;
        int I_comp_level();
        double cov;

        process_args( argc, argv );

        while( fscanf( fp, "%s", id ) != EOF )
                neff++;

        rewind( fp );

        if( (effectp = (struct level *) malloc( neff * sizeof( struct level))) == NULL ){
                fprintf( stderr, "random_r: Cannot allocate enough space\n");
                exit( -1 );
        }

        for(i=0; i<neff; i++){
                fscanf( fp, "%s", id );
                strcpy( (effectp+i)->id, id );
                (effectp+i)->index = i + 1;
        }
```

```
        qsort( (char *) effectp, neff, sizeof( struct level ), I_comp_level );


        fprintf( fpo, NULL_HEADER );

        while( !(fscanf( fpp, "%s", id ) == EOF ||
            fscanf( fpc, "%s", dummy ) == EOF )) {
                row++;

                if( fscanf( fpr, "%s", rhs_value ) == EOF ){
                        fprintf( stderr, "random_r: Premature EOF on RHS file\n");
                        exit( -1 );
                }
                if( !strcmp(dummy, UNKNOWN) )
                        cov = 0;
                else{
                        cov = atof( dummy );


                        if( strcmp( rhs_value, UNKNOWN ) != NULL ){
                                strcpy( d.id, id );
                                if( (dx = (struct level *) bsearch( (char *) &d,
                                                        (char *) effectp,
                                                        neff,
                                                        sizeof( struct level ),
                                                        I_comp_level ))
                                == NULL ){
                                if( !supress_flag ){
                                        fprintf( stderr, "gen_z: WARNING: Effect level %s not found
in effect list.\n",
                                                id );
                                        fprintf( stderr, "\tMatrix may be unusable.\n");
                                   }
                                } else {
                                        nelem++;
                                        fprintf( fpo, "%d %d %e\n", row, dx->index, cov );
                                }
                        }
                }
        }

        rewind( fpo );
        fprintf( fpo, "SPARSE %d %d %d\n", row, neff, nelem );

        exit(0);
}

int I_comp_level( ep1, ep2 )
struct level *ep1, *ep2;
{
        return( strcmp( ep1->id, ep2->id ) );
}
Syntax()
{
```

```
        fprintf( stderr, "random_r: Syntax: random_r -d (data vector) -e (effect list)\n\t-r (obs vector) -c
(cov vector) -o (output incidence matrix)\n");
        exit(1);
}

process_args( argc, argv )
int argc;
char *argv[];
{
        int c;
        extern char *optarg;
        short dflg=FALSE, eflg=FALSE, rflg=FALSE, cflg=FALSE, oflg=FALSE;

        while( (c=getopt( argc, argv, "d:e:r:c:o:s" )) != -1 ){

            switch( c ) {

                case 'd':
                        dflg = TRUE;
                        if( (fpp = fopen( optarg, "r" )) == NULL ){
                                fprintf( stderr, "gen_z: Cannot open %s for input.\n", optarg );
                                exit( -1 );
                        }
                        break;

            case 'e':
                eflg = TRUE;
                if( (fp = fopen( optarg, "r" )) == NULL ){
                    fprintf( stderr, "gen_z: Cannot open %s for input.\n", optarg );
                    exit( -1 );
                }
                break;

            case 'r':
                rflg = TRUE;
                if( (fpr = fopen( optarg, "r" )) == NULL ){
                    fprintf( stderr, "gen_z: Cannot open %s for input.\n", optarg );
                    exit( -1 );
                }
                break;

            case 'c':
                cflg = TRUE;
                if ( (fpc = fopen( optarg, "r" )) == NULL ){
                    fprintf( stderr, " random_r: Cannot open %s for output.\n", optarg );
                    exit( -1 );
                }
                break;

            case 'o':
                oflg = TRUE;
                if( (fpo = fopen( optarg, "w" )) == NULL ){
                    fprintf( stderr, "gen_z: Cannot open %s for output.\n", optarg );
                    exit( -1 );
                }
                break;
```

```
                        case 's':
                                supress_flag = TRUE;
                                break;

                        case '?':
                                Syntax();
                }
        }

        if( !dflg || !eflg || !rflg || !cflg || !oflg )
                Syntax();


        return;
}
```

APPENDIX C

Results Tables and Figures

Table C.1. Number of observations (N), BLUP Fixed effects estimates for age of dam (AOD) and adjusted weaning weight (WWTadj), SE for weight at age 2yr to 4yr in Red Angus cattle

	2yr		3yr		4yr	
Effect (2yr)	N	Estimate (kg) (SE)	N	Estimate (kg) (SE)	N	Estimate (kg) (SE)
AOD (yr)						
2	1,816	-14.09 (1.960)	1,129	-14.52 (2.686)	915	-15.81 (3.341)
3	1,294	-13.39 (2.112)	900	-12.98 (2.784)	658	-9.36 (3.556)
4	913	-7.03 (2.292)	729	-5.87 (2.892)	536	-7.05 (3.756)
5 to 9	2,706	.00 (.000)	2,094	.00 (.000)	1,559	.00 (.000)
10	230	-0.14 (4.050)	187	-5.29 (5.190)	139	4.11 (6.698)
11	166	-15.28 (4.832)	125	-9.22 (6.319)	102	-16.06 (7.995)
12	126	-10.99 (5.512)	88	-12.58 (7.831)	61	-5.97 (10.361)
13+	168	-18.34 (4.964)	132	-20.54 (6.692)	94	-23.14 (8.721)
WWT adj (kg)	-	.035(.0159)	-	.023 (.020)	-	.017 (.0251)

Table C.2. Number of observations (N), BLUP Fixed effects estimates for age of dam (AOD) and adjusted weaning weight (WWTadj), SE for adult weight at age 5yr to 7yr in Red Angus cattle

	5yr		6yr		7yr	
Effect	N	Estimate, kg (SE)	N	Estimate (SE)	N	Estimate (SE)
AOD (yr)						
2	735	-15.75 (3.673)	574	-14.05 (4.225)	516	-12.41 (4.436)
3	548	-6.75 (3.873)	475	-6.67 (4.329)	400	-6.40 (4.717)
4	470	-6.15 (4.036)	357	-5.73 (4.666)	280	-3.03 (5.173)
5 to 9	1,279	.00 (.000)	1,028	.00 (.000)	835	.00 (.000)
10	117	-2.79 (7.495)	80	2.53 (9.086)	67	-7.07 (9.889)
11	80	-3.12 (8.748)	66	-8.94 (10.193)	53	-16.91 (10.762)
12	56	-5.14 (11.588)	45	-9.21 (12.769)	32	-26.09 (14.806)
13+	85	-16.99 (8.770)	65	-21.28 (10.808)	56	-11.68 (11.933)
WWTadj (kg)		.016 (.0282)		-.014 (.0313)		.098 (.0334)

Table C.3. Number of observations (N), BLUP Fixed effects estimates for age of dam (AOD) and adjusted weaning weight (WWTadj), SE for weight at age 8yr to 10yr in Red Angus cattle

	8yr		9yr		10yr	
Effect	N	Estimate, kg (SE)	N	Estimate (SE)	N	Estimate (SE)
AOD (yr)						
2	399	-9.10 (5.219)	333	-11.82 (5.567)	241	-8.07 (6.976)
3	302	-2.26 (5.507)	239	-3.57 (6.100)	178	-4.55 (7.572)
4	236	1.25 (5.865)	210	2.48 (6.328)	121	3.67 (8.897)
5 to 9	683	.00 (.000)	535	.00 (.000)	354	.00 (.000)
10	56	-2.36 (11.249)	49	-4.96 (12.829)	22	27.01 (18.320)
11	41	-3.99 (12.445)	40	-1.00 (12.436)	18	-.85 (20.364)
12	28	-10.43 (17.048)	16	-6.01 (20.094)	15	15.05 (22.288)
13+	40	-21.27 (14.946)	31	-9.66 (15.750)	27	-16.14 (16.986)
WWTadj (kg)	-	.010 (.0382)	-	-.057 (.0397)	-	.119 (.0514)

Table C.4. Number of subsamples (N), median heritability (h^2) estimate, mean, and 95% CI for each trait of two-trait analysis for ages to 2 to 10 yr

	Trait 1		Trait 2	
Run (N)	Median h^2	95% CI (Median)	Median h^2	95% CI (Median)
2.3 (24)	.67	.58 to.84	.61	.56 to.67
2.4(28)	.52	.51 to .57	.57	.54 to.61
2.5(24)	.56	.54 to.62	.72	.67 to.75
2.6(23)	.53	.51 to .58	.58	.52 to .62
2.7(24)	.54	.52 to .57	.69	.62 to .75
2.8(23)	.54	.53 to .60	.60	.54 to .73
2.9(0)	-	-	-	-
2.10(0)	-	-	-	-
3.4(22)	.68	.59 to .93	.68	.63 to .74
3.5(23)	.59	.56 to .62	.71	.63 to .74
3.6(24)	.56	.54 to .62	.69	.54 to .76
3.7(23)	.54	.47 to .55	.73	.67 to .79
3.8(25)	.50	.46 to .54	.71	.64 to .76
3.9(20)	.50	.45 to .54	.79	.66 to .86
3.10(3)	.43	.35 to .45	.87	.65 to .87
4.5(25)	.69	.58 to .75	.71	.66 to .80
4.6(19)	.43	.33 to .61	.61	.58 to .76
4.7(17)	.56	.42 to .64	.62	.53 to .73
4.8(19)	.53	.47 to .58	.56	.47 to .68
4.9(18)	.37	.30 to .45	.67	.59 to .79
4.10(0)	-	-	-	-
5.6(23)	.56	.49 to .62	.67	.63 to .71
5.7(21)	.55	.50 to .64	.71	.59 to .80
5.8(19)	.45	.39 to .56	.62	.46 to .78
5.9(17)	.40	.33 to .49	.72	.50 to .82
5.10(0)	-	-	-	-
6.7(10)	.64	.25 to .82	.51	.34 to .66
6.8(24)	.62	.57 to .75	.54	.42 to .63
6.9(23)	.54	.42 to .64	.62	.47 to .70
6.10(4)	.48	.10 to .53	.68	.51 to .79
7.8(13)	.37	.22 to .99	.43	.39 to .69
7.9(19)	.46	.36 to .71	.68	.59 to .80
7.10(0)	-	-	-	-
8.9(11)	.22	.14 to .99	.34	.29 to .63
8.10(4)	.33	.02 to .37	.75	.48 to .96
9.10(0)	-	-	-	-

*rounded interval to 1.00

Table C.5. Residual variances for trait 1 and trait 2 from multivariate analyses of Red Angus mature weight data

		Trait 1	Trait 2	
Run (N)	median	95% CI (median)	median	95% CI (median)
2.3 (24)	2,434.35	2095.64 to 3128.41	4102.43	3722.33 to 5184.28
2.4(28)	3,356.62	3212.49 to 3928.21	8784.69	7228.22 to 10184.80
2.5(24)	2,994.31	2686.62 to 3450.34	5780.05	4993.17 to 7140.86
2.6(23)	4,244.52	3962.05 to 43451.56	11081.80	7634.59 to 15248.50
2.7(24)	3,518.21	3325.95 to 3892.35	7693.10	6121.94 to 9194.96
2.8(23)	3,426.00	2933.29 to 3645.0	9120.24	6077.54 to 15542.50
2.9(0)	-	-	-	-
2.10(0)	-	-	-	-
3.4(22)	3,551.04	1459.72 to 4398.70	4830.49	3945.90 to 5988.95
3.5(23)	4,267.77	3633.94 to 5067.91	4267.77	3633.94 to 5067.91
3.6(24)	4,459.98	4218.03 to 5342.42	5475.09	4447.12 to 7098.01
3.7(23)	4,569.95	4131.52 to 5133.58	4783.81	3773.46 to 5661.52
3.8(25)	5,102.86	4270.95 to 5745.73	8571.94	5892.80 to 10009.90
3.9(20)	5,598.98	5115.02 to 6332.39	7157.98	4658.01 to 12214.90
3.10(3)	6,643.34	6531.19 to 7692.54	72688.60	11832.60 to 99947
4.5(25)	4,727.82	4231.61 to 5254.09	4167.77	3491.60 to 5328.39
4.6(19)	8,018.53	6439.36 to 9761.73	7377.70	5611.51 to 8882.08
4.7(17)	6,478.44	5126.22 to 8461.77	5599.28	4272.47 to 8453.13
4.8(19)	7,916.93	7430.03 to 8970.20	7904.87	5897.84 to 12621.10
4.9(18)	8,994.39	7669.56 to 11113.30	9686.86	6333.23 to 14890.0
4.10()	-	-	-	-
5.6(23)	7,205.81	5924.06 to 8379.18	7457.14	6141.76 to 8718.35
5.7(21)	6,746.64	5595.16 to 8537.69	4990.68	4009.18 to 7384.09
5.8(19)	10,283.70	8121.32 to 11749.20	8367.54	6734.67 to 13521.20
5.9(17)	7,862.31	6952.60 to 11354.60	11698.2	8340.98 to 15018.8
5.10()	-	-	-	-
6.7(10)	7,080.62	3379.94 to 12330.70	9970.45	5981.71 to 13988.60
6.8(24)	7,093.88	4950.05 to 9519.50	7960.18	7100.29 to 9020.16
6.9(23)	9,263.72	7150.93 to 12007.3	9831.35	8404.99 to 13202.80
6.10(4)	14,336.10	12642.80 to 16508.3	28117.15	14426 to 33111.1
7.8(13)	9,425.56	6940.99 to 16550.20	13008.20	8389.78 to 26373.30
7.9(19)	9,067.63	6826.1 to 11371.40	9317.86	5315.40 to 19560.00
7.10(0)	-	-	-	-
8.9(11)	10915.40	1671.70 to 18260.6	28439.10	13346.60 to 44323.7
8.10(4)	19578.03	15290.2 to 24980.8	49640.52	3154.49 to 134818
9.10(0)	-	-	-	-

Table C.6. Additive genetic variances for trait 1 and trait 2 from multivariate analyses of Red Angus mature weight data

		Trait 1	Trait 2	
Run (N)	median	95% CI (median)	median	95% CI (median)
2.3 (24)	5397.33	3933.99 – 10932.0	7209.80	3964.21-10459.30
2.4(28)	4007.07	3402.31-4684.13	13427.45	11624.50-14192.0
2.5(24)	3888.02	3630.74-4513.46	14794.35	12070.50 – 17980.3
2.6(23)	4244.50	3962.05 – 4351.56	14798.5	12115.90 – 19034.7
2.7(24)	4294.74	3793.16 – 4654.43	19175.05	13315.2 – 21890.2
2.8(23)	4230.57	3889.36 – 4888.27	19466.70	12490.2 – 28941.4
2.9(0)	-	-	-	-
2.10(0)	-	-	-	-
3.4(22)	7908.53	5988.39-18877.50	9594.62	8377.91-14065.1
3.5(23)	6443.01	5686.84-7779.33	13794.6	9784.43-15799.4
3.6(24)	6058.29	5581.53-6592.31	11803.20	8856.08-17093.20
3.7(23)	5512.52	4095.59-5987.07	22261.2	16323.1-28057.4
3.8(25)	5158.74	4351.1-5633.09	19056.10	16323.1-30891.0
3.9(20)	5439.99	4922.71-6284.70	27314.0	18494.6-33525.2
3.10(3)	4988.40	4212.93-5464.18	134545.0	80125.4-674520.0
4.5(25)	10155.30	7343.71-14267.0	13312.20	10411.40-14795.7
4.6(19)	6077.40	4866.97 – 8014.74	13606.3	10021.6 – 20666.8
4.7(17)	8047.01	5680.72-10078.1	11240.2	6792.0-17963.8
4.8(19)	9821.44	6695-10843.5	13420.5	7847.15-19539.6
4.9(18)	5590.62	4349.25-8153.06	21991.1	11033.7-35546.5
4.10(0)	-	-	-	-
5.6(23)	9114.79	6202.92 – 12705.30	16065.1	14518.5 – 19767.7
5.7(21)	8544.51	6798.65 – 10210.3	13881.70	10874.90-19844.4
5.8(19)	8493.85	6467.1 – 11422.3	16279.3	8026.25 – 29489.5
5.9(17)	5636.02	4382.37 – 7080.68	29992.2	18750.1 – 44036.3
5.10(0)	-	-	-	-
6.7(10)	13215.50	4194.89-18591.1	10599.89	4669.22-17031.1
6.8(24)	11385.45	10027.3-16245.9	9584.07	6503.36-11549.20
6.9(23)	10631.2	8830.04 – 14217.6	16767.8	12078.80-27454.2
6.10(4)	12291.75	1826.18-16653.3	40635.3	34106.6-117235
7.8(13)	6588.28	3883.71-96255.1	18634.50	5527.33-23175.2
7.9(19)	11261.1	5005.47-16270.6	23642.9	16662.8-31951.0
7.10(0)	-	-	-	-
8.9(11)	4256.03	2163.26 – 74547.6	19284.0	5748.81-40097.6
8.10(4)	7999.50	586.9-12892.70	79867.40	35019.-353328
9.10(0)	-	-	-	-

Table C.7. Median phenotypic (co)variances for cow weight at ages 2 to 10 yr in Red Angus Cattle (multivariate analyses). Variances are pooled along the diagonal

Age (yr)	2 (kg^2)	3	4	5	6	7	8	9	10
2	**1,579.17**	1,412.35 (1,160.63 to 1,581.44)	1,877.44 (1,547.58 to 1,954.95)	1,611.04 (1,491.77 to 1,813.79)	2,091.45 (1,625.44 to 2,644.36)	1,837.92 (1,511.16 to 2,072.59)	1,882.31 (1,271.33 to 2,918.54)	-	-
3		**2,287.29**	1873.29 (1,768.60 to 2,246.18)	18401.11 (1,629.98 to 2,334.42)	1,433.53 (1,254.45 to 1,783.41)	1,602.07 (1,416.98 to 1,760.582)	2,103.44 (1,806.24 to 2,637.58)	2,374.53 (1,819.46 to 2,829.73)	4,039.86 (3,523.84, 7,024.85)
4			**3,482.27**	2,356.14 (2,098.92 to 2,510.58)	2,206.43 (1,760.99 to 2,817.67)	2,073.37 (1,337.79 to 3,139.57)	2,320.84 (1,902.91 to 2,778.68)	2,513.07 (1,753.64 to 3,098.91)	-
5				**3,531.27**	2,785.05 (2,493.75 to 3,46.94)	2,169.67 (1,875.14 to 3,093.98)	2,620.10 (2,333.80 to 3,413.66)	2,971.33 (2,547.29 to 3,644.45)	-
6					**4,549.57**	2,959.14 (2,118.27 to 3,553.46)	2,366.34 (2,152.85 to 2,948.13)	2,955.64 (2,352.25 to 3,240.52)	4,077.72 (3,312.57 to 5,762.00)
7						**4,079.29**	2,776.42 (2,534.33 to 4,379.14)	3,364.11 (2,808.83 to 4,869.78)	-
8							**8,686.86**	3,986.20 (2,777.61 to 5,286.818)	5,380.84 (2,939.29 to 13,488.00)
9								**8,044.49**	-
10									**27,618.31**

All variances are averages of the median estimates for that age.

Table C.8. Median and 95% confidence limits of genetic and residual covariances for weight in Red Angus Cattle at ages 2 to 10 yr (multivariate analyses). Genetic covariances are above the diagonal and residual covariances below the diagonal genetic and residual variances along the diagonal

Age (yr)	2 (kg^2)	3	4	5	6	7	8	9	10
2	**893.39 (gen)** **684.69 (res)**	1214.05 1134.18 to 1426.24	1378.13 1197.39 to 1483.88	1477.27 1385.75 to 1578.86	1519.13 1338.76 to 1746.53	1582.56 1460.12 to 1694.63	1685.35 1199.71 to 2003.62	-	-
3	10.15 -246.90 to 196.69	**1252.36 (gen)** **984.57 (res)**	1887.69 1756.61 to 2165.39	1721.73 1570.04 to 2008.20	1530.86 1433.88 to 1840.55	1641.74 1349.79 to 1839.88	1785.09 1511.78 to 2123.70	2252.98 1900.67 to 2338.76	4816.74 3400 to 6671
4	370.45 295.08 to 522.11	-32.28 -239.54 to 88.13	**1842.67 (gen)** **1461.74 (res)**	2109.57 2012.13 to 2423.02	1682.85 1568.91 to 2156.47	1759.92 1323.14 to 2422.93	2129.19 1567.77 to 2536.36	2153.75 1500.41 to 2758.11	-
5	134.68 99.79 to 323.43	188.15 45.57 to 268.77	20.93 -129.21 to 166.24	**2165.19(gen)** **1360.75(res)**	2479.52 1893.93 to 2805.99	1817.54 1649.59 to 2751.03	2150.21 1522.43 to 2790.52	2438.43 2155.60 to 728.31	-
6	497.63 234.51 to 809.50	-50.61 -103.17 to 37.01	268.54 120.45 to 736.20	464.18 306.41 to 696.49	**2668.44(gen)** **1786.16(res)**	1923.14 1511.93 to 2994.22	2121.31 1862.40 to 2612.98	2722.19 2362.71 to 2917.46	3780.43 2667.50 to 4643.59
7	146.09 -22.68 to 304.44	28.56 -49.79 to 77.06	170.45 -59.73 to 418.43	172.11 119.72 to 448.97	428.64 -76.64 to 1649.93	**2804.13(gen)** **1520.87(res)**	2201.67 1866.43 to 3004.13	3146.88 2303.06 to 3892.36	-
8	141.94 -22.11 to 605.58	337.60 162.60 to 468.08	296.62 78.59 to 626.15	674.25 487.11 to 81.84	60.77 -66.67 to 573.42	791.44 530.99 to 2361.16	**2794.51(gen)** **2206.20(res)**	2388.22 1078.07 to 5378.03	4114.67 1328.93 to 10756.74
9	-	139.12 -105.41 to 251.18	201.51 7.88 to 380.79	407.62 95.70 to 902.38	182.56 87.98 to 507.93	629.66 189.36 to 1465.29	1290.49 -394.01 to 2874.59	**4764.54(gen)** **2609.61(res)**	-
10	-	139.97 -2613.64 to 2240.17	-	-	720.45 -149.07 to 1144.57	-	1368.36 -142.38 to 4403.33	-	**17485.70(gen)** **10361.16(res)**

Simulated data analysis: software validation

Table C.9. Median additive genetic variance component estimates, 95% CI, and standard error of the mean (SEM) for the intercept term (b0) from simulated mature weight data

No. of observations	No. of Converged Subsamples[1]	Median Genetic Variance (SEM)	95% CI
2[2]	0	_	_
3	3	5,392.94 (4,135.73)	4730.46 to 17455.90
4	15	2,477.57 (204.50)	1,907.94 to 3,101.79
5	15	1,563.27 (115.53)	1,446.67 to 1,720.34
8	15	1,559.96 (41.71)	1,378.76 to 1,646.54
True Value		1,429.45	_

[1]Number of Method R subsamples that yielded converged estimates.
[2]There were no converged subsamples at 2 observations per animal

Table C.10. Median additive genetic covariance component estimates, 95% CI, and standard error of the mean (SEM) for the intercept (b0) and linear (b1) term from simulated mature weight data

No. of observations	No. of Converged Subsamples[1]	Genetic Cov(b0,b1)	95% CI
2[2]	0	_	_
3	3	-1,187.88 (1,085.51)	-3,910.20 to 302.55
4	15	-116.26 (15.64)	-147.88 to 39.07
5	15	-3.45 (7.11)	-22.56 to 5.13
8	15	-12.88 (2.50)	-20.10 to 6.93
True Value		-35.58	_

[1]Number of Method R subsamples that yielded converged estimates.
[2]There were no converged subsamples at 2 observations per animal

Table C.11. Median additive genetic variance component estimates, 95% CI, and standard error of the mean (SEM) for the linear term (b1) from simulated mature weight data

No. of observations	No. of Converged Subsamples[1]	Genetic Var(b1)	95% CI
2[2]	0	_	_
3	3	402.89 (277.55)	27.23 to 981.48
4	15	31.91 (5.41)	27.17 to 44.28
5	15	35.50 (3.28)	27.55 to 42.37
8	15	27.82 (.84)	24.98 to 29.49
True Value		22.21	_

[1]Number of Method R subsamples that yielded converged estimates.
[2]There were no converged subsamples at 2 observations per animal

Table C.12. Median permanent environment variance component estimates, 95% CI, and standard error of the mean (SEM) for the intercept term (b0) from simulated mature weight data

No. of observations	No. of Converged Subsamples[1]	Permanent Environment Var(b0)	95% CI
2	0	_	_
3	3	2,374.81 (393.84)	1369.87 to 2671.46
4	15	1,237.44 (141.65)	650.55 to 1700.97
5	15	706.02 (77.77)	378.43 to 805.05
8	15	804.44 (18.59)	741.95 to 832.57
True Value		514.19	_

[1]Number of Method R subsamples that yielded converged estimates.
[2]There were no converged subsamples at 2 observations per animal

Table C.13. Median permanent environmental covariance component estimates between the intercept (b0) and linear term (b1), 95% CI, and standard error of the mean (SEM) in parentheses from simulated mature weight data

No. of observations	No. of Converged Subsamples[1]	Permanent Environment Cov(b0,b1)	95% CI
2	0	-	-
3	3	-491.44 (126.76)	-492.14 to –111.48
4	15	-110.73 (17.10)	-136.21 to –47.30
5	15	13.46 (7.19)	-10.93 to 30.91
8	15	-27.15 (1.58)	-32.66 to –24.02
True Value		-12.95	_

[1]Number of Method R subsamples that yielded converged estimates
[2]There were no converged subsamples at 2 observations per animal

Table C.14. Median permanent environment variance component estimates, 95% CI, and standard error of the mean (SEM) for the linear term (b1) from simulated mature weight data

No. of observations	No. of Converged Subsamples[1]	Permanent Environment Var(b1) (SEM)	95% CI
2	0	_	_
3	3	93.62 (29.97)	11.14 to 106.96
4	15	23.03 (2.55)	15.47 to 28.44
5	15	4.41 (1.20)	1.40 to 7.64
8	15	10.57 (.33)	10.19 to 11.72
True Value	_	8.02	_

[1]Number of Method R subsamples that yielded converged estimates
[2]There were no converged subsamples at 2 observations per animal

Table C.15. Median residual variance component estimate, 95% CI, and standard error of the mean (SEM) for simulated mature weight data

No. of observations	No. of Converged Subsamples[1]	Residual Variance	95% CI
2	0	–	–
3	3	4,335.99 (1,195.68)	1145.77 to 5035.00
4	15	2,454.24 (101.04)	2071.65 to 2768.81
5	15	2,439.72 (48.67)	2210.62 to 2506.10
8	15	2,090.28 (4.61)	2082.26 to 2107.76
True Value		1,645.40	–

[1]Number of Method R subsamples that yielded converged estimates
[2]There were no converged subsamples at 2 observations per animal

Table C.16. Number of foundation animals per group 2yr old weight group, additive genetic group solutions for stayability on both the underlying and percentage probability scale, and estimated standard errors for stayability in Red Angus cattle

Group[1] 2yr. old weight (Avg MW EBV)	No. of foundation animals	EBV for Stayability (Underlying)(SE)	Average EBV for Stayability group ± 2 SE	EBV for Stayability (% probability)
1	1,038	.00 (.00)		.00
2	1,037	-.28 (.090)	-.46 to -.10	-11.19
3	1,037	-.01 (.086)	-.16 to .18	.33
4	1,037	.12 (.081)	-.04 to .28	4.84

[1]Additive genetic groups for 2 yr old weight. 1=Low to 4 = High

Table C.17. Number of foundation animals per 2 yr old weight group, number of 2 yr old weights and stayability observations, average 2 yr old wt. EBV(kg), and average accuracy per genetic group in Red Angus cattle

Group[1] 2yr. Mature weight	No. of foundation animals	No. of weight / stayability observations	Avg. 2 yr old wt. EBV, kg	Avg. Accuracy
1	1,038	499 / 854	-12.9	.275
2	1,037	169 / 723	-1.5	.116
3	1,037	126 / 740	1.4	.107
4	1,037	441 / 840	13.7	.198

[1]Additive genetic groups for 2yr old weight. 1=Low to 4 = High
[2]Grouped by number of observations into even numbered groups

Table C.18. Number of foundation animals per 2yr old weight group, additive genetic group solutions for stayability on both the underlying and percentage probability scale, and estimated standard errors for stayability in Red Angus cattle

Group[1] 2yr. old weight	No. of foundation animals	EBV for Stayability (Underlying)(SE)	Average EBV for Stayability group ± 2 SE	EBV for Stayability (% probability)
1	254	.00 (.00)	0	0
2	607	.438 (.154)	.13 to .75	16.93
3	2,433	.176 (.130)	-.084 to .44	6.99
4	590	.440 (.145)	.15 to .73	17.02
5	265	.503 (.176)	.15 to .86	19.26

[1]Additive genetic groups for 2 yr old weight. 1=Low to 5 = High
[2]Grouped by standard deviation from the mean additive genetic group

Table C.19. Number of foundation animals per 2yr old weight group, additive genetic group solutions for stayability on both the underlying and percentage probability scale, and estimated standard errors for stayability in Red Angus cattle

Group[1] 2yr. old weight	No. of foundation animals	EBV for Stayability (Underlying)(SE)	Average EBV for Stayability group ± 2 SE	EBV for Stayability (% probability)
1	220	0 (.00)	0	0
2	3,595	.23 (.135)	-.04 to 0.50	9.20455
3	318	.45 (.169)	.12 to .79	17.5072
4	16	1.45 (.685)	.08 to 2.82	42.6618

[1]Additive genetic groups for 2 yr old weight. 1=Low to 4 = High
[2]Grouped by range of EBV into equal length strides.

Table C.20. Number of foundation animals per 3yr old weight group, additive genetic group solutions on both the underlying and percentage probability scale, and standard errors for stayability in Red Angus cattle

Group[1] 3yr. old weight	No. of foundation animals	EBV for Stayability (Underlying)(SE)	Average EBV for Stayability group ± 2 SE	EBV for Stayability (% probability)
1	1,049	.00 (.000)	0	.10
2	1,048	-.28 (.087)	-.46 to -.11	-11.15
3	1,048	-.08 (.084)	-.25 to .09	-3.29
4	1,048	.008 (.080)	-.15 to .17	.34

[1]Additive genetic groups for 3 yr old weight. 1=Low to 4 = High

Table C.21. Number of foundation animals per weight group, number of 3 yr old weight records, average 3 yr old wt. EBV, kg, and average accuracy per genetic group in Red Angus cattle

Group[1] 3yr. old weight	No. of foundation animals	No. of wt. / stayability observations	Avg. 3 yr old wt. EBV, kg	Avg. Accuracy
1	1,049	315 / 848	-11.2	.274
2	1,048	56 / 742	-1.0	.118
3	1,048	62 / 755	1.1	.111
4	1,048	294 / 812	12.0	.199

[1]Additive genetic groups for 3 yr old weight. 1=Low to 4 = High

Table C.22. Number of foundation animals per 3yr old weight group, additive genetic group solutions for stayability on both the underlying and percentage probability scale, and estimated standard errors for stayability in Red Angus cattle

Group[1] 3yr. old weight	No. of foundation animals	EBV for Stayability (Underlying)(SE)	Average EBV for Stayability group ± 2 SE	EBV for Stayability (% probability)
1	216	0 (.00)	0 to 0	0.1
2	628	-.192 (.156)	-.50 to .12	-7.62
3	2,548	-.299 (.130)	-.56 to -.04	-11.76
4	570	-.104 (.146)	-.40 to .19	-4.16
5	231	-.012 (.177)	-.37 to .34	-.49

[1]Additive genetic groups for 3 yr old weight. 1=Low to 5 = High
[2]Grouped by standard deviation from the mean additive genetic group

Table C.23. Number of foundation animals per 3yr old weight group, additive genetic group solutions for stayability on both the underlying and percentage probability scale, and estimated standard errors for stayability in Red Angus cattle

Group[1] 3yr. old weight	No. of foundation animals	EBV for Stayability (Underlying)(SE)	Average EBV for Stayability group ± 2 SE	EBV for Stayability (% probability)
1	96	.00 (.00)	0 to 0	.10
2	3,841	-.07 (.170)	-.41 to .27	-2.80928
3	254	.12 (.202)	-.28 to .53	4.89655
4	2	-1.68 (2.80)	-7.29 to 3.93	-45.3563

[1]Additive genetic groups for 3 yr old weight. 1=Low to 4 = High
[2]Grouped by range of EBV into equal length strides.

Table C.24. Number of foundation animals per 5yr old weight group, additive genetic group solutions for stayability on both the underlying and percentage probability scale , and estimated standard errors for stayability in Red Angus cattle.

Group[1] 5yr old weight	No. of foundation animals	EBV for Stayability (Underlying)(SE)	Average EBV for Stayability group ± 2 SE	EBV for Stayability (% probability)
1	1,017	.00(0)	.00	.00
2	1,016	-.43631(.088)	-.61 to -.26	-.25978
3	1,017	-.09042(.082)	-.26 to .07	.074204
4	1,016	-.05931(.080)	-.22 to .10	.100409

[1]Additive genetic groups for 5 yr old weight. 1=Low to 4 = High

Table C.25. Number of foundation animals per 5 yr old weight group, number of weight records, average weight EBV, and average accuracy per genetic group in Red Angus cattle.

Group[1] 5yr. old weight	No. of foundation animals	No. of wt. / stayability observations	Avg. 5 yr old wt. EBV, kg	Avg. Accuracy
1	1,017	178 / 806	9.9	.268
2	1,016	27 / 769	1.1	.130
3	1,017	59 / 798	.8	.113
4	1,016	166 / 784	10.6	.195

[1]Additive genetic groups for 5 yr old weight. 1=Low to 4 = High

Table C.26. Number of foundation animals per 5yr old weight group, additive genetic group solutions for stayability on both the underlying and percentage probability scale , and estimated standard errors for stayability in Red Angus cattle.

Group[1] 5yr. old weight	No. of foundation animals	EBV for Stayability (Underlying)(SE)	Average EBV for Stayability group ± 2 SE	EBV for Stayability (%)
1	224	0 (.0)	0 to 0	.10
2	558	-.32 (.153)	-.62 to -.012	-12.46
3	2,529	-.48 (.122)	-.72 to -.24	-18.43
4	525	-.32 (.142)	-.60 to -.03	-12.39
5	230	-.19 (.166)	-.52 to .15	-7.37

[1]Additive genetic groups for 5 yr old weight. 1=Low to 5 = High
[2]Grouped by standard deviation from the mean additive genetic group

Table C.27. Number of foundation animals per 5yr old weight group, additive genetic group solutions for stayability on both the underlying and percentage probability scale, and estimated standard errors for stayability in Red Angus cattle

Group[1] 5yr. old weight (Avg MW EBV)	No. of foundation animals	EBV for Stayability (Underlying)(SE)	Average EBV for Stayability group ± 2 SE	EBV for Stayability (%)
1	55	0 (.00)	0 to 0	0
2	3,873	-.55 (.181)	-.91 to -.19	-20.76
3	136	-.22 (.237)	-.70 to .25	-8.77
4	2	.59 (1.82)	-3.05 to 4.24	22.30

[1]Additive genetic groups for 5 yr old weight. 1=Low to 4 = High
[2]Grouped by range of EBV into equal length strides.

Table C.28. Number of foundation animals per 2yr old weight group by yrl wt group, additive genetic group solutions for stayability on both the underlying and percentage probability scale, and estimated standard errors for stayability in Red Angus cattle

Group[1] 2yr. old weight by ywt(AVG MW EBV/YW EBV)	No. of foundation animals	EBV for Stayability (Underlying)(SE)	Average EBV for Stayability group ± 2 SE	EBV for Stayability (%)
11 (-29.9 / -27.6)	519	0 (.00)	0 to 0	0
12 (-26.8 / -.2)	519	.23 (.126)	-.02 to .48	9.07
21 (-3.4 / -29.4)	519	-.29 (.130)	-.55 to -.03	-11.31
22 (-3.2 / 1.4)	518	-.09 (.120)	-.33 to .15	-3.47
31 (3.0 / -26.9)	519	.12 (.124)	-.13 to .37	4.84
32 (3.2 / 3.2)	518	.12 (.117)	-.11 to .36	4.89
41 (24.1 / -14.2)	519	.17 (.118)	-.07 to .41	6.72
42 (36.3 / 17.6)	518	.32 (.122)	.07 to .56	12.41

[1]Additive genetic groups for 2 yr old wt by yearling wt . 11 =Low 2 yr old wt and low yearling weight EBV to 42 = High 2 yr old wt and high yearling wt EBV.

Table C.29. Number of foundation animals per 3yr old weight group by yrl wt group, additive genetic group solutions for stayability on both the underlying and percentage probability scale, and estimated standard errors for stayability in Red Angus cattle

Group[1] 3yr. old weight by ywt (AVG MW EBV/YW EBV)	No. of foundation animals	EBV for Stayability (Underlying)(SE)	Average EBV for Stayability group ± 2 SE	EBV for Stayability (%)
11(-24.6 / -28.6)	525	0 (.0)	0 to 0	0
12(-24.2 / 1.7)	524	.39(.12)	.14 to .63	15.05
21(-2.5 / -27.7)	524	-.24(.13)	-.50 to .01	-9.56
22(-2.5 / 2.7)	524	.03(.12)	-.21 to .27	1.18
31(2.4 / -25.9)	524	.18(.12)	-.06 to .43	7.29
32(2.5 / 4.2)	524	.06(.12)	-.18 to .29	2.34
41(21.3 / -17.3)	524	.10(.12)	-.14 to .34	3.85
42(31.3 / 15.0)	524	.32(.12)	.09 to .56	12.69

[1]Additive genetic groups for 3 yr old wt by yearling wt . 11 =Low 3 yr old wt and low yearling weight EBV to 42 = High 3 yr old wt and high yearling wt EBV.

Table C.30. Number of foundation animals per 5yr old weight group by yrl wt group, additive genetic group solutions for stayability on both the underlying and percentage probability scale, and estimated standard errors for stayability in Red Angus cattle

Group[1] 5yr. old weight by ywt (AVG MW EBV/YW EBV)	No. of foundation animals	EBV for Stayability (Underlying)(SE)	Average EBV for Stayability group ± 2 SE	EBV for Stayability (%)
11(-21.1 / -29.1)	509	0(.00)	0 to 0	0.15
12(-22.2 / 1.6)	508	.42(.125)	.17 to .67	16.13
21(-2.4 / -27.6)	508	-.35(.132)	-.61 to -.08	-13.56
22(-2.3 / 2.1)	508	-.15(.120)	-.39 to .09	-6.00
31(1.7 / -23.0)	509	.09(.120)	-.15 to .32	3.44
32(1.7 / 3.6)	508	.14(.115)	-.09 to .37	5.45
41(19.9/ -20.7)	508	.01(.121)	-.23 to .25	.42
42(26.9/ 12.8)	508	.29(.118)	.06 to .53	11.58

[1]Additive genetic groups for 5 yr old wt by yearling wt 11 =Low 5 yr old wt and low yearling weight EBV to 42 = High 5 yr old wt and high yearling wt EBV.

Table C.31. Number of foundation animals per birth wt group, additive genetic group solutions for stayability on both the underlying and percentage probability scale, and estimated standard errors for stayability in Red Angus cattle

Group[1] Birth weight (avg BW EBV, kg)	No. of foundation animals	EBV for Stayability (Underlying)(SE)	Average EBV for Stayability group ± 2 SE	EBV for Stayability (% probability)
1(-1.9)	970	0(.00)	0	.00
2(-.2)	969	-.11(.092)	-.30 to .08	-4.38
3(.7)	970	.17(.090)	-.01 to .35	6.69
4(2.3)	969	.23(.090)	.05 to .41	9.20

[1]Additive genetic groups for birth wt.. 1=Low to 4 = High

Table C.32. Number of foundation animals per weaning weight wt(maternal) group, additive genetic group solutions for stayability on both the underlying and percentage probability scale , and estimated standard errors for stayability in Red Angus cattle

Group[1] Weaning weight-maternal (avg WW EBV, kg)	No. of foundation animals	EBV for Stayability (Underlying)(SE)	Average EBV for Stayability group ± 2 SE	EBV for Stayability (% probability)
1 (-5)	970	0	0	0
2 (-1.7)	969	.01 (.088)	-.16 to .19	.52
3 (.4)	970	.16 (.088)	-.01 to .33	6.23
4 (4.2)	969	.62 (.097)	.45 to .80	23.33

[1]Additive genetic groups for weaning wt.(maternal). 1=Low to 4 = High

Table C.33. Number of foundation animals per weaning wt direct group, additive genetic group solutions for stayability on both the underlying and percentage probability scale , and estimated standard errors for stayability in Red Angus cattle

Group[1] Weaning weight(direct) (avg EBV, kg)	No. of foundation animals	EBV for Stayability (Underlying)(SE)	Average EBV for Stayability group ± 2 SE	EBV for Stayability (% probability)
1(-10.1)	970	0	0	0.
2(-3.7)	969	.02(.091)	-.16 to .21	.99
3(-.6)	970	.21(.089)	.03 to .38	8.13
4(4.9)	969	.44(.089)	.26 to .61	16.86

[1]Additive genetic groups for weaning weight 1=Low to 4 = High

Table C.34. Number of foundation animals per yearling wt group, additive genetic group solutions for stayability on both the underlying and percentage probability scale, and estimated standard errors for stayability in Red Angus cattle

Group[1] Yearling weight (avg EBV, kg)	No. of foundation animals	EBV for Stayability (Underlying)(SE)	Average EBV for Stayability group ± 2 SE	EBV for Stayability (% probability)
1(-16.5)	970	0(0)	0	.10
2(-6.4)	969	.13(.089)	-.05 to .31	5.23
3(-1.9)	970	.18(.087)	.01 to .35	7.09
4(7.5)	969	.36(.089)	.18 to .54	14.04

[1]Additive genetic groups for yearling wt. 1=Low to 4 = High